FORESTBIO

Management of biodiversity in a range of Irish forest types

Final Report

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Acknowledgements

Cite as: O'Halloran, J., Irwin, S. , Kelly, D. L., Kelly, T. C., Mitchell, F. J. G., Coote, L., Oxbrough, A., Wilson, M.W., Martin, R. D., Moore, K., Sweeney, O., Dietzsch, A. C., Walsh, A., Keady, S., French, V., Fox, H., Kopke, K., Butler, F. and Neville, P. 2011. Management of biodiversity in a range of Irish forest types. Report prepared for the Department of Agriculture, Fisheries and Food. 391pp.

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Executive Summary

The forest industry in Ireland, and throughout Europe, is no longer focussed exclusively on timber production, but now has multiple goals and functions. These include the provision of a range of wood products, biodiversity conservation, carbon sequestration and use for recreation. This diversification in forest use is driven by state and EU policies, and supported by several measures and processes, including Sustainable Forest Management (SFM). Conservation of biodiversity is at the core of international environmental initiatives, and forests, both plantations and native woodlands, have an important role to play in the achieving this objective.

Ireland has an unusual forest landscape, characterised by small plantations embedded in a matrix of un-forested land that is largely dominated by agriculture. This is in contrast with much of the rest of Northern Europe, where large areas of continuous forest cover are common. As recently as 6000 years ago, native pine (*Pinus sylvestris*), oak (*Quercus* sp.), elm (*Ulmus glabra*) and alder (*Alnus glutinosa*) forests covered much of the Irish landscape. However, extensive deforestation by man coupled with a change to a cooler, wetter climate, led to a decline in forest cover to around 1% by the 1900s. Today, forest cover has again increased to 10% of land area, primarily through plantation establishment on previously un-forested lands, with native woodlands constituting only around 1%. This decrease in Ireland's forest cover and subsequent extensive afforestation, almost exclusively with non-native tree species during the twentieth century, have undoubtedly been associated with some loss of native forest biodiversity. State-sponsored afforestation is ongoing, and the Irish government aims to further increase forest cover to 14% by 2030. The value of plantation forests for biodiversity is typically considered to be low, although this overlooks the potential for enhancing the biodiversity value of an area through sympathetic management. For example, targeting areas of particularly poor biodiversity value for afforestation or planting native woodland tree species.

Although the earlier COFORD funded BIOFOREST project made significant progress in providing fundamental data on the biodiversity of Irish afforestation plantations, very little research has been carried out to date on reforestation and intimately mixed-species plantations, i.e. forest types that are of increasing importance in Ireland. Sympathetic management of these forest types requires knowledge of the biota present and the prevailing ecological processes that underpin their multiple objectives. The FORESTBIO project was designed to address gaps in our knowledge by assessing the biodiversity of second rotation and mixed-species plantation forests, but also of native woodlands to provide insight into typical Irish forest flora and fauna in semi-natural situations. In addition to this the project set out to identify biodiversity indicators that can be directly used to inform SFM plans in Ireland. This report details the advances in knowledge that have been made by researchers during the project.

Surveys of ground vegetation, epiphyte, invertebrate (ground- and canopy-dwelling spiders and beetles, and lepidoptera) and bird diversity were carried out at 60 sites throughout Ireland. The study sites comprised 20 Sitka spruce reforestation plantations (5 each of 4 age classes), 20 mixed species plantations (5 Norway spruce/oak, 5 Norway spruce/Scots pine and 10 pure Norway spruce stands as controls) and 20 native woodlands (10 oak-dominated and 10 ash-dominated). Data on reforestation plantations were compared with data on afforestation plantations collected during the BIOFOREST project, and some supplementary surveys of additional afforestation plantations were carried out where necessary. Biodiversity surveys were conducted using standardised sampling methods. A canopy fogging

technique was used for an in-depth study of canopy invertebrate biology (supported by IRCSET). This is the first time that this technique has been used extensively in research in Ireland, and two new invertebrate species records for Ireland were identified in samples collected from native oak woodland canopies. A detailed survey of deadwood in native woodlands and plantation forests was also conducted at a sub-set of forest sites. An investigation of the potential of terrestrial laser scanning for use in the measurement of structural proxies for biodiversity in forests was also undertaken (supported by the EPA).

This study found that the different taxonomic groups displayed similar patterns in species richness and community composition over the forest cycle in afforestation and reforestation of Sitka spruce plantations. Species richness was typically high at the beginning and/or end of the cycle and low during the middle stages. Trends were also broadly similar between afforestation and reforestation plantations, with the only differences related to retention of species between rotations, the presence of large, complex brash piles at early stage reforestation sites and the higher canopy cover in reforestation. The different taxonomic groups also displayed similar patterns when comparing their community composition across stages in the forest cycle; composition was generally most distinctive in the early stages of both afforestation and reforestation plantations.

The inclusion of a broadleaved species (oak) or a light-canopied conifer (Scots pine) in an intimate mixture with Norway spruce had little effect on the diversity or community composition of most of the taxa studied. The exceptions were those groups specifically adapted to living or feeding on native broadleaved trees; the epiphytes also showed a direct response to the addition of a light-canopied conifer. The proportion of Scots pine and oak in the majority of the mixtures studied was less than 40%, and most of the planted oak trees had been outcompeted by surrounding Norway spruce, such that they formed an understorey layer rather than part of the main canopy. It is likely that mixed tree species planting could have a more positive effect on forest biodiversity through the planting of more compatible tree species mixtures, or management that allows the secondary species to reach the canopy.

The oak and ash native woodlands supported broadly similar numbers of bird and invertebrate species, though this differed for ground vegetation and epiphytes. The communities supported between woodland types differed for invertebrates and plants, and for the latter group well-defined plant communities were found. Management of both oak and ash woodlands can therefore increase biodiversity at the landscape scale. Other woodland types in Ireland may also support distinct biotic assemblages, but further investigation is required to elucidate this.

Native woodlands were generally more species rich and supported different communities to plantations. Where similar or greater numbers of species were supported in plantations, the communities differed from those in native woodlands, and where communities were similar, more species were supported in native woodlands. Ground-dwelling beetles were an exception; as this group is composed of generalists. Since forest plantations are the predominant forest type in Ireland, the preservation or extension of existing native woodlands, or management of plantations to encourage native-woodland characteristics, would typically enhance biodiversity at both stand and landscape scales.

The history of extensive deforestation and exploitation of forests for wood resources in Ireland was evident in the paucity of large-diameter logs and snags found in both native woodlands and plantation forests in this study. Deadwood is one of the most important components of forest ecosystems, and one of the

factors that most clearly distinguish woodlands with natural characteristics from more intensively managed forests. Despite the low levels of deadlwood recorded in Irish forests, deadwood was positively related to diversity of a range of taxa in the forests investigated.

A number of potential structural and functional indicators of diversity have been identified for various taxonomic groups. Our data show that although some relatively easily surveyed groups, such as vascular plants and birds, were congruent with many of the other taxa when looking across all study sites, the similarities in response were not strong enough to warrant use of these taxa as surrogates at the scales we studied. In order to capture a wide range of biotic variation, assessments of biodiversity in Irish forests must either encompass several taxonomic groups, or else rely on the use of structural or functional indicators of diversity. However, this will not be possible for poorly-studied taxonomic groups, such as saproxylic invertebrates that feed on deadwood, until further research is undertaken to improve our understanding of their ecological requirements and associations.

The results of this study are discussed in the context of their implications for policy and practice. Data collected during this project were compiled in a GIS database that allows access, visualisation and further analyses of the dataset, and this can be easily distributed and updated with future research. A range of recommendations for forest management has been produced based on the findings of this study. This research will improve understanding of the factors influencing biodiversity in forests and help the forestry sector to develop sound strategies for SFM, and achieve its objectives of protecting forest biodiversity while continuing to produce wood biomass of adequate quality and in sufficient quantity.

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1. Introduction

One hundred and fifty seven countries, including Ireland, signed the Convention on Biological Diversity (CBD) at the United Nations Conference on Environment and Development (UNCED) in 1992. The main objective of the CBD was the conservation and sustainable use of biological diversity, or 'biodiversity' at all scales. Biodiversity encompasses all variation between, within and around living things, including diversity of ecosystems, habitats and species, as well as genetic and molecular diversity within species and populations. Although the term was coined just twenty-five years ago (Wilson, 1988), it is arguably the most widespread and fundamental concept in modern conservation and ecological thinking. Biodiversity is widely recognised as being of vital importance to society, providing ecosystem services and increasing ecological stability, with explicitly economic consequences. It also affects the quality of human lives in ways that are no less valuable, but are much harder to quantify (Hassan *et al.*, 2006). Forests harbour a large proportion of global biodiversity, including more than half of all terrestrial species (FAO, 2001), and play a central role in the functioning of the biosphere (Larsson, 2001). The importance of managing forests sustainably and in a manner compatible with biodiversity conservation was recognised internationally at UNCED in the Statement of Forest Principles. In a European context, the Helsinki Process comprised a series of meetings and agreements by EU member states in the 1990s, aimed at promoting and assessing progress towards sustainable management of forests in Europe. Since then, the concept of Sustainable Forest Management (SFM), supported by international certification schemes, has emerged as one of the foremost tools for achieving compatibility between forest industries and the provision of ecosystem services, including the conservation of forest biodiversity. Forestry is an important industry in Europe and is becoming increasingly important in Ireland, where grant-aided forestry must now be SFM certified (Forest Service, 2000a). One of the main driving forces for Sustainable Forest Management is the need for environmental certification as a marketing tool demonstrating that timber is produced in a sustainable way (i.e. not damaging to the environment or the future capacity of an area to grow healthy forests). In order to achieve Ireland's ambition of establishing 1 million ha of forest plantations (approximately 14% of land area) by the year 2030 (COFORD, 2009), forest management practices must be underpinned by a thorough understanding of Ireland's forest biodiversity.

Although Ireland was once extensively forested, today just 10% (0.67 million ha) of its surface area is covered by forests. This represents one of the lowest levels of forest cover in any EU country, where the average forest cover is now approaching 50%. Eighty-seven percent of these forests are plantations, the majority of which (97%) are dominated by conifers (MCPFE Liaison Unit Warsaw, 2007), with non-native Sitka spruce (*Picea sitchensis*) (nomenclature follows (Stace, 1997) for vascular plants, Smith (2004) for mosses, Paton (1999) for liverworts and Coppins (2002) for lichens, unless otherwise stated) being the most frequently planted tree species (53% of the forest estate, EPA, 2008). Native woodlands today constitute about % of forested lands in Ireland (Department of Agriculture and Food, 2003). This makes plantation forests potentially of greater importance to forest biodiversity than in regions where native woodland predominates. However, although Ireland's native woodlands are limited in their spatial extent, the value of their biodiversity is disproportionately high, providing a reference point against which more recently established forests can be compared.

At present the ratio of broadleaved to conifer species planted in Ireland is low (Forest Service, 2004), although there has been a shift in recent years towards the planting of more broadleaves. Current forestry policy aims to increase the proportion of broadleaves to 30% of the national forest estate (Department of

Agriculture, 1996), and since 1998 the proportion of broadleaves in planting has risen from 19% to 41% (Forest Service, 2004) in response to a number of factors. Firstly, the Forest-Farm Partnership Scheme has led to the planting of more lowland agricultural areas which, being more fertile, are suitable for a greater number of tree species than upland areas (Teagasc: Irish Agriculture and Food Development authority, 2005). Secondly, the *Irish Forest Biodiversity Guidelines* (Forest Service, 2000b) recommend planting a mixture of tree species, to enhance plantation biodiversity. All new planting must contain a minimum of 10% broadleaves (Forest Service, 2000c). Similarly, new plantings of conifers must contain a minimum of 20% diverse conifers which, in Ireland, are species other than Sitka spruce or Lodgepole pine (*Pinus contorta*) (McAree, 2002). However, although the planting of mixed species trees is widely recommended (Peterken, 1986; Bibby *et al.*, 1989; Forest Service, 2001) very little research has been carried out on the species combinations which have the greatest potential to enhance forest biodiversity. This is especially important in an Irish context, where mixes commonly consist of two or more non-native species planted together, and may be of less biodiversity value than a mix of native and non-native species planted together.

The prevalent model of forest management in the twentieth century focused almost entirely on wood production, but pressures from international agreements and the demands of society are acting to make modern forests more multifunctional. Management of such forests requires knowledge not only of the trees and timber production, but also of the biota and prevailing ecological processes that underpin the potential benefits and diverse products of these commercial forests. This, in turn, requires an understanding of the factors influencing the biodiversity of our remaining native woodlands as it is likely that managed forests will only support forest-associated species where Sustainable Forest Management regimes reflect the dynamics of natural forests (Haila *et al.*, 1994). The full potential of Irish plantations can only be realised when the ecology of our native woodlands and their flora and fauna is understood, and the factors influencing forest biodiversity have been identified.

There have been few studies of biodiversity in Irish forests, particularly in the commercial plantations that dominate the forest estate. The necessity for more information on these is underscored by the increasing emphasis placed by internationally agreed SFM standards on the enhancement of forest biodiversity. The BIOFOREST Project, which increased our understanding of biodiversity in plantations during a four year investigation covering over 100 sites throughout Ireland, concluded that, although afforestation can positively affect biodiversity, it can also have deleterious effects (Iremonger *et al.*, 2007). A total of 57 recommendations were made to promote types of management and policies that would enhance the biodiversity value of plantations. BIOFOREST was initiated during a programme of vigorous afforestation that aimed to expand forest cover from 9% to 17% within a period spanning three decades. Much of the forest estate was in its first rotation, and so the project focused mainly on newly established forests in their first commercial rotation, especially forests dominated by Sitka spruce.

While there is still an emphasis on forest expansion, the nature of the forest estate is changing, as first-rotation forests are harvested by clearfelling, and second rotation (also known as restock or reforestation) forests are planted in their stead. These plantings have been affected by new policies aimed at diversifying the forest estate, which encourage combinations of species that were not commonly planted until recently. The more conventional species such as Sitka spruce and Lodgepole pine continue to be planted, but their dominance in the Irish forest estate is diminishing according to industry regulations (and Government Policy) that require new plantings to incorporate a variety of tree species. Many native

broadleaves that have traditionally been regarded as unproductive (or else have more recently been neglected by the forest industry in favour of faster-growing conifers) are now planted as part of many commercial plantings, as well as in forests established as part of dedicated initiatives such as the Native Woodland Scheme. These recent developments provide an opportunity for the forest industry to achieve new ecological standards, and to ensure compliance with international agreements, using research based knowledge. This study of a range of different forest types will contribute to a greater understanding of the new types of forest appearing in the Irish landscape, improve our knowledge of Ireland's native woodland heritage, and enable more effective management of our forests for biodiversity.

Considering the issues outlined above, this project has four main objectives:

1. To determine the biodiversity of second rotation forests, forests composed of different mixes of tree species, and native woodlands.
2. To make comparisons between forest types and with data from BIOFOREST project sites to increase our understanding of the variety of forests in Ireland today.
3. To identify indicators of biodiversity for different forest types and describe monitoring techniques for the future in permanently marked study sites.
4. To identify measures to enhance the biodiversity of the different forest types, including second rotation forests and first rotation mixes under conventional afforestation management regimes.

2. Background

2.1 Epiphytes

Epiphytes are organisms that live on plants, or in the dead outer tissues of plants, without drawing water or food from their living tissues (Barkman, 1958). Their complete dependence on woody plants makes obligate epiphytes particularly sensitive to forest management practices (Coote, 2007). In Ireland, epiphytes are comprised mainly of mosses, liverworts and lichens, but also include a few vascular plant species that can be found growing on trees, such as polypody ferns (*Polypodium spp.*). From an ecological perspective, epiphytes are important indicators of climate change, forest structure and ecosystem health due to their sensitivity to microclimatic conditions (Gradstein *et al.*, 1996). Their-value as biological indicators of pollution is well known and some lichens are particularly sensitive to sulphur dioxide pollution and can accumulate metals (Richardson, 1987). Epiphytes also play important roles in forest hydrology (Pócs, 1982; Jarvis, 1999) and in nutrient cycling (Nadkarni, 1994), and can provide food, shelter and nest material for forest invertebrates and vertebrates (Gerson and Seaward, 1977; Richardson and Young, 1977). For example, epiphytic lichen abundance may have a positive effect on the numbers and biomass of invertebrates which, in turn, are an important food source for many bird species (Pettersson *et al.*, 1995).

The high proportion of conifers in Ireland's plantation forests makes them potentially important as hosts for epiphyte vegetation. Nearly all epiphyte studies carried out in Ireland so far have been in native broadleaved woodland and scrub habitats (Richards, 1938; Phillips, 1959; Mitchell, 1964; Folan and Mitchell, 1970; Kelly, 1975; McCarthy, 1980; Kirby and O'Connell, 1982; McCarthy *et al.*, 1986; Fox *et al.*, 2001) which are, compared to forestry plantations, a minority habitat in Ireland. To date, the only epiphyte studies in Irish forestry plantations are by Coote (2007) and Coote *et al*. (2008). Similarly, studies on epiphytes in Britain have primarily explored native woodlands (e.g. Martin, 1938; James *et al.*, 1977; Farmer *et al.*, 1991), although recent years have seen an increase in the number of studies on non-native conifer plantations and their potential for biodiversity (Ratcliffe and Peterken, 1995; Humphrey *et al.*, 2002a). However, our knowledge of coniferous species as hosts for epiphyte communities still derives mainly from studies in continental Europe (Halonen *et al.*, 1991; Hyvärinen *et al.*, 1992; Hilmo, 1994; Esseen *et al.*, 1996; Hilmo, 2002; Hilmo and Holien, 2002; Felton *et al.*, 2010; Nascimbene *et al.*, 2010; Wannebo-Nilsen *et al.*, 2010) including studies where epiphyte communities were sampled in mixed forests (Dettki and Esseen, 1998; Uliczka and Angelstam, 1999; Moe and Botnen, 2000; Dettki and Esseen, 2003; Felton *et al.*, 2010) and compared between coniferous and broadleaved host species.

In their native range, conifers can host large numbers of epiphytes, including specialist species (Minore, 1979; Ellyson and Sillett, 2003; Wannebo-Nilsen *et al.*, 2010). However, when introduced as a non-native plantation tree, they may host fewer epiphytic species due to the lack of an epiphytic flora adapted to the particular substrate provided by their bark (Wannebo-Nilsen *et al.*, 2010) or the low levels of host-species diversity in many commercially planted forests (Felton *et al.*, 2010). Plantations, especially of evergreen species, may experience lower light levels than native forests, which can further reduce epiphyte communities (Moe and Botnen, 2000). Structural heterogeneity is a key factor for the diversity of macroepiphytes, and the lower epiphyte species richness in plantation stands is often related to their structural homogeneity (Dettki and Esseen, 1998). This includes the absence of very old trees, which in general have been found to host a larger number and greater biomass of epiphyte species than younger

trees (Esseen *et al.*, 1996; Uliczka and Angelstam, 1999) as well as the absence of different age classes of trees within a stand (epiphyte species composition undergoes a turnover from young to old trees (Hilmo and Holien, 2002)). Although it is likely that epiphyte communities in Irish native woodlands and plantation forests are affected by the above mentioned factors, epiphytes have received insufficient study in Ireland to confirm this. Such information is vital for sustainable management of forest biodiversity in Ireland.

2.2 Ground vegetation

Ground vegetation diversity is one of the most important elements of biodiversity in forest ecosystems (French, 2005). It plays an important role in forest ecosystem functioning, both directly and indirectly. It can account for a high proportion of annual litterfall and allow for rapid return of nutrients to the soil, thereby contributing to forest productivity (Ford and Newbould, 1977; Moore and Lee Allen, 1999). Ground vegetation diversity also contributes to the diversity of heterotrophic organisms, stabilising the biogeochemical cycle by balancing production and mineralisation (Larsen, 1995). It can influence bird diversity (Donald *et al.*, 1998; Sweeney *et al.*, 2010b; Wilson *et al.*, 2010b) and mammal community composition (Carey and Harrington, 2001) and can provide habitats for insects (Humphrey *et al.*, 1999) and other invertebrates important to ecosystem functioning (French, 2005). The presence of ground vegetation can also promote percolation of water and minimise erosion (Larsen, 1995), and can aesthetically enhance plantation forests (Smith *et al.*, 2005).

Until recently, little data had been published on the ground vegetation communities of Irish plantation forests and most studies were site specific and had low levels of replication (French, 2005). The BIOFOREST project (Iremonger *et al.*, 2007) was the first large-scale project investigating plantation forest diversity, including ground vegetation communities, and began to fill some of the gaps in the knowledge that existed (Iremonger *et al.*, 2007). Little research has been carried out on the factors affecting ground vegetation diversity in reforestation plantations. Previous research on reforestation in Ireland by Cooper *et al.* (2008) investigated early stages of reforestation (0 – 11 years) established on dredged sediments along the banks of a river. In Britain, Eycott *et al.* (2006) studied ground vegetation community composition in reforested pine plantations and modelled ground vegetation development over successive rotations of plantations established on peatland and heath were developed by Peterken (2001) and Hill (1979).

There is also a dearth of information available on ground vegetation in intimately mixed plantations in Ireland, with existing knowledge derived mostly from studies carried out in Britain (Kirby, 1988; Mason and Baldwin, 1995; Mason, 2006) and Sweden (Saetre *et al.*, 1997). Until recently, the level of research on ground vegetation communities in Irish native woodlands was moderate, with most studies covering a narrow range of sites or forest types (Perrin *et al.*, 2008a). In Northern Ireland, the 'Back on the Map' project (The Woodland Trust, 2007b) compiled a comprehensive inventory of ancient and long-established woodland in the region. The National Survey of Native Woodlands (Perrin *et al.*, 2008a) was the first systematic national scale survey of native woodlands in the Republic of Ireland aimed at habitat and wildlife conservation. However, the main aims of that survey were to produce an inventory and classification of native woodlands and to examine their conservation value and threat status. It did not include a detailed investigation of the drivers of vegetation types or patterns of diversity.

Attempts to apply phytosociological classifications of native woodland communities in Britain and Ireland to the vegetation communities of plantations have found that, while many plantation communities do not satisfactorily fit any of the native woodland classifications, some similarities do exist (Wallace *et al.*, 1992; Ferris *et al.*, 2000a; Wallace, 2003; French, 2005). There have been few field studies directly comparing plantations and native woodlands and, while they have found native woodlands to be more species rich than plantations (Magurran, 1988; Fahy and Gormally, 1998; Coroi *et al.*, 2004), their results are informative only at a local scale. The most comprehensive comparison to date was made by Humphrey *et al.* (2003), who found that the bryophyte communities of some British plantations were similar to those of native woodlands (Humphrey *et al.*, 2002a). However, work on vascular plant communities has included only two native pinewoods and focussed on comparing vegetation communities to phytosociological community classifications (Ferris *et al.*, 2000a). French *et al.* (2008) described the vegetation communities of a range of Irish plantation types, but there have been no large-scale field surveys directly comparing the vegetation communities of plantations and native woodlands in Ireland to date.

2.3 Invertebrates

Invertebrates are an important component of forest biodiversity, inhabiting all parts of the forest ecosystem, including the soil, litter, herb and understorey layers, as well as the canopy. They have functional importance in food webs, acting as predators and as a food source for mammals and birds (Buse and Good, 1993; Wilson *et al.*, 1999), but also as decomposers and pollinators (Kevan, 1999; Mayer, 2008). They are typically less studied in forest biodiversity research than taxa that are more easily surveyed, such as plants or birds, particularly in Ireland where there is a lack of specialist taxonomic expertise. However, in recent years large scale projects such as BIOFOREST and BIOSCAPE have included taxa such as spiders (Araneae), beetles (Carabidae) and hoverflies (Syrpidae), providing baseline knowledge of these groups in conifer plantations in Ireland (Oxbrough *et al.*, 2005; Gittings *et al.*, 2006; Oxbrough *et al.*, 2006a; Oxbrough *et al.*, 2006b; Oxbrough *et al.*, 2007; Mullen *et al.*, 2008). The Irish *Forest Biodiversity Guidelines* (Forest Service, 2000b) recommend a suite of measures to enhance biological diversity in plantations, but make no explicit mention of invertebrates, the most diverse taxonomic group. Furthermore, although most of the are aimed at the scale of the stand or the plantation, many of the processes affecting invertebrates take place on a smaller scale (Niemelä and Spence, 1994; Pearce *et al.*, 2004).

2.3.1 Ground-dwelling invertebrates

Ground-dwelling spiders and Carabid beetles are frequently used to assess habitat 'quality' in a wide variety of forested ecosystems (Rainio and Niemelä 2003; Pearce and Venier, 2006). They are relatively easily captured and identified, and their ecology and behaviour is well known compared to those of other invertebrate taxa. In addition to this, they are sensitive to changes in vegetation structure (Ings and Hartley, 1999; Sanders *et al.*, 2008), which often reflects variation in canopy species or structural development (Oxbrough *et al.*, 2005; Mullen *et al.*, 2008). Both spiders and beetles inhabit all parts of a forest, from the litter to the canopy, allowing the comparison of communities in these taxa across all vertical strata. Additionally, spiders can be classified into guilds according to their hunting strategies (for example active hunters, ambush predators and various types of web builders) which adds a further dimension to the interpretation of ecological data. Lastly, both Carabids and spiders also respond to

gradients of moisture or climate which may reflect differences in habitat quality (De Bakker *et al.*, 2000; Jukes *et al.*, 2002; Gurdebeke *et al.*, 2003; Saetersdal *et al.*, 2003).

2.3.2 Lepidoptera

Lepidoptera, comprising butterflies and moths, is one of the largest insect orders with 160,000 named species (New, 2004), and is among the most taxonomically well known groups of forest insects (Summerville *et al.*, 2004). Lepidoptera are critical to the functioning of many ecosystems, with species having roles as selective herbivores, pollinators and prey for migratorial passerines and small mammals (Summerville *et al.*, 2004). Combined with their strong association with vegetation structure and composition (Lomov *et al.*, 2006), this makes Lepidoptera diversity and community structure well-suited to indicating ecological variation in forests and forested landscapes (Summerville *et al.*, 2004). To date, the only study that explicitly compared the Lepidoptera diversity of Irish native woodlands with that of plantation forests was restricted to two study sites (Magurran, 1985). FORESTBIO is the first project to examine Irish Lepidoptera across a large geographic scale and across a wide range of forest habitats.

2.3.3 Canopy-dwelling invertebrates

Canopy biology is a relatively new science discipline (having first been used in the late 1960s) that seeks to investigate the ecological and community links between mobile and sessile organisms in a forest canopy (Lowman and Wittman, 1996). The canopy of a forest is defined as '*the top layer of a forest or wooded ecosystem consisting of overlapping leaves and branches of trees, shrubs or both*' (Lowman and Wittman, 1996). Undertaking research in forest canopies is exceptionally worthwhile due to the ecological importance of canopy processes, including forest-atmosphere nutrient cycling and the dominating effect of canopies on the microclimate of the forest understorey (Barker and Pinard, 2001). Forests are also the most complex of all terrestrial ecosystems, and forest canopies make up the bulk of the biomass in forest ecosystems and contain a major proportion of the diversity of organisms on Earth (Lowman and Wittman, 1996), the majority of which are invertebrates. Despite this, there has been relatively little research on invertebrates in forest canopies worldwide because they are difficult to access and sample efficiently. However, in recent decades, canopy access methods have improved greatly, due to the availability of increasingly reliable hardware, such as dirigible rafts, improved arboreal climbing and mountaineering equipment, canopy cranes, and canopy foggers (Lowman and Wittman, 1996).

2.4 Birds

Birds are an important component of every terrestrial ecosystem. They are involved in ecological processes such as plant dispersal (Gómez, 2003) and are important scavengers (Selva *et al.*, 2005), and predation from birds can exert top-down control on invertebrate populations (Skoczylas *et al.*, 2007; Gunnarsson *et al.*, 2009). In Europe, many woodland birds species have suffered declines (Fuller *et al.*, 2005; Gregory *et al.*, 2007). These declines, coupled with the important role that birds play in forests, means that investigating bird communities and understanding what aspects of forests are most important to birds is vital to the conservation of forest biodiversity. Bird communities change in different stages of the forest cycle (Fuller and Browne, 2003; Wilson *et al.*, 2006) and may differ between native and plantation forests (Donald *et al.*, 1998; Sax, 2002). Specialist birds are more likely to be absent from plantations

(Zurita *et al.*, 2006; Paritsis and Aizen, 2008), probably due to their more demanding habitat requirements. At present, we know little about the bird communities of second rotation forests, particularly in winter, or how the generalist bird fauna of Ireland utilises native and plantation forests. There is also very little literature on the bird communities of mixed species plantations. This research will therefore be useful in addressing several knowledge gaps.

2.5 Deadwood

Deadwood plays an important part in forest ecology, and should be explicitly considered in SFM strategies aiming to promote biodiversity and ecosystem integrity. Deadwood influences many processes, such as nutrient cycling (Hafner and Groffman, 2005) and germination (Kennedy and Quinn, 2001), and is associated with the life-histories of a variety of specialist flora and fauna (Nordén *et al.*, 2004b; Kappes, 2006; Smith, 2007). The volume and diversity of deadwood in forest stands will determine habitat availability and heterogeneity for many species that utilise this resource (Lindhe *et al.*, 2005; Hottola and Siitonen, 2008). Typically, management intensity of forests is negatively related to deadwood volume (Green and Peterken, 1997; Marage and Lemperiere, 2005). The management of most plantations is more intensive than that of natural stands and, in Ireland, is undertaken on the basis of short commercial rotations (approximately 50 years), with periodical thinning, and harvesting by clearfelling (Forest Service, 2000a). Such management is unlikely to result in the development of old-growth characteristics, such as large living and dead trees, a wide variety of tree agess within a stand, large fallen logs and high levels of deadwood (Lindenmayer *et al.*, 1999; Siitonen *et al.*, 2000; Bobiec, 2002), unless management specifically targets these attributes. Despite the importance of information on deadwood to forest managers seeking to maximise biodiversity and the known link between deadwood and biodiversity, little information is available on deadwood in Irish native woodlands.

2.6 Terrestrial laser scanning

The biodiversity of all taxa in forests is influenced by structural complexity. Although this relationship is well established (Hunter, 1999), precise and repeatable measures of structural diversity are often difficult to achieve in practice. Because traditional methods of structural complexity and deadwood assessment require many field visits, emerging technologies such as remote sensing present an opportunity to automate and improve forest structure survey methods (Weltz *et al.*, 1994; Innes and Kock, 1998). Terrestrial laser scanning (TLS), also known as ground-based Lidar, is a rapidly developing technology that has huge potential for yielding data on forest structure at a previously unattainable level of accuracy and resolution of detail. Terrestrial laser scanning has been developed to capture detailed, three-dimensional data about an object's dimensions, spatial positioning, texture and colour. In recent years, it has been adapted for the forest industry where it is now used for taking measurements from standing timber in a non-destructive manner in order to inform harvesting decisions and reduce waste (Boston and Murphy, 2003). This technology is being developed for application to standing timber measurement by a local Irish company, Treemetrics Ltd., based in Co. Cork (www.treemetrics.com), but its potential as a tool for biodiversity research and management has not yet been exploited. The requirement for collaboration between remote sensing and biodiversity research communities to fully exploit the potential of remote sensing in biodiversity studies is well recognised, but collaborative work between these two fields in the quest for biodiversity conservation remains in its infancy. The FORESTBIO project joined forces with

Treemetrics in an EPA funded project to test the usefulness of terrestrial laser scanning for measurement of forest structure and prediction of plant, bird and invertebrate diversity at FORESTBIO sites.

2.7 Cross-taxon analysis

Assessments of biodiversity are often required to identify sites and 'hotspots' that are particularly rich in biodiversity, and networks of reserves that complement one another in the range of species and habitats they protect. They are also carried out to gauge the impact of different management practices on biodiversity. However, despite its importance and the apparent ease with which it can be defined, measuring biodiversity is far from straightforward. This is partly because there are several different components of biological diversity that apply at different levels of taxonomic organisation and geographic scales. These include measures of the number and distinctiveness of genes (genetic diversity), species (species diversity) and higher taxonomic levels (Noss, 1990). In terms of geographic and ecological scale, alpha diversity typically describes the composition (in terms of number and evenness of species) within a community, beta diversity is the variation between different habitats or biotypes, and gamma diversity is the variation across all habitats or biotypes in a region (Whittaker, 1977). A successful assay of biodiversity requires an understanding of which of these various components are most relevant to a particular situation.

A complete assessment of species or genetic diversity is impracticable on all but the smallest of scales (Noss, 1990). One way in which the gap between the taxonomic scope of a survey and the full range of plant and animal species that contribute to the biodiversity of an area can be bridged is through the use of indicators (Reid *et al.*, 1993). These can include environmental factors and processes that either affect or derive from variation in fauna and flora: structural indicators (which include habitat at different scales and variables related to vegetation structure), functional indicators (encompassing ecological processes, properties of trophic networks, ecosystem services and human activity and its consequences) (Noss, 1990; Ferris and Humphrey, 1999) and biotic indicators such as surrogate taxa. At its most basic, surrogacy involves inferring the diversity in one taxon from the diversity of another. Surrogacy can be considered on different levels, in terms of both the information used from one taxon, and the information inferred about the other. If metrics such as species richness and evenness are closely correlated between two taxa, one can infer the probable diversity of one taxon from the results of a survey of the other (Blair, 1999). Alternatively, one can use surrogacy at the level of species composition – inferring unknown information about the species composition of one taxon from variation in the relative abundance of species in another (Kremen, 1992). It is possible to employ surrogacy at higher taxonomic levels than species, either between taxa or within a taxon, using diversity at a higher level to indicate diversity at the species level (Williams and Gaston, 1994).

Previous studies that have investigated the usefulness of surrogacy have arrived at various conclusions, some considering surrogate taxa to be a useful tool for providing data about unsurveyed taxa (Rodrigues and Brooks, 2007; Gioria *et al.*, 2010), and others cautioning that relationships between taxa are often too weak or too variable to infer information efficiently about one taxon from another (Andelman and Fagan, 2000; Carmel and Stoller-Cavari, 2006). Studies that have considered surrogacy at relatively broad geographical scale and over a broad range of habitat and environmental variation have typically found

more strongly in favour of surrogacy than studies considering a limited scope of geographical and environmental variation (Lewandowski *et al.*, 2010; van Weerd and de Haes, 2010).

One of the strengths of a multi-disciplinary project like FORESTBIO lies in the fact that several very different taxonomic communities were investigated by specialists within the same group of sites. This enables us to investigate the relationships between the different taxa we studied and to assess the extent to which information derived from one taxon may inform us about another. Only after carrying out such detailed projects across a wide taxonomic range can we assess the adequacy of surveys that focus on one or a few. Few studies are suited to looking at cross-taxon patterns in biodiversity, as this requires sampling of multiple taxa within the same areas and across the range of habitats under investigation. FORESTBIO is the most comprehensive survey of biodiversity in Irish forests carried out to date, covering a broad range of native woodland and plantation forest types, and compiling data on the communities of plant, invertebrate and vertebrate taxa. In particular, the sampling of species in each of these groups from the upper canopy as well as from the lower vegetation layers makes this study unique among Irish studies to date and one that is well suited to the investigation of cross-taxon congruence and the potential for surveying of some taxa to act as surrogates for others.

2.8 GIS database

The FORESTBIO database captures data made available by the researchers that participated in this project and provides an updateable system that allows access, visualisation and further analysis of the spatial data component within the FORESTBIO project. The FORESTBIO database will be integrated in the overall PLANFORBIO research program database, which has the goal to provide a 'one-stop-shop' for the spatial data component and related tabular information of the whole project. Data visualisation will be provided in two ways:

1. via ArcGIS, a fully functional GIS that allows further analyses and in depth querying of the data but requires a licence for ArcGIS 9.2 or 9.3 and
2. via ArcReader, which does not require a licence and has a more restricted GIS functionality.

2.9 Forest Policy

Conservation and enhancement of forest biodiversity has an important part to play in the ongoing development of the Irish forest estate (Anon, 2000b). Biodiversity conservation in Irish forests is supported by legal and regulatory frameworks at local, national and international levels. At national level these include the Forestry Act 1956, the Wildlife Act 1976 (repealed by the Wildlife Amendment Act 2000), and the Environmental Protection Agency Act 1992. The Earth Summit held in Rio de Janeiro in 1992 led to the UN Convention on Biological Diversity (CBD). Ireland ratified the CBD in 1996 and is obliged under this convention to produce national biodiversity strategies. The CBD has seven thematic programmes of work, one of which is 'Forest Biodiversity'. This is reflected in Ireland's National Biodiversity Plan (Anon, 2002b), where one of the sixteen themes addressed is 'Forestry'. The National Biodiversity Plan was produced in 2002 in accordance with Article 6 of the Rio Convention on Biological Diversity by the National Parks and Wildlife Service (NPWS) (Anon, 2002b).

The National Biodiversity Plan (NBP) provides for the conservation and sustainable use of biodiversity in all stages of the forest cycle in plantation forests and in native woodlands through 22 actions that specifically address maximising the biodiversity value of Irish forests. These include enhanced training in ecology and biodiversity conservation in the agricultural sector, expansion of the existing forest and biodiversity research programme, updating of the forest legislation, increasing annual broadleaved tree planting and the introduction of guidelines on forest biodiversity. The NBP also sets out a number of initiatives in relation to native woodlands aimed at increasing the area of semi-natural woodlands through the creation of new woodlands. These include the the Native Woodland Scheme (which includes measures aimed at establishing new native woodlands, as well as conserving existing woodlands), and the Peoples Millennium Forest Project (Anon, 2000b).

The Government's Strategic Plan for the development of forestry is set out in Growing for the Future (Anon, 1996), and is based on the principles of Sustainable Forest Management (SFM). It aims to greatly increase forest cover in Ireland from the current level 10% forest cover to 14% by 2030. The Forest Service is committed to ensuring that this expansion takes place in the context of careful consideration of the conservation and enhancement of biodiversity in all its forms—species, habitat and genetic (McAree, 2002). SFM in Ireland is guided by various instruments including the Code of Best Forest Practice – Ireland, the Irish National Forest Standard and the Forest Biodiversity Guidelines (Anon, 2000b; Anon, 2000a). The Forest Biodiversity Guidelines (Anon, 2000b) focus on conserving biodiversity in Ireland's forests and require that 15% of forest area be given ABE (Area for Biodiversity Enhancement) status and made subject to measures aimed at promoting biodiversity. These include the protection of small-scale habitats and open spaces, the encouragement of a more varied age class and canopy structure, the careful timing of operations to minimise wildlife disturbance, the retention of old growth trees and deadwood and the control of invasive species. In line with measures aimed at increasing species diversity in Irish forests and increasing the proportion of broadleaves the national forest estate to 30%, all new planting must contain a minimum of 10% broadleaves, and conifer plantations must contain a minimum of 20% diverse conifers (species other than Sitka spruce and Lodgepole pine) (McAree, 2002). The Forest Biodiversity Guidelines recognise that tree species diversity in a plantation contributes to the biodiversity value of a forest and recommend that broadleaved species are favoured as much as possible. While species compatibility with the site is recognised by the recommendations as being of paramount importance, they also favour planting of mixes including different native species, in order to promote structural complexity in the canopy. Furthermore, the retention of old growth trees and deadwood in forests is recommended (Anon, 2000b).

3. Methods

3.1 Study design and site selection

The aim of the FORESTBIO project is to assess biodiversity in a range of Irish forest habitats in order to address some of the key issues outlined above. The project also aims to identify biodiversity indicators that can be used to directly inform Sustainable Forest Management plans. In order to fulfil these objectives the biodiversity surveys were divided into three main areas:

- Biodiversity survey of reforested sites (with comparisons to BIOFOREST afforestation data).
- Biodiversity survey of various mixed species forests.
- Biodiversity survey of native woodlands.

A total of 60 sites were surveyed, mostly during the 2007 and 2008 field seasons, resulting in 20 sites sampled for each of the three key areas outlined above.

Botanical, invertebrate, ornithological surveys of these forests were mainly conducted during 2007 and 2008, with a small amount of fieldwork conducted in 2009. Biodiversity surveys were conducted at all sites during the summer months, unless otherwise stated in the text. Surveys were undertaken of:

- Epiphytes (lower trunk and canopy)
- Ground vegetation
- Ground-dwelling invertebrates (including some Lepidoptera surveys)
- Canopy-dwelling invertebrates
- Birds
- Deadwood

In some cases it was not possible to include all taxa at each site, and further data on the taxa studied at each site are provided in Appendix 1. In addition to these surveys, an investigation of Terrestrial Laser Scanning for forest biodiversity assessment was conducted.

3.1.1 Afforestation and reforestation survey

The aim of this survey was to investigate the biodiversity of afforested and reforested Sitka spruce (*Picea sitchensis*) plantations at different stages of the forest cycle. Coillte Teoranta, the Irish semi-state forestry body, provided the Forest database used to identify second-rotation plantations in the following age classes: age class I (4-6 years), age class II (9-16 years), age class III (20-29 years) and age class IV (30-50 years) in ArcGIS (ESRI ArcMap V3.2 and 9.2). A total of 20 plantations were surveyed, comprising five forests from each age class. We adopted a clustered approach, each cluster consisting of four sites (one from each age class) located in close proximity to one another, to minimise the potentially confounding influence of abiotic and climatic variation. This project was a continuation of an earlier investigation of the biodiversity of afforestation (first-rotation plantations) conducted as part of the BIOFOREST project (Smith *et al.*, 2005). We therefore selected second-rotation plantations that were planted in situations that resembled, as closely as possible, the previous land uses of the sites used in the first-rotation study. This was to ensure that comparisons between rotations would not be confounded by large variations in site productivity. Clusters were located to ensure a representative geographical spread across the country (Fig. 3.1). Sitka spruce was the dominant (> 90% cover) tree species at all sites. The five clusters of sites we selected are described in Table 3.1.

Table 3.1: Second rotation forest plantations selected for study in FORESTBIO. The 20 sites are divided into 5 geographic clusters, each of which is comprised of four sites of the following age-classes: age class I (4-6 years), age class II (9-16 years), age class III (20-29 years), and age class IV (30-50 years).

Site name	Code	Cluster	County	Location	Age class	Structural group
Ballyteige	BYTIE	East	Wicklow	T063846	IV	Commercially mature
Stranahely Wood	SWMID	East	Wicklow	S984957	III	Closed-maturing
Fauna	FAUNA	East	Wicklow	S928954	II	Thicket
Threewells	THREE	East	Wicklow	T149825	I	Pre-thicket
Baunreagh	BAUNR	Midlands	Laois	N298021	IV	Re-opening
Cullenagh	CULLE	Midlands	Laois	S493900	III	Closed-maturing
Sheskin	SHKIN	Midlands	Offaly	N252077	II	Thicket
Capard	CAPAR	Midlands	Laois	N372074	I	Pre-thicket
Rearour	REARO	South	Cork	X005861	IV	Re-opening
Ballyanthony	BYANT	South	Cork	W991877	III	Closed-maturing
Knockacool	KKCOO	South	Cork	W975845	II	Thicket
Boola	BOOLA	South	Waterford	X060850	I	Pre-thicket
Quitrent Mountain	QUITR	Southwest	Cork	R679149	IV	Commercially mature
Meenytinny	MEENY	Southwest	Cork	R243148	III	Closed-maturing
Tooreenascarty	TARTY	Southwest	Kerry	R09116	II	Thicket
Glengort	GLENG	Southwest	Limerick	R192218	I	Pre-thicket
Chevy Chase	CHEVY	West	Galway	R534982	IV	Commerically Mature
Bohatch	BOHAT	West	Clare	R695905	III	Closed-maturing
Derrykeel	DYKEE	West	Galway	R527999	II	Thicket
Reyrawer	REYRA	West	Galway	M535021	I	Pre-thicket

For the joint analysis of afforested and reforested sites, the sites were reclassified into Structural groups. During the BIOFOREST project, first rotation (afforestation) Sitka spruce plantations of 4 age classes were studied: 4-6 years, 9-16 years, 25-29 years, 35-50 years (see Iremonger *et al*. (2007) for further details). It was found that stands within an age class exhibited a large amount of variation in structural attributes. Factors such as climatic variation, soil type and moisture etc. influence the growth rate of trees within each age class. Although age can directly influence biodiversity in plantation forests (through colonisation or dispersal mechanisms), most age-related effects are mediated through stand structure and its influence on the below canopy environment. For these reasons, a structural classification of the forests was employed which used tree height, mean DBH and canopy cover in a cluster analysis to delineate the following structural groups which it was felt more adequately represented the various stages of the forest cycle than tree age per se: Pre-thicket, Thicket, Closed-maturing, Re-opening, Commercially mature (Table 3.1).
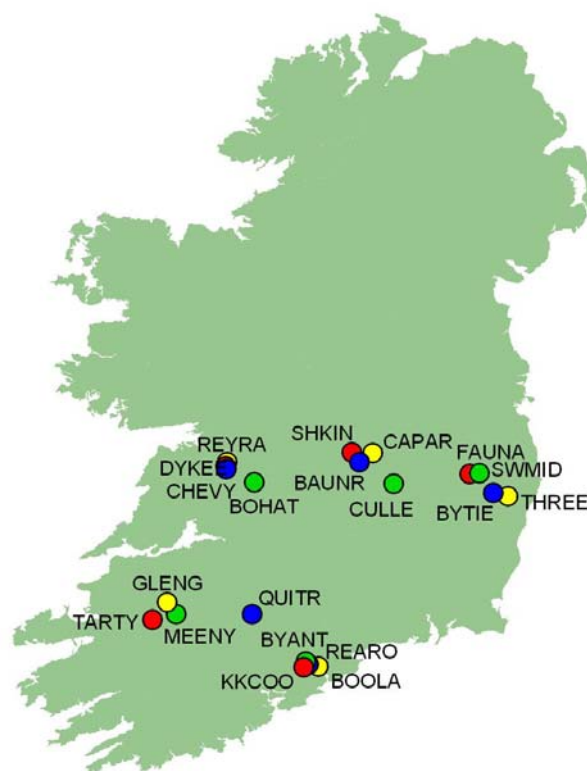
Figure 3.1: Distribution of study clusters throughout Ireland: ● = Age class I; ● = Age class II; ● = Age class III; ● = Age class IV.

3.1.2 Mixed tree species survey

After initial exploration of a forest database to determine what types of mixed plantations existed in the landscape, Norway spruce (*Picea abies*) was chosen as the primary plantation tree. Sitka spruce would have been preferable because of its importance in the plantation forest estate in Ireland and the availability of data collected from Sitka spruce plantations for this and other projects, but suitable mixed plantations were not available. Oak (*Quercus* spp.) and Scots pine (*Pinus sylvestris*) were chosen as the secondary mix species. Oak has been one of the most widespread native trees in the Irish landscape since the end of the last glaciation, while Scots pine was Ireland's only native pine, and the only one of three native Irish conifers (the other two are yew (*Taxus baccata*)) and juniper (*Juniperus communis*)) to be commonly included in commercial plantings in this country. Both of these trees are associated with acid to neutral soils and are often planted in intimate mixes with Norway spruce. Plantations containing both Norway spruce and either oak or Scots pine are referred to as 'mixes'. Five Norway spruce/oak mixes and five Norway spruce/Scots pine mixes and ten nearby stands of pure Norway spruce were selected, resulting in 20 forests in total to be studied. In all mixed study sites, the secondary mix species accounted for between 5 and 40% of the planted crop and was intimately mixed with the primary tree species (i.e. not clumped, but distributed more or less evenly throughout the stand).

ArcGIS v9.2 and forestry databases were used to select both pure and mixed plantation forests. To minimise environmental and abiotic variation, mixed and pure forests were located in geographic pairs, as close to each other as possible. Most pairs were within 5-10km of each other, but in one instance this was not possible due to a lack of suitable plantations, and the mixed and pure forests were located approximately 50km apart (Table 3.2 and Fig. 3.2).

Table 3.2: Mixed and pure Norway spruce plantations selected for study. Mixed sites consists of a plantation where Norway spruce is the dominant planting species and is planted in an 'intimate' mix with either oak (5 pairs) or Scots pine (5 pairs). The other sites are 'pure' Norway spruce plantations.

Site name	Code	County	Location	Site type
Parkanaur	PARKM	Tyrone	H736612	Norway spruce/oak mix
Woodburn	WOODM	Antrim	J375915	Norway spruce/oak mix
Gosford	GOSFM	Armagh	H970403	Norway spruce/oak mix
Thomastown	THOMM	Offaly	N141096	Norway spruce/oak mix
Garrynagree	GARRM	Waterford	C213869	Norway spruce/oak mix
Castle Archdale	CASTM	Fermanagh	H186600	Norway spruce/Scots pine mix
Jenkin	JENKM	Fermanagh	H501413	Norway spruce/Scots pine mix
Mote Park	MOTEM	Roscommon	M889616	Norway spruce/Scots pine mix
Crab	CRABM	Tipperary	S276569	Norway spruce/Scots pine mix
Coolacullig	COOLM	Cork	N452749	Norway spruce/Scots pine mix
Parkanaur	PARKP	Tyrone	H737612	Pure Norway spruce
Woodburn	WOODP	Antrim	J373919	Pure Norway spruce
Gosford	GOSFP	Armagh	H972410	Pure Norway spruce
Bogderries	THOMP	Offaly	N093077	Pure Norway spruce
Grallagh	GARRP	Waterford	C163834	Pure Norway spruce
Kesh	CASTP	Fermanagh	H124655	Pure Norway spruce
Jenkin	JENKP	Fermanagh	H496418	Pure Norway spruce
Mote Park	MOTEP	Roscommon	M907604	Pure Norway spruce
Crab	CRABP	Tipperary	S276569	Pure Norway spruce
Ballard	COOLP	Cork	R877063	Pure Norway spruce
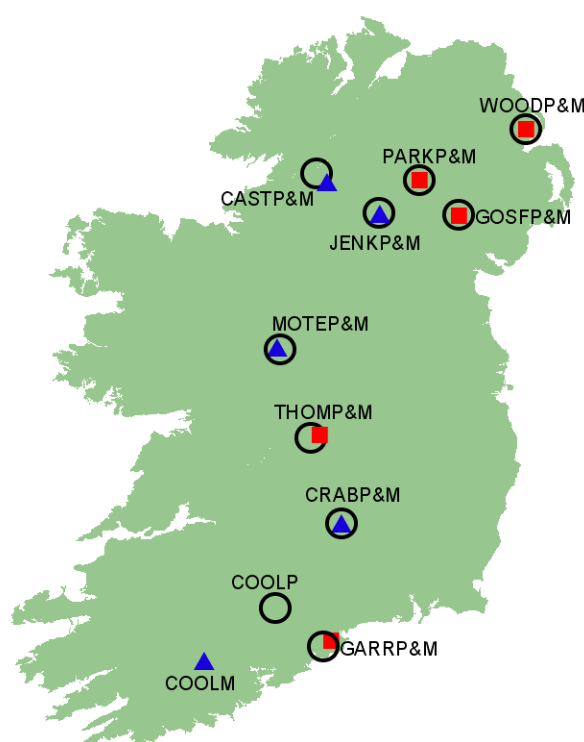
Figure 3.2: Map of Ireland showing mixed tree species survey sites. Norway spruce/Scots pine mixes are represented by blue triangles, Norway spruce/oak mixes are represented by red squares, and pure Norway spruce forests are indicated by open black circles.

3.1.3 Native woodlands survey

Twenty native woodlands were selected for study throughout the island of Ireland, all a minimum of 4ha in size (Table 3.3 and Fig. 3.3). Ten sites were oak-birch-holly woodlands (classified as WN1 by Fossitt (2000) and henceforth oak woodlands), which occur on acid or base poor, reasonably well-drained soils and are usually dominated by sessile oak *Quercus petraea*. The other ten sites were oak-ash-hazel woodlands (classified as WN2 by Fossitt (2000)), which occur on more base-rich soils (henceforth ash woodlands). Site visits were carried out to cross-check canopy species composition on the ground against the database inventory, and woodlands with more than occasional presence of beech (*Fagus sylvatica*), cherry laurel (*Prunus laurocerasus*), rhododendron (*Rhododendron ponticum*), and conifers (e.g. *Picea abies, Picea sitchensis, Pinus sylvaticus*) were excluded from selection. Oak woodlands were comprised of a minimum of 50% oak in the canopy and had an understorey dominated by birch and holly. To avoid too much overlap with the oak woodlands (the two types naturally grade into each other in many woodlands), it was ensured that cover of ash was < 10% across the site. Ash woodlands had a minimum of 25% ash in the canopy, an understorey dominated by ash and hazel, and a level of oak cover lower than that of ash. In both woodland types canopy height was a minimum of 6m.

Table 3.3: WN1 (oak) and WN2 (ash) native woodland sites selected for study. The canopies of WN1 woodlands were comprised of a minimum 50% oak, while the canopies of WN2 woodlands comprised a minimum of 25% ash and always contained a lower proportion of oak than of ash.

Site name	Code	County	Location*	Site type
Drummin Wood	DRUMM	Galway	R516997	WN1 (oak)
Prohus	PROHU	Cork	W268737	WN1 (oak)
Knocknabrandaun	KKBRA	Waterford	S246136	WN1 (oak)
Ballyarr	BYARR	Donegal	C185203	WN1 (oak)
Kilmacrea	KCREA	Wicklow	T231850	WN1 (oak)
Uragh	URAGH	Kerry	V836627	WN1 (oak)
Tomnafinnoge	TOMNA	Wicklow	T017697	WN1 (oak)
Brownstown Wood	BROWN	Kilkenny	S655295	WN1 (oak)
Breen Wood	BREEN	Antrim	D120336	WN1 (oak)
Rostrevor Wood	ROSTR	Down	J186172	WN1 (oak)
St John's Wood	STJON	Roscommon	M990569	WN2 (ash)
Cuildermot	DERMO	Galway	M280386	WN2 (ash)
Oughtnadrin	OUGHT	Donegal	G935743	WN2 (ash)
Drummans Island	DRISL	Roscommon	G837046	WN2 (ash)
Killough Hill	KILLO	Tipperary	S113515	WN2 (ash)
Dromore Nature Reserve	DROMO	Clare	R353863	WN2 (ash)
Killavalla Wood	KILLA	Tipperary	R950716	WN2 (ash)
Gole Wood	GOLEW	Fermanagh	H335248	WN2 (ash)
Greenaun North	GREEN	Leitrim	G791339	WN2 (ash)
Carrickbreeny	CRICK	Donegal	G930712	WN2 (ash)

* National Grid 6 point references
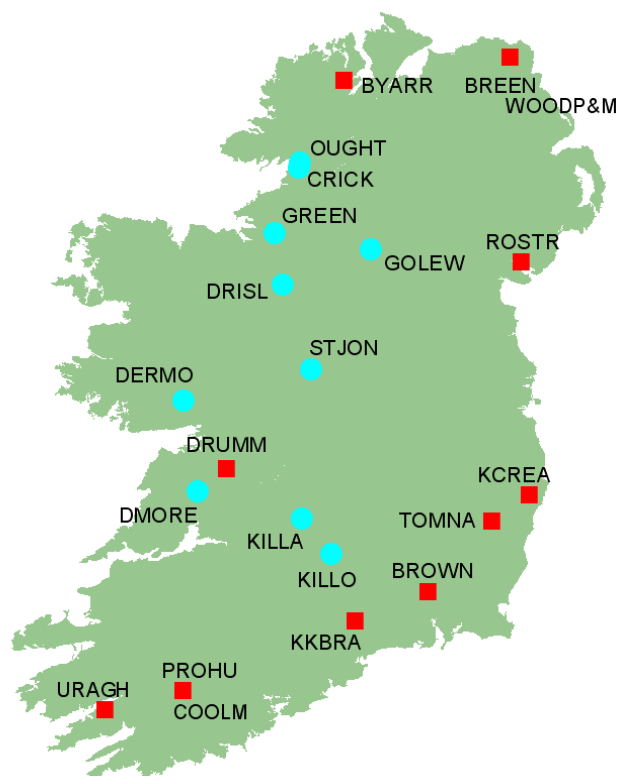
Figure 3.3: Map of Ireland showing native woodland survey sites. Ash woodlands are represented by light blue circles, and oak woodlands are represented by red squares.

Oak and ash woodlands in the Republic of Ireland were selected on the basis of their presence on 1840s Ordnance Survey maps, while those in Northern Ireland were selected from a database of ancient and long-established woodland (The Woodland Trust, 2007a). This was in order to minimise potential differences in floral and faunal communities as a result of differences in woodland age. However, due to a lack of suitable sites, we included two woodlands that were not present on the 1840s maps or the database. Following analysis we found that these woodlands did not differ significantly from the others and so results are presented for all woodlands. The native woodlands all currently receive little or no management intervention.

3.2 Biodiversity surveys

3.2.1 Epiphytes

3.2.1.1 Lower trunk epiphytes

Three 10m × 10m plots were studied at each site (Appendix 1). The plots were located at least 50m from the forest or woodland edge, and at least 50m apart, in areas that were considered to be representative of the site as a whole. Within each plot, the percentage cover of lichens, bryophytes and vascular plants (including ivy) up to two metres above ground level was recorded on living and dead trees using a five-point DAFOR scale (except for the reforestation sites where a presence/absence score was used) with D = dominant, A = abundant, F = frequent, O = occasional, R = rare. Each point on the scale was subsequently assigned an approximate percentage cover-value as follows: D = 70%, A = 30%, F = 5%, O = 0.2%, R = 0.04%. The number of trees, and the height and percentage cover (to the nearest 5%) of the canopy and understorey (≥ 2m tall) were recorded. The diameter at breast height (DBH, 1.3m) and the number of individuals of each tree species with a height ≥ 2m for planted trees and a DBH of ≥ 5cm for naturally regenerating trees were recorded. Stand basal area was subsequently calculated from these data. The total number of different host species in the plot, including trees and shrubs, was calculated and referred to as 'total host SR'. The total volume of snags was also calculated. Annual precipitation was calculated using data from Sweeney *et al*. (2003).

Hemispherical photographs were taken at the centre of each 10m x10m plot using a tripod-mounted Nikon Coolpix 8400 digital camera with a Nikon LC-ER2 fisheye lens. The camera was erected at 1.3m above ground, levelled and oriented towards magnetic north. The images were later analysed using Gap Light Analyzer 2.0 software (Frazer *et al.*, 1999) and percentage canopy openness was estimated. Slope (^{o}) and aspect were also recorded at each plot, and elevation was subsequently estimated from Discovery and Discoverer series Ordnance Survey maps. Aspect was transformed from degrees to a linear scale using the equation "A' = cos (45-A) + 1" (Beers *et al.*, 1966), where A is the aspect in degrees and A' is the transformed aspect. Using this transformation, southwest, the warmest and driest aspect in the northern hemisphere, receives a value of zero and northeast, the coldest, has a value of two. The intermediate aspects of southeast and northwest are both transformed to one. The position of each plot was recorded with a GPS (Global Positioning System). The proximity to old woodland, defined as areas marked as woodland (deciduous, coniferous or mixes) or scrub on the third edition 6":1 mile ordnance survey maps (1900-1913), and the area of old woodland (km^2) within a 1km radius were recorded for each site. Nomenclature follows (Stace, 1997) for vascular plants, Smith (2004) for mosses, Paton (1999) for liverworts and Coppins (2002) for lichens.

3.2.1.2 Canopy epiphytes

Epiphytes were studied at different heights on the trunk of a tree in 20 native woodland survey sites, 20 mixed tree species survey sites and in the five mature sites from the reforestation survey (Appendix 1). At each site, eight plots on a single trunk of the dominant tree species (oak, ash, Norway spruce or Sitka spruce) were sampled. All plots were 50cm high, but plot width varied according to trunk size. Plot width was 25cm or half the girth of the trunk cylinder, whichever was the smaller measurement.

Plots were assigned to four different height zones on the tree: tree base (B), lower (L), middle (M) and upper (U) tree trunk. The tree base zone was bounded at its lower extremity by the the point where the trunk emerged from the soil or needle litter. The centre of the lower zone plot was at breast height (1.3m),

while the centres of the middle and upper zone plots were at one-third and two-thirds of the height of the tree, respectively. For each height zone, two plots were studied on opposite sides of the trunk the aspect of these plots being centred on magnetic north and south. Tree-climbing techniques were used to study the middle and upper zones. This involved the use of a rope and harness and, in the case of conifers, climbing spurs. Branches were removed with a pruning saw where necessary to facilitate upward movement in the tree.

Within each plot, the identity of all epiphyte species was recorded and their percentage cover was estimated to the nearest 5%. Below 5% two different levels of cover were distinguished: 3% (indicating cover of 1-5%) and 0.5% (indicating cover < 1%). Total cover occasionally exceeded 100% for plots where plants of different species shared the same horizontal space. Data for the base and lower plots of two mixed plantation trunks and upper plot data for five native woodland trees (two ash and three oak trunks) were not recorded. To identify differences in species richness and assemblages between mature reforestation and afforestation plantations, we compared the reforestation data from this study with a subset of data from five afforestation sites sampled in 2003 and 2004 by Coote (2007). Afforestation sites were selected to be as similar as possible to reforestation sites in their soil type and age (Table 3.4).

Table 3.4: Characteristics of Sitka spruce afforestation sites (data collected by Coote (2007)) and reforestation sites (data collected in this study) used in further analyses.

Site name	Code	County	Grid Ref	Age (yrs)	Elevation (m)	Soil type
Afforestation						
Ballysmuttan	BMUT	Wicklow	O047 145	38	325	Podzol
Fuhiry	FURY	Cork	W146 734	41	290	Podzol
Meentinny	MEEN	Cork	R245 135	32	320	Peaty podzol
Mungacullin	MUNG	Wicklow	S954 683	42	280	Brown earth
Toureenmacauliffe	REAN	Cork	R256 200	39	380	Peat
Reforestation						
Ballyteige	BYTIE	Wicklow	T067 846	36	270	Gley
Baunreagh	BAUNR	Laois	N297 021	30	255	Gley
Chevy Chase	CHEVY	Galway	R534 983	37	60	Brown podzolic
Quitrent	QUITR	Cork	R678 148	35	240	Peat
Rearour	REARO	Cork	X004 860	35	150	Podzol

3.2.2 Ground vegetation

3.2.2.1 Vegetation sampling

Three 10m × 10m plots were studied in each site and were identical to those plots studied for lower trunk epiphytes. These were located at least 50m from the edge of the area of woodland, and at least 50m apart, in areas which were representative of the site as a whole. Within each plot, the percentage cover of each terrestrial (including saxicolous and saproxylic) species was estimated to the nearest 5%. Below 5% two different cover-abundance units were distinguished: 3% (indicating cover of 1-5%) and 0.5% (indicating cover < 1%). Algae and non-lichenised fungi were not recorded. For bryophytes and lichens, only species forming patches more than 10cm^2 were recorded. Species not forming patches of this size

but which were frequently occurring were also recorded. No minimum patch size was used for the sites studied during the BIOFOREST project. Nomenclature follows (Stace, 1997) for vascular plants, (Smith, 2004) for mosses, (Paton, 1999) for liverworts and (Coppins, 2002) for lichens.

3.2.2.2 Environmental and structural data sampling

Slope was recorded at each plot and elevation was estimated from Discovery and Discoverer series Ordnance Survey maps. For the comparison of forest types, the presence or absence of a steep slope (> 15°) was noted and annual precipitation was estimated using data from Sweeney *et al.* (2003). The diameter at breast height (DBH, 1.3m) of all planted trees ≥ 2m tall and all unplanted trees of ≥ 5cm DBH was recorded and the number (density) and species of these trees was noted. For the mixed tree species survey, the ratio of the number of oak or Scots pine to Norway spruce trees was calculated for each plot. For the native woodland survey and comparison of forest types, the presence or absence of grazing was determined based on presence of dung and/or trampling and damage to vegetation.

Within each 100m^2 plot, percentage cover (nearest 5%, as above) of the following vegetation strata was recorded: canopy, understorey (≥ 2m tall), shrub layer (< 2m tall, including climbers and prostrate woody species), field layer (non-woody), and bryophyte and lichen layer. For the afforestation-reforestation survey comparison and the comparison of forest types, in order to make the data collected during the BIOFOREST project (Smith *et al.*, 2005) and the current project comparable, the shrub layer excluded brambles and briars, but included climbing species; the cover of the bramble/briar layer (*Rubus fruticosus* agg. & *Rosa* spp.) was recorded separately; the field layer was separated into ferns, graminoids (grass, rush and sedge) and forbs (broadleaved herbaceous plants); and lichens were not considered, making the ultimate layer the bryophyte layer. These structural data were subsequently used to calculate an index of structural diversity using Simpson's reciprocal diversity index (1/D).

The percentage cover of the following ground cover categories was also recorded: bare soil, leaf litter (including broadleaved tree and herbaceous litter) and fine woody debris (FWD, < 10cm diameter). In the reforestation and mixed tree species plantations the cover of needle litter and brash piles (piles of deadwood left on site following thinning and/or clearfell) were recorded. For the afforestation-reforestation survey comparison, FWD and needle litter cover were combined in order to make the data comparable with the BIOFOREST project data. The total volume of coarse woody debris (CWD, ≥ 10cm diameter) was recorded and, for the mixed tree species survey, the cover of CWD was also estimated. Hemispherical photographs were taken at the centre of the 10m x 10m plot using a tripod-mounted Nikon Coolpix 8400 digital camera with a Nikon LC-ER2 fisheye lens. The camera was erected at 1.3m above ground, levelled and oriented towards magnetic north. The images were later analysed using Gap Light Analyzer 2.0 software (Frazer *et al.*, 1999) and percentage canopy openness was calculated.

Five soil samples were collected to a depth of 10cm, or to 5cm in the BIOFOREST sites, from near the corners and the centre of the 10m x 10m plot, and bulked in the field. Soil pH was determined for the bulked, field moist samples at the earliest opportunity, using a glass electrode pH meter on a suspension of soil and distilled water. Samples were air dried prior to analysis for organic matter content (LOI - 550°C x 5 hrs), total nitrogen and total phosphorus. Bulk density was calculated from loss-on-ignition data according to the method of Jeffrey (1970), and these data were used to convert the total nitrogen and total phosphorous data from a per weight to a per volume basis. For the native woodland survey, percentage soil carbon content was estimated by dividing the organic matter content values by 1.724, a widely used

conversion (Howard and Howard, 1990). Carbon/nitrogen ratios were subsequently calculated. Soil type was determined in the field from the soil samples, where deep enough, or from a soil pit, according to the Irish classification (Gardiner and Radford, 1980). For the native woodland survey, the presence of poorly drained peat or gley soils was noted. For the comparison of forest types, drainage was estimated on a four point scale (very good, good, moderate, poor).

Proximity to old woodland, defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the third edition 6" O.S. maps (1900-1913), and the area of old woodland within 1km were recorded for all but two sites, where a 3rd edition map was unavailable. For the afforestation and reforestation survey comparison, it was noted whether a site was on or adjacent to old woodland. For the comparison of forest types it was also noted whether the sites were on or adjacent to historic woodland, defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the first edition 6" O.S. maps (1837-1842). For the plantations, information on previous land use and the age of the stand was subsequently collected from forest managers. Information on the native woodland site history was scarce, but all available information was obtained from various sources (Bohan, 1997; Rackham, 2006; The Woodland Trust, 2007b; Perrin *et al.*, 2008a) on certain sites considered to be ancient woodland, those formerly coppiced or felled and those with conservation designations.

3.2.3 Ground-dwelling invertebrates and lepidoptera

3.2.3.1 Ground–dwelling invertebrates

Pitfall traps were used to collect spiders and Carabid beetles within the forest stands, a method which has been widely used to sample ground-dwelling invertebrates in forested habitats (Oxbrough *et al.*, 2005; Mullen *et al.*, 2008; Yu *et al.*, 2008; Ziesche and Roth, 2008). Although it is an efficient method, it should be noted that pitfall catches are dependent on a species' density and activity and so do not represent a measure of absolute abundance (Curtis, 1980). Three sampling plots were established in each site adjacent (< 10m) to the ground vegetation and lower trunk epiphyte survey plots. Each sampling plot was comprised of five pitfall traps spaced 2-4m apart. Each pitfall trap consisted of a plastic cup, approximately 7cm in diameter and 9cm in depth. A bulb corer of similar dimensions to the cup was used to make a hole in the ground in which to sink the cup so that it was flush with the soil surface and soil disturbance around the trap was minimized. Two drainage holes were cut horizontally, 1 cm from the top of the cup and traps were filled with ethylene glycol to a depth of 1cm to act as a killing and preserving agent. There was considerable animal disturbance (> 80% trap loss) at two sites sampled during 2007 (BAUNR and BYANT), so these sites were re-sampled during the same period in 2008. To reduce the impact of animal disturbance a combination of protective wire mesh boxes (mesh size was approximately 3cm to allow ground-dwelling invertebrates to pass through) and wire mesh 'roofs' held 5cm above the ground by plastic pegs and attached to electric fence units were used. To identify any potential influence of the protective devices or of sampling across years two further sites were re-sampled in 2008 which were located in close proximity to the disturbed sites, were of similar age class and had a full set of pitfall traps collected during the previous year for comparison. All traps were set in mid May of 2007 or 2008 and left *in situ* for 9 weeks giving a total of 61-63 trapping days. However, traps in the reforestation survey were left *in situ* for an additional 21 days in order for comparisons to be made with BIOFOREST project data. The contents of all traps were emptied every three weeks.

Spider assemblage data from afforested sites sampled during the BIOFOREST project were used for comparison with reforested sites. Twenty three first rotation sites were sampled during 2001-02 with between four and seven replicate sites for each age class. A similar pitfall trapping protocol was followed with the exception that five sampling plots were established in each of the first rotation stands. Traps in the first rotation stands were set in mid June in either 2001 or 2002 and were left *in-situ* for 9-10 weeks giving a total of 64-71 trap days. These comparisons and those of the reforestation forest cycle utlised structural groupings (see general methods section) rather than age classes. A full protocol for the sampling in the BIOFOREST afforestation sites, identical to that used in this study, is outlined in Oxbrough (2005).

At each sampling plot, metrics of stand structure were measured including Canopy openness (by hemispherical photography), diameter at breast height (DBH) and Tree height. A soil sample was also taken at each plot and Organic content and pH were subsequently determined. Cover of vegetation layers was estimated within a 1m^2 quadrat surrounding each of the five pitfall traps in a plot using the following classification: Ground layer vegetation (< 10cm); Lower vegetation layer (> 10cm - 50cm); Upper vegetation layer (> 50cm - 200cm) and Understorey layer (> 200cm). Coverage was estimated to the nearest 5 %, with values of between 1-5% recorded as 3% and coverage of less than 1% allocated 0.5 %. Other ground cover types (i.e. rocks, bare soil, litter) and the amount of deadwood in each of the following categories were also recorded by this method: Coarse woody debris (CWD, diameter ≥ 10cm at widest point); Fine woody debris (FWD diameter < 10cm); Brash pile (accumulated deadwood as a result of felling/thinning, various diameters). Lastly, the depth of litter was measured within each quadrat. For the analyses a mean value was calculated across the five quadrats to obtain a representative value per plot. The method for collection of plant species richness and composition data is described in the ground vegetation section of this report.

The spiders and Carabid beetles (hereafter referred to as beetles) were sorted from the pitfall samples and adults were identified to species level using Roberts (1993) and Luff (2007). Nomenclature follows these texts. Species from both taxa were assigned to habitat preferences using the literature, primarily Roberts (1993), Forsythe (2000a), Harvey (2002), Luff (2007) and Nolan (2010). A full list of species collected, their authorities and habitat associations are given Appendices 2 and 3.

3.2.3.2 Lepidoptera

Lepidopteran sampling took place only as part of the mixed tree species survey and so data are only available for this survey and for the comparison of forest types (see Appendix 1). Light traps were used to sample the Lepidoptera. These are the most commonly adopted method for sampling Lepidoptera, as they capture the widest range of species of moth of any trapping technique (Fry and Waring, 2001). Actinic Heath light traps were used as they are relatively light weight, making them more suitable to remote places accessed by foot, and are cheap in comparison with other trap types. In addition the actinic tube light is cold in operation and so is not damaged by rain. Light trapping was carried out over a six week period between early June and mid July 2008. This was timed to correspond with the peak flight season for the majority of moth species in Ireland.

Two light traps were deployed in each forest stand, adjacent to two of the pitfall-lower trunk epiphyte-ground vegetation plots. Each trap was spaced a minimum of 100m apart and never in direct line of sight, to prevent light interference between the traps. The traps were placed in the centre of a white sheet

measuring 1.5m x 1.5m to increase visibility, delineating a cut-off point in terms of counting species around the trap whilst making sure there is no bias towards more conspicuous species. The traps were deployed in a stand before dusk on each sampling night and were automatically turned on and off by an attached light sensor at sunset and sunrise. Trapping was only carried out on nights where the temperature was 10°C at dusk, when wind was not in excess of Beaufort force 4-5 (13-24 mph), and when persistent or heavy rain was not forecast for the night. Geographic pairs of mixed and pure sites were always sampled on the same night to ensure that variation in weather between trapping nights did not affect between-pair comparisons. For the native woodlands it was only possible to sample one stand per night due to the geographical spread of sites. At dawn, netting was placed over each trap and white sheet to ensure moths captured did not escape. Lepidoptera (hereafter referred to as moths) were identified in the field using Waring (2007) and nomenclature follows this text. Ambiguous specimens were photographed for later identification, and, where necessary, were killed in a jar using 30% ammonia, stored in a cooling box, and pinned for later identification by one of the foremost experts of Irish Lepidoptera, Mr Ken Bond. For analyses, species were assigned to habitat preferences using the literature (Emmet and Heath, 1991; Gittings and Bond, 2008). A full list of species, their authorities and habitat associations are given in Appendix 4.

3.2.4 Canopy-dwelling invertebrates

3.2.4.1 Canopy-fogging method

Canopy fogging has become one of the most popular of sampling methods for researchers working on canopy invertebrates. It provides access to invertebrate populations in tall canopies while enabling access-related disturbance to be kept to a minimum, due to the lack of requirement for access structures. However, it does have some disadvantages. The areas one can sample using this method may restricted due to difficulties in accessing remote or densely vegetated areas with the heavy and cumbersome equipment needed for fogging. The method is also limited by weather conditions, with at least several hours of dry, still weather required for successful sampling. It is known that canopy fogging does not sample certain groups that live within the tree itself, such as gall formers and leaf miners (Stork and Hammond, 1997). This method may also overlook sessile animals, those in webs and cocoons or those attached by silken threads (Stork and Hammond, 1997). Some aphids and other sucking insects may not fall if they have not removed their stylets before succumbing to the insecticide, and semi-permanently or permanently attached phloem feeders will not be sampled (Stork and Hammond, 1997). Adult bark beetles (Scolytidae) and other wood-inhabiting groups may also not be accurately represented in fogging samples, where they tend to be present in low numbers, whereas, when malaise traps are used in the same trees, these bark-burrowing species are caught in larger numbers (Stork and Hammond, 1997). Therefore, fogging is not generally regarded as a good method for sampling insects found in burrows in bark, under bark, deep in the wood, in rot holes or in nests (Stork and Hammond, 1997). However, on the whole, a study by Stork and Hammond, (1997), showed that nearly twice as many insect species associated with oaks were collected by fogging when compared with malaise traps.

Canopy fogging field trials began in late May 2007. Initially a water-based insecticide (AquaPy) was chosen for use in the fogging machine, as it is a more environmentally friendly option than a petrol-based insecticide, and any subsequent residue left on the trees is less likely to cause damage to the foliage and invertebrates present. However, initial field trials found that the water-based fog was not visible and therefore it was not possible to accurately direct the fog into the area of canopy chosen for survey. In light

of this, it was decided to use a petrol-based insecticide with white vapour that is clearly visible and therefore easier to direct into the target canopy.

Field trials indicated that diurnal variation in wind conditions and dewfall restrict the period suitable for fogging on the vast majority of days to between 6am and 9am each morning. Fogging should be undertaken only in still, dry weather, as invertebrates will stick to damp or wet leaves and not fall onto the collectors (Connolly, 1992). It is therefore inadvisable to fog immediately after dawn, as morning dew has not yet had a chance to evaporate. In terms of wind, sampling should not be carried out when there is enough of a breeze to move the leaves of the trees, as the fog will then spread laterally and may not reach the top of the canopy (Stork and Hammond, 1997). This means that fogging can be carried out in wind speeds of no more than 6-9kph, which often limits the time suitable for fogging to before 9am, even on relatively still days. This restricted the number of sites sampled to one per day, except where sites were in close proximity to one another. Additionally, the time spent fogging was restricted by inclement weather (many days were unsuitable for fogging due to damp conditions or rising wind speeds), and the unusually high number of days of rainfall in the summers of 2007, 2008 and 2009. The year 2008 was the wettest summer in Ireland since records began, until 2009, which was even wetter (Met Éireann, 2010a).

The experimental nature of the fogging fieldwork meant that optimum methodology and associated limitations were not finalised until the last week of August and first fortnight of September in 2007. The periods of peak abundance for the target invertebrate taxa had passed by this time (Connolly, 1992), which meant that the results from 2007 were not comparable to the following years. It was also found that age class I and II Sitka spruce sites were unsuitable for fogging due to fire risk (in the case of age class II sites) and trees that were too small and widely spaced (in age class I sites), and therefore canopy invertebrates were not sampled in these age classes.

3.2.4.2 Canopy invertebrate sampling

Canopy fogging was carried out during the summer months from April to August 2008 and 2009 (Appendix 5), to coincide with the major periods of activity-abundance of the target taxa (Connolly, 1992). A petrol-driven fogging machine (SwingFog SN50-PE, supplied by SwingTec Ltd, Germany) was used with a natural pyrethroid (Pybuthrin 33, supplied by Spray-Chem Ltd, Dublin). This petrol-based insecticide is non-persistent in the environment, has no phytotoxic effects and (at the levels used by this method) is not harmful to mammals or birds (Casida, 1980; Straw *et al.*, 1996). Canopy fogging disperses an aerosol insecticide (usually pyrethrins) in ultra low volume (ULV) droplets into the tree canopy. ULV techniques produce droplets that are much smaller than those produced by spraying, and provide a method whereby pesticides are applied in minimum volumes with highly accurate doses (Connolly, 1992). The insecticidal fog is generated by the injection of the pesticide through a nozzle into the exhaust of the fogging machine's engine, which produces droplets that are less than 5μm in diameter (Connolly, 1992). The fog produced is clearly visible and rises through the canopy in still conditions, allowing its progress to be easily followed (Connolly, 1992). The insecticidal fog rapidly kills or incapacitates canopy invertebrate fauna (Connolly, 1992). Fallen invertebrates are then collected using an arrangement of plastic sheets, trays or funnels, which are set up under the fogged canopy (Connolly, 1992). Sheets suspended under the canopy are more suitable than ground sheets, as they reduce the risk of contamination by 'tourist' invertebrates (i.e. invertebrates not based in the sampled area).

Within each forest one area was selected for the fogging plot, which was representative of the forest as a whole and at least 50m from the forest perimeter to reduce possible edge effects (Ozanne *et al.*, 1997). A 'target' tree was selected at the centre of each fogging plot. Target trees were oak in oak woodlands and Norway spruce/oak mix plantations, ash in ash woodlands, Norway spruce in pure Norway spruce stands, and Sitka spruce in afforesation or reforestation Sitka spruce stands. Sampling of the canopy is not limited to the target tree using the canopy fogging technique, as inevitably the canopy of surrounding trees is interspersed with the target canopy and so this was also sampled. This may have included Norway spruce in the mix plantation stands, or understorey species in the native. However, as the investigation of broad patterns in canopy invertebrate community composition between native broadleaved and non-native coniferous forest types was the main research aim, small-scale differences within forest types are unlikely to confound the results.

Prior to fogging, 16 plastic sheets with a combined area of $24m^2$ ($1.5m^2$ per sheet) were suspended above the ground in the fogging plot on 1m high wooden rods pushed into the ground and attached to the sheets at each corner. This area is known to adequately sample the diversity of canopy invertebrates. Each sample sheet was suspended so that it would slope downwards towards its middle, preventing invertebrates from falling off the edge of the sheets and reducing the chances of escape by recovering insects (Stork and Hammond, 1997). Sampling sheets were arranged around the target tree on the eight cardinal and ordinal compass bearings (N, NE, E, se etc.). Two sheets were aligned lengthwise on each compass bearing and sample sheets were separated by 0.5m from each other and from all trees (Fig. 3.4). During fogging, one person operated the fogging machine while an assistant instructed the operator where to direct the fog in order to maximise the exposure of the target area of canopy to the insecticide. Each canopy was fogged for approximately 6 to 9 minutes, until fully covered in insecticidal fog. Sample sheets were left in place for 3 hours after fogging finished (Stork and Hammond, 1997), and the catches from 16 sample sheets from one site were pooled. Samples were collected *in situ* using soft paintbrushes to brush invertebrates into bottles containing 70% alcohol before the insects could recover from the effects of the insecticide.
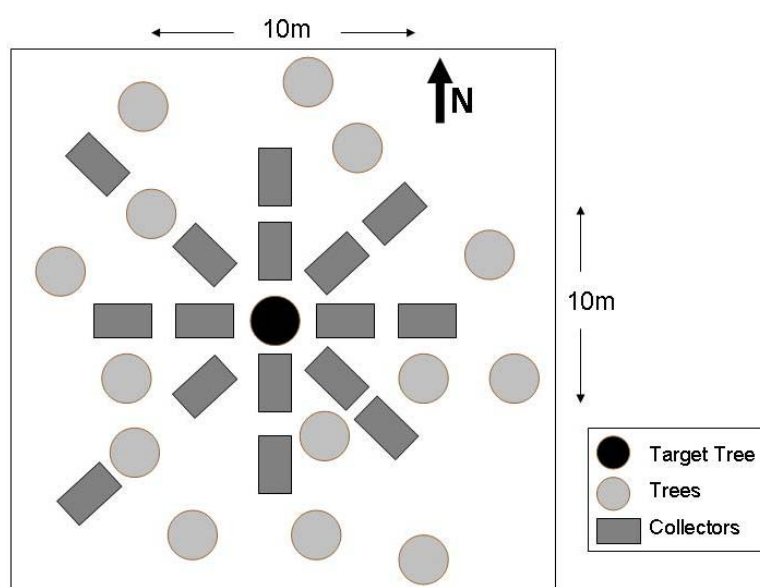
Figure 3.4: Layout of canopy invertebrate collection sheets in the fogging plots.

3.2.4.3 Canopy invertebrate identification

Target taxa were sorted in the laboratory and adults from the Orders Araneae (spiders) and Coleoptera (beetles) were identified to species level using the available literature (Joy, 1932; Majerus and Kearns, 1989; Morris, 1990; Morris, 1991; Roberts, 1993; Luff, 2007). Species-level identification of all individuals was not possible due to the large numbers of specimens caught, but all taxa were identified to either Family or Order, to provide a general overview and comparison of the numbers of individuals and relative community composition of the canopy invertebrate fauna present in the different site types. Adults from the Orders Diptera (true flies) and Hemiptera (true bugs) were identified to family level (primarily using Unwin, 2001; Oosterbroek, 2006), while all other invertebrates were enumerated and assigned to Order using Chinery (1993). Nomenclature of all species, families and Orders follows Fauna Europaea (2004). Basic training in taxonomy and species-level identification was provided by postdoctoral researchers in UCC, and verification of species identities were confirmed by experts and entomologists familiar with the groups sampled (see acknowledgements).

All spider and beetle species identified were assigned categories based on their feeding guild and habitat preferences (see Table 3.5 for descriptions of these categories and Appendix 6 for a detailed account of the species assigned to these categories) using the available literature (primarily Harvey *et al.*, 2002; Buckland and Buckland, 2006). Habitat preferences were assigned to species depending on the habitats they were typically associated with or recorded in. Beetle species were also categorised according to their rarity (JNCC, 2010). Such categorisation was unnecessary for the spider species sampled, as all of these were classified as common species.

Table 3.5: Feeding guild, rarity and habitat preference categories assigned to canopy spiders and beetles

Feeding Guild Categories	Category Abbreviation
Spiders building orb webs	Orb Web
Spiders building scaffold webs	Scaffold web
Spiders building sheet webs	Sheet web
Spiders or beetles actively hunting other invertebrates	Active Hunters
Beetles feeding on live plant matter, herbivores, phytophages	Phytophagous
Beetles feeding on plant and animal debris, scavengers, omnivores	Detritivorous
Beetles feeding on fungi and rotting plant matter	Mycetophagous
Beetles feeding on deadwood	Xylophagous
Rarity Categories	
Common or ubiquitous	Common
Locally distributed or widespread but restricted to certain habitats, uncommon, or rare	Local
New Irish record	New Irish record
Red-listed* in the UK	RDB/Notable B
Habitat Preference Categories	
Predominantly associated with coniferous forest	Conifers
Predominantly associated with broadleaved forest	Broadleaves
Predominantly associated with forests/forest of any kind	Mixed Forest
No association with forest, open habitats preferable or species is ubiquitous in many habitats.	Generalist

*Red-Listed according to the JNCC (2010)

Although there are currently no Red-lists for the majority of invertebrate species in Ireland, the UK Red-List categorisation was used in the absence of anything available from an Irish perspective. The above categories could not be applied to family- or Order-level data. Reference collections of all identified spider and beetle species were made, and are stored in the museum of the School of Biological, Earth & Environmental Sciences, UCC.

3.2.4.4 Environmental and habitat measurements

At each fogging plot, several environmental and habitat variables were recorded to form a 'map' of the environmental and structural metrics present, including elevation, slope and aspect of the plots. Average canopy height (to the nearest 0.1m), diameter at breast height (DBH) at 1.3.m for all trees ≥ 2m tall, and number of trees ≥ 2m tall. Coarse woody debris (CWD: diameter ≥ 10cm at widest point) and Fine woody eebris (FWD: diameter ≤ 10 cm) coverage were estimated at each plot within four $1m^2$ quadrats placed 1m to the N, S, E and W of the fogged target tree. Woody debris coverage was estimated to the nearest 5%, with values of 1–5% recorded as 3%, and those of ≤ 1% allocated 0.5%. A mean value for coverage of CWD and FWD was calculated across the four quadrats to obtain a standardized value per fogging plot. Average minimum and maximum temperatures for the day of fogging were estimated using Met Éireann daily temperature ranges and the nearest weather station to each site (Met Éireann, 2010a). Canopy openness was estimated from digital hemispherical photography using Gap Light Analyzer V.2 (Frazer *et al.*, 1999) at a location two metres to the south of the target tree at each fogging plot.

3.2.5 Birds

3.2.5.1 Bird surveys

Birds were surveyed using point counts (Bibby *et al.*, 2000). Six (or, if forests were too small, between 4 and 5) point counts were placed in each forest to ensure reliable density estimates and to standardise survey effort. Points were randomly placed a minimum of 100m apart in edge and interior habitat. Counts lasted for 10 minutes, during which time all birds seen and heard within 50 metres of the observer were recorded and their distances from the observer noted. Counts were conducted on days without strong wind (less than Beaufort scale 4) or persistent rain. Thirty-six of the sixty study sites were also surveyed in the winters (November – February) of 2007-2008 and 2008-2009, with 18 sites surveyed in each winter (Appendix 1). These forests were visited twice in winter to ensure comparability of data with that collected during the breeding season. There was a gap of approximately 4 – 6 weeks between the first and second winter visits in each forest. One age class III forest was visited only once in winter due to an error, and two points in one pure Norway spruce plantation only received one winter visit due to unexpected tree felling. Because of the number of study sites in each survey, it was necessary to survey forests in both the morning and afternoon. During the breeding season, one of the visits to each site was carried out between 0800 and 1100 hours, and the other between 1400 and 1700 hours. Each point therefore received both a morning and an afternoon count. A similar approach was adopted in the winter, with morning counts being conducted from 0930 – 1200, and afternoon counts taking place between 1200 and 1430. This approach has been used before and may help to reduce any diurnal bias due to particular species being more or less active at a particular time of day (Wilson *et al.*, 2006). Densities of all species were calculated for the early and late counts and the maximum of these two values was used as the density of a species.

3.2.5.2 Bird communities

Bird metrics extracted from the data were population density, species richness and mean Simpson's reciprocal diversity index (Simpson's diversity). EstimateS (Colwell, 2006) was used to randomly resample the data 500 times to generate a mean Simpson's diversity for every site to ensure that there was no effect of sample size on the index. Species richness was calculated as the cumulative number of species recorded over two visits. Due to their significance from a conservation perspective, and their importance to the bird fauna of temperate regions, migrant species were analysed both as a component of total bird density and separately. Individuals that were detected in flight were excluded from analysis, along with individuals of the Corvidae (with the exception of Jay, *Garrulus glandarius*,) Hirundinidae and Motacillidae as their presence cannot be assumed to indicate a breeding association with forests. Eleven species were identified as being forest specialists: Blackcap (*Sylvia atricapilla*), Bullfinch (*Pyrrhula pyrrhula*), Blue Tit (*Cyanistes caeruleus*), Chiffchaff (*Phylloscopus collybita*), Crossbill (*Loxia curvirostra*), Great Tit (*Parus major*), Garden Warbler (*Sylvia borin*), Long-tailed Tit (*Aegithalos caudatus*), Spotted Flycatcher (*Muscicapa striata*), Treecreeper (*Certhia familiaris*) and Woodcock (*Scolopax rusticola*). All of these either have a strong association with all forest habitats in Ireland, or else specialise in one type of forest habitat (e.g. coniferous or broadleaved) to the exclusion of the other.

3.2.5.3 Vegetation and habitat recording

Vegetation variables were estimated visually in a 30m radius from each point and expressed as percentage cover. These variables included canopy cover and height, cover and height of the understorey (a vegetation layer taller than the shrub layer but beneath the canopy), shrub cover (woody vegetation under 2m), field layer cover (non-woody vegetation under 2m in height), ground layer cover (mosses and liverworts) and needle litter cover. In the winter survey, the percentage cover of evergreen plant species, and of those common species that provide berries in winter was also recorded (Table 3.6). An attempt was made to quantify berry production at each point count but was not practical because much of the ivy occurred at too great a height to be examined. However, it is reasonable to assume that the greater the cover of berry-producing plant species, the more berries are present. For each of these variables, the mean value across both visits was calculated for each point. The value for each site was calculated as the mean percentage cover from all point counts. Analyses of bird data also incorporated habitat information from other parts of the FORESTBIO study. This included mean diameter at breast height (DBH) of all crop trees; tree basal area (m^2 per 10x10 plot) and the number of stems in the plot (including crop trees > 2m tall and non-crop trees > 5cm DBH), derived from the three 10x10 metre ground vegetation and lower trunk epiphyte plots (see ground vegetation section above); and a measure of canopy openness derived from hemipsherical photographs (see ground vegetation methods). All values for these variables were converted to site averages before analysis. Measures of patch size, prevalence of open space and presence or absence of rides were derived from aerial photos. While it was possible to measure forest patch size for most of the native woodland sites, which comprised discrete blocks of forest set in a matrix of non-forest habitat, most plantations were embedded in a larger area of plantation forest making calculation of a meaningful size for each forest patch impossible.

Table 3.6: Evergreen and berry-producing plant species recorded during the study. Nomenclature follows Stace (1997).

Common name	Scientific name	Evergreen	Berries
Elder	*Sambucus nigra*	No	Yes
Gorse	*Ulex europaeus*	Yes	No
Guelder rose	*Viburnum opulus*	No	Yes
Hawthorn	*Crataegus monogyna*	No	Yes
Heather	*Calluna vulgaris*	Yes	No
Holly	*Ilex aquifolium*	Yes	Yes
Honeysuckle	*Loniceria periclymenum*	No	Yes
Ivy	*Hedera helix*	Yes	Yes
Mountain ash	*Sorbus aucuparia*	No	Yes
Spindle	*Euonymus europaeus*	No	Yes
Tutsan	*Hypericum androsaemum*	Yes	Yes
Yew	*Taxus baccata*	Yes	Yes

3.2.5.4 Density estimation

Distance (Thomas *et al.*, 2006) was used to derive species densities from field observations. Both the identity of a species (Alldredge *et al.*, 2007) and the habitat in which it is observed (Schieck, 1997) may affect the detectability of birds. Ideally, each species-habitat combination should therefore be analysed using a separate detection function, however we did not have enough bird observations to make this possible. Each species was therefore assigned to one of four species detection groups, which depended on the method of detection, the distribution of detections in five 10 metre distance bands and knowledge of the species' ecology. Therefore, species in the same detection group were judged to have roughly similar detectability. Detection groups differed between the breeding season and winter, because bird behaviour differs according to seasons. Because habitat may also affect the detectability of birds (Schieck, 1997), study sites were allocated to habitat detection groups based either on study site type (for comparisons between native woodland and plantation forests, and between different growth stages of second rotation plantation forest) or on groupings derived from cluster analysis in PC-ORD (McCune and Mefford, 2006) using the vegetation data collected in each forest. Akaike's Information Criteria (AIC) was used to select between four models for fitting of the detection function: Uniform + Cosine, Uniform + Polynomial, Half normal + Hermite and Hazard-rate + Cosine (as recommended by Buckland *et al*. (2001). For each site, the population densities of all species for both the early and late counts were calculated, and the density of a species taken as the maximum of these two values. When comparing density data with those derived from previous studies, densities were corrected using annual rates of population increase calculated by the Countryside Bird Survey (Coombes *et al.*, 2009), and models run both with the original and corrected data.

In winter, flocking birds are a potential source of bias when using *Distance* to estimate bird density if detectability is biased by flock size (Newson *et al.*, 2005). The occurrence of mixed-species flocks also complicates the estimation of species' densities. To check whether detectability was affected by flock size, correlations of flock size and both distance from the observer and probability of detection were carried out in *Distance*, where significant correlations would have indicated that detectability was affected by flock size. This was repeated for each site group, each detection group and for each species that was

commonly detected in flocks. Flock size did not have a significant effect on detectability in any of the site groups or detection groups. Among the species detected in flocks, only Goldcrest showed a significant increase in detectability when it was part of a mixed-species flock. As a result, Goldcrest was analysed separately from all other species. To generate winter densities for species in mixed-species flocks, we entered 'flock' at the observation level in *Distance*. Mixed-species flocks were placed in the same detection group as the species that typically comprised the flocks (group 1). The density output for mixed-species flocks was divided, in the correct proportion, between each species that comprised the flock. This density was then added to the calculated individual density for each species to obtain the total density of a species. The contribution of mixed-species flocks to the total density of a species was typically low for all species (< 5%) except for Long-tailed Tit (up to 100%). Density was calculated for both the first and second visits for each species, and the maximum of the two visits taken to be the species' density.

3.2.6 Deadwood surveys

Deadwood surveys were conducted at the 20 native woodland sites, and also at five age class IV (30-50 years old) reforestation plantation forests throughout Ireland (Appendx 1). ArcGIS v9.2 was used to randomly place ten 30m transect start points in each of the 25 forest patches. Prior to visiting the site, each transect was assigned one of eight compass bearings which denoted transect orientation from the start point (making sure that the assigned bearing did not take the transect outside of the study site) to ensure that there was no observer bias either towards or away from large logs or snags (Ringvall and Ståhl, 1999). Between seven and 10 transects were conducted in each forest patch depending on size and terrain. Line-intersect sampling (Kirby *et al.*, 1998) was used to calculate the volume of logs in all of the forest patches. All logs greater than or equal to five centimetres in diameter at the point of intersection with the transect line were recorded in one of five size classes: 5 - 10 cm, 11 - 20 cm, 21 - 30 cm, 31 - 40 cm and > 40 cm. These intersections were then converted to volume of fallen wood (m^3 ha^{-1}) per transect using the mean diameter of measured logs in each size class. The mean of the volumes calculated from each transect was then taken as the site volume. Five centimetres was used as a minimum log diameter to ensure comparability with as many published studies as possible (Sweeney *et al.*, 2010b). Logs were assigned to one of three decomposition classes: 1: intact (still solid with bark attached); 2: part rotted (bark absent and beginning to decompose) and 3: well-rotted (crumbly).

Standing deadwood features greater than two meters in height were classed as snags. All snags with a diameter at breast height (DBH) greater than 5 cm and within two metres either side of the transect line were recorded. Snags were placed in the same three rot categories as were used for logs. Snag density was subsequently calculated. It was not possible to calculate snag volume as the height of snags was not measured. All stumps (standing deadwood less than two meters in height) located within two meters each side of the transect line were also recorded and used to calculate deadwood volume contained in stumps (Sweeney *et al.*, 2010b).

3.2.7 Terrestrial laser scanning

In order to investigate the use of Terrestrial Laser Scanning for forest biodiversity assessment, a subset of FORESTBIO sites was assessed using TLS (Appendix 1). A total of 10 sites were selected for this work, of which 4 were native woodlands and 6 were commercial conifer plantations. Scans were conducted

during both summer and winter. A Faro laser scanner (LS 880HE) was used to carry out the sampling. The scanning hardware was used to generate a point cloud description of an area of forest (Fig. 3.5). A point cloud description is an array of points comprising a 3D image of the scanned forest. Each point is represented by its x, y and z coordinates, along with an intensity measure that can be used to derive information associated with angle and texture. These data were used to derive structural information with relevance to forest structure and biodiversity including:

1. Tree diameter at breast height (DBH).
2. Tree height (to a point up the stem where diameter is approximately 70mm).
3. Deadwood (volume of logs and both volume and density of snags).
4. Coefficient of Variation (%) of estimated biomass between 1.82m and 15.82m above ground.
5. Open space (distance between trees).
6. Standing volume per hectare.

Figure 3.5: Three-dimensional images produced using terrestrial laser scanning at a native woodland (left) and in a Sitka spruce plantation (right).

The objective of the study was to determine whether a number of specific biodiversity measures could be predicted from the structural information in terrestrial laser scan data. The specific biodiversity measures we considered were: beetle species richness, bird species richness, canopy invertebrate species richness, ground vegetation species richness and spider species richness. Values for these metrics were taken from the surveys of flora and faunacarried out at the laser-scanned sites.

3.3 Data analysis

3.3.1 Epiphytes

Total epiphyte, moss, liverwort, lichen and vascular plant species richness (SR) were calculated for each 10m x 10m x 2m plot at the tree bases and lower trunks (referred to as lower trunk epiphytes) as well as for each 50cm x 25cm plot at different height zones on the tree trunks (referred to as canopy epiphytes). For the lower trunk epiphytes, mosses and liverworts were often combined to give bryophyte SR. Data relating to species identified only to generic level were handled so that their inclusion did not cause an overestimation of species richness. If no other species belonging to the genus of an unidentified specimen were present within the plot, then the specimen was considered an additional species. If other species belonging to the genus of an unidentified specimen were present within the plot, then the specimen was excluded from species richness counts. Affinity for epiphytism was calculated after Coote (2007), using information from Irish and British literature (Watson, 1981; Jermy *et al.*, 1982; Hubbard, 1984; Clapham *et al.*, 1987; Grime *et al.*, 1988; Smith, 1990; Hill *et al.*, 1991; Hill *et al.*, 1992; Purvis *et al.*, 1992; Fitter and Peat, 1994; Hill *et al.*, 1994; Webb *et al.*, 1996; Paton, 1999; Dobson, 2000; Preston *et al.*, 2002; Smith, 2004). Each species was classified as having low affinity (mostly recorded in non-epiphytic situations), medium affinity (frequently occurring in epiphytic and non-epiphtic situations) or high affinity for epiphytism (species typically recorded as epiphytes). Species richness in each of these categories was also calculated.

To explore differences in epiphyte composition and relative abundance in both lower trunk and canopy epiphyte communities, ordination analyses were carried out using non-metric multidimensional scaling (NMS), a technique particularly suited to analysis of ecological communities (McCune and Grace, 2002). Percentage cover data were organised into matrices with species in columns and sample plots in rows. Bray-Curtis dissimilarities were calculated as distance measures on untransformed data. Final ordinations were performed with a maximum of 500 iterations, an instability criterion of 0.0000001, 250 real runs and 250 random runs for randomisation tests (McCune and Grace, 2002). Varimax rotations were used to maximise the alignment of the plots with one primary ordination axis (Kaiser, 1958; Mather, 1976). This simplifies the interpretation of results because, after rotation, each plot tends to be associated with one of the ordination axes more strongly than with the other axes (Bloomfield and Davis, 1994).

For lower trunk epiphytes, environmental variables were included in the ordination analysis and correlated to the ordination axes using Pearson correlation. Multi-response Permutation Procedures (MRPP) were used to test for significant differences between the epiphyte assemblages of the different forest types of the mixed tree species survey and the four age classes of the reforestation cycle The MRPP test statistic T measures effect size whereas the test statistic *A* describes within group homogeneity compared to random expectation. If all items are identical within groups, then $A = 1$. If heterogeneity within groups equals heterogeneity expected by chance, then $A = 0$ (McCune and Grace, 2002). Additionally, indicator species (McCune and Grace, 2002) within epiphytic communities were identified for each of the nine forest types covered in the three surveys. A perfect indicator species (with an indicator-value of 100) would be one that is unique to one habitat and is found in all samples from that habitat (Dufrêne and Legendre, 1997b). Indicator-values were tested for statistical significance using a randomisation (Monte Carlo) technique. This significance test compares the observed maximum indicator-value for each species with values based on 1000 randomisations (McCune and Grace, 2002). There were two main criteria for a

species to be an indicator: a significant Monte Carlo P-value of < 0.05 and an indicator-value of at least 25 (McCune and Grace, 2002).

We investigated the influence of forest type, height zone and aspect on canopy epiphyte communities using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001). We employed three-way models with the three variables specified as fixed factors and using 9,999 Monte Carlo permutations of raw data during each run (Anderson and Ter Braak, 2003). Differences in biodiversity, structural and functional variables between site types were tested using non-parametric and categorical statistical analyses, because some subsets of the dataset did not conform to parametric assumptions but showed a Poisson distribution typical for count data. Differences among groups were tested using the Kruskall Wallis test followed by Mann-Whitney U tests (using U^* as test statistic corrected for ties) and/or Mood Median tests. In some cases, both the unadjusted pairwise comparison results and results adjusted with the sequential Šidák method (Day and Quinn, 1989) are presented. For lower trunk epiphytes, associations between diversity measures and structural and functional variables were examined using Spearman's correlations. A P-value of < 0.05 was deemed a significant result.

For canopy epiphytes, Poisson generalised linear models (GLM, Zuur *et al.*, 2009) with log link functions were used to investigate variation in the species richness of plots according to forest type, height zone and aspect. We used the log link function with likelihood-ratio inference as the chi-square statistics because they are seen as more reliable than Wald statistics (Agresti, 2007). In all cases, type III analyses were carried out with deviance as a scale parameter and a robust estimator for the covariance matrix. Analyses included forest type, height zone and aspect as fixed factors. For each response variable, all possible models (main effects and/or two-way interactions and/or full factorial models) were fitted and assessed. Akaike's Information Criterion corrected for small sample sizes (AICc) was used to rank and weight the models (Burnham and Anderson, 2004). Among all models, the model with the lowest AICc value was assumed to fit the data best (Agresti, 2007) and was selected for further pairwise comparisons among all levels of its significant predictors. For these *a posteriori* comparisons, estimated marginal means were calculated and multiple pairwise comparisons were adjusted applying the sequential Šidák method (Day and Quinn, 1989).

Univariate analyses were performed with MINITAB 15 (MINITAB, 2007) or SPSS 16 (SPSS, 2007). All multivariate analyses were conducted using PC-ORD 5.26 (McCune and Mefford, 2006) or PERMANOVA 1.6 (Anderson, 2005). If not stated otherwise, data presented are means and standard errors.

3.3.2 Ground vegetation

Both plot level and site level data were used in the analysis. Site level data were calculated from plot level data by averaging values from the three 10m x 10m plots. While plot level data are more sensitive to heterogeneity in richness and ecological processes, site level data provide a general overview of associations between forest vegetation communities and any underlying causal factors (Smith *et al.*, 2005). In all but the native woodlands survey, the canopy (all planted species in the case of plantations) was excluded from analyses to allow for a better assessment of differences in the below-canopy layers at the sites.

The following biodiversity metrics were calculated for each plot: total species richness (SR), vascular plant species richness, non-vascular plant (bryophyte and lichen) species richness (or bryophytes only in the case of the afforestation and reforestation survey comparison and the comparison of forest types). Species diversity was calculated using Simpson's reciprocal diversity index (1/D) for the native woodland survey and comparison of forest types. For this calculation, % cover-values for canopy species were included to prevent ambiguous results (French, 2005). All species were classified according to their affinity for woodland after Smith *et al.* (2005), using additional information from Irish and British literature (Watson, 1981; Jermy *et al.*, 1982; Hubbard, 1984; Clapham *et al.*, 1987; Grime *et al.*, 1988; Smith, 1990; Hill *et al.*, 1991; Hill *et al.*, 1992; Purvis *et al.*, 1992; Fitter and Peat, 1994; Hill *et al.*, 1994; Webb *et al.*, 1996; Paton, 1999; Dobson, 2000; Preston *et al.*, 2002; Smith, 2004). Based on the information collected, plants were classified as having low (usually found in non-woodland habitats), moderate (frequently occurring in both woodlands and unwooded habitats) or high affinity for woodland (typical woodland species). In the plantations, in order to relate the vegetation communities to environmental conditions, vascular plants were also classified according to their ecological strategy as competitors (C), stress tolerators (S) or ruderals (R), or a combination of these categories, according to Grime *et al.*'s CSR theory (Grime *et al.*, 1988). The species richness of plants in the above categories was calculated for each plot. Mean weighted Ellenberg values (Hill *et al.*, 2004; Hill *et al.*, 2007) for moisture (F) and nitrogen (N) for all species were calculated for each plot. For the mixed tree species survey, the cover of vascular and non-vascular species was calculated for each plot.

For the afforestation and reforestation survey comparison, βsim was used as a metric to represent species turnover. It is calculated according to the formula βsim = min(*b,c*) / *a* + min(*b,c*) where *a* comprises the total number of species that occur in both plots i.e. species continuity; *b* comprises the total number of species that occur in the neighbouring plot but not in the focal one; and *c* comprises the total number of species that occur in the focal plot but not in the neighbouring one. It has an upper limit of 1 (no species in common) and lower limit of 0 (all species in common). βsim was calculated in the beta.sim package (Baselga, 2009) for R (R Development Core Team, 2010) which computes a distance matrix using Simpson pairwise dissimilarity measure.

Generalised linear models, using a Poisson distribution, were used to identify environmental variables related to total and typical woodland species richness at the sites for comparisons between the afforestation and reforestation surveys and between all forest types. Where data were analysed at the plot level, Generalised Linear Mixed Models (GLMMs; Zuur *et al.*, 2009) were used, as plots were nested in sites. Spatial autocorrelation was dealt with by using site as a random effect. Multi model inference (Burnham and Anderson, 2002) was used to assess sets of models. Following data exploration, variables that were deemed ecologically meaningful were included in the model, provided that they were not collinear with more meaningful variables. Interaction terms were included where deemed ecologically relevant. Variables were transformed where necessary to decrease the influence of outliers. Models comprising all possible combinations of variables and interactions (but all containing forest type as a fixed variable in the comparison between all forest types, and canopy cover as a fixed variable in the comparison between afforestation and reforestation) were tested in order to quantify the relative importance of all variables and interactions. Akaike's Information Criterion corrected for small sample sizes (AIC*c*) was used to rank and weight the models. A confidence set of models was selected for the comparison of forest types with a cumulative Akaike weight of ≤ 0.95 (i.e. a 95% probability that the best model is being selected) and a set of models within 2 units of the lowest AIC*c* was selected for the

afforestation and reforestation survey comparison. The importance of each variable was estimated by calculating the cumulative Akaike weights of the models containing that variable. Average coefficients and standard errors were also calculated within the confidence set. Analyses were undertaken using R version 2.11.0 (R Development Core Team, 2010) and the nlme (Pinheiro *et al.*, 2009), lme4 (Bates and Sarkar, 2006) and MuMln (Barton, 2009) packages.

To examine patterns in ground vegetation communities for the afforestation and reforestation survey comparison and mixed tree species surveys, a non-metric multidimensional scaling (NMS) ordination, using slow and thorough autopilot settings, was performed with species percentage cover data. This technique has been found to be particularly suited to analysis of ecological communities (McCune and Grace, 2002). NMS axes are arbitrary (Legendre and Legendre, 1998), so varimax rotation was used to simplify the interpretation of results (Bloomfield and Davis, 1994). Flexible-beta cluster analysis, with beta set to 0.25, was used in conjunction with indicator species analysis (Dufrêne and Legendre, 1997a) to classify and define ground vegetation communities in the native woodland survey and comparison of forest types. The different levels of clustering were compared using the sum of significant indicator-values (Dufrêne and Legendre 1997). Only indicator-values of 25 or over were considered to be useful species indicators (Dufrêne and Legendre, 1997a). Indicator species analysis was also used to identify indicator species for various groups.

Differences in biodiversity, structural and functional variables between site types were tested using parametric statistics where possible, and data transformations and/or non-parametric statistics if required. To test for differences between two groups, T-tests or non-parametric Mann-Whitney U tests were used. To test for differences among groups, ANOVAs or non-parametric Kruskall Wallis tests were used as appropriate, followed by Tukey's HSD, non-parametric Mann-Whitney U tests or Mood's Median tests. Associations between diversity measures and structural and functional variables were examined using Spearman's correlations. *Post-hoc* P-value corrections were not applied due to the criticism that they are too conservative, as they reduce the level for significance below the usual 0.05 and thus significant relationships may be missed (Dytham, 2003). Therefore, where significant relationships were found, the form of the relationship was investigated in more detail and these relationships were viewed with caution where they did not appear to be ecologically meaningful.

Multi-response Permutation Procedures (MRPP) with Sørenson distance measures were used to test for differences in vegetation communities among the mixed tree species survey forest types. The distance matrices were rank transformed in order to correct for loss of sensitivity as community heterogeneity increases and to make the MRPP results more analogous in theory to NMS (Brandtberg *et al.*, 2000). MRPP reports a test statistic T with P-value, (more negative values of T represent stronger separation between groups). However, the P-value is not independent of sample size, so the derived test statistic *A* is used to describe separation between groups. This statistic approaches 1 when distances within groups are smaller than distances between groups, and is 0 when distances between and within groups are equal. Values of *A* for ecological communities are commonly below 0.1 while those above 0.3 are considered high (McCune and Mefford, 2006). Multivariate analyses were conducted using PC-Ord 5.6 (McCune and Mefford, 2006) and univariate analyses with SPSS 16 (SPSS, 2007) and Minitab versions 13 and 15 (Minitab, 2000; MINITAB, 2007).

For the comparison of forest types, Canonical Correspondence Analysis (CCA) was used to examine the influence of the environmental variables on species composition, and Detrended Correspondence Analysis (DCA) was used to obtain estimates of gradient lengths (in standard deviation (S.D.) units of species turnover). Species recorded only once were made supplementary to the ordinations and rare species were down-weighted. Variables were checked for outliers, and transformations applied to canopy cover (cubed), and annual precipitation and CWD volume (log transformed) to reduce the influence of outliers for these variables. Nominal environmental data were converted to zero/one dummy variables. Total phosphorus and the area of old woodland within 1km were excluded from the ordinations due to missing values. Automatic forward selection was used to identify the variables best related to the species data. Variables displaying (multi)collinearity, as assessed by examining pairplots and variance inflation factors (VIFs) (values greater than 12 suggest multicollinearity), and/or non-significance were removed. Monte Carlo tests, with an unrestricted permutation structure, were used to assess the significance of the environmental variables with 499 permutations for preliminary analyses and 9999 for final solutions. Ordinations were performed using CANOCO for Windows Version 4.51 (ter Braak and Smilauer, 1998).

3.3.2.1 Comparison of forest types

In the comparison of forest types for the ground vegetation, data from all native woodland (20) and mix tree species survey sites (20) and all age class IV (> 30 years) reforestation sites (5) were included in the analysis (Appendix 1), along with data collected in the summers of 2001-03 from first rotation Sitka spruce (11), larch (8) and ash (11) sites aged 30 years or over during the BIOFOREST project 3.1.2 (Smith *et al.*, 2005) (Appendix 7).

3.3.3 Ground-dwelling invertebrates and Lepidoptera

For the spiders and beetles datasets derived from sampling periods of different durations were used in different analyses, in order to maximise sample size while making sure that collection periods matched between all groups being compared in each analysis. For comparisons across the forest cycle in the reforestation survey all four pitfall collections (12 weeks sampling) were used. For comparisons with afforestation (BIOFOREST) data the first pitfall collection from reforestation sites was excluded from analysis, so that the dataset derived from the last 9 weeks of sampling. For the sections dealing with mixed tree species, native woodlands and comparison of forest types sections data deriving from the first three rounds of pitfall collections (9 weeks) were used.

A combination of Non-metric Multidimensional Scaling analysis (NMS) and Multi-Response Permutation Procedures (MRPP with Sorensen distance measure) was used to examine differences in invertebrate species assemblages between the forest types. A variation of MRPP, MRBP (Multi-Response Block Procedure) incorporates a blocking variable so that geographically paired, mixed and pure stands could be analysed. In addition, for the Native woodlands section PERMANOVA (R package Vegan) was used (with forest type nested within year and 5000 permutations). This test allows for a factorial comparison of non-parametric multivariate data and is analogous to ANOVA for univariate data (Anderson, 2001). The following parameter setup was used for NMS: Sorensen distance measure; 500 maximum number of iterations; Random Starting coordinates; 250 runs with real data; Step down in dimensionality (Initial step length = 0.2); 250 runs with randomized data; Varimax rotation. Indicator Species Analysis was used to determine species which were affiliated with particular forest types (McCune and Grace, 2002).

Relative abundance data were used in these multivariate analyses, so that differences in trap efficiency between plots, which may be attributed to variation in vegetation structure, is reduced (Melbourne, 1999). For comparisons across years, presence-absence data was used unless otherwise stated. For moths, presence-absence data was used in ordinations, as catches of individuals from light traps may be influenced by weather conditions, moon phase (Williams, 1961; Bowden, 1973) and differences in the length of time between sunrise and sunset over the 6 week sampling period. In addition, preliminary analyses revealed a strong effect of sampling month, where assemblages sampled in July were markedly different from those sampled in June (MRPP: T = -11.09, A = 0.04, P ≤ 0.00001). It was therefore decided to exclude the stands sampled during July from the NMS analyses so that this strong trend in the data did not confound any potential relationship with forest type. All multivariate comparisons were carried out at the plot level with the exception of the comparison of forest types section where mean values where calculated from the three pitfall plots or two moth traps per site.

Differences in species metrics (richness, relative abundance and Berger-Parker dominance index) between the forest types were tested using either one-way ANOVA with Tukey post-hoc test or paired T tests where appropriate. When data did not meet parametric assumptions after transformation a non-parametric Kruskal-Wallis with Nemenyi post-hoc test (Zar, 1996) or Mann Whitney U test was used. In the reforestation survey, species richness at each plot was standardised to 60 trap days using individual-based rarefaction curves (Gotelli and Colwell, 2001), to control for differences between plots in length of sampling period (60-71 days). For moths, expected species richness for each trap was calculated using individual based rarefaction so that differences in number of individuals (due to weather conditions etc.) did not bias the analyses. In addition, for comparisons of moth species richness, ANCOVA was used with trap date as a covariable.

To identify potential indicators and drivers of invertebrate diversity, the relationships between species metrics and habitat variables were examined. Where datasets had less than 30 samples, Pearson's correlations or Spearman's (non-parametric) correlations were used. Where datasets had a sufficient number of samples, Generalised Linear Mixed Models (GLMM) were used with a Poisson distribution. Site was included in the model as a random factor and interaction terms were only included if data exploration identified a possible relationship with the dependent variable. Highly collinear variables (Pearson r > 0.60) were removed prior to modelling. Model selection was performed using AIC (Akaike Information Criteria) following the methods outlined in Zuur (2009) and as such non-significant variables were retained if they improved the overall model fit. The use of GLMMs to model ecological data is becoming more frequent as they can incorporate nested data and deal with spatial autocorrelation. However, it should be noted that as the core mathematics in GLMM is complex, interpretation of relationships at lower levels of significance (e.g. P = 0.01-0.05) should be treated with caution (Zuur *et al.*, 2009). For analyses of the relationship between moth species richness measures (after rarefaction) and environmental variables Generalised Additive Models (GAMs) were used. These analyses utililised site level data and thus did not require a mixed-model approach for nested data. A Poisson GLM, detected overdispersion, and corrected the standard errors using a quasi-GLM model where the variance is given by $\varphi \times \mu$, where μ is the mean and φ the dispersion parameter was used to approximate a poisson distribution for count data, because moth species richness values were non-integer after rarefaction.

Where appropriate, Bonferroni corrections were applied to ANOVAs and correlations, and all percentage cover data were arcsine transformed. All multivariate analyses were out carried in PCORD Version 5.10

and ANOVAs, ANCOVAs, Paired T tests, and Kruskal Wallis tests were carried out in SPSS Version 17 whereas Mann Whitney *U* was carried out in the ExactRankTests package (Hothorn and Hornik, 2010) of R version 2.11.1 (R Development Core Team, 2010). Rarefaction curves were constructed using Biodiversity Pro (reforestation survey) or in the Vegan R package (Oksanen *et al.*, 2010) (Mixed tree species survey/comparison of forest types). All correlations were carried out in R, as were GLMMs in the LMe4 package (Bates and Maechler, 2010) and GAMs and GAMMs in mgcv package (Wood, 2008).

3.3.4 Canopy-dwelling invertebrates

Singletons were excluded from canopy arthropod assemblage analyses, to remove the influence of rare species that were sampled in one forest type only, and species abundance data was log (x+1)-transformed to reduce the influence of highly abundant species (McCune and Grace, 2002). A Multi-Response Permutation procedure (MRPP) was used to test for differences in species composition between forest types when site numbers differed between forest types, and a permutation-based non-parametric MANOVA (PerMANOVA) procedure (McCune and Grace, 2002) was used when each forest type had the same number of sites. Relative Sorensen distance measures were used for MRPP and PerMANOVA. The following weighting option was used for MRPP: $C_i = n_i/\Sigma n_i$, where n_i is the number of items in group *I*, Σn_i is the number of items in all groups, and C_i is the weight applied to each item in group.

Differences in assemblage composition were forest types were graphed using a Hierarchial Cluster Analysis of the log (x+1)-transformed species abundance data and setup parameters as follows: Sorensen Distance Measure, Flexible Beta Linkage Method (Beta = -0.25), dendrogram scale log-transformed, and distance among groups scaled by Wishart's Objective Function. Differences in relative species composition were analysed using the Indicator Species Analysis (ISA) method of Dufrêne and Legende (1997) described in McCune and Grace (2002), followed by a Monte Carlo Test of the significance of the observed maximum indicator-value for each species using 1000 permutations. Differences in total canopy invertebrate abundance between forest types could be attributable to the differences in vertical canopy structure (and thus habitat volume) between conifers and deciduous broadleaved trees. To account for this potential bias, individual-based rarefied species richness was calculated (Lande *et al.*, 2000; Magurran, 2004), using species abundance data pooled by forest type. Rarefaction curves were constructed for each taxon investigated at each forest type, and richness values adjusted to correspond to the smallest total number of individuals caught in any one forest type (Magurran, 2004; Berndt *et al.*, 2008).

Variation in the mean relative species richness of feeding guilds, rare and common species, and the habitat associations of species were compared between forest types using exact T-testing for non-parametric proportional data. Environmental and habitat variables were compared between all forest types using one-way ANOVAs and Tukey post-hoc tests for parametric data, and exact Mann-Whitney tests for non-parametric data. Environmental and habitat variables were correlated with species richness values for canopy spiders and beetles at each forest site using Spearman's two-tailed correlations for non-parametric data. MRPP and PerMANOVA procedures, Hierarchial Cluster Analysis and ISA analyses were carried out in PCOrd Version 5.10 (McCune and Mefford, 1997), while means testing and correlation

analyses were carried out in SPSS 15.0 (SPSS, 2002). Individual-based rarefaction curves (± 95% C.L.) were constructed using Ecosim (Gotelli and Entsminger, 2001).

Relative abundances of the three most abundant canopy invertebrate orders in the afforestation and reforestation surveys, comprising > 90% of all individuals caught in these forest types, were compared using exact T-testing for non-parametric proportional data. Total abundances of these orders were also correlated with predatory spider and beetle species richness using Spearman's Rho two-tailed correlations for non-parametric data.

Due to adverse weather conditions half the native woodlands (three oak and three ash woodlands) were sampled in 2008, with the remaining six native woodlands sampled in 2009. Thus, inter-annual differences in species density and/or activity could influence the data. In particular, more abundant species are likely to be present across both years, but rarer species, specifically singletons, may not be (Norris, 1999; Relys *et al.*, 2002; Oxbrough *et al.*, 2010). To examine this potentially confounding influence for the comparison of native woodlands and age class IV Sitka spruce plantations, community assemblage composition and species richness metrics were compared between native oak and ash woodlands sampled in 2008 and those sampled in 2009, both when singletons were included and excluded (doubletons were not excluded as they had the chance to be sampled in either year) (Norris, 1999). A permutation-based non-parametric MANOVA (PerMANOVA) procedure was used to examine assemblage composition (using log(x+1)-transformed species abundance data) between years in native oak and ash woodland (McCune and Grace, 2002). There were no significant differences in assemblage composition in native oak woodlands between years, or in native ash woodlands between years, either when all species were included or when singletons were removed. There were also no significant differences (P > 0.05) in mean species richness or mean abundance of canopy invertebrates between years. Thus it was not deemed necessary to include year as an additional factor in the comparison of native woodlands and age class IV Sitka spruce plantations. Additionally, three of the age class IV Sitka spruce stands sampled were afforested sites, while the remaining three were reforested (and thus had been through two complete forest rotations rather than one). Thus, differences in species richness and/or assemblages between Sitka spruce forest rotations could influence the data. Therefore, community assemblage composition and species richness metrics were compared between afforested and reforested age class IV Sitka spruce stands, both with singletons included and excluded. Rarefaction curves (± 95% confidence limits) were compared at the smallest total number of individuals caught at any one forest type (i.e. at the end-point of the afforested Sitka spruce curve for spiders (33 individuals) and at the end-point of the reforested Sitka spruce curve for beetles (29 individuals)) (Magurran, 2004; Berndt *et al.*, 2008). A permutation-based non-parametric MANOVA (PerMANOVA) procedure (McCune and Grace, 2002) was also used to examine assemblage composition (using log(x+1)-transformed species abundance data) between rotations in age class IV Sitka spruce forests (McCune and Grace, 2002). There were no significant differences in mean or rarefied species richness or assemblage composition of spiders or beetles between afforested and reforested Sitka spruce, either when all species were included or when singletons were removed. Thus it was not deemed necessary to include forest rotation as an additional factor in the comparison of native woodlands and age class IV Sitka spruce plantations.

3.3.5 Birds

Before modelling, data were checked for normality, colinearity and outliers using Brodgar (Highland Statistics LTD, 2007). Potential explanatory variables that were collinear with other variables in a model were not included. Data transformations (log, cube root and fourth root) were applied where appropriate to reduce the effect of outliers and to normalise data before carrying out parametric tests. Relationships between bird metrics, vegetation and structural variables, and site types were investigated using Poisson Generalised Linear Models (GLM), ANOVA and Tukey HSD post-hoc tests, non-parametric Mann-Whitney U test and Kruskal-Wallis with Dunn's post-hoc test. For GLMs, forwards and backwards selection was used to select a model start point using minimum AIC. Models were then re-run dropping the least significant explanatory variable until all remaining variables were significant. Poisson GLMs comparing variables between different site types were typically run as separate models for each bird metric or environmental variable under investigation, with site type specified as the sole explanatory variable. GLMs were checked for overdispersion and corrected if necessary by fitting a quasi-GLM model where the variance is given by $\varphi \times \mu$, where μ is the mean and φ the dispersion parameter. The relationship between winter and breeding bird assemblages was assessed by season, by carrying out Spearman's rank correlation on species richness, Simpson's diversity and total bird density in the two seasons. Only those forests that had been surveyed in both the breeding season and in winter were considered. GLMs were carried out using Brodgar (Highland Statistics LTD, 2007), other statistical tests were carried out using SPSS (SPSS Inc., 2006) or by hand.

Nonmetric Multidimensional Scaling (NMS) using species densities was used to examine the species composition between age classes as it can deal with non-normal and zero rich data (McCune and Grace, 2002). This was performed in PC-ORD (McCune and Mefford, 2006) using random starting coordinates and a Sørenson distance measure and by carrying out 250 runs with real data and 250 with randomised data. The difference in NMS axis scores between the bird communities of different study sites was evaluated using Analysis of Similarity (ANOSIM) carried out in Primer (Primer-E Ltd, 2006). Indicator species analysis (Dufrêne and Legendre, 1997b) was carried out in PC-ORD to identify the species typical of different forest types. Indicator-values were derived from the relative abundance and relative frequency of the species in each group to produce an indicator-value. This value was then tested for statistical significance using a Monte Carlo test. Only species with an indicator-value of ≥ 40% and with $P < 0.05$ were considered.

Rank-abundance curves were used to investigate differences in bird community structure in a particular forest age class. The slope of a rank-abundance curve is an indicator of the evenness of a community, shallower slopes indicating more even communities (Magurran, 2004). The slopes of the rank abundance curves in a particular age class were compared in turn using a Kolmogorov-Smirnov two-sample test.

The findings of this study were compared with those of a recent study of first-rotation forests in Ireland (Wilson *et al.*, 2006) to investigate differences in both vegetation and the bird community between rotations. Mann-Whitney U tests were used to compare vegetation, while Generalised Linear Models (GLM) assuming a Poisson distribution were used to compare species richness, total bird density and migrant density between first and second rotation forests. Poisson GLM was deemed most suitable as species richness is count data, and densities are derived from count data (Zuur *et al.*, 2009). To perform this test, we used a model with only one explanatory variable, rotation, and carried out a GLM for each combination of age class and response variable (species richness; total bird density and migrant density).

In each of these models, the significance of just one explanatory variable (rotation) was tested against the null model. Models were checked for overdispersion and corrected using a quasi-GLM model where the variance is given by $\varphi \times \mu$, where μ is the mean and φ the dispersion parameter if necessary. To check whether any difference between rotations was due to natural population increase in the time period (5 years) between the studies, densities were corrected using annual rates of population increase calculated by the Countryside Bird Survey (Coombes *et al.*, 2009) and models run both with the original and corrected data.

3.3.6 Deadwood

ANOVA and a Tukey HSD post-hoc test were used to compare the mean volume of deadwood contained in stumps and snag density between the three site types. The log volume data did not meet the assumptions of parametric tests and therefore a Kruskal-Wallis test with a Dunne's post-hoc was used. Graphs of log volumes and snag densities revealed one ash site in each with an outlying value that could not be addressed by transformations. Analysis was run with and without these sites and it was found that their inclusion did not alter the outcome of the results. Therefore results are presented for all data points. A log volume outlier was also found in plantation forests and was removed from analysis. This site contained large areas of wind-throw and therefore did not represent a typically managed plantation.

3.3.7 Cross-taxon analysis

In this section we compare trends in species richness, forest-associated species richness and community composition across the various forest types studied between the taxonomic groups. We do this using both a review of results from individual sections of this study and a formal, quantitative, data analysis. For forest-associated species richness we used the ground vegetation (total, vascular and non-vascular) typical woodland (high affinity for woodland) species richness, the ground-dwelling spider and beetle and Lepidoptera forest-associated species richness, the canopy-dwelling spider and beetle conifer, broadleaved, mixed forest and deadwood specialists combined, the epiphyte high affinity for epiphytism (typical epiphyte) species richness and the forest specialist bird species richness. We also review the factors that correlate with the biodiversity of the different groups in order to identify indicators of biodiversity and to test the indicators proposed by a previous study of the biodiversity in plantation forests.

3.3.7.1 Review of results of different taxa surveys

In order to compare the trends in species richness, forest-associated species richness and community composition for each taxonomic group and to identify similarities and differences among them, we reviewed the results of the preceding taxonomic sections for the different forest types. We also compiled graphs illustrating species richness and forest-associated species richness of all of the taxonomic groups among various forest types. In these graphs, a diagonal line indicates equal species richness in both forest types and the position of a taxonomic group above or below this line indicates a positive influence on species richness of one of the forest types in comparison to the other.

3.3.7.1 Formal data comparison

3.3.7.1.1. Data selection

For each taxonomic group, a data matrix was collated containing species identities as columns and all sites of the surveyed forest types as rows. Individuals identified to generic levels were only included in the matrix if no other species belonging to the genus of an unidentified specimen was present within any other site. Data matrices formed the base for calculations of species richness (SR) and forest-associated species richness (FaSR) for each taxonomic group at each site.

3.3.7.1.2 Data analysis

Species richness and forest-associated species richness values for each taxonomic group were correlated with values for every other taxonomic group for each forest type as well as for each survey (reforestation, mixed tree species and native woodlands) separately. Since some of the datasets did not conform to parametric assumptions, non-parametric Spearman's rank correlations were used throughout. Significance values were not adjusted with e.g. the Bonferroni method after conducting multiple comparisons on the same data sets, because there are some mathematical and practical objections in the application of such corrections (Moran, 2003). However, in some cases, both unadjusted and sequentially Dunn-Šidák adjusted (Day and Quinn, 1989; Sokal and Rohlf, 1995) results of pairwise comparisons are presented. Correlations were not only evaluated with regard to their significance, but also their strength. Where $r > 0.7$, such strong correlations in species richness between taxonomic groups may be considered as evidence that variation in the diversity of one group is mirrored strongly enough by the other to be useful for predictive purposes in biodiversity surveys (Heino, 2010).

In order to explore the similarities in community composition and relative abundance among different taxonomic groups in different forest types and to identify surrogate taxa, the Procrustes rotation method was used (Jackson, 1995; Peres-Neto and Jackson, 2001). First, ordination analyses were carried out using non-metric multidimensional scaling (NMS) (McCune and Grace, 2002). Bray-Curtis dissimilarities were calculated as distance measures on untransformed data. All matrices were resolved in three-dimensional ordinations. The NMS scores of each taxonomic group were then best fitted with the scores of each other taxonomic group using rotation, reflection and dilation to find an optimal superimposition. Such a Procrustes rotation process minimises the residual sum-of-squares (m_{12}) between the two matrix configurations (Peres-Neto and Jackson, 2001). The value of the sum-of-the-squared residuals between corresponding coordinates in both configurations can be used as a metric of correlation (Gower, 1971); the lower the value, the greater the degree of association between the ordinations, i.e. the concordance between datasets. By using a permutation test called PROTEST, the best fit of the two investigated ordinations can then be tested for difference from a relationship occurring by chance (PROTEST, Jackson, 1995). PROTEST uses a correlation-like statistic $r = \sqrt{(1 - m_{12})}$ derived from the symmetric Procrustes sum-of-squares, which can be interpreted similarly to the Pearson correlation index r^2 (Peres-Neto and Jackson, 2001): larger-values of r indicate a better concordance between two matrices. Both matrices are identical if $r = 1$.

In addition, individual residuals between homologous site observations were interpreted separately (Peres-Neto and Jackson, 2001): a mean residual value for each site across all pairwise taxonomic Procrustes rotations (21 pairwise combinations of the seven taxonomic groups - ground vegetation, lower trunk epiphytes, canopy epiphytes, ground-dwelling spiders, ground-dwelling beetles, canopy-dwelling

invertebrates and birds) was calculated and compared between forest types. Larger-values of mean residual distance are associated with sites and/or forest types which show little concordance between the investigated taxa in the relationship between community compositions in one site or forest type in comparison with another. The Procrustes analysis and PROTEST were carried out in R (R Development Core Team, 2010) using the Vegan R package (Oksanen *et al.*, 2010), whereas the correlation analyses and comparison of Procrustes residuals were calculated in SPSS (SPSS, 2007).

3.3.8 GIS database

All data collected during the FORESTBIO project have being compiled into a Geodatabase. A number of documents have been compiled to facilitate data collection and storage including:

- A data help document to ensure that the minimum of required spatial information is supplied to facilitate individuals that choose to supply the data in xls format and not as a shape file.
- A metadata help document to support the use of the ArcCatalog wizard, and informing contributors to the database as to how to make sure that their metdata comply with INSPIRE Directive standards
- A metadata template compatible with the standards of the INSPIRE Directive, for researchers who choose not to utilise the ArcCatalog wizard.

The original data were stored by researchers either in shape file format or on xls spreadsheets. The data were then converted into File Geodatabase Feature Class for spatial data and tables for non spatial data components. All converted data were included into an ESRI Geodatabase. The data stored in the Geodatabase can be viewed via an ArcMap template created for that purpose or via Arc Catalogue, which also allows access to the Metadata and easy viewing of tables associated with the spatial data component of the database.

4. Results

4.1 Epiphytes

4.1.1 Afforestation and reforestation survey

4.1.1.1 Lower trunk epiphytes across the reforestation cycle

A total of 70 species were recorded from the plots; 39 lichens, 14 mosses, 15 liverworts and 2 vascular plants. Twenty five species occurred only once (14 lichens, 9 bryophytes and 2 vascular plants) and only 12 species occurred in 25% or more of the plots. The most common species was the moss *Kindbergia praelonga,* occurring in 67% of the plots. The liverwort *Microlejeunea ulicina* occurred with 49% frequency while the lichens *Dimerella pineti* and *D. lutea* occurred with 47% and 45% frequency. Total species richness ranged from 0 to 28 species per plot with a mean of 9.11 (± 0.83 se). A total of 29 epiphyte species were recorded in age class I (25 lichens and 4 bryophytes), 52 species in age class II (30 lichens and 22 bryophytes), 31 species in age class III (15 lichens and 16 bryophytes) and 42 species in age class IV (19 lichens and 23 bryophytes).

Total species richness (SR) was significantly different among the four age classes (H = 9.65, P = 0.022, Table 4.1). Age class I had the lowest total SR, which increased to its highest in age class II, dropped significantly lower in age class III (U^* = -2.86, P = 0.004) and increased again toward age class IV but did not reach the high level achieved in age class II. Lichens and bryophytes showed a similar trend although bryophytes reached their highest SR in age class IV (Table 4.1). Vascular epiphytes remained low in number and were only present in the older age class III and IV sites. Lichens were higher in number than bryophytes in age class I and II with bryophytes more numerous in age class III and IV. The typical epiphyte SR showed a similar trend to total epiphyte SR although there was little recovery in species richness in age class IV (Table 4.1).

As well as being generally the most diverse, age class II plots also had the highest total host SR and a higher level of canopy openness than both age class III and IV (Table 4.1). Age class I plots had the highest canopy openness (significantly higher than age class II (U^* = -3.69, P = 0.001), and this decreased to its lowest in age class III (significantly lower than age class I (U^* = -3.78, P = 0.001), increasing again from age class III to age class IV plots due to thinning of the trees. Age class IV sites were significantly closer to old woodland and had the largest area of old woodland within 1km, mainly due to the fact that one site was planted on old woodland. Drainage, elevation, slope and aspect were relatively uniform across the age classes (Table 4.1).

Table 4.1: Mean ±se diversity of epiphytes on lower trunks and environmental variables for the four age classes. Significance of differences between age classes tested with non-parametric Kruskal-Wallis and Mann Whitney U. Different letters in superscript indicate significant differences (P < 0.05) between age classes for a variable.

	Age class I (n=11)	Age class II (n=14)	Age class III (n=15)	Age class IV (n=15)
Diversity				
Total epiphyte SR	6.1±2.2^{AB}	12.6±1.4^{A}	6.4±0.8^{B}	10.8±1.7^{A}
Lichen SR	4.3±1.6^{AB}	6.4±0.9^{A}	2.5±0.4^{B}	3.9±0.4^{AB}
Bryophyte SR	1.8±0.7^{A}	6.1±0.7^{B}	3.9±0.6^{AB}	6.9±0.6^{AB}
Vascular plant SR	0.0±0.0^{A}	0.0±0.0^{A}	0.1±0.1^{A}	0.1±0.1^{A}
Typical epiphyte SR	1.8±0.7^{A}	5.1±0.9^{C}	2.3±0.4^{AB}	2.7±0.4^{B}
Environmental				
Canopy openness (%)	59.2±3.2^{A}	13.0±4.2^{B}	2.7±0.3^{C}	7.2±0.5^{BC}
Understorey cover (%)	1.7±1.0^{A}	3.7±1.4^{A}	0.4±0.2^{A}	1.0±1.0^{A}
Basal area (m^2)	0.03±0^{A}	0.23±0.03^{B}	0.49±0.03^{C}	0.56±0.05^{C}
Average DBH (cm)	3.48±0.14^{A}	9.9±0.94^{B}	18.7±1^{C}	35.1±1.5 ^{D}
Total tree number	21.5±1.7^{AB}	24.8±2.8^{A}	15.9±1.1^{B}	6.1±0.5^{C}
Total host SR	1.5±0.2^{AB}	1.9±0.2^{A}	1.4±0.1^{AB}	1.1±0.1^{B}
Slope (°)	5.0±0.6^{A}	5.0±0.8^{A}	7.1±1.1^{A}	6.1±1.3^{A}
Aspect*	0.7±0.2^{A}	1.1±0.2^{A}	0.9±1.2^{A}	0.6±0.2^{A}
Elevation (m)	225.9±18.2^{A}	220.4±19.5^{A}	245.3±13.6^{A}	192.3±20.7^{A}
Annual precipitation (mm)	1261±72.9^{A}	1329±57.2^{A}	1364±65.0^{A}	1302±31.3^{A}
Distance to old woodland (km^2)	6.6±1.4^{A}	6.6±1.1^{A}	7.08±0.7^{A}	4.65±0.8^{B}
Area of old woodland (km^2)	0.11±0.06^{A}	0.16±0.06^{A}	0.05±0.02^{A}	0.5±0.20^{B}

*Transformed from degrees to a linear scale.

The NMS ordination (Fig. 4.1) used 52 of the 55 plots as three of the plots from age class I contained no species. The NMS suggested a 3-D solution was optimum. The four age classes did not form four distinct clusters and there was extensive overlap among the age classes. Age class I plots were the most variable group. MRPP analysis on the species assemblages using age class as the defining factor showed them to be significantly different from each other at the plot level (T = -13.76, A = 0.12, P ≤ 0.001) and pairwise comparisons showed all age classes to be significantly different from each other (Table 4.2). The MRPP result showed that age class IV plots were the least homogenous with both age class I and II plots, which were most similar to each other (Table 4.2). Axis 1 mainly separated high elevation from low elevation plots (Table 4.3). Axis 3, which generally represented the continuum from age class I to age class IV from the top to bottom of the axis, was correlated with the structural variables which changed through the plantation cycle, such as average DBH, canopy openness etc. (Table 4.3).
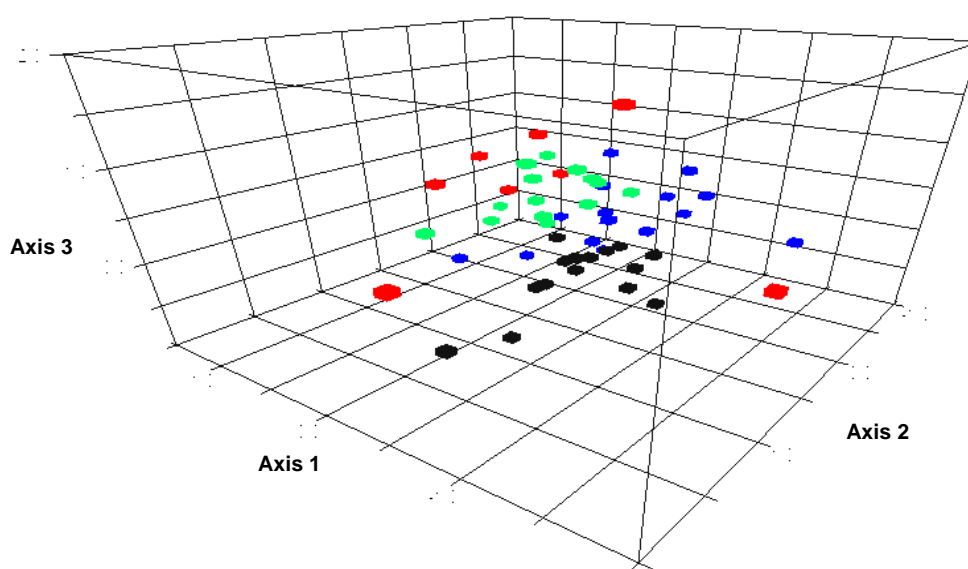
Figure 4.1: NMS ordination of the lower trunk epiphyte composition (3-D solution: stress = 19.57) of age classes I (red), II (green), III (blue) and IV (black) of the reforestation plots. The three axes accounted for over 75% of the variation: axis 1 = 24%, axis 2 = 25%, axis 3 = 26%.

Table 4.2: MRPP results of lower trunk epiphyte species assemblages defined by age class. T = effect size, A = within group homogeneity. Significant P–values (< 0.05) are indicated in bold.

	Age class I			Age class II			Age class III		
	T	A	P-value	T	A	P-value	T	A	P-value
Age class II	-2.9	0.03	**0.01**						
Age class III	-6.7	0.08	**<0.01**	-5.8	0.06	**<0.01**			
Age class IV	-10.1	0.13	**<0.01**	-11.6	0.13	**<0.01**	-8.4	0.08	**<0.01**

Table 4.3: Pearson's coefficient of correlations between environmental variables and the three axes from the NMS ordination of the lower trunk epiphyte composition in reforested plantations. Significant results (P < 0.05) are highlighted in bold. The columns are ordered to show the stronger correlations first in descending order.

	Axis 1	Axis 2	Axis 3
Average DBH	-0.22	-0.05	**-0.75**
Basal area	-0.16	-0.23	**-0.73**
Canopy openness	0.16	-0.03	**0.59**
Total tree number	**0.36**	-0.03	**0.56**
Elevation	**0.36**	-0.03	-0.14
Distance to old woodland	**0.29**	0.17	0.19

There were three significant indicator species for age class I (Table 4.4). Two of these were pioneer lichen species characteristic of well-lit, damp situations (Purvis *et al.*, 1992; Dobson, 2000). Age class II had five significant indicators species. These species were mainly characteristic of well-lit, humid and well drained situations (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004). Age class III had just one

significant indicator, *Metzgeria furcata* (Table 4.4). This liverwort species has a wide ecological range, occurring on all but the most acid trees and rocks. It is tolerant of drought and is a pioneer species (Paton, 1999). Age class IV had eight significant indicators. Six of these indicator species are shade-tolerant, calcifuge and require moist conditions (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004).

Table 4.4: Indicator species of lower trunk epiphytes for the four age classes with indicator-values given. Species were considered significant indicators (highlighted in bold) if they had an indicator-value of ≥ 25 and a P-value < 0.05. Group: L = lichen, B = bryophyte and V = vascular plant. Affinity for epiphytism: L = low, M = medium, H = high.

Species	Group	Affinity	Age class I	Age class II	Age class III	Age class IV
Fuscidea lightfootii	L	H	**43**	9	0	0
Fellhanera bouteillei	L	M	**27**	20	0	0
Lecanora symmicta	L	M	**25**	0	0	0
Colura calyptrifolia	B	M	19	**48**	0	0
Ramalina farinacea	L	H	8	**40**	0	0
Parmotrema chinense	L	M	1	**35**	2	6
Dimerella lutea	L	M	7	**33**	8	6
Frullania dilatata	B	H	2	**30**	2	1
Metzgeria furcata	B	M	0	13	**38**	0
Lepraria incana	L	M	0	0	1	**61**
Hypnum jutlandicum	B	M	1	12	1	**43**
Metzgeria temperate	B	H	1	7	9	**43**
Hypnum resupinatum	B	M	0	2	2	**41**
Lophocolea bidentata	B	M	1	6	3	**35**
Porina leptalea	L	M	0	1	5	**35**
Microlejeunea ulicina	B	H	1	17	8	**34**
Pseudotaxiphyllum elegans	B	L	0	0	0	**27**

The results of the correlations (Table 4.5) between total SR and typical epiphyte SR and the environmental variables measured for all age classes combined showed a significant negative correlation with elevation and a significant positive correlation with total host SR; old woodland area was also positively correlated for typical epiphyte SR. When the analysis was calculated excluding age class I plots (it was felt this age class may not have had sufficient time to develop relationships with the variables measured as epiphytes are slow to colonise (Benzing, 1990; Uliczka and Angelstam, 1999)) total host SR became the most strongly correlated variable and additional variables emerged as correlates; old woodland area was positively correlated with both total and typical epiphyte SR, as was canopy openness. When the four age classes were examined separately, the total SR of age class I was positively influenced only by a higher level of rainfall. Total epiphyte SR of age class II was positively correlated with total host SR while typical epiphyte SR in this stage was positively correlated with area of old woodland. In age class III, old woodland area was identified as important for total SR with no correlations for typical epiphyte SR. The total and typical epiphyte SR of age class IV was positively influenced by total host SR and negatively by elevation.

Table 4.5: Spearman's correlations between total SR of lower trunk epiphytes or typical epiphyte SR and the various environmental variables for all plots combined, for age class II, III and IV plantations combined; and for each age class separately. Only significant correlations (P < 0.05) are shown and the direction of the relationship is indicated with + or – respectively. Correlations are shown with the largest r-value first and in descending order thereafter.

	Total epiphyte SR	Typical epiphyte SR
All age classes (n = 55)	- Elevation** + Total host SR*	- Elevation** + Total host SR** + Old woodland area*
All age classes excluding age class I (n = 44)	+Total host SR** + Old woodland area** - Elevation ** +Annual Precipitation* +Canopy openness*	+Total host SR** +Old woodland area* - Average DBH* - Elevation* + Total tree number* + Canopy openness*
Age class I (n = 11)	+ Annual precipitation*	*No significant correlations*
Age class II (n = 14)	+ Total host SR *	+ Old woodland area* - Average DBH*
Age class III (n = 15)	+ Old woodland area**	*No significant correlations*
Age class IV (n = 15)	+ Total host SR* - Elevation*	+Total host SR* - Elevation*

*P < 0.05; **P < 0.01

4.1.1.2 Canopy epiphytes in mature afforested and reforested plantations

In age class IV afforestation and reforestation plantations, data from 80 plots from ten Sitka spruce trees were analysed (Table 4.6). Trees in age class IV Sitka spruce plantations were host to 14.3±2.1 species per trunk, of which 4.6±1.0 species are recognised as typical epiphyte species. Of all species per trunk, 5.0±1.2 were lichens, 4.2±0.8 mosses, 4.8±0.4 liverworts and 0.3±0.2 vascular plants. Trunks in reforestation plantations were significantly richer in their overall epiphyte species as well as in their lichen species when compared to trunks in afforestation sites (Table 4.7).

Table 4.6: Counts of all canopy epiphyte species, liverworts, lichens, mosses and vascular plant species in afforestation and reforestation plantations.

Species counts	All plantations	Afforestation sites	Reforestation sites
All epiphytes	46	24	39
Lichens	20	6	19
Liverworts	9	8	7
Mosses	15	9	12
Vascular plants	2	1	1

Table 4.7: Mean canopy epiphyte species richness, richness of species with high epiphyte affinity (typical epiphytes), richness of liverworts, lichens, mosses and vascular plant species (±standard errors) across all plots in afforested and reforested Sitka spruce plantations. Non-parametric Mann-Whitney test results are displayed for their comparison. Significant differences between afforested and reforested trunks are indicated in bold.

Species richness	Afforestation	Reforestation	*U**	P
N	5	5		
All epiphytes	10.4±1.57	18.2±3.06	-2.01	**0.04**
Typical epiphytes	2.8±0.80	6.4±1.44	-1.79	0.07
Lichens	2.2±0.58	7.8±1.59	-2.52	**0.01**
Liverworts	4.0±0.63	5.6±0.40	-1.93	0.05
Mosses	3.8±0.92	4.6±1.40	-0.43	0.67
Vascular plants	0.4±0.25	0.2±0.20	-0.66	0.51

Table 4.8: Model parameters for best fitted models and results (Likelihood ratio χ^2, degrees of freedom DF and significance value P) of GLM analyses on species richness for different taxonomic levels of canopy epiphytes in age class IV Sitka spruce afforestation and reforestation plantation plots. Significant factors and interactions are marked in bold.

	Value	χ^2	DF	P
Total SR				
Deviance/DF	1.24			
AICc for best fitted model	366.8			
Best fit model predictors				
Forest type (F)		25.34	1	**<0.001**
Height zone (H)		6.46	3	0.09
F x H		7.91	3	**0.048**
Typical epiphyte SR				
Deviance/DF	1.08			
AICc for best fitted model	252.5			
Best fit model predictors				
Forest type		28.49	1	**<0.001**
Lichen SR				
Deviance/DF	0.78			
AICc for best fitted model	284.8			
Best fit model predictors				
Forest type		54.87	1	**<0.001**
Liverwort SR				
Deviance/DF	0.65			
AICc for best fitted model	239.8			
Best fit model predictors				
Forest type		10.07	1	**0.002**
Moss SR				
Deviance/DF	0.93			
AICc for best fitted model	228.6			
Best fit model predictors				
Height zone		22.73	3	**<0.001**
Vascular plant SR				
Deviance/DF	0.35			
AICc for best fitted model	41.7			
Best fit model predictors				
Forest type		0.57	1	0.45

Sitka spruce trunks in age class IV plantations held 4.85±0.32 species per plot, of which 1.8±0.18 species can be regarded typical epiphyte species. We recorded 3.0±0.22 lichens, 1.4±0.14 mosses, 1.8±0.12 liverworts and 0.1±0.03 vascular plants per plot. In afforestation sites 3.5±0.33 epiphytic species were found per plot whereas 6.2±0.47 species were found per plot in reforestation sites. Generalised linear models which included forest type or height zone or these two factors and their interaction best described the data for the investigated taxonomic groups (Table 4.8). Aspect of a plot or any of its interaction terms were not important predictors for species richness in any of the fitted models (GLM, $\chi^2 \leq 0.77$, P ≥ 0.38).

Pairwise *a posteriori* comparisons showed that middle and upper plots on Sitka spruce trees in afforestation plantations were significantly more species poor in their overall epiphyte species richness than plots of the same height zones on Sitka spruce trunks in reforestation plantations (Fig. 4.2). Species richness of typical epiphytes, lichens or liverworts significantly differed between the two plantation types (Table 4.9), whereas species richness of mosses significantly decreased with increasing height in both plantation types. Species richness of vascular plant species was very low and not significantly different between different height zones or forest types (Table 4.9).
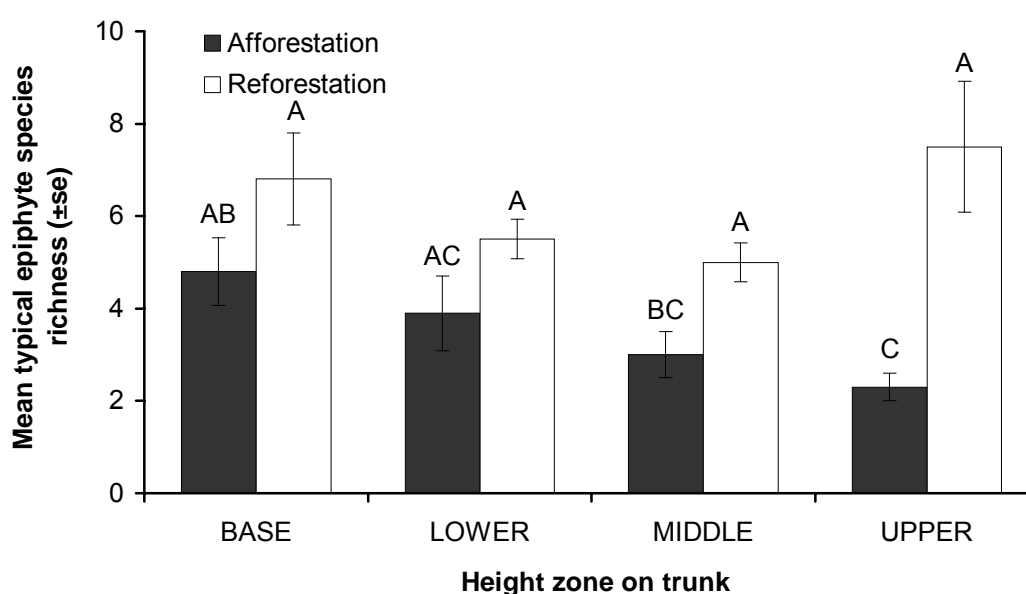
Figure 4.2 Mean canopy epiphyte species richness (±standard errors) for plots on Sitka spruce trunks in afforestation and reforestation plantations. Columns with different labels represent data which significantly differ from each other in their species richness at an α-level < 0.05. *N* = 10 for any height zone × forest type combination.

Table 4.9: Mean species richness of investigated taxonomic groups of canopy epiphytes (±standard errors) in plots of different height zones on Sitka spruce trunks in afforestation and reforestation plantations. Letters refer to pairwise *a posteriori* comparisons of GLM analyses. Comparisons were only made where a factor (forest type, height zone or their interaction) was significant in the model. In cases where groups do not share any letter they are significantly different from each other at an α-level < 0.05. Letters are not shown where comparisons were not made i.e. where a factor was not significant.

Species richness	Height zone (N_{Aff}, N_{Ref})	Total		Afforestation		Reforestation	
Typical epiphytes	Base (10, 10)			0.7±0.26		2.2±0.33	
	Lower (10, 10)			0.9±0.23		2.4±0.22	
	Middle (10, 10)			1.0±0.21		2.4±0.43	
	Upper (10, 10)			1.3±0.33		3.4±0.93	
	Total			1.0±0.13	A	2.6±0.27	B
Lichens	Base (10, 10)			1.4±0.30		4.1±0.60	
	Lower (10, 10)			1.6±0.37		3.8±0.20	
	Middle (10, 10)			2.2±0.25		3.9±0.31	
	Upper (10, 10)			1.8±0.29		5.2±1.02	
	Total			1.8±0.16	A	4.3±0.31	B
Liverworts	Base (10, 10)			1.9±0.43		2.5±0.34	
	Lower (10, 10)			1.7±0.40		2.2±0.25	
	Middle (10, 10)			1.4±0.27		1.8±0.20	
	Upper (10, 10)			0.8±0.13		2.4±0.31	
	Total			1.5±0.17	A	2.2±0.14	B
Mosses	Base (10, 10)	2.4±0.33	A	2.6±0.52		2.1±0.41	
	Lower (10, 10)	1.6±0.23	AB	1.8±0.44		1.3±0.15	
	Middle (10, 10)	0.9±0.17	B	0.7±0.30		1.0±0.15	
	Upper (10, 10)	0.9±0.22	B	0.4±0.22		1.3±0.33	
Vascular plants	Base (10, 10)			0.1±0.10		0.2±0.13	
	Lower (10, 10)			0.1±0.10		0±0	
	Middle (10, 10)			0.1±0.10		0±0	
	Upper (10, 10)			0±0		0±0	

Using the multivariate species cover data for NMS, an ordination with three dimensions was favoured. Stress of the final 3-dimensional solution was 18.2 with a final instability of 0.1746 (Fig. 4.3). This ordination solution explained 44.9% of the variation in the original data whereby axes 1, 2 and 3 accounted for 11.0%, 11.9% and 21.9% respectively. With some overlap, forest types were separated within the ordination space along axis 2 and height zones within each forest type were also separated (Fig. 4.3). However, plots within the same height zone did not clearly cluster together or form a continuum but were rather thinly spread (Fig. 4.3). Axis 1 was negatively correlated with typical epiphyte species richness (r = -0.23, P < 0.05) whereas typical epiphyte species richness was positively associated with axis 2 (r = 0.44, P < 0.01). Axis 2 was also positively correlated with lichen species richness (r = 0.44, P < 0.01). The main significant negative correlations with axis 3 were moss (r = 0.50, P < 0.01) and liverwort species richness (r = 0.33, P < 0.01).
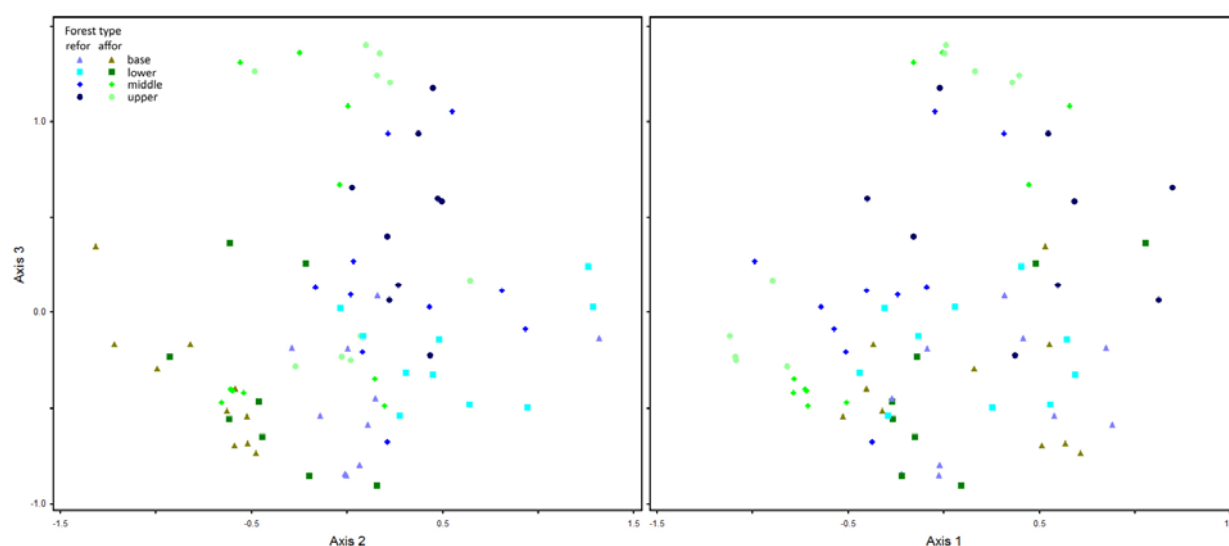
Figure 4.3: Three-dimensional ordination of plots in afforested (affor) and reforested (refor) Sitka spruce plantations. Each data point represents the cumulative canopy epiphyte cover and species assemblage of an individual north or south facing plot sampled at a specific height zone on a spruce trunk.

PERMANOVA showed significant differences in species assemblages between forest types, height zones and an interaction of these two factors (F, H and F x H; Table 4.10). Assemblages did not differ between north and south facing plots (NS) or any interaction terms with this factor (Table 4.10). Pairwise *a posteriori* comparisons on the interaction term between forest type and height zone revealed that plots on Sitka spruce trunks in afforested sites significantly differed from plots in reforested sites in their species composition and cover for each of the four height zones (T = 1.94, P ≤ 0.011 for all tests). In both afforested and reforested stands, base plots showed a significantly different species composition and cover from middle and lower plots (T ≥ 1.74, P < 0.017), and lower and middle plots were significantly different in their species assemblage from upper plots (T > 1.79, P < 0.004), whereas the base and lower plots as well as the lower and middle plots were more similar to each other in their species composition and cover (T < 1.37, P ≥ 0.086 and T < 1.40, P > 0.053 respectively).

Table 4.10: Permutational multivariate analysis of variance (PERMANOVA) on species composition and cover of canopy epiphytes. Significant effects are indicated in bold.

Source	DF	MS	*F*	P	Denom
Forest type (F)	1	17420.44	4.66	**0.0001**	Res
Height zone (H)	3	12814.21	3.43	**0.0001**	Res
Aspect N vs S (NS)	1	520.37	0.14	1.0000	Res
F x H	3	7869.65	2.10	**0.0003**	Res
F x NS	1	1345.86	0.36	0.9941	Res
H x NS	3	1523.83	0.41	0.9999	Res
F x H x NS	3	1136.03	0.30	1.0000	Res
Residual (Res)	64	3739.62			
Total	79				

4.1.2 Mixed tree species survey

4.1.2.1 Lower trunk epiphytes

A total of 73 species were recorded from the mixed tree species survey plots; 41 lichens, 8 liverworts, 16 mosses and 8 vascular plants. Twenty three species occurred only once (18 lichens, 3 bryophytes and 2 vascular plants) and only 15 species occurred in more than 25% of plots. The most common species was the moss *Kindbergia praelonga*, which occurred in 93% of the plots; the liverwort *Metzgeria furcata* occurred in 78% and the lichens *Dimerella pineti* and *D. lutea* occurred in 66% and 60%, respectively. Total epiphyte species richness (SR) in these sites ranged from 3 to 23 species per plot with a mean of 10.83 ± 0.65. The pure Norway spruce plots ranged from 3 to 18 species, the Norway spruce/Scots pine mix plots from 6 to 23 species and the Norway spruce/oak mix plots (hereafter referred to as oak mixes) from 4 to 18 species.

Scots pine mixes had a significantly higher total SR ($U^* = -3.2$, P = 0.001), bryophyte SR ($U^* = -2.58$, P = 0.01) and typical epiphyte SR ($U^* = -2.66$, P = 0.008) than pure Norway spruce plantations and significantly more vascular species than both pure Norway spruce plantations ($U^* = -2.87$, P = 0.004) and oak mixes ($U^* = -2.2$, P = 0.04) (Table 4.11). The Scots pine mixes also had significantly more typical epiphyte species compared to the pure Norway spruce plantations ($U^* = -2.66$, P = 0.008, Table 4.11). The Scots pine mix plots had a significantly higher canopy openness than either pure Norway spruce ($U^* = -2.31$, P = 0.021) or oak mix plots ($U^* = -3.4$, P = 0.0001). Oak mixes had on average the lowest canopy openness of the three plantation types and the lowest percentage of understorey cover - significantly lower than the Scots pine mixes ($U^* = -3.4$, P = 0.045) (Table 4.11).

The NMS ordination (Fig. 4.4) suggested a 3-D solution was optimum. The three plantation types did not form three distinct clusters. The pure Norway spruce plots had the most overlap with the Scots pine mixes but, with the exception of three plots, the oak mixes were separated from the other plantation types. These three plots were different as they contained *Quercus robur* as opposed to *Quercus petraea* and were the lowest, 3rd lowest and 5th lowest plots for canopy openness compared to other oak mix plots. MRPP analysis on the species assemblages using plantation type (pure Norway spruce, Scots pine mix, oak mix) as the defining factor showed a significant difference among types (T = -2.59, A = 0.02, P = 0.02). Pairwise comparisons showed the differences to be between the pure Norway spruce plots and the oak mixes, with the difference between oak mixes and Scots pine mixes close to significance (Table 4.12). Axis 2 had the strongest correlations and mainly separated plots that occur near old woodland, at lower elevations and that had a higher number of tree species and fewer snags from plots that were further away from old woodland, occurred at higher elevations and had fewer trees species and numerous snags (Table 4.13). Axis 1 also separated plots near old woodland from those that were not. Axis 3, which explained most of the original variation (Fig. 4.4), was not significantly correlated with any of the environmental variables recorded.

Table 4.11: Values for lower trunk epiphyte diversity and environmental variables in the three plantation types (mean ± se). Significance of differences tested with non-parametric Kruskal-Wallis and Mann Whitney U. Different letters in superscript indicate significant differences (P < 0.05) between the plantation types for the variable.

	Pure Norway spruce (n=28)	Norway spruce/ Scots pine mix (n=15)	Norway spruce/ oak mix (n=15)
Diversity			
Total SR	8.8±0.7[A]	14.3±1.4[B]	11.1±1.2[AB]
Lichen SR	3.9±0.4[A]	6.6±1.0[A]	4.1±0.4[A]
Bryophyte SR	4.3±0.4[A]	6.2±0.6[B]	6.2±0.8[AB]
Vascular plant SR	0.6±0.1[A]	1.5±0.3[B]	0.7±0.2[A]
Typical epiphyte SR	1.9±0.2[A]	4.3±0.8[B]	2.3±0.3[AB]
Environmental			
Canopy openness (%)	6.3±0.8[A]	7.9±0.8[B]	4.4±0.5[A]
Understorey cover (%)	0.4±0.2[A]	5.0±1.9[B]	0.3±0.2[A]
Basal area (m^2/100m^2)	0.6±0.0[A]	0.5±0.0[A]	0.5±0.1[A]
Average DBH(cm)	28.4±1.2[A]	25.8±1.6[A]	28.2±1.5[A]
Total tree number	10.1±0.9[A]	10.5±1.3[A]	7.5±0.6[A]
Total host SR	1.1±0.1[A]	3.2±0.3[B]	2.0±0.0[C]
Total volume of snags (m^3)	0.1±0.1[A]	0.2±0.1[A]	0.1±0.1[A]
Slope (°)	4.6±1.1[A]	1.9±0.6[B]	4.4±0.9[AB]
Aspect*	0.8±0.1[A]	1.2±0.2[B]	0.4±0.1[AB]
Elevation (m)	110.2±11.9[A]	97.3±14.1[A]	127.7±16.9[A]
Annual precipitation (mm)	1079±48.5[A]	1111±27.1[A]	1079±48.5[A]
Distance to old woodland (m)	350±72[A]	425±98[A]	644±114[A]
Old woodland area (km^2)	0.26±0.1[A]	0.29±0.1[A]	0.24±0.1[A]

* Transformed from degrees to a linear scale.

Table 4.12: MRPP results of lower trunk epiphyte species assemblages defined by plantation type. T = effect size, A = within group homogeneity. Significant P-values (< 0.05) are indicated in bold.

	Pure Norway spruce			Norway spruce/Scots pine mix		
	T	A	P	T	A	P
Norway spruce/Scots pine mix	-1.2	0.01	0.12			
Norway spruce/oak mix	-2.4	0.02	**0.03**	-1.8	0.02	0.06

Table 4.13: Pearson's coefficient of correlations between environmental variables and the three axes from the NMS ordination of the lower trunk epiphyte composition in pure and mixed plantations. Significant results are highlighted in bold (P < 0.05). The columns are ordered to show the stronger correlations first in descending order.

	Axis 1	Axis 2	Axis 3
Old woodland area	**-0.33**	**0.51**	0.15
Distance to old woodland	**0.33**	**-0.42**	-0.22
Elevation	0.25	**-0.40**	0.00
Total volume of snags	0.10	**-0.37**	-0.18
Total host SR	-0.05	**0.32**	-0.20
Understorey cover	**-0.28**	0.15	-0.05
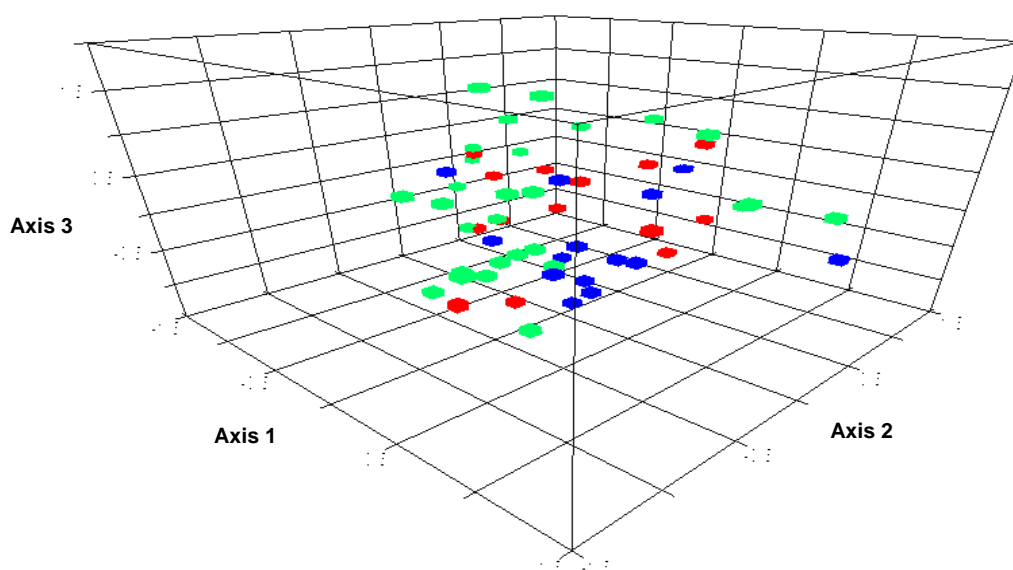
Figure 4.4: NMS ordination of the lower trunk epiphyte composition (3-D solution: stress = 16.23) of pure Norway spruce (green), Norway spruce/Scots pine mix (red) and Norway spruce/oak mix (blue) plots. The three axes accounted for 70% of the variation: axis 1 = 17%, axis 2 = 19%, axis 3 = 34%.

Four significant indicator species were found for Scots pine mixes (Table 4.14). These species are characteristic of humid and well lit situations and are mainly acid tolerant (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004). There were three significant indicators for oak mix plots. These were a mixture of shade tolerant species that prefer higher illumination. They are all characteristic of drier situations (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004) and all occurred on both Norway spruce and oak. None of the indicator species for either mix type had a low affinity for epiphytism. There were no indicator species for the pure Norway spruce plots.

Table 4.14: Indicator species of lower trunk epiphytes for the three plantation types with indicator-values given. Species were considered significant indicators (highlighted in bold) if they had an indicator-value of ≥ 25 and a P-value < 0.05. Groups: L = lichen, B = bryophyte and V = vascular plant. Affinity for epiphytism: M = medium, H = high.

Species	Group	Norway spruce/Scots pine mix	Norway spruce/ oak mix	Pure Norway spruce	Affinity
Microlejeunea ulicina	B	**33**	1	8	H
Eurhynchium striatum	B	**29**	0	4	M
Parmotrema chinense	L	**26**	0	0	M
Polypodium vulgare	V	**26**	1	0	M
Isothecium myosuroides	B	8	**57**	2	M
Neckera complanata	B	2	**30**	0	M
Radula complanata	B	2	**26**	0	H

Significant positive correlations were found (Table 4.15) between both total epiphyte SR and typical epiphyte SR and total host SR, understorey cover and canopy openness for all plots combined and for the Scots pine mixes; understorey cover was also significantly correlated for the pure Norway spruce plantations. Total host SR was rarely more than the number of planted tree species in the plot and had a

maximum of four species. Distance to old woodland and elevation were also significantly negatively correlated with typical epiphyte SR for all plots and for Scots pine mix plots; this variable was also negatively correlated with total epiphyte SR in Scots pine mixes. There were few significant correlations between total SR or typical epiphyte SR with any of the investigated variables for the pure Norway spruce plantations and none for the oak mix plots.

Table 4.15: Spearman's correlations between total SR of lower trunk epiphytes or typical epiphyte SR and the environmental variables of the plots from all the three plantation types combined and for each type separately. Only significant correlations (P < 0.05) are shown and the direction of the relationship is indicated with + or – respectively. Significant correlations are listed in descending order of r-value.

	Total Epiphyte SR	**Typical epiphyte SR**
All plots (n = 58)	+Total host SR** +Understorey cover** +Canopy openness*	+ Understorey cover** + Total host SR** -Elevation** -Distance to old woodland* +Canopy openness*
Pure Norway spruce (n = 28)	+Aspect** +Understorey cover*	+Understorey cover**
Norway spruce/Scots pine mix (n = 15)	-Distance to old woodland** +Understorey cover** -Elevation** +Total host SR* +Old woodland area*	+Understorey cover** -Distance to old woodland** -Elevation** +Total host SR*
Norway spruce/oak mix (n = 15)	*None*	*None*

Spearman's correlation significance: *P < 0.05; **P < 0.01

4.1.2.2 Canopy epiphytes

In the mixed tree species survey, we recorded epiphyte communities on Norway spruce trunks from 154 plots (Table 4.16). Summing the data from all trunk plots per individual tree, Norway spruce trees in pure and mixed Norway spruce plantations were inhabited by an average of 15.5±1.5 species, of which 5.4±0.9 species showed a high epiphyte affinity. We identified a mean of 7.3±0.8 lichens, 3.1±0.5 mosses, 1.4±0.3 liverworts and 0.9±0.3 vascular plant species per trunk. Norway spruce trees in pure and mixed plantations did not significantly differ in their species richness for any taxonomic group, but the highest figures for all groups were from trees grown in Scots pine mix plantations (Table 4.17).

Table 4.16: Counts of all canopy epiphyte species, liverworts, lichens, mosses and vascular plant species in the mixed tree species survey.

Species counts	**Total**	**Pure Norway spruce**	**Norway spruce/ Scots pine mix**	**Norway spruce/ oak mix**
All epiphytes	62	37	50	31
Lichens	31	18	27	14
Liverworts	10	8	9	6
Mosses	14	7	10	10
Vascular plants	7	4	5	1

Table 4.17: Mean total canopy epiphyte species richness, richness of species with high epiphyte affinity (typical epiphytes), richness of liverworts, lichens, mosses and vascular plant species (±standard errors) across all plots in pure and mixed Norway spruce plantations. Non-parametric Kruskal-Wallis test results are displayed.

Species richness	Pure Norway spruce	Norway spruce/ Scots pine mix	Norway spruce/oak mix	*H*	P
N	9	5	4		
Total	13.8±1.40	20.6±3.86	13.0±2.68	3.1	0.21
Typical epiphytes	4.1±0.82	9.2±2.27	3.8±0.85	4.6	0.10
Lichens	6.4±0.58	10.0±2.28	6.0±1.08	3.4	0.18
Liverworts	4.2±0.57	4.4±0.25	3.5±0.65	1.2	0.54
Mosses	2.1±0.26	4.8±1.20	3.3±0.95	3.8	0.15
Vascular plants	1.0±0.37	1.4±0.68	0.3±0.25	2.5	0.29

At a plot level, Norway spruce plots contained an average of 5.1±0.2 species, of which 1.4±0.1 species showed a high epiphyte affinity. We identified a mean of 2.3±0.1 lichens, 1.1±0.1 mosses, 1.5±0.1 liverworts and 0.2±0.1 vascular plant species per plot. Generalised linear models were fitted to the dataset and compared with each other. Data for all taxonomic groups were best described by models including forest type and/or height zone or these two factors and their interaction (Table 4.18). Aspect of a plot or any of its interaction terms were not important predictors for species richness in any of the fitted models (GLM, $\chi^2 \leq 1.13$, P ≥ 0.56).

Pairwise *a posteriori* comparisons showed that plots on Norway spruce trees in Scots pine mix plantations differed significantly in their total epiphyte species richness from plots in the two other plantation types (Fig. 4.5). Species richness of typical epiphytes, lichens and liverworts significantly increased with greater heights although in some cases this relationship was observed in Scots pine mix plantations only (Table 4.19). In contrast, species richness of mosses and vascular plants decreased with increasing heights and significantly differed between forest types (Table 4.19).
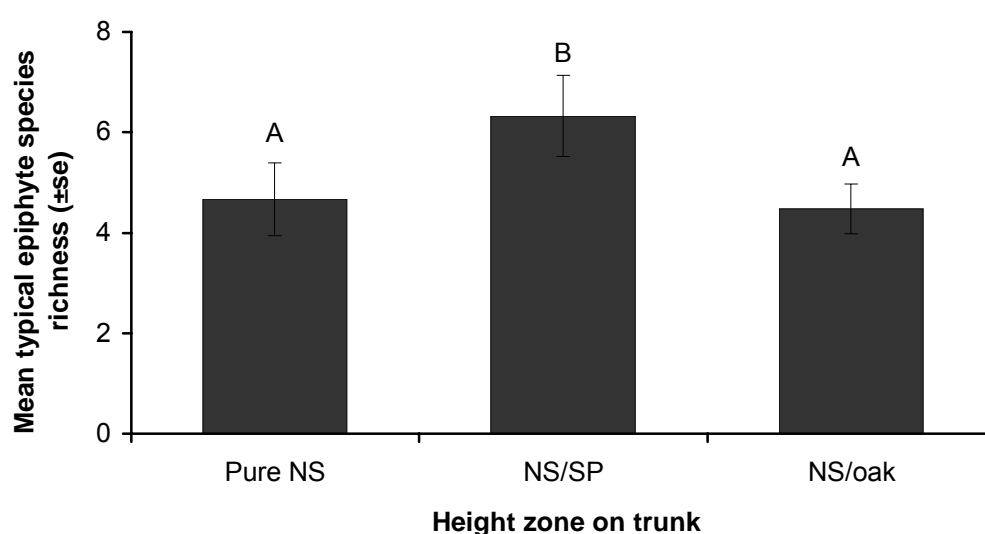
Figure 4.5: Mean canopy epiphyte species richness (±standard errors) for plots on Norway spruce trunks in different types of plantations. Columns with different labels represent data which significantly differ from each other in their species richness at an α-level of 0.002. $N_{pure NS}$ = 78, $N_{NS/SP}$ = 40, $N_{NS/oak}$ = 36. Pure NS = Pure Norway spruce, NS/SP = Norway spruce/Scots pine mix and NS/oak = Norway spruce/oak mix.

Table 4.18: Model parameters for best fitted models and results (Likelihood ratio χ², degrees of freedom DF and significance value P) of GLM analyses on species richness for different taxonomic levels of canopy epiphytes in pure and mixed Norway spruce plantation plots. Significant factors and interactions are marked in bold.

	Value	χ^2	DF	P
Total SR				
Deviance/DF	1.12			
AICc for best fitted model	693.4			
Best fit model predictors				
Forest type		14.93	2	**<0.001**
Typical epiphyte SR				
Deviance/DF	1.15			
AICc for best fitted model	446.2			
Best fit model predictors				
Forest type (F)		20.84	2	**<0.001**
Height zone (H)		41.00	3	**<0.001**
F x H		14.54	6	**0.024**
Lichen SR				
Deviance/DF	1.29			
AICc for best fitted model	566.8			
Best fit model predictors				
Forest type		4.57	2	0.10
Height zone		10.51	3	**0.015**
Liverwort SR				
Deviance/DF	1.05			
AICc for best fitted model	471.9			
Best fit model predictors				
Forest type (F)		0.54	2	0.76
Height zone (H)		10.58	3	**0.014**
F x H		15.81	6	**0.015**
Moss SR				
Deviance/DF	0.55			
AICc for best fitted model	466.9			
Best fit model predictors				
Forest type		15.86	2	**<0.001**
Height zone		15.59	3	**0.001**
Vascular plant SR				
Deviance/DF	0.62			
AICc for best fitted model	161.1			
Best fit model predictors				
Forest type		19.93	2	**<0.001**
Height zone		45.86	3	**<0.001**

Table 4.19: Mean species richness (SR) (±standard errors) of typical epiphytes (TE), lichens (L), liverworts (H), mosses (M) and vascular plants (VP) in plots of different height zones for pure Norway spruce plantations (NS), Norway spruce/Scots pine mix (NS/SP) and Norway spruce/oak mix (NS/oak) plantations. Letters refer to pairwise *a posteriori* comparisons of GLM analyses. Comparisons were only made where a factor (forest type, height zone or their interaction) was significant in the model. In cases where groups do not share any letter they are significantly different from each other at an α-level < 0.05. Letters are not shown where comparisons were not made i.e. where a factor was not significant.

SR	Height zone	Total		Forest type					
	($N_{NS, NS/SP, NS/oak}$)			NS		NS/SP		NS/oak	
TE	Base (19, 10, 8)			0.8±0.22	AC	0.8±0.36	AC	0.5±0.19	A
	Lower (19, 10, 8)			0.9±0.24	AC	1.7±0.42	AB	0.4±0.26	A
	Middle (20, 10, 10)			0.8±0.14	A	3.3±0.50	B	0.7±0.21	A
	Upper(20, 10, 10)			1.5±0.28	AC	4.1±0.66	B	2.6±0.54	BC
L	Base (19, 10, 8)	1.6±0.21	A	1.7±0.33		1.4±0.34		1.4±0.42	
	Lower (19, 10, 8)	2.4±0.30	AB	2.5±0.41		2.8±0.68		1.8±0.53	
	Middle (20, 10, 10)	2.8±0.28	B	2.5±0.32		3.9±0.74		2.1±0.53	
	Upper(20, 10, 10)	2.3±0.25	AB	1.7±0.29		2.9±0.53		2.7±0.56	
H	Base (19, 10, 8)			2.0±0.38	AB	0.8±0.29	A	0.9±0.35	A
	Lower (19, 10, 8)			1.1±0.21	A	1.2±0.29	AB	1.3±0.41	AB
	Middle (20, 10, 10)			1.2±0.16	A	1.9±0.35	AB	1.4±0.31	AB
	Upper(20, 10, 10)			1.5±0.21	AB	2.9±0.46	B	1.9±0.57	AB
M	Base (19, 10, 8)	1.5±0.12	A	1.3±0.11		1.7±0.26		1.9±0.35	
	Lower (19, 10, 8)	0.9±0.12	B	0.6±0.11		1.5±0.30		0.8±0.16	
	Middle (20, 10, 10)	0.9±0.09	B	0.8±0.09		1.4±0.16		0.5±0.17	
	Upper(20, 10, 10)	1.1±0.13	B	0.9±0.15		1.4±0.40		1.1±0.18	
	Total			0.9±0.06	A	1.5±0.14	B	1.0±0.14	A
VP	Base (19, 10, 8)	0.6±0.17	A	0.6±0.18		1.2±0.49		0±0	
	Lower (19, 10, 8)	0.2±0.06	AB	0.2±0.09		0.3±0.15		0±0	
	Middle (20, 10, 10)	0.1±0.05	AB	0.2±0.08		0±0		0.1±0.10	
	Upper(20, 10, 10)	0.05±0.03	B	0.1±0.07		0±0		0±0	
	Total			0.2±0.06	A	0.4±0.15	A	0.03±0.03	B

Using the multivariate species cover data for NMS, an ordination with three dimensions was favoured. Stress of the final 3-dimensional solution was 21.8 with a final instability of 0.0024 (Fig. 4.6). This ordination solution explained 43.0% of the variation in the original data whereby axes 1, 2 and 3 accounted for 16.8%, 14.3% and 12.0% respectively. Plots of each forest type did not cluster together but widely overlapped with plots of the other forest types. However, plots within the same height zone grouped more closely together and formed a continuum according to the position on the trunk (Fig. 4.6). Axis 1 was positively correlated with moss species richness (r = 0.36, P < 0.01) and negatively correlated with lichen (r = 0.43, P < 0.01) and typical epiphyte species richness (r = 0.33, P < 0.01). Typical epiphyte species richness was also negatively associated with axis 2 (r = 0.31, P < 0.01) whereas axis 3 was positively related with moss species richness (r = 0.35, P < 0.01).

We used plots of a random subset of sites (for pure Norway spruce plantations: CASTP, GARRP, MOTEP, PARKP; for Scots pine mix: CASTM, COOLM, CRABM, MOTEM; for oak mix: GARRM, PARKM, THOMM, WOODM) in order to create a balanced design necessary for PERMANOVA. The analysis showed significant differences in species assemblages both among forest types and among height zones

(F and H, Table 4.20). Assemblages did not differ between north and south facing plots or any interaction terms (Table 4.20). Pairwise *a posteriori* comparisons among forest types showed significant differences between pure Norway spruce and Scots pine mix plantations (T = 1.64, P = 0.006) as well as oak mix plantations (T = 1.71, P = 0.005); however, the two mixed plantation types did not differ significantly in their species composition and cover (T = 1.20, P = 0.13). Base plots hosted in general a significantly different species assemblage and cover of epiphyte species in comparison to every other height zone (T > 2.00, P < 0.001). This was also true for upper plots, which differed significantly from any other height zone in their species composition (T > 1.32, P = 0.043). However, base and middle plots did not significantly differ in their species composition and cover (T = 1.08, P = 0.28).
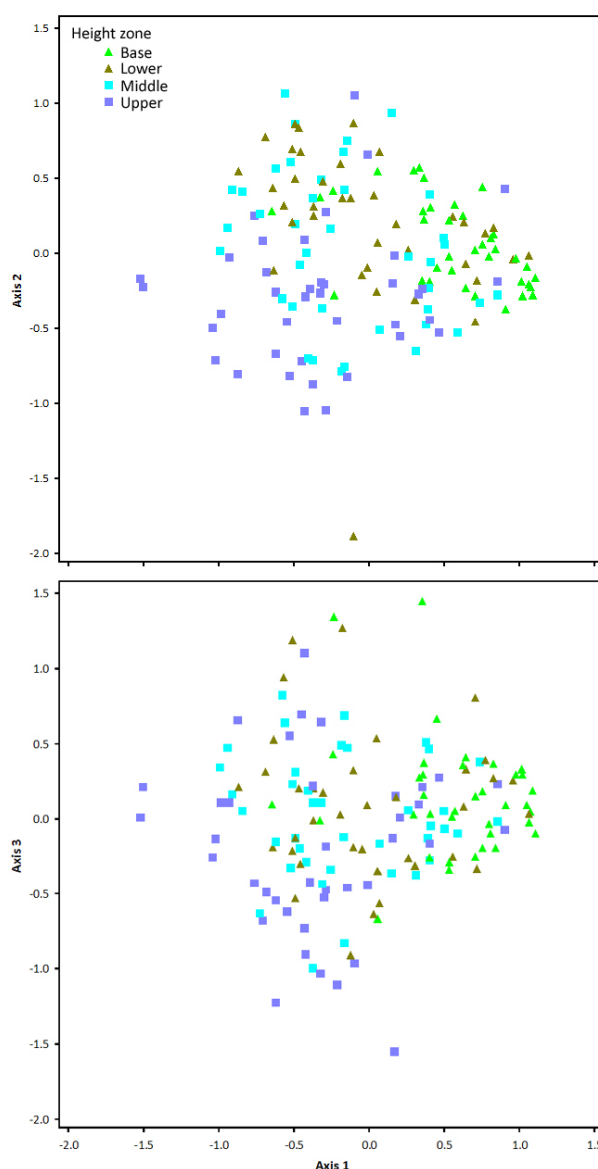
Figure 4.6: Three-dimensional ordination of plots in pure and mixed Norway spruce plantations. Each data point represents the cumulative canopy epiphyte cover and species assemblage of an individual north or south facing plot sampled at a specific height zone on a spruce trunk.

Table 4.20: Permutational multivariate analysis of variance (PERMANOVA) on species composition and cover of canopy epiphytes. Significant effects are indicated in bold.

Source	DF	MS	*F*	P	Denom
Forest type (F)	2	8779.43	2.41	**0.0013**	Res
Height zone (H)	3	14219.09	3.90	**0.0001**	Res
Aspect N vs S (NS)	1	2949.92	0.81	0.6426	Res
F x H	6	4522.52	1.24	0.0917	Res
F x NS	2	2340.41	0.64	0.9297	Res
H x NS	3	1490.92	0.41	1.0000	Res
F x H x NS	6	1379.18	0.38	1.0000	Res
Residual (Res)	72	3650.11			
Total	95				

4.1.3 Native woodlands survey

4.1.3.1 Lower trunk epiphytes

A total of 195 species were recorded from the native woodland plots made up of a total of 121 lichens, 22 liverworts, 32 mosses and 20 vascular plants. Oak woodland contained a total of 127 species: 80 lichens, 12 liverworts, 19 mosses and 16 vascular plants. Ash woodland contained a total of 142 species: 88 lichens 18 liverworts, 27 mosses and 9 vascular plants.

Thirty one species occurred only once (25 lichens, 5 bryophytes and 1 vascular plant). Only 15 species occurred in 30% or more of the plots; the most common taxa were the moss *Isothecium myosuroides*, which occurred in 81% of the plots, the liverwort *Metzgeria furcata* which occurred in 80% and the moss *Thuidium tamariscinum* which occurred in 76%. Ash was significantly more species rich on average than oak (U^* = -3.61, P < 0.001, Table 4.21), mainly due to a significantly higher bryophytes species richness. However, oak woodland supported significantly more vascular species, although number of vascular epiphytes was low overall. Ash woodland was found to support more typical epiphyte species (Table 4.21). Ash woodlands contained more trees per sample plot and these had a significantly smaller mean DBH and total basal area compared to oak woodland. This was related to the significantly higher understorey cover in ash plots, which led to significantly lower canopy openness compared to the oak plots (Table 4.21). Ash woodland plots also had a significantly lower slope and elevation and a lower annual precipitation than oak woodland (Table 4.21).

The NMS ordination (Fig. 4.7) suggested a 2-D solution was optimum and showed a clear separation between oak woodland and ash woodland plots. Multi-Response Permutation Procedure (MRPP) analysis on the species assemblages using woodland type (oak and ash) as the defining factor showed a significant difference from each other (T = -28.1, A = 0.17, P = < 0.001). The majority of the significant correlations were along Axis 2 (Table 4.22) and these were mainly related to significant differences in variables between oak and ash woodlands (Table 4.21), which were reasonably well separated along this axis.

Table 4.21: Mean ±se of lower trunk epiphyte diversity and environmental variables for oak and ash woodlands. Significant differences between the woodland types tested with non-parametric Mann Whitney U. A significant difference (P < 0.05) between variables is indicated by different letters.

	Oak (n=30)	Ash (n=29)
Diversity		
Total epiphyte SR	24.3±1.6^A	32.7±1.4^B
Lichen SR	13.0±1.2^A	16.9±1.0^A
Bryophyte SR	8.6±0.6^A	13.5±0.6^B
Vascular plant SR	2.5±0.4^A	1.9±0.2^B
Typical epiphyte SR	8.4±0.7^A	13.2±0.8^B
Environmental		
Canopy openness (%)	6.1±0.6^A	3.7±0.4^B
Understorey cover (%)	33.9±5.2^A	64.8±5.3^B
Basal area (m^2/100m^2)	0.45±0.03^A	0.35±0.03^B
Average DBH (cm)	22.8±2.5^A	11.9±0.7^B
Total tree number	12.9±1.8^A	23.8±2.2^B
Total host SR	3.0±0.2^A	3.7±0.2^A
Slope (^{o})	12.6±1.5^A	8.5±1.5^B
Aspect*	1.0±0.1^A	1.2±0.1^A
Elevation (m)	103 ± 8.6^A	66±11^B
Annual precipitation (mm)	1269±42.7^A	1101±15.2^B

*Transformed from degrees to a linear scale
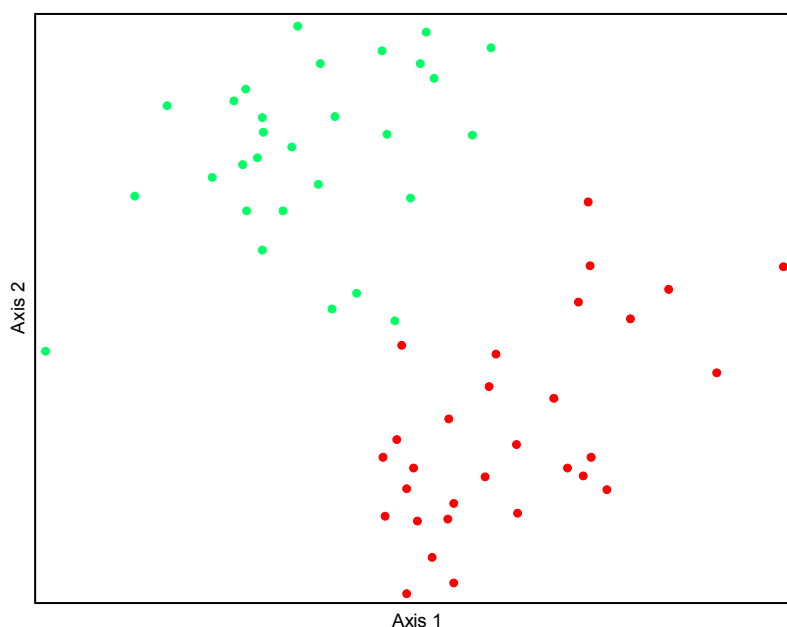
Figure 4.7: Epiphytes on lower trunks (0-2m) in oak woodland and ash woodland plots: 2D varimax rotated NMS ordination (stress = 18.59). The two axes accounted for 71% of the variation: axis 1 = 31% and axis 2 = 40%. Oak plots (n = 30) are red and ash plots (n = 29) are green.

Table 4.22: Pearson co-efficient of correlations between variables and the two axes from the NMS ordination of lower trunk epiphytes in oak and ash woodland plots. Significant results are highlighted in bold (P ≤ 0.05)

	Axis 1	Axis 2
Average DBH	0.12	**-0.64**
Total tree number	-0.24	**0.56**
Typical epiphyte SR	-0.22	**0.54**
Canopy Openness	0.15	**-0.47**
Total SR	-0.14	**0.46**
Basal area	0.20	**-0.38**
Total host SR	0.01	**0.36**
Understorey Cover	-0.27	**0.54**
Elevation	0.15	**-0.29**

There were ten significant indicator species for the oak woodland plots and 20 for the ash woodland plots (Table 4.23). The oak woodland indicator species were made up of 4 bryophytes, 5 lichens and 1 vascular plant (*Polypodium vulgare* agg.) while the ash woodland indicator species were made up of 11 bryophytes and 9 lichens. Oak woodland had two indicator species with high affinity for epiphytism (Table 4.23), which are common on smooth bark in sheltered situations (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004) while the other eight were mainly medium affinity epiphytes. Ash woodland contained a higher proportion of high affinity indicator species (eight out of 20) compared to oak woodland, all species which are also common on smooth-barked deciduous trees in sheltered woodland (Purvis *et al.*, 1992; Paton, 1999; Dobson, 2000; Smith, 2004). Some of the ash woodland lichen indicator species, such as *Arthonia cinnabarina* and *Graphina anguina* were common on both *Fraxinus excelsior* and *Corylus avellana* in the ash woodlands in this study.

Significant positive correlations (P < 0.05) were found for both the total SR and typical epiphyte SR of oak woodland and ash woodland plots combined (n = 59) with total tree number and understorey cover while a negative correlations was found with average DBH per plot (Table 4.24). All of these variables are related to the presence of an understorey at the sites. While the species richness of host species was not correlated with total epiphyte SR, typical epiphyte SR was positively correlated with this variable for all plots combined and for oak woodlands. There were no significant correlations between total or typical epiphyte SR in the ash woodland plots and the variables measured.

Table 4.23: Indicator species of lower trunk epiphytes for oak and ash woodlands with their indicator-values shown. Species were considered significant indicators (highlighted in bold) if they had an indicator-value of ≥ 25 and a P-value < 0.05. Group: L = lichen, B = bryophyte and V = vascular plant. Affinity for epiphytism: L = low, M = medium, H = high.

Species	Group	Affinity	Oak	Ash
Isothecium myosuroides	B	M	**88**	6
Hypnum andoi	B	M	**83**	0
Thelotrema lepadinum	L	H	**72**	2
Dicranum scoparium	B	M	**69**	0
Graphis elegans	L	H	**69**	4
Polypodium vulgare	V	M	**59**	0
Cladonia coniocraea	L	M	**56**	3
Lepraria incana	L	M	**51**	1
Rhytidiadelphus loreus	B	L	**43**	0
Lecanactis abietina	L	M	**27**	0
Arthonia cinnabarina	L	H	0	**96**
Graphis scripta	L	H	0	**96**
Neckera complanata	B	M	0	**96**
Pyrenula macrospora	L	H	0	**86**
Metzgeria furcata	B	M	2	**81**
Radula complanata	B	H	0	**76**
Isothecium alopecuroides	B	M	0	**73**
Eurhynchium striatum	B	M	0	**65**
Frullania dilatata	B	H	0	**61**
Normandina pulchella	L	M	8	**55**
Homalothecium sericeum	B	M	0	**55**
Zygodon viridissimus	B	M	0	**55**
Graphina anguina	L	H	0	**48**
Bacidia arceutina	L	M	0	**45**
Pertusaria leioplaca	L	H	6	**42**
Climacium dendroides	B	L	0	**38**
Thamnobryum alopecurum	B	M	0	**34**
Lejeunea patens	B	M	2	**30**
Leptogium gelatinosum	L	M	0	**30**
Pertusaria hymenea	L	H	4	**28**

Table 4.24: Spearman's correlation results between (a) total SR of lower trunk epiphytes and (b) typical epiphyte SR and the environmental variables of the plots from the oak and ash woodlands combined and for each type separately. Only significant correlations (P < 0.05) are shown and the direction of the relationship is indicated with + or – respectively. Significant correlations are arranged in descending order by r-value.

(a) Total epiphyte SR		
Oak and ash combined	Oak	Ash
-Average DBH** -Elevation** +Total tree number** +Understorey cover* -Slope*	*No significant correlations*	*No significant correlations*
(b) Typical epiphyte SR		
Oak and ash combined	Oak	Ash
-Average DBH** +Total tree number** -Elevation* +Understorey cover* +Total host SR*	+Total host SR*	*No significant correlations*

Spearman's correlation significance: * P < 0.05; ** P < 0.01

4.1.3.2 Canopy epiphytes

In native woodlands, epiphyte species were recorded from 150 plots (Table 4.25). On a trunk level (data summed across all trunk plots within an individual tree), trees in native woodlands were inhabited by an average of 35.8±8.7 species, of which 13.5±6.4 species showed a high epiphyte affinity. We identified a mean of 21.9±8.4 lichens, 6.6±2.1 mosses, 4.7±1.6 liverworts and 2.5±1.8 vascular plant species per trunk. Ash woodlands and oak woodlands did not significantly differ in their epiphytic species richness for most taxonomic groups (Table 4.26). However, ash trunks showed a higher diversity of high epiphyte affinity species than oak trunks (Table 4.26). On a plot level, native woodland plots contained an average of 10.1±0.5 species, of which 3.5±0.3 species showed a high epiphyte affinity. We identified a mean of 5.8±0.4 lichens, 2.2±0.1 mosses, 1.5±0.1 liverworts and 0.7±0.1 vascular plant species per plot. An average of 11.1±0.7 epiphytic species per plot was found on ash trunks compared with an average of 9.1±0.6 species per plot on oak trunks.

Table 4.25: Canopy epiphyte species counts, as well as liverwort, lichen, moss and vascular plant species counts, in native woodlands.

Species counts	Native woodlands	Oak	Ash
All epiphytes	174	106	131
Lichens	104	73	87
Liverworts	17	13	12
Mosses	22	12	22
Vascular plants	11	8	10

Table 4.26: Mean canopy epiphyte species richness, richness of typical epiphytes, richness of liverworts, lichens, mosses and vascular plant species (±standard errors) across all plots of ash and oak trunks. Non-parametric Mann-Whitney test results are displayed for their comparison. Significant differences (P < 0.05) between ash and oak trunks are indicated in bold.

Species richness	Oak	Ash	U*	P
N	7	8		
All epiphytes	32.7±3.45	38.5±2.81	-1.45	0.15
Typical epiphytes	9.3±2.13	17.1±1.67	-2.32	**0.02**
Lichens	19.4±3.20	24.1±2.90	-0.70	0.49
Liverworts	4.3±0.68	5.1±0.52	-1.42	0.16
Mosses	5.9±0.55	7.3±0.84	-0.82	0.41
Vascular plants	3.1±0.46	2.0±0.76	-1.47	0.14

Generalised linear models were fitted to the dataset and compared with each other. Data for all taxonomic groups were best described by models including forest type (ash vs. oak), height zone (base, lower, middle, upper) and an interaction between these two factors (Table 4.27). Aspect (north vs. south) of a plot or any interaction term containing aspect was not an important predictor for species richness in any of the fitted models (GLM, $\chi^2 \leq 2.42$, P $\geq$ 0.12).

Pairwise *a posteriori* comparisons revealed significant differences in total epiphyte species richness per plot in relation both to height zone and to host tree species (Fig. 4.8). A significant increase in species richness related to increasing height was apparent on oak trunks for typical epiphyte species richness, lichen species richness and liverwort species richness (Table 4.28). There was no height gradient for liverwort species richness in plots on ash trunks and moss or vascular plant species richness on oak trunks (Table 4.28). However, species richness of mosses and vascular plants in plots on ash trunks decreased with increasing height (Table 4.28)
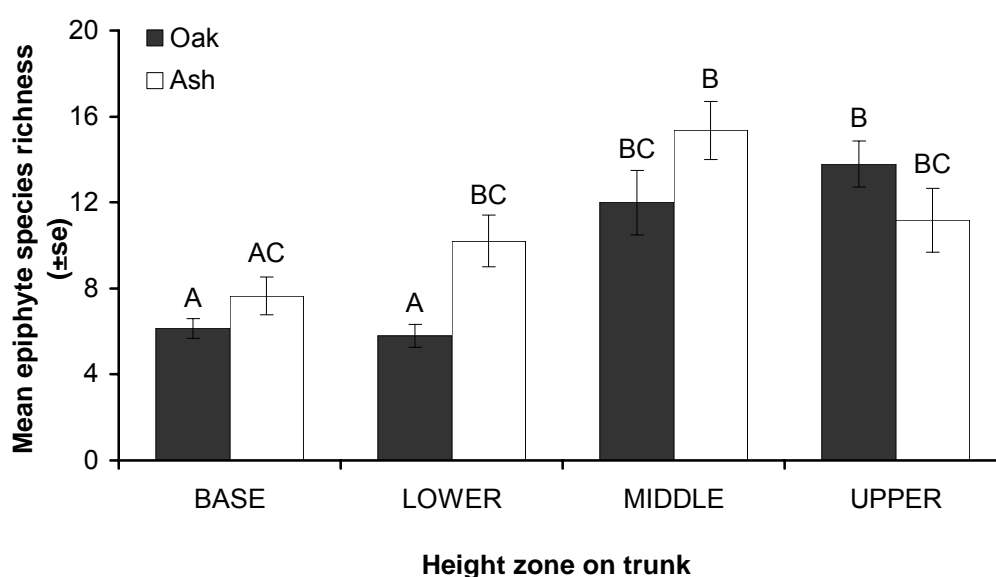
Figure 4.8: Mean canopy epiphyte species richness (±se) for plots of different height zones on ash and oak trunks. Where two columns do not share any letter, they represent plots which significantly differ from each other in their epiphyte species richness at an α-level < 0.05. *N* = 20 for any height zone × woodland type combination except for upper plots on oak (*N* = 14) and ash trees (*N* = 16).

Table 4.27: Model parameters for best fitted models and results (Likelihood ratio χ^2, degrees of freedom DF and significance value P) of GLM analyses on species richness for different taxonomical levels of canopy epiphytes in native woodland plots. Significant factors and interactions are marked in bold.

	Value	χ^2	DF	P
Total SR				
Deviance/DF	2.20			
AICc for best fitted model	929.1			
Best fit model predictors				
Forest type (F)		6.66	1	**0.01**
Height zone (H)		58.43	3	**<0.001**
F x H		11.80	3	**0.008**
Typical epiphyte SR				
Deviance/DF	2.35			
AICc for best fitted model	676.1			
Best fit model predictors				
Forest type (W)		35.41	1	**<0.001**
Height zone (H)		110.73	3	**<0.001**
W x H		12.10	3	**0.007**
Lichen SR				
Deviance/DF	2.33			
AICc for best fitted model	811.1			
Best fit model predictors				
Woodland type (W)		3.10	1	**0.08**
Height zone (H)		135.31	3	**<0.001**
W x H		4.47	3	0.22
Liverwort SR				
Deviance/DF	1.41			
AICc for best fitted model	476.2			
Best fit model predictors				
Woodland type (W)		5.52	1	**0.02**
Height zone (H)		13.28	3	**0.004**
W x H		8.92	3	**0.03**
Moss SR				
Deviance/DF	0.71			
AICc for best fitted model	485.0			
Best fit model predictors				
Woodland type (W)		0.59	1	0.44
Height zone (H)		31.95	3	**<0.001**
W x H		19.79	3	**<0.001**
Vascular plant SR				
Deviance/DF	0.82			
AICc for best fitted model	293.6			
Best fit model predictors				
Woodland type (W)		4.49	1	**0.03**
Height zone (H)		52.87	3	**<0.001**
W x H		15.88	3	**0.001**

Using the multivariate species data for NMS, an ordination with three dimensions was favoured. Stress of the final 3-dimensional solution was 17.4 with a final instability of 0.00013 (Fig. 4.9). This ordination solution explained 49.7% of the variation in the original data whereby axes 1, 2 and 3 accounted for 17.5%, 17.6% and 15.7% respectively. Plots within the same height zone sampled within either oak or ash woodlands grouped closely together (Fig. 4.9). Axis 1 was significantly ($P < 0.01$) correlated to total epiphyte species richness ($r = 0.53$), typical epiphyte species richness ($r = 0.65$) and the number of lichens ($r = 0.54$) whereas axis 3 was negatively correlated with the number of typical epiphyte species ($r = -0.50$, $P < 0.01$). Axis 2 was significantly correlated to the number of typical epiphyte species ($r = 0.46$, $P < 0.01$) and lichen species ($r = 0.59$, $P < 0.01$).

Table 4.28: Mean richness of species with high epiphyte affinity (typical epiphytes), richness of liverworts, lichens, mosses and vascular plant species (±standard errors) within plots at different height zones on ash and oak trunks. Letters after the mean values refer to pairwise *a posteriori* comparisons of GLM analyses. Comparisons were only made where a factor (forest type or height zone or their interaction) was significant in the model. Height zone × woodland type combinations within each taxonomic group which do not have any letter in common are significantly different from each other at an α-level < 0.05.

Species richness	Height zone (N_{oak}, N_{ash})	Oak		Ash		Total	
Typical epiphytes	Base (20, 20)	0.1±0.07	A	1.2±0.44	AC		
	Lower (20, 20)	0.7±0.22	A	3.9±0.67	B		
	Middle (20, 20)	3.4±0.83	BC	8.7±0.92	D		
	Upper (14, 16)	4.8±1.13	BD	6.7±0.93	BD		
Lichens	Base (20, 20)	1.5±0.29		1.6±0.39		1.6±0.24	A
	Lower (20, 20)	3.0±0.52		5.1±0.75		4.1±0.48	B
	Middle (20, 20)	7.8±1.17		11.3±1.04		9.5±0.82	C
	Upper (14, 16)	9.0±1.14		8.6±1.34		8.8±0.88	C
Liverworts	Base (20, 20)	0.7±0.18	A	1.3±0.33	AC		
	Lower (20, 20)	0.7±0.19	A	1.9±0.41	AC		
	Middle (20, 20)	1.6±0.29	AC	2.3±0.31	BC		
	Upper (14, 16)	2.2±0.41	BC	1.5±0.24	AC		
Mosses	Base (20, 20)	2.7±0.26	AC	3.5±0.38	C		
	Lower (20, 20)	1.7±0.17	BD	2.5±0.32	ABC		
	Middle (20, 20)	1.9±0.16	AB	1.8±0.27	ABD		
	Upper (14, 16)	2.3±0.24	ABC	0.9±0.27	D		
Vascular plants	Base (20, 20)	1.3±0.18	A	1.4±0.28	AB		
	Lower (20, 20)	0.5±0.15	BD	0.8±0.20	ABCE		
	Middle (20, 20)	0.8±0.14	ABC	0.1±0.07	D		
	Upper (14, 16)	0.3±0.13	CD	0.1±0.09	DE		
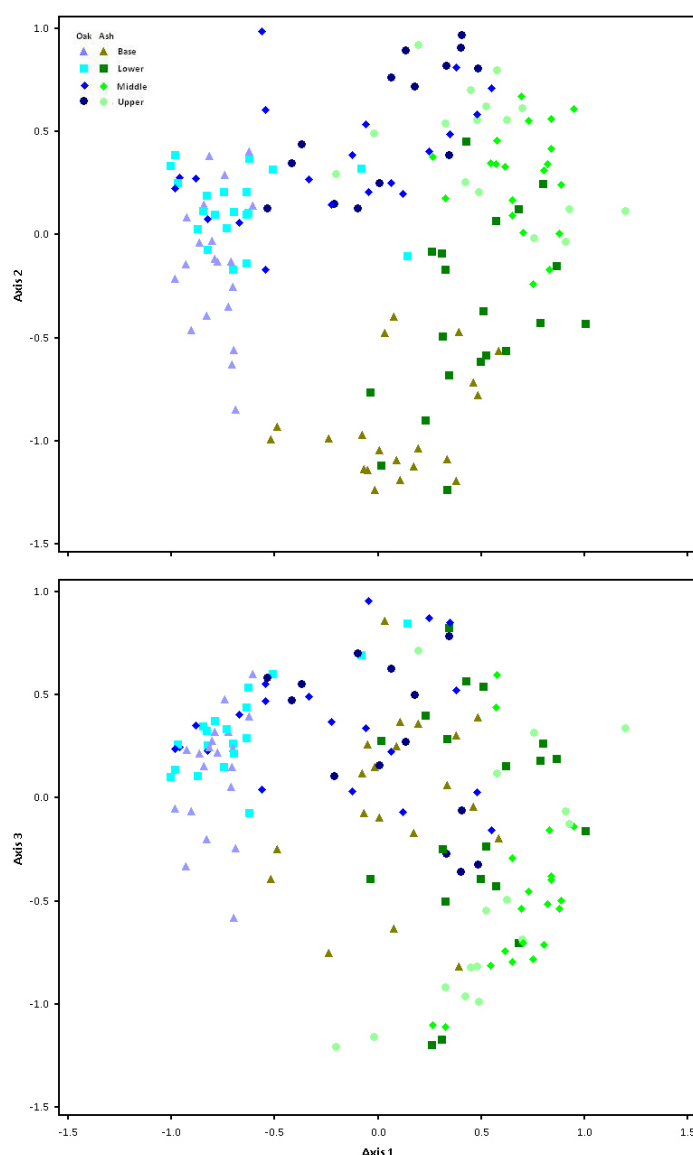
Figure 4.9: Three-dimensional ordination of sampled native woodland plots. Each data point represents the cumulative canopy epiphyte cover and species assemblage of an individual north or south facing plot sampled at a specific height zone on either an oak or an ash tree.

PERMANOVA showed significant differences between species assemblages on oak and ash trees depending on the investigated height zone (F x H, Table 4.29). Assemblages did not differ between north and south facing plots (NS, Table 4.29) or any interaction terms with this factor. Pairwise *a posteriori* comparisons on the interaction term between tree species (oak vs. ash) and height zone (base, lower, middle, upper) revealed that ash trees differed significantly from oak trees in their species composition and cover for each of the four height zones (T = 1.94, P = 0.0001 for all tests). On ash trees each of the zones showed a significantly different species composition and cover from any other (T > 1.30, P < 0.034). For oak trees, however, only the base and lower plots were significantly different from each other as well as from the middle and upper plots (T > 1.63, P < 0.031); the middle and upper plots were relatively similar to each other in their species composition and cover (T = 1.28, P = 0.121).

Table 4.29: Permutational multivariate analysis of variance (PERMANOVA) on species composition and cover of canopy epiphytes. Significant effects are indicated in bold.

Source	DF	MS	*F*	P	Denom
Forest type (F)	1	60924.52	18.07	**0.0001**	Res
Height zone (H)	3	16132.47	4.78	**0.0001**	Res
Aspect N vs S (NS)	1	2077.13	0.62	0.8909	Res
F x H	3	10544.55	3.13	**0.0001**	Res
F x NS	1	2031.11	0.60	0.8980	Res
H x NS	3	1283.46	0.38	1.0000	Res
F x H x NS	3	1264.62	0.38	1.0000	Res
Residual (Res)	96	3371.81			
Total	111				

4.1.4 Comparison of forest types

4.1.4.1 Canopy epiphytes

In the canopy epiphyte survey, a total of 189 species were recorded from 344 plots. Of these taxa, there were 127 lichens, 20 liverworts, 28 mosses and 14 vascular plant species. Epiphyte species richness differed significantly between forest types (Kruskal Wallis *H* = 25.3, P < 0.001); trunks in native woodlands hosted significantly more epiphyte species than trunks in pure or mixed conifer plantations (Fig. 4.10). Native ash woodlands were also significantly richer in typical epiphytes, lichens and mosses than pure conifer plantations (Table 4.30). Native oak woodlands held an intermediate number of species of these taxonomic groups. They were significantly more species rich in typical epiphytes, lichens, mosses and vascular plants than pure Norway spruce plantations (Table 4.30). In a number of cases, native woodlands, especially ash woodlands, were also more species rich in these taxa than mixed conifer plantations, although Norway spruce/Scots pine mix plantations held a similar number of typical epiphyte and lichen species to oak woodlands (Table 4.30).
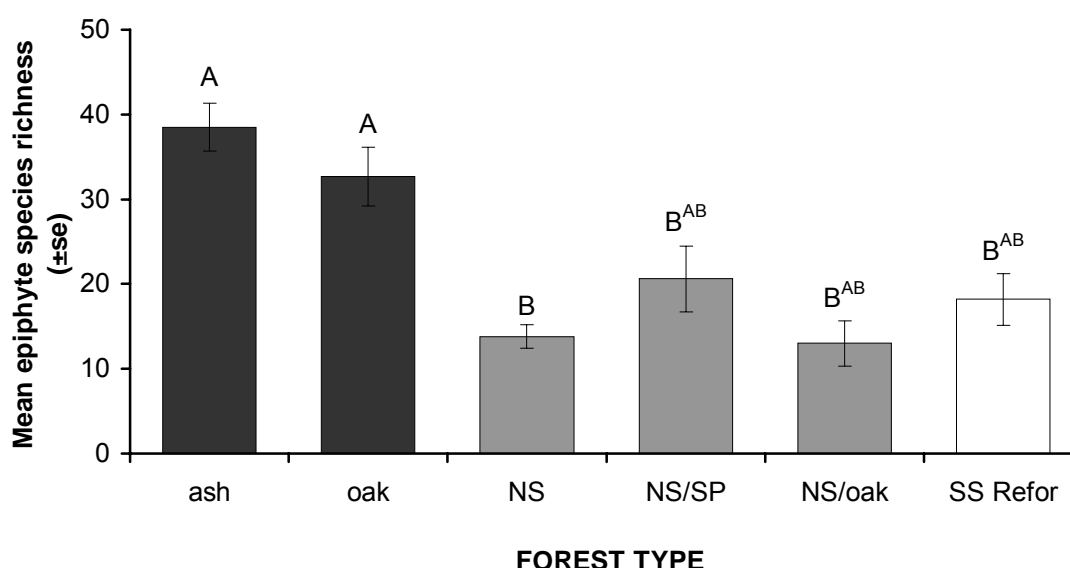
Figure 4.10: Mean canopy epiphyte species richness (±standard errors) on trunks in native woodlands (ash or oak) and pure or mixed conifer plantations (pure Norway spruce = NS, Norway spruce/Scots pine mix = NS/SP, Norway spruce/oak mix = NS/oak, reforested Sitka spruce = SS Refor). Different letters indicate a significant difference in epiphyte species richness between two forest types at an α-level < 0.05. Superscript letters refer to changes in such a significant difference after adjustment of significance values (sequential Šidák method). For sample sizes see Table 4.30.

Cover data for all forest types on a plot level could not be resolved in a meaningful NMS ordination; stress of a three-dimensional solution was 31.8 with a final instability of 0.1039. Such an ordination would only explain 8.7% of the variation in the original data and could not be interpreted in a reliable way. Therefore species assemblages on a plot level were not further analysed or presented via NMS ordinations and the cumulative cover of all eight surveyed plots on each tree was used instead; trees with fewer than 8 plots surveyed were excluded from analysis.

An NMS ordination with three dimensions provided the best resolution when including the multivariate data across sites of all forest types. Stress of the final 3-dimensional solution was 13.1 with a final instability of < 0.00001 (Fig. 4.11). The ordination explained 80.8% of the variation in the original data whereby axes 1, 2 and 3 accounted for 34.2%, 27.3% and 19.3% respectively. Axis 2 was most strongly correlated with total epiphyte SR ($r = 0.49$, $P < 0.01$) and SR of mosses ($r = 0.49$, $P < 0.01$) whereas axis 1 was strongly negatively correlated with total epiphyte SR ($r = 0.73$, $P < 0.01$) and also with typical epiphyte SR ($r = 0.69$, $P < 0.01$) and lichen SR ($r = 0.68$, $P < 0.01$). Axis 3 only negatively correlated with the species richness of liverworts ($r = 0.40$, $P < 0.05$). Oak woodland sites and ash woodland sites both formed separate groups within the ordination space and could be discriminated from mixed or pure conifer plantation sites except for one Sitka spruce reforestation site (CHEVY) which grouped with native oak woodland sites (Fig. 4.11). The remaining plantation sites clustered together within the space that was characterised by low numbers of total epiphytes and of typical epiphyte species (Fig. 4.11).

Table 4.30: Mean richness of canopy epiphyte species with high epiphyte affinity (typical epiphytes), richness of liverworts, lichens, mosses and vascular plant species (±standard errors) across all plots in native woodlands (ash or oak) or pure or mixed conifer plantations (NS = Norway spruce, Refor SS = Reforested Sitka spruce, SP = Scots pine). Non-parametric Kruskal-Wallis test results are displayed and indicated in bold where significant. Significant differences in species richness of a particular taxonomic group between forest types are indicated by different letters (pairwise *a posterior* Mann-Whitney tests, α-level < 0.05). Superscript letters refer to changes in such significant differences after adjustment of significance values (sequential Šidák method).

Taxonomic group	Ash		Oak		Pure NS		NS/SP mix		NS/oak mix		Refor SS		*H*	P
N	8		7		9		5		4		5			
Typical epiphytes	17.1±1.67	A	9.3±2.13	C^{AB}	4.1±0.82	B	9.2±2.27	C^{AB}	3.8±0.85	CB^{AB}	6.4±1.44	CB^{AB}	21.6	**<0.001**
Lichens	24.1±2.90	A	19.4±3.20	AC^{AB}	6.4±0.58	B	10.0±2.28	BC^{AB}	6.0±1.08	B^{AB}	7.8±1.59	B	22.7	**<0.001**
Liverworts	5.1±0.52		4.3±0.68		4.2±0.57		4.4±0.25		3.5±0.65		5.6±0.40		8.4	0.14
Mosses	7.3±0.84	A	5.9±0.55	AC^{A}	2.1±0.26	B	4.8±1.20	ABC^{AB}	3.3±0.95	BD^{AB}	4.6±1.40	CD^{AB}	19.7	**0.001**
Vascular plants	2.0±0.76	AB^{A}	3.1±0.46	A	1.0±0.37	B^{A}	1.4±0.68	B^{A}	0.3±0.25	B^{A}	0.2±0.20	B^{A}	16.1	**0.007**
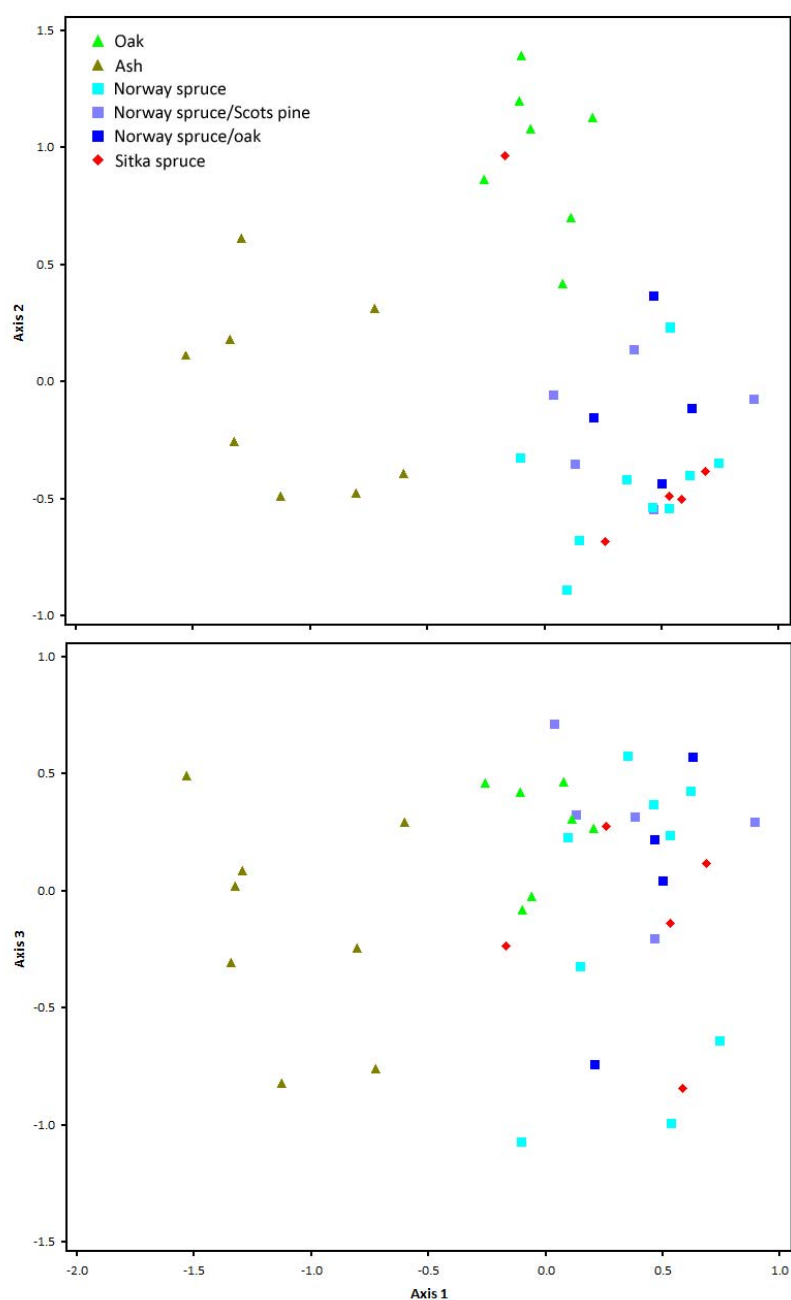
Figure 4.11: Three-dimensional ordination of native woodland sites and sites in pure and mixed conifer plantations. Each data point represents the cumulative canopy epiphyte cover and species assemblage of all eight surveyed plots on an oak, an ash or a spruce tree.

4.2 Ground vegetation

4.2.1 Afforestation and reforestation survey

4.2.1.1 Species richness

A total of 267 ground vegetation species were recorded from both rotations in the 100m^2 plots, comprising 178 vascular plants and 89 bryophytes (Appendix 8 and Smith *et al.*, 2005). Forty four typical woodland species were recorded in afforestation and 58 in reforestation. Unique species recorded in afforestation numbered 113 (of which 14% are typical woodland species) and 31 species were unique to reforestation (38% of which are typical woodland species). There were no red data list species recorded (Curtis and McGough, 1988). *Stachys officinalis* (betony) was recorded in a mature reforestation stand established on old woodland and adjacent to existing woodland. It is on the Flora Protection Order (Anon, 1999b) list and is a 'notable' species (rare species typically found in woodland, or species indicative of long-established woodland) of the 30 listed by Perrin *et al.* (2008a).

Over the afforestation cycle the increase in the Commercially mature stage was to significantly higher levels than Pre-thicket (Table 4.31). There was no significant increase in vascular SR over the afforestation cycle; however, there was an increase in bryophyte SR. The afforestation closed-maturing stage had the lowest SR of the cycle but SR in the re-opening stage was not significantly different to that of the Pre-thicket or Thicket stages. For reforestation there was a decrease in SR to its lowest level in the closed-maturing stage followed by an increase, however, by the Commercially mature stage SR had not significantly increased above the levels found in Pre-thicket. The Commercially mature stage was significantly more species rich than all stages other than Pre-thicket and the closed-maturing had significantly lower SR than all but the re-opening stages. There were significant increases in typical woodland species richness over both afforestation and reforestation. The stages with the significantly highest SR differ between rotations, being the Commercially mature stage in afforestation and both the Pre-thicket and Commercially mature stages in reforestation. Where there was a lack of significant differences in diversity metrics between the same stages of the two rotations some general trends could still be discerned. There was a trend for higher species richness in afforestation than reforestation (only significantly so in closed-maturing stages), except in Pre-thicket, where reforestation had more species than afforestation (non-significant). There were similar trends to that of species richness for vascular and bryophyte species richness but there was only one significant difference between comparable stages of the two rotations; bryophyte SR was significantly higher in closed-maturing afforestation than reforestation. There was significantly higher typical woodland species richness in reforestation Pre-thicket compared to afforestation Pre-thicket but no other comparable stages of the two rotations were significantly different, although there was a trend for higher-values in afforestation. Species turnover (βsim) was generally higher in afforestation than reforestation; significantly so in the Pre-thicket, Thicket and Commercially mature stages. Significant differences in species richness were calculated between afforestation Commercially mature and reforestation Pre-thicket stages to investigate what, if any, changes occur between the two successive rotations. Species richness, bryophyte SR and typical woodland SR were significantly lower in the Pre-thicket reforestation stage than in the afforestation Commercially mature stage.

Table 4.31: Mean (± se) diversity metrics of ground vegetation in each structural stage of afforestation (Affor) and reforestation (Refor). Numbers in brackets after stages are numbers of observations in Affor and Refor respectively. Species richness = SR. Significant differences between groups and within groups tested with non-parametric Mann Whitney (U). Differences between stages in each rotation ($P < 0.05$) indicated with different capital letters before mean value; "*" differences ($P < 0.05$) between the same stage of the two rotations; differences between afforestation Commercially mature and reforestation Pre-thicket a ($P \leq 0.05$), b ($P < 0.001$).

		Pre-thicket (22, 15)	Thicket (18, 15)	Closed-maturing (21, 15)	Re-opening (12, 6)	Commercially mature (17, 9)
Total SR	Affor	[A]23.6 ±2.0	[A]20.8 ± 1.3	[B]12.5 ± 1.4 *	[AB]19.2± 3.4	[C]33.1± 2.6 a
	Refor	[A]28.7 ± 1.9 a	[B]16.3 ± 1.6	[C]8.2 ± 1.2 *	[BC]12.2± 2.1	[A]26.9 ± 2.6
Vascular SR	Affor	[A]19.1 ± 1.5	[B]10.5 ± 1.1	[C]3.7 ± 1.0	[BC]8.0 ± 2.5	[A]19.6 ± 2.2
	Refor	[A]18.3 ± 1.0	[B]7.9 ± 0.9	[C]3.1 ± 0.6	[BC]4.0 ±1.8	[A]15.0 ± 2.9
Bryophyte SR	Affor	[A]4.5 ± 0.9 *	[B]10.3 ± 0.9	[B]8.8 ± 1.1 *	[ABC]11.2 ± 1.7	[C]13.5 ±0.7 a
	Refor	[AC]10.5 ±1.2 * a	[A]8.5 ± 0.9	[B]5.1 ± 0.8 *	[A]8.2 ± 0.8	[C]11.9 ± 1.1
Typical woodland SR	Affor	[A]1.7 ± 0.3 *	[B]6.5 ± 0.4	[B]5.3 ± 0.5	[B]7.9 ± 1.2	[C]12.7 ± 0.9 b
	Refor	[A]6.8 ± 0.7 * b	[A]5.7 ± 0.6	[A]5.1 ± 0.5	[A]6.2 ± 1.1	[B]13.1 ± 1.2
βsim	Affor	[AB]0.4± 0.1 *	[A]0.4±0.1 *	[B]0.3 ± 0.1	[B]0.3 ± 0.1	[B]0.4 ± 0.1 *a
	Refor	[AB]0.3 ± 0.1* a	[A]0.3±0.1 *	[B]0.2 ± 0.1	[AB]0.3 ± 0.1	[AB]0.3 ± 0.1 *

4.2.1.2 Community composition

The varimax rotated NMS ordinations shown in Fig. 4.12 were based on the species composition of the ground vegetation at the site level. The most distinct group was the Pre-thicket afforestation sites, which were clearly separated from all of the other site types along axis 2 (Fig. 4.12). Axis 2 was correlated with canopy cover ($r_s = - 0.631$, $P \leq 0.01$), CWD volume ($r_s = - 0.659$, $P \leq 0. 01$), pH ($r_s = - 0.612$, $P \leq 0. 01$), Ellenberg drainage ($r_s = 0.530$, $P \leq 0. 01$) and elevation ($r_s = - 0.512$, $P \leq 0. 01$). Axis 3 correlated with canopy cover ($r_s = 0.528$, $P \leq 0.01$), CWD volume ($r_s = - 0.384$, $P \leq 0.01$) and area of oldwood ($r_s = 0.356$, ≤ 0.01). Axis 1 correlated with canopy cover ($r_s = - 0.406$ $P \leq 0.01$), CWD volume ($r_s = - 0.659$, $P \leq 0. 05$), LOI ($r_s = -0.501$, $P \leq 0. 01$), Ellenberg fertility ($r_s = 0.530$, $P \leq 0. 01$) and distance to oldwood ($r_s = 0.444$, $P \leq 0. 05$). The afforestation Pre-thicket sites had a higher variability in species composition when compared to reforestation Pre-thicket, shown by the fact that the sites were spread over a larger area in the ordination space. Moreover, although the Pre-thicket stages of the two rotations were widely separated in ordination space, the Commercially mature stages for both rotations were relatively close. Heterogeneity in vegetation composition among sites within a structural stage means that there was extensive overlap among some structural stages. The ordination also showed that reforestation communities were more similar to each other (sites relatively clustered) compared to afforestation communities (sites more spread out). Although the afforestation commerically mature and reforestation Pre-thicket sites appear to ordinate closely within dimension 2 and 3 of the ordination (Fig. 4.12a), they were slightly separated along axis 1 (Fig. 4.12b).
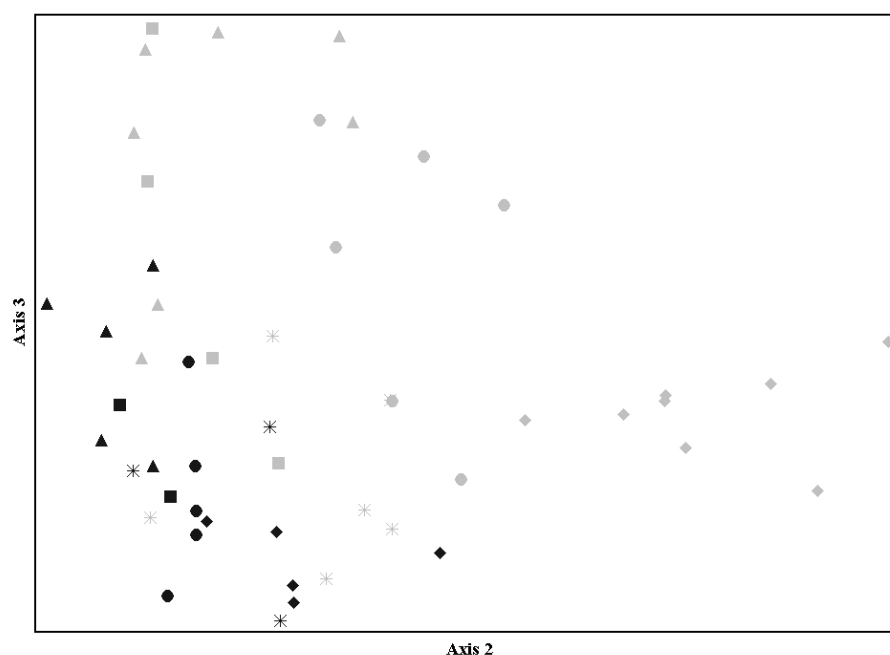
Figure 4.12a: Axes 2 and 3 of varimax rotated NMS ordination of species composition for afforestation (grey symbols) and reforestation (black symbols) sites at different stages of the forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; ✳ Commerically mature. Cumulative variation in the data explained by the ordination is 75.9% with Axis 1 accounting for 11.9%, Axis 2 for 32.3% and Axis 3 for 31.7%. Final stress = 12.09, Final instability = 0.00000.
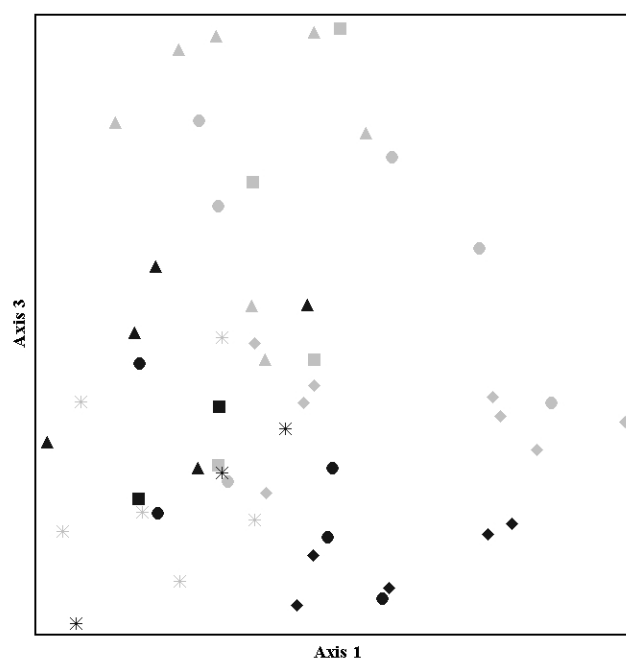
Figure 4.12b: Axes 1 and 3 of varimax rotated NMS ordination of species composition for afforestation (grey symbols) and reforestation (black symbols) sites at different stages of the forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; ✳ Commerically mature. Cumulative variation in the data explained by the ordination is 75.9% with Axis 1 accounting for 11.9%, Axis 2 for 32.3% and Axis 3 for 31.7%. Final stress = 12.09, Final instability = 0.00000.

The ordination also highlights species turnover between afforestation and reforestation rotations as most reforestation stages occupied different areas of the ordination from their corresponding afforestation stage. Species turnover was formally assessed with βsim and, overall, turnover is relatively low between rotations (Table 4.32, inter-rotational values); however, it was highest at earlier stages of the rotations, lowest at re-opening and increased slightly again at Commercially mature stages. βsim was also calculated between the successive stages (in terms of the chronosequence) of each rotation and, for both rotations, higher species turnover occured between earlier stages than at later stages. The difference was more pronounced in afforestation (Table 4.32, intra-rotational values). The highest βsim is between the two successive rotations i.e. between afforestation Pre-thicket and reforestation Commercially mature (0.55). The βsim between rotations i.e. afforestation Commercially mature and reforestation Pre-thicket is relatively low (0.35).

Table 4.32: βsim on a scale representing no species turnover (0) to complete species turnover (1) between stages of rotations. Values in bold and italics are inter-rotational values for the same structural stage and bold, underlined values are intra-rotational values for successive stages within each rotation.

			Reforestation							
			Pre-thicket	**0.4**	Thicket	**0.37**	Closed-maturing	**0.37**	Re-opening	**0.2**	Commercially mature
Afforestation	Pre-thicket		*0.39*		0.45		0.45		0.5		0.55
		0.25									
	Thicket		0.43		*0.35*		0.25		0.25		0.45
		0.36									
	Closed-maturing		0.43		0.43		*0.38*		0.32		0.47
		0.32									
	Re-opening		0.46		0.4		0.29		*0.19*		0.37
		0.04									
	Commercially mature		0.35		0.27		0.27		0.13		*0.28*

4.2.1.3 Structural, environmental and site history variables

Table 4.34 shows some of the structural, environmental and site history variables measured for each stage. Canopy cover was greater in reforestation than afforestation throughout the forest cycle although only significantly so in the Pre-thicket and Commercially mature stages. DBH was significantly greater in reforestation Pre-thicket than afforestation, but by the Thicket stage this difference was non-significant. In the re-opening and Commercially mature stages the difference had switched and the afforestation stands had significantly higher DBH than reforestation. Structural diversity followed a similar trend to that of species diversity over the forest cycle for both rotations - high during early stages, lowest during the closed-maturing stage (but not significantly different in the re-opening stages) and increasing in the Commercially mature stages. For afforestation it increased to levels significantly higher than Pre-thicket but for reforestation the Commercially mature levels were not significantly different to Pre-thicket or Thicket. CWD volume was higher in reforestation compared to afforestation, significantly so in the earlier stages. Reforestation sites had more acidic soils than afforestation; however, the difference between comparable stages was significant only between the early stages. For all stages, except Thicket, afforestation had a higher LOI than reforestation, but the difference was only significant between re-opening stages.

Table 4.34: Mean ±se structural and environmental variables in each structural stage of afforestation (Affor) and reforestation (Refor). Number in brackets after stage is number of observations (n) in Affor and Refor respectively. For pH the median and interquartile range is shown. Proximity to old woodland indicates the number of sites in each stage on/adjacent to old woodland. Significant differences between groups and within groups tested with non-parametric Mann Whitney (U) where applicable. Differences between stages in each rotation (P ≤ 0.05) indicated with different capital letters; "*" differences (P ≤ 0.05) between the same stage of the two rotations; differences between afforestation Commercially mature and reforestation Pre-thicket a (P ≤ 0.05), b (P ≤ 0.001).

		Pre-thicket (22, 15)	Thicket (18, 15)	Closed-maturing (21, 15)	Re-opening (12, 6)	Commercially mature (17, 9)
Canopy cover (%)	Affor	[A]28.9 ± 2.7 *	[BC]78.9±41	[B]86.2±2.4	[C]71.7±5.1	[D]55.0 ± 1.9 *a
	Refor	[A]47.7±3.0 *a	[BC]81.0±3.9	[B]90.0±3.0	[C]0.8 ± 2.7	[C]71.7±4.1 *
DBH (cm)	Affor	[A]3.6 ± 0.3 *	[B]12.7 ±0.6	[C]19.4 ±0.7	[D]24.1±1.0 *	[E]39.3 ± 1.0 *b
	Refor	[A]9.2 ± 1.6 *b	[A]12.8 ±1.7	[B]18.2±1.2	[BC]23.6±3.1 *	[C]26.7 ± 3.2 *
Structural diversity (1/D)	Affor	[A]2.3 ± 0.1 *	[AB]2.2±0.2	[C]1.4 ±0.1	[BC]1.7 ± 0.2	[D]3.1 ± 0.2
	Refor	[A]3.5 ± 0.1 *	[B]2.5 ± 0.2	[C]1.5 ± 0.1	[C]1.9 ± 0.1	[AB]3.0 ± 0.4
CWD volume (m^3/100m^2)	Affor	0.0 ± 0.0	[A]0.2 ± 0.2 *	[B]0.1 ± 0.1 *	[C]0.2 ± 0.2	[BC]0.3 ± 0.1
	Refor	[A]0.3 ± 0.1	[A]0.3 ± 0.1 *	[B]0.6 ± 0.1 *	[AB]0.3 ± 0.1	[AB]0.4 ± 0.1
Soil pH	Affor	[A]5.1 ± 1.9 *	[A]5.1 ± 0.8 *	[B]4.4 ± 1.3	[B]4.2 ± 0.2	[B]4.5 ± 0.4
	Refor	[A]4.2 ± 0.9 *	[A]4.0 ±0.5 *	[A]4.3 ± 0.4	[A]4.1 ± 0.7	[A]4.3 ± 0.9
LOI (%)	Affor	[AB]43.5 ± 7.5	[AB]35.7±6.9	[AB]31.5±5.0	[A]48.5±9.8*	[B]24.2± 3.3
	Refor	[AB]33.8±7.2	[B]40.6±7.1	[AB]25.8±4.3	[A]14.8±2.2 *	[A]16.9±3.6
Ellenberg moisture (F)	Affor	[A]6.4 ±0.2 *	[AB]6.2±0.2	[BC]5.9±0.2	[C]5.8±0.2	[C]5.8±0.1
	Refor	[A]5.8±0.1 *	[A]6.0± 0.1	[A]5.9±0.1	[A]5.7 ±0.3	[A]5.8 ±0.2
Ellenberg nitrogen (N)	Affor	[AB]4.2 ±0.3	[AB]4.2±0.3	[AB]4.0±0.2	[A]3.7±0.2 *	[B]4.4±0.2 a
	Refor	[AB]3.7±0.3 a	[A]3.8±0.2	[AB]4.2±0.2	[AB]4.4±0.1 *	[B]4.3±0.1
Distance to old woodland (m)	Affor	[AB]550.1± 80.4	[A]775.3± 51.9	[BC]414.7± 86.4	[ABC]513.3±147.2	[C]194.4± 35.0 a
	Refor	[A]729.9 ±104.1 a	[A]785.7± 56.6	[A]562.1± 104.9	[B]67.7± 29.8	[AB]522.4± 144.9
Proximity to old woodland	Affor	0	0	1	1	2
	Refor	1	0	1	1	1 ‡

Ellenberg indicator-values for moisture (F) indicate that afforestation Pre-thicket sites were significantly wetter than reforestation Pre-thicket with no significant difference between any other stage of rotations. Ellenberg indicator-values for soil nitrogen (N) suggest that fertility was significantly higher in the reforestation than afforestation re-opening stage but there was no significant difference for any other stage. In terms of the differences between the end of the first and beginning of the second rotation (afforestation Commercially mature and reforestation Pre-thicket) values for Ellenberg N were significantly different. Of the reforestation sites, one re-opening and one Commercially mature site were on areas that

had been old woodland. That these sites were old woodland in at least 1900 and that they were, at the time of survey, nearing the end of their second rotation indicates that these sites may have been woodland directly prior to afforestation. One Commercially mature afforestation site was scrub prior to planting. For afforestation sites in the closed-maturing to Commercially mature stages and for reforestation sites in the re-opening and Commercially mature stage there were sites established on areas that had been old woodland. Distance to old woodland showed no significant differences between rotations. Previous land use of afforestation sites by proportion in each rotation was 57.6% grassland or rough grazing, 39.6% unknown and 2.8% scrub and of reforestation sites (before afforestation) 92.8% grassland or rough grazing and 7.2% bog/heath. There were significant differences in stand age between rotations in two stages; Thicket (afforestation 10.7 ± 0.33, reforestation 13 ± 0.51, P ≤ 0.01) and Commercially mature (afforestation 42.2 ± 1.0, reforestation 36 ± 0.29, P ≤ 0.001) with some afforestation Commercially mature sites up to 10 years older than reforestation Commercially mature sites.

4.2.1.4 Drivers of diversity

Correlation analysis was carried out between species richness and typical woodland species richness and environmental variables not included in the models for each rotation. Only significant correlations (P < 0.05) are reported. For both rotations FWD & needle cover was negatively correlated with species richness (afforestation; r_s = - 0.52, P ≤ 0.001: reforestation; r_s = - 0.74, P ≤ 0.001). Large complex brash piles (only found in reforestation Pre-thicket stages) were significantly positively correlated with species richness (r_s = 0.55, P ≤ 0.01) and with bryophyte species richness (r_s = 0.54, P ≤ 0.05) for reforestation. In afforestation Ellenberg N was positively correlated (r_s = 0.30, P ≤ 0.01) with species richness and elevation was negatively correlated (r_s = - 0.27, P ≤ 0.05). Correlations with typical woodland species richness were leaf litter (afforestation; r_s = - 0.41, P ≤ 0.001), elevation (afforestation; r_s = 0.29, P > 0.01), distance to oldwood (afforestation; r_s = 0.26, P ≤ 0.05) and FWD & needle cover (reforestation; r_s = -0.30, P ≤ 0.05). Multimodel inference resulted in a set of two models for total species richness (Table 4.35). Canopy cover, rotation, CWD volume, structural diversity and the canopy cover: CWD volume interaction were the relatively most important predictors from this set of models, while pH was the relatively least important as it was a fixed term in the model set. Age did not appear in the model set.

Table 4.35: Akaike weights for the set of two models selected within 2 units of the lowest AIC*c* for total species richness and the relative importance (R.I.) for each variable and interaction term.

	1	2	R.I.
Canopy cover	X	X	1
CWD volume	X	X	1
Canopy cover : CWD volume	X	X	1
Structural diversity	X	X	1
Rotation	X	X	1
pH	X		0.58
Akaike weight (ωi)	0.58	0.42	

The averaged model parameters predicted lower species richness in reforestation compared to afforestation. pH had a negative average model parameter so higher species richness in the more acidic sites was predicted. The interaction term canopy cover:CWD volume was investigated further and showed that, for all volumes of CWD, an increase in canopy cover was associated with a decrease in total species richness. However, the association between CWD volume and total species richness changed at differing

values of canopy cover. There was a positive association between total species richness and CWD volume at low canopy covers (< 40%) and at canopy covers of 60-70%. However, at intermediate (40-55%) and high (> 70%) canopy covers there was a negative association between CWD volume and species richness.

Multimodel inference resulted in a set of three models for typical woodland species richness (Table 4.36). Canopy cover, DBH, and structural diversity were the relatively most important predictors from this set of models, while Ellenberg nitrogen (N) and pH were relatively less important. Rotation, proximity to old woodland, LOI or Ellenberg moisture (F) did not appear in the model set.

Table 4.36: Akaike weights for the set of three models selected within 2 units of the lowest AICc for mean typical woodland species richness and the relative importance (R.I.) for each variable.

	1	2	3	R.I.
Canopy cover	X	X	X	1.00
DBH	X	X	X	1.00
Structural diversity	X	X	X	1.00
Ellenberg nitrogen (N)		X		0.29
pH			X	0.21
Akaike weight (ωi)	0.50	0.29	0.21	

The averaged model parameters and pair plot results showed a positive non-linear association between mean typical woodland species richness and canopy cover (up to approximately 60% it was positively associated but at higher-values the relationship was negative). The associations between typical woodland species richness and both DBH and structural diversity were also positively linear. There was a negative non-linear association between typical woodland species richness and pH and Ellenberg nitrogen.

4.2.2 Mixed tree species survey

4.2.2.1 Species richness

A total of 189 ground flora species were recorded in the 100m^2 plots, comprising 153 vascular plant, 31 bryophyte and 2 lichen species (Appendix 8). Due to the low occurrence of lichens in this study, non-vascular richness and cover are equivalent to bryophyte richness and cover. There were no species recorded from the vascular plant red data list (Curtis and McGough, 1988) or the Flora Protection Order (Anon, 1999a) and no non-vascular species that are listed as rare in Holyoak (2003). However, two 'notable' species (defined as a rare species typically found in woodland or a species indicative of long-established woodland) of the 30 listed by Perrin *et al.* (2008a) were found. *Prunus padus* (bird cherry) and *Carex strigosa* (thin-spiked wood-sedge) were found in a Norway spruce/Scots pine mix plantation established in an area that was previously old woodland. Over 32% of vascular plant and 31% of non-vascular species were recorded only once, as were the two lichen species, *Cladonia coniocraea* and *Lepraria incana*. The vast majority of non-vascular species were recorded as having less than 1% cover, with only 6 species recorded with cover greater than 5%. Almost 50% of non-vascular species recorded in this survey were growing on deadwood.

There were no significant differences in species richness metrics between the three forest types (Table 4.37). However, a trend is evident with Scots pine mixes and pure sites having almost equal species richness, while the oak mixes have the lowest species richness (except non-vascular richness where they have the highest). From Table 4.37 we see that for all forest types the majority of vascular species were competitors and stress tolerant, with ruderal numbers the lowest, and there were no significant differences in strategies of plants between the three forest types.

Table 4.37: Mean diversity metrics (SR - species richness) ± standard error. No significant differences (P ≤ 0.05) were found between forest types with Kruskal-Wallis non-parametric test.

	Norway spruce/ Scots pine (n=15)	Norway spruce/oak (n=15)	Pure Norway spruce (n=30)
Diversity metrics			
Total SR	24.3 ± 2.2	22.1 ± 1.3	24.8 ± 2.1
Vascular SR	14.7 ± 2.2	12 ± 1.2	14.9 ± 2
Non-vascular SR	9.6 ± 0.8	10.1 ± 0.8	9.9 ± 0.6
Typical woodland SR	14.6 ± 1.3	12.2 ± 0.8	13.2 ± 1
Competitor SR	13.9 ± 2.1	11.4 ± 1.1	14.1 ± 1.9
Stress tolerant SR	13.8 ± 2.0	10.7 ± 1.1	13.3 ± 1.7
Ruderal SR	6.9 ± 1.4	5.7 ± 0.8	7.5 ± 1.3

4.2.2.2 Structural and environmental variables

There were few significant differences in the mean structural, geographic, functional and compositional attributes of species among forest types although there were some ecologically relevant relationships highlighted (Table 4.38).

Canopy openness was significantly greater in the Scots pine mixes than other two forest types and was lowest in the oak mixes. Canopy cover was divided up into that of Norway spruce and of the mix component (Scots pine or oak) and the canopy cover of Norway spruce was significantly greater in the Scots pine mix than the oak mix. There was significantly higher cover of the oak in the oak mix than there was of Scots pine in the Scots pine mix. The DBH of Norway spruce was lowest in the Scots pine mixes and, not surprisingly, highest in the pure sites and. The DBH of the mix species was significantly lower in the oak mixes than in the Scots pine mixes. Although there were no significant differences in structural diversity between the forest types, there were between covers of certain vegetation layers e.g. the Scots pine mix had the highest vascular, non-vascular and understorey covers. Oak in the oak mixes undoubtedly added to the stand's structural diversity as it was present as understorey, however, it was included in calculations for structural diversity as part of the canopy as it was planted. There was a large variation between the forest types in the distance to and percentage of sites on/adjacent to old woodland. None of the forest types differed significantly in terms of soil variables. CWD cover was significantly lower in pure sites than in the oak mixes. There were no significant differences in brash pile, FWD or needle litter covers between the forest types although, from field observations, more recent thinning had been carried out in the Scots pine mixes and pure sites than in the oak mixes.

Table 4.38: Mean values ± standard error of structural, geographic, functional and compositional variables for the three forest types (exception pH, median ± interquartile range). Significance tested with non-parametric Kruskal-Wallis test followed by Mann Whitney (U) post hoc test.Values for variable are significantly different (P ≤ 0.05) between the forest types if indicated by a different letter. All variables are from 100 m^2 plots.

Variable (unit)	Norway spruce/ Scots pine (n=15)	Norway spruce/ oak (n=15)	Pure Norway spruce (n=30)
Structural			
Canopy openness (%)	8.0 ± 0.9^A	4.5 ± 0.5^B	6.3 ± 0.8^B
Canopy cover main (%)	60.0 ± 4.4^A	55.7 ± 5.1^B	80.0 ± 1.7^C
Canopy cover mix (%)	10.4 ± 1.7^A	24.7 ± 4.6^B	n/a
DBH main species (cm)	27.2 ± 2.1^A	36.4 ± 1.7^B	28.6 ± 1.2^C
DBH mix species (cm)	18.2 ± 2.5^A	15.4 ± 1.2^B	n/a
Ratio of mix to main	0.5 ± 0.1^A	0.1 ±0.3^B	n/a
Planted tree density (no./100m^2)	10.5 ± 1.4	7.5 ± 0.6	9.8 ± 0.9
Structural diversity (1/D)	3.0 ± 0.3	2.4 ± 0.2	2.3 ± 0.2
Understorey cover (%)	5.0 ± 2.0^A	0.4 ± 0.2^B	0.4 ± 0.2^B
Compositional			
Vascular cover	52.9 ± 11.5 ^{A}	27.1 ± 7.3 ^{B}	28.7 ± 10.0 ^{A}
Non-vascular cover	65.7 ± 6.2 ^{A}	45.0 ± 5.8 ^{B}	43.7 ±5.7 ^{B}
Geographic			
Distance to old woodland (m)	425.3 ± 98.2	643.8 ± 114.4	326.2 ± 68.8
On/adjacent to old woodland (% sites)	10.0	30.0	60.0
Functional			
Soil pH	4.2 ± 1.4	4.1 ± 0.8	4.3 ± 0.7
Ellenberg N (fertility)	4.9 ± 0.1	4.7 ± 0.2	4.7 ± 0.1
CWD cover	3 ± 0.4^{AB}	3.4 ± 0.4^A	2.4 ± 0.3^B
Brash piles (%)	3.9 ± 1.8	1.3 ± 1.1	4.0 ± 1.1
FWD (%)	21.3 ± 4.1	21.0 ± 2.3	18.2 ± 2.4
Needle cover (%)	31.1 ± 5.9	36.0 ± 6.2	49.6 ± 5.7

4.2.2.3 Community composition

The varimax rotated NMS ordination shown in Fig. 4.13 is based on the species composition of the ground vegetation and shows the differences among sites; however, there was no separation of any one forest type in ordination space, indicating that the forest types did not support substantially different communities. Two pure Norway spruce sites that separated out from other sites (positioned at the bottom of axis 3) were notable for their low total and typical woodland species richness and low canopy openness and high needle litter cover. The ordination shows several geographically close sites occurring very close in ordination space highlighting the similarities in communities between these mixed and pure sites. The joint plots superimposed on the ordination highlighted the correlations of environmental and structural variables with the axes. Axis 3 mainly represented a strong gradient in Ellenberg N (fertility) and structural diversity values with a weaker gradient in needle litter cover while axis 2 represented weaker gradients in structural diversity and needle litter cover.

MRPP analysis using forest type as the defining factor was carried out to help interpret the NMS results. There were no significant differences found overall or pairwise among the forest types (P > 0.05) at the site level.
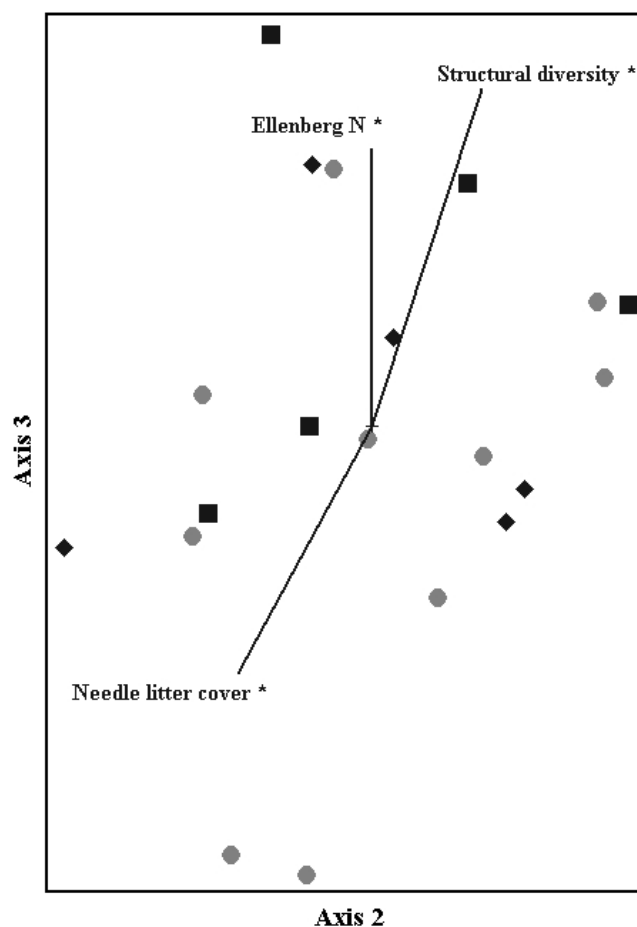
Figure 4.13: Axes 2 and 3 of the varimax rotated NMS ordination of ground vegetation species composition for Norway Spruce / oak mixes ♦, Norway Spruce / Scots pine mixes ■ and pure Norway spruce sites ●. Joint plot superimposed on ordination highlighting the relationship between sites (ordination scores) and environmental variables: * Pearson's coefficient significant at < 0.05 level. Cumulative variation in the data explained by the ordination is 88.3% with Axis 3 accounting for 60.8%, Axis 2 for 14.4% and Axis 1 for 13.1%. Final stress = 9.6, Final instability = 0.00000.

4.2.2.4 Structural and functional diversity indicators

Canopy openness was positively associated with total and vascular richness (Table 4.39) while structural diversity was significantly positively correlated with all diversity metrics with the exception of non-vascular SR. High planted tree density and distance to old woodland were strongly negatively correlated with all species metrics with the exception of non-vascular SR. Brash pile cover was positively associated with vascular SR whereas FWD and needle cover were negatively associated with all species metrics, with the exception of non-vascular SR, and with each other (r_s = 0.528, P ≤ 0.01). None of the variables tested were significantly correlated with non-vascular SR.

Table 4.39: Significant Spearman's (r_s) correlations between mean diversity metrics and measured variables for all forest types (n = 60). * indicates significance at P ≤ 0.05, ** P ≤ 0.01. "–" indicates correlation is negative.

	Total SR	Vascular SR	Non-vascular SR	Typical woodland SR
Structural				
Canopy openness (%)	0.386*	0.455**		
Structural diversity (1/D)	0.685**	0.740**		0.640**
Planted tree density (no./100m^2)	-0.491**	-0.613**		-0.522**
Geographic				
Distance to old woodland (m)	-0.396**	-0.486**		-0.454**
Functional				
Brash piles (%)		0.325*		
FWD (%)	-0.570**	-0.612**		-0.590**
Needle litter (%)	-0.387**	-0.459**		-0.407**

Spearman's correlation significance: *P ≤ 0.05; **P ≤ 0.01. *r* = 1.0.

4.2.3 Native woodlands survey

4.2.3.1 Species richness and vegetation communities

A total of 227 species was recorded in the survey, 125 vascular plants and 102 non-vascular plants (Appendix 8). No species listed in the Red Data Book for vascular plants (Curtis and McGough, 1988), in the Vegetation Protection Order (Anon, 1999a), or bryophytes listed as rare in Holyoak (2003) were found at the sites. However, two of the 30 'notable' species listed by Perrin *et al.* (2008a), that is, rare species typically found in woodland, or species which are indicative of long-established woodland, were found in four of the ash woodland sites: *Melica uniflora* in one site and *Anemone nemorosa* in four. A total of 110 species was recorded in the oak woodlands and 186 in the ash woodlands, with 41 species only recorded in the oak woodlands and 121 species only in the ash woodlands. Total species richness ranged from 16.3 to 61.3 species per site with a mean of 33.9 (± 2.7se).

Of the species recorded, 27 were classified as having a low affinity for woodland, 117 a moderate affinity and 81 a high affinity. Two species identified to genus only could not be classified. In the oak sites, only 5.7% of species had a low affinity for woodland, while 59.4% had a moderate and 34.9% a high affinity. In the ash sites 12.5% of species had a low affinity for woodland, while 48.4% had a moderate and 39.1% a high affinity.

Flexible beta cluster analysis of the plots using the vegetation species covers indicated the difference in vegetation communities between the oak and ash woodlands (Figure 4.14). Ash woodlands were significantly more species rich and diverse than oak woodlands (Table 4.40). Structurally, ash woodlands were more diverse in their vegetation layers and the presence of a substantial understorey, mainly of *Corylus avellana*, resulted in significantly more trees with a smaller DBH on average and significantly lower canopy openness (Table 4.40). Oak woodland plots had substantial cover of leaf litter, significantly higher than the ash woodlands, and had significantly less bare ground. Ash woodlands had significantly more deadwood in the form of both fine and coarse woody debris. In terms of soil chemistry, ash woodlands had significantly higher pH, total nitrogen, total phosphorus and C/N ratio and significantly

lower LOI than oak woodlands. The proportion of plots with presence of grazing and poorly drained soils was higher in ash woodlands.

Table 4.40: Values of various diversity metrics, structural and functional variables (mean ± standard error, with the exception of pH – median ± interquartile range) for the ground vegetation plots in native oak and ash woodlands. Those variables with significantly different values for oak and ash (P ≤ 0.05) are indicated by a different letter.

	Oak	Ash
Diversity		
Total SR	26.5± 1.4[A]	41.3± 2.3[B]
Vascular SR	13.7± 0.7[A]	26.0± 1.7[B]
Non-vascular SR	12.7± 0.8[A]	15.3± 0.8[B]
Species diversity (1/D)	4.5± 0.3[A]	7.3± 0.4[B]
Typical woodland SR	14.7± 0.5[A]	25.5± 1.1[B]
Structural & Functional		
Structural diversity (1/D)	3.0± 0.1[A]	3.7± 0.1[B]
No. of Trees (No./100m^2)	12.9± 1.8[A]	24.0± 2.1[B]
Average DBH (cm)	22.8± 2.5[A]	11.9± 0.6[B]
Canopy Openness (%)	6.1± 0.6[A]	3.7± 0.4[B]
Bare soil (%)	0.6± 0.2[A]	1.9± 0.5[B]
Leaf Litter (%)	75.8± 3.4[A]	28.7± 3.0[B]
FWD cover (%)	5.1± 0.9[A]	8.9± 1.0[B]
CWD volume (m^3/100m^2)	0.18± 0.03[A]	0.54± 0.10[B]
Soil pH	4.0± 0.6[A]	6.1± 1.5[B]
Total N (g/l)	3.34± 0.14[A]	4.35±0.25[B]
Total P (g/l)	0.31± 0.03[A]	0.48± 0.04[B]
LOI (%)	30.9± 3.9[A]	19.8± 1.9[B]
C/N Ratio	22.2± 0.6[A]	15.3± 0.3[B]
Grazing‡	*40.0*	*50.0*
Poorly drained soils‡	*20.0*	*30.0*

‡Presence/absence variables: percentage of sites in each group with presence of the variables indicated

Owing to the obvious differences between them, cluster and indicator species analysis was carried out separately for the oak and ash plots. This analysis suggested a four cluster solution was the optimum for the oak plots and these clusters are indicated on the cluster dendrogram (Fig. 4.14). The significant indicator species for each cluster are shown in Table 4.41. In many cases, plots from the same site did not cluster together, indicating the amount of variation in vegetation composition within, as well as among, sites.
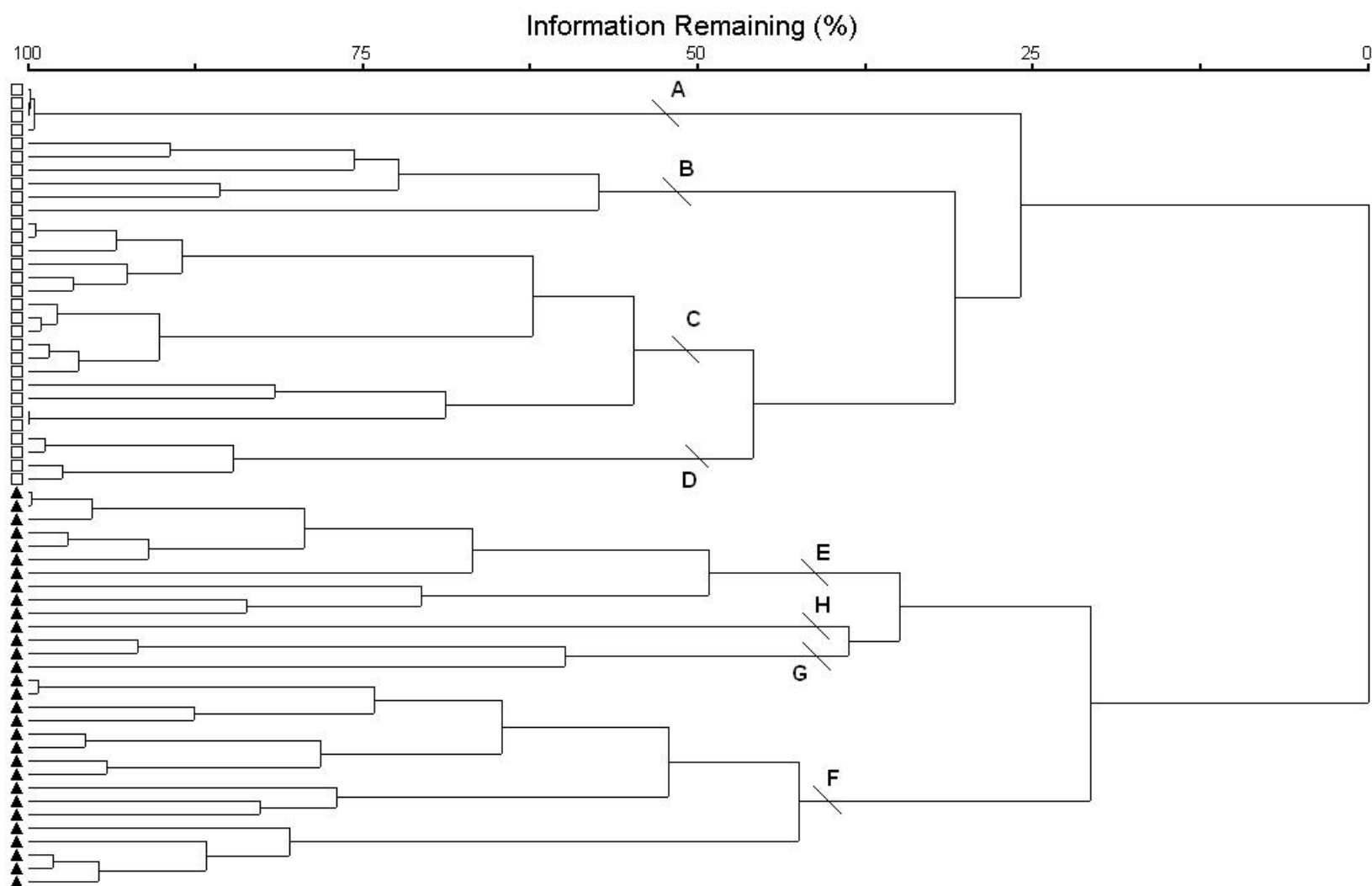
Figure 4.14: Dendrogram from the flexible beta cluster analysis of the ground vegetation communities of the native oak □ and ash ▲ woodland plots. Letters A-H indicate the eight cluster groups formed from the separate analysis of oak and ash plots.

Table 4.41: Significant indicator species for the ground vegetation native oak plot cluster groups. Cluster groups are indicated by letters. Indicator-values greater than 25 for each species are highlighted in bold.

Species	A	B	C	D
Luzula sylvatica	**81**	4	10	0
Dicranum bonjeanii	**75**	0	0	0
Dicranum scoparium	**56**	6	2	4
Cladonia chlorophaea	**50**	0	0	0
Ulota crispa s.l.	**50**	0	0	0
Athyrium filix-femina	**44**	0	1	0
Quercus petraea	**30**	17	**27**	**26**
Polytrichastrum formosum	0	**64**	13	13
Thuidium tamariscinum	1	**60**	14	23
Betula pubescens	0	**57**	6	13
Frullania tamarisci	4	**50**	7	0
Plagiothecium undulatum	4	**50**	7	0
Hedera helix	0	23	**70**	4
Dryopteris affinis	0	0	**56**	0
Ilex aquifolium	1	**38**	**52**	9
Rubus fruticosus agg.	1	2	9	**86**
Oxalis acetosella	2	9	4	**77**
Holcus mollis	0	0	0	**50**
Stellaria holostea	0	12	0	**46**

Cluster A contains four plots in which *Luzula sylvatica* almost completely dominated the field layer. Non-vascular species had low cover and were mainly confined to deadwood. This cluster had the lowest total, vascular and typical woodland species richness and diversity and had significantly lower structural diversity than all other clusters due to the dominance of the canopy and field layers (Table 4.42). Trees in the plots were large and few in number and canopy openness was high. Leaf litter cover in the plots was also high and grazing was absent. None of the plots were on poorly drained soils. Cluster B contains six plots which had higher *Betula pubescens* cover and lower oak cover than the other plots. This was the only cluster for which *Quercus petraea* was not a good indicator species. This cluster had the highest total, vascular, non-vascular and typical woodland species richness and the highest species diversity and structural diversity of all the clusters (Table 4.42). Trees were small on average and canopy openness was relatively high, while leaf litter cover was relatively low and little CWD was present. Grazing was present in half the plots in the cluster and one third of plots had poorly drained soils. Cluster C contains 16 plots which had high *Ilex aquifolium* cover. *Hedera helix* was also common and often occurred with high cover. In a couple of the plots, *Vaccinium myrtillus* was dominant in place of *I. aquifolium*. Species richness was moderate but typical woodland species richness was relatively high. This cluster had one of the least open canopies and a relatively low structural diversity. Leaf litter cover was also high and grazing was present in slightly less than half the plots. Few plots were on poorly drained soils. Cluster D contains four plots which had high *Rubus fruticosus* cover. There were no bryophyte or lichen indicators for this group and non-vascular species richness was the lowest of all clusters, with total and typical woodland species richness also relatively low. Canopy openness in this cluster was also low. Grazing was present in half the plots and none occurred on poorly drained soils.

For the ash plots, cluster and indicator species analysis suggested four clusters were the optimum. These clusters are indicated on the cluster dendrogram (Fig. 4.14). As one cluster contained a single plot, indicator species could not be calculated. The indicator species for each of the remaining three clusters are shown in Table 4.43.

Cluster E contains ten plots which had a dense understorey, mainly of *Corylus avellana*. Total species richness, and vascular and non-vascular richness and species diversity in this cluster were the highest of all clusters and a high number of typical woodland species were supported (Table 4.42). The dense understorey meant that canopy openness was low, but structural diversity remained high. Bare soil cover was relatively high and resulted from grazing by large herbivores in the plots in combination with poorly drained soils. Cluster F contains 16 plots from five sites which had abundant *Hedera helix* and *Thamnobryum alopecurum*. The *C. avellana* understorey was also substantial and *Q. petraea* occurred in the canopy. Species richness was the lowest of all three ash clusters but was still relatively high. Canopy openness was low but, again, structural diversity remained high. CWD volume was the highest of the three ash clusters. Grazing was only present in a few plots and none of the plots were on poorly drained soils. Cluster G contained three plots from a single site which had a non-native element, notably *Acer pseudoplatanus* with occasional *Fagus sylvatica*. Total species richness was high but non-vascular species richness was the lowest of the ash clusters, as was species diversity. Structural diversity was also the lowest but was still relatively high. Cover of bare soil was high - an indication of grazing by cattle. The amount of deadwood was low. Soil pH was significantly more acid than the other ash clusters and total phosphorus and organic matter content were significantly higher: however the C/N ratio was not significantly different. None of the plots occurred on poorly drained soils. The remaining plot, which formed cluster H, was exceptional in its very low canopy cover which, in combination with a low understorey cover, made it a very open plot. It was the most species rich and diverse plot studied and had the highest structural diversity. The high CWD volume was as a result of a number of fallen dead trees in the plot which had opened up a canopy gap. Total nitrogen and phosphorous levels were high and the C/N ratio was relatively low.

Table 4.42: Values of diversity metrics and structural and functional variables (mean ± standard error, with the exception of pH – median ± interquartile range) for the four native oak (A-D) and three native ash ground vegetation plot cluster groups (E-G) and the values for the single plot ash cluster (H). Values for each variable are significantly different between the cluster groups for oak (lowercase) or ash (uppercase) if indicated by a different letter.

Forest type	Oak				Ash			
Cluster group	A	B	C	D	E	F	G	H
n	4	6	16	4	10	16	3	1
Diversity								
Total SR	21.5^a ± 1.7	34.7^b ± 2.2	25.8^a ± 1.8	22.0^{ab} ± 3.5	52.2^A ± 3.0	33.0^B ± 1.5	38.7^B ± 3.9	72.0
Vascular SR	10.5^a ± 1.4	17.2^b ±1.4	13.7^{ab} ± 0.8	12.0^{ab} ± 0.8	34.8^A ± 2.1	19.1^B ± 1.0	26.7^A ± 3.2	46.0
Non-Vascular SR	11.0^a ± 0.7	17.5^b ± 1.2	12.1^a ± 1.1	10.0^a ± 2.9	17.4^A ± 1.2	13.9^B ± 0.7	12.0^B ± 1.2	26.0
Species diversity (1/D)	2.7^a ± 0.1	7.0^b ± 0.3	4.1^c ± 0.3	4.4^{abc} ± 0.6	7.9^A ± 0.9	6.9^A ± 0.4	6.0^A ± 0.7	10.2
Typical woodland SR	12.8^a ±1.3	16.2^a ± 0.9	15.1^a ± 0.6	13.3^a ± 1.7	30.4^A ±1.9	22.4^B ± 1.1	23.3^{AB}± 1.2	33.0
Structural & Functional								
CWD volume (m^3/100m^2)	0.21^a ± 0.07	0.08^a ± 0.05	0.20^a ± 0.04	0.24^a ± 0.08	0.49^A ± 0.17	0.60^A ± 0.13	0.21^A ± 0.16	1.08
Structural diversity (1/D)	2.21^a ±0.08	3.68^c ± 0.20	2.90^b ± 0.12	3.25^{bc} ± 0.28	3.74^A ± 0.13	3.79^A ± 0.08	3.06^A ± 0.29	4.06
No. of Trees (No./100m^2)	4.0^a ± 1.8	13.7^a ± 2.8	14.9^a ± 3.0	12.5^a ± 1.2	25.1^A ± 2.7	25.6^A ± 3.4	15.0^A ± 3.8	14.0
Average DBH (cm)	39.7^a ± 8.4	16.7^a ± 2.4	21.7^a ± 3.6	19.1^a ± 1.3	11.1^A ± 0.7	11.9^A ± 1.0	14.7^A ± 1.3	10.0
Canopy openness (%)	10.7^a ± 1.0	7.5^{ab} ± 1.5	4.7^b ± 0.6	4.7^{ab} ± 0.6	3.0^A ± 0.2	3.5^A ± 0.4	4.9^A ± 1.1	9.79
Bare soil (%)	0.0^a ± 0.0	0.9^a ± 0.8	0.4^a ± 0.2	1.5^a ± 0.9	3.6^A ± 1.2	0.6^B ± 0.2	2.8^B ± 1.3	3.0
Leaf Litter (%)	87.5^a ± 1.4	50.8^b ± 7.4	81.9^a ± 3.3	77.5^{ab} ± 7.2	28.5^A ± 4.2	30.0^A ± 4.2	26.7^A ± 16.9	15.0
FWD Cover (%)	0.5^a ± 0.0	4.8^{ab} ± 1.8	5.6^b ± 1.2	7.8^b ± 2.9	8.1^A ± 1.4	11.1^{AB} ± 1.2	2.0^B ± 1.5	3.0
Soil pH	3.8^a ± 0.9	3.8^a ± 0.3	4.2^a ± 0.5	4.2^a ± 0.7	5.5^A± 1.3	6.3^A ± 1.0	4.6^B ± 0.0	6.5
Total N (g/l)	3.21^a ± 0.19	3.64^a ± 0.20	3.28^a± 0.24	3.23^a ± 0.09	4.06^A ± 0.24	4.23^A ± 0.41	5.30^A ± 0.05	6.45
Total P (g/l)	0.41^a ± 0.12	0.24^a ± 0.04	0.28^a ± 0.05	0.42^a ± 0.02	0.35^A ± 0.02	0.49^A ± 0.05	0.74^B± 0.02	0.85
C/N	23.0^a ± 1.6	22.6^a ± 1.4	22.5^a ± 0.9	19.3^a ± 0.4	15.9^A ± 0.4	15.0^A ± 0.5	15.0^A ± 0.3	12.6
LOI (%)	25.0^a± 5.2	44.7^a± 11.4	30.9^a± 5.4	16.3^a± 1.1	19.4^A± 3.4	18.3^A± 2.9	26.7^B± 0.67	28.0
Grazing‡	*0.0*	*50.0*	*43.8*	*50.0*	*100.0*	*6.3*	*100.0*	*100.0*
Poorly drained soils‡	*0.0*	*33.3*	*18.8*	*0.0*	*90.0*	*0.0*	*0.0*	*0.0*

‡Presence/absence variables: percentage of sites in each group with presence of the variables indicated

Table 4.43: Significant indicator species for the ground vegetation native ash plot cluster groups. Cluster groups are indicated by letters. Indicator-values greater than 25 for each species are highlighted in bold.

Species	E	F	G
Geranium robertianum	**94**	0	3
Primula vulgaris	**84**	1	0
Geum urbanum	**82**	9	0
Deschampsia caespitosa	**80**	0	0
Hookeria lucens	**70**	2	0
Carex sylvatica	**67**	3	3
Fissidens taxifolius	**64**	1	0
Carex remota	**59**	0	0
Salix cinerea	**57**	1	0
Thuidium tamariscinum	**56**	**30**	14
Corylus avellana	**54**	**35**	10
Brachypodium sylvaticum	**50**	2	0
Fragaria vesca	**48**	0	0
Blechnum spicant	**40**	0	0
Neckera complanata	2	**91**	0
Thamnobryum alopecurum	1	**88**	9
Hedera helix	**26**	**71**	1
Dryopteris affinis	4	**65**	8
Euonymus europaeus	0	**55**	0
Arum maculatum	9	**54**	0
Quercus petraea	0	**50**	0
Poa trivialis	1	0	**98**
Veronica montana	4	0	**92**
Dryopteris filix-mas	2	1	**90**
Hyacinthoides non-scripta	3	1	**89**
Veronica chamaedrys	9	1	**84**
Rhytidiadelphus loreus	1	3	**78**
Acer pseudoplatanus	2	16	**69**
Veronica officinalis	0	0	**67**
Lysimachia nemorea	2	0	**64**
Glechoma hederacea	0	1	**63**
Ranunculus repens	2	0	**61**
Cardamine flexuosus	1	0	**58**
Epilobium montanum	1	0	**58**
Eurhynchium striatum	**26**	16	**58**

4.2.3.2 Relationship between structural and functional variables and diversity measures

For the oak plots, correlation analysis identified leaf litter cover and structural diversity as having significant correlations with the diversity measures. Leaf litter was strongly negatively correlated with all of the diversity measures and structural diversity positively correlated with all but vascular species richness (Table 4.44). Deadwood variables were also correlated with the diversity measures, with CWD volume negatively correlated with both total and vascular species richness and FWD cover positively correlated

with species diversity (1/D). Soil chemistry was also found to be important, with soil pH and total phosphorus negatively correlated with non-vascular species richness. Average DBH was negatively correlated with species diversity (1/D). Occurrence on poorly drained soils resulted in significantly higher total and vascular species richness and the presence of grazing led to significantly higher species diversity (1/D) and typical woodland species richness.

Table 4.44: Relationships between the ground vegetation native oak plot diversity measures and various structural and functional variables calculated with a) Spearman's correlations for continuous variables and b) Mann Whitney U tests for presence/absence variables. Only significant (P ≤ 0.05) results are shown with the variables ordered from highest to lowest r-value and U-value respectively and the direction of the relationship indicated with + or –.

Total SR	Vascular SR	Non-vascular SR	Species diversity (1/D)	Typical woodland SR
a)				
- Leaf litter***	- Leaf litter**	- Leaf litter***	+ Structural 1/D***	- Leaf litter**
+ Structural 1/D**	-CWD Vol. **	- pH**	- Leaf litter***	+ Structural 1/D*
- CWD Vol.*		+ Structural 1/D**	+FWD Cover*	
		-Total P*	-Average DBH*	
b)				
+Poorly drained*	+Poorly drained*		+Grazed*	+Grazed*

Significance: * P ≤ 0.05; ** P ≤ 0.01; ***P ≤ 0.001

For the ash plots, bare soil and the cover of FWD were significantly correlated with a number of the diversity measures; the former positively correlated with all but species diversity (1/D) and the latter negatively correlated with all but non-vascular species richness and species diversity (Table 4.45). Species diversity was most strongly correlated with structural diversity, the relationship being positive, while the soil parameters of total nitrogen and organic matter content (LOI) were negatively correlated with this diversity measure. The volume of CWD was also positively correlated with species diversity. Occurrence on poorly drained soils and the presence of grazing both resulted in significantly higher-values of all of the diversity measure with the exception of species diversity (1/D).

Table 4.45: Relationships between the ground vegetation native ash plot diversity measures and various structural and functional variables calculated with a) Spearman's correlations for continuous variables and b) Mann Whitney U tests for presence absence variables. Only significant (P ≤ 0.05) results are shown with the variables ordered from highest to lowest r-value and U-value respectively and the direction of the relationship indicated with + or –.

Total SR	Vascular SR	Non-vascular SR	Species diversity (1/D)	Woodland SR
a)				
+ Bare soil**	- FWD Cover**	+Bare soil*	+ Structural 1/D***	- FWD Cover *
- FWD Cover*	+Bare soil**		- Total N*	+ Bare soil*
			- LOI*	
			+ CWD Volume*	
b)				
+Poorly drained***	+Poorly drained***	+Grazed*		+Poorly drained**
+Grazed***	+Grazed***	+Poorly drained*		+Grazed***

Significance: * P ≤ 0.05; ** P ≤ 0.01; ***P ≤ 0.001

4.2.4 Comparison of forest types

4.2.4.1 Species richness and typical woodland species richness

A total of 317 species was recorded at the sites, with 209 recorded in the native woodlands and 268 in the plantations (Appendix 8; Smith *et al* 2005; French 2005). No species listed in the Red Data Book for vascular plants (Curtis and McGough, 1988) or bryophytes listed as rare in Holyoak (2003) were found at the sites. However, *Stachys officinalis* (betony), which is listed in the Vegetation Protection Order (Anon, 1999a) was recorded in a Sitka spruce plantation established on historic woodland and adjacent to existing remnants of this woodland. It is also oneof the 30 'notable' species listed by Perrin *et al.* (2008a), that is, rare species typically found in woodland, or species which are indicative of long-established woodland. Four additional 'notable' species were found at the sites: *Carex strigosa* and *Prunus padus* in a Norway spruce plantation established on historic woodland, and *Melica uniflora* and *Anemone nemorosa* in native ash woodlands. Species with a low affinity for woodland accounted for 12.4% of species in native woodlands compared to 28.4% of species in plantations, while species with a high affinity for woodland accounted for 37.3% of species in native woodlands and 31.7% of species in plantations. A total of 49 species was recorded only in native woodlands and 108 only in plantations; however, 53.7% of the species found only in plantations had a low affinity for woodland compared with only 16.3% of the species found only in native woodlands.

On average, native woodlands were significantly more species rich than plantations, in their total species richness and in the number of vascular plants, bryophytes and typical woodland species they supported (Table 4.46). They also had significantly higher species diversity according to Simpson's reciprocal index (1/D). Structurally, the most striking difference was in the understorey cover, which was significantly higher in native woodland, as was shrub cover. Cover of the other layers did not differ significantly and there was no significant difference in the volume of CWD.

Table 4.46: Values (mean ± se) of the diversity and structural variables recorded for the ground vegetation in the native woodlands and plantations. Values with different letters indicate significant differences between them at the P ≤ 0.05 level.

	n	Plantations 55	Native 20
Diversity			
Total SR		24.2 ± 1.5[A]	33.5 ± 2.3[B]
Vascular SR		13.6 ± 1.0[A]	19.8 ± 2.0[B]
Bryophyte SR		10.6 ± 0.4[A]	13.6 ± 0.9[B]
Species diversity (1/D)		4.1 ± 0.2[A]	5.9 ± 0.5[B]
Typical woodland SR		11.4 ± 0.6[A]	20.1 ± 1.6[B]
Structural layers			
Canopy (%)		74.0± 1.5[A]	74.4 ± 2.5[A]
Understorey (%)		2.4 ± 0.9[A]	49.0 ± 6.5[B]
Shrub (%)		8.3 ± 1.9[A]	15.6 ± 3.4[B]
Fern (%)		6.3 ± 1.0[A]	8.0 ± 1.6[A]
Graminoid (%)		13.5 ±3.1[A]	15.1 ± 4.6[A]
Forb (%)		9.1± 2.0[A]	10.7 ± 3.5[A]
Bramble/briar (%)		12.3 ± 2.7[A]	9.1 ± 2.8[A]
Bryophyte (%)		44.5± 3.4[A]	38.3 ± 5.4[A]
CWD volume (m^3)		0.25 ± 0.03[A]	0.36 ± 0.07[A]

Native ash woodlands were significantly more species rich and diverse than all other forest types and supported significantly more vascular plant and typical woodland species (Table 4.47). Native oak woodlands were not significantly different in their species richness and species diversity from the four plantation types studied and did not support significantly more typical woodland species than the Norway spruce (including all pure Norway spruce and all Norway spruce/oak (hereafter referred to as oak mixes) and Norway spruce/Scots pine mixes combined) or ash plantations.

Table 4.47: The mean (± se) values for diversity and selected environmental variables for the ground vegetation in different forest types. Variables are significantly different (P ≤ 0.05) between forest types if indicated by a different letter.

	Plantations				Native	
	Sitka spruce	**Norway spruce**	**Larch**	**Ash**	**Oak**	**Ash**
n	**16**	**20**	**8**	**11**	**10**	**10**
Diversity						
Total SR	23.3^A ± 2.9	23.8^A ± 1.9	24.8^A ± 0.9	25.2^A ± 1.9	26.1^A ± 2.3	40.9^B ±3.7
Vascular SR	11.9^A ± 2.4	14.0^A ± 1.9	12.0^A ± 0.7	16.1^A ± 1.7	13.7^A ± 1.1	26.0^B ± 2.7
Bryophyte SR	11.4^{AB} ± 0.9	9.8^{AD} ± 0.5	12.8^{BC} ± 0.7	9.2^A ± 0.8	12.4^{BCD} ± 1.3	14.9^C ± 1.1
Species diversity (1/D)	3.4^A ± 0.4	3.8^{AB} ± 0.4	4.9^{BC} ± 0.3	5.2^C ± 0.3	4.5^{ABC} ± 0.5	7.3^D ± 0.6
Typicla woodland SR	9.8^{AB} ± 1.2	13.3^C ± 1.0	7.2^A ± 0.7	12.6^{BC} ± 1.1	14.7^C ± 0.7	25.5^D ± 1.9
Environmental						
Canopy cover	68.5^A ± 3.3	77.6^A ± 1.9	76.0^A ± 2.2	73.8^A ± 3.7	79.8^A ± 2.3	69.0^A ± 3.8
CWD volume	0.27^{AB} ± 0.05	0.30^A ± 0.05	0.11^B ± 0.02	0.24^B ± 0.12	0.18^{AB} ± 0.03	0.54^C ± 0.10
Drainage†	3^{AB} ± 2	2^{BC} ± 1	4^D ± 0	4^{AD} ± 2	2^{CE} ± 1	2^{BE} ± 2
Grazing‡	*12.5*	*5.0*	*75.0*	*45.4*	*20.0*	*40.0*
Historic woodland‡	*18.8*	*50.0*	*25.0*	*72.7*	*90.0*	*90.0*

§ Includes all pure Norway spruce and all Norway spruce/oak and Norway spruce/Scots pine mixes
† Median +/- interquartile range reported: 1 = poor, 2 = moderate, 3 = good, 4 = very good
‡Presence/absence variables: percentage of sites in each group with presence of the variables indicated

Multimodel inference selected a set of eight models in the 95% confidence set for total species richness (Table 4.48). Forest type, canopy cover and their interaction had the highest importance values and CWD volume and its interaction with forest type had the lowest of the six variables and two interactions included in the models. Plots of species richness versus canopy cover at the six different forest types (Fig. 4.15) indicate a negative association with canopy cover in the Sitka spruce and Norway spruce sites and no strong relationship in the other four forest types. The relative importance of the remaining three variables was high. The average model parameters for the eight models predict a slight negative association between species richness and improved drainage. Being located on/adjacent to historic woodland is also predicted to have a slight negative association with species richness but grazing is predicted to have a positive association.

Table 4.48: The Akaike weights for the 95% confidence set of models and the cumulative Aikake weight (wtAIC) for each variable for ground vegetation total species richness (SR). Interaction terms are indicated by an x.

Model No.	1	2	3	4	5	6	7	8	wtAIC
Total SR									
Forest type	X	X	X	X	X	X	X	X	1.00
Canopy cover	X	X	X	X	X	X	X	X	1.00
Forest type x Canopy cover	X	X	X	X	X	X	X	X	1.00
Drainage	X	X		X	X	X		X	0.82
Grazing	X		X	X	X		X	X	0.77
Historic woodland	X	X			X		X	X	0.74
CWD			X	X		X	X	X	0.37
Forest type x CWD			X				X		0.18
Akaike weight (ωᵢ)	0.36	0.17	0.14	0.11	0.10	0.06	0.04	0.03	
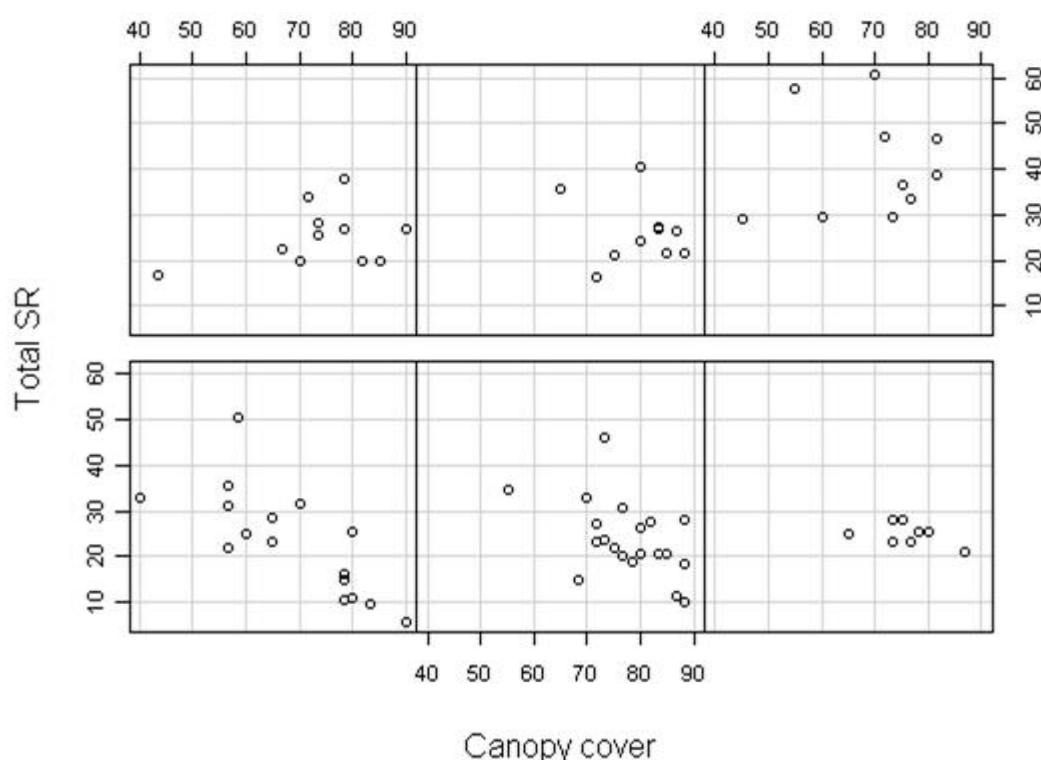
Figure 4.15: Plot of total species richness versus percentage canopy cover for the ground vegetation for the six site types. Top row L-R: ash plantation, oak native woodland and ash native woodland. Bottom row L-R: Sitka spruce, Norway spruce, larch.

For typical woodland species richness, a set of nineteen models was selected in the 95% confidence set (Table 4.49). Historic woodland, forest type and drainage had the highest importance values, with forest type and historic woodland appearing in all nineteen models. Canopy cover had a relatively high importance value also. Grazing, the interaction between forest type and canopy cover and CWD volume had relatively low importance values. Location on/adjacent to historic woodland was predicted to have a

positive association with typical woodland species richness and increased drainage a negative one, although with a slight improvement at the highest drainage level. Canopy cover was predicted to have a negative association with typical woodland species richness and grazing and CWD volume a slight positive association.

Table 4.49: The Akaike weights for the top nine of the 19 models in the 95% confidence set of models and the cumulative Aikake weight (wtAIC) for each variable from all 19 models for ground vegetation typical woodland species richness (SR).

Model No.	**Typicl woodland SR**									
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**wtAIC**
Historic woodland	X	X	X	X	X	X	X	X	X	1.00
Forest type	X	X	X	X	X	X	X	X	X	1.00†
Drainage	X	X		X	X		X	X	X	0.70
Canopy cover		X	X			X	X	X	X	0.54
Grazing				X		X			X	0.26
Forest type x Canopy cover			X			X	X			0.25
CWD					X			X		0.16
Akaike weight (ω$_i$)	0.25	0.16	0.09	0.07	0.06	0.06	0.05	0.04	0.04	

†Forest type was fixed to appear in all models so value must be 1.00

4.2.4.2 Vegetation communities

Following flexible beta cluster analysis, a six cluster solution had the highest sum of significant indicator-values, however this resulted in two clusters with heterogeneous vegetation community composition so an eight cluster solution was selected. These 8 clusters are indicated in Fig. 4.16.

Sites did not always cluster according to their forest type and plantations and native woodlands clustered together in clusters II and IV. Cluster II contains all ten native ash woodlands, seven ash plantations and one pure Norway spruce plantation; all of these plantation sites were low elevation sites located on or near old woodland which was also historically wooded. It is the most species rich and diverse cluster and a high number of typical woodland species are supported (Table 4.50). Sites in the cluster also have a high volume of CWD on average. French *et al.* (2008) classified the ground vegetation community of the ash plantations in this cluster as 'basophilic forest' and had previously noted the similarity of the vegetation in these plantations to that of native ash woodland.

Cluster IV contains twelve plantations, with representatives from all four plantation types, and two native oak woodlands. Vascular species richness is high and a moderate number of typical woodland species are supported. French *et al.* (2008) described a ground vegetation community named 'bramble-dominated', applicable to the sites in this cluster, which was present in plantations at all stages of development but which had a relatively open canopy in common.
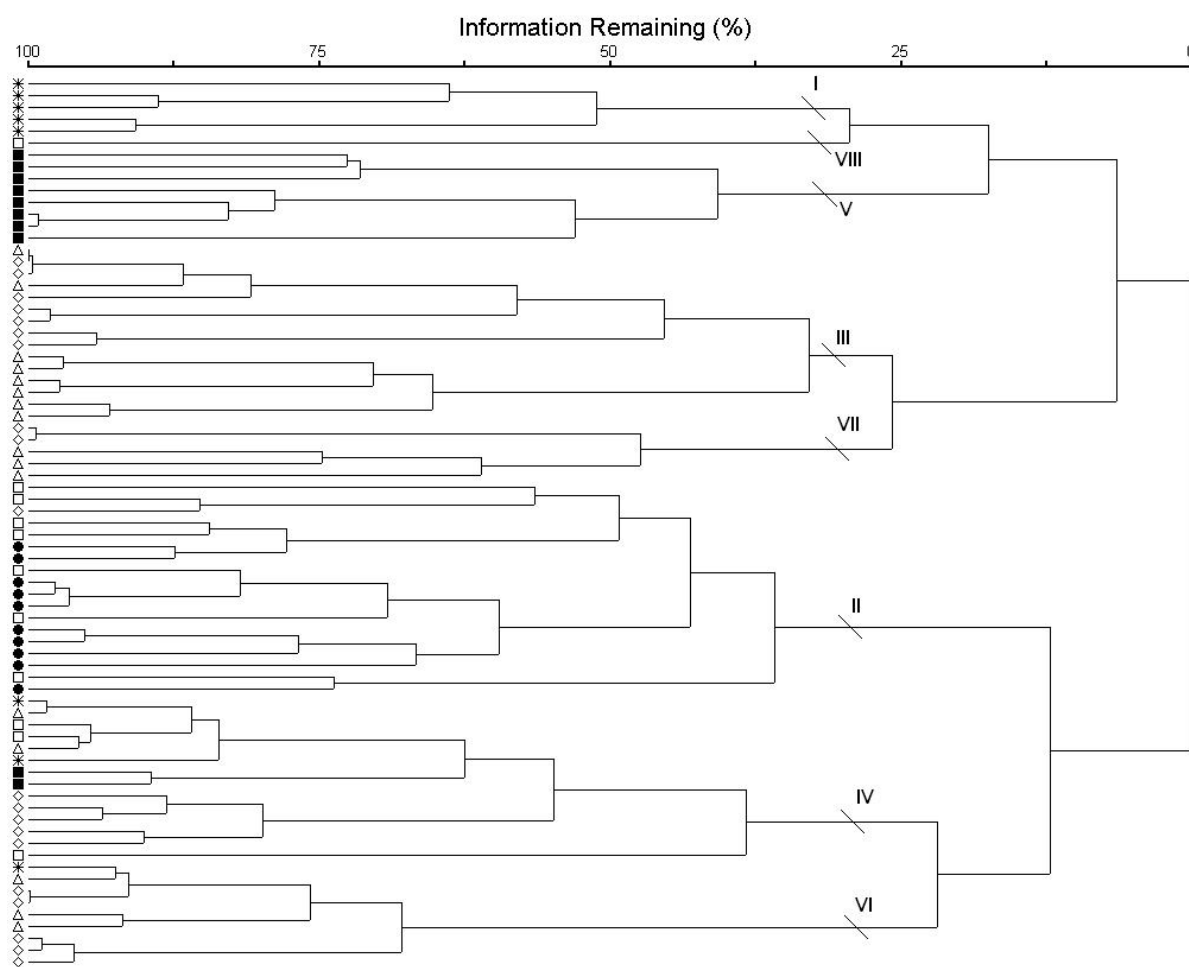
Figure 4.16: Dendrogram from the flexible beta cluster analysis of the ground vegetation composition of Sitka spruce △, Norway spruce ◇, Japanese larch ✳, ash plantation □, native oak woodland ■ and native ash woodland ● sites. Symbols I-VIII indicate the eight cluster groups.

All other clusters contain solely plantations or native woodlands. Cluster I contains larch plantations which support few typical woodland species (Table 4.50) and have a vegetation community described by French *et al.* (2008) as 'acidophilic forest: grass-dominated', although some sites also have affinities to their 'heath' vegetation community. Cluster III contains Sitka spruce and Norway spruce plantations which have a ground vegetation described as 'acidophilic woodland – bryophyte dominated' by French *et al.* (2008), support relatively few vascular plants and have low species diversity on average. Cluster V contains the remaining eight native oak woodlands which have a vegetation community typical of this forest type. Cluster VI contains Sitka spruce, Norway spruce and a single larch plantation with a vegetation community dominated by *Thuidium tamariscinum*, with *Athyrium felix-femina*, *Cardamine flexuosa*, *Hypericum pulchrum* and *Veronica serpyllifolia* also common, which was not previously described by French *et al*. (2008). It has high species richness, particularly vascular species richness, and supports a reasonable number of typical woodland species. The majority of the sites in this cluster were planted on or adjacent to old and historic woodland. Cluster VII contains Sitka spruce and Norway spruce plantations which have a vegetation community described by French *et al.* (2008) as 'Closed canopy conifer forest: 2nd stage' and are extremely species poor and support few typical woodland species. Cluster VIII contains a single ash plantation from a very poorly drained site.

Table 4.50: The mean (± se) values for the diversity and environmental variables for the ground vegetation for clusters I-VII. Variables are significantly different between clusters (P ≤ 0.05) if indicated by a different letter.

Cluster	I	II	III	IV	V	VI	VII
n	5	18	15	14	8	9	5
Diversity							
Total SR	24.9^{AB}	33.3^{A}	20.6^{B}	26.8^{A}	27.2^{AB}	30.8^{A}	11.1^{C}
	±0.9	±2.9	± 1.6	± 2.1	± 2.5	± 3.0	±2.0
Vascular SR	12.2^{AC}	21.1^{B}	9.8^{C}	16.1^{AB}	14.1^{AC}	19.6^{AB}	2.5^{D}
	± 0.6	± 2.1	± 1.5	± 2.0	± 1.3	± 2.5	± 0.7
Bryophyte SR	12.7^{A}	12.2^{A}	10.8^{A}	10.7^{A}	13.1^{A}	11.1^{A}	8.6^{A}
	± 0.8	± 1.0	± 0.8	± 0.8	± 1.4	± 1.0	± 1.6
Species diversity (1/D)	4.9^{A}	6.4^{B}	2.9^{C}	5.0^{A}	4.5^{A}	4.9^{A}	1.3^{D}
	± 0.2	± 0.5	± 0.2	± 0.3	± 0.5	± 0.3	± 0.1
Typical woodland SR	6.7^{A}	20.8^{B}	9.8^{CD}	11.9^{DE}	15.1^{F}	15.2^{BEF}	6.1^{AC}
	± 0.3	± 1.7	± 0.8	± 1.1	± 0.6	± 1.5	± 1.5
Forestry							
Canopy cover	76.3^{AB}	73.2^{AB}	74.2^{AB}	67.2^{A}	80.4^{BC}	72.8^{AB}	85.0^{C}
	± 1.3	± 2.7	± 2.4	± 3.6	± 2.7	± 3.5	± 2.4
Grazing‡	80.0	33.3	0.0	28.6	25.0	33.3	0.0
Geographic							
Elevation	291.0^{A}	62.4^{B}	176.8^{C}	135.8^{CD}	87.1^{BD}	111.9^{BD}	231.0^{ACD}
	± 28.9	± 11.2	± 18.0	± 15.3	± 10.7	± 31.7	± 54.8
Annual precipitation	1302^{AC}	1068^{B}	1176^{AB}	1137^{AB}	1292^{AC}	1129^{AB}	1425^{C}
	± 47	± 35	± 42	± 45	± 84	± 54	± 129
Steep slope‡	100.0	27.8	20.0	35.7	37.5	22.2	60.0
Historic Woodland‡	40.0	94.4	20.0	21.4	100	77.8	0.0
Edaphic							
Soil pH†	4.0A^{B}	5.9^{D}	4.3^{C}	4.2^{AC}	3.9^{B}	4.4^{C}	4.3^{AC}
	± 0.5	± 0.9	± 0.3	± 0.6	± 0.4	± 0.6	± 0.3
LOI	52.8^{A}	19.6^{B}	32.3^{AB}	18.8^{B}	34.1^{AB}	25.7^{BC}	39.8^{AC}
	± 9.2	± 2.0	± 6.4	± 2.1	± 7.0	± 6.7	± 10.9

‡Presence/absence variables, proportion of sites in each group with presence of the variables indicated

†Median ± interquartile range reported

With a maximum gradient length of 4.207 S.D. units, the preliminary DCA ordination confirmed that CCA was the appropriate model to use on the vegetation data. Automatic forward selection identified twelve variables that were included in the final model (Table 4.51). Sitka spruce and Norway spruce were selected despite their non-significance, as forest type was considered a single variable with six states rather than six separate variables. The total variance in the species data is 5.356 and the estimated total variance explained by the environmental variables selected is 1.958 (36.6%). The eigenvalues for the first three axes are 0.539, 0.417 and 0.287 respectively. The first canonical axis is highly significant according to Monte Carlo tests with 9999 permutations (F = 7.047, P = 0.0001) as is the sum of all eigenvalues (F = 3.301, P = 0.0001).

The relationship between the environmental variables used in the final CCA ordination and the six forest types are shown in the biplot in Fig. 4.17. Overall, forest type was an important variable in explaining variation in the species data. There was a clear separation along Axis 1 between all native ash woodlands and ash plantations with the basophilic woodland vegetation type (but not the single Norway spruce plantation) and all other groups (with the exception of the single ash plantation which formed the eighth cluster). The three ash woodlands with the bramble-dominated vegetation type were separated from the rest of the ash plantations. Axis 1 mainly represented a gradient in soil pH. The positive association of total phosphorus with this axis also suggested a soil fertility gradient. Elevation and annual precipitation were strongly negatively associated with this axis while historic woodland and old woodland area were both positively associated. Axis 2 represented a separation between the native oak woodlands and all other forest types, with one of the two oak woodlands with the bramble-dominated ground flora slightly separated from the rest of the oak woodlands along this axis. Spruce plantations were mainly found towards the negative end of this axis. The remaining clusters did not separate well, indicating that the CCA model did not adequately explain the variation in species composition for these sites.

Table 4.51: The environmental variables used in the CCA ordination of the ground vegetation composition of the sites. The variance explained (Lambda-A), order selected, F-statistic and significance of each variable are shown.

Category	Variable	Lambda-A	Order selected	F
Forest	Forest type: Sitka spruce	0.07	11	1.20
Forest	Forest type: Norway spruce†	-	11†	-
Forest	Forest type: Japanese larch	0.23	3	3.90**
Forest	Forest type: Ash plantation	0.13	5	2.29**
Forest	Forest type: Oak native	0.38	2	6.02**
Forest	Forest type: Ash native	0.19	4	3.17**
Forest	Grazing	0.11	8	1.93**
Geographic	Elevation	0.12	6	2.08**
Geographic	Steep slope	0.09	9	1.69*
Geographic	Annual precipitation	0.08	10	1.53*
Geographic	Historic woodland	0.10	7	1.93**
Edaphic	Soil pH	0.46	1	6.81**

* Environmental variable significant at $P \leq 0.05$ (Monte Carlo test of significance).
** Environmental variable significant at $P \leq 0.01$ (Monte Carlo test of significance).
†The six forest type variables are a linear combination therefore all information for Norway spruce is represented once all other forest type variables are selected. Norway spruce includes all pure Norway spruce and all Norway spruce/oak and Norway spruce/Scots pine mixes.
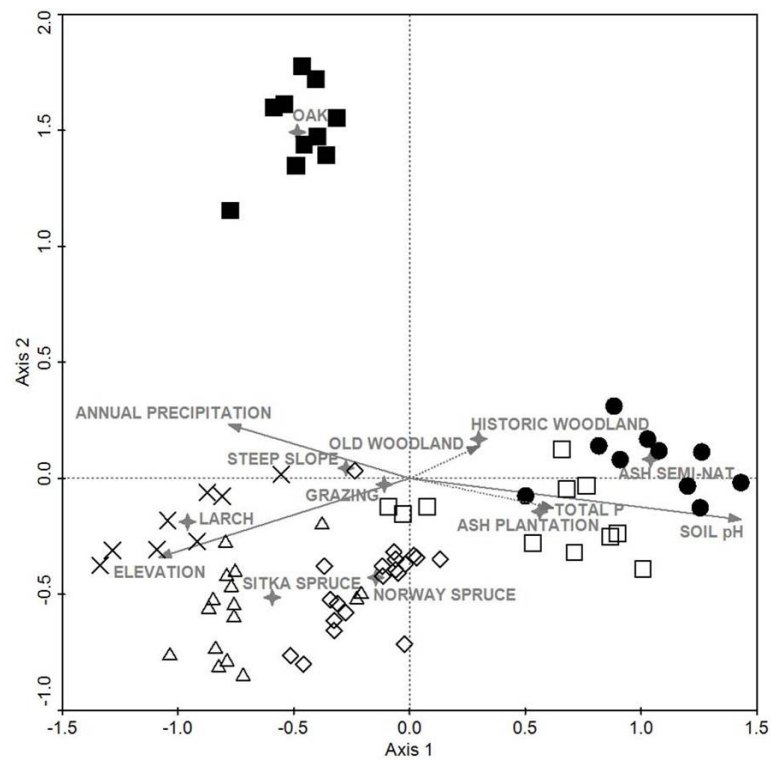
Figure 4.17: CCA biplot indicating the relationship between the six forest types and the environmental variables (✦indicates nominal environmental variables; supplementary variables indicated by dotted lines). Symbols indicate forest types: Sitka spruce △, Norway spruce ◇, Japanese larch ✕, ash plantation □, native oak woodland ■,native ash woodland ●.

4.3 Ground-dwelling invertebrates and Lepidoptera

4.3.1 Afforestation and reforestation survey

A total of 12,661 spiders were identified belonging to 134 species (Appendix 2) and 13,442 beetles from 47 species (Appendix 3). The most abundant spider species were from the Linyphiidae family and included *Lepthyphantes zimmermanni* (17%)*, Saaristoa abnormis* (8%) and *Monocephalus fuscipes* (8%). The most abundant beetle species were *Abax parallelepipedus* (54%), *Pterostichus melanarius* (15%) and P*. madidus* (9%).

4.3.1.1 Invertebrate diversity across the forest cycle of second rotation plantations

Two axes were recommended by the NMS ordination of spider assemblages (Fig. 4.18) (r^2 = 0.79 correlation between final solution and original distance space, Axis 1 = 0.62, Axis 2 = 0.17). Across Axis 1 the plots were distinguished by structural development with the Pre-thicket and Thicket plots separated relatively well into their respective structural groups. In contrast, the more developed stands overlapped with each other and were more tightly clustered across both axes. Cover of upper and lower vegetation layer and organic content of the soil were positively correlated with this axis whilst canopy cover, litter depth, cover of needle litter and fine woody debris displayed a negative relationship. Across Axis 2 half of the Pre-thicket plots along with three Commercially mature plots from the same site were separated from the others and cover of vascular ground vegetation was positively correlated with this axis.

Figure 4.18: NMS ordination of spider assemblages across second rotation forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; ✳ Commercially mature. Variables with a Pearson correlation coefficient significant at P ≤ 0.05 are shown. Correlation between original dataset and ordination space r^2 = 0.79: Axis1 r^2 = 0.62, Axis 2 r^2 = 0.17, Final Stress = 18.1; Final Instability = 0.0001.

A three dimensional solution was recommended by the NMS ordination of beetle assemblages represented (r^2 = 0.94 correlation between final solution and original distance space) (Fig. 4.19). Across Axis 1 (r^2 = 0.40) the Pre-thicket and Thicket plots were broadly separated from those with a more developed canopy with the exception of three plots from the same Pre-thicket site. Axis 1 was positively correlated with organic content of the soil and negatively correlated with soil pH and also longitude. Across Axis 2 (r^2 = 0.30), the majority of the Pre-thicket plots were separated from the Thicket stands and some of

the more structurally developed plots, which is likely to be related to their greater cover of lower vegetation layer. *Abax parallelepipedus*, which represented 54% of the total captures, was highly positively correlated with Axes 1 (Pearson r = 0.87) and 2 (Pearson r = 0.74), thus these axes are likely to be highly influenced by the presence of this species, particularly in the tightly clustered group of Thicket stands, where few other species were present. Axis 3 (r^2 = 0.24) did not represent any changes in assemblage structure across the forest cycle, however it may reflect differences in the presence of two species which do not appear to occur in high numbers together i.e. P. *melanarius* which constituted 15% of the total captures was negatively associated with Axis 3 (Pearson r = -0.43) and P. *niger* which constituted 4% of the captures, was positively associated with this axis (Pearson r = 0.69).
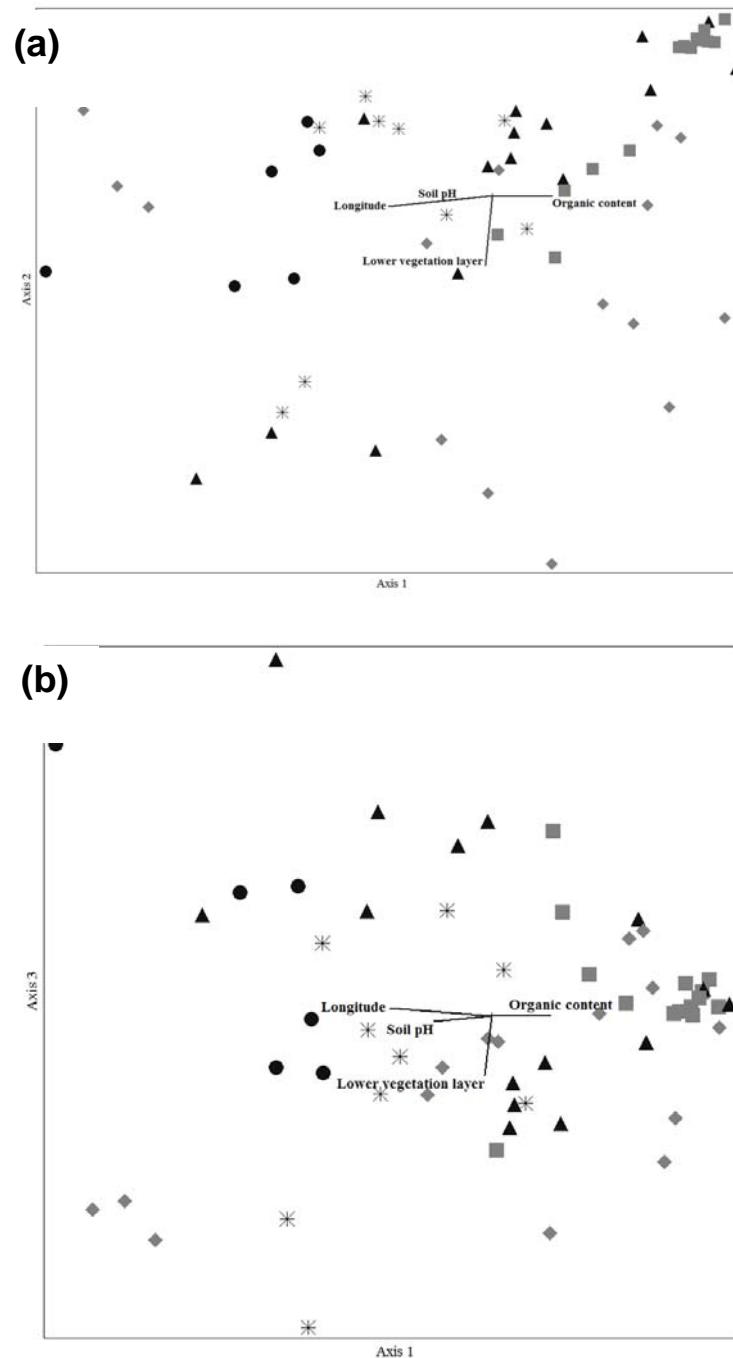
Figure 4.19: NMS ordination of beetle assemblages across second rotation forest cycle: ♦ Pre-thicket, ■ Thicket, ▲ Closed-maturing, ● Reopening, ✳ Commercially mature. a) Axes 1 and 2; and b) Axes 1 and 3. Correlation between original dataset and ordination space r^2 = 0.94: Axis1 r^2 = 0.40, Axis 2 r^2 = 0.30; Axis 3 r^2 = 0.24, Final Stress = 9.30; Final Instability = 0.0001.

Spider species richness was significantly greater in the younger stands than in those with a more developed canopy whilst beetle species richness increased in the later stages of the forest cycle (Table 4.52). For both taxa, richness and relative abundance of open habitat species was greatest in the Pre-thicket stands whereas the richness and relative abundance of forest-associated species increased with forest structural development. A similar trend was shown by the Berger-Parker dominance index for spiders, which was significantly higher towards the end of the forest cycle. The relative abundance of beetle species with a preference for forest habitats was greatest in the Thicket stands, as was dominance, however this is likely to reflect captures of *A. parallelepipedus* which is associated with forest habitats, and was the most abundant beetle at this structural stage and the whole dataset.

Table 4.52: Mean (±se) values per plot of species metrics among the structural groups in second rotation forests. Significance tested with parametric ANOVA (*F*) and non-parametric Kruskal-Wallis (*H*) with Tukey and Nemenyi posthoc tests respectively. Test statistics in bold are significant after Bonferroni correction.

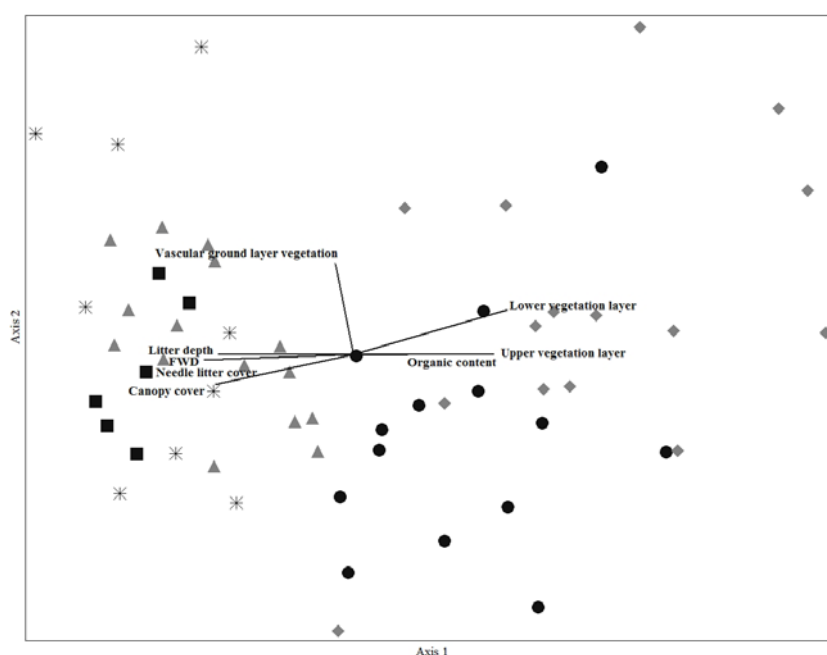|	Pre-thicket (P)	Thicket (T)	Closed-maturing (C)	Re-opening (R)	Commercially mature (M)	ANOVA DF $_{4,54}$	Post Hoc comparisons
Spiders							
Species richness[a]	22.3 ±1.5	16.9 ±1.0	12.9 ±0.8	12.8 ±1.3	13.1±0.7	***F = 13.43***	P > T,C,R,M; T > C
Dominance	0.22 ±0.02	0.25 ±0.03	0.30 ±0.02	0.35 ±0.03	0.33 ±0.03	*F* = 3.97**	P < R,M
Open species richness	5.53 ±0.65	2.07 ±0.53	0.27 ±0.12	0	0.11 ±0.11	***H = 42.66***	P > T,C,R,M; T > C,R,M
Forest species richness	3.93 ±0.42	4.43 ±0.27	5.60 ±0.40	6.17 ±0.60	6.11 ±0.35	***F= 6.02***	P < C,R,M; T < R,M
Open relative abundance	0.26 ±0.04	0.06 ±0.03	0.01 ±0	0	0.01 ±0	***H = 43.81***	P > T,C,R,M
Forest relative abundance	0.24 ±0.03	0.41 ±0.03	0.46±0.03	0.48 ±0.09	0.61±0.03	***F = 12.39***	P < T, C+R+M; T < M
Beetles							
Species richness[a]	9 ±1.2	7.1 ±1.1	8.3 ±0.8	13.2 ±5.4	12 ± 0.9	*F* = 4.29**	T < R,M
Dominance	0.49 ±0.04	0.83 ±0.05	0.61 ±0.05	0.33 ±0.13	0.45 ±0.04	***F = 16.53***	T > P,C,R,M; C > R
Open species richness	2.20 ±0.48	0.93 ±0.29	0.53 ±0.17	1.00 ±0.41	0.89 ±0.26	***H = 16.79***	P > T,C
Forest species richness	1.73 ±0.21	2.36 ±0.31	3.20 ±0.24	4.67 ±0.62	4.11 ±0.57	***F = 10.33***	P < C, R, M; T < R, M
Open relative abundance	0.17 ±0.03	0.01 ±0.01	0.01 ±0	0.01 ±0	0.02 ±0.01	***H= 34.74***	P > T,C,R,M
Forest relative abundance	0.44 ±0.05	0.85 ±0.04	0.65 ±0.06	0.40 ±0.05	0.60 ±0.07	***F = 10.18***	T > P,C,R,M; C > P,

[a] Square root transformed; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

Nearly four times as many spider species were identified by Indicator Species Analysis in the Pre-thicket plots than in any of the other structural groups, seven of which were associated with open habitats (Table 4.53). By contrast, only four species were affiliated with the Thicket plots, although one of these, *A. ramosa,* was associated with forest habitats. In the more structurally developed groups, between two and four species were identified and these were predominately associated with forested habitats. Indicator Species Analysis identified one beetle species in the Pre-thicket stands which has a preference for open habitats (Table 4.54) whereas for the Thicket structural group, no species were identified. One species was identified as an indicator of the Closed-maturing structural group and this was associated with

forested habitats. For the Re-opening group eight species were identified, one of which was associated with forested habitats, but also one with open habitats, whereas of the four species identified in the Commercially mature structural group only one had a preference for forested habitats.

Table 4.53: Spider species identified in each structural group by Indicator Species Analysis and their habitat preference. Species with a significant indicator-value (P ≤ 0.05) are shown in bold.

	Indicator Value (%)					
	Pre-thicket (n = 15)	Thicket (n = 14)	Closed-maturing (n = 15)	Re-opening (n = 6)	Commercially mature (n= 9)	Habitat preference
Pardosa pullata	**70*****	1	0	0	0	Open
Pocadicnemis pumila	**68*****	9	0	0	0	Open
Dismodicus bifrons	**53****	14	0	0	0	Generalist
Walchenaeria vigilax	**47****	0	0	0	0	Generalist
Pardosa nigriceps	**46****	2	0	0	0	Open
Trochosa terricola	**45****	2	0	0	0	Generalist
Pepnocranium ludicrum	**40****	1	0	0	0	Generalist
Bathyphantes parvulus	**40****	0	0	0	0	Open
Metpobactrus prominulus	**36***	0	0	0	0	Generalist
Ero cambridgei	**33****	0	0	0	0	Generalist
Pardosa amentata	**33****	0	0	0	0	Open
Lepthyphantes ericaeus	**33****	6	12	0	3	Generalist
Neriene clathrata	**31***	2	0	0	0	Generalist
Pocadicnemis juncea	**30***	2	0	0	0	Open
Oedothorax gibbosus	**26***	3	0	0	0	Open
Walckenaeria acuminata	3	**47****	6	1	5	Generalist
Agyneta ramosa	32	**42****	12	2	5	Forest
Agyneta conigera	1	**37****	2	0	0	Generalist
Ozyptila trux	1	**33***	0	0	0	Generalist
Monocephalus fuscipes	3	21	**38*****	15	13	Forest
Pelocopsis nemoralis	0	0	**38****	2	1	Forest
Centromerus dilutus	0	10	**35***	13	10	Generalist
Lepthyphantes zimmermanni	6	7	**32***	31	23	Generalist
Diplocephalus latifrons	0	0	4	**54*****	33	Forest
Asthenargus paganus	2	6	17	**40****	13	Forest
Robertus lividus	7	11	13	**36***	5	Generalist
Lepthyphantes tenebricola	0	0	2	21	**55****	Forest
Lepthyphantes flavipes	0	0	6	4	**48****	Forest

Significance of Monte Carlo tests: * P ≤ 0.01; ** P ≤ 0.005; ***P ≤ 0.001

Table 5.45: Beetle species identified in each structural group by Indicator Species Analysis and their habitat preference. Species with a significant indicator-value (P ≤ 0.05) are shown in bold.

	Indicator Value (%)					
	Pre-thicket (n = 12)	**Thicket (n = 14)**	**Closed-maturing (n = 15)**	**Re-opening (n = 6)**	**Commercially mature (n= 9)**	**Habitat preference**
Carabus granulatus	**63*****	4	1	2	13	Open
Cychrus caraboides	1	1	**53*****	21	7	Forest
Pterostichus madidus	1	0	0	**77*****	16	Generalist
Notiophilus biguttatus	0	0	11	**63*****	24	Generalist
Calathus rotundicollis	0	0	0	**61*****	4	Forest
Pterostichus nigrita	16	12	8	**42****	5	Generalist
Loricera pilicornis	0	0	1	**38****	15	Generalist
Pterostichus melanarius	7	5	14	**38***	29	Generalist
Amara plebeja	0	0	0	**33***	0	Generalist
Bembidion lampros	6	1	0	**30***	0	Open
Nebria brevicollis	0	0	0	36	**55****	Forest
Pterostichus niger	0	0	1	1	**44****	Generalist
Leistus terminatus	1	2	3	10	**33***	Generalist
Paranchus albipes	0	0	0	0	**22***	Generalist

Significance of Monte Carlo tests: * P ≤ 0.05; ** P ≤ 0.01; ***P ≤ 0.001

4.3.1.2 Relationship between environmental variables and invertebrates in second rotation forests

In the Pre-thicket stands, species richness of both beetles and open habitat associated spiders was positively related to cover of lower vegetation layer (Table 4.55). A similar trend was observed for the relative abundance of open-associated spiders, but they were also negatively related to needle litter and upper vegetation layer cover. In contrast, beetle dominance (which represents the abundance of the most dominant beetle, the forest species *Abax parallelepipedus*) and beetles associated with forested habitats were negatively related to lower vegetation layer. These metrics as well as forest-associated spider species were positively related to variables which indicate forest development (canopy cover and height, and needle litter cover). In the Thicket stands, spider richness, abundance and open-associated species were negatively related to canopy cover, canopy height, mean DBH and brash cover, whereas forest species were positively related to litter depth. In the Thicket stands, beetle abundance was positively related to needle litter cover, whereas forest beetle species were negatively related to cover of shrub layer, upper vegetation layer and brash. In the more developed structural groups, abundance and dominance of both spiders and beetles were positively related to canopy height, cover and mean DBH. Furthermore, beetles associated with forests were positively related to litter depth and ground layer vegetation cover.

Table 4.55: Relationship between species metrics and environmental variables within each structural group (n = number of plots). Only significant (P < 0.05) Spearman's correlations are shown and the direction of the relationship indicated with + or – respectively. Correlations significant after Bonferroni correction are shown in bold.

	PreThicket (n = 15)	Thicket (n = 14)	Closed maturing (n = 15)	Re-opening + Commercially mature (n = 15)
Spiders				
Total S		- Canopy cover**		
Abundance		- Canopy cover**	- Soil pH*	- Litter depth*
Dominance			+ Canopy height* + DBH*	+ Canopy cover*
Open S	+ Lower vegetation layer*	- DBH* - Canopy cover** - Brash*		
Forest S	+ Canopy height*	+ Litter depth*		- Soil pH*
Open RA	**+ Lower vegetation layer**** - Upper vegetation layer* - Needle litter cover* + Soil pH*	- Canopy height* - Canopy cover* + Lower vegetation layer* - Brash**		
Forest RA	**+ Canopy cover **** + Needle litter* -Soil pH*		- Canopy height* - DBH**	**+ DBH****
Beetles				
Total S	+ Lower vegetation layer*	+ Soil pH**		
Abundance		+ Needle litter*	**+ Canopy height**** + DBH**	+ Soil pH*
Dominance	- Lower vegetation layer* + Canopy cover*	- Soil pH* - Brash*	**+ DBH**** + Litter depth**	
Open S	+ Soil pH*			
Forest S	+ DBH* + Shrub*	- Upper vegetation layer** **- Shrub layer**** + Soil pH** - Brash**		- Organic content*
Open RA	**+ Brash****	**- Brash****		
Forest RA	**-** Lower vegetation layer** + Upper vegetation layer** + Canopy cover* -Soil pH**	- Soil pH* + Organic content*	+ DBH**	+ Ground layer vegetation* + Needle litter** - Organic content*

Spearman's correlation significance: *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001; S = Species richness; RA = Relative abundance.

Overall, there were conflicting patterns in the relationship between species metrics and edpahic factors (soil pH and organic content) across the forest cycle. In the Pre-thicket stage for both taxa there was a positive relationship with soil pH and open species and a negative relationship with forest species. However, in the later stages of the forest cycle soil pH is negatively related to spider abundance and forest species richness but positively related to beetle abundance. Organic content was positively related to relative abundance of beetle forest species at several structural stages, which is in contrast with a negative relationship between this variable and species richness of forest beetle species. Across the structural groups there were no significant correlations between the species metrics and FWD and CWD (excluding brash piles).

4.3.1.3 Spider diversity between first and second rotation plantation forests

A two dimensional solution was recommended by the NMS ordination of spider assemblages, with an r^2 = 0.81 for the correlation between final solution and the between original distance space (Fig. 4.20), with Axis 1 accounting for 0.50 and Axis 2 for 0.31. Overall, the spider assemblages were distinguished by both rotation and structural development; first and second rotation plots were separated from each other but arranged in a similar pattern with increasing structural development. The most distinct group was the first rotation Pre-thicket plots which were clearly distinguished from all of the other plots across Axis 1, which was negatively related to soil pH. In addition, the difference between Pre-thicket and Thicket second rotation plots was not as great as that of first rotation. In contrast, the more developed stands displayed similar levels of variation across the axes for both first and second rotation. Variables related to tree development such as canopy cover and height, were positively associated with both axes whereas lower vegetation layer cover was negatively associated with both axes. In each of the structural groups, the spider assemblages differed significantly between rotations though in the Re-opening group the difference was not as large (MRPP, Pre-thicket: T = -14.8, P ≤ 0.0001, A = 0.27; Thicket: T = -14.7, P ≤ 0.0001, A = 0.22; Closed-maturing: T = -9.4, P ≤ 0.00001, A = 0.10; Re-opening: T = -2.1; P = 0.03, A = 0.09; Commercially mature: T = -4.2, P ≤ 0.0007, A = 0.09).
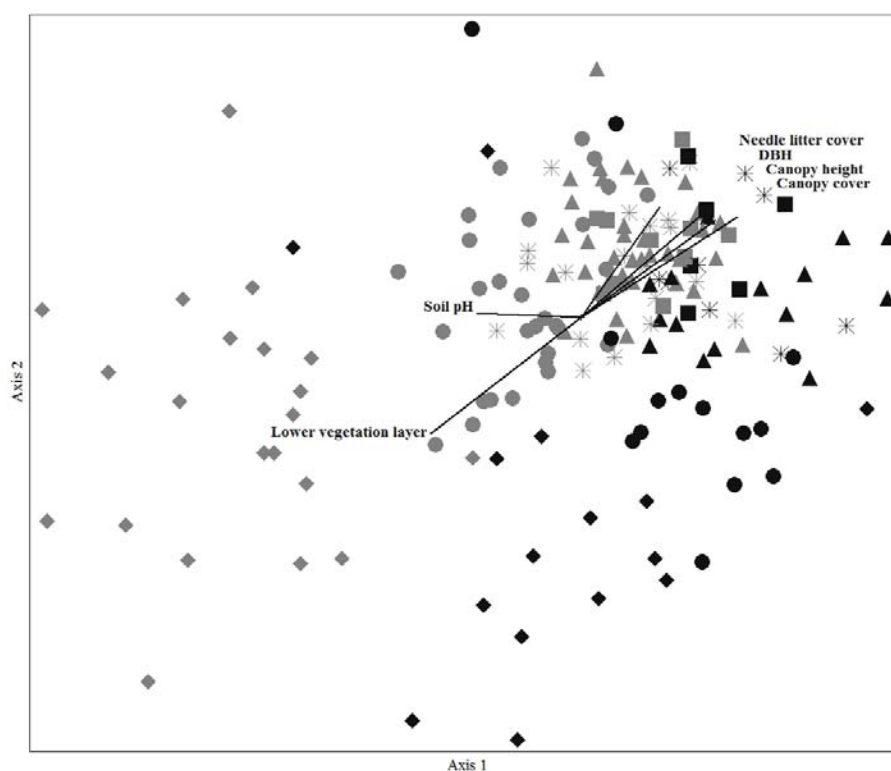
Figure 4.20: NMS ordination of spiders in first (grey symbols) and second (black symbols) rotation plantations at different structural stages of the forest cycle: ♦ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Re-opening; ✳ Commercially mature. Correlation between original dataset and ordination space r^2 = 0.81: Axis1 r^2 = 0.50, Axis 2 r^2 = 0.31, Final Stress = 21.42; Final Instability = 0.0006.

Overall, 44 of the spider species sampled were unique to first rotation stands and 19 to second rotation. For both rotations, the majority of the unique species were encountered in the early stages of the forest

cycle (Table 4.56); however, in the first rotation stands the number of unique species was also relatively high in the Commercially mature structural group. Both expected (corrected for trap days) and observed species richness were significantly higher in first rotation than second rotation stands across all stages of the forest cycle with the exception of the Pre-thicket stands. The number of species with a preference for open habitats was generally lower in second rotation stands, though this difference was only significant in the Commercially mature structural group. A significantly greater number of species with a preference for forested habitats were sampled in the second rotation Pre-thicket stands, however there was no difference in the number of these species between rotations in the other structural groups.

Table 4.56: Total number of unique species and mean ±se spider species richness (S) per plot between first and second rotation plantation forests within each structural group. Significance tested with parametric ANOVA (F) and non-parametric Kruskal-Wallis ANOVA (H). Test statistics shown in bold are significant after Bonferroni correction (P < 0.05).

	Unique species	Observed S	Expected S†	Open S	Forest S
Pre-Thicket (n = 35, DF $_{1,34}$)					
1st Rotation	24	17.0 ± 1.4	16.5 ± 1.3	4.9 ± 0.5	1.1 ± 0.2
2nd Rotation	12	17.5 ± 1.6	17.3 ± 1.6	4.2 ± 0.7	2.8 ± 0.4
ANOVA	-	n.s	n.s	n.s	*F* = 14.9***
Thicket (n = 42, DF $_{1,41}$)					
1st Rotation	22	18.8 ± 0.8	17.7 ± 1.1	1.8 ± 0.3	4.4 ± 0.3
2nd Rotation	6	13.2 ± 1.1	13.1 ± 0.7	1.3 ± 0.4	3.4 ± 0.4
ANOVA	-	*F* = 16.8***	*F* = 12.6***	n.s	n.s
Closed-maturing (n = 49, DF $_{1,48}$)					
1st Rotation	9	14.0 ± 0.4	13.2 ± 0.3	0.34 ±0.1	4.7 ± 0.2
2nd Rotation	3	11.3 ± 0.8	11.2 ± 0.7	0.2 ±0.1	5.0 ± 0.4
ANOVA	-	*F* = 8.3**	*F* = 12.9***	n.s	n.s
Re-opening (n = 15, DF $_{1,14}$)					
1st Rotation	4	14.6 ±0.8	13.9 ±0.7	0	5.6 ± 0.5
2nd Rotation	1	11.2 ±1.4	11.1 ±1.4	0	5.3 ± 0.5
ANOVA	-	*F* = 5.4*	n.s	n.s	n.s
Commercially mature (n = 28, DF $_{1,27}$)					
1st Rotation	13	17.8 ±1.1[a]	17.0 ±1.0[a]	1.0 ± 0.2	6.3 ± 0.2
2nd Rotation	2	11.4 ±0.7[a]	11.4 ±0.7[a]	0	5.4 ± 0.4
ANOVA	-	*F* = 16.7***	*F* = 14.6***	*U* = 36**	n.s

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001
† Standardised by trap day; [a] Data square root transformed

4.3.1.4 Environmental variables in first and second rotation plantation forests

Structural variables (canopy cover, mean DBH, tree height) were similar between rotations during the early stages of the forest cycle although canopy cover was significantly greater in second rotation Pre-thicket stands than in those of first rotation (Table 4.57). However, towards the end of the forest cycle, canopy height and mean DBH, and canopy cover and DBH were greater in second rotation for the Re-opening and Commercially mature groups respectively. In contrast cover of FWD was greater in first rotation stands in the later stages of the forest cycle, though this was only significant in the Commercially mature structural group. Overall, cover of ground layer vegetation was significantly greater in second rotation stands (excepting the Closed-maturing group), whilst cover of the lower vegetation layer was

greater in first rotation stands, though only significantly so for the Thicket and Commercially mature groups. Soil pH was higher in the first rotation stands at the beginning of the forest cycle but did not differ significantly in the more developed stands. Needle litter cover showed contrasting trends, being greater in first rotation Thicket stands but higher in second rotation Closed-maturing stands.

Table 4.57: Mean ±se environmental variables between first and second rotation forests within each structural group. Significance tested with parametric ANOVA (F) and non-parametric Kruskal-Wallis ANOVA (H). Test statistics shown in bold are significant after Bonferroni correction. Only environmental variables with a mean coverage of > 5% within a structural group are included.

	Canopy cover (%)	Canopy height (m)	Mean DBH (cm)	Fine Woody Debris (%)	Ground vegetation (%)	Lower vegetation layer (%)	Needle Litter (%)	Soil pH
Pre-Thicket (n = 35, DF $_{1,34}$)								
1st Rotation	27.5 ±3.1	2.4 ±0.2	3.4 ±0.4	0	6.3 ±0	52.3 ±0.1	0.1 ±0.1	5.3 ±0.2
2nd Rotation	47.7 ±3	2.9 ±0.1	3.4 ±0.1	0.12 ±0.1	47.7 ±4.9	57.3 ±8.9	0.2 ±0.1	4.2 ±0.1
ANOVA	***F = 20.2****	n.s	n.s	n/a	***U = 6****	n.s	n/a	***U = 27****
Thicket (n = 42, DF $_{1,41}$)								
1st Rotation	78.3 ±2.9	6.1 ±0.4	12 ±0.5	0.8 ±0.2	33.1 ±4.8	25.1 ±4	53 ±4.9	5.1 ±0.1
2nd Rotation	80 ±4.1	6.3 ±0.3	9.3 ±0.9	2.3 ±0.5	77.4 ±6	2.3 ±0.6	24.6 ±6	4 ±0.1
ANOVA	n.s	n.s	F = 8.25**	n/a	***F = 33.7****	U = 91.5**	***U = 73.5****	***U = 16.5****
Closed-maturing (n = 49, DF $_{1,48}$)								
1st Rotation	86 ±1.6	12.4 ±0.4	19.3 ±0.7	11 ±2.1	18.1 ±2.9	0.5 ±0.5	75.9 ±2.5	4.6 ±0.1
2nd Rotation	90 ±3	13.9 ±1	18.7 ±1	6.1 ±1.5	13.1 ±4.2	0.1 ±0	84.7 ±7.3	4.3 ±0.1
ANOVA	n.s	n.s	n.s	n.s	n.s	n/a	***F = 23.2****	n.s
Reopening (n = 15, DF $_{1,14}$)								
1st Rotation	69.1 ±4.7	19.2 ±0.4	21.1 ±1	17 ±4.3	16.5 ±3.1	7.6 ±6.2	67.6 ±6.6	4.6 ±0.2
2nd Rotation	80.8 ±2.7	21.5 ±0.5	31.7 ±2.2	8.6 ±2	44.2 ±12.5	0.1 ±0.1	60.1 ±11.9	4.2 ±0.2
ANOVA	n.s	F = 11.38**	***F = 26.8****	n.s	U = 9*	n.s	n.s	n.s
Commercially mature (n = 28, DF $_{1,27}$)								
1st Rotation	53.3 ±1.8	21.9 ±0.4	37.0 ±1.3	15.5 ±2.0	60.7 ±4.4	29.6 ±5.7	21.8 ±4.5	4.57±0.08
2nd Rotation	71.7 ±4.1	26.4 ±0.9	37.3 ±1.8	8.3 ±1.4	91.6 ±10.4	6.3 ±2.3	21.9 ±6.9	4.40 ±0.16
ANOVA	***U = 27.5****	***F = 33.4****	n.s	U = 45*	U = 38.5*	U = 41*	n.s	n.s

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

4.3.2 Mixed tree species survey

Preliminary analyses of the beetle data revealed that the main ordination axis (r = 0.69) was primarily describing the difference in relative abundance of one species, *A. parallelepipedus*, which is not found in the more Northern sites (Pearson correlation between Axis1 scores and *A. parallelepipedus:* r = 0.92, n = 59, P ≤ 0.0001). Thus it was decided to exclude this species from the ordination analyses so that it did not obscure trends of the majority of the species sampled related to forest type or environmental variables.

A total of 6313 adult spiders were identified in belonging to 77 species (Appendix 2) and 9325 adult beetles involving 37 species (Appendix 3) whereas 96 moth species from 1247 individuals were collected (Appendix 4). Of these, 24 spider species and 10 beetle species were classified as being associated with forested habitats. For moths, 46 species were associated with trees: on 35 species with a larval feeding preference for broadleaved trees, 9 for conifer trees, one a generalist (both conifers and broadleaves) and one associated with lichens on trees. Commonly encountered species included *Lepthyphantes zimermanni* (20% of total adult individuals) and *Lepthyphantes tenebricola* (12%) for spiders, *Abax parallelepipedus*, (39%) and *Pterostichus madidus* (14%) for beetles, and Grey Pine Carpet (*Thera obeliscata*) and Map-winged Swift (*Hepialus fusconebulosa*) representing 17% and 11% of the individuals respectively for moths.

4.3.2.1. Invertebrate assemblages between mixed and pure plantations

There was no significance difference in assemblage composition between either mix type and the geographically paired pure stands examined using MRBP, although this difference was approaching significance for spiders in Norway spruce/oak mixes (hereafter referred to as oak mixes) (T = 1.58, P = 0.06, A = 0.02). The NMS ordinations for each taxon also show no clear difference among the sampling plots by forest type, which suggests that other environmental factors may be driving differences between the assemblages, such as ground vegetation, litter cover and plant species richness (Figs 4.21 – 4.23). However, when examining axes scores of the geographically paired mix and pure sites within a particular forest type some general trends can be seen. For beetles (Fig. 4.21), the Norway spruce/Scots pine mixes (hereafter referred to as Scots pine mixes) generally had lower Axis 2 scores than their geographically paired pure stands with the exception of 1 site pair, MOTE, which were very similar in position, whereas for the oak mixes only three mix stands exhibited lower Axis 2 scores than their geographically matched pure stand (GOSF, PARK, WOOD). This axis was positively related to needle litter cover and negatively related to ground layer vegetation and plant species richness, suggesting some difference in ground habitat structure, along this axis and between forest types.
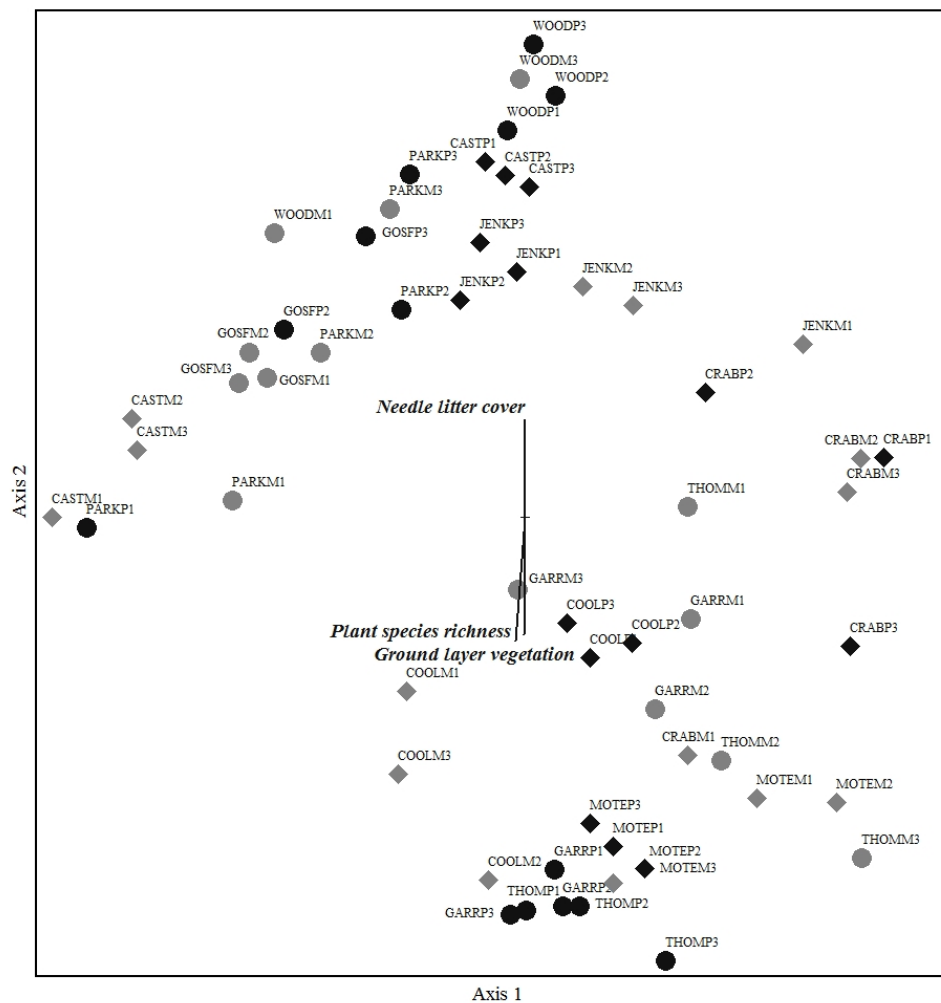
Figure 4.21: NMS ordination of Carabid beetle assemblages among the sampling plots: ◆ Norway spruce/Scots pine mix; ◆ Matching pure to Norway spruce/Scots pine mix; ● Norway spruce/oak pine mix ● Matching pure to Norway spruce/oak pine mix. 'M' or 'P' after site codes refers to mix or pure stand, number denotes plot number. Axis 1 r ^{2} = 0.23; Axis 2 r ^{2} = 0.59; Final stress = 17.1; Final instability = 0.001.

For spiders (Fig. 4.22), in general Scots pine mixes had higher mean site axis scores across Axis 2 with the exception of JENK, whereas for the oak mixes only 3 of the 5 geographically matched site pairs had higher axis scores (GARR, PARK, THOM). This axis was negatively correlated with needle litter cover, again suggesting a broad difference in habitat structure on the ground between mix and pure stands. In contrast, the moth assemblages did not show any broad trend between mix and pure stands across either axis (Fig. 4.23) but there was a separation of Scots pine mixes and their geographically paired pure stands from the oak mixes and their pures across Axis1. Axis 2, however, which represented the majority of the explained data, was not related to differences in stand type, but was positively related to leaf litter cover and negatively related to canopy height, but this was mostly explained by the differences at three plots.
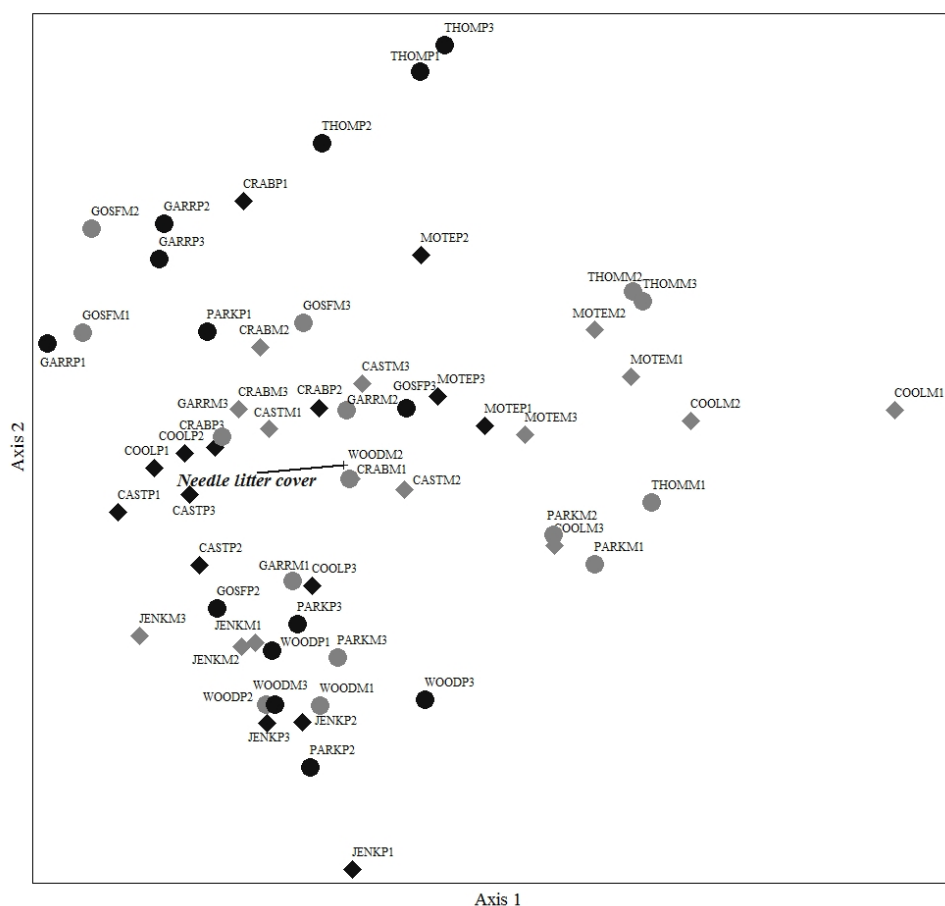
Figure 4.22: NMS ordination of spider assemblages among the sampling plots: ♦ Norway spruce/Scots pine mix; ♦ Matching pure to Norway spruce/Scots pine mix; ● Norway spruce/oak mix ● Matching pure to Norway spruce/oak mix. 'M' or 'P' after site codes refers to mix or pure stand, number denotes plot number. Axis 1 r^2 = 0.24; Axis 2 r^2 = 0.25; Final stress = 12.2; Final instability = 0.0001.

4.3.2.2. Species associations among plantation types

Using Indicator Species Analysis, only one beetle species was identified as having a affinity (high relative frequency and abundance) for a particular stand type; *Pterostichus melanarius* in oak mixes (Indicator-value 47.2%, P = 0.04). This species is commonly found in both open and forested habitats but has a preference for moister areas (Anderson, 2001). Several generalist spider species were identified including *Aygneta subtilis* which was found to be characteristic of both mix stand types (Indicator-value 68.8%, P = 0.03; 60.3%, P = 0.03 in oak and Scots pine respectively); and, *Centromerus dilutus* characteristic of Scots pine mixes (40.1%, P = 0.05). In the pures *Lepthyphantes flavipes* and *Neriene peltata* (69.5%, P = 0.04 and 38.0%, P = 0.02 respectively) were indicators of matching pures for oak mixes and *Lepthyphantes tenebricola* for those matching Scots pine mixes (64.6%, P = 0.02). *L. flavipes and L. tenebricola* are associated with forested habitats whereas *N. peltata* is typically found on low vegetation or bushes in more shaded habitats (Harvey *et al.*, 2002; Nolan, 2010). For moths, no species were identified using Indicator Species Analysis between mixed and pure stand types but an additional analysis was conducted between the oak mix/matching pure group and Scots pine mix/matching pure group as there was evidence that these supporting different assemblages (Fig. 4.23). Barred Red (*Hylaea fasciaria)*, which has a larval food preference for conifers and Common Wave (*Cabera exanthemata*), with a larval

food preference on willow were indicators of the Scots pine mix/matching pure group (45.5%, P = 0.004 and 43.2%, P = 0.02 respectively), but there were no moth species indicators of the oak mix/pure group.
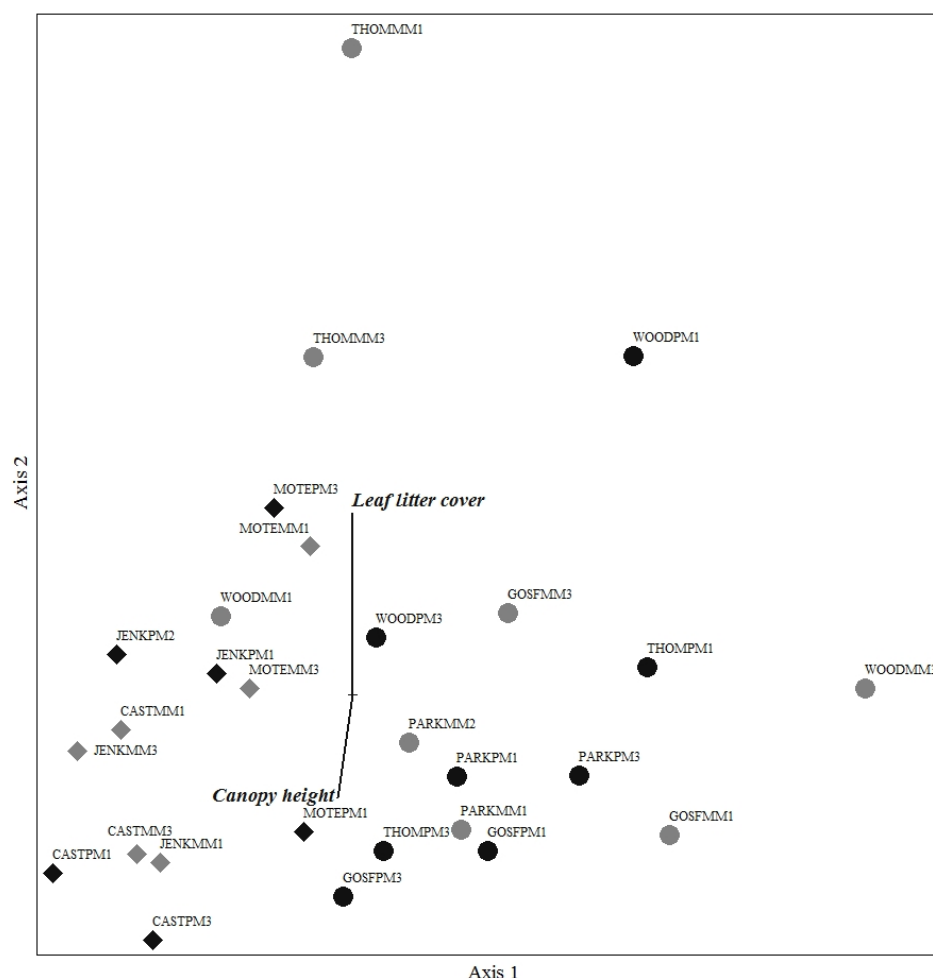
Figure 4.23: NMS ordination of moth assemblages among the sampling plots: ♦ Norway spruce/Scots pine mix; ♦ Matching pure to Norway spruce/Scots pine mix; ● Norway spruce/oak mix ● Matching pure to Norway spruce/oak mix. 'M' or 'P' after site codes refers to mix or pure stand, number denotes plot number. Axis 1 r^2 = 0.16; Axis 2 r^2 = 0.41; Final stress = 12.3; Final instability = 0.0001.

4.3.2.3. Species richness and habitat associations among plantation types

Overall, mix and pure stands supported a similar number of species and relative abundance of forest-associated species across the three taxa (Table 4.58).

4.3.2.4. Environmental attributes between mixed and pure stands

There was no difference in stand structure or habitat variables between mix and pure stands (Table 4.59), with the exception of leaf litter cover which was significantly higher in the oak mix stands compared with the matching pure stands. Interestingly, overall the Scots pine mixes and their geographically matched pures generally displayed greater canopy openness than the Oak pairs, although mean DBH and tree height were similar. However, when DBH within mix types is examined, oak trees within the mix have significantly lower mean DBH than Norway spruce trees within the same mix (mean oak DBH = 16.1

±2.5SD; mean spruce = 35.3 ±6.8SD, T = 6.9 $_{DF = 4}$, P = 0.002) whereas the spruce trees in the oak mix had a significantly larger DBH than those in the matching pures (mean spruce DBH in oak mix = 35.3 ±6.8SD; mean spruce in pure = 30.3 ±4.6 T = 3.66 $_{DF = 4}$, P = 0.02). In contrast, there was no difference between the DBH of Scots pine trees or Norway spruce trees between mix and pure stands (mean Scots pine DBH = 25.0 ±3.9; mean spruce = 27.6 ±6.9, T = 0.89 $_{DF = 4,}$ P = 0.43 and mean spruce DBH in Scots pine mix = 27.6 ±6.9SD; mean spruce in pure = 25.9 ±8.8SD, T = 0.47 $_{DF = 4}$, P = 0.66 respectively).

Table 4.58: Mean (±SD) species metrics between mix and pure stands, tested for significance with Paired T-tests between geographically paired stands (DF = 4).

	Norway spruce/oak			Norway spruce/Scots pine		
	Mix	**Pure**	**Paired T-test**	**Mix**	**Pure**	**Paired T-test**
Spiders#						
Total S	16.0 ±2.9	15.4 ±3.6	n.s	16.5 ±2.3	15.0 ±2.9	n.s
Forest-associated S	6.87 ±1.07	6.90 ±1.27	n.s	6.80 ±1.64	6.86 ±1.28	n.s
Forest-associated species RA	0.46 ±0.14	0.53 ±0.08	n.s	0.37 ±0.11	0.56 ±0.11	n.s
Beetles#						
Total S	8.6 ±1.7	7.1 ±1.0	n.s	7.2 ±1.3	9.7 ±2.8	n.s
Forest-associated S	2.73 ±0.98	2.83 ±1.0	n.s	2.06 ±1.11	3.13 ±1.34	n.s
Forest-associated species RA	0.44 ±0.24	0.57 ±0.22	n.s	0.44 ±0.25	0.49 ±0.18	n.s
Moths§						
Observed S	19.8 ±9.7	20.4 ±7.9	n.s	20.2 ±7.2	21.6 ±5.9	n.s
Expected S†	11.1 ±2.5	10.9 ±1.9	n.s	9.6 ±1.3.6	10.4 ±2.4	n.s
Observed Forest-associated S	8.2 ±3.6	8.8 ±2.5	n.s	9.8 ±4.3	10.2 ±3.4	n.s
Expected forest-associated S†	4.1 ±0.7	3.9 ±0.8	n.s	3.9 ±0.7	3.9 ±1.2	n.s
Conifer-associated S	3 ±1.4	3.2 ±0.8	n.s	3 ±1	3.4 ±1.5	n.s
Broadleaved-associated S	3.6 ±2.4	4.4 ±3.2	n.s	5.6 ±4.0	5.6 ±1.8	n.s

\# Mean values calculated per plot within a site; § Mean values per site † after rarefaction
S = Species Richness, RA = Relative Abundance

Table 4.59: Mean ±SD (per plot within a site) structural and habitat characteristics between mix and pure stands, tested for significance using paired T tests between geographically paired stands (DF = 4).

	Oak			Scots pine		
	Mix	**Pure**	**Paired T test**	**Mix**	**Pure**	**Paired T test**
Stand structure						
Canopy openness (%)	4.4 ±1.5	4.4 ±1.1	-0.38	7.9 ±2.6	8.01 ±4.7	-0.36
Mean DBH (cm)	28.9 ±4.7	30.3 ±4.6	0.19	27.1 ±5.7	25.9 ± 8.8	0.33
Tree height (m)	22.0 ±2.4	21.5 ±2.8	0.78	21.6 ±2.8	20.8 ±3.1	0.96
Number of planted stems	7.3 ±3.0	8.2 ±4.1	1.91	8.8 ±3.7	10.2 ±5.6	0.66
Vegetation cover and richness						
Ground layer vegetation cover (%)	69.1 ±11.2	70.0 ±24.0	-0.07	89.1 ±21.8	66.3 ±42.1	1.4
Lower vegetation layer cover (%)	12.4 ±8.7	13.9 ±14.3	-0.47	20.3 ±19.8	20.0 ±33.8	0.03
Upper vegetation layer cover (%)	0	0		0	0	
Understorey cover	0.33 ±0.49	0.27 ±0.42	0.78	5.0 ±5.7	0.4 ±0.8	1.82
Total plant species richness	24.4 ±3.4	25.6 ±9.3	-0.29	26.9 ±7.3	27.9 ±13.8	-0.14
Litter and soil						
Needle litter cover (%)	26.7 ±18.9	43.3 ±10.3	-1.09	13.6 ±17.1	34.4 ±38.0	-1.04
Leaf litter cover (%)	**11.9 ±7.2**	**0.3 ±0.7**	**3.97***	0.37 ±0.59	0.2 ±0.3	0.75
Litter depth (cm)	1 ±0.6	1.6 ±1.2	-1.07	0.40 ±0.66	0.88 ±1.06	-0.78
Soil pH	4.1 ±0.2	4.1 ±0.3	0.01	4.4 ±0.6	4.3 ±0.1	0.44

* $P \leq 0.05$

4.3.3 Native woodlands survey

Overall 3539 spiders were identified in 12 families and 97 species, of which 80 species were collected in the oak woodlands and 74 in the ash (Appendix 2). The most commonly captured species in both woodland types were *Lepthyphantes zimmermanni* (27% of total catch)*, Agyneta ramosa* (8%) and *Lepthyphantes tenebricola* (5%). In total, 26 of the species sampled were associated with forested habitats, nine with open habitats and 15 with moist habitats (Appendix 2). A total of 6510 Carabid beetles were collected involving 45 species with 33 in the oak woodlands and 38 in the ash (Appendix 3). The most abundant species included *Abax parallelepipedus* (39% of the total catch), *Pterostichus melanarius* (14%) and *Pterostichus madidus*. In total 11 of the species sampled were associated with forested habitats, 11 with open habitats and 17 with moist habitats (Appendix 3).

4.3.3.1. Invertebrate diversity in oak and ash native woodlands

The spider assemblages differed significantly by forest type (nested within year) and also by sampling year (PERMANOVA $F_{1,53}$ = 5.82, P ≤ 0.001 and $F_{1,53}$ = 5.48, P ≤ 0.001 respectively). Figure 4.24 shows the NMS ordinations of spider assemblages sampled during 2007 and 2008. The 2007 spider assemblages were primarily distinguished by woodland type across Axis 1 (r^2 = 0.34), with the exception of all three plots from St John's (STJON) ash woodland. This axis was negatively related to cover of understorey vegetation and leaf litter, and positively related to cover of lower vegetation layers, plant species richness and soil pH. Axis 2 (r^2 = 0.32) did not distinguish assemblages by geographical location

or woodland type and was positively related to the number of stems. Axis 3 ($r^2 = 0.20$) was strongly correlated with longitude (Pearson r = 0.69) indicating a difference in the assemblages sampled across an east-west gradient. However, as this axis did not distinguish the assemblages by woodland type or measured environmental variables it is not presented here.

For the spider assemblages sampled in 2008, oak and ash woodlands were largely separated in the ordination space, with oak woodland plots displaying greater variation in assemblage structure across Axis 1 (Fig. 4.24). Axis 1 was positively related to litter depth and lower vegetation layer cover and negatively related to total plant richness and that of woody species. Axis 3 did not separate stands by forest type, but was negatively related spider species richness and positively related to longitude. Axis 3 ($r^2 = 0.23$) distinguished two plots of the same oak woodland site from the others and may be related to litter depth, which was relatively high in these two plots, ranging from 3-4.2cm in comparison with 0-2.5cm for the remaining plots. However, as Axis 3 mostly represents the difference of two plots from the others it is not shown here.

The beetle assemblages differed significantly by forest type (nested within year) and sampling year (PERMANOVA $F_{1,53}$ = 10.87, P ≤ 0.001 and $F_{1,53}$ = 8.04, P ≤ 0.001 respectively). Figure 4.25 shows the NMS ordinations of the beetle assemblages sampled during 2007 and 2008. Two axes were recommended by the NMS ordination of 2007 beetle assemblages (r^2 = 0.74 correlation between final solution and original distance space). The final stress for this ordination was relatively high (22.8) so not too much emphasis should be placed on specific plot placement in the ordination space, however broad patterns can still be considered reliable (McCune and Grace, 2002). Axis 1 (r^2 = 0.49) did not distinguish the plots by forest type or geographical location, but separated sites with higher vascular plant species richness to some degree. Axis 2 (r^2 = 0.26) broadly distinguished the sites by forest type. This axis was positively related to litter cover and canopy height and negatively related to cover of ground layer vegetation, fine woody debris and number of stems.
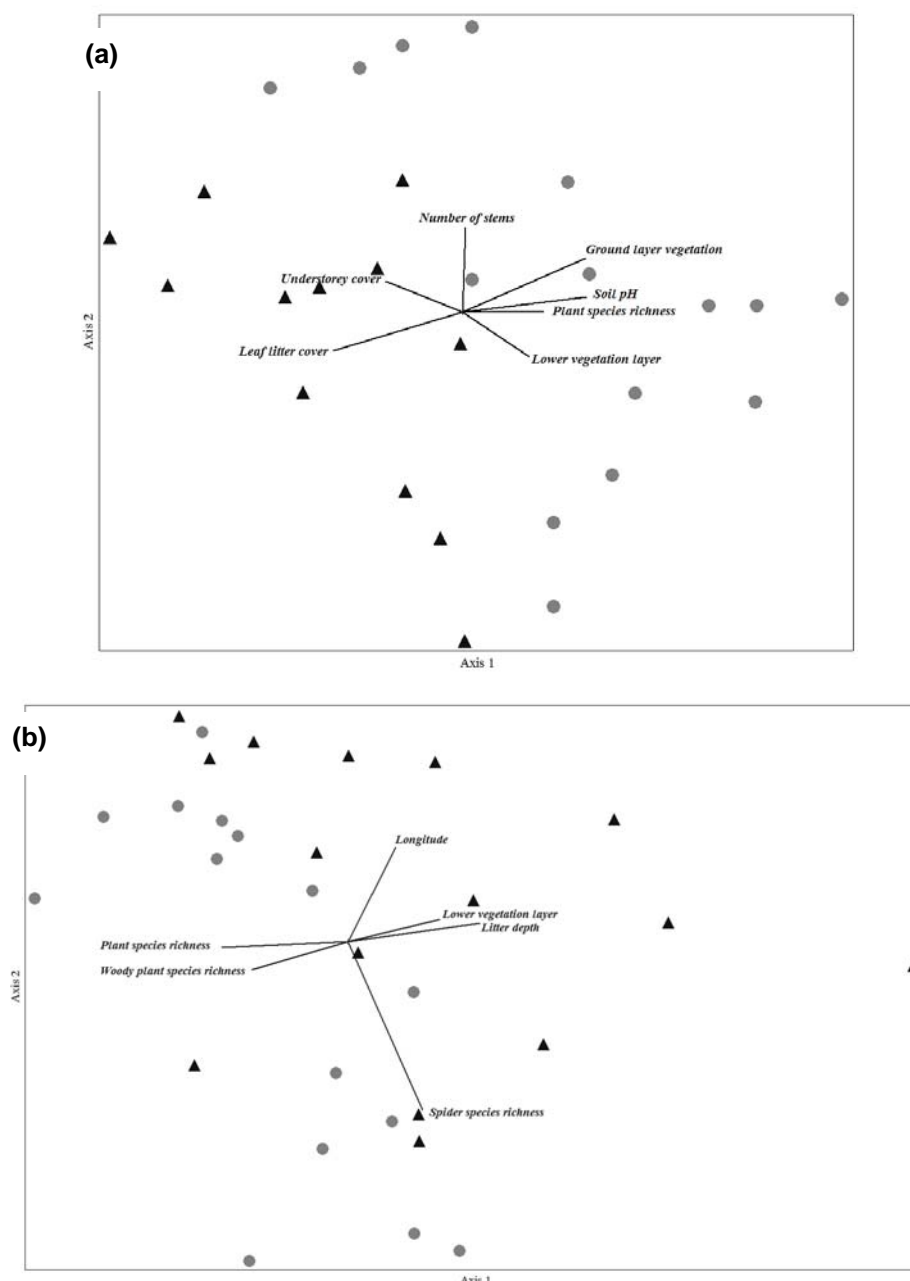
Figure 4.24: NMS ordination of spider assemblages in native oak (▲) and ash (●) woodland plots from: a) 2007 sampling season: Axis 1 r^2 = 0.34, Axis 2 r^2 = 0.32; Final stress = 11.27; Final instability = 0.00001; and; (b) 2008 sampling season: Axis 1 r^2 = 0.37, Axis 2 r^2 = 0.29; Final stress = 11.39; Final instability = 0.00001. Environmental variables are shown if Pearson correlation r^2 with axes > 0.2.

A three dimensional solution was recommended for the NMS ordination of the 2008 beetle assemblages (r^2 = 0.91 correlation of the final solution and the original distance space) (Fig. 4.25). Axis 2 (r^2 = 0.57) primarily distinguished the oak woodlands in the north east from the other plots which had greater litter depth and cover of lower field layer vegetation. The remaining oak woodland plots were distinguished from the majority of the ash woodlands across this axis and Axis 1 (r^2 = 0.22), and were related to litter cover and DBH of trees. The ash woodlands generally had higher plant species richness, ground layer vegetation and canopy cover. Axis 3 (r^2 = 0.12) was primarily related to soil pH (Pearson r = -0.57) rather than forest type, and it is not shown here.
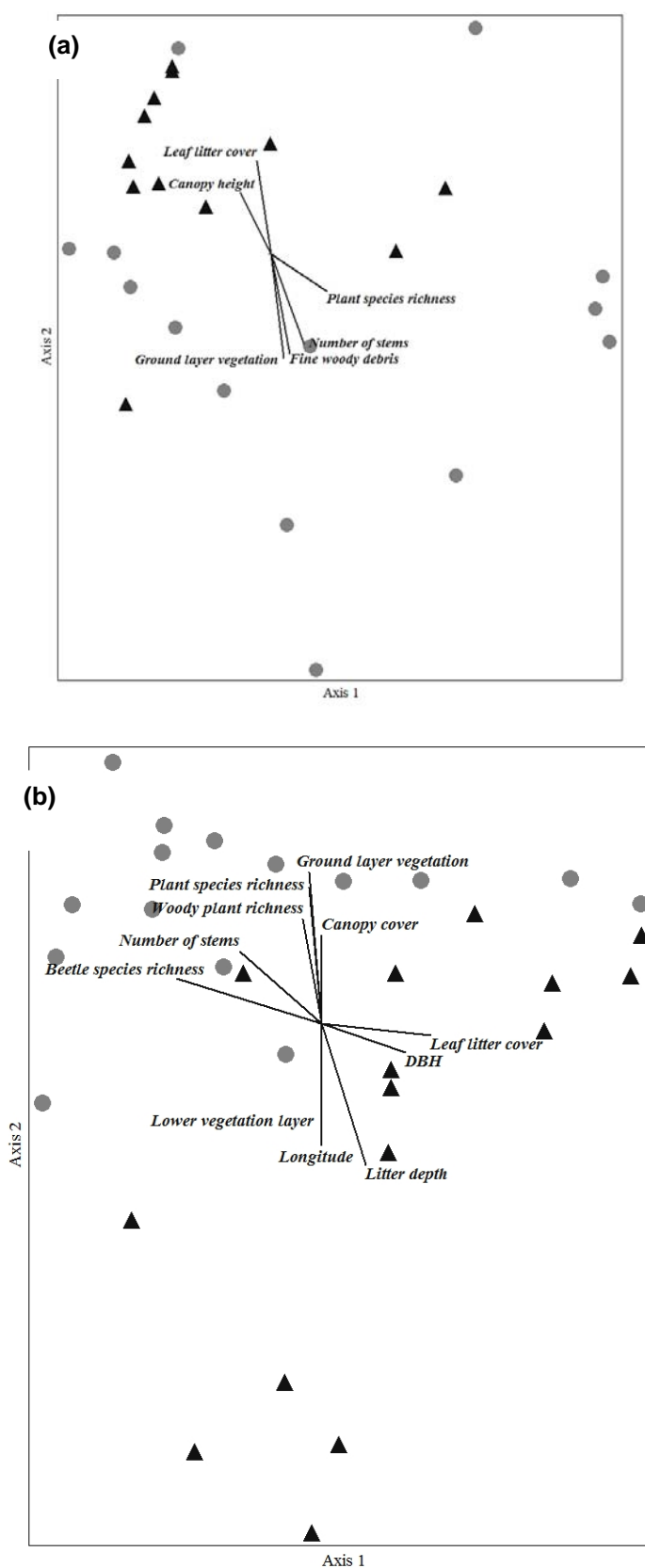
Figure 4.25: NMS ordination of beetle assemblages in native oak (▲) and ash (●) woodland plots: (a) 2007 sampling season: Axis 1 r^2 = 0.48, Axis 2 r^2 = 0.26; Final stress = 22.8, Final instability = 0.006; (b) 2008 sampling season: Axis 1 r^2 = 0.22, Axis 2 r^2 = 0.57. Final stress = 9.94, Final instability = 0.001. Environmental variables are shown if Pearson correlation r^2 with axes > 0.2.

Overall, spider species richness was greater in the oak woodlands, though this difference was only significant during the 2007 sampling season, however, spider species associated with forest, open and moist habitats were similar in richness and relative abundance between woodland types (Table 4.60). The species richness of beetles was significantly greater in ash woodlands sampled in 2008 whereas no difference was found in 2007. However, richness of forest and moist habitat associates showed consistent patterns across years, being greater in ash woodlands. Relative abundance of forest-associated species showed an inconsistent pattern being significantly greater in oak woodlands (in 2007 only). However, this was largely due to differences in the capture of *A. parallelepidedus*, which constituted a mean of 96% (0.01se) of the forest-associated beetles in the 2007 oak woodlands compared to 65% (0.11se) of those in the 2007 ash woodlands. Beetle and spiders species associated with open habitats were similarly low between the forest types.

Table 4.60: Mean (±se) spider and beetle species metrics per plot between woodland types within each year tested with parametric ANOVA *F* and non-parametric Mann-Whitney *U*. Test statistics shown in bold are significant after Bonferroni correction.

	2007			2008		
Variable	**Oak**	**Ash**	**Test statistics DF = 1,25**	**Oak**	**Ash**	**Test statistics DF = 1,28**
Spiders						
Species richness	14.8 ±0.9	11.9 ±0.8	*F* **= 6.1***	16.2 ±0.9	14.1 ±1.3	n.s
Forest S	6.7 ±0.6	5.1 ±0.6	n.s	7.1 ±0.4	5.3 ±0.7	n.s
Open S	0.3 ±0.1	0.2 ±0.1	n.s	0.1 ±0.1	0.6 ±0.1	n.s
Moist S	0.3 ±0.1	0.3 ±0.1	n.s	0.3 ±0.1	0.5 ±0.2	n.s
Forest RA	0.38 ±0.04	0.50 ±0.04	n.s	0.38 ±0.04	0.42 ±0.04	n.s
Open RA	0.01 ±0.01	0.01 ±0.02	n.s	0.01 ±0.01	0.01 ±0.01	n.s
Moist RA	0.01 ±0.01	0.01 ±0.02	n.s	0.01 ±0.01	0.01 ±0.01	n.s
Beetles						
Species richness	7.8 ±1.9	7.7 ±3.1	n.s	7.1 ±0.5	11.3 ±0.9	*F* **= 16.4*****
Forest S	1.9 ±0.1	2.6 ±0.2	*F* **= 4.2***	2.1 ±0.2	3.8 ±0.3	*F* = 22.3***
Open S	1.2 ±0.8	0.7 ±0.9	n.s	0.5 ±0.1	1 ±0.2	n.s
Moist S	2.3 ±0.3	2.5 ±0.5	n.s	1.9 ±0.2	3.5 ±0.5	*F* **= 10.5****
Forest RA	0.59 ±0.20	0.30 ±0.23	*F* = 12.3**	0.53 ±0.24	0.50 ±0.23	n.s
Open RA	0.04 ±0.01	0.02 ±0.01	n.s	0.02 ±0.01	0.07 ±0.02	n.s
Moist RA	0.13 ±0.03	0.24 ±0.04	*F* = 4.2*	0.10 ±0.02	0.30 ±0.04	*U* **= 40****

S = Species Richness, RA = Relative Abundance
* P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001. n.s = Non Significant

Indicator Species Analysis identified nine spider species with an affinity for oak woodlands and four species for ash (Table 4.61). All but one of these species were sheet web builders from the family Linyphiidae, and many of these were associated with forest habitats. In both sampling years species with high indicator-values in oak woodlands included *A. paganus, R. lividus* and to a lesser extent *W. dysderoides* and T*. pallens*, whereas in ash woodlands *D. concolor* and *C. scabrosa* were more common. *L. pallidus* showed conflicting patterns across the years having high indicator-values in the 2007 ash woodlands but higher indicator-value in the oak woodlands during 2008 sampling.

Table 4.61: Indicator Species Analysis of Carabid beetle assemblages between the native woodlandtypes within each sampling year. Significant percentage indicator-values determined with the Monte Carlo test are shown in bold.

	2007 sites		2008 sites		Habitat preference	Moisture preference	Feeding behaviour
	Oak	Ash	Oak	Ash			
Spiders							*Hunting strategy*
Agyneta conigera	**33***	0	4	2	Generalist	Eurytopic	Sheet web
Asthernargus paganus	**42****	0	**51****	0	Forest	Eurytopic	Sheet web
Centromerus dilutus	17	0	**50***	0	Generalist	Eurytopic	Sheet web
Ceratinella scabrosa	4	30	0	**67*****	Generalist	Eurytopic	Sheet web
Diplostylor concolor	0	**71*****	11	31	Forest	Eurytopic	Sheet web
Gonatium rubellum	6	2	**33***	0	Forest	Eurytopic	Sheet web
Lepthyphantes pallidus	1	**49***	40	3	Generalist	Eurytopic	Sheet web
Lepthyphantes tenebricola	28	38	21	**69***	Forest	Eurytopic	Sheet web
Microneta viaria	**69*****	2	13	24	Forest	Eurytopic	Sheet web
Robertus lividus	**53****	1	**58****	1	Generalist	Eurytopic	Scaffold web
Tapinocyba pallens	29	1	**47****	0	Forest	Eurytopic	Sheet web
Walckenaeria acuminata	37	30	**57***	9	Generalist	Eurytopic	Sheet web
Walckenaeria dyderoides	**52****	1	30	1	Generalist	Eurytopic	Sheet web
Carabid beetles							*Prey preference*
Abax parallelepipedus	**81*****	14	41	59	Forest	Eurytopic	Generalist predator
Badister bullatus	0	7	0	**33***	Generalist	Eurytopic	Snails
Carabus granulatus	39	6	4	**59***	Generalist	Moist	Generalist predator
Carabus problematicus	17	0	0	**65*****	Forest	Eurytopic	Generalist predator
Leistus fulvibarbis	0	**33***	0	7	Forest	Eurytopic	Collembola
Loricera pilicornis	**45***	1	5	**76****	Generalist	Eurytopic	Collembola
Nebria brevicollis	23	15	1	**81*****	Forest	Eurytopic	Generalist predator
Notiophilus biguttatus	**57***	4	3	29	Generalist	Eurytopic	Collembola
Pterostichus madidus	27	32	6	**71***	Generalist	Eurytopic	Generalist predator
Pterostichus melanarius	36	30	12	**80****	Generalist	Moist	Generalist predator
Pterostichus niger	26	22	**92*****	3	Generalist	Eurytopic	Generalist predator
Pterostichus strenuus	10	12	1	**58***	Generalist	Eurytopic	Generalist predator
Trechus obtusus	4	**59***	5	**50***	Generalist	Eurytopic	Generalist predator

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

In contrast to spiders, fewer beetle species were identified as indicators of oak woodlands (four) in comparison with ash (nine), and most high indicator-values were from ash woodlands sampled during 2008 (Table 4.61). Several indicator species were associated with forest habitats, however only *T. obtusus,* a generalist species, was found to have a high indicator-value in both years within the same woodland type (ash). The ash woodlands also had two species with high indicator-values associated with

moist habitats. *A. parallelepipedus* had relatively high indicator-values across both forest types and years suggesting it is a forest generalist species in Ireland.

4.3.3.2. Environmental characteristics of oak and ash native woodlands

In terms of woodland structure, the sites were different between sampling years: those studied in 2007 were similar in canopy cover, tree height and DBH between woodland types, whereas the 2008 oak woodlands had lower canopy cover, but greater tree height and DBH than the ash woodlands sampled in that year (Table 4.62). The number of stems, however, was similarly high in the ash woodlands across both years. Plant species richness and cover of ground vegetation was higher in the ash woodlands in both years, whereas cover of lower vegetation layer was greater and understorey cover was lower in the 2008 oak woodlands. Cover and depth of litter was significantly greater in oak woodlands as was soil organic content, whereas soil pH was greater in ash woodlands. Amount of deadwood (coarse and fine woody debris) was similarly low (< 5% cover) in both woodland types.

Table 4.62: Mean (±se) cover of environmental variables between the woodland types sampled in each year tested with non-parametric Mann-Whitney *U*. Test statistics in shown bold are significant after Bonferroni correction.

Variable	2007			2008		
	Oak	Ash	*U* (DF = 1,25)	Oak	Ash	*U* (DF = 1,28)
Woodland structure						
Canopy height (m)	17.4 ±1.4	16 ±0.9	n.s	21.5 ±1.5	18.5 ±1.2	n.s
DBH (cm)	14 ±1.3	11.6 ±0.9	n.s	31.3 ±3.8	12.1 ±0.8	*U* = **10.0*****
No. of stems‡	28 ±4	145 ±31	*U* = **3.0*****	55 ±15	526 ±109	*U* = **9.5*****
Plant richness and cover						
Total plant species richness	25.3 ±2.1	35 ±2	*U* = 32.5**	26.8 ±2.1	47.8 ±3.5	*U* = **18.5*****
Woody species richness	7.8 ±0.5	9.7 ±0.5	*U* = 37.5**	6.7 ±0.5	10.6 ±0.7	*U* = **27.0*****
Vascular plant species richness	5.6 ±0.7	11.5 ±7.8	*U* = 38**	6.9 ±0.8	20.5 ±2.2	*U* = **13.5*****
Non-vascular plant species richness	11.8 ±1.5	13.5 ±0.7	n.s	13.2 ±1.2	16.8 ±1.3	*U* = 60.5*
Ground layer vegetation cover (%)	18.7 ±4.2	92.5 ±2.7	*U* = **0*****	27.1 ±7	77.7 ±4.4	*U* = **18.0*****
Lower vegetation layer cover (%)	25.6 ±6.1	31.1 ±4.2	n.s	57.6 ±5.7	16 ±4.6	*U* = **13.5*****
Understorey cover (%)	30 ±6.5	29.3 ±5.6	n.s	16.1 ±5	37.6 ±4.9	*U* = 60.5*
Canopy cover (%)	96.1 ±0.4	96.5 ±0.4	n.s	91.6 ±0.8	96.1 ±0.6	*U* = **23.5*****
Deadwood, litter and soil						
Coarse Woody debris cover (%)	1.3 ±0.4	4.6 ±0.9	*U* = **23.0*****	1.9 ±0.4	3 ±0.8	n.s
Fine Woody Debris cover (%)	2.6 ±0.3	3.9 ±0.5	n.s	2.6 ±0.2	3.4 ±0.5	n.s
Litter cover (%)	71.3 ±5.8	17.1 ±2.8	*U* = **0.5*****	55.3 ±5.6	30.7 ±4.7	*U* = **43.5****
Litter depth (cm)	1.4 ±0.3	0.3 ±0.1	*U* = **29.0*****	2.1 ±0.2	0.6 ±0.1	*U* = **22.0*****
Soil pH	4.1 ±0.1	6.2 ±0.2	*U* = **0*****	3.9 ±0.1	5.8 ±0.3	*U* = **2.0*****
Organic content (%)	25 ±7.1	13.1 ±1	n.s	37.9 ±4.8	26.5 ±2.9	n.s

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001. n.s: Non Significant

4.3.3.3. Relationship between spider and Carabid beetle diversity and environmental characteristics

At the plot level, cover of ground and lower vegetation layers and forest type were related to overall spider species richness (Table 4.63). There were also two significant interactions, between both ground and lower vegetation layer, and forest type where these variables had a relationship in oak woodlands but negative in ash. Forest spider species showed a smiliar trend (and interaction) with lower vegetation layer cover. Overall beetle species richness was related to sampling year (being higher in 2008), and negatively related to litter depth, however, forest beetle species richness was not related to any of the variables. There was a negative relationsiph with slope for total richness of both taxa. At the site and landscape level only one correlation was significant: forest beetle richness was positively related to latitude in ash woodlands (Spearman's = 0.85, P = 0.002).

Table 4.63: Stand scale relationships between species metrics and environmental characteristics using Generalized Linear Mixed Models with Poisson distribution (n = 57 plots). Interaction terms are denoted by X.

	Spiders		Beetles	
	Model parameters	**Test statistics (z)**	**Model parameters**	**Test statistics (z)**
Total species richness	Forest type	$z = 2.94**$	Sampling year	$z = -3.34**$
	Ground layer vegetation cover	$z = 1.97*$	Litter depth	$z = -2.62$
	Ground layer vegetation cover X Forest type - Ash	$z = -3.11**$	Slope	$z = -2.54*$
	Lower vegetation layer cover X Forest type - Ash	$z = -3.03**$		
	Lower vegetation layer cover	$z = 2.04*$		
	Slope	$z = -1.97*$		
Forest-associated species richness	Forest type	$z = -0.21$	None significant	
	Lower vegetation layer cover	$z = 0.62$		
	Lower vegetation layer cover X Forest type - Ash	$z = -2.14*$		

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

4.3.4 Comparison of forest types

A three dimensional solution was recommended for the NMS ordination of spider assemblages among forest sites (r^2 = 0.76 correlation between original distance and ordination matrices, Axes 1-3 representing r^2 0.24, 0.26 and 0.26 respectively) (Fig. 4.26). The spider assemblages were broadly distinguished by forest type, primarily through a separation of the plantations from the native woodlands, but also with a gradual separation of mixes from pures. The native woodlands were related to greater understorey cover, leaf litter and soil pH, particularly in the ash woodlands; whilst the plantations were related to greater needle litter cover. Overall, the native woodland sites were more widely spread across both axes in comparison with the plantations. Axis 3 represents a further separation of the spider assemblages, likely driven by the relative abundance of the *Lepthyphantes zimmermanni,* which is highly correlated with this axis (Pearson correlation *r* = 0.79). This is species is highly abundant in a range of habitats, but favours

more shaded situtions. This axis was also positively related to canopy cover (Pearson correlation r = 0.42), but as it was not related to the main forest types it is not presented here.
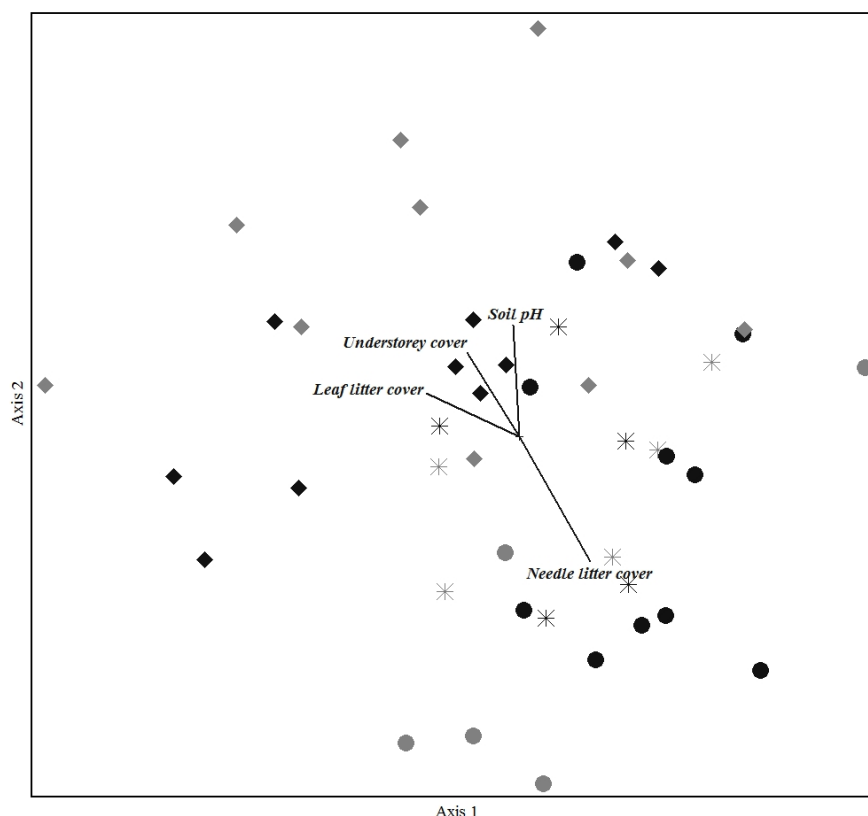
Figure 4.26: NMS ordination of spider assemblages among the forest sites: ♦ = Oak native woodland; ♦ = Ash native woodland; ● = Sitka spruce plantation; ● = Norway spruce plantation; ✱ = Norway spruce/oak mix plantation; ✱ = Norway spruce/Scots pine mix plantation. a) Axis 1 r^2 = 0.24; Axis 2 r^2 = 0.26; Final stress = 15.41; Final instability = 0.00001.

The NMS ordination of beetle assemblages (total r^2 = 0.89, Axis 1 = 0.68; Axis 2 = 0.21) primarily distinguished the sites by geographical location, with nine of the ten plantations in the north of the island of Ireland separated from the majority of the other sites in central and southern regions (Fig. 4.27). This is exemplified by the correlation of latitude with both axes. The more northerly plantations generally had higher needle litter cover, as shown by the positive correlation between Axis 1 and this variable (Pearson r = -0.47). The native woodlands were clustered with the plantations in the central and southern regions, though there is a slight distinction of these by native woodland type across Axis 2. However, there were no consistent differences between the plantation types.

For the NMS ordination of moth assemblages a three dimensional solution was recommended with a total r^2 of 0.72 (Fig. 4.28). Across Axis 1 (r^2 = 0.24) the native woodlands were distinguished from the plantation forests, with oak and ash woodlands broadly separated from each other across Axis 2 (r^2 = 0.21). However, the plantations were not distinguished by forest type. The native woodlands were related to canopy and understorey cover and plant species richness, and the oak woodlands were particularly associated with higher lower vegetation layer and leaf litter cover. The plantations were related to needle litter cover and longitude. Axis 3 (r^2 = 0.27) was not related to forest type or and of the environmental variables measured, but was negatively related to moth species richness (Pearson r = -0.49), however this axis is not presented here.
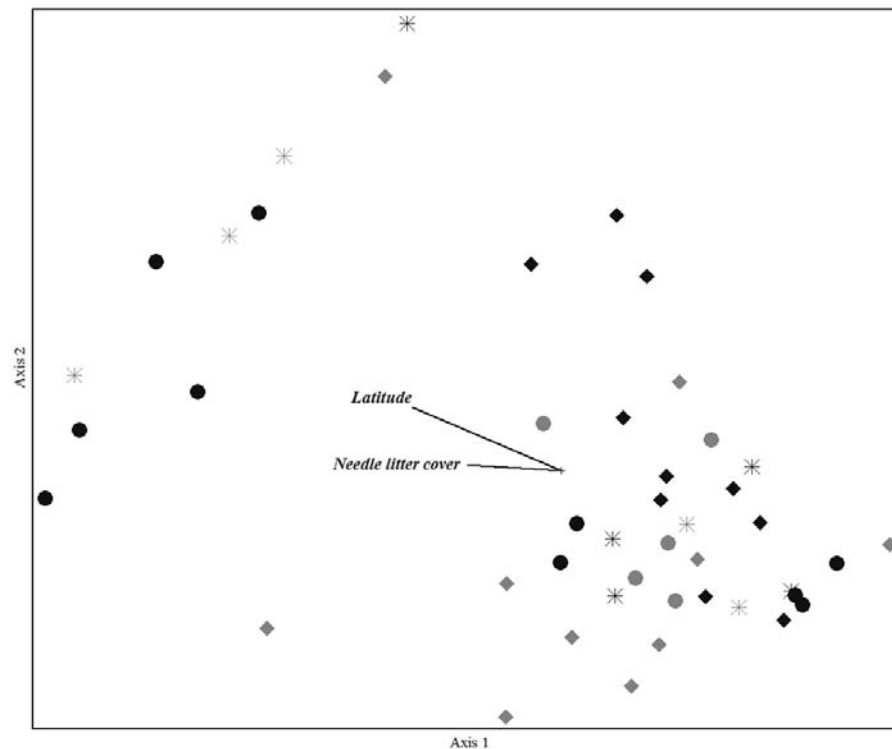
Figure 4.27: NMS ordination of beetle assemblages among the forest sites: ♦ = Oak native woodland; ♦ = Ash native woodland; ● = Sitka spruce plantation; ● = Norway spruce plantation; ✳ = Norway spruce/oak mix plantation; ✳ = Norway spruce/ Scots pine mix plantation. Axis 1 r^2 = 0.68; Axis 2 r^2 = 0.21; Final stress = 13.81; Final instability ≤ 0.00001.
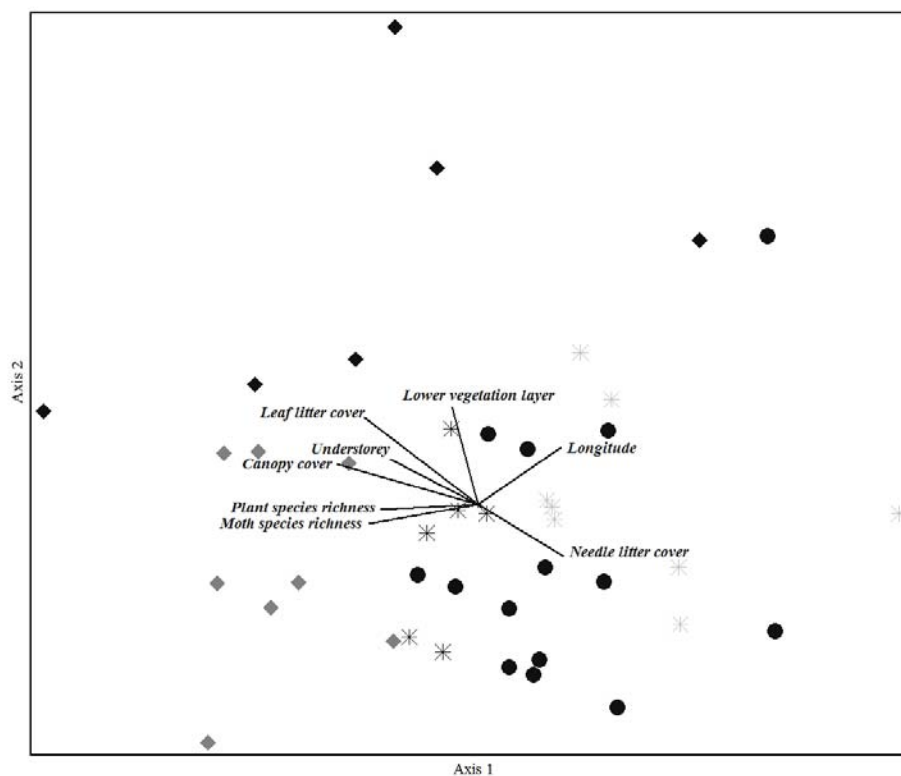
Figure 4.28: NMS ordination of moth assemblages among the forest types: ♦ = Oak native woodland; ♦ = Ash native woodland; ● = Norway spruce plantation; ✳ = Norway spruce/oak mix plantation ; ✳ Norway spruce/Scots pine mix plantation. Axis 1 r^2 = 0.24; Axis 2 r^2 = 0.21; Final stress = 13.24; Final instability ≤ 0.00001. Joint biplot variables represent percentage cover unless otherwise stated.

4.3.4.1 Species associated with plantations and native woodlands

Indicator Species Analysis revealed 20 spider species associated with either plantations or native woodlands, 12 of which were associated with forest habitats (Table 4.64). Six forest-associated spider species were identified for either plantation forests or native woodlands, and all of these were captured in relatively low numbers in the other forest type, with the exception of *L. tenebricola.* This species was an indicator of the plantations, but also had a relatively high indicator-value in the native woodlands, suggesting that it is more of a forest generalist. By contrast, only one forest-associated beetle species (*C. rotundicollis*) was identified as being associated with a particular forest type and this was an indicator of the plantations. The remaining species with significant indicator-values were habitat generalists. Ten moth species were identified as being associated with either plantation forests or native woodlands, all but one of which were associated with tree species (Table 4.65). In the plantations, four of the six species identified were associated with conifer trees, all of which were unqiue to plantations. A further species was also identified as an indicator that has a preference for both broadleaved and conifer trees. In the native woodlands three of the species identified were associated with broadleaved trees and one with grasses.

Table 4.64: Percent indicator-value of spider and beetle species between the plantations and native woodlands derived using Indicator Species Analysis. Significant indicator-values are shown in bold type.

	Plantation (n = 25)	Native woodland (n = 20)	Habitat association
Spiders			
Diplocephalus latifrons	**81***	6	Forest
Asthenargus paganus	**77***	9	Forest
Lepthyphantes flavipes	**74**	6	Forest
Lepthyphantes tenbricola	**65***	29	Forest
Robertus lividus	**60***	16	Generalist
Centromerus dilutus	**55***	10	Generalist
Porrhomma pallidum	**43***	1	Generalist
Erigonella hiemalis	**35***	0	Forest
Maro minutus	**34***	2	Generalist
Pelecopsis nemoralis	**30***	0	Forest
Saaristoa abnormis	29	**64**	Generalist
Walckenaeria acuminata	20	**65**	Generalist
Agyneta ramose	8	**70**	Forest
Diplocephalus picinus	4	**49**	Forest
Microneta viaria	1	**65**	Forest
Dicybium tibiale	1	**62**	Forest
Diplostylor concolor	1	**53**	Forest
Micrargus herbigradus	1	**32***	Generalist
Linyphia hortensis	0	**30**	Forest
Walckenaeria cuspidate	0	**25***	Generalist
Beetles			
Notiophilus biguttatus	**85***	6	Generalist
Calathus rotundicollis	**75***	0	Forest
Pterostichus nigrita	**36**	0	Generalist
Pterostichus strenuous	3	**54**	Generalist
Agonum fuliginosum	0	**44**	Generalist
Bembidion manniheimmi	0	**25**	Generalist

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

Table 4.65: Percent indicator-value of moth species between the plantations and native woodlands derived using Indicator Species Analysis. Significant indicator-values are shown in bold type.

	Plantations (n = 20)	Native woodlands (n =10)	Larval food preference
Thera obeliscata	**79****	0	Conifer
Thera Britannica	**68****	0	Conifer
Odontopera bidentata	**62***	9	Broadleaves and conifer
Macaria liturata	**60****	0	Conifer
Cabera exanthemata	**49***	1	Broadleaves
Hylaea fasciaria	**40***	0	Conifer
Ochropacha duplaris	2	**64*****	Broadleaves
Biston betularia	1	**36***	Broadleaves
Phalera bucephala	0	**39***	Broadleaves
Protodeltote pygarga	0	**29***	Grasses

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

Excluding singletons and doubletons, two forest spider species were unique to the native woodlands: *L. hortensis*, which is associated with deciduous forest; and P. *listeri* a species associated with mixed forest (Table 4.66). These species were collected in 6 and 4 sites respectively, suggesting an affiliation for broadleaved woodlands rather than plantations. For beetles, two species were unique to a forest type: P*. oblongopunctatus*, which was collected in two oak woodland sites and *O. obscurus* in two ash woodlands. This latter species is known from wet forested habitats. Four moth species were unique to the plantation forests: *M. liturata* (from 12 sites), which was identified as an indicator species (Table 4.65), but also *E. abietaria* (from 6 sites), *D. ribeata* (from 4 sites), and *H. fasciaria* (from 8 sites). All of these species are associated with conifers as the larval food plant. Three moth species were unique to the native woodlands, all of which have a larval preference for broadleaved trees, though they were only sampled in a few sites: *A. sylvata* (1 site), *G. papilionaria* (2 sites) and P*. rectangulata* (1 site).

Table 4.66: Unique forest-associated species to either plantation or native woodland among the taxa (excluding singletons or doubletons). Values represent number of individuals captured.

	Plantations	Native woodlands	Habitat association
Spiders			
Linyphia hortensis	0	11	Deciduous forest
Pachygnatha listeri	0	16	Mixed forest
Beetles			
Oxysehpalus obscurus	0	57	Forest
Pterstichus oblongopunctatus	0	4	Forest
Moths			
Hylaea fasciaria	15	0	Conifer
Eupithecia abietaria	10	0	Conifer
Abraxas sylvata	0	5	Broadleaves
Pasiphila rectangulata	0	4	Broadleaves
Geometra papilionaria	0	5	Broadleaves
Deileptenia ribeata	4	0	Conifer
Macaria liturata	22	0	Conifer

4.3.4.2 Species richness in plantations and native woodlands

Across the taxa, total number of species and the various habitat associates did not differ between plantation forests and native woodlands (Table 4.67), with the exception of conifer associated moth species which were supported in higher numbers in the plantations.

4.3.4.3 Relationship between invertebrate diversity and environmental variables

In native woodlands, spider species richness was related to forest type, cover of the lower vegetation layers and slope (Table 4.67). Beetles species richness was also negatively related to slope, and additionally litter depth and sampling year, which is probably related to different structural features in the oak woodlands sampled between 2007 and 2008 (see native woodland survey section for details). However, there were no significant relationships between beetle forest species and the environmental variables measured. Within the plantations, total spider richness was positively related to forest type, being higher in the mixes. However, there was also a significant interaction between canopy cover and forest type, where richness was negatively associated with canopy cover in the mix plantations. Total spider richness was also negatively related to fine woody debris cover. No variables were significant for forest-associated spider species. Total and forest-associated beetle species richness were negatively related to both ground layer vegetation cover and soil organic content in the plantations. There was also a negative relationship between forest-associated beetles and forest type, with fewer species in the mixes. At the larger scale no land cover variables were significant for spiders or beetles within 200m or 1km of the sampling plots.

Table 4.67: Mean ±se species richness between plantations and native woodlands for each taxa. Relationships examined for significance with non-parametric Kruskal Wallis *H*, parametric ANOVA *F* DF = $_{3,41}$ (spiders and beetles) and ANCOVA DF = $_{3,26}$ (moths) with sample date as a covariable.

	Plantations	Native woodlands	ANOVA *F*
***Spiders*#**	n = 25	n = 20	
Total species richness	15.0 ±0.6	14.2 ±0.7	n.s.
Forest-associated species richness	6.6 ±0.2	6.2 ±0.4	n.s.
***Beetles*#**			
Total species richness	8.8 ±0.5	8.5 ±0.6	n.s.
Forest-associated species richness	2.9 ±0.2	2.6 ±0.2	n.s.
***Moths*§**	n = 20	n = 10	
Total species richness	20.5 ±1.6	21.4 ±1.9	n.s.
Expected species richness†	10.5 ±0.5	11.3 ±0.6	n.s.
Forest-associated species richness	9.3 ±0.7	8.1 ±0.9	n.s.
Expected forest-associated species richness†	3.9 ±0.2	4.0 ±0.2	n.s.
Broadleaved-associated species richness	6.4 ±0.7	7.9 ±0.8	n.s.
Conifer-associated species richness	2.9 ±0.2	0.2 ±0.2	*F* = 57.1***

*P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001;† After rarefaction
Mean richness per plot within each site; §Total richness per site

Canopy height was positively related to both total and forest moth species richness (Table 4.68), however for both metrics there was also a significant interaction between forest type and canopy height with a negative relationship in both woodland types. Both richness measures were also positively related to forest type in the woodlands, being higher in both woodland types. For total species richness there was also a negative relationship with ground vegetation cover and a positive relationship with plant species richness. There was only one significant variable at the larger scale: a negative relationship between expected forest species richness and total mature plantation within 1km.

Table 4.68: Relationship between expected moth species richness and environmental variables within stands and at 200m and 1km scales using GAMs with (quasi-) Poisson distribution, n = 30.

	Model parameters	Test statistics
Expected species richness†	Canopy height	T = 4.78***
	Canopy height X Forest type - Ash	T = -2.55*
	Canopy height X Forest type - Oak	T = -3.89***
	Forest type - Ash	T = 2.30*
	Forest type - Oak	T = 3.98***
	Ground layer vegetation	T = -2.82*
	Plant species richness	T = 3.22**
Expected forest-associated species richness†	Canopy height	T = 2.37*
	Canopy height X Forest type - Ash	T = -1.99**
	Canopy height X Forest type - Oak	T = -2.99**
	Forest type - Ash	T = 1.79
	Forest type - Oak	T = 2.92**
	Total mature plantation 1km	T = -3.80***

†After rarefaction

4.4 Canopy-dwelling invertebrates

4.4.1 Afforestation and reforestation survey

4.4.1.1 Canopy spider diversity

In total, 23 spider species were identified from 582 adult individuals (Appendix 9). The three most common spider species encountered across all forest types (age class IV afforested, age class IV reforested, age class III afforested, and age class III reforested Sitka spruce plantations) were *Neriene peltata* (Araneae: Linyphiidae), *Paidiscura pallens* (Araneae: Theridiidae) and *Pelecopsis nemoralis* (Araneae: Linyphiidae), which combined made up approximately 63% of the total spider abundance (see Appendix 9 for more details). *Neriene peltata* is a habitat generalist, and is not specifically associated with woodland habitat, while *Paidiscura pallens* and *Pelecopsis nemoralis* are both mixed-forest-associated species.

There were no significant differences (P > 0.05) in mean abundances, rarefied species richness or assemblage composition of canopy spiders among any of the forest types, either when all species were included or when singletons were removed. Additionally, there were no significant spider Indicator species for any of the forest types.

There were several significant differences (P < 0.05, 2-tailed T-test, 2 DF) in the proportional guild composition (mean relative species richness ± se) of spiders among forest types (Table 4.69). It was notable that there were no actively hunting spider species sampled at any of the Sitka spruce forests, while sheet-web spinning spiders (Family Linyphiidae) were the dominant group, comprising at least 75% of all individuals (Table 4.69). Age class IV reforested, age class III afforested and age class III reforested plantations had significantly higher proportions of orb-web spinners compared to age class IV afforested plantations, as there were no individuals from this guild present at the latter forest type (Table 4.69). Age class IV afforested plantations also had a significantly higher proportion of sheet-web spinning spiders compared to age class IV reforested plantations. There were no other significant differences in the relative proportions of spider guilds among forest types. There were no significant differences in the relative proportions of spider species habitat associations among the four forest types surveyed, and all spider species sampled were classified as common.

4.4.1.2 Canopy beetle diversity

Fewer beetles were sampled in comparison to spiders, with 20 species identified from 181 individuals (Appendix 10). The three most abundant Coleoptera species overall comprised approximately 57% of all beetle individuals. *Malthodes marginatus* (a predatory species) and *Strophosoma melanogrammum* (a phytophage) are both mixed forest-associates, while *Rhagonycha lignosa* is a generalist predator (see Appendix 10 for more details). Similarly to spiders, there were no significant differences (P > 0.05) in mean abundances, rarefied species richness, or assemblage composition for beetle species-level data, either when all species were included or when singletons were removed. There were no significant beetle Indicator species for any of the forest types.

There were several significant differences (P < 0.05, 2-tailed T-test, 2 DF) in the proportional guild composition (mean relative species richness ± se) of beetles among forest types (Table 4.69). Age class IV afforested and age class III reforested plantations had significantly higher proportions of mycetophagous beetles compared to age class IV reforested and age class III afforested plantations, as there were no mycetophagous species sampled in the latter two forest types (Table 4.69). Almost half of

all beetles at afforested age class III plantations were phytophagous species; this value was significantly higher than the values for that guild at all three other forest types. In contrast, afforested age class III plantations had the lowest proportion of predatory beetles of all the forest types, and this was significantly lower compared to both age class IV and age class III reforested plantations. Age class III reforested plantations had a significantly lower proportion of xylophagous species compared to all other forest types.

Table 4.69: Proportional spider and beetle guild composition (mean relative species richness ± se) across afforested and reforested Sitka spruce forests at two age classes.

	Age class III afforested (IIIA)	Age class IV afforested (IVA)	Age class III reforested (IIIR)	Age class IV reforested (IVR)	Significant differences (z-score)
Spider Guilds					
Orb web	0.08 ± 0.02	0.00 ± 0.0	0.10 ± 0.03	0.05 ± 0.02	IVA < IIIA (3.26)*, IIIR (3.23)*, IVR (3.15)*
Scaffold Web	0.12 ± 0.04	0.11 ± 0.03	0.10 ± 0.03	0.21 ± 0.05	
Sheet Web	0.80 ± 0.05	0.89 ± 0.03	0.81 ± 0.05	0.75 ± 0.06	IVA > IVR (2.01)*
Beetle guilds					
Mycetophagous	0.00 ± 0.00	0.04 ± 0.01	0.11 ± 0.03	0.00 ± 0.00	IVA > IIIA (3.13)*, IVR (3.13)*; IIIR > IIIA (3.38)*, IVR(3.38)*;
Phytophagous	0.45 ± 0.08	0.23 ± 0.06	0.14 ± 0.04	0.17 ± 0.05	IIIA > IVA (2.13)*, IIIR (3.40)*, IVR(2.99)*
Predator	0.39 ± 0.08	0.51 ± 0.08	0.69 ± 0.07	0.67 ± 0.07	IIIR > IIIA (2.89)*, IVR(2.58)*
Xylophagous	0.16 ± 0.05	0.22 ± 0.06	0.06 ± 0.02	0.17 ± 0.05	IIIR < IIIA (2.20)*, IVA(2.74)*, IVR (2.25)*,

Significance Levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

There were no significant differences in the proportions of forest generalists and forest specialists among forest types. However, there were several significant differences in the specific habitat associations of beetle species among forest types (Table 4.70). There were no broadleaved-associated beetle species sampled at either age class IV or age class II reforested sites, but broadleaved-associated species were sampled at both age classes in afforested plantations (Table 4.70). No conifer-associated species were sampled at age class IV afforested plantations, which was significantly lower than at all other forest types. There were no significant differences in habitat associations of the remaining beetle species among forest types.

In total, there were two Red-listed beetle species sampled at Sitka spruce forests, neither of which were phytophagous: the predatory *Malthodes guttifer* (Coleoptera: Cantharidae) (1 individual at one forest) and the xylophagous *Athous (Orthathous) campyloides* (Coleoptera: Elateridae) (20 individuals at 6 forests) (Appendix 11). Reforested age class III sites had a significantly lower mean relative species richness of rare species compared to all other plantation forest types.

4.4.1.3 Other taxa

In addition to spiders and beetles, 46,571 Diptera (true flies) were identified to family-level and 174,281 invertebrates from 20 other taxa were identified to Order or Super-family-level (See Appendices 12 and 13 for full list of all taxa identified). The three most abundant taxa overall were Diptera, Hemiptera and

Collembola (21%, 27% and 48% of all individuals, respectively); these three Orders alone comprised between 90% and 96% of all the taxa identified (including spiders and beetles) across the four forest types (Table 4.71).

Approximately half of all the Diptera sampled were from the Chironomidae family, with the second and third most abundant families being the Ceratopogonidae and Cecidomyiidae (~38% and ~3% of all individuals, respectively). Thus, over 90% of the Diptera sampled belonged to only three families, with 30 families comprising less than 10% of all individuals (Appendix 12). Collembola and Aphididae dominated the remaining taxa, while 21 other Orders made up the remaining 4% of individuals (Appendix 13).

Table 4.70: Habitat associations of beetle species (mean relative species richness ± se) across afforested and reforested Sitka spruce forests at two age classes.

	Age class III afforested (IIIA)	Age class IV afforested (IVA)	Age class III reforested (IIIR)	Age class IV reforested (IVR)	Significant differences (z-score)
Habitat Association					
Broadleaves	0.06 ± 0.02	0.08 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	IVA > IVR (3.27)*; IIIA > IIIR (3.20)*
Conifers	0.15 ± 0.04	0.00 ± 0.00	0.11 ± 0.03	0.17 ± 0.05	IVA < IIIA (3.51)*, IIIR (3.38)* IVR (3.60)*
Deadwood	0.29 ± 0.07	0.22 ± 0.06	0.36 ± 0.08	0.25 ± 0.07	ns
Mixed Forest	0.21 ± 0.05	0.30 ± 0.07	0.22 ± 0.06	0.33 ± 0.07	ns
None	0.23 ± 0.06	0.39 ± 0.08	0.31 ± 0.07	0.25 ± 0.06	ns
Rarity Category					
Notable B[a]	0.17 ± 0.05	0.18 ± 0.05	0.06 ± 0.02	0.17 ± 0.05	IIIR < IIIA (2.20)*, IVA(2.36)*, IVR (2.25)*

Significance Levels: ns: not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. [a]Red-listed according to the JNCC (2010)

While there were no significant differences in total abundances of the three most abundant Orders, there were several significant differences among forest types in their mean relative abundances (Table 4.71). The relative proportion of Diptera (mean relative abundance ± se) at age class III afforested plantations was significantly lower than at both age class IV forest types, while there was a significantly lower proportion of Collembola at age class IV afforested plantations compared to both age class III forest types.

Total Collembolan abundances were negatively correlated with the proportional species richness of scaffold- (Spearman's correlation coefficient: -0.797; $P < 0.001$; n = 12, 2-tailed) and sheet-web spinning spiders (Spearman's correlation coefficient: -0.844; $P < 0.001$; n = 12, 2-tailed), but there were no significant correlations between any of the other taxa or guilds mentioned above.

Table 4.71: Total and mean relative abundances (± se) of the three most abundant taxa at four Sitka spruce plantation forest types.

	Family	Age class III afforested (IIIA)	Age class IV afforested (IVA)	Age class III reforested (IIIR)	Age class IV reforested (IVR)	Significant differences (z-score)
Total abundance	Diptera	4082	17322	9075	16092	n.s.
	Aphidoidea	12017	18662	15813	12288	n.s.
	Collembola	37766	1359	49882	17633	n.s.
Relative abundance	Diptera	0.17 ± 0.05	0.46 ± 0.08	0.31 ± 0.07	0.39 ± 0.08	IIIA < IVA* (2.98), IVR* (2.38)
	Aphidoidea	0.41 ± 0.08	0.39 ± 0.08	0.31 ± 0.07	0.33 ± 0.07	n.s.
	Collembola	0.32 ± 0.07	0.11 ± 0.03	0.28 ± 0.07	0.23 ± 0.06	IVA < IIIA* (2.69), IIIR* (2.28)
Total proportional abundance		**0.90**	**0.96**	**0.90**	**0.95**	

Significance Levels: ns: not significant; *P < 0.05;

4.4.1.4 Structural variables among forest types and correlations with species metrics

There was a significant difference (P < 0.017, T = 3.95, 2DF) in the diameter at breast height (DBH) (cm ± se) of trees between age class IV and age class II reforested plantations (32.58 ± 5.90 and 19.60 ± 4.90, respectively), but there were no other significant differences among forest types for the measured structural variables. Canopy openness was highly significantly positively correlated with the total species richness of sheet-web spinning spiders (Spearman's correlation coefficient: 0.835; P < 0.001; n = 12, 2-tailed) at each site. There were no other significant correlations between measured environmental variables, richness and/or abundance values for the any of the other taxa sampled.

4.4.2 Mixed tree species survey and comparison of native oak woodlands with mixed and pure plantations

In total, 1057 individuals and 89 species were identified, comprising 355 spiders from 22 species and 5 families and 702 beetles from 67 species and 20 families (Appendices 9 and 11, respectively). Canopy spiders were dominated by three species, which comprised 70% of the total spider catch (*Parapelecopsis nemoralis* at 27%, *Neriene peltata* at 22%, and *Paidiscura pallens* at 21%). In contrast, the three most abundant canopy beetle species amounted to approximately 30% of the total beetle catch (*Strophosoma melannogrammum* at 12%, *Malthodes guttifer* 1852 at 10%, and *Aphidecta obliterata* at 9%), and eighty-six other species represented the remainder. Although many open-habitat associated or generalist species were caught in the forest canopies, all of the most abundant species in both taxa were woodland-associates: the majority being associated with mixed forests, but one beetle species *Aphidecta obliterata* (Coleoptera: Coccinellidae) was specifically associated with conifers and was only found in mix and pure plantations.

4.4.2.1 Canopy invertebrate diversity

Mean spider abundances were higher in native oak woodland, followed by pure Norways spruce plantations, and finally Norways spruce/oak mix (hereafter referred to as oak mix) plantations, but values were not significantly different among forest types (Table 4.72). Mean spider species richness was also higher in native oak woodland compared to both plantation types, but again these did not differ significantly. Mean beetle abundances and species richness also showed a general trend of being higher in native woodlands compared to the plantations, although these differences were not significant. Rarefied species richness for both taxa showed the same trend as mean species richness, with native oak woodlands showing relatively higher rarefied species richness, but with no significant differences among forest types (Table 4.72).

Table 4.72: Species abundance and richness metrics for canopy spiders and beetles among forest types.

Site Type	Mean abundance (± se)	Mean species richness (± se)	Rarefied species richness (±95% CI)
Spiders			
Pure plantations	26.00 ± 16.50	3.67 ± 1.45	8.21 ± 1.21
Oak mix plantations	22.00 ± 1.15	4.30 ± 0.88	8.69 ± 0.69
Native oak woodland	35.17 ±6.15	6.67 ± 0.21	11.24 ± 3.24
Beetles			
Pure plantations	34.00 ± 14.36	10.00 ± 4.93	23.50 ± 2.50
Oak mix plantations	51.00 ± 50.24	10.33 ± 3.27	19.55 ± 3.55
Native oak woodlands	74.50 ± 41.78	18.00 ± 7.03	27.37 ± 5.37

4.4.2.2 Spider community composition

Spider assemblage composition differed significantly between native oak woodlands and pure plantations (A = 0.075, T = -1.88, P < 0.05), but there were no significant differences between native oak woodlands and oak mix plantations, or between oak mix and pure plantations. Cluster analysis did not show a clear separation among any of the forest types for spider assemblage composition (Fig. 4.29). Indicator Species Analysis did not identify any spider species in this study as characteristic of a particular forest type.

Pure plantations supported half the number of spider guilds compared to native oak woodland and oak mix plantation forests, as the proportion of sheet-web spinners (Family Linyphiidae) in pure plantations (~89% of all individuals) was highly significantly different to the proportion of that guild in both native oak woodland (P < 0.001) and oak mix plantations (P < 0.01) (Table 4.73). In contrast, only approximately half of the species were comprised of sheet web builders in oak mix plantations and native oak woodlands, which also supported active hunting and orb web building spiders.

All of the spider species sampled were either habitat generalists or forest generalists associated with mixed forests, rather than being specifically associated with a conifer or broadleaved species (Appendix 11), and there were no significant differences in relative species richness of habitat generalists or forest-associated spider species across forest types.
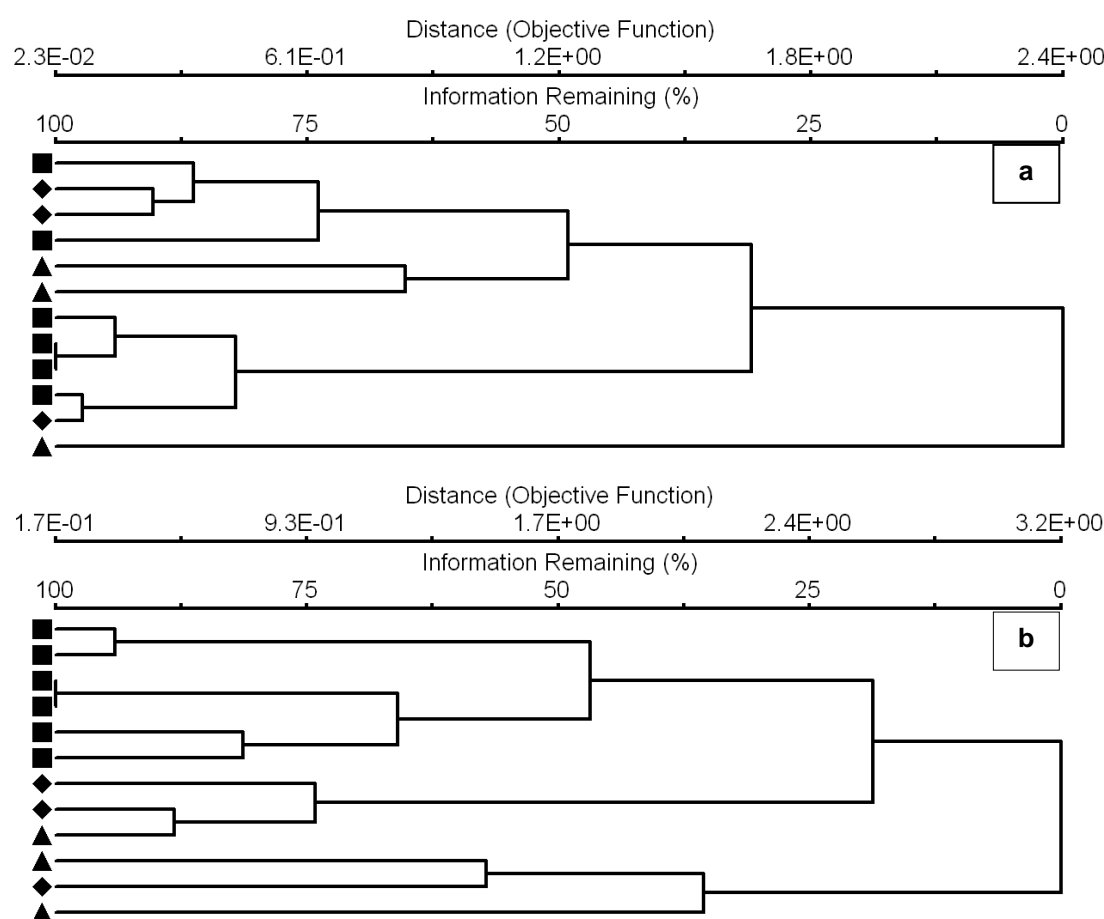
Figure 4.29: Cluster dendrogram of **(a)** canopy spider assemblage similarity and **(b)** canopy beetle assemblage similarity among forest types: (■) native oak woodlands; (♦) Norway spruce/oakmix plantations; (▲) pure Norway spruce plantations.

4.4.2.3 Beetle community composition

In contrast to spiders, beetle assemblage composition was highly significantly different between native oakd woodlands and oak mix plantations (A = 0.075, T = -3.06, P < 0.01), but not among the other forest types. Clustering of beetle assemblage composition clearly separated native oak woodlands from both plantation forest types (Fig. 4.30b). Indicator Species Analysis did not identify any beetle species as characteristic of a particular forest type in this study.

There were significant differences in beetle guild composition among the forest types, with almost half (43%) of all beetle species sampled in native oak woodlands being phytophagous (Table 4.73), which was almost double the proportion (mean relative number) of phytophagous beetle species (23%) caught in oak mix plantations and almost five times higher than that in pure plantations (8%). Pure plantations contained a significantly higher proportion of actively hunting and detritiphagous beetle species, compared to native oak woodlands, while the proportion of both these guilds at oak mix plantations was intermediate between the two other forest types, and not significantly different from either (Table 4.72). There were no significant differences in the relative proportions of species from any other beetle guild across forest types.

Unlike the spider species sampled, there were significant differences in the habitat associations of beetle species among forest types. The proportion of broadleaved-associated beetle species present in native oak woodlands (48%) was significantly higher (P < 0.05) than in both plantation types. There were no conifer-associated beetles sampled in native oak woodlands, which was significantly lower than the proportion of those species sampled in both plantation forest types (Table 4.74). There was a slight increase in the proportion of broadleaved-associated species present in oak mix plantations, when compared to pure plantations, but this difference was not significant and there were no significant differences in the habitat associations of generalist, mixed-forest or deadwood-associated beetle species across forest types.

4.4.2.4 Rarity of canopy invertebrates

There were no Red-listed (according to the Joint Nature Conservation Committee, 2010) spider species sampled in any forests. However, oak mix plantations had a significantly lower proportion of Red-listed beetle species when compared to both native oak woodland (P < 0.01) and pure plantation forests (P < 0.05) (Table 4.74). Only two Red-listed species were sampled from both native oak woodland and plantation forests: *Malthodes guttifer* (seventy-one individuals in native oak woodlands, one individual in a pure plantation) and *Stenichnus (Cyrtoscydmus) poweri* (one individual in a native oak woodland, one individual in a pure plantation), while one Red-listed species was sampled from plantation forests only, and four other Red-listed species were sampled from native oak woodlands only (Appendix 10).

Two new Irish species records were verified from this research, both of which were found only in native oak woodlands. Two individuals of the Linyphiid spider *Entelecara acuminata* were sampled in one woodland (Martin, 2009) (verified by Dr. Anne Oxbrough), while four individuals of the Anobiid beetle *Anobium inexspectatum* were sampled in two different woodlands (Martin, R In Press) (verified by Dr. Roy Anderson, Belfast). *E. acuminata* is a common predator often found on trees, bushes and herbaceous vegetation in the UK (Harvey *et al.*, 2002). *A. inexspectatum* is on the UK beetle Red-list, is known to be xylophagous on a variety of wood types, and is generally specific to deciduous forests in association with old ivy (*Hedera helix*) (Buckland and Buckland, 2006).

4.4.2.5 Habitat variables among forest types

There were no significant differences in structural variables measured at each fogging plot among forest types, with the exception of mean diameter at breast height (DBH) of the fogged trees. Mean DBH (± se) of Norway spruce trees in pure plantations was significantly greater (1-tailed paired T-test, T = -5.504, P < 0.05, 2 DF) than that of oak trees in oak mix plantations (27.5 ± 2.4cm and 14.9 ± 1.2cm, respectively). Mean DBH of oak trees at native oak woodlands was intermediate (19.0 ± 2.9cm) between Norway spruce at pure plantations and oaks at oak mix plantations, and was not significantly different from either (P > 0.05).

Table 4.73: Guild composition of canopy spiders and beetles (mean relative species richness ± se) among forest types.

	Native oak woodlands (NO)	Oak mix plantations (Mix)	Pure plantations (Pure)	Significant differences (z-score)[a]
Spiders				
Active Hunters	0.05 ± 0.03	0.06 ± 0.06	0.00 ± 0.00	Pure < NO (6.33)*** & Mix (3.18)*
Orb Web	0.19 ± 0.05	0.06 ± 0.06	0.00 ± 0.00	Pure < NO (7.45)*** & Mix (3.18)*; Mix < NO (4.42)**
Scaffold Web	0.20 ± 0.03	0.36 ± 0.07	0.11 ± 0.11	Pure < NO (2.15)* & Mix (2.99)*
Sheet web	0.55 ± 0.03	0.53 ± 0.18	0.89 ± 0.11	Pure > NO (6.39)*** & Mix (4.04)**
Beetles				
Active Hunters	0.34 ± 0.06	0.47 ± 0.15	0.59 ± 0.24	Pure > NO (2.82)*
Phytophages	0.43 ± 0.04	0.23 ± 0.04	0.08 ± 0.05	NO > Mix (2.66)* & Pure (7.24)***; Mix > Pure (2.36)*
Mycetophages	0.12 ± 0.03	0.10 ± 0.02	0.08 ± 0.05	n.s
Detritiphages	0.01 ± 0.01	0.03 ± 0.03	0.05 ± 0.05	Pure > SN (2.53)*
Xylophages	0.10 ± 0.03	0.17 ± 0.13	0.19 ± 0.16	n.s.

[a]N = 6 for native oak woodland, N = 3 for both plantation forest types, 2-tailed T-tests for proportional data, 2DF. Significance Levels: n.s.: not significant; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

Table 4.74: Habitat associations and rarity of beetles (mean relative species richness ± se) from the canopies of native oak woodlands, Norway spruce/oak mix plantations and pure Norway spruce plantations.

	Native oak woodlands (NO)	Oak mix plantations (Mix)	Pure plantations (Pure)	Significant differences (z-score)[a]
Habitat Association				
Generalist	0.14 ± 0.03	0.22 ± 0.11	0.23 ± 0.01	n.s.
Broadleaves	0.48 ± 0.03	0.29± 0.02	0.23 ± 0.01	NO > Mix (2.42)* & Pure (3.58)*
Conifers	0.00 ± 0.00	0.10 ± 0.02	0.23 ± 0.01	NO < Mix (3.35)* & Pure (3.88)*
Mixed Forest	0.23 ± 0.04	0.16 ± 0.05	0.14 ± 0.07	n.s.
Deadwood	0.14 ± 0.03	0.23 ± 0.10	0.16 ± 0.05	n.s.
Rarity				
Red-listed	0.13 ± 0.03	0.03 ± 0.02	0.08 ± 0.03	Mix < SN (4.83)** & Pure (2.02)*

[a]N = 6 for native oak woodlands, N = 3 for both plantation forest types, 2-tailed T-tests for proportional data, 2DF. Significance Levels: n.s.: not significant; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

4.4.3 Comparison of forest types

4.4.3.1 Canopy spider diversity and community composition

In total, 524 spiders were identified from 8 families and 29 species (Appendix 9). Almost two-thirds (61%) of all spiders sampled across the three forest types (native oak and ash woodlands and age class IV Sitka spruce plantations) were comprised of three species. These were *Tetragnatha montana* (~18% of all spiders), *Neriene peltata* (~22% of all spiders) and *Paidiscura pallens* (~22% of all spiders). However, the three most abundant spider species differed between forest types. Notably, T*. montana* was not sampled in any Sitka spruce forests, and *Pelecopsis nemoralis* was relatively dominant in this forest type instead (42% of all individuals in Sitka spruce forests), while *Metellina mengei* was slightly more abundant than *N. peltata* in ash woodlands (13% and 10% of all individuals, respectively) (see Appendix 9 for more details). T*.montana* and *M. mengei* are both classified as ubiquitous habitat generalists, while *N. peltata*, P*. pallens* and P*. nemoralis* are all mixed forest-associated species.

Rarefied spider species richness at Sitka spruce forests was significantly lower than at both oak (Mann-Whitney U = 23.50; P < 0.05; n = 6 for each forest type) and ash (Mann-Whitney U = 22.50; P < 0.05; n = 6 for each forest type) native woodlands (Fig. 4.30). However, there were no significant differences between rarefied spider species richness values in native ash and oak woodlands (P > 0.05) (Fig. 4.30).

There were highly significant differences in spider assemblage composition between forest types (F = 4.389; P < 0.001; 2 DF). Pairwise comparisons between forest types demonstrated that the spider assemblages in Sitka spruce plantations were highly significantly different to those present in both native ash (T = 2.873, P < 0.01) and oak (T = 1.885, P < 0.01) woodlands, while oak and ash woodlands were not significantly different from one another (T = 1.255, P > 0.05). *Pelecopsis nemoralis* was identified as a significant Indicator species (Monte Carlo test of significance of observed maximum Indicator-value = 52.5, P < 0.05, 1000 permutations) for Sitka spruce forests, but there were no significant spider Indicator species for either native woodland type. P*. nemoralis* is a sheet-web building spider (Family Linyphiidae) associated with mixed forests. A Cluster Analysis dendrogram of spider species assemblages showed a distinct separation between Sitka spruce sites and all the native woodlands sites, although ash and oak native woodland sites did not clearly separate from one another (Fig. 4.31).

There were several significant differences in guild composition (mean proportional species richness ± se) between forest types for spider species (Table 4.75). There were no actively hunting spiders sampled in Sitka spruce forests, and the species richness of this group was highly significantly lower (P < 0.001) than in both native woodland types, although ash woodlands also had a significantly higher (P < 0.01) proportion of active hunters compared to oak woodlands. This pattern was also observed for orb-web spinning spiders. In contrast to the above two guilds, the proportion of sheet web-spinning spiders was significantly higher (P < 0.01) in Sitka spruce forests than it was in both oak and ash woodlands, as over 80% of all spiders in Sitka spruce forests were sheet-web spinners (Table 4.75). Ash woodlands also had a significantly lower proportion of this sheet-web spinners than oak woodlands (P < 0.05). The proportion of scaffold-web spinners did not vary significantly across forest types.
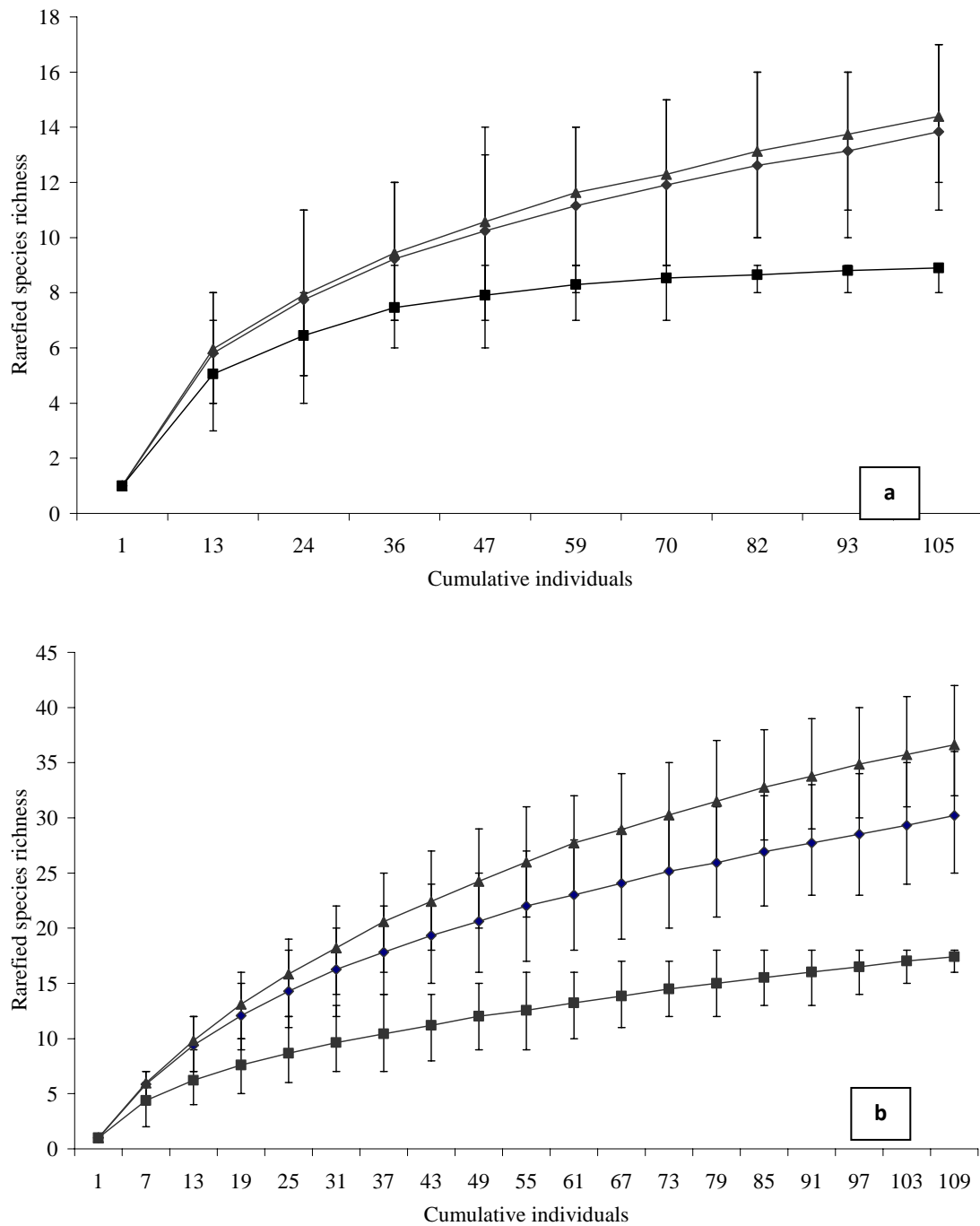
Figure 4.30: Rarefied species richness (± 95% C.I.) of **(a)** canopy spiders and **(b)** canopy beetles among forest types: (▲) native ash woodlands; (♦) native oak woodlands; (■) age class IV Sitka spruce forests.

a

Distance (Objective Function)

| 1.2E-02 | 5.4E-01 | 1.1E+00 | 1.6E+00 | 2.1E+00 |

Information Remaining (%)

| 100 | 75 | 50 | 25 | 0 |

Distance (Objective Function)

| 1.8E-02 | 1.2E+00 | 2.3E+00 | 3.4E+00 | 4.6E+00 |

Information Remaining (%)

| 100 | 75 | 50 | 25 | 0 |
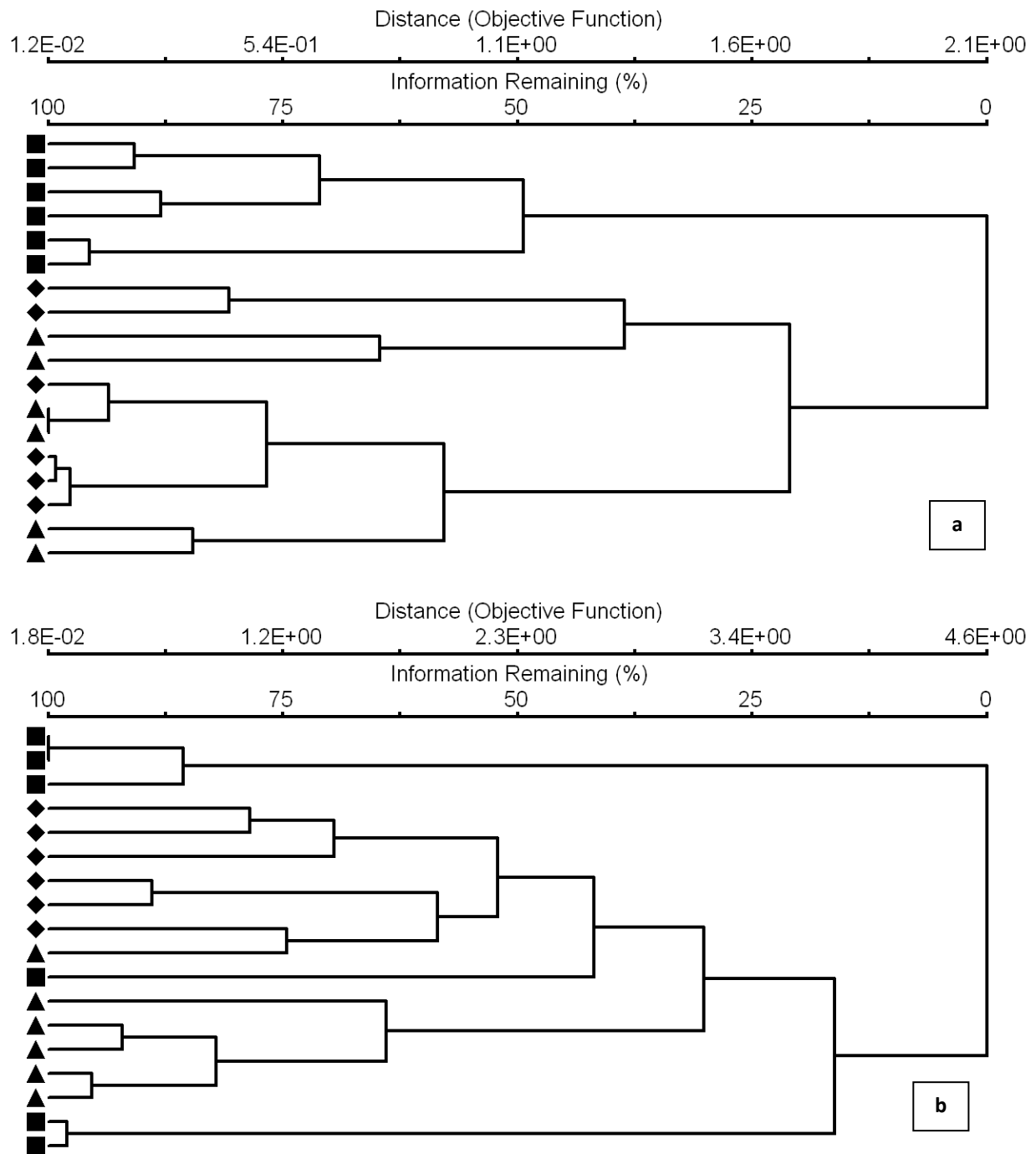
Figure 4.31: Cluster dendrogram of **(a)** canopy spider assemblage similarity and **(b)** canopy beetle assemblage similarity among forest types: (▲) native ash woodlands; (♦) native oak woodlands; (■) age class IV Sitka spruce forests.

Table 4.75: Guild composition of canopy spiders and beetles (mean relative species richness ± se) among forest types.

Guild	Ash	Oak	Sitka spruce plantations (SS)	Significant differences (z-score)[a]
Spiders				
Active Hunters	0.14 ± 0.02	0.05 ± 0.01	0.00 ± 0.00	SS < Ash (6.97)***, Oak (6.33)***; Oak < Ash (4.06)**
Orb Web	0.31 ± 0.04	0.19 ± 0.03	0.02 ± 0.00	SS < Ash (7.97)***, Oak (6.47)***; Oak < Ash (2.59)*
Scaffold Web	0.21 ± 0.03	0.20 ± 0.03	0.16 ± 0.02	n.s.
Sheet web	0.35 ± 0.04	0.55 ± 0.04	0.82 ± 0.02	SS > Ash (10.42)***, Oak (5.52)** Oak > Ash (3.67)*
Beetles				
Active Hunters	0.28 ± 0.03	0.34 ± 0.04	0.59 ± 0.04	SS > Ash (5.80)**, Oak (4.39)**
Phytophages	0.34 ± 0.04	0.43 ± 0.04	0.20 ± 0.03	SS < Ash (2.98)*, Oak (4.66)**
Mycetophages	0.16 ± 0.02	0.12 ± 0.02	0.02 ± 0.00	SS < Ash (6.17)***, Oak (5.48)**
Detritiphages	0.03 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	SS < Ash (6.17)***, Oak (6.06)***; Oak < Ash (3.62)*
Xylophages	0.19 ± 0.03	0.10 ± 0.02	0.19 ± 0.03	Oak < Ash (3.02)*, SS (3.01)*

[a]N = 6 for all forest types, 2-tailed T-tests for proportional data, 2DF. Significance Levels: n.s.: not significant; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

There were also significant differences among forest types in the habitat associations of spider species (mean proportional species richness ± se). Sitka spruce forests had a relatively high proportion (~94%) of mixed forest-associated species, which was highly significantly different ($P < 0.001$) to the proportion of these species in both native woodland types, although oak woodlands also had a significantly higher proportion ($P < 0.05$) of these species than ash woodlands (Table 4.76).

4.4.3.2 Canopy beetle diversity and community composition

In total, 880 adult beetles from 23 families and 78 species were identified and the three most abundant beetle species across all forest types were relatively less dominant than for spiders, comprising almost one quarter (~24%) of the total individuals sampled (*Acalles (Acalles) misellus* (~7% of all beetles), *Malthodes marginatus* (~8% of all beetles) and *Malthodes guttifer* 1852 (~9% of all beetles)) (see Appendix 10 for more details). However, as with spiders, the three most abundant beetle species differed between forest types. No individuals of the phytophagous weevil *Acalles misellus* were sampled in Sitka spruce forests, as this species is specifically associated with broadleaved forest, and only one individual of *M. guttifer* (Notable B on the UK Red-list) was sampled in Sitka spruce forests, although both *Malthodes* spp. are primarily aphidophagous predators associated with mixed forests.

Table 4.76: Habitat associations of spiders and beetles and rarity of beetles (mean relative species richness ± se) in this study.

	Ash	Oak	Sitka spruce plantations (SS)	Significant differences (z-score)[a]
Spiders				
Mixed Forest	0.42 ± 0.04	0.64 ± 0.04	0.94 ± 0.04	SS > Ash (12.59)***, Oak (7.75)***; Oak > Ash (3.90)*
Beetles				
Generalist	0.28 ± 0.03	0.14 ± 0.02	0.32 ± 0.04	Oak < Ash (3.56)*, SS (4.40)**
Broadleaves	0.44 ± 0.04	0.48 ± 0.04	0.04 ± 0.01	SS < Ash (9.50)***, Oak (10.49)***
Conifers	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.01	SS > Ash (6.55)***, Oak (6.55)***
Mixed Forest	0.16 ± 0.02	0.22 ± 0.02	0.32 ± 0.04	SS > Ash (3.74)*, Oak (2.17)*
Deadwood	0.13 ± 0.02	0.16 ± 0.02	0.23 ± 0.03	SS > Ash (3.07)*, Oak (2.05)*
Red-listed species	0.12 ± 0.02	0.11 ± 0.02	0.17 ± 0.02	SS > Oak (2.15)*

[a]N = 6 for all forest types, 2-tailed T-tests for proportional data, 2DF. Significance Levels: *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

In contrast to the overall pattern of low beetle species dominance across all forest types, almost 57% of beetles in Sitka spruce forests were comprised of three species: the generalist predator *Rhagonycha (Rhagonycha) lignosa* (~15%), the mixed forest-associated phytophagous weevil *Strophosoma (Strophosoma) melannogrammum* (~15%) and *M. marginatus* (~26%). The three most abundant species in ash woodlands were all broadleaved-associates; the aphidophagous predator *Halyzia sedecimguttata* (~5% of all individuals at ash woodlands), and two phytophagous weevils, *Orchestes (Salius) fagi* and *A. misellus* (11% and 18% of all individuals at ash woodlands, respectively). *Salpingus planirostris*, *Polydrusus (Polydrusus) tereticollis* and *M. guttifer* were the three most abundant species in oak woodlands (9%, 10% and 16% of all individuals, respectively). *S. planirostris* is a mixed forest-associated predator, while P. *tereticollis* is a phytophagous broadleaved forest-associated species.

Rarefied beetle species richness at Sitka spruce forests was highly significantly lower than at both oak (Mann-Whitney U = 69.50; P < 0.001; n = 6 for each forest type) and ash (Mann-Whitney U = 61.50; P < 0.001; n = 6 for each forest type) native woodland types and, in fact, rarefied beetle species richness at Sitka spruce forests was almost half that in native ash woodlands (Fig. 4.30). However, there were no significant differences between rarefied beetle species richness values in native ash and oak woodlands (P > 0.05) (Fig. 4.30).

Beetle assemblage composition also differed significantly between forest types (F = 3.938; P < 0.001; 2 DF). However, in contrast to spider assemblages, beetle assemblages were significantly different among all three forest types (pairwise comparisons). Sitka spruce plantations were highly significantly different to those present in both native ash (T = 2.190, P < 0.01) and oak (T = 1.810, P < 0.01) woodland types, while oak and ash woodlands were also highly significantly different from one another (T = 1.943, P < 0.01). There were five significant Beetle Indicator species for each of the native woodland types (Table

4.77). With the exception of *Athous (Athous) haemorrhoidalis*, all of the beetle Indicator species for both native woodland types were associated with mixed or broadleaved forest, while *Orchesia (Clinocara) minor* is also on the UK Red-list (Table 4.77). In comparison to spiders, there was a less distinct separation in the Cluster Analysis dendrogram between forest types for beetle species assemblages (Fig. 4.31). Three of the Sitka spruce forests separated quite distinctly from the remaining forests, but, although all oak woodlands were situated adjacent to each other in the dendrogram, they were clustered with the ash woodlands and the remaining three Sitka spruce forests.

There were also several significant differences in guild composition (mean proportional species richness ± se) between forest types for beetles (Table 4.75). In contrast to spiders, active hunters were the most dominant beetle guild in Sitka spruce forests, and were present in significantly higher ($P < 0.01$) relative proportions than in both native woodland types (Table 4.75). There were also significantly lower ($P < 0.05$) proportions of both phytophagous and mycetophagous beetle species in Sitka spruce forests compared to both native woodland types. Although there were relatively low proportions of detritiphagous species across all forest types, no individuals from this guild were sampled in Sitka spruce forests, which had a highly significantly lower ($P < 0.001$) species richness than in both native woodland types. However, ash woodlands also had a significantly higher ($P < 0.05$) proportion of this guild compared to oak woodlands (Table 4.75). Oak woodlands had a significantly lower proportion ($P < 0.05$) of xylophagous beetle species compared to both ash woodlands and Sitka spruce forests.

Similarly to the pattern observed for spider species, Sitka spruce forests had a significantly higher ($P < 0.05$) proportion of mixed forest-associated beetle species compared to both native woodland types, although ash and oak woodlands did not differ from each other in this case (Table 4.76). Oak woodlands had the lowest relative proportion of generalists ($P < 0.05$) compared to both ash woodlands and Sitka spruce forests, while Sitka spruce forests had highly significantly lower ($P < 0.001$) proportions of broadleaved-associated species compared to both native woodland types. In contrast, no conifer-associated beetle species were sampled in either native woodland type; this was a highly significantly lower ($P < 0.001$) proportion than in Sitka spruce forests. Sitka spruce forests also had a significantly higher ($P < 0.05$) proportion of deadwood-associated species compared to both native woodland types (Table 4.76); approximately 35% of all beetles sampled at Sitka spruce forests were *Malthodes marginatus*, which is a predatory species whose larvae develop in deadwood (Appendix 4). Although only two out of the nine Red-listed species sampled in this study were found in Sitka spruce forests (eight individuals of the generalist xylophage *Athous (Orthathous) campyloides* and one individual of the mixed forest-associated predator *Malthodes guttifer*), these forests still contained the highest relative proportion of Red-listed beetle species: almost 17% of the 18 species, which was significantly higher ($P < 0.05$) than in oak woodlands (Table 4.76).

Five beetle species (out of a total of fifty-two) sampled had been classified as being specifically associated with oak trees. However, three beetle species classified as oak-associated in this study were also sampled in ash woodlands. Two of these were phytophagous weevils which were also sampled in oak woodlands (*Coeliodes rana* and *Orchestes quercus*), and one predatory species which was only sampled in ash woodlands (*Malthinus fasciatus*) (Appendices 10 and 11). No beetle species sampled in ash

woodlands were specifically associated with ash trees, and none of the above species were sampled in Sitka spruce forests**.**

Table 4.77: Beetle Indicator species for native ash and oak woodlands.

Species	Family	Guild	Habitat Association	Observed maximum Indicator Value
Ash				
Acalles (Acalles) misellus	Curculionidae	Phytophage	Broadleaved forest	92.6***
Athous (Athous) haemorrhoidalis	Elateridae	Xylophage	Generalist	69.3**
Halyzia sedecimguttata	Coccinellidae	Mycetophagous/Aphidophagous	Broadleaved forest	54.8*
Orchesia (Clinocara) minor[a]	Melandryidae	Mycetophagous	Broadleaved forest	83.3**
Polydrusus (Eustolus) ptreygomalis	Curculionidae	Phytophage	Broadleaved forest	66.7*
Oak				
Cis boleti	Ciidae	Mycetophagous	Mixed forest	54.7*
Dromius (Dromius) quadrimaculatus	Carabidae	Predatory	Mixed forest	53.9*
Nalassus laevioctostriatus	Tenebrionidae	Phytophagous	Broadleaved forest	66.7*
Polydrusus (Polydrusus) tereticollis	Curculionidae	Phytophage	Broadleaved forest	66.7*
Salpingus ruficollis	Salpingidae	Predator	Broadleaved forest	76.6**

[a]Notable B (JNCC 2010). Significance level: *P < 0.05; ** P < 0.01; ***P < 0.001.

4.4.3.3 Other taxa

48,741 true flies (Diptera) and 38,791 true bugs (Hemiptera) were identified to family-level (for details, see Appendices 12 and 13 respectively), while 32,923 individuals were identified from 27 other taxa. Even at these relatively high taxonomic levels (Family-level and higher), broad patterns were evident across forest types. Although native woodlands had much lower total abundances overall compared to Sitka spruce plantations for Dipteran and Hemipteran families, and all other taxa, total richness at all taxonomic levels examined was higher in both native woodlands types compared to that in Sitka spruce plantations (Appendices 6, 13 and 14). Additionally, Sitka spruce plantations were consistently more dominated (> 50% of all individuals) by one group at each taxonomic level examined (Table 4.78). For example, the Chironomidae were the most abundant Dipteran family at Sitka spruce plantations, comprising almost two thirds of all individuals, which was very highly significantly different (P < 0.001) to the mean proportional abundance of that family in both native woodland types (Table. 4.78). In addition, almost 90% of all Diptera individuals at Sitka spruce plantations were comprised of only three families; Chironomidae (~58%), Ceratopogonidae (~25%) and Psychodidae (~5%). In contrast, the relative dominance of each family was lower in both native ash and oak woodland types, where the three most dominant families comprised ~48% and ~70% of all individuals, respectively (Table 4.78).

The Aphidiidae completely dominated Sitka spruce plantations, comprising almost 100% of all Hemipteran individuals (Table 4.78 and Appendix 14). In contrast, the relative dominance of each Hemipteran family was highly significantly lower (P < 0.001) in both native woodland types; Cicadellidae made up the greatest proportion of Hemiptera at native ash and oak woodlands, and comprised only ~28% and ~32% of all individuals, respectively (Table 4.78).

This pattern was also evident at higher taxonomic levels, whereby Collembola comprised over half of all individuals in Sitka spruce plantations, which was significantly higher (P < 0.001) relative proportions than in both native woodland types. Notably, Collembola and Psocoptera together comprised approximately three quarters of all individuals in Sitka spruce forests (Table 4.78). In contrast, Hymenoptera were the most dominant group in both native ash and oak woodlands (approximately 37% and 29% of all individuals, respectively). Native ash woodlands contained significantly lower (P < 0.05) mean relative proportions of Psocoptera compared to both native oak woodlands and Sitka spruce plantations, while Sitka spruce plantations had significantly lower (P < 0.05) mean relative proportions of Acari and immature Araneae (spiders) compared to both native woodland types (Table 4.78).

Apart from the Chironomidae, there were several other significant differences among forest types for mean relative Dipteran family composition (only families comprising greater than 5% of individuals in at least one forest type were examined in analyses); the proportional abundances of Cecidomyiidae, Dolichopodidae, Empidiidae/Hybotidae, Lauxaniidae and Sciariidae were significantly higher (P < 0.05) in both native woodland types compared to Sitka spruce plantations (Table 4.78). Additionally, oak woodlands had significantly higher mean proportional abundances of Empididae/Hybotidae compared to both other forest types, and proportional abundances of Dolichopodidae and Sciaridiae were significantly higher in native ash woodlands compared to oak woodlands (Table 4.78).

There were strikingly significant differences in the mean relative proportions of Hemipteran families across forest types (only families comprising greater than 5% of individuals in at least one forest type were examined in analyses); the mean proportional abundances of Aphidiidae and Psyllidae were significantly higher (P < 0.05) in native ash and oak woodlands, while oak woodlands had significantly higher mean proportional abundances of Miridae compared to those of ash (Table 4.78).

Rarefied Dipteran family richness (± 95% confidence limits, 1000 iterations) at Sitka spruce plantations (16.90 ± 3.90) was significantly lower than at both native ash (40.88 ± 0.88) (Mann-Whitney U = 41.50; P < 0.001; n = 6 for each forest type) and oak woodlands (35.70 ± 2.70) (Mann-Whitney U = 60.50; P < 0.001; n = 6 for each forest type). In fact, both native ash and oak woodlands had more than double the rarefied family richness of Sitka spruce plantations. Native ash woodlands also had significantly higher rarefied Dipteran family richness compared to native oak woodlands (Mann-Whitney U = 378.50; P < 0.001; n = 6 for each forest type). Rarefied Hemipteran family richness (± 95% confidence limits, 1000 iterations) at Sitka spruce plantations (1.98 ± 0.02) was significantly lower than at both native ash (10.50 ± 0.22) (Mann-Whitney U = 378.50; P < 0.001; n = 6 for each forest type) and oak woodlands (9.91 ± 0.10) (Mann-Whitney U = 10.50; P < 0.001; n = 6 for each forest type). However, there were no differences in rarefied Hemipteran family richness between native woodland types. Notably, both native woodland types had almost five times the rarefied Hemipteran family richness of Sitka spruce plantations.

Table 4.78 Mean relative abundances (± se) of Dipteran and Hemipteran families and other taxa among forest types (only taxa comprising greater than 5% of individuals in at least one forest type were included in analyses).

	Ash	Oak	Sitka spruce plantations (SS)	Significant differences (z-score)[a]
Diptera Families				
Cecidomyiidae	0.08 ± 0.01	0.09 ± 0.01	0.01 ± 0.00	SS < Ash (5.42)**, Oak (5.67)**
Ceratopogonidae	0.18 ± 0.02	0.24 ± 0.03	0.25 ± 0.03	n.s.
Chironomidae	0.18 ± 0.02	0.23 ± 0.03	0.58 ± 0.04	SS > Ash (8.68)***, Oak (6.96)***
Dolichopodidae	0.05 ± 0.01	0.02 ± 0.00	0.00 ± 0.00	SS < Ash (6.33)***, Oak (6.04)***; Ash > Oak (4.23)**
Empididae/Hybotidae	0.12 ± 0.02	0.23 ± 0.03	0.04 ± 0.01	SS < Ash (4.05)**, Oak (6.15)***; Oak > Ash (3.17)*
Lauxanidae	0.05 ± 0.01	0.04 ± 0.01	0.00 ± 0.00	SS < Ash (6.31)***, Oak (6.23)***
Psychodidae	0.04 ± 0.01	0.01 ± 0.00	0.05 ± 0.01	Oak < Ash (4.74)**, SS (5.19)**
Sciaridae	0.12 ± 0.02	0.06 ± 0.01	0.03 ± 0.00	SS < Ash (5.03)**, Oak (3.36)*; Ash > Oak (2.63)*
Hemiptera Families				
Anthocoridae	0.26 ± 0.03	0.31 ± 0.04	0.00 ± 0.00	SS < Ash (8.13)***, Oak (8.71)***
Aphidiidae	0.24 ± 0.03	0.10 ± 0.01	1.00 ± 0.00	SS > Ash (25.38)***, Oak (61.29)***; Ash > Oak (4.13)**
Cicadellidae	0.28 ± 0.03	0.32 ± 0.04	0.00 ± 0.00	SS < Ash (8.38)***, Oak (8.83)***
Miridae	0.14 ± 0.02	0.22 ± 0.03	0.00 ± 0.00	SS < Ash (7.00)***, Oak (7.74)***; Oak > Ash (2.31)*
Psyllidae	0.06 ± 0.01	0.01 ± 0.00	0.00 ± 0.00	SS < Ash (6.39)***, Oak (6.09)***; Ash > Oak (4.71)**
Other Taxa				
Acari	0.10 ± 0.02	0.11 ± 0.02	0.05 ± 0.01	SS < Ash (2.81)*, Oak (3.19)*
Aranae (Immature)	0.28 ± 0.03	0.28 ± 0.03	0.02 ± 0.00	SS < Ash (7.76)***, Oak (7.76)***
Coleoptera (Larvae)	0.07 ± 0.01	0.07 ± 0.01	0.06 ± 0.01	n.s.
Collembola	0.03 ± 0.01	0.02 ± 0.00	0.51 ± 0.04	SS > Ash (11.44)***, Oak (11.84)***
Hymenoptera	0.37 ± 0.04	0.29 ± 0.03	0.09 ± 0.01	SS < Ash (6.87)***, Oak (5.44)**
Psocoptera	0.06 ± 0.01	0.21 ± 0.03	0.25 ± 0.03	Ash < Oak (5.16)**, SS (5.86)**

[a]N = 6 for all forest types, 2-tailed T-tests for proportional data, 2DF. Significance Levels: n.s: not significant; *P ≤ 0.05; **P ≤ 0.01; ***P ≤ 0.001

4.4.3.4 Habitat variables

Canopy height in Sitka spruce forests was significantly greater (P < 0.05) than in both native woodland types, while ash woodlands contained significantly more trees per 100m^2 plot compared to Sitka spruce forests (Table 4.79). The diameter at breast height (DBH) and canopy openess of ash woodlands was significantly lower (P < 0.05) than in oak woodlands, but there were no significant differences for these variables between the other forest types. There were no significant correlations between habitat variables and richness values for any of the taxa sampled.

Table 4.79 Mean (± se) structural variables among forest types. Significance tested with non-parametric Mann-Whitney U.

Structural Variable	Ash	Oak	Sitka spruce plantations (SS)	Significant differences (U)[a]
Canopy height (m)	17.98 ± 1.24	17.72 ± 1.44	22.50 ± 1.06	SS > Ash (4.00)*, Oak (3.00)**
DBH (cm)	11.63 ± 0.94	21.56 ± 4.06	25.17 ± 4.77	Ash < Oak (5.00)*
Canopy cover (%)	69.17 ± 4.10	81.11 ± 2.18	79.22 ± 1.19	Ash < Oak (4.50)*
No. of trees in 100m^2 plot	22.78 ± 4.36	14.56 ± 4.33	8.67 ± 0.82	Ash > SS (0.00)**

[a]N = 6 for all forest types. Exact 2-tailed significance levels: *P ≤ 0.05; **P ≤ 0.01

4.5 Birds

4.5.1 Afforestation and reforestation survey

4.5.1.1 Community structure in second-rotation forests

A total of 51 species were recorded in second-rotation plantation forests in this study. Of these, 31 species were used in analysis. Of the 31 species, 24 were detected in Age class I (with 8 species unique to this age-class), 21 in Age class II (with 0 uniques), 20 in Age class III (with 1 unique) and 17 in Age class IV forests (with 0 uniques) (Table 4.80). NMS ordination explained 96% of the variation in the species density data in second-rotation forests with Axis 1 accounting for 89% and Axis 2, 7%. The ordination identified three main groups of sites: Age class I separated from the rest of the age classes along Axis 1 and showed a large amount of inter-site variation across Axis 2. Age class II separated from Age class I across Axis 1 and, to a lesser extent, across Axis 2. Age class II also separated from age class III and IV across Axis 1. However, age class III and IV did not separate clearly from each other along either axis one or two (Fig. 4.32). These two age classes were therefore combined into a Closed canopy age class for further analyses and hereafter the names of the equivalent structural stages of Pre-thicket and Thicket are used for age class I and II respectively. There was no significant difference between the rank abundance curves in any of the stages (Kolmogorov-Smirnov: Pre-thicket v Thicket: Z = 0.48, P > 0.05; Pre-thicket v Closed canopy: Z = 1.02, P > 0.05; Thicket v Closed canopy: Z = 0.93, P > 0.05) (Fig. 4.33).

Indicator species for Pre-thicket included Lesser Redpoll (Indicator-value 80%, P < 0.01) and Whitethroat (80%, P < 0.01). Indicators for Thicket were Chaffinch (62%, P < 0.01); Coal Tit (41%, P < 0.01); Dunnock (63%, P < 0.05); Song Thrush (57%, P < 0.05); and Robin (50%, P < 0.01) while indicator species for the Closed canopy stage were Coal Tit (56%, P < 0.01) and Goldcrest (66%, P < 0.01) (Fig. 4.32).
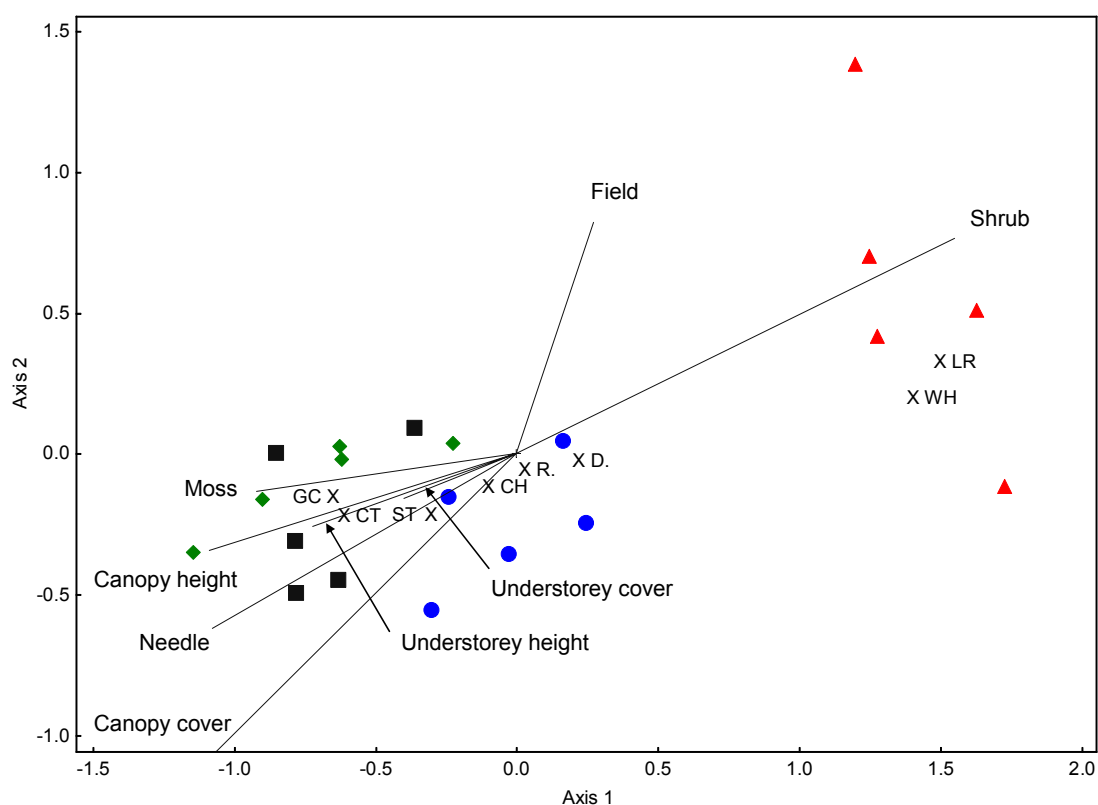
Figure 4.32: NMS biplot of site bird species densities and vegetation components in second-rotation Sitka spruce plantations. ▲ = age class I, ● = age class II, ■ = age class III, ♦ = age class IV. Axis 1, r^2=0.89, Axis 2, r^2=0.070. Final stress for 2D solution = 6.961, Final instability = 0.00000. Species with an indicator-value of 40% or more and with a P-value of < 0.05 are displayed with the symbol X. CH = Chaffinch (*Fringilla coelebs*); CT = Coal Tit (*Periparus ater*); D. = Dunnock (*Prunella modularis*); GC = Goldcrest (*Regulus regulus*); LR = Lesser Redpoll (*Carduelis flammea*); R. = Robin (*Erithacus rubecula*); ST = Song Thrush (*Turdus philomelos*) WH = Whitethroat (*Sylvia communis*).
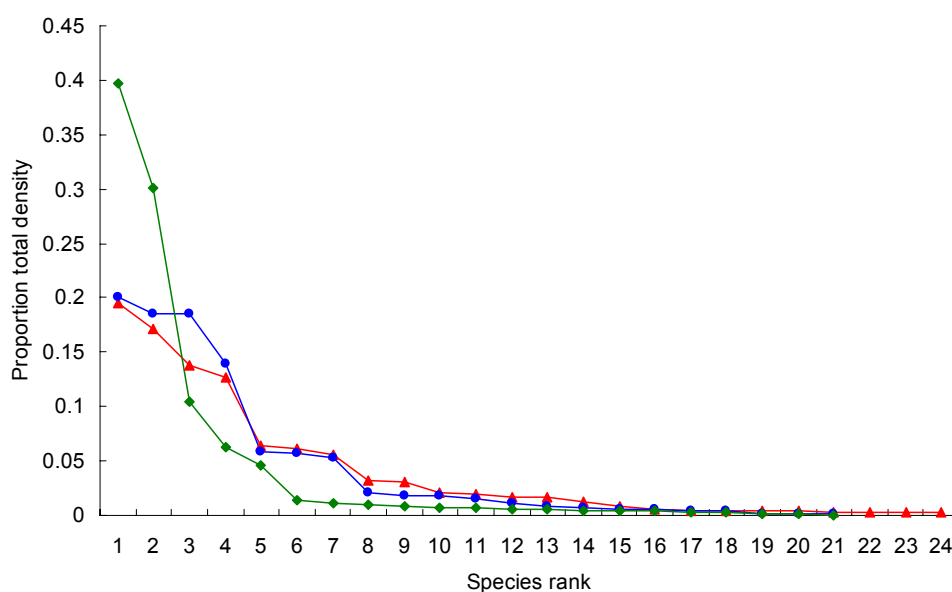
Figure 4.33: Rank-abundance curves of bird assemblages in Pre-thicket (▲); Thicket (▲) and Closed canopy (▲) second-rotation Sitka spruce plantations.

Table 4.80: Bird species listed alphabetically according to their common names, their population densities (No. ha^{-1} ± se) in four first (data derived from (Wilson *et al.*, 2006) and second-rotation forest age classes and their rate of natural population change as identified by Coombes *et al.* (2009). The detection groups to which each species was assigned is also noted (DG)

Species	Scientific name	DG	Annual population change (%)	Age class I		Age class II		Age class III		Age class IV	
				1st rotation	2nd rotation	1st rotation	2nd rotation	1st rotation	2nd rotation	1st rotation	2nd rotation
Blackbird	*Turdus merula*	1	+0.77	0.48(0.34)	0.53(0.18)	2.45(0.63)	1.31 (0.30)	1.46(0.40)	1.17(0.30)	0.49(0.18)	0.40 (0.10)
Blackcap (M)	*Sylvia atricapilla*	1	+16.08*	0.04(0.04)	0.06(0.06)	0.32(0.12)	0.35 (0.28)	0.46(0.46)	0.89(0.39)	0	0.32 (0.19)
Blue Tit	*Cyanistes caeruleus*	4	+1.57*	0.08(0.08)	0	0.38(0.38)	1.14 (0.76)	0.06(0.06)	0.36(0.36)	0	0.48 (0.48)
Bullfinch	*Pyrrhula pyrrhula*	2	+6.66*	0.17(0.17)	0.11(0.11)	0.73(0.35)	0	0.08(0.08)	0	0.08(0.08)	0
Chaffinch	*Fringilla coelebs*	3	+1.04*	0.82(0.48)	1.69(0.33)	3.34(0.96)	8.52 (1.26)	6.17(1.80)	2.61(0.67)	5.79(0.67)	4.51 (0.92)
Chiffchaff (M)	*Phylloscopus collybita*	1	-0.77	0.17(0.17)	0.06(0.06)	0.66(0.55)	0.92 (0.38)	0.26(0.11)	0.5(0.14)	0.16(0.07)	0.05 (0.05)
Coal Tit	*Periparus ater*	4	+2.09*	0.26(0.26)	0.84(0.42)	1.54(0.53)	12.30(2.78)	4.93(1.21)	18.64(2.96)	4.42(0.27)	15.44(3.18)
Cuckoo (M)	*Cuculus canorus*	1	+1.78	0	0	0	0	0	0.12 (0.12)	0	0
Dunnock	*Prunella modularis*	2	+0.34	0.46(0.21)	1.61(0.54)	1.17(0.48)	3.47 (0.91)	0.13(0.08)	0.95 (0.28)	0	0
Goldcrest	*Regulus regulus*	4	+2.63*	1.46(0.85)	0.33(0.22)	3.64(1.05)	11.33(2.02)	9.00(0.73)	24.72(3.15)	9.19(2.04)	20.30(3.81)
Goldfinch	*Carduelis carduelis*	3	+9.87*	0.23(0.23)	0.09(0.09)	0.10(0.10)	0	0	0	0	0
Grasshopper Warbler (M)	*Locustella naevia*	1	+4.12	0.03(0.03)	0.11(0.11)	0	0	0	0	0	0
Great Tit	*Parus major*	3	+2.77*	0.12(0.12)	0.44(0.13)	0.27(0.27)	0.36 (0.15)	0.53(0.18)	0.05(0.05)	0.09(0.09)	0.33(0.17)
Greenfinch	*Carduelis chloris*	3	-0.7	0	0	0.53(0.53)	0	0	0	0	0
Jay	*Garrulus glandarius*	2	DD	0	0	0	0.23 (0.22)	0	0.26 (0.16)	0	0.54 (0.26)
Lesser Redpoll	*Carduelis flammea*	3	+12.72*	1.92(0.37)	0.54(0.17)	2.41(0.84)	0	0.37(0.22)	0	0.35(0.20)	0
Linnet	*Carduelis cannabina*	3	1.88	1.07(0.56)	0.80(0.60)	0	0	0	0	0	0
Long-tailed Tit	*Aegithalos caudatus*	4	1.29	0	0	0.07(0.07)	0.67(0.67)	0.15(0.15)	1.05 (0.68)	0	0
Meadow Pipit	*Anthus pratensis*	2	-1.18*	2.02(0.70)	1.49(1.23)	0.16(0.16)	0.45(0.45)	0	0	0	0
Mistle Thrush	*Turdus viscivorus*	1	-3.30*	0	0.06(0.06)	0.33(0.21)	0.12(0.07)	0.20(0.14)	0.06	0.40(0.33)	0.15 (0.10)
Pheasant	*Phasianus colchicus*	1	+2.86*	0	0.23(0.23)	0	0.07(0.07)	0	0	0.06(0.06)	0
Reed bunting	*Emberiza schoeniclus*	3	+3.04*	1.19(0.91)	0.17(0.17)	0	0	0	0	0	0
Robin	*Erithacus rubecula*	2	-1.08*	0.80(0.38)	5.18(0.81)	5.30(0.85)	11.31(1.22)	5.57(1.19)	7.26 (0.74)	2.77(0.97)	4.64 (1.25)

Species	Scientific name	DG	Annual population change (%)	Age class I		Age class II		Age class III		Age class IV	
				1st rotation	2nd rotation	1st rotation	2nd rotation	1st rotation	2nd rotation	1st rotation	2nd rotation
Sedge Warbler (M)	*Acrocephalus schoenobaenus*	1	+2.99*	0.11(0.11)	0	0	0	0	0	0	0
Siskin	*Carduelis spinus*	3	DD	0.33(0.27)	0	0.33(0.23)	0.12 (0.11)	0.07(0.07)	0.05 (0.05)	0.32(0.18)	0
Skylark	*Alauda arvensis*	1	-2.67*	0.05(0.05)	0	0	0	0	0	0	0
Song Thrush	*Turdus philomelos*	1	+0.55	0.11(0.11)	0.12(0.07)	1.66(0.68)	1.07 (0.43)	0.50(0.43)	0.42 (0.21)	0.05(0.05)	0.21 (0.21)
Sparrowhawk	*Accipiter nisus*	2	DD	0	0.1 (0.10)	0	0	0.07(0.07)	0	0.20(0.15)	0
Stonechat	*Saxicola torquata*	2	+6.32*	0.12(0.12)	0.43(0.43)	0	0	0	0	0	0
Treecreeper	*Certhia familaris*	2	-2.19	0.10(0.10)	0	0	0.23 (0.23)	0.13(0.07)	0	0.12(0.05)	0.35 (0.14)
Whitethroat (M)	*Sylvia communis*	1	+3.78	0.16(0.16)	3.36(1.48)	0	0	0	0.13 (0.13)	0	0.27 (0.27)
Willow Warbler (M)	*Phylloscopus trochilus*	1	+3.20*	1.00(0.12)	3.67(0.55)	1.84(0.65)	3.24(0.58)	0.15(0.09)	0.22 (0.22)	0.22(0.09)	0.11 (0.07)
Woodpigeon	*Columba palumbus*	1	+2.30*	0	0	0.45(0.27)	0.47(0.18)	0.17(0.06)	0.06 (0.06)	0.12(0.07)	0.50 (0.21)
Wren	*Troglodytes troglodytes*	1	+1.73*	1.86(0.46)	4.55(0.37)	2.45(0.61)	3.59(0.40)	2.00(0.65)	2.64 (0.91)	0.58(0.16)	2.63 (0.79)

[1] (M) denotes migrant species

[1] DD denotes Data Deficient species, * indicates statistically significant increase or decrease

4.5.1.2. Species richness, total bird density and migrant bird density

There was no significant difference in mean species richness between Pre-thicket, Thicket or Closed canopy (H = 1.28, P > 0.05). Total bird density was significantly different between the atages (H = 11.17; P < 0.01). Both Thicket (Q = 2.78, P < 0.05) and Closed canopy (Q = 2.69, P < 0.05) had significantly higher bird density than Pre-thicket, but there was no significant difference between Thicket and Closed canopy (Q = 0.52, P > 0.05). Migrant density also differed significantly between the stages (H = 12.88, P < 0.01), being significantly lower in Closed canopy than in Thicket (Q = 2.53, P < 0.05) and Pre-thicket (Q = 3.02, P < 0.01). However, there was no significant difference in migrant density between Thicket and Pre-thicket (Q = 0.86, P > 0.05) (Table 4.81).

4.5.1.3 Comparison with first-rotation forests

Shrub cover in Pre-thicket was significantly higher in the second rotation than the first (U = 0, P < 0.05) while field layer cover was significantly higher in the first rotation than in the second (U = 0, P < 0.05). Canopy cover and height did not differ significantly between rotations. In Thicket, only field layer cover differed significantly between rotations, being higher in the first rotation than the second (U = 0, P < 0.05). In Closed canopy, both canopy cover (U = 16, P < 0.05) and field layer cover (U = 10, P < 0.01) were significantly higher in the first rotation than in the second (Table 4.82).

Table 4.81: Mean species richness, total bird density and migrant bird density (± se) in three age classes in first (data derived from (Wilson *et al.*, 2006) and second-rotation plantation forests. A significant difference between rotations is indicated in the appropriate second-rotation column

	Species Richness		Total bird density		Migrant bird density	
	1st Rotation	2nd rotation	1st Rotation	2nd Rotation	1st Rotation	2nd Rotation
Pre-thicket	12.75 (2.17)	12.60 (1.21)	15.16 (2.67)	26.57 (4.98)**	1.51 (0.14)	7.26 (1.93)**
Thicket	14.50 (1.32)	13.20 (1.50)	30.11 (4.56)	61.24 (4.84)**	2.82 (0.57)	4.51 (0.67)
Closed canopy	12.75 (1.79)	11.20 (0.77)	29.05 (3.79)	56.73 (4.62)**	0.43 (0.09)	1.34 (0.44)

Table 4.82: Canopy height and percentage cover (± se) of vegetation variables from first (data from Wilson *et al.*, 2006) and second rotation forests in three stages. Stage names differ from those used in (Wilson *et al.*, 2006): Pre-thicket = Younger; Thicket = Intermediate and Closed canopy = Older. Significant differences between rotations are indicated in the appropriate column

	Canopy height		Canopy Cover		Shrub cover		Field layer cover	
	1st Rotation	2nd Rotation	1st Rotation	2nd Rotation	1st Rotation	2nd Rotation	1st Rotation	2nd Rotation
Pre-thicket	2.2 (0.2)	2.8 (0.3)	24.7 (6.7)	29.8 (3.1)	11.4 (5.4)	46.3 (4.2)*	89.0 (4.9)*	31.3 (10)
Thicket	5.7 (0.6)	5.9 (0.4)	62.0 (7.0)	75.3 (5.1)	15.0 (6.9)	12.0 (3.0)	48.1 (10.0)*	17.2 (3.4)
Closed canopy	12.6 (0.6)	13.1 (1.1)	73.0 (2.9)*	64.8 (2.4)	4.2 (1.4)	5.5 (1.9)	37.5 (8.8)**	11.7 (5.9)

Species richness did not differ significantly between rotations in any of the three stages (Pre-thicket, Z = -0.063, P > 0.05; Thicket, Z = -0.522, P > 005; Closed canopy Z = -0.947, P > 0.05). Species richness of forest specialists did not differ between rotations (Z = 0.00, one-tailed P > 0.05) but was lower in Pre-

thicket than in older stages (Z = 1.82, P < 0.05). Total bird density was significantly higher in the second-rotation in all three stages (Pre-thicket, T = 2.137 P < 0.01; Thicket, T = 3.860, P < 0.01; Closed canopy, T = 4.963, P < 0.01), and migrant bird density was significantly higher in the second rotation in Pre-thicket (T = 3.394, P < 0.01). Density of forest specialists did not differ between rotations (Z = 0.30, one-tailed P > 0.05) but was lower in Pre-thicket than in older stages (T = 2.10, P < 0.05). There was no significant difference in migrant density between rotations in the other stages (Thicket, Z = 0.433, P > 0.05; Closed canopy, Z = -0.217, P > 0.05) (Table 4.81).

Correcting the data for natural population increase resulted in a decrease of between 5 and 10% in total bird density in each atage (Fig. 4.34). When re-analysed, there was no significant difference in total bird density between rotations in Pre-thicket (T = 1.88, P = 0.07), but total bird density remained significantly higher in the second rotation in both Thicket (T = 3.637, P < 0.01) and Closed canopy (T = 4.361, P < 0.01). Migrant density remained significantly higher in the second rotation in Pre-thicket (T = 3.309, P < 0.01).

The difference in density between rotations in Thicket and Closed canopy is largely driven by two abundant species: Coal Tit and Goldcrest (Table 4.80). Because of their numbers in the field, density estimates generated using *Distance* are particularly susceptible to observer bias for these species. To test whether the observed differences were influenced by these species, the values for these species were removed and the data, corrected for population increase, re-analysed. Total bird density was significantly higher in the second rotation in Pre-thicket and Thicket (Pre-thicket, T = 2.183, P < 0.04; Thicket, T = 2.047, P = 0.05) in the second rotation, but there was no significant difference between rotations in Closed canopy (T = 0.363, P = 0.72) (Fig. 4.35). Species richness and migrant density were unaffected by the removal of these species from analysis.
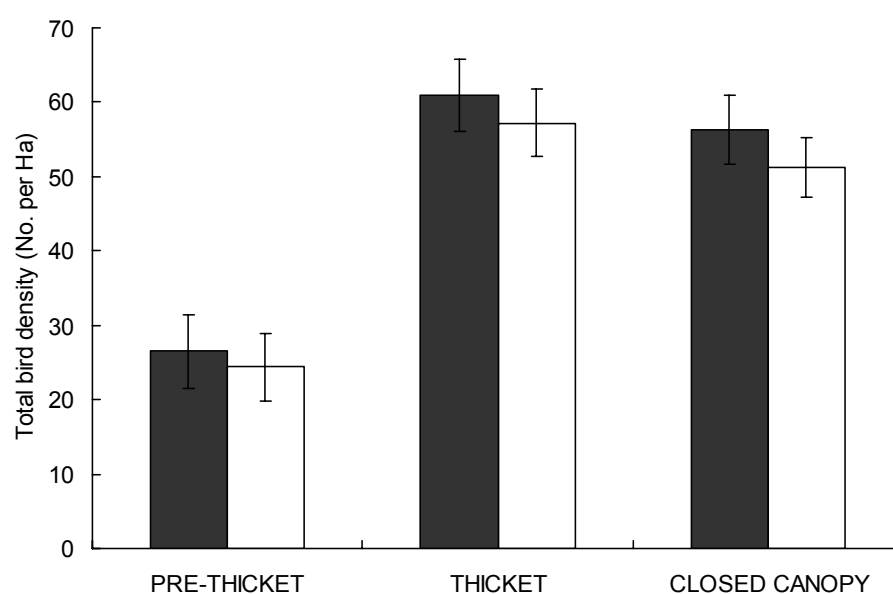
Figure 4.34: Total bird density (± se) before (dark bars) and after (open bars) correcting for natural population increase.
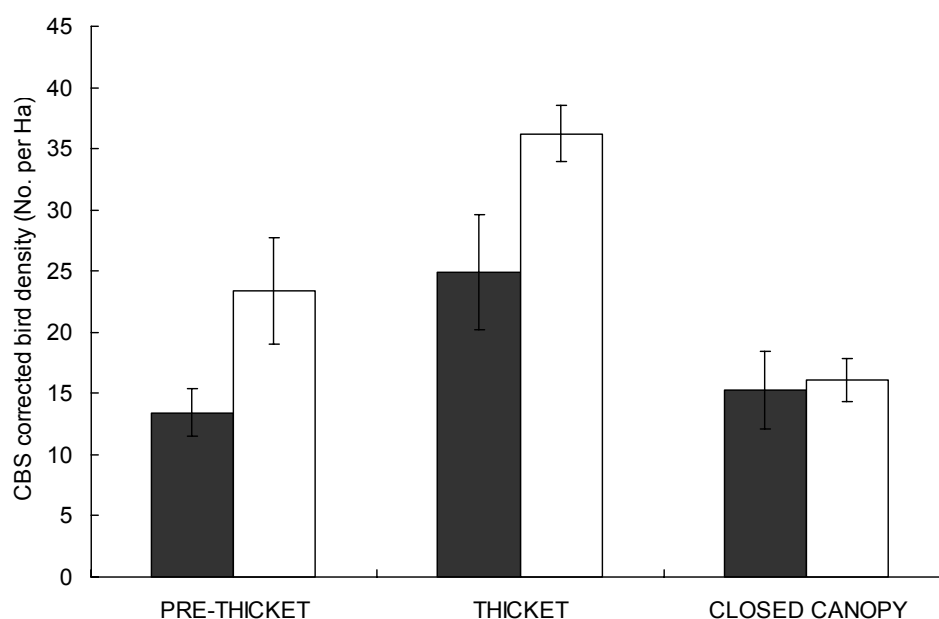
Figure 4.35: Total bird density corrected for natural population increase and excluding Coal Tit and Goldcrest, in three stages in first (dark bars) and second (light bars) rotation Sitka spruce plantations.

4.5.2 Mixed tree species survey

4.5.2.1 Density, species richness and Simpson's diversity

Twenty-five species in total were used in analysis. Of these, 23 were detected in pure Norway spruce, 20 in Norway spruce/oak mixes (hereafter referred to as oak mixes) and 22 in Norway spruce/Scots pine mixes (hereafter referred to as Scots pine mixes). Of the 25 species, 16 attained their highest population densities in the Scots pine mixes, four in the oak mixes and five in pure Norway spruce (Table 4.83). Ordination revealed no clear differences between the mixed and pure plantations (Fig. 4.36). Similarly, indicator species analysis was not very informative. Blackcap (indicator-value 61%, P = 0.03) and Song Thrush (indicator-value 67%, P < 0.01) were indicators for the Scots pine mixes. Woodpigeon was an indicator species for all three forest types (Scots pine mixes 55%, oak mixes 20% and pure Norway spruce 26%, P = 0.02). There were no indicator species exclusive to either the oak mixes or to pure Norway spruce.

To visualise more clearly any differences between the bird communities of the different forest types, we graphically represented the proportion of the total bird density contributed by each species. Although the community structure was roughly similar between the forest types, the two most common species, Coal Tit and Goldcrest, accounted for a smaller proportion of the total bird density in both types of mixed plantations than in pure Norway spruce (Fig. 4.37). The models revealed no significant differences in either species richness or Simpson's diversity between the mixed plantations and pure Norway spruce. Total bird density was significantly higher in the Scots pine mixes than in oak mixes (Z = -2.33, P < 0.05) or pure Norway spruce (Z = -3.16, P < 0.01) (Fig. 4.38).

4.5.2.2 Vegetation and birds

There was no significant difference between canopy cover, field layer cover, tree basal area, mean DBH, number of stems or the proportion of open space between the different forest types (Table 4.84). Both oak mixes (Z = 5.008, P < 0.01) and Scots pine mixes (Z = 3.019, P < 0.01) had significantly higher understorey vegetation cover than pure Norway spruce, but there was no significant difference in understorey cover between oak mixes and Scots pine mixes. Scots pine mixes had significantly higher shrub cover than either oak mixes (Z = 2.814, P < 0.01) or pure Norway spruce (Z = 5.531, P < 0.01), and oak mixes had significantly higher shrub cover than pure Norway spruce (Z = 2.161, P = 0.03). Scots pine mixes had significantly higher ground layer cover than either oak mixes (Z = 3.617, P < 0.01) or pure Norway spruce (Z = 3.954, P < 0.01), but there was no significant difference between oak mixes and pure Norway spruce. The canopy of Scots pine mixes had a significantly higher degree of openness than oak mixes (Z = 2.531, P < 0.01). However, there was no difference in canopy openness between Scots pine mixes and pure Norway spruce or between oak mixes and pure Norway spruce (Table 4.84).

Table 4.83: Species detected in pure Norway spruce (Pure NS); Norway spruce/oak mix plantations (NS:O); and Norway spruce/Scots pine mix plantations (NS:SP), the detection group to which each was assigned and their mean population density (No. ha^{-1} ± se). Also shown is the mean bird density for each forest type.

Species	Detection group	Scientific name	Pure NS	NS:O	NS:SP
Blackbird	1	*Turdus merula*	1.39 (0.34)	1.14 (0.39)	2.85 (0.99)
Blackcap	1	*Sylvia atricapilla*	0.52 (0.15)	0.49 (0.23)	1.6 (0.62)
Blue Tit	4	*Cyanistes caeruleus*	1.23 (0.44)	4.96 (1.61)	3.46 (1.82)
Bullfinch	2	*Pyrrhula pyrrhula*	0.27 (0.18)	0.28 (0.28)	0.54 (0.35)
Chaffinch	3	*Fringilla coelebs*	3.78 (0.33)	4.06 (0.93)	4.46 (0.60)
Chiffchaff	1	*Phylloscopus collybita*	0.23 (0.11)	0.32 (0.14)	0.97 (0.56)
Coal Tit	4	*Periparus ater*	19.19 (2.05)	14.93 (2.58)	22.82 (3.89)
Crossbill	3	*Loxia curvirostra*	0.06 (0.06)	0	0
Dunnock	2	*Prunella modularis*	1.05 (0.50)	1.40 (0.59)	2.14 (0.98)
Garden Warbler	1	*Sylvia borin*	0.03 (0.03)	0	0
Goldcrest	4	*Regulus regulus*	19.53 (1.56)	16.93 (3.46)	19.51 (1.84)
Great Tit	3	*Parus major*	0.43 (0.31)	0.58 (0.27)	0.45 (0.26)
Jay	2	*Garrulus glandarius*	1.00 (0.52)	1.31 (0.77)	0.74 (0.54)
Long-tailed Tit	4	*Aegithalos caudatus*	1.27 (0.42)	1.33 (0.06)	1.39 (0.85)
Mistle Thrush	1	*Turdus viscivorus*	0.44 (0.17)	0.40 (0.19)	0.67 (0.26)
Pheasant	1	*Phasianus colchicus*	0	0	0.19 (0.12)
Robin	2	*Erithacus rubecula*	4.94 (0.76)	8.14 (1.91)	8.53 (1.19)
Siskin	3	*Carduelis spinus*	0.03 (0.03)	0.06 (0.06)	0.09 (0.09)
Song Thrush	1	*Turdus philomelos*	0.36 (0.13)	0.46 (0.33)	1.68 (0.42)
Spotted Flycatcher	2	*Muscicapa striata*	0	0	0.34 (0.34)
Treecreeper	2	*Certhia familaris*	0.96 (0.27)	2.51 (0.45)	1.76 (0.69)
Willow Warbler	1	*Phylloscopus trochilus*	0.23 (0.20)	0.06 (0.06)	0.21 (0.15)
Woodcock	2	*Scolopax rusticola*	0.25 (0.25)	0	0
Woodpigeon	1	*Columba palumbus*	1.29 (0.21)	1.08 (0.42)	2.92 (0.97)
Wren	1	*Troglodytes troglodytes*	2.79 (0.62)	3.15 (0.58)	4.91 (1.16)
Mean bird density			**61.26 (2.79)**	**63.58 (5.82)**	**82.22 (5.88)**

Table 4.84: Range and mean (± se) of vegetation and structural variables in pure Norway spruce (pure NS); Norway spruce/oak mix plantations (NS:O) and Norway spruce/Scots pine mix plantations (NS:SP). Significant differences between the forests are noted, test statistics and P-values are given in the text.

	Canopy Cover (%)	Understorey cover (%)	Shrub cover (%)	Field layer cover (%)	Ground layer cover (%)	DBH (cm)	Basal area (m^2)	Number of stems	Proportion open space	Canopy openness (%)
Range Pure NS	47.33 – 81.25	2.42 – 11.25	1.83 – 67.87	6.25 – 39.00	14.75 – 53.75	22.00 – 39.74	0.42 – 0.68	5.33 – 19.67	0.02 – 0.21	3.28 – 12.82
Mean Pure NS	65.67 (10.81)	5.95 (0.92)	29.59 (7.81)	18.47 (3.96)	35.16 (4.60)	28.60 (1.93)	0.58 (0.04)	9.80 (1.46)	0.07 (0.02)	6.22 (1.14)
Range NS:O	55.42 – 66.67	5.83 – 22.33	12.42 – 61.47	2.42 – 30.08	20.00 – 55.00	22.96 – 33.58	0.35 – 0.64	6.00 – 11.33	0.01 – 0.13	2.44 – 5.44
Mean NS:O	59.75 (1.93)	14.53 (2.78)	36.55 (8.88)	15.22 (4.82)	34.07 (7.29)	28.23 (2.14)	0.53 (0.05)	7.53 (0.97)	0.05 (0.02)	4.36 (0.67)
Range NS:SP	51.25 – 74.50	1.67 – 20.08	3.50 – 91.83	3.08 – 37.20	15.92 – 77.50	17.30 – 32.66	0.44 – 0.66	6.00 – 17.00	0 – 0.03	5.08 – 11.81
Mean NS:SP	59.57 (9.01)	10.64 (3.64)	47.88 (17.87)	15.49 (5.82)	48.60 (10.28)	25.76 (2.75)	0.51 (0.05)	11.07 (2.10)	0.01 (0.01)	7.96 (1.17)
Significant Differences	None	NS:SP & NS:O > Pure NS	NS:SP > NS:O; NS:O > Pure NS	None	NS:SP > NS:O & Pure NS	None	None	None	None	NS:SP > NS:O

The results of all models investigating the relationships between bird metrics and vegetation are summarised in Table 4.85. The only explanatory variable related to Simpson's diversity was shrub cover which had a positive influence (P = 0.019). The explained deviance of the model was 56%. Shrub cover was also positively related to species richness (P = 0.032), with 57% of deviance explained. Total bird density was positively related to shrub cover (P < 0.01) and the presence of rides in forest stands (P < 0.01), and negatively related to field layer cover (P < 0.01). 87% of the variation was explained by the model in this instance.
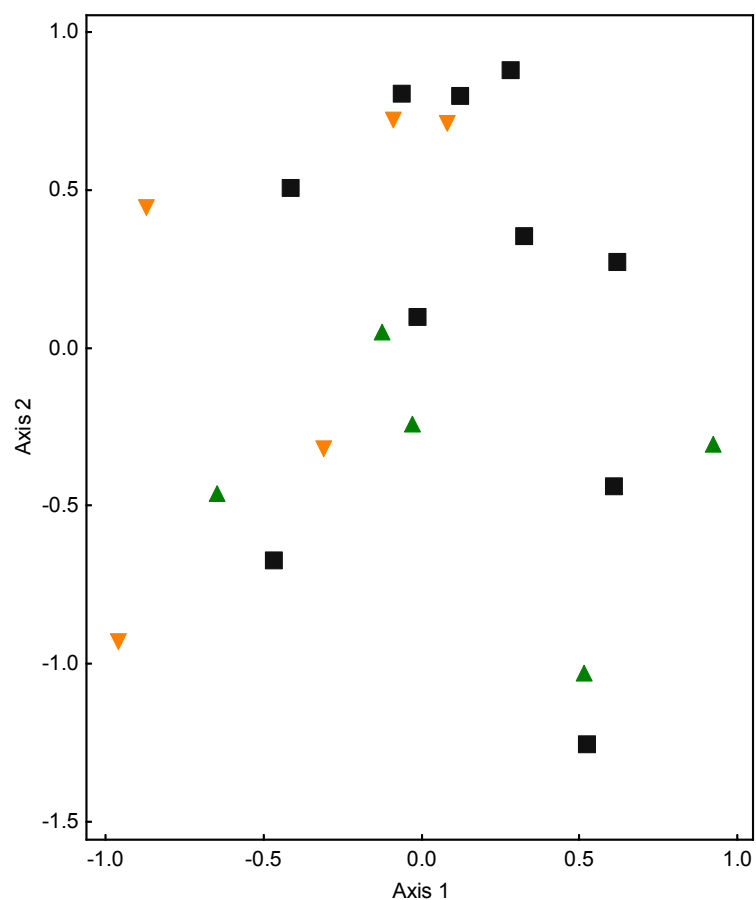
Figure 4.36: NMS ordination of species densities. Final stress for three-dimensional solution = 9.10 after 120 iterations; final instability = 0. Axis 1, r^2 = 0.17; Axis 2, r^2 = 0.37; Axis 3, r^2 = 0.36; cumulative r^2 = 0.90. ▲ = Norway spruce/oak mix plantation; ▲ = Norway spruce/Scots pine mixed plantation; ■ = pure Norway spruce plantation.
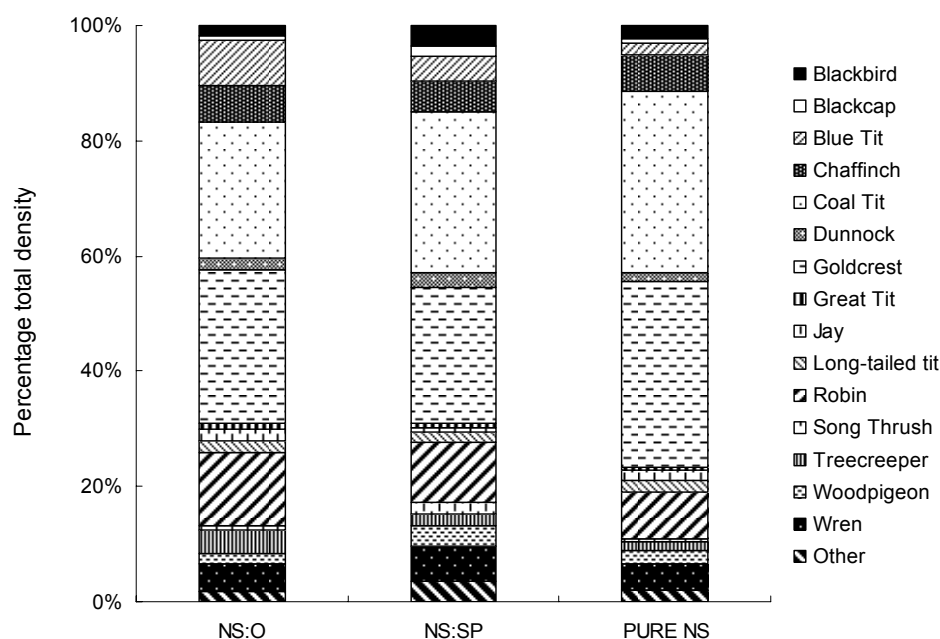
Figure 4.37: Stacked bar chart, using species densities, illustrating the bird communities in Norway spruce/oak mix plantations (NS:O); Norway spruce/Scots pine mix plantations (NS:SP) and pure Norway spruce (PURE NS) plantation forests.

Table 4.85: Results of General Linear Models investigating relationships between Simpson's diversity, bird species richness and bird density with vegetation and structural variables in three plantation forest types.

Response variable	Null deviance	Residual deviance	Intercept	Significant explanatory variable	Estimate	Z	P
Simpson's diversity	9.863	4.374	1.960	Shrub cover	0.006	2.355	0.019
Species richness	8.023	3.442	2.490	Shrub cover	0.005	2.150	0.032
Bird density	51.869	6.681	4.029	Shrub cover	0.004	3.477	< 0.01
				Ride presence	0.175	2.703	< 0.01
				Oak mix	-0.180	-2.328	0.020
				Pure Norway spruce	-0.213	-3.159	< 0.01
				Field layer cover	-0.007	-2.778	< 0.01
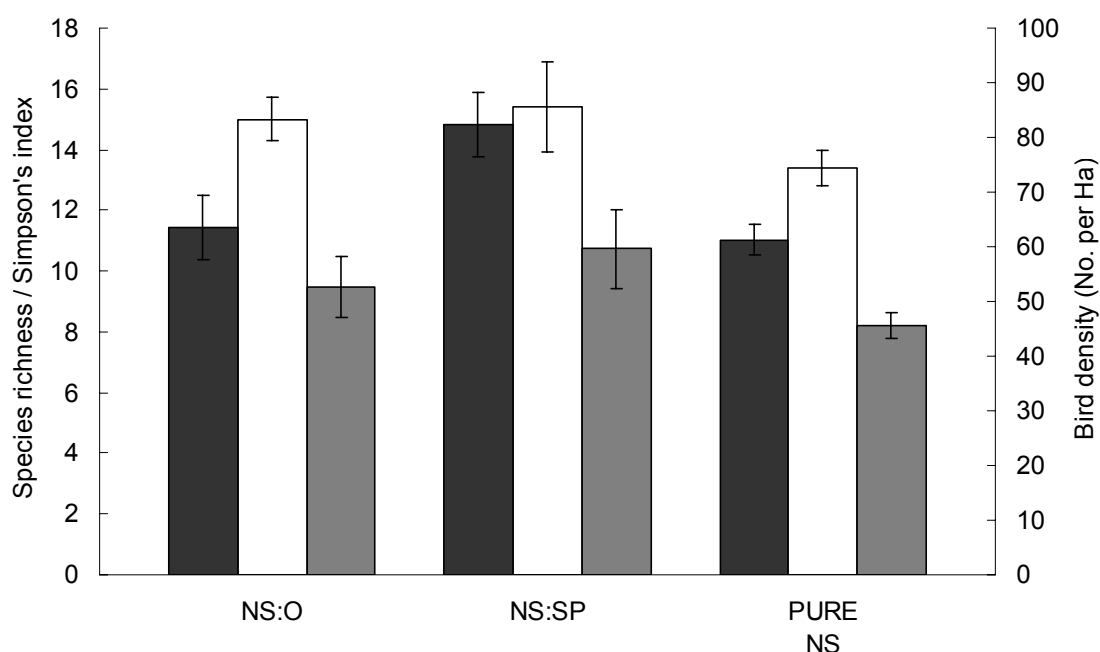
Figure 4.38: Total bird density (black bars), species richness (open bars) and Simpson's diversity (grey bars) (± se) in Norway spruce and oak mixed plantations (NS:O); Norway spruce and Scots pine mixed plantations (NS:SP) and pure Norway spruce (PURE NS) plantation forests.

4.5.3 Comparison of plantations and native woodlands

The differences between native woodlands (both oak and ash) and Sitka spruce plantations were investigated.

4.5.3.1 Ordination and indicator species analysis

Having excluded species detected in flight and those groups that were not of interest, 27 species were included in the analysis. Twenty species were recorded in age class II and 17 in age class IV Sitka spruce plantations. Twenty-one species were recorded in ash woodlands and all 27 in oak woodlands.

The ordination represents a gradient from high canopy cover and simple understorey and ground vegetation structure in the Sitka spruce plantations, through to oak and ash woodlands which had increased shrub, field layer and understorey cover (Fig. 4.39). Age class III and IV Sitka spruce plantations separated clearly from oak and ash woodlands along both Axis 1 (31% of variation) and Axis 2 (58% variation). However, Oak and Ash woodlands did not separate from each other along either axis, nor did age class III and IV plantations. Final stress for the 2 dimensional ordination was 13.57. Indicator species analysis revealed at least two indicators in each woodland type with considerable overlap of indicators between the woodland types (Table 4.86; Fig. 4.39). ANOSIM revealed significant differences in the bird community between Age class IV Sitka spruce plantations and oak woodlands (R = 0.725, P < 0.01); between age class IV Sitka spruce plantations and ash woodlands (R = 0.804, P < 0.01); between age class III Sitka spruce plantations and oak woodlands (R = 0.841, P < 0.01) and between age class III Sitka spruce plantations and ash woodlands (R = 0.951, P < 0.01). There were no significant differences between age class III and IV Sitka spruce plantations (R = 0.104, P = 0.22) or between oak and ash woodlands (R = -0.012, P = 0.51).
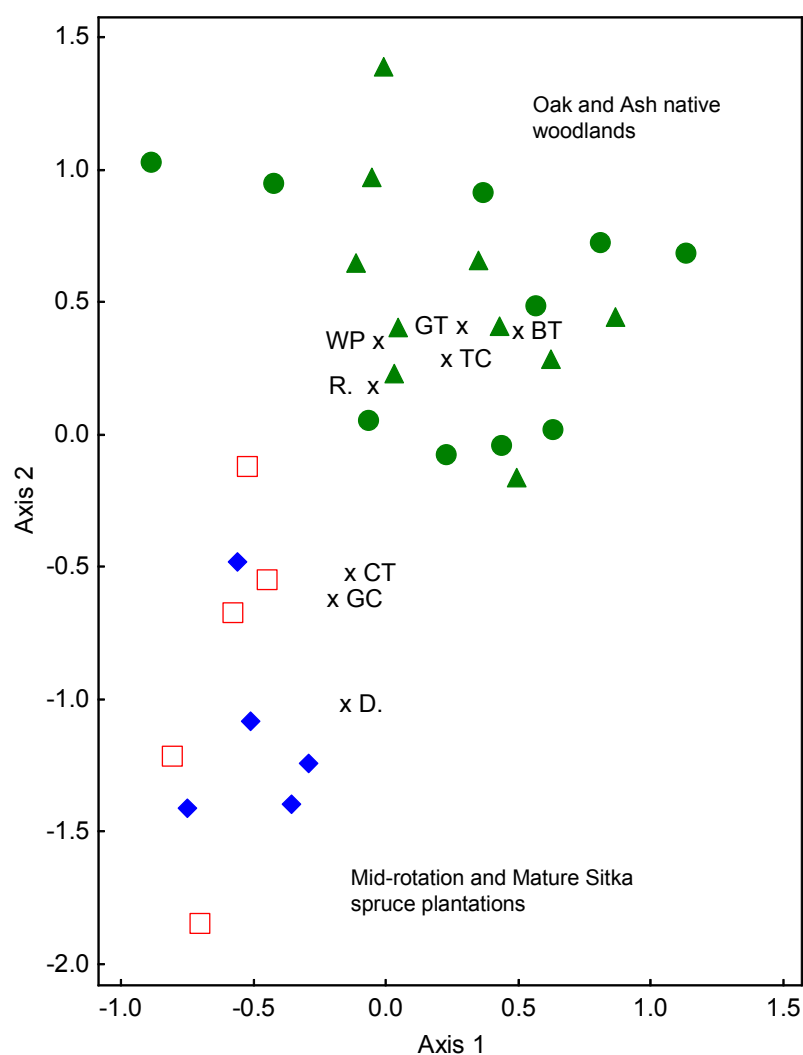
Figure 4.39: NMS ordination of species densities in Age class III and Age class IV Sitka spruce plantations, and in Oak and Ash native woodlands. Axis 1, r^2 = 0.31, Axis 2, r^2 = 0.58, cumulative r^2 = 0.90. ☐ = Age class III; ◆ = Age class IV; ● = Oak; ▲ = Ash. Indicator species with an indicator-value of 25% or more with P < 0.05 are marked with the symbol x. BT = Blue tit; CT = Coal tit; D. = Dunnock; GC = Goldcrest; GT = Great tit; R. = Robin; TC = Treecreeper; WP = Wood Pigeon. Rough site grouping are indicated on the plot. Final stress for the 2-dimensional solution = 13.57.

Table 4.86: Indicator species (indicator-value, % of perfect indication) in Age class III and age class IV Sitka spruce plantations and and in oak and ash native woodlands.

Species	Age class III	Age class IV	Oak	Ash
Dunnock	68**	-	-	-
Robin	25*	-	32*	27*
Coal Tit	32*	39*	-	-
Goldcrest	34*	42*	-	-
Blue Tit	-	-	51**	43**
Great Tit	-	-	26**	60**
Treecreeper	-	-	36*	46*
Woodpigeon	-	-	25**	46**

4.5.3.2 Bird density, species richness and Simpson's diversity

We found no significant difference in total bird density among the woodland types ($F_{3, 26}$ = 1.21, P > 0.05). There was no significant difference in mean density of forest specialists between either age class III (2.9 ± 1.0) and age class IV (1.5 ± 0.6) plantations or between oak (13.8 ± 2.1) and ash (14.3 ± 1.5) native woodlands, but native woodlands held significantly higher densities of forest specialist birds than plantations (Z = -6.39, P < 0.001). However, species richness was significantly different among woodlands (H_c = 84.18, DF = 3, P < 0.01), with oak woodlands having significantly higher species richness than age class III (Q = 2.70, P < 0.05) and IV (Q = 3.25, P < 0.01) Sitka spruce plantations and ash woodlands having significantly higher species richness than age class IV Sitka spruce plantations (Q = 3.12, P < 0.05). Species richness did not differ significantly between the other forest types. There was no significant difference in mean species richness of forest specialists between either age class III (2.4 ± 0.7) and IV (2.2 ± 0.5) plantations or between oak (5.6 ± 0.5) and ash (5.8 ± 0.4) native woodlands, but native woodlands held significantly more forest specialist species than plantations (Z = -3.97, P < 0.001). Simpson's diversity was also significantly different between woodlands ($F_{3,26}$ = 29.40, P < 0.01). Both oak and ash woodlands had significantly higher Simpson's diversity than either age class III (Oak: Q = 4.41, P < 0.05; Ash: q = 6.27, P < 0.01) or age class IV Sitka spruce plantations (Oak: q = 6.44, P < 0.01; Ash: q = 8.31, P < 0.01). Simpson's diversity did not differ significantly between age class III and age class IV Sitka spruce plantations, or between oak and ash woodlands (Fig. 4.40). It was evident from the raw data that Coal Tit and Goldcrest accounted for a large proportion of the bird density in plantation forests. To visualise their influence we plotted total bird density without these species (Fig. 4.41).

The GLM fitted to the total bird density data was found to be overdispersed. This was corrected by using a quasi-GLM model where the variance is given by $\varphi \times \mu$, where μ is the mean and φ the dispersion parameter. Year of study was positively related to total bird density, while understorey cover was negatively related to total bird density, although the explained deviance of the model was relatively low (24%). In contrast, understorey cover was associated with increasing species richness in a GLM with 55% of the deviance explained (Table 4.87). Understorey cover, shrub cover, field layer cover and mean number of stems were all significantly related to Simpson's diversity. The regression model explained a high proportion of the variation in the data (adjusted R^2 = 0.77) (Table 4.88).

Table 4.87: Significant explanatory variables and their relationship to total bird density and species richness as identified by GLM.

Response variable	Null deviance	Residual deviance	Intercept	Significant explanatory variable	Estimate	Z or T	P
Density	83.978	63.434	4.023	Understorey cover	-0.004	-2.526	0.018
				Year	0.214	2.359	0.026
Richness	19.554	10.824	2.456	Understorey cover	0.006	2.926	< 0.01

Table 4.88: Significant explanatory variables and their relationship to Simpson's diversity as identified by linear regression.

Response variable	Adjusted R^2 of model	Intercept	Significant explanatory variable	Estimate	T	F	DF	P
Simpson's diversity	0.745	6.210	Understorey cover	0.034	2.619	25.14	4,25	0.012
			Shrub cover	0.049	3.487			< 0.01
			Number of stems	0.058	2.982			0.032
			Field layer cover	0.030	2.268			< 0.01
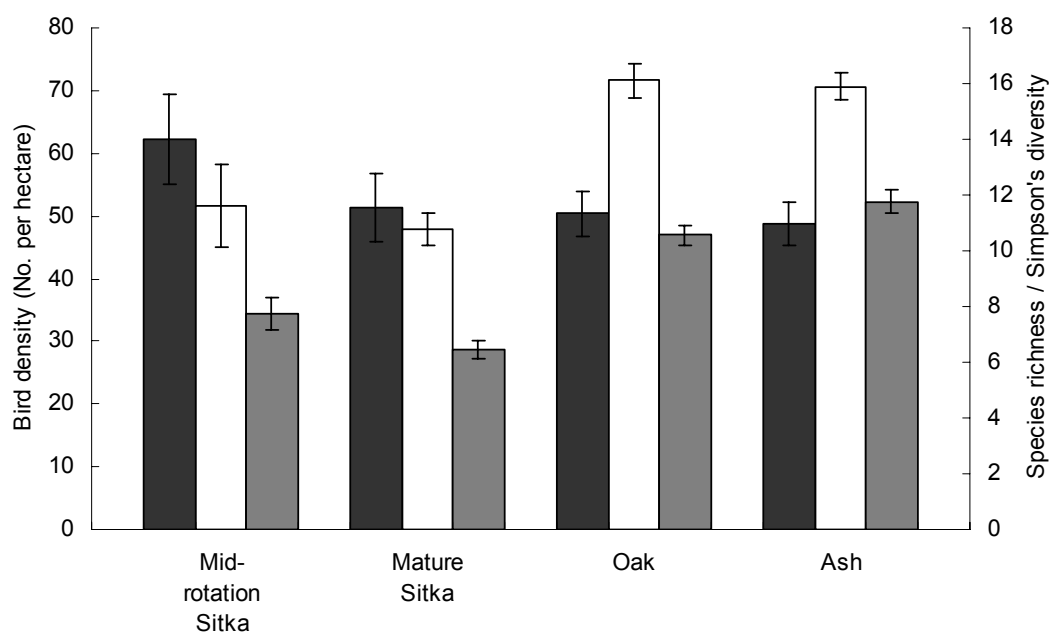
Figure 4.40: Total bird density (black bars), species richness (open bars) and Simpson's diversity (grey bars) (± se) in age class III (Mid-rotation in the graph above) and IV (Mature in the graph above) Sitka spruce plantations and in oak and ash native woodlands.
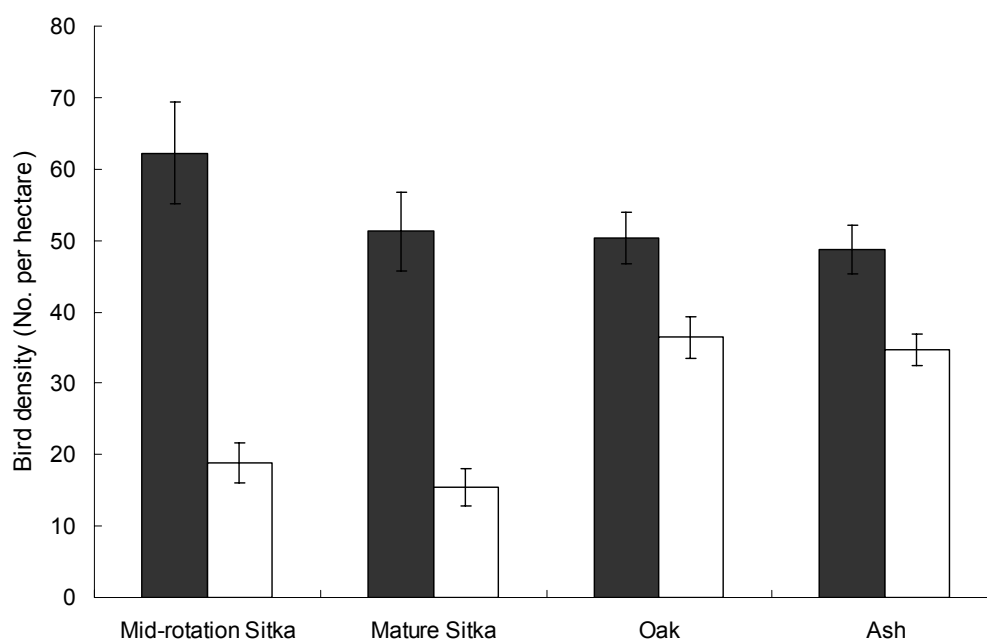
Figure 4.41: Mean bird density (± se) in age class III and IV Sitka spruce plantations and oak and ash native woodlands when all species are included (black bars) and following the removal of Coal Tit and Goldcrest (open bars)

4.5.4 Comparison of forest types in winter and breeding season

4.5.4.1 Ordination

In total, 41 species were recorded in the winter study. Species detected in flight were excluded, and we excluded some species from *Distance* analysis for comparability with the breeding season (Motacillidae and Corvidae with the exception of Jay). Woodcock and Sparrowhawk were also excluded from density analysis as their detections did not fit closely with other species in detection groups and there were too few observations to analyse separately. We were able to generate density estimates for 28 species (Table 4.89).

Ordination resulted in some discernable differences between the different forest types in winter (Fig. 4.42) but the patterns were much less pronounced than those seen during the breeding season (Fig. 4.43). There was also much greater variation in the bird assemblages within each forest type in winter as indicated by the distance between points representing the same site type. There was some overlap in the indicator species between forest type and seasons, but other species were specific to particular forest types and seasons. No species were indicative of age class IV Sitka spruce or pure Norway spruce in either season, while age class III Sitka spruce had no indicator species in the breeding season and age class II Sitka spruce had no indicator species in winter (Table 4.90).

Table 4.89: Species analysed as part of winter fieldwork, the detection group into which they were placed and their mean population densities (No. ha^{-1} ± se) in seven types of plantation forests and two types of native woodland (SS = Sitka spruce, NS:O = Norway spruce/oak mixes, NS:SP = Norways spruce/Scots pine mixes, Pure NS = pure Norways spruce.

Species	Scientific name	DG	Age class I SS	Age class II SS	Age class III SS	Age class IV SS	NS:O	NS:SP	Pure NS	Oak	Ash
Blackbird	*Turdus merula*	2	0.71 (0.42)	2.74 (1.33)	0.67 (0.67)	0.17 (0.17)	3.99 (0.99)	4.72 (0.71)	1.90 (0.48)	5.60 (1.48)	11.04 (2.50)
Blackcap	*Sylvia atricapilla*	2	0.00	0	0	0	0	0	0	0	0.14 (0.14)
Blue Tit	*Cyanistes caeruleus*	1	0.32 (0.32)	0.32 (0.32)	0.76 (0.57)	0	3.00 (0.93)	3.16 (1.64)	2.22 (0.85)	12.41 (4.84)	8.88 (3.00)
Bullfinch	*Pyrrhula pyrrhula*	2	1.35 (0.82)	0	0	0	0	0.14 (0.14)	0	0.47 (0.36)	0.59 (0.27)
Chaffinch	*Fringilla coelebs*	3	0.48 (0.31)	3.66 (2.13)	8.00 (1.05)	0.66 (0.47)	0.19 (0.19)	1.23 (1.23)	0.66 (0.59)	0.78 (0.34)	1.70 (1.24)
Crossbill	*Loxia curvirostra*	3	0	0.30 (0.30)	0	0.36 (0.36)	0	0	0	0	0
Coal Tit	*Periparus ater*	1	5.69 (1.85)	7.37 (1.80)	26.68 (3.05)	11.86 (3.58)	9.90 (1.99)	8.64 (0.97)	10.12 (1.80)	11.39 (1.74)	6.80 (1.46)
Dunnock	*Prunella modularis*	3	3.62 (0.80)	0.91 (0.52)	0	0.13 (0.13)	1.45 (0.31)	1.24 (0.86)	1.11 (0.38)	0.67 (0.47)	0.29 (0.13)
Goldcrest	*Regulus regulus*	4	12.29 (1.61)	33.13 (3.39)	34.92 (6.30)	29.69 (5.38)	27.92 (1.61)	25.29 (1.27)	25.08 (3.09)	26.01 (4.35)	23.74 (4.14)
Goldfinch	*Carduelis carduelis*	3	0.24 (0.12)	0	0	0	0	0	0.07 (0.07)	0.12 (0.12)	0
Great Tit	*Parus major*	3	0.59 (0.42)	0.91 (0.53)	0.37 (0.31)	0.28 (0.28)	0.75 (0.38)	0.30 (0.15)	0.41 (0.15)	3.22 (0.90)	3.61 (1.32)
Jay	*Garrulus glandarius*	2	0	0.47 (0.47)	0	0	0.17 (0.17)	0	0.10 (0.10)	2.94 (1.31)	1.38 (0.75)
Linnet	*Carduelis cannabina*	3	0.12 (0.12)	0	0	0	0	0	0	0	0
Lesser Redpoll	*Carduelis flammea*	3	0.12 (0.12)	0	0.04 (0.04)	0	0	0	0	0.20 (0.20)	0.10 (0.10)
Long-tailed Tit	*Aegithalos caudatus*	1	0	0	0.32 (0.32)	0	2.18 (2.18)	1.37 (0.75)	0.84 (0.38)	4.30 (2.09)	9.36 (1.88)
Mistle Thrush	*Turdus viscivorus*	2	0	0.45 (0.45)	0.19 (0.19)	0	0	1.79 (1.79)	0.09 (0.09)	0.18 (0.18)	0.15 (0.15)

Species	Scientific name	DG	Age class I SS	Age class II SS	Age class III SS	Age class IV SS	NS:O	NS:SP	Pure NS	Oak	Ash
Meadow Pipit	*Anthus pratensis*	3	0.36 (0.36)	0.6 (0.6)	0	0	0	0	0	0	0
Pheasant	*Phasianus colchicus*	2	0	0	0	0	0	0	0.09 (0.09)	0.27 (0.27)	0.15 (0.15)
Robin	*Erithacus rubecula*	2	9.70 (2.67)	14.70 (5.26)	6.40 (0.63)	2.33 (0.79)	7.47 (1.89)	9.98 (0.73)	6.40 (1.34)	7.43 (1.16)	7.93 (2.12)
Reed Bunting	*Emberiza schoeniclus*	3	0.12 (0.12)	0	0	0	0	0	0	0	0
Redwing	*Turdus iliacus*	2	0	0	0	0	0.16 (0.16)	0	0	0	1.38 (0.54)
Stonechat	*Saxicola torquata*	3	0.25 (0.25)	0	0	0	0	0	0	0	0
Siskin	*Carduelis spinus*	3	0.24 (0.24)	2.13 (0.61)	2.08 (2.08)	0.26 (0.26)	0.43 (0.02)	0.30 (0.30)	0.06 (0.06)	0	0.10 (0.10)
Song Thrush	*Turdus philomelos*	2	0	0.45 (0.45)	1.22 (0.30)	0	0	0.59 (0.34)	0.17 (0.17)	0.34 (0.34)	2.79 (0.91)
Treecreeper	*Certhia familaris*	1	0	0	0	0.96 (0.53)	1.78 (0.30)	3.24 (1.06)	3.63 (0.52)	9.52 (1.65)	6.80 (1.17)
Woodpigeon	*Columba palumbus*	2	0	0.47 (0.47)	2.00 (2.00)	0.17 (0.17)	0	0.70 (0.70)	0.09 (0.09)	0.74 (0.39)	3.16 (1.81)
Wren	*Troglodytes troglodytes*	2	11.84 (3.83)	2.80 (0.82)	1.29 (0.42)	0.34 (0.17)	4.05 (1.39)	8.30 (1.82)	4.18 (0.68)	3.72 (0.93)	5.90 (0.77)
	Site Mean		48.04 (3.77)	71.41 (7.97)	84.92 (10.63)	47.20 (8.60)	63.45 (4.36)	70.98 (5.94)	57.20 (3.95)	90.29 (14.14)	95.98 (11.70)
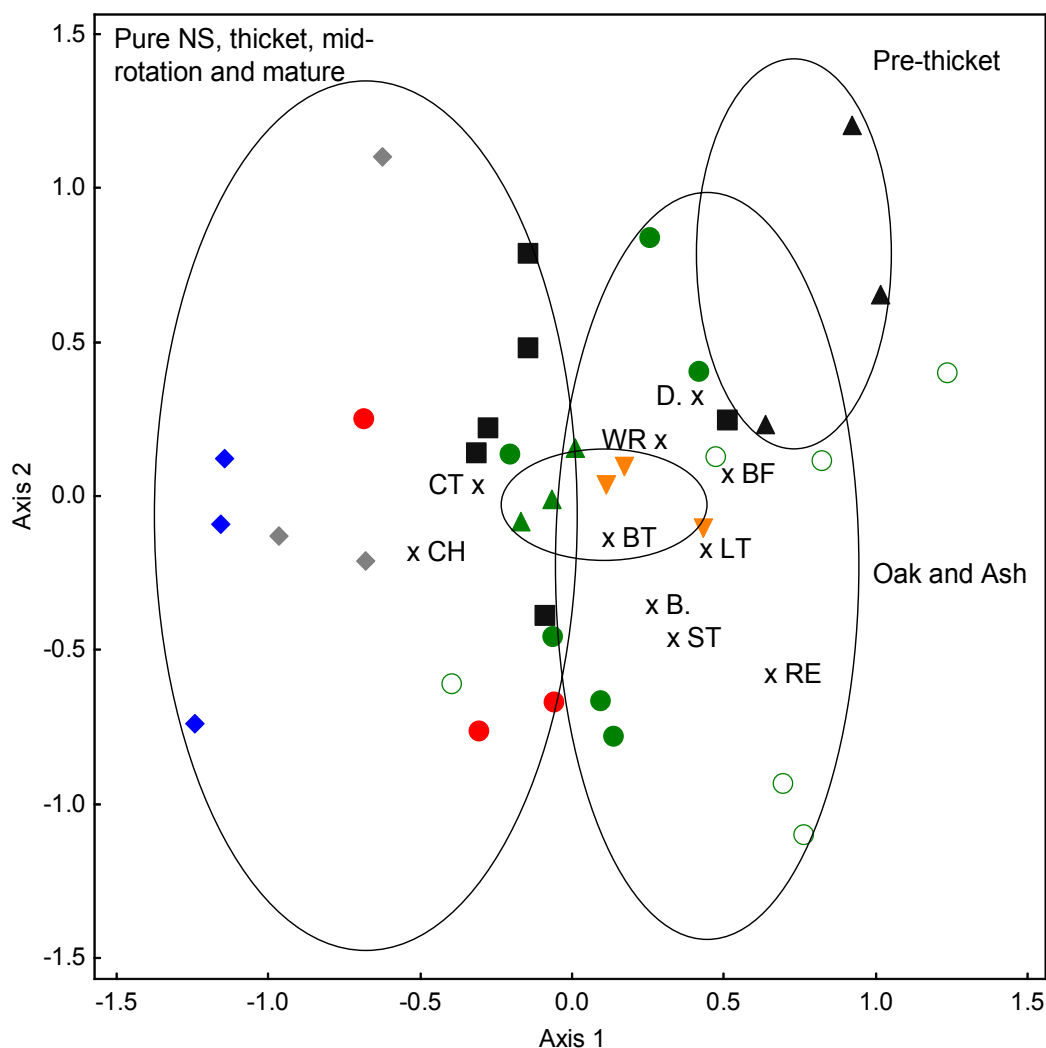
Figure 4.42: NMS ordination of bird densities in 24 plantation forests and 12 native woodlands in winter. Rough site groupings are indicated on the plot. Final stress for three-dimensional solution = 9.2; final instability = 0; number of iterations = 88. Axis 1, r^2 = 0.37; Axis 2, r^2 = 0.27, Axis 3, r^2 = 0.29. Cumulative r^2 = 0.93. ▲ = age class I Sitka spruce; ● = age class II Sitka spruce; ◆ = age class III Sitka spruce; ◆ = age class IV Sitka spruce; ■ = Pure Norway spruce; ▲ = Norways spruce/oak (NS:O) mix; ▼ = Norway spruce/Scots pine (NS: SP) mix; ● = Oak native woodland; ○ = Ash native woodland. Also shown are indicator species: B. = Blackbird; BF = Bullfinch; BT = Blue Tit; CH = Chaffinch; CT = Coal Tit; D. = Dunnock; LT = Long-tailed Tit; RE = Redwing; ST = Song Thrush; WR = Wren.
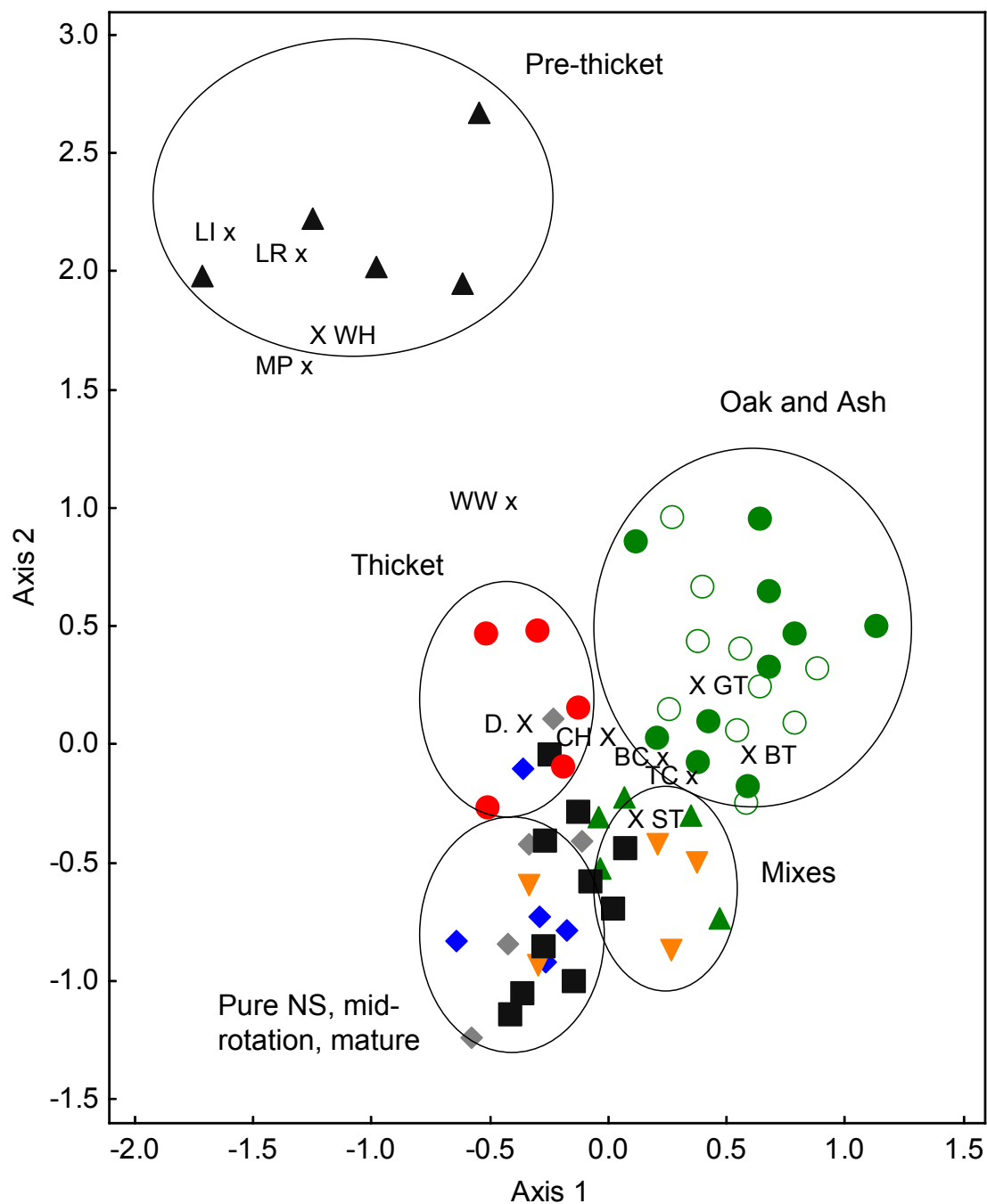
Figure 4.43: NMS ordination of breeding bird densities obtained from 40 plantation forests and 20 native woodlands. Final stress for two-dimensional solution = 13.19; final instability = 0; number of iterations = 119. Axis 1, r^2 = 0.41; Axis 2, r^2 = 0.51; cumulative r^2 = 0.92. ▲ = age class I Sitka spruce; ● = age class II Sitka spruce; ◆ = age class III Sitka spruce; ◆ = age class IV Sitka spruce; ■ = Pure Norway spruce; ▲ = Norway spruce/oak (NS:O) mix; ▼ = Norway spruce/Scots pine (NS:SP) mix; ● = Oak native woodland; ○ = Ash native woodland. Also shown are indicator species: BC = Blackcap; BT = Blue Tit; CH = Chaffinch; D. = Dunnock; GT = Great Tit; LI = Linnet; LR = Lesser Redpoll; MP = Meadow Pipit; ST = Song Thrush; TC = Treecreeper; WH = Whitethroat; WW = Willow Warbler.

Table 4.90: Indicator species in each of seven plantation forest types and in oak and ash native woodlands in the breeding season and winter. % of perfect indication is derived from the both the abundance and frequency of occurrence of each species in each forest type. NS:O = Norway spruce/oak mix, NS:SP = Norways spruce/Scots pine mix, Pure NS = pure Norway spruce

Forest type	Breeding season indicator species (% of perfect indication)	Winter indicator species (% of perfect indication)
Age class I	Linnet (40)	Bullfinch (53)
	Lesser Redpoll (80)	Dunnock (38)
	Meadow Pipit (46)	Wren (28)
	Whitethroat (70)	
	Willow Warbler (43)	
Age class II	Chaffinch (32)	-
	Dunnock (32)	-
	Willow Warbler (38)	-
Age class III	-	Chaffinch (46)
	-	Coal Tit (27)
	-	Song Thrush (22)
Age class IV	-	-
NS:O	Blue Tit (21)	-
	Treecreeper (26)	-
NS:SP	Blackcap (25)	Wren (20)
	Song Thrush (30)	
Pure NS	-	-
Oak	Blue Tit (28)	Blue Tit (40)
		Long-tailed Tit (20)
Ash	Blue Tit (23)	Blackbird (35)
	Great Tit (37)	Blue Tit (29)
	Treecreeper (20)	Long-tailed Tit (51)
		Redwing (60)
		Song Thrush (42)

4.5.4.2 Species richness, Simpson's diversity and bird density

There was a significant difference in species richness (H = 22.71, DF = 8, P < 0.01), Simpson's diversity (H = 25.51, DF = 8, P < 0.01) and bird density (H = 19.98, DF = 8, P = 0.01) between the forest types in winter. Dunne's post-hoc indicated that oak had significantly higher species richness than both age class III (Q = 3.24, P < 0.05) and IV (Q = 3.62, P < 0.05) Sitka spruce. There was no significant difference in species richness between any of the other forest types. Simpson's diversity was significantly higher in both oak (Q = 3.51, P < 0.05) and ash (Q = 3.64, P < 0.01) woodlands than in age class IV Sitka spruce, but there was no differences between any of the other forest types. The post-hoc tests found no significant differences in bird density between the different forest types despite the initial test indicating a significant difference. However, the pattern for density was similar to that of species richness and Simpson's diversity with the lowest density in Mature Sitka spruce and the highest in native woodland (Table 4.91).

Table 4.91: Winter and breeding season species richness (to nearest whole number); Simpson's diversity and total bird density (± se) in seven types of plantation forests and in oak and ash native woodlands. NS:O = Norway spruce/oak mix, NS:SP = Norways spruce/Scots pine mix, Pure NS = pure Norway spruce

Forest Type	Species richness		Simpson's diversity		Bird density	
	Winter	Breeding	Winter	Breeding	Winter	Breeding
Age class I	11 (1.53)	13 (1.21)	6.48 (1.07)	7.34 (0.71)	48.04 (3.77)	26.57 (4.98)
Age class II	11 (1.16)	13 (1.49)	5.72 (0.19)	9.19 (1.11)	71.41 (7.97)	61.24 (4.84)
Age class III	9 (0.67)	12 (1.50)	5.59 (0.51)	7.75 (0.57)	84.92 (10.63)	62.23 (7.15)
Age class IV	7 (1.33)	11 (0.58)	4.04 (0.17)	6.44 (0.30)	47.20 (8.60)	51.23 (5.43)
NS:O	12 (0.88)	15 (0.71)	7.44 (1.30)	9.47 (1.01)	63.45 (4.36)	63.58 (5.79)
NS:SP	13 (0.58)	15 (1.47)	8.32 (0.81)	10.74 (1.29)	70.98 (5.94)	82.22 (5.86)
Pure NS	11 (0.26)	14 (0.72)	7.79 (0.24)	8.19 (0.42)	57.20 (3.95)	61.26 (2.79)
Oak	13 (0.91)	16 (0.62)	9.88 (0.54)	10.57 (0.37)	90.29 (14.14)	50.36 (3.62)
Ash	15 (0.73)	16 (0.48)	9.66 (0.66)	11.76 (0.42)	95.98 (11.70)	48.79 (3.40)

4.5.4.3 Vegetation and structural attributes

For species richness, model selection removed all explanatory variables except for ivy (*Hedera helix*) cover and the number of stems, but only ivy was significantly related to species richness (Z = 2.61, P < 0.01). This model explained 31% of variation. The selection procedure investigating Simpson's diversity and the vegetation variables removed all variables except understorey cover and field layer cover, but only understorey cover was significantly associated with Simspon's diversity (Z = 3.22, P < 0.01) with 44% of variation explained. The initial bird density model identified holly (*Ilex* aquifolium) cover (T = 3.76, P < 0.01) and the density of stems (T = 2.17, P < 0.05) as the two influential explanatory variables. However, model validation using Cook's distance revealed this model to contain two influential points. When these points were removed and the data re-analysed, ivy cover (T = 3.67, P < 0.01), evergreen shrub cover (T = -2.73, P = 0.01) and density of stems (T = 5.16, P < 0.01) were all significantly related to total bird density. 57% of variation was explained by this model (Table 4.92).

4.5.4.4 Patterns across seasons

Both species richness (r_s = 0.53, P < 0.01) and Simpson's diversity (r_s = 0.59, P < 0.01) were significantly positively correlated between the breeding season and winter for all study sites (Fig. 4.44). Bird density did not correlate significantly between winter and the breeding season (r_s = -0.01, P = 0.94). However, when Goldcrest and Coal Tit were removed from analysis, the correlation between bird density in winter and the breeding season was significant (r_s = 0.57, P < 0.01) (Fig. 4.45).

Table 4.92: Explanatory variables significantly influencing winter species richness and Simpson's diversity, identified using Poisson GLM, and winter bird density identified using Quasi-Poisson GLM.

Response variable	Null deviance	Residual deviance	Intercept	Significant explanatory variable	Estimate	Z or T	P
Species richness	21.70	15.07	2.34	Ivy	**0.06**	**2.61**	< 0.01
Simpson's diversity	22.91	12.94	1.75	Understorey cover	0.12	3.22	< 0.01
Bird density	237.87	101.65	3.87	Ivy	**0.08**	**3.67**	< 0.01
				Evergreen shrub	-0.01	-2.73	0.01
				Stem density	0.02	5.16	< 0.01
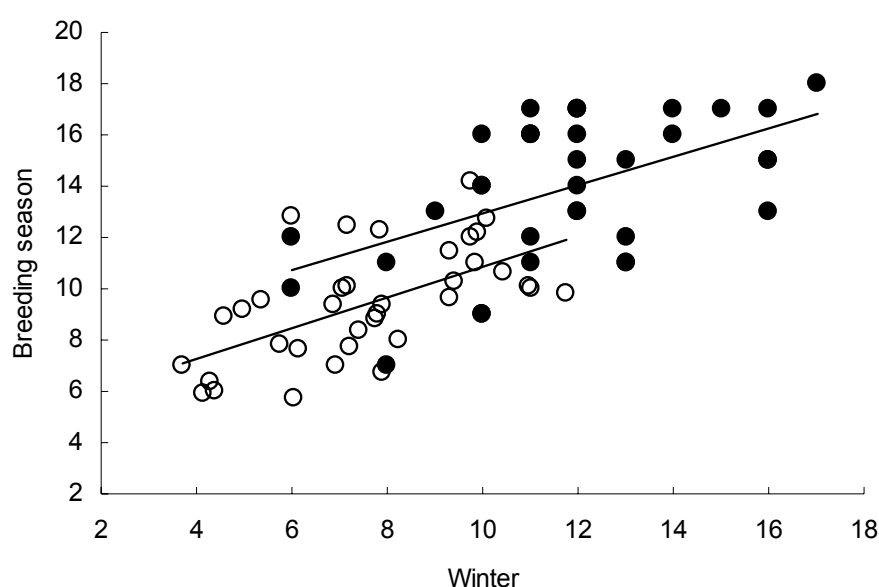
Figure 4.44: Scatterplot of Simpson's diversity (open circles) and species richness (closed circles) in 12 native woodlands and 24 plantation forests in the breeding season and winter. Simpson's diversity r^2 = 0.35; Species richness r^2 = 0.28.

Neither winter species richness (Z = 0.45, P = 0.45, explained deviance = 12%), Simpson's diversity (Z = 0.26, P = 0.80, explained deviance = 2%) or bird density (T = 0.60, P = 0.56, explained deviance = 3%) (Fig. 4.46a) showed any relationship with forest area in winter. The relationship between bird density and forest area was not improved by removing the outliers. This pattern was in contrast to the breeding season where bird density was significantly negatively related to forest area after removing the four largest outliers (Fig. 4.46b).
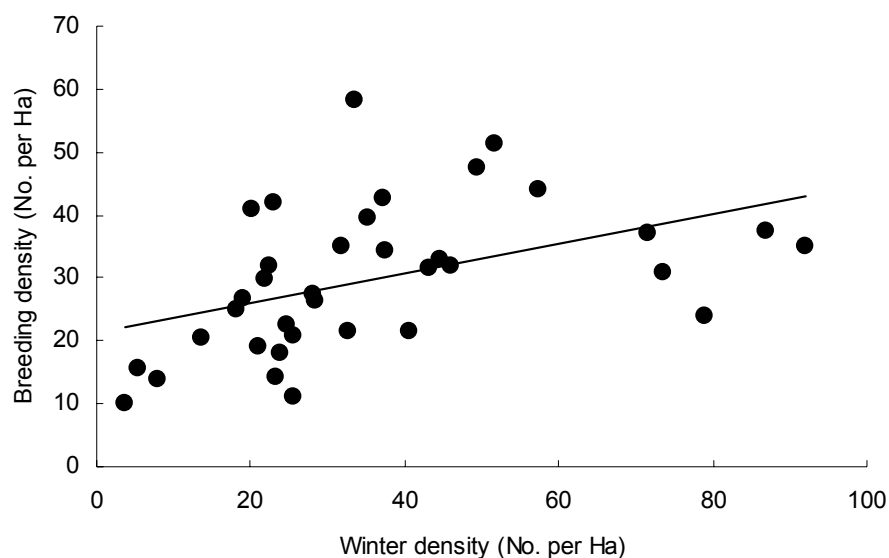
Figure 4.45: Scatterplot of total bird density (number ha^{-1}) in 12 native woodlands and 24 plantation forests in the breeding season and winter, after excluding Goldcrest and Coal Tit from analysis. r^2 = 0.20.
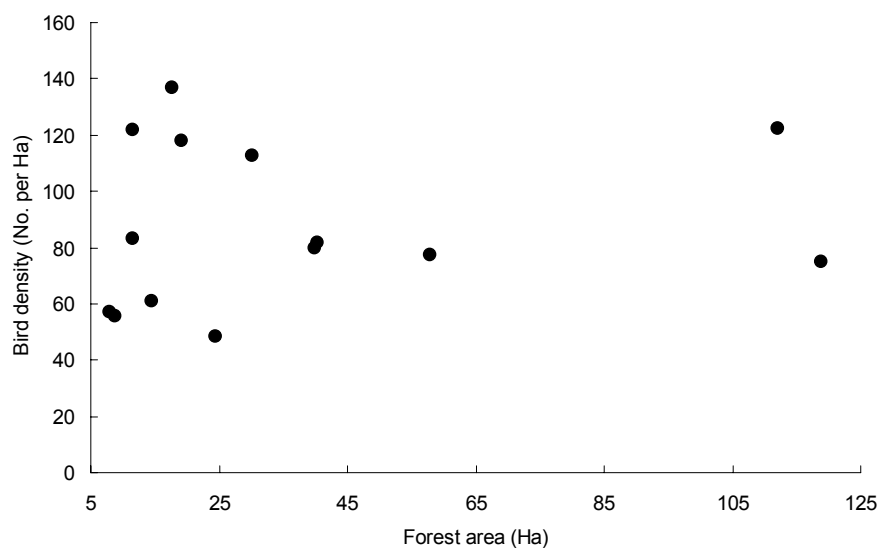
Figure 4.46a: Scatterplot of bird density against forest area in winter.
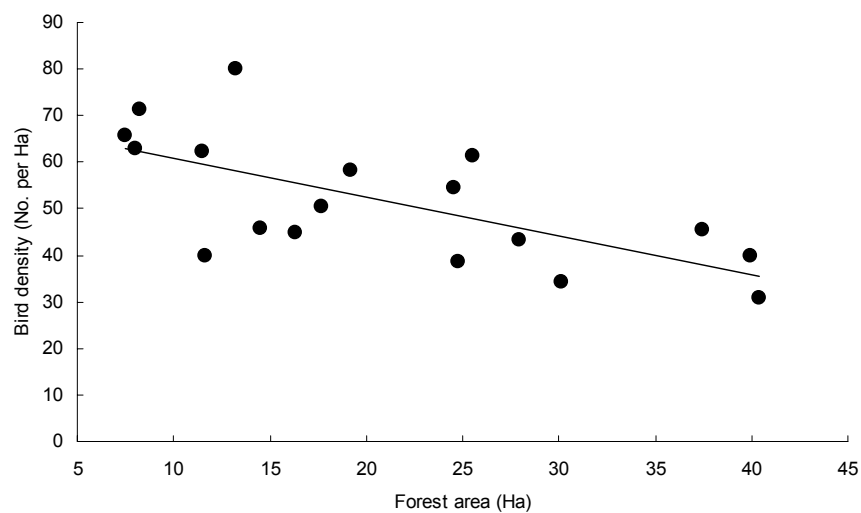
Figure 4.46b: Scatterplot of bird density against forest area in the breeding season. r^2 = 0.47.

4.6 Deadwood

The mean volume of logs in oak woodlands was 20.68 ± 1.87 m^3 ha^{-1} (range: 15.01 - 25.94 m^3 ha^{-1}; median = 21.19 m^3 ha^{-1}). The mean log volume in ash woodlands was 27.06 ± 1.32 m^3 ha^{-1} (range: 24.49 - 30.67 m^3 ha^{-1}; median = 25.39 m^3 ha^{-1}) and the mean log volume in age class IV Sitka spruce plantations was 13.55 ± 1.90 m^3 ha^{-1} (range: 8.74 – 18.97 m^3 ha^{-1}; median = 13.24). We found a significant difference in log volume between the three forest types (Kruskal-Wallis H = 11.64; P < 0.01). Dunn's post-hoc indicated no significant difference between the log volumes of oak and ash woodlands (Q = 1.58, P > 0.05) or between oak and plantation forests (Q = 1.49, P > 0.05), but ash woodlands had significantly higher log volumes than plantations (Q = 2.99, P < 0.01). In all forests, over 90% of all recorded logs were less than 20 cm in diameter. In plantations, no logs over 40 cm in diameter were recorded while in each of oak and ash woodlands, logs of this size were rare (Table 4.93). Most recorded logs in all size classes were part rotted, except in the largest category where half of recorded logs were well-rotted (Fig. 4.47).

Table 4.93: Size distribution of recorded logs and snags in oak and ash native woodlands and age class IV Sitka spruce plantation forests before and (after) correcting for survey effort. Size of logs is expressed as cm diameter while snags are cm DBH.

	Forest type					
	Oak		Ash		Plantation	
Size Class	% Logs	% Snags	% Logs	% Snags	% Logs	% Snags
5-10	**62 (57)**	**65 (61)**	**68 (66)**	**56 (46)**	**66 (69)**	**70 (70)**
11-20	**29 (35)**	**27 (32)**	**25 (26)**	**37 (45)**	24 (21)	30 (30)
21-30	**6 (6)**	**6 (6)**	6 (6)	7 (9)	8 (9)	0 (0)
31-40	**1 (1)**	**1 (1)**	1 (1)	0 (0)	1 (1)	0 (0)
> 40	**2 (1)**	**1 (0)**	< 1 (< 1)	0 (0)	0 (0)	0 (0)

In oak woodlands, mean snag density was 92.22 ± 3.28 ha^{-1} (range: 81.34 – 100.39 ha^{-1}; median = 90.86 ha^{-1}), and in ash woodlands, mean snag density was 89.52 ha^{-1} ± 7.79 (range: 61.03 – 107.27 ha^{-1}; median = 89.52 ha^{-1}). Snag density in plantations was 72.26 ± 30.24 snags ha^{-1} (range: 11.90 – 170.73 snags ha^{-1}; median = 59.52). There was no significant difference between the density of snags in the three forest types (Kruskal-Wallis H = 0.74; P > 0.05). Snag size distribution over all forests closely resembled that of logs with over 90% of all recorded snags under 20 cm DBH. We recorded only two snags greater than 30 cm DBH (both in oak woodlands) and only one of these (0.5%) was greater than 40 cm DBH. However this snag was removed after correcting for survey effort (Table 4.93). As in the case of logs, most snags were categorised as part-rotted. All 30 snags recorded in plantations were under 20cm DBH and none were classed as well-rotted (Fig. 4.48).
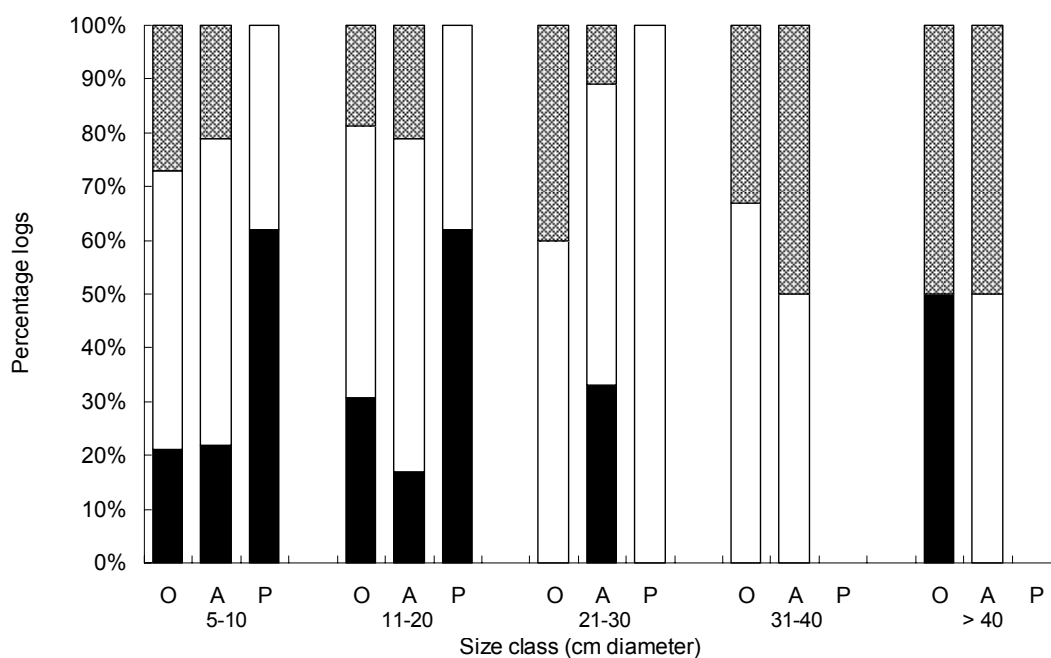
Figure 4.47: Percentage of recorded logs in each size class in each rot category (Intact = black section; Part-rotted = open section; Well-rotted = shaded section). O = Oak; A = Ash and P = age class IV Sitka spruce plantation.
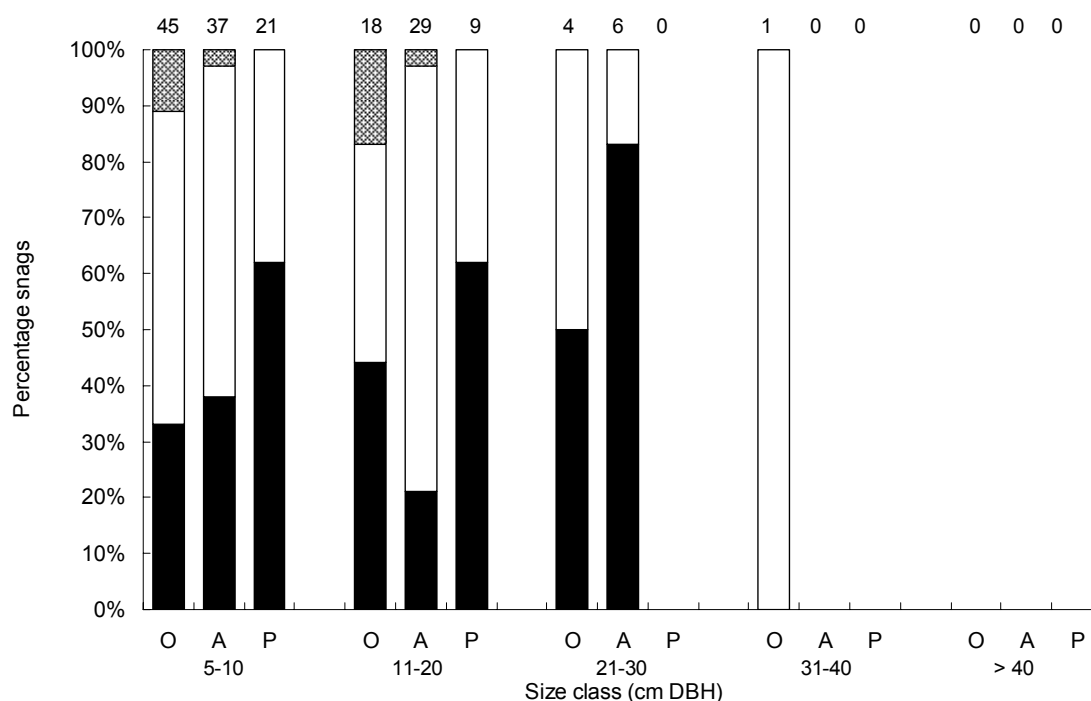
Figure 4.48: Percentage of recorded snags in each size class in each rot category (Intact = black section; Part-rotted = open section; Well-rotted = shaded section). O = Oak; A = Ash and P = age class IV Sitka spruce plantation. Actual numbers (corrected for survey effort) are shown above the bars.

Mean stump volume in plantations was 25.40 ± 5.16 m^3 ha^{-1} (range: 14.32 - 42.61 m^3 ha^{-1}), in oak woodlands mean stump volume was 6.07 ± 2.71 m^3 (range: 4.33 – 8.01 m^3 ha^{-1}) and in ash woodlands, the mean stump volume was 7.90 ± 3.52 m^3 ha^{-1} (range: 4.66 – 11.34 m^3 ha^{-1}). There was a significant difference in volume of deadwood contained in stumps in the three forest types ($F_{2,\ 14}$ = 12.00, P < 0.01). The stump volume in plantations was significantly higher than that in oak (q = 6.32, P < 0.01) or ash (q = 5.72, P < 0.01) forests. There was no significant difference in the stump volumes of oak and ash woodlands. The distribution of stumps between the different rot classes in oak and ash woodlands was similar, with most classed as part-rotted. Most stumps in plantation forests were classed as intact (Fig. 4.49).
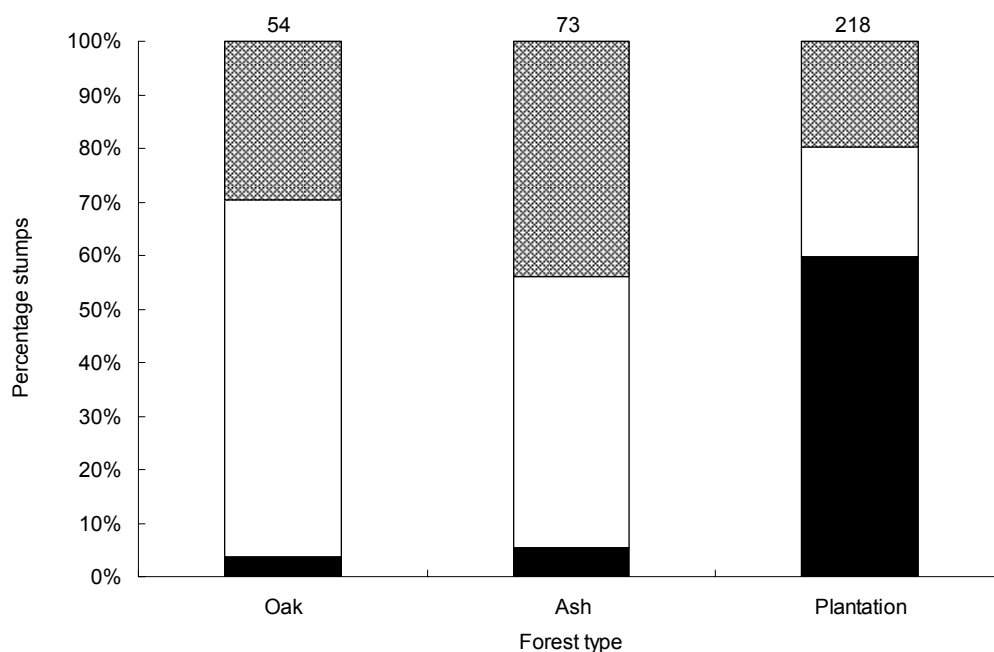
Figure 4.49: Percentage of recorded stumps in each forest type in each rot category (Intact = black section; Part-rotted = open section; Well-rotted = shaded section) in native oak and ash woodlands and age class IV Sitka spruce plantation forests. Actual numbers (corrected for survey effort) are shown above the bars.

4.7 Terrestrial laser scanning

Terrestrial Laser Scanning was used to determine diameter at breast height (DBH), a proxy for tree height, deadwood volume and density, vertical variation of biomass over a specific range of heights and open space at a subset of FORESTBIO sites (Appendix 1; Tables 4.94 and 4.95). DBH was derived from scans of the forest structure at all sites and also measured manually during surveys of ground vegetation biodiversity. A strong correlation was found between the two methods of DBH measurement, although the intercept was not near to zero (Fig. 4.50). Tree height (measured from forest floor to a point on the stem where diameter was approximately 70mm) was derived from the scans of all sites. A strong correlation was found between it and DBH. The distance between trees was used as a measure of open space in the forests in this study. The X and Y coordinates of trees that made the analysis possible were determined using AutoStem, commercial software made available by TreeMetrics Ltd. The greatest spread of distance between trees was in oak native woodland, followed by age class III Sitka spruce plantations and then by age class IV Sitka spruce plantations (Table 4.94). No significant relationships were found between any of the measures of forest structure extracted from scan data and species richness of any of the taxa under investigation. Total species richness at all plots in each site and average species richness at all plots in each site were both investigated.
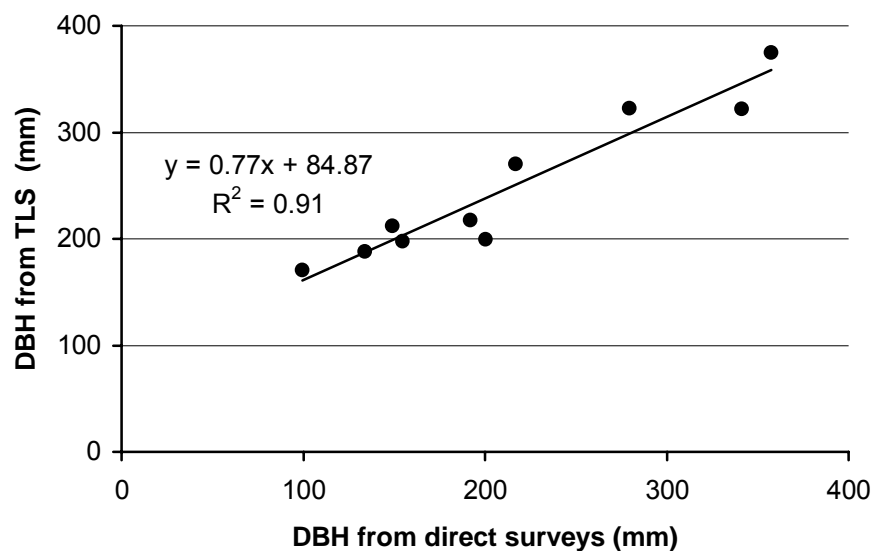
Figure 4.50: The relationship between diameter at breast height (DBH) (mm) measured using Terrestrial Laser Scanning (TLS) and by direct measurement in the field.

Table 4.94: Structural information retrieved from point clouds in each forest type during summer and winter (mean values where n > 1).

Treatment		n	DBH (mm)	Tree height (m)	Nearest neighbour distance (m)	Standing volume (m^3 ha^{-1})	Vegetation (%)*
Native Woodlands							
Oak	Winter	4	193.7	12.3	2.3	55.5	99.1
Oak	Summer	4	197.2	12.3	2.4	52.0	93.5
Sitka Spruce Plantations							
Age class IV	Winter	1	356.4	20.4	3.2	330.6	37.0
Age class IV	Summer	3	339.7	20.7	3.24	394.71	47.7
Age class III	Summer	3	222.5	14.2	2.77	67.0	149.2

* Coefficient of Variation of estimated biomass from 1.82m to 15.82m above ground.

Table 4.95: Deadwood in each forest type during summer and winter (mean values where n > 1).

Treatment		n	Logs* (m^3 ha^{-1})	Snags* (No ha^{-1})	Snags* (m^3 ha^{-1})
Native Woodlands					
Oak	Winter	4	0.8	62.8	10.0
Oak	Summer	4	0.29	46.3	3.8
Sitka Spruce Plantations					
Age class IV	Winter	1	0.4	0	0
Age class IV	Summer	3	0.5	11.5	0.5
Age class III	Summer	3	0.3	35.6	0.8

* Minimum Diameter 50mm

Data-mining was used to predict each of five biodiversity measures based on the physical descriptions obtained of the forests using laser scanning. The following biodiversity measures were considered:

- Ground-dwelling beetle species richness
- Bird species richness
- Canopy-dwelling invertebrate species richness
- Ground vegetation species richness
- Ground-dwelling spider species richness

A number of regression techniques were used to predict each of the 5 biodiversity measures. The regression techniques were as follows:

- Pace Regression
- Multilayer Perceptron
- Linear Regression
- Least Median Squares
- REPTree

The correlation coefficients between the true biodiversity measure derived from manual surveys and the predictions generated by each regression technique are shown in Table 4.96.

Table 4.96: Correlation coefficients (R^2) between actual and predicted biodiversity using five regression techniques.

	Pace Regression	Multi-layer perceptron	Linear Regression	Leastmedsq	REPTree
Ground vegetation	0.77	0.93	0.77	0.73	0.85
Ground-dwelling beetles	0.85	0.92	0.84	0.65	0.82
Ground-dwelling spiders	0.68	0.93	0.61	0.17	0.76
Canopy Invertebrates	0.95	0.99	0.94	0.81	0.92
Birds	0.80	0.92	0.83	0.57	0.90

There was greater performance of the function Multilayer Perceptron over the other functions based on correlation coefficients undergoing paired corrected T-test. There was no human-readable rule output by Multilayer Perceptron (as is normal) and the function that received second place in the ranking was REPTree, which produced a human-readable decision tree (the equivalent of a rule). The best performing function that produced a very human-readable rule (as an equation) was Linear Regression. Figure 4.51 shows the results of application of Linear Regression to Ground vegetation species richness. Canopy-dwelling invertebrates were the most suited biodiversity measure to the combination of Multilayer Perceptron with the attributes that comprised the data set for canopy-dwelling invertebrates. Correlation coefficient (R^2) was 0.99.
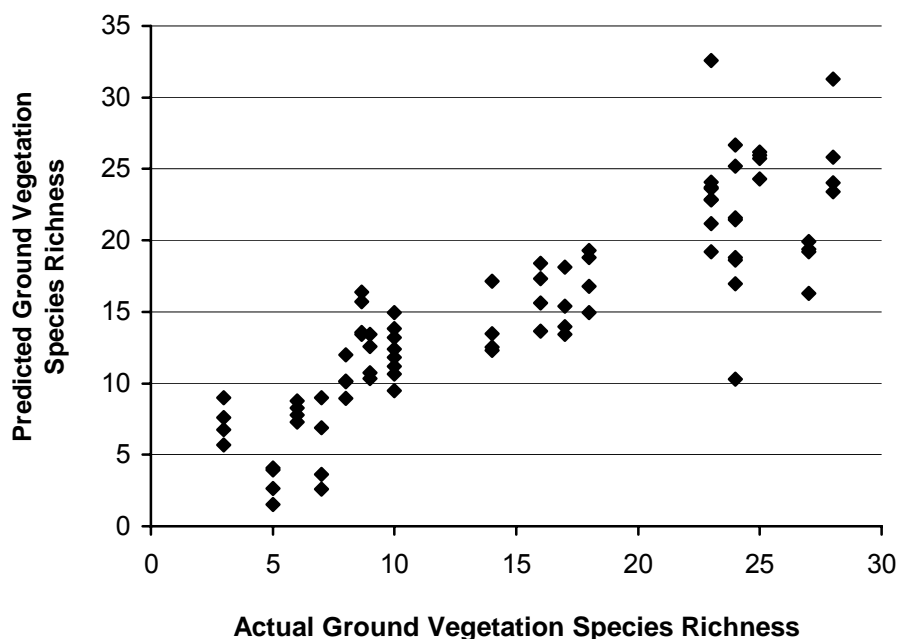
Figure 4.51: An example biodiversity predictor for ground vegetation richness obtained using Linear Regression.

4.8 Cross-taxon analysis

4.8.1 Informal comparison

4.8.1.1 Afforestation and reforestation survey

4.8.1.1.1 Trends across the forest cycle

4.8.1.1.1.1 Trends in species richness

In reforestation, the ground vegetation groups (total, vascular and non-vascular) and the ground-dwelling spiders showed a similar trend early in the forest cycle with high species richness in the Pre-thicket stage (age class I) when the canopy was at its most open and low species richness in the intermediate stages when the canopy was closed and little light could penetrate (Table 4.97). Conversely, ground-dwelling beetles and lower trunk epiphytes had low species richness in the Pre-thicket stage (age class I), with a lack of specialist open habitat beetles, particularly for poorly drained peat soils, and slow colonization rates for epiphytes cited as possible causes. There was generally relatively high species richness in the Commercially mature stage when the canopy was beginning to open again, other than for the ground-dwelling spiders, which remained relatively species poor, with few species seeming able to exploit the relatively Closed canopy conditions. Total species richness of birds did not differ significantly across the cycle. Trends in species richness across the forest cycle were similar in afforestation and reforestation, other than for the non-vascular ground vegetation and ground-dwelling spiders, and these differences will be discussed in the comparison of afforestation and reforestation below.

Table 4.97: Trends in total species richness across the afforestation (A) and reforestation (R) cycle for structural stages and age classes. The terms High and Low relate to relative species richness between the stages of a rotation and do not refer to species richness relative to other forest types.An arrow indicates a trend of increasing species richness from the beginning to end of a rotation.

Structural stage		Pre-thicket	Thicket	Closed-maturing	Reopening	Commercially mature
Age class		I	II	III		IV
Ground vegetation	A	High		Low		High
(total)	R	High		Low		High
Vascular plants	A	High		Low		High
	R	High		Low		High
Non-vascular plants	A	Low	⟶			High
	R	High		Low		High
Ground-dwelling	A	High	High	Low	Low	High
spiders	R	High	Low	Low	Low	Low
Ground-dwelling	A			(Not studied)		
beetles	R	Low	Low	Low	High	High
Canopy-dwelling	A	(Not studied)		No statistically significant differences		
spiders	R	(Not studied)		No statistically significant differences		
Canopy-dwelling	A	(Not studied)		No statistically significant differences		
beetles	R	(Not studied)		No statistically significant differences		
Lower trunk	A			(Not studied)		
epiphytes	R	Low	High	Low		High
Birds	A			No statistically significant differences		
	R			No statistically significant differences		

Note: Lepidoptera were not studied in this survey and canopy epiphytes were only sampled in age class IV

The species richness of forest-associated species in reforestation (Table 4.98) showed a general trend of increasing with structural development, with the exception of the lower trunk typical epiphytes which were most species rich in the Thicket stage (age class II). This may be related to the fact that typical epiphytes have an association with trees, rather than with forests *per se*, and may either show a preference for certain host species or be relatively light demanding. Trends were similar for afforestation and reforestation.

Table 4.98: Trends in forest-associated species richness across the afforestation (A) and reforestation (R) cycle. The terms High and Low relate to relative species richness between the stages of a rotation and do not refer to species richness relative to other forest types. An arrow indicates a trend of increasing species richness from the beginning to end of a rotation.

Structural stage		Pre-thicket	Thicket	Closed-maturing	Reopening	Commercially mature
Age class		I	II	III		IV
Ground vegetation	A	Low		───────────────────▶		High
(total)	R	Low	Low	Low	Low	High
Ground-dwelling	A	Low		─────────────────▶		High
spiders	R	Low		─────────────────▶		High
Ground-dwelling	A			(Not studied)		
beetles	R	Low		─────────────────▶		High
Canopy-dwelling	A	(Not studied)		No statistically significant differences		
spiders	R	(Not studied)		No statistically significant differences		
Canopy-dwelling	A	(Not studied)		No statistically significant differences		
beetles	R	(Not studied)		No statistically significant differences		
Lower trunk	A			(Not studied)		
epiphytes	R	Low	High	Low		Low
Birds	A	Low	High	High		High
	R	Low	High	High		High

Note: Lepidoptera were not studied in this survey

4.8.1.1.1.2 Trends in community composition

The general trend in community composition for the different taxonomic groups was for the earlier stages of the reforestation cycle to be more distinct, with composition becoming more similar in the later stages of the cycle. This is related to the presence of a varied open habitat flora and fauna in the early stages, with more specialisation as the canopy closes. For the ground vegetation, the Pre-thicket stage (age class I) had a relatively distinct vegetation composition, but vegetation composition was relatively similar between the sites within this stage. For all other groups, the Pre-thicket stage (age class I) showed much greater variation between sites compared to the other structural stages. For the ground-dwelling spiders and beetles, and the birds, Pre-thicket (age class I) and Thicket (age class II) sites were relatively distinct and separated from the later stages, although for the ground-dwelling beetles this was confounded somewhat by geographic location. For all groups, other than the lower-trunk epiphytes, the later stages had relatively similar community composition, with little variation between sites. The lower trunk epiphytes were the only group that had a significantly different community composition in all age classes.

4.8.1.1.2 Comparison of trends between afforestation and reforestation

4.8.1.1.2.1 Trends in species richness

The trends in total species richness exhibited by the different taxonomic groups could be divided into three responses; higher species richness in afforestation, higher species richness in reforestation or no difference between rotations. The ground vegetation groups and the ground-dwelling spiders showed a trend of higher species richness in afforestation sites compared to reforestation, except at the Pre-thicket stage (age class I). This was related to the higher canopy cover in reforestation sites over the whole cycle, although canopy cover was only significantly higher in the Pre-thicket (age class I) and Commercially mature stages. Beyond the Pre-thicket stage (age class I) for the ground-dwelling spiders, the higher species richness in afforestation was significant for all stages while the differences in total ground vegetation and non-vascular species richness were only significant at the closed-maturing stage. At the Pre-thicket stage (age class I), there was no significant difference in ground-dwelling spider species richness between rotations, while non-vascular (bryophytes only) species richness was significantly higher in reforestation sites at this stage. This was believed to be related for both groups to the retention of species between rotations, which was assisted for non vascular plants by the presence of brash piles in Pre-thicket reforestation containing deadwood residues from the previous rotation. The birds showed no significant difference between rotations nor did the canopy-dwelling spiders and beetles. However, the canopy invertebrates were only studied in the later stages of the cycle and were studied in different afforestation sites to the other taxonomic groups; these sites displayed no difference in canopy cover between rotations. The canopy epiphytes were the only group which showed significantly higher species richness in reforestation in the later stages of the cycle. However, they were also studied at different afforestation sites to the other taxonomic groups and the rotations were compared by age class (all age class IV) rather than structural stage, suggesting that there could have been confounding differences in structural development between rotations.

For forest-associated species richness, both the ground vegetation and ground-dwelling spiders showed significantly higher-values in Pre-thicket (age class I) reforestation than afforestation sites. Again this was likely related to the retention of species between rotations and the presence of brash piles in Pre-thicket reforestation. Conversely, there were more typical canopy epiphyte species in the later stages of reforestation, although this difference was not significant.

4.8.1.1.2.2 Trends in community composition

The general trend was for a convergence in community composition between rotations through the forest cycle. For both the ground vegetation and ground-dwelling spiders the Pre-thicket stage (age class I) was the most distinct and the first three structural stages appeared to have relatively distinct community composition. This was most likely related to the different pre-planting habitats in the afforestation sites, while all reforestation sites were previously plantation forest. Ground-dwelling spiders also showed a significant difference between rotations in the later stages of the rotation, possibly related to differences in canopy openness between rotations, although these stages were the most similar between rotations. Canopy epiphytes also showed a significant difference in their community composition in the later stages, while canopy invertebrates showed no difference.

4.8.1.2 Mixed tree species survey

4.8.1.2.1 The effect of planting Scots pine or oak with Norway spruce

4.8.1.2.1.1 Trends in species richness

The majority of the taxonomic groups studied showed no or only a weak effect of the addition of either Scots pine or oak to Norway spruce (Fig. 4.52). This was believed to be related to the low proportion of the secondary mix species in the plantations and the incompatibility of the mix partners, particularly the oak, which remained as an understorey tree. The ground vegetation groups (total, vascular and non-vascular), ground-dwelling spiders and beetles, Lepidoptera, canopy-dwelling spiders and beetles, and birds showed no significant differences in species richness in either of the mix types compared to the pure plantations. The lower trunk and canopy epiphytes were the only groups that showed a significantly higher species richness in Norway spruce/Scots pine mixes but they showed no effect of adding oak to Norway spruce. This was attributed to the significantly higher canopy openness in Scots pine mixes, due to the light canopy of Scots pine, which also resulted in regeneration of understorey broadleaved tree and shrub species, which acted as additional host species for epiphytes.
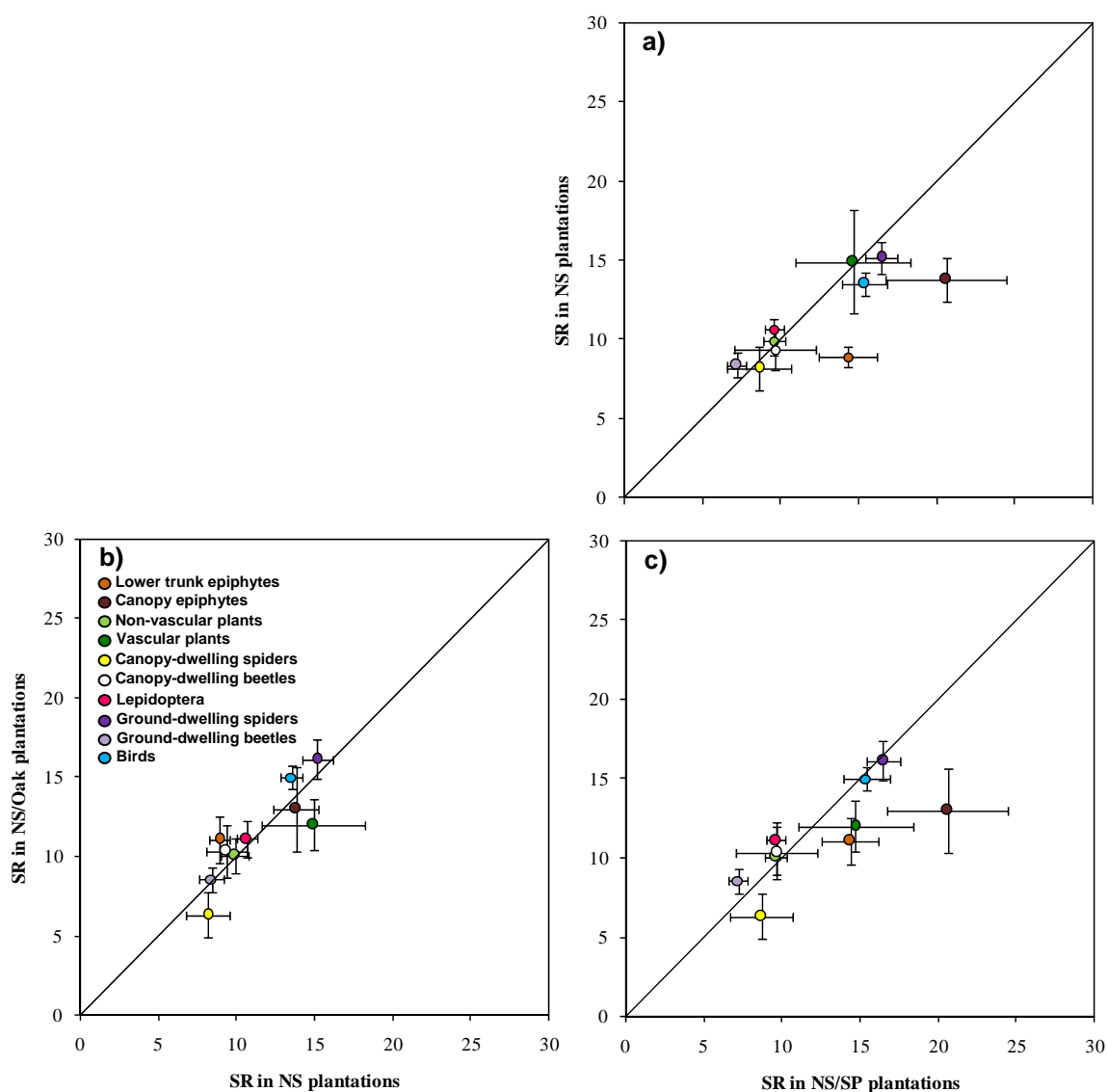
Figure 4.52: Mean species richness (SR) (±se) of the different taxonomic groups in (a) pure Norway spruce (NS) and (b and c) mixed Norway spruce/oak (NS/oak) plantations in relation to mean species richness of these taxonomic groups in (b) pure NS and (a and c) mixed Norway spruce/Scots pine (NS/SP) plantations.

The same pattern was evident for the species richness of forest-associated species, where the lower-trunk and canopy epiphytes were the only groups that showed any significant effect of the addition of a Scots pine compared to pure Norway spruce plantations, with more typical epiphytes found on the lower trunks of trees in Scots pine mixes and in the middle and upper trunks of Norway spruce in the same mix type (Fig. 4.53). Again no effect was found for the addition of oak to Norway spruce. There was a trend of increased forest-associated canopy-dwelling beetle richness in Norway spruce/oak mixes, which was probably related to the higher number of phytophagous forest beetles which are adapted to feeding on broadleaved trees.
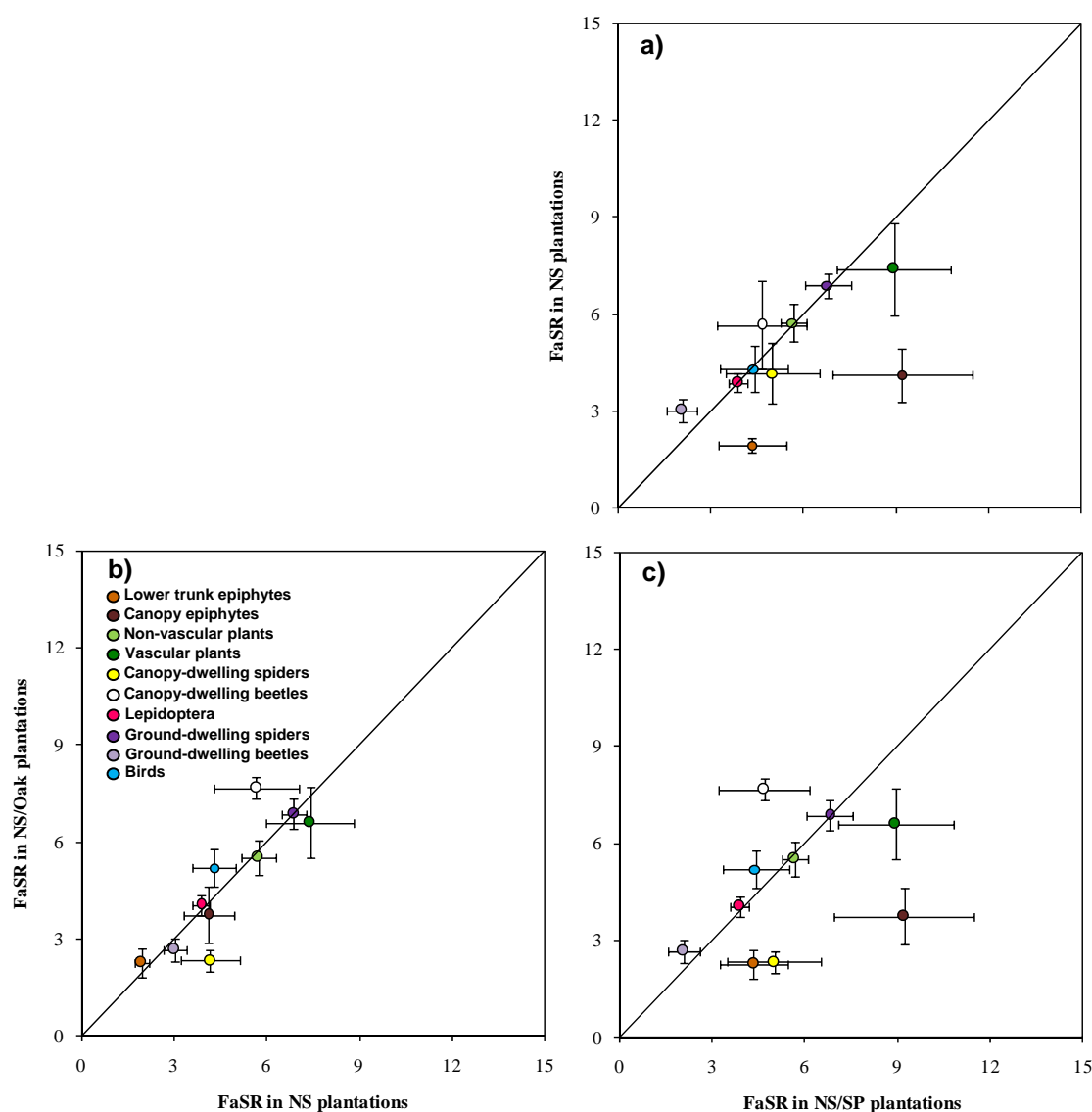
Figure 4.53: Mean forest-associated species richness (FaSR) (±se) of the different taxonomic groups in (a) pure Norway spruce (NS) and (b and c) mixed Norway spruce/oak (NS/oak) plantations in relation to mean forest-associated species richness of these taxonomic groups in (b) pure NS and (a and c) mixed Norway spruce/Scots pine (NS/SP) plantations.

4.8.1.2.1.2 Trends in community composition

As with the species richness measures, the only significant difference in community composition between mixed and pure Norway spruce sites was found for lower trunk and canopy epiphytes. These groups showed differences in community composition in pure Norway spruce plantations compared to both mix

types but no difference between the two different mix types. This was attributed to the presence of broadleaved understorey host tree species, in the form of the planted oaks in the oak mixes and naturally regenerating broadleaved trees and shrubs in the Scots pine mixes. For ground-dwelling spiders, the difference in community composition between pure Norway spruce plantations and oak mixes was close to significance.

4.8.1.3 Native woodlands survey

4.8.1.3.1 Differences between oak and ash native woodlands

4.8.1.3.1.1 Trends in species richness

The majority of groups showed no difference in species richness between the two native woodland types (Fig. 4.54a). However, the ground vegetation groups (total, vascular and non-vascular) and lower trunk epiphytes were significantly more species rich in ash than in oak woodlands, although there was no difference in canopy epiphyte richness between oak and ash trees. Previous large-scale research on the ground vegetation of the two native woodland types suggests that there is no difference in species richness between them in Ireland and that the ash woodlands studied may have been richer in ground vegetation than the average. Ground-dwelling beetles were significantly more species rich in ash woodlands in 2008 while ground-dwelling spider species richness was higher in oak than ash woodlands, significantly so in 2007. The presence of deep litter layers in oak woodlands may be the reason for these differences, as ground-dwelling spiders seem to be able to exploit the micro-habitat conditions created, while the more generalist ground-dwelling beetles cannot.

Figure 4.54: a) Mean species richness (SR) (±se) of the different taxonomic groups in ash woodlands in relation to mean species richness of these taxonomic groups in oak woodlands. b) Mean forest-associated species richness (FaSR) (±se) of different taxonomic groups in ash woodlands in relation to mean forest-associated species richness of these taxonomic groups in oak woodlands.

For forest-associated species, the typical woodland ground vegetation and lower trunk typical epiphyte species richness were again significantly higher in ash than oak woodlands and, in this instance, there were also significantly more canopy typical epiphytes on ash than oak trees (Fig. 4.54b), possibly related to differences in bark chemistry between these tree species. Ground-dwelling forest beetles were also significantly more species rich in ash than oak woodlands, and this may be related to the lower number of

beetle species adapted to living in acidic conditions. The other groups did not differ significantly in their forest-associated species richness between the two woodland types, although there was a trend of higher canopy-dwelling beetle richness in oak woodlands. This may be due to the historic presence of oak in the landscape, combined with its current rarity, which may have led to more phytophagous beetle specialists on oak.

4.8.1.3.1.2 Trends in community composition

While the majority of groups showed no difference in the species richness measures, there was more distinction between oak and ash woodlands in community composition. The difference was particularly marked for the ground vegetation, as is to be expected given that the sites were selected to represent two different vegetation types, which occur on strongly acid and base-rich soils respectively. The lower trunk and canopy epiphytes and the canopy-dwelling beetle communities were also quite distinct. For the epiphytes this may be related to differences in bark chemical and physical characteristics between oak and ash trees and between trees in oak and ash woodlands, which is also affected by soil pH. For canopy-dwelling beetles the difference may be related to the greater number of forest specialist species in oak woodlands. The ground-dwelling spiders and beetles and the Lepidoptera showed broad separation but there was a degree of overlap in composition between the two woodland types. Ground-dwelling invertebrates respond particularly to differences in structural complexity which did show a degree of overlap between woodland types. Lepidoptera respond more to availability of larval food plants and, while vegetation composition was distinct, there was a degree of overlap in species between the two forest types e.g. oak trees present in some ash woodlands. There was no difference in community composition between oak and ash for the canopy-dwelling spiders or the birds. Canopy-dwelling spiders are unlikely to be affected by relatively small scale difference in structure between ash and oak canopies, as both support a diverse array of prey types. Both woodland types also provide similar habitats for birds, with differences in vegetation structure more important than the dominant tree species.

4.8.1.4 Comparison of forest types

4.8.1.4.1 Comparison of native woodlands and plantations

4.8.1.4.1.1 Trends in species richness

Although different plantation types were compared to native oak and ash woodlands in the different taxonomic sections, some clear trends could be identified (Figs. 4.55 and 4.56). Canopy-dwelling spiders and beetles were significantly more species rich in oak and ash woodlands than in Sitka spruce plantations, with canopy-dwelling beetles also more species rich in these native woodland types than in mixed and pure Norway spruce plantations. For the canopy-dwelling spiders this is likely due to the structural unsuitability of conifer canopies for certain spider guilds, while for canopy-dwelling beetles it is likely due to the lack of beetle guilds in the Irish fauna, which specifically feed on conifer tissues. Epiphytes were significantly more species rich in both oak and ash native woodlands than in any spruce plantation types and birds were more species rich in these native woodland types than in Sitka spruce plantations. For the canopy epiphytes this is probably due to the acidic bark of conifers and the lower light levels beneath conifer canopies; the latter factor can lead to reduced structural diversity and particularly lower cover of understorey and shrub layers, which may also explain the low diversity of birds. Ground vegetation and vascular species richness were only significantly greater in ash woodlands than plantations, with oak woodlands similar in total and vascular species richness to all plantation types examined and with similar non-vascular species richness to spruce plantations. Ash supported more non-

vascular species than spruce plantations. The higher species richness in ash is probably related to the lower light levels in spruce plantations, possibly combined with lower pH levels, since fewer plant species are adapted to strongly acidic conditions. The lack of any difference between oak woodlands and plantations may be related to the fact that the oak woodlands studied were not, on average, among the more species rich Irish oak woodlands, combined with the fact that a number of the plantations studied were located on or adjacent to historic woodland; the latter appeared to enrich the ground vegetation. Ground-dwelling spiders, ground-dwelling beetles and Lepidoptera showed no significant differences between native woodlands and spruce plantations. For the ground-dwelling spiders and Lepidoptera this was due to the presence of two different suites of forest specialists which were able to exploit the conditions in native woodlands and plantations respectively, while the ground-dwelling beetles were strongly influenced by geographic location rather than forest type, which may indicate a lack of forest specialist species in Ireland.
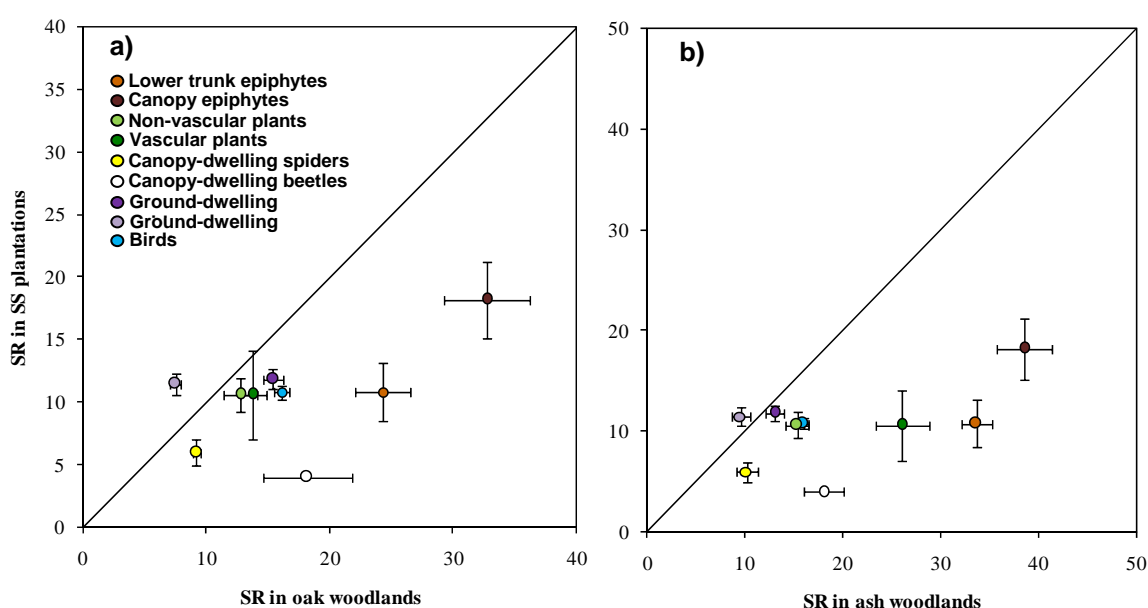
Figure 4.55: Mean species richness (SR) (±se) of the different taxonomic groups (a) in oak and (b) ash woodlands in relation to mean species richness of these taxonomic groups in age class IV reforested Sitka spruce (SS) plantations. Note that Lepidoptera were not sampled in SS plantations.
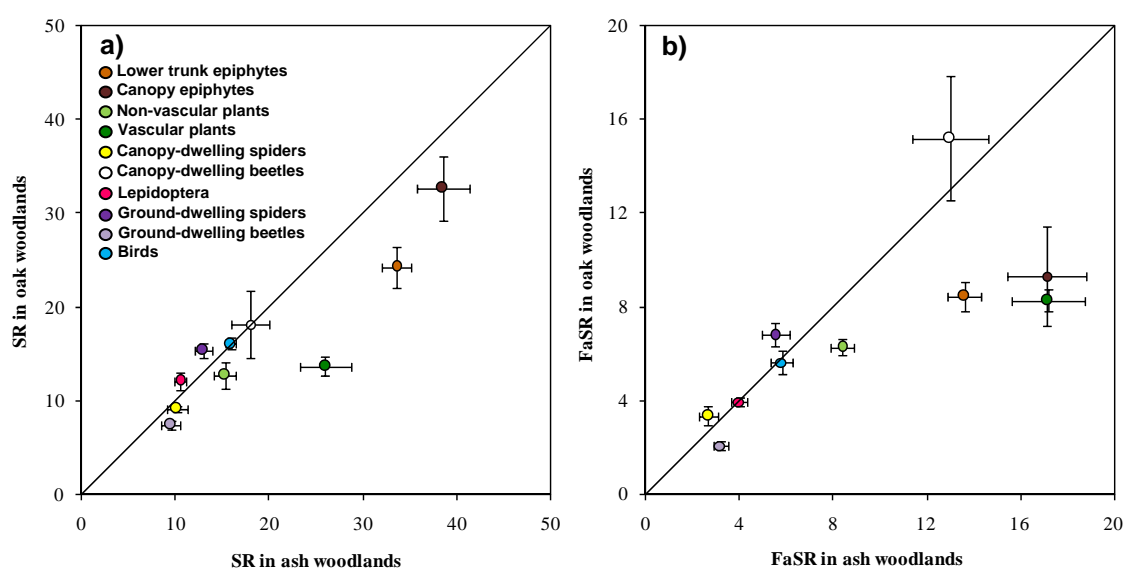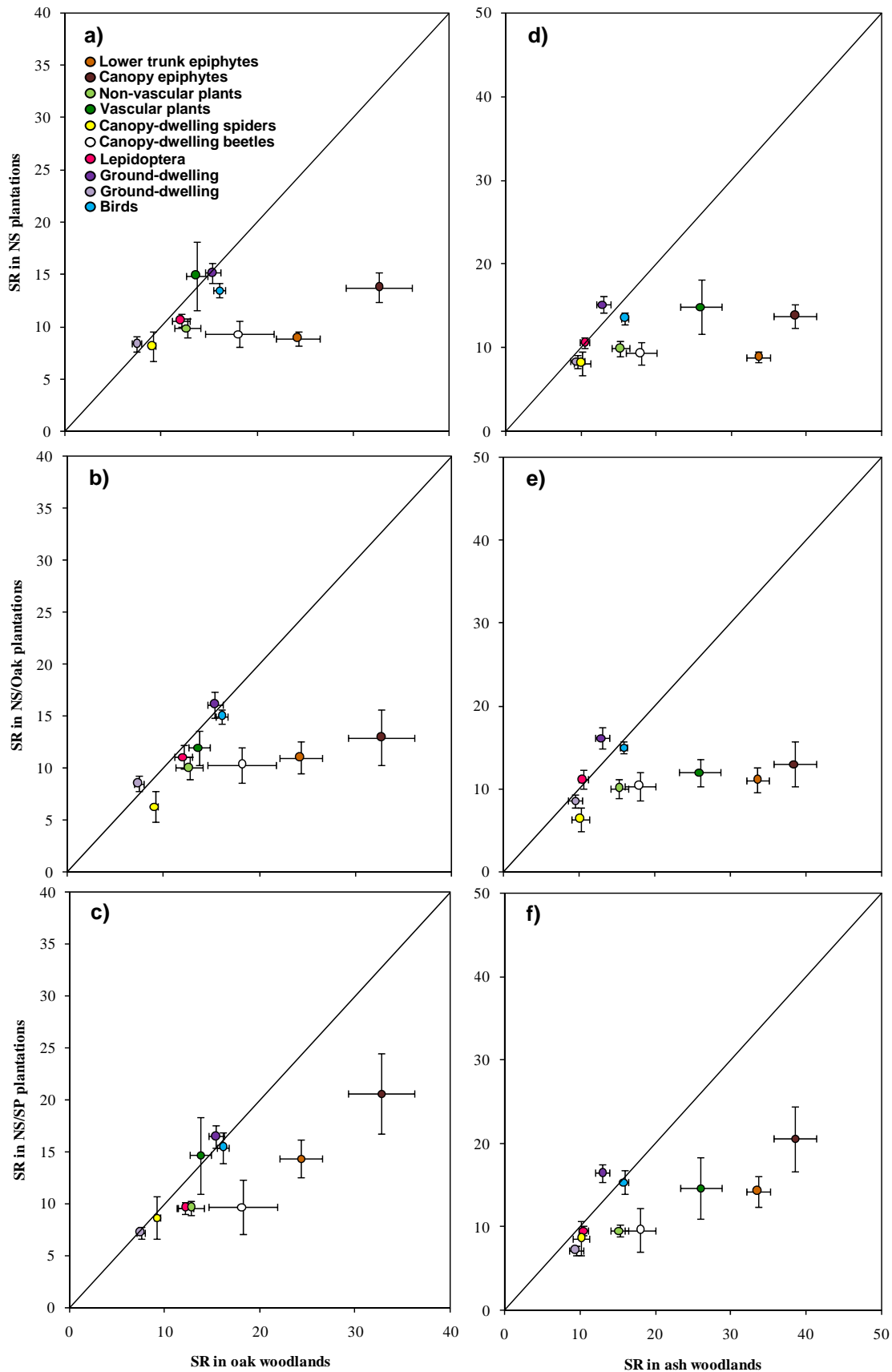
Figure 4.56: Mean species richness (SR) (±se) of the different taxonomic groups in (a-c) oak and (d-f) ash woodlands in relation to mean species richness of these taxonomic groups in (a and d) pure Norway spruce (NS) and (b, c, e and f) Norway spruce/oak (NS/oak) and Norway spruce/Scots pine (NS/SP) mix plantations.

For forest-associated species richness, some different trends were evident (Figs 4.57 and 4.58). There were significantly more typical epiphytes in ash woodlands than in any of the spruce plantation groupings examined, while oak woodlands supported similar numbers of canopy epiphyte species to Norway spruce/Scots pine mix plantations. For the ash woodlands this may be related to bark physical and chemical characteristic, as discussed above, while the similarity in canopy epiphytes between oak trees in oak woodlands and Norway spruce trees in Scots pine mixes may be related to the more open canopy in this mix type. For the ground vegetation, only ash woodlands had significantly more typical woodland species (mainly vascular species) than all plantation types examined while oak woodlands did not have more species than the Norway spruce mixed and pure plantations combined. The reasons for these differences are probably the same as those for total species richness discussed above. Birds had more forest-associated species in native woodland than in Sitka spruce plantations, while canopy-dwelling beetles had more species in native woodlands than spruce plantations in general. Again, the reasons for these differences are likely to be the reduced structural diversity in plantations, which is important to birds, and the lack of phytophagous beetles specialised to feeding on conifers, as discussed above. Ground-dwelling spiders, beetles and Lepidoptera again showed no significant differences between the native woodlands and plantations, which was related to the occurrence of two different suites of forest specialists in native woodlands and plantations, respectively.
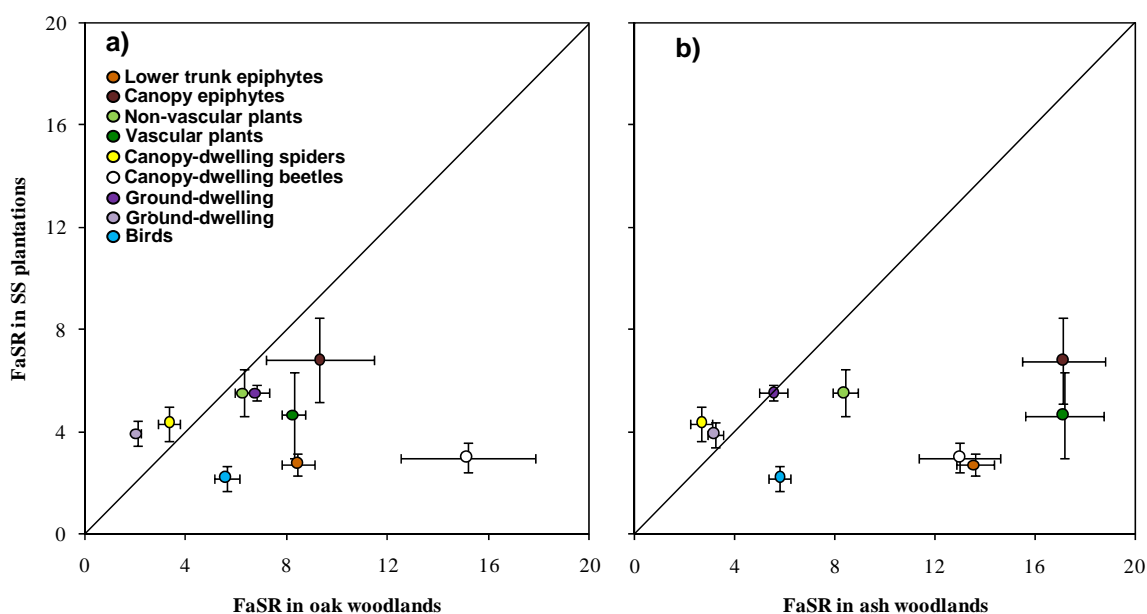
Figure 4.57: Mean forest-associated species richness (FaSR) (±se) of the different taxonomic groups (a) in oak and (b) ash woodlands in relation to mean forest-associated species richness of these taxonomic groups in mature reforested Sitka spruce (SS) plantations. Note that Lepidoptera were not sampled in SS plantations.
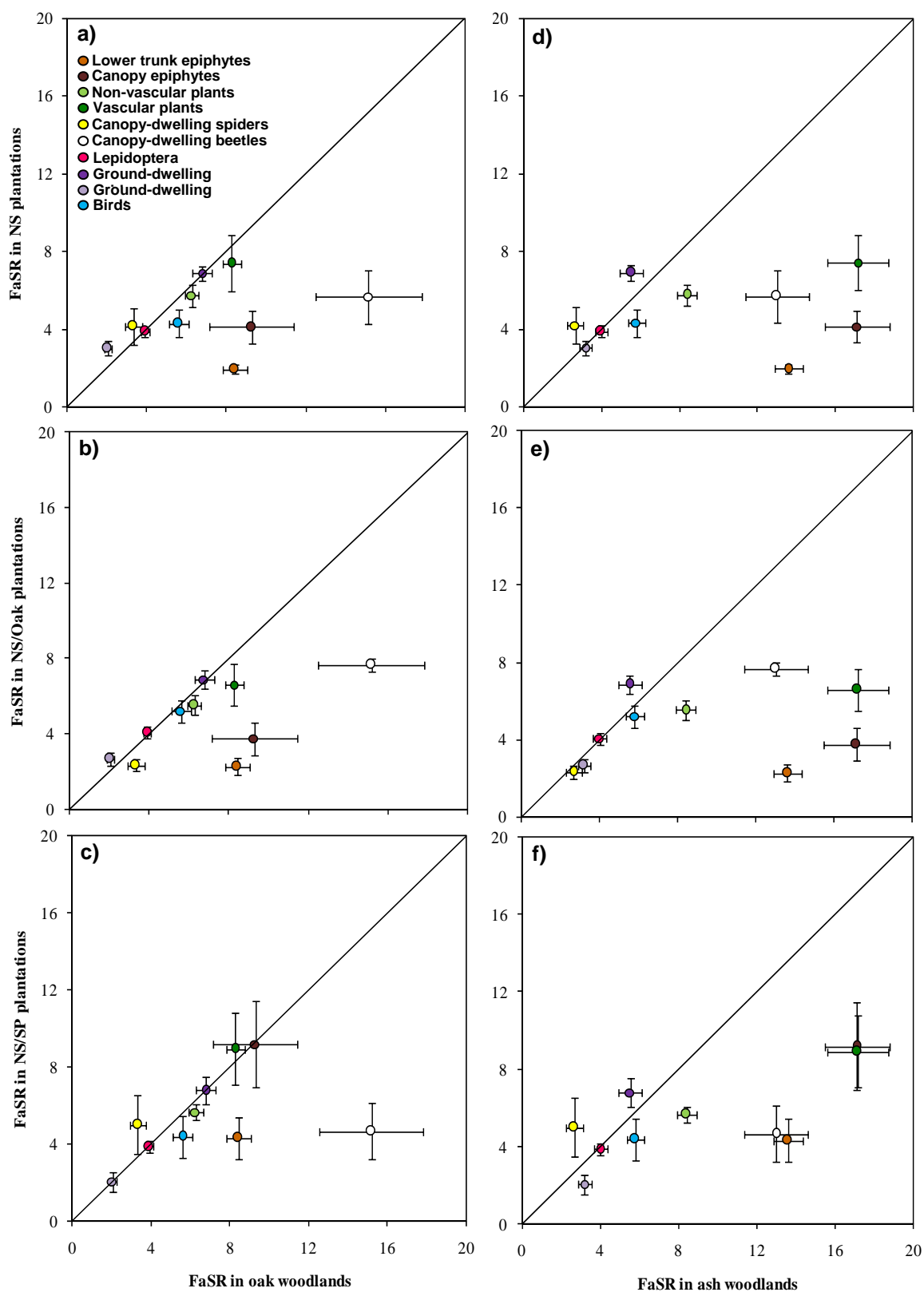
Figure 4.58: Mean forest-associated species richness (FaSR) (±se) of the different taxonomic groups in (a-c) oak and (d-f) ash woodlands in relation to mean forest-associated species richness of these taxonomic groups in (a and d) pure Norway spruce (NS) and (b, c, e and f) Norway spruce/oak (NS/oak) and Norway spruce/Scots pine (NS/SP) mix plantations.

4.8.1.4.1.2 Trends in community composition

Compared to the trends in species richness, the trends in community composition between native oak and ash woodlands and plantations were more similar among the taxonomic groups with the majority having different communities in native woodlands and plantations. For the birds and Lepidoptera, there was clear separation of native woodlands and spruce plantations, while the separation for ground-dwelling spiders was less distinct. For the birds this was probably related to the lower structural diversity of plantations, as well as differences in the diet preferences of certain species, while differences in larval food preferences may explain the difference for Lepidoptera. For the ground-dwelling spiders, while different suites of forest-associated species were adapted to the different structural features in native woodlands and plantations, there was probably some structural overlap, especially in more open plantations. There was a general separation of native woodlands and conifer plantations for the ground vegetation, although two oak woodlands had a similar bramble (*Rubus fruticosus* agg.) dominated composition to more open plantations, while a single Norway spruce and several ash plantations (a forest type not examined for the other taxonomic groups) located on or adjacent to historic woodland sites were found to have similar communities to native ash woodlands. The bramble dominated vegetation type was seen to be a species-poor one, which was related to low grazing levels. The source of plant propagules provided by historic woodland seemed important in determining the plant communities in plantations. For the canopy epiphytes, while native woodlands were generally clearly separated from plantations, one Sitka spruce plantation had a similar community to oak woodlands, which was attributed to its openness, the presence of a naturally regenerated understorey and its location on and adjacent to historic woodland. For the canopy-dwelling spiders, native woodlands had different communities to pure spruce plantations but oak woodlands were not significantly different to oak mix plantations, while canopy-dwelling beetles were significantly different between native woodlands and spruce plantations. For the canopy-dwelling spiders, differences in habitat structure and prey availability between coniferous and broadleaved trees are likely to be the reason for the patterns observed. The differences for canopy-dwelling beetles may be related to the abundance of prey for predators in spruce, combined with the lack of beetle guilds which specifically feed on conifer tissues, resulting in different suites of species. Ground-dwelling beetles were the only group that did not show any clear separation between native woodlands and plantations and were separated instead by geographic location. The lack of forest specialist beetles may be the reason for this lack of distinction.

4.8.2 Formal comparison

4.8.2.1 Reforestation survey

4.8.2.1.1 Species richness

Apart from significant positive correlations of vascular plant and lower trunk epiphyte species richness with non-vascular ground vegetation species richness, no other taxonomic pairs were significantly related to each other in reforestation Sitka spruce plantations of all age classes (Fig. 4.59). There was a strong positive trend of association between canopy epiphyte and lower trunk epiphyte species richness, which could be sufficiently strong for considering the two taxa as surrogates (≥0.7; Heino, 2010), however, our sample sizes were small and this relationship was not significant (Fig. 4.59).

Species richness of all the taxonomic groups of plants (vascular and non-vascular ground vegetation, lower trunk and canopy epiphytes) was positively associated with each other. This was mainly due to a strong positive correlation between the species richness of these plant groups in reforested plantations of

age class I (Appendix 15) and age class IV (Appendix 16), while they were barely associated with each other in age class II and III plantations (Appendices 17 and 18). Species richness of ground- and canopy-dwelling invertebrates and birds did not show a consistent positive or negative pattern of relationships with the species richness of plant taxa or of the other animal taxa (Fig. 4.59, Appendices 15-18).

4.8.2.1.2 Forest-associated species richness

As for species richness, the number of significant correlations between forest-associated species richness (faSR) of any two taxonomic groups was very low; forest-associated species richness of vascular and non-vascular ground vegetation as well as of ground-dwelling spiders and beetles were the only taxonomic groups significantly related to each other in reforestation Sitka spruce plantations of all age classes (Fig. 4.60). This was mainly due to strong positive correlations between faSR of these groups in reforested plantations of age class I (Appendix 19) and (in the case of ground-dwelling invertebrates) of age class III (Appendix 20), while they were not significantly associated with each other in age class II and IV plantations (Appendices 21 and 22).

Although the associations of forest-associated species richness of lower trunk epiphytes, ground-dwelling spiders, ground-dwelling beetles and birds to the majority of other taxonomic groups were positive in plantations of all age classes (Fig. 4.60), none of these correlations were sufficiently strong for considering a taxonomic pair as surrogates (≥0.7; Heino, 2010). Forest-associated species richness of vascular and non-vascular ground vegetation and of canopy epiphytes and canopy invertebrates did not show a consistent strong positive or negative pattern of relationship with faSR of the other taxonomic groups (Fig. 4.60, Appendices 19 – 22) except for strong positive correlations of ground vegetation faSR in plantations of age class I (Appendix 19) and of canopy invertebrate faSR in plantations of age class III (Appendix 20) to faSR of the majority of the other taxonomic groups.
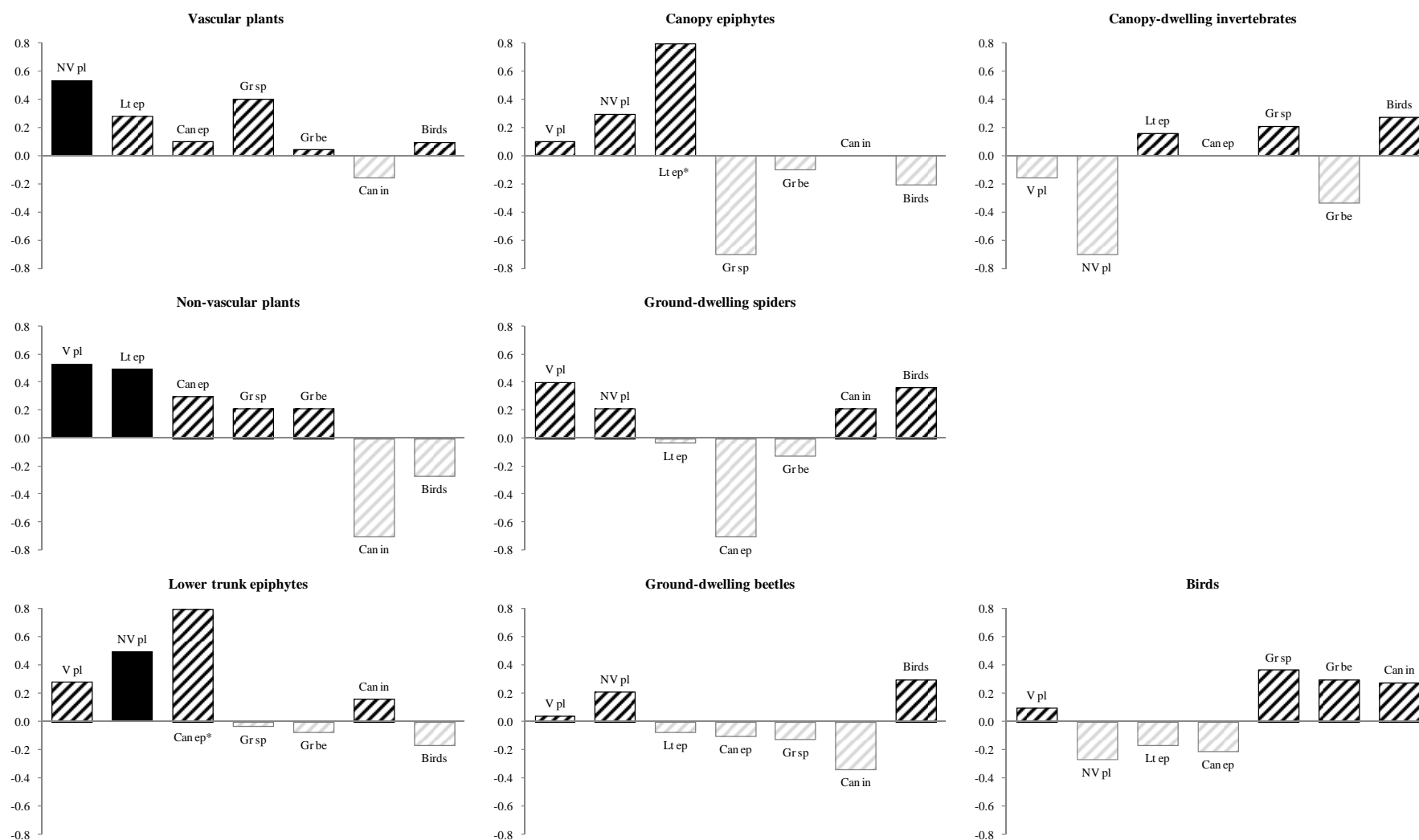
Figure 4.59: Coefficients for correlations between species richness of investigated taxa in reforested plantations (age classes I, II, III and IV combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. *N* = 20 for any of the correlations between vascular plants (V pl), non-vascular plants (NV pl), lower trunk epiphytes (Lt ep), ground-dwelling spiders (Gr sp), ground-dwelling beetles (Gr be) and birds. *N* = 5 for correlations between canopy epiphytes (Can ep) and these taxa. *N* = 6 for correlations between canopy-dwelling invertebrates (Can in) and these taxa. *N* = 3 for the correlation between canopy epiphytes and canopy-dwelling invertebrates. Lepidoptera (Lepi) were not sampled in reforested plantations. An asterisk (*) behind a taxonomic name indicates that these taxonomic pairs might be considered as surrogates relevant for biodiversity surveys due to a correlation coefficient > 0.7 (Heino, 2010).
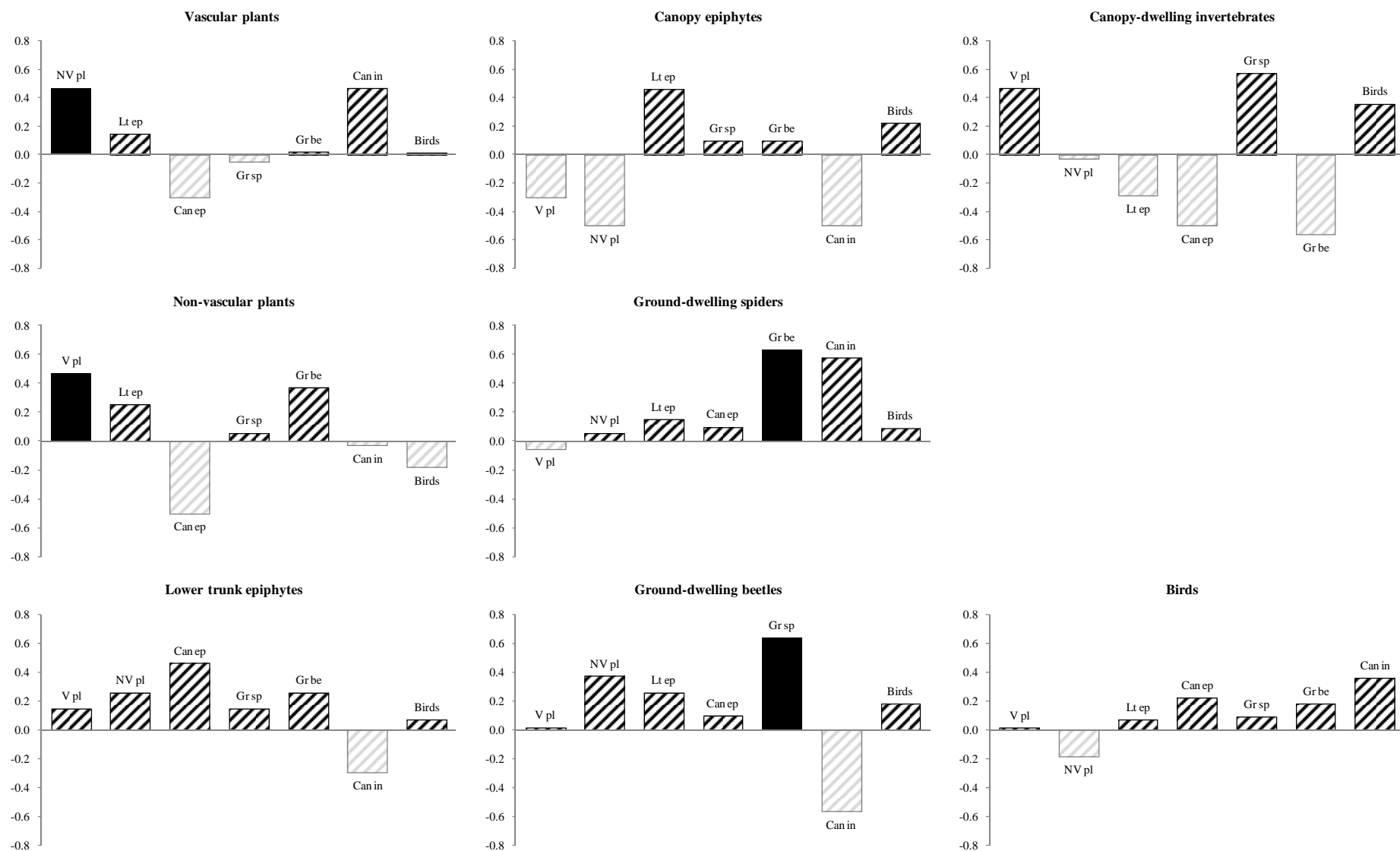
Figure 4.60: Coefficients for correlations between forest-associated species richness of investigated taxa in reforested plantations (age classes I, II, III and IV combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. For taxonomic abbreviations see legend of Fig. 4.59. N = 20 for any of the correlations between V pl, NV pl, Lt ep, Gr sp, Gr be and birds. N = 5 for correlations between Can ep and these taxa. N = 6 for correlations between Can in and these taxa. N = 3 for the correlation between Can ep and Can in. None of the correlation coefficients was ≥ 0.7, the level above which taxonomic pairs could be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

4.8.2.2 Mixed tree species survey

4.8.2.2.1 Species richness

Species richness of five of the nine taxonomic groups investigated (vascular ground vegetation, lower trunk and canopy epiphytes, canopy-dwelling invertebrates and birds) was positively and often significantly correlated to species richness of the majority of the other taxonomic groups in pure and mixed Norway spruce plantations (Fig. 4.61), with lower trunk epiphytes, vascular ground vegetation and canopy-dwelling invertebrates revealing the highest numbers of significant relationships (4, 3 and 3 respectively). However, only the correlation between species richness of canopy epiphytes and canopy invertebrates was sufficiently strong (≥0.7; Heino, 2010) for considering the two taxonomic groups as surrogates in pure and mixed Norway spruce plantations. The positive relationships of species richness of these five taxonomic groups to any other taxonomic group were mainly due to positive correlations revealed in Norway spruce/Scots pine mix plantations (11 strong and/or significant correlations out of 29 investigated correlations, Appendix 23), while species richness of these groups was barely associated with each other or with species richness of the other groups in pure Norway spruce and Norway spruce/oak mix plantations (3 and 5 strong and/or significant correlations out of 29 investigated correlations, respectively, Appendices 24 and 25).

Species richness of non-vascular ground vegetation, ground-dwelling spiders and Lepidoptera did not show a consistent positive or negative pattern of relationships with species richness of the other taxa (Fig. 4.61, Appendices 23-25). However, species richness of ground-dwelling beetles was negatively correlated with species richness of most of the other taxonomic groups.

4.8.2.2.2 Forest-associated species richness

Although forest-associated species richness (faSR) of vascular and non-vascular ground vegetation, lower trunk epiphytes, ground-dwelling spiders, Lepidoptera and birds was positively related to faSR of the majority of other taxonomic groups (Fig. 4.62), very few of these relationships were significant correlations and none of them was sufficiently strong (≥0.7; Heino, 2010) for considering any taxonomic group as a surrogate for any other taxonomic group. While faSR of canopy epiphytes and canopy-dwelling invertebrates did not reveal any consistent positive or negative pattern of relationship with species richness of the other taxa, faSR of ground-dwelling beetles was negatively correlated with faSR of most of the other taxonomic groups (Fig. 4.62, Appendices 26-28). The positive relationships between forest-associated species richness of the investigated taxonomic groups were mainly due to positive correlations revealed in Norway spruce/Scots pine mix plantations (Appendix 27), while there were very few significant and/or strong correlations revealed in pure Norway spruce and Norway spruce/oak mix plantations (Appendices 26 and 28).
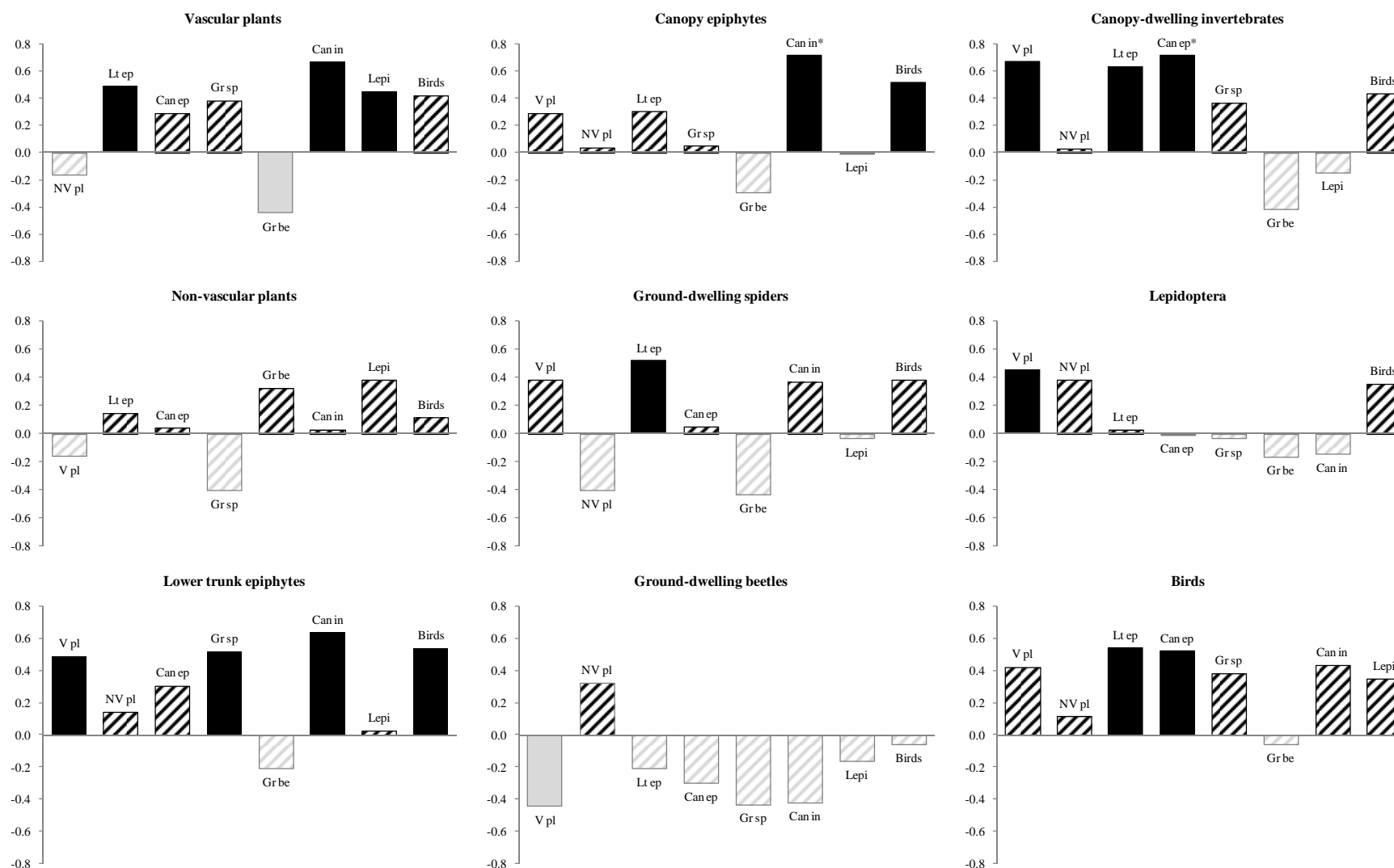
Figure 4.61: Coefficients for correlations between species richness of investigated taxa in pure and mixed plantations (pure Norway spruce, Norway spruce/Scots pine mix and Norway spruce/oak mix combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. For taxonomic abbreviations see legend of Fig. 4.59. N = 20 for any of the correlations between V pl, NV pl, Lt ep, Gr sp, Gr be, Lepi and birds. N = 18 for correlations between Can ep and these taxa. N = 12 for correlations between Can in and these taxa. N = 12 for the correlation between Can ep and Can in. An asterisk (*) behind a taxonomic name indicates that these taxonomic pairs might be considered as surrogates relevant for biodiversity surveys due to a correlation coefficients > 0.7 (Heino, 2010).
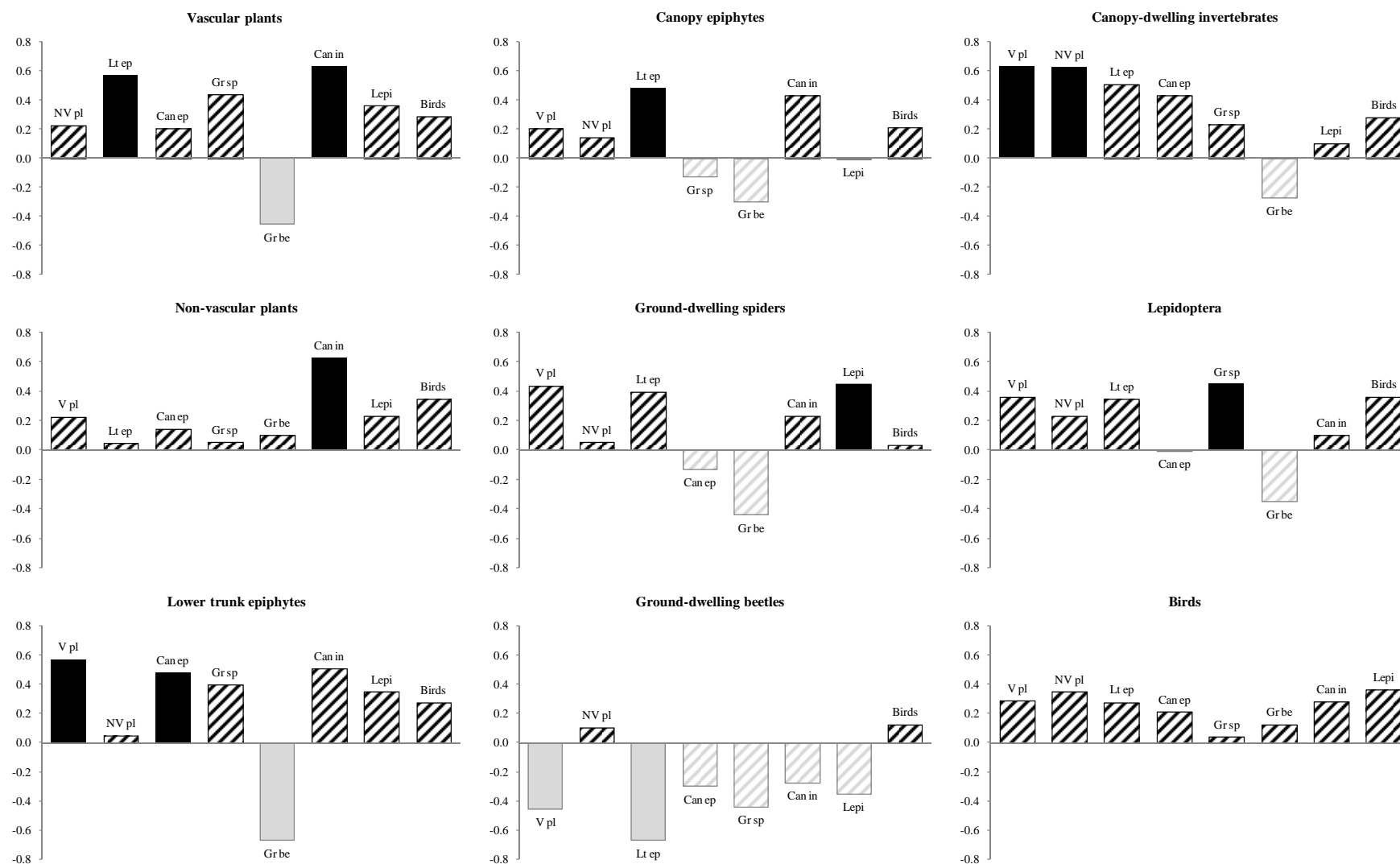
Figure 4.62: Coefficients for correlations between forest-associated species richness of investigated taxa in pure and mixed plantations (pure Norway spruce, Norway spruce/Scots pine mix and Norway spruce/oak mix combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. For taxonomic abbreviations see legend of Fig. 4.59. N = 20 for any of the correlations between V pl, NV pl, Lt ep, Gr sp, Gr be, Lepi and birds. N = 18 for correlations between Can ep and these taxa. N = 12 for correlations between Can in and these taxa. N = 12 for the correlation between Can ep and Can in. None of the correlation coefficients was > 0.7, the leve above which taxonomic pairs could be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

4.8.2.3 Native woodlands survey

4.8.2.3.1 Species richness

While species richness of all taxonomic plant groups (vascular and non-vascular ground vegetation, lower trunk and canopy epiphytes) was positively and in most cases significantly correlated with each other and the species richness of ground-dwelling beetles, species richness of most animal taxa was not consistently positively correlated with species richness of the other taxonomic groups in native woodlands (Fig. 4.63). On the contrary, species richness of canopy-dwelling invertebrates, Lepidoptera and birds was negatively (but not significantly) associated to species richness of the majority of other taxonomic groups (Fig. 4.63). Only species richness of ground-dwelling beetles was positively and often significantly correlated to species richness of most other taxonomic groups due to strong significant positive correlations in oak woodlands (Appendix 29) but not in ash woodlands (Appendix 30).

Two positive correlations were sufficiently strong (≥0.7; Heino, 2010) for considering these two taxonomic pairs as surrogates in native woodlands (Fig. 4.63): the strong positive correlation between species richness of vascular and non-vascular ground vegetation mirrored the significant correlations separately revealed in oak and ash woodlands (Appendices 29 and 30). Although species richness of vascular ground vegetation and lower trunk epiphytes were also found to be strongly positively correlated when looking at oak and ash woodlands combined, they were not significantly correlated when looking at oak and ash woodlands separately (Fig. 4.63 vs Appendices 29 and 30).

4.8.2.3.2 Forest-associated species richness

Forest-associated species richness (faSR) of vascular and non-vascular ground vegetation, lower trunk and canopy epiphytes, ground-dwelling beetles and canopy-dwelling invertebrates was positively related to faSR of the majority of other taxonomic groups (Fig. 4.64), and, except for canopy-dwelling invertebrates, these positive correlations were significant. Two of these correlations (between faSR of vascular ground vegetation and lower trunk epiphytes and between faSR of non-vascular ground vegetation and ground-dwelling beetles, Fig. 4.64) were found to be sufficiently strong (≥0.7; Heino, 2010) for considering the taxonomic pairs as surrogates. However, when looking at oak and ash woodlands separately, a strong positive correlation between faSR of non-vascular ground vegetation and ground-dwelling beetles was only present in ash but not in oak woodlands, and there was no significant positive correlation found for faSR of vascular ground vegetation and lower trunk epiphytes (Appendices 31 and 32). These inconsistencies in the analyses of combined and separate faSR data imply that none of the taxonomic groups can be regarded as a reliable surrogate for biodiversity surveys in native Irish woodlands (Heino, 2010). Forest-associated species richness of canopy-dwelling spiders, Lepidoptera and birds did not reveal any consistent positive pattern of relationships with species richness of the other taxa (Fig. 4.64, Appendices 31 and 32).
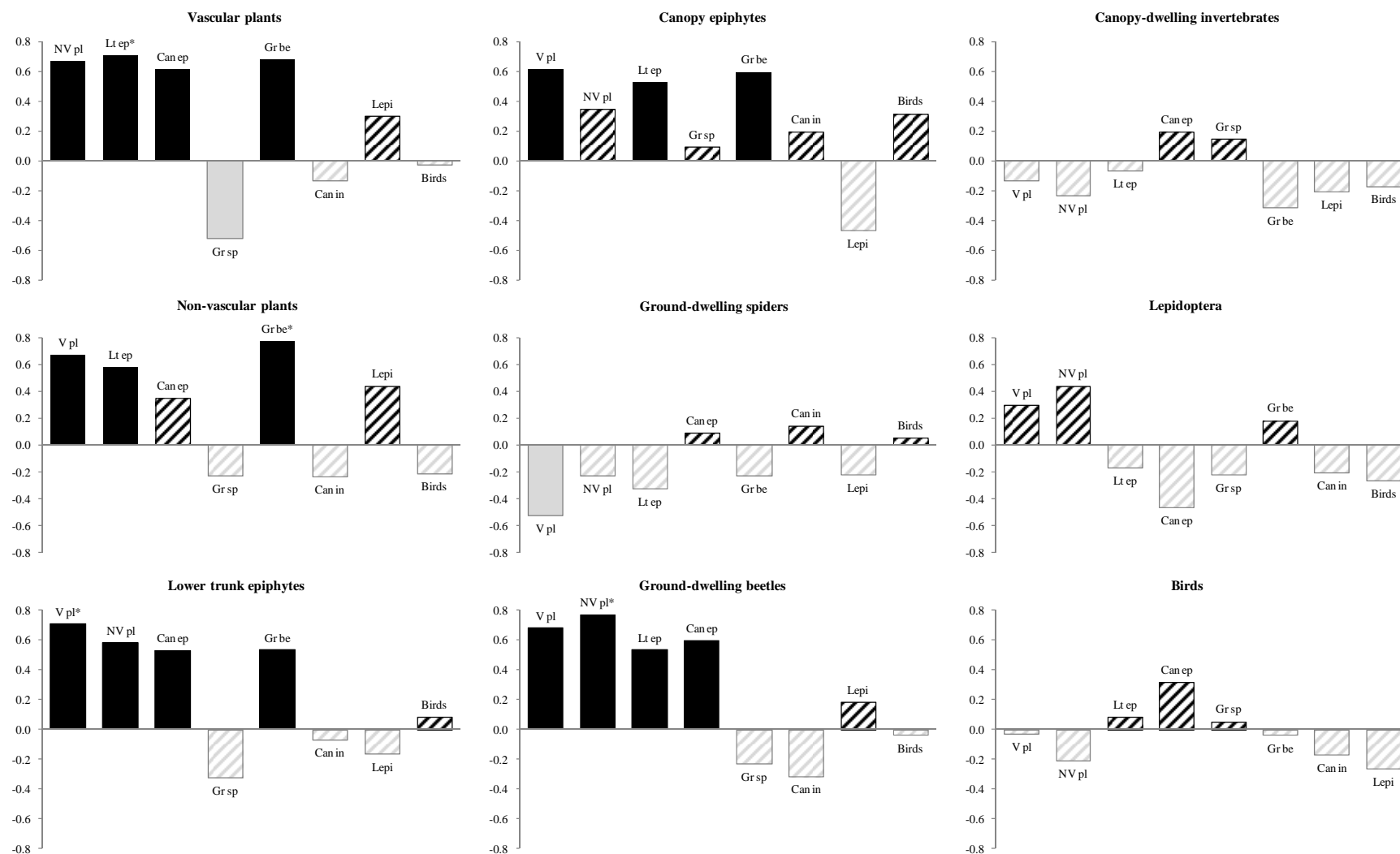
Figure 4.63: Coefficients for correlations between species richness of investigated taxa in native woodlands (ash and oak combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. For taxonomic abbreviations see legend of Fig. 4.59. N = 20 for any of the correlations between V pl, NV pl, Lt ep, Gr sp, Gr be and birds. N = 15 for correlations between Can ep and these taxa. N = 12 for correlations between Can in and these taxa. N = 10 for correlations between Lepi and these taxa. N = 8 for the correlation between Can ep and Can in, N = 7 for the correlation between Can ep and Lepi and N = 8 for the correlation between Can in and Lepi. An asterisk (*) behind a taxonomic name indicates that these taxonomic pairs might be considered as surrogates relevant for biodiversity surveys due to a correlation coefficients > 0.7 (Heino, 2010).

Figure 4.64: Coefficients for correlations between forest-associated species richness of investigated taxa in native woodlands (ash and oak combined). Black represents a positive and grey a negative association between taxa. Solid boxes indicate that correlations were significant (P ≤ 0.05) and hatched boxes indicate otherwise. For taxonomic abbreviations see legend of Fig. 4.59. N = 20 for any of the correlations between V pl, NV pl, Lt ep, Gr sp, Gr be and birds. N = 15 for correlations between Can ep and these taxa. N = 12 for correlations between Can in and these taxa. N = 10 for correlations between Lepi and these taxa. N = 8 for the correlation between Can ep and Can in, N = 7 for the correlation between Can ep and Lepi and N = 8 for the correlation between Can in and Lepi. An asterisk (*) behind a taxonomic name indicates that these taxonomic pairs might be considered as surrogates relevant for biodiversity surveys due to a correlation coefficients > 0.7 (Heino, 2010).

4.8.2.3 Comparison of forest types

4.8.2.3.1 Generalised Procrustes analysis

After rotation of NMS ordinations of any two taxonomic groups, Procrustes randomisation tests in PROTEST indicated significant concordances between assemblage ordinations of the majority of taxonomic groups (Table 4.99), except for ground-dwelling beetles, whose NMS ordination did not significantly correlate with most of the other ordinations. Many of the Procrustes concordances were highly significant, but none were sufficiently strong ($r>0.7$) to regard any taxonomic groups as surrogate taxa (Heino, 2010). The two taxonomic groups closest to being regarded as surrogates were canopy epiphytes and lower trunk epiphytes (Table 4.99).

Table 4.99: Correlation coefficient of a symmetric Procrustes rotation (*r*), number of sites used for NMS ordinations (*N*) and level of significance (P) evaluating the concordance between the NMS scores (calculated for each investigated taxonomic group sampled on a site level in all forest types combined) after Procrustes rotation. All tests were based on 10,000 permutations. Significant results (P ≤ 0.05) are indicated in italic; results, which remained significant at P ≤ 0.05 after Šidák adjustment, are highlighted in bold.

|		Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Birds
Ground vegetation	*r*	**0.5936**	**0.6542**	**0.5437**	*0.2647*	**0.5195**	**0.5919**
	N	**60**	**38**	**60**	*60*	**30**	**60**
	P	**0.0001**	**0.0001**	**0.0001**	*0.0392*	**0.0004**	**0.0001**
Lower trunk epiphytes	*r*		**0.6958**	**0.4686**	0.2058	**0.5079**	**0.5829**
	N		**38**	**60**	60	**30**	**60**
	P		**0.0001**	**0.0001**	0.2529	**0.0002**	**0.0001**
Canopy epiphytes	*r*			**0.4211**	0.3034	**0.5651**	**0.5602**
	N			**38**	38	**23**	**38**
	P			**0.0011**	0.0863	**0.0003**	**0.0001**
Ground-dwelling spiders	*r*				**0.3171**	0.3576	**0.5960**
	N				**60**	30	**60**
	P				**0.0047**	0.0740	**0.0001**
Ground-dwelling beetles	*r*					0.3490	**0.3047**
	N					30	**60**
	P					0.0794	**0.0080**
Canopy-dwelling invertebrates	*r*						**0.5217**
	N						**30**
	P						**0.0003**

Analyses of Procrustes residuals (Fig. 4.65) revealed that taxonomic groups mirrored each other's community composition and abundance significantly better when sampled in pure Sitka spruce plantations of age classes II, III or IV, in native oak woodlands or in Norway spruce/Scots pine mix plantations. In contrast, community responses towards Sitka spruce plantations of age class I were significantly more variable among different taxonomic groups, i.e. the spatial arrangement of age class I plantation sites in the NMS ordinations was significantly more variable among taxonomic groups.
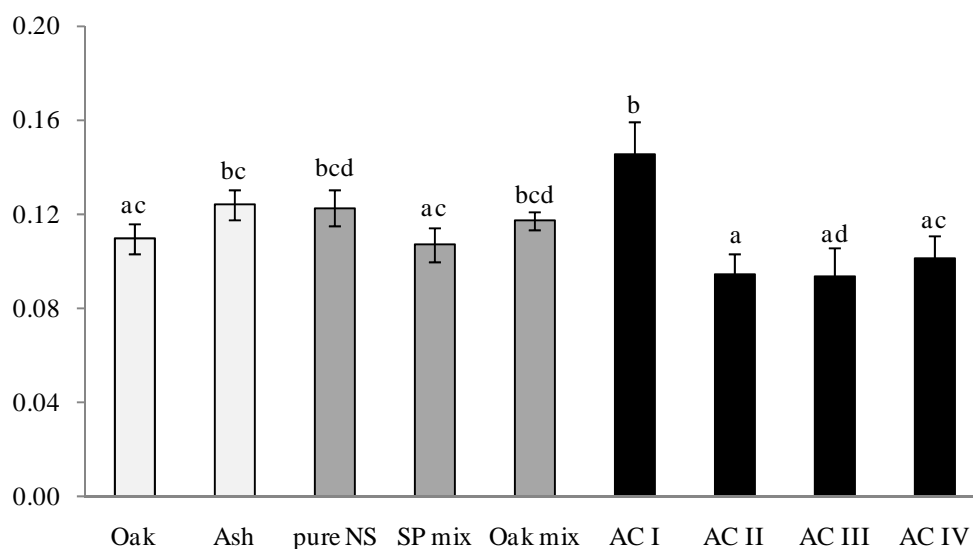
Figure 4.65: Mean Procrustes residuals (±se) across pairwise taxonomic comparisons and sites within each forest type: native oak and ash woodlands; pure Norway spruce (pure NS), Norway spruce/Scots pine (SP mix) and Norway spruce/oak (Oak mix) mix plantations; Sitka spruce plantations of age classes (AC) I, II, III and IV. Forest types that are represented by columns, which do not share any letter in common, are significantly different in their residuals from each other at P ≤ 0.05. Low mean residual values indicate that taxonomic groups respond similarly in their community composition and abundance to this particular forest type compared to the other forest types.

4.9 Findings of special conservation relevance

A number of relatively rare and interesting species were recorded during the ground vegetation surveys. *Salix x pontederiana* (a hybrid between the willows *Salix cinerea* and *Salix purpurea*) was a new record for Ireland and was found at Glengort, Co. Limerick (GLENG) in an age class I Sitka spruce reforestation plantation. *Stachys officinalis* (betony) is on the Flora Protection Order, which legally protects our rarest species. It is also a 'Notable' species, that is a rare species typically found in woodland, and/or a species indicative of long-established woodland (Perrin *et al.*, 2008a). It was recorded at Chevy Chase in Co. Galway (CHEVY) in an age class IV Sitka spruce reforestation stand established on historic woodland and adjacent to existing remnants of this woodland. Additional 'Notable' species recorded in plantations established on historic woodland were *Carex strigosa* (thin-spiked wood-sedge) and *Prunus padus* (bird cherry), both recorded at Mote Park, Co. Roscommon (MOTEM), a Norway spruce/Scots pine mix. Another 'notable' species was *Melica uniflora* (wood melick), recorded in ash woodland at Carrickbreeny, Co. Donegal (CRICK). In terms of bryophytes, *Daltonia splachnoides* (Fig. 4.66) was recorded at Glengort, Co. Limerick (GLENG) in an age class I Sitka spruce reforestation plantation (Bosanquet *et al.* 2010). Red data lists detail the potential risk that a species could become extinct in the wild and *Daltonia splachnoides* is classified as 'Vulnerable' in the Red Data Book of British Mosses and Liverworts (Church *et al.*, 2001) and it is listed as "Near Threatened" in Europe (Anon., 1995). The fact that this species is confined to the western fringe of Europe and is well represented in south-western Ireland is of conservation importance at the European scale. *Sphagnum girgensohnii*, was a new record for Co. Offaly and will most probably appear as "Near threatened" in the soon to be published Irish Red Data Book for bryophytes (N. Lockhart, *Pers. Comm.*). It was recorded at Sheshkin, Co. Offaly (SHKIN), an age class II reforestation plantation. *Plagiothecium laetum* has only been recorded twice before in Ireland (Holyoak, 2003) and is likely to appear as "Vulnerable" in the upcoming Irish Red Data Book. It was recorded at Fauna, Co. Wicklow (FAUNA) in an age class II Sitka spruce reforestation plantation.

Figure 4.66: *Daltonia splachnoides* (photo by Sam Bosanquet).

Several forest species of ground-dwelling invertebrate and Lepidopteran fauna were collected solely in native woodlands. This may suggest a degree of specialisation to more natural or undisturbed forests and the low cover of natural forest in Ireland may be a limiting factor in their distribution. These species included the forest associated spiders *Pachygnatha listeri* and *Linyphia hortensis*. *P. listeri* (family

Tetragnathidae) is typically found in low vegetation in ancient or well established old woodlands (Harvey *et al.*, 2002). Species from this genus build orb webs as juveniles but are active hunters as adults (Roberts, 1993). Ten individuals were sampled in Uragh oak woodland, Co. Kerry (URAGH), two in Gole Wood, Co. Fermanagh (GOLEW) and four in St Johns Wood, Co. Roscommon (STJON), both ash woodlands, suggesting a widespread distribution across the island. Across Europe this species is widespread with a palaearctic distribution, however there is insufficient data to assess its status in Ireland (Nolan, 2010), *L. hortensis* (family Linyphiidae) builds sheet webs on low vegetation and is typically found in both forest interior and edges. Individuals were collected in two oak woodlands: Rostrevor Wood, Co, Down (ROSTR, 2 individuals) and Tomnafinnoge, Co. Wicklow (TOMNA, 1 individual); and in four ash woodlands: Carrickbreeny, Co. Donegal (CRICK, 2 individuals), Greenaun, Co. Leitrim (GREEN, 3 individuals), Killavalla, Co. Tipperary (KILLA, 2 individuals), Oughtnadrin, Co. Donegal (OUGHT, 1 individual). This species is relatively widespread across Europe with a palaearctic distribution, however there is currently insufficient data to assess its status in Ireland (Nolan, 2010). The lack of records for both of these forest species may also be a reflection of their preferred micro-habitat - low vegetation layers, which are not efficiently sampled using pitfall traps, the most widely used spider collection method in Ireland.

Two forest associated Carabid beetles were unique to the native woodlands: *Oxyselaphus obscurus* and *Pterstichus oblongopunctatus. O. obscurus* was collected in two ash woodlands with 55 individuals found in Dromore Wood, Co. Clare (DROMO) and 2 individuals in St Johns Wood, Co Roscommon (STJON). This species is typically known from wet woodlands or heavily vegetated sites and is widespread across the Northern hemisphere. It is found all over Ireland, though sparsely distributed (Anderson, 2006), *P. oblongopunctatus* was collected in two oak woodlands: Breen Wood, Co. Antrim (BREEN, 3 individuals) and Brownstown Wood, Co. Kilkenny (BROWN, 1 individual). This species is typically found under decaying bark or stones in woodlands (Anderson, 2006). It occurs throughout Europe, but has a patchy distribution across the British Isles (Anderson, 2006). In Ireland at least, this may reflect the lack of recording in suitable habitats.

Three forest associated moth species were found solely in native woodlands: *Abraxas sylvata*, *Pasiphila rectangulata* and *Geometra papilionaria. A. sylvata,* or Clouded Magpie, has a larval feeding preference of Wych elm and English elm (Emmet and Heath, 1991). Five individuals were collected in Rostrevor Wood, Co. Down (ROSTR) and on the island of Ireland it has a scarce distribution, with most current records in the north (Tyner, 2010). *P. rectangulata*, or Green pug, was collected in Tomnafinnoge Wood, Co. Wicklow (TOMNA) 4 individuals). This species has a larval food preference for trees such as apple, cherry and blackthorn (Emmet and Heath, 1991) and is widespread across Ireland (Tyner, 2010). *G. papilionaria* or Large Emerald, has a feeding preference of birch, but also occasionally alder, hazel and beech (Emmet and Heath, 1991). This moth species was collected in two oak woodlands: Brownstown, Co.Kilkenny (BROWN, 4 individuals) and Rostrevor, Co. Down (ROSTR, 1 individual). Across Ireland this species in widespread and locally common (Tyner, 2010).

No ground-dwelling spider or beetle species were found exclusively in plantations, however four moth species were only collected only in these forests: *Hylaea fasciaria* (Barred red)*, Eupithecia abietaria* (Cloaked pug)*, Deileptenia ribeata* (Satin beauty)*, Macaria liturata* (Tawny-barred angle). All of these

species utilise conifers as a larval food plant, including trees of natural or semi-natural in origin (Yew, Scots pine) but also non-native trees (Norway spruce, Douglas fir (*Pseudotsuga menziesii*), Sitka spruce, Noble fir (*Abies procera*), Silver fir (*Abies alba*))

Two new species records were recorded for Ireland during the canopy fogging of native oak woodlands. One male and one female specimen of the spider *Entelecara acuminata* (Wider) (Fig. 4.67) were captured at Brownstown Wood in Co. Kilkenny (BROWN), while four specimens of the beetle *Anobium inexspectatum* Lohse (Fig. 4.68) were captured at Drummin Wood in Co. Galway (DRUMM) and Uragh Wood, Co. Kerry (URAGH). *Entelecara acuminata* is locally common but patchily distributed in southern England, is rarer in northern England and has been recorded in Scotland (Harvey *et al.*, 2002). Investigation of the distribution, status and habitat requirements of this species in Britain suggested that it could have been present in Ireland (McFerran, 1997a), but may have previously gone undetected in Ireland due to its arboreal lifestyle and small size (1.8-2.4 mm). *Anobium inexspectatum* is also on the UK Red List. This species is generally found in association with old broadleaved trees, and in particular with stems of ivy (*Hedera helix)* growing on these broadleaves. *Anobium inexspectatum* feeds on deciduous wood only, and is rarely found in conifers.

Figure 4.67: *Entelecara acuminata* (Araneae: Linyphiidae).

Canopy spider species assemblages from native Irish ash and oak woodlands differed from those found in plantations, with *Clubiona brevipes, Araneus diadematus*, *Entelecara acuminata* and *Hahnia montana* being found exclusively in native woodlands, while *Porrhomma convexum* was found only in Sitka Spruce plantations and *Lepthyphantes obscurus* only in coniferous plantations (Sitka spruce, Norway spruce or Norway spruce/Scots pine mixes). Additionally, eight Red-listed (JNCC, 2010) beetle species were sampled in various forest types, and several of these were woodland specialists. *Coeliodes transversealbofasciatus* feeds on *Quercus* spp. (oak) and was sampled only in native oak woodlands. *Kyklioacalles roboris* is a xylophage and was sampled in native ash and oak woodlands, while the predatory *Malthodes guttifer* was sampled in both broadleaved and coniferous woodlands. *Mniophila muscorum* feeds on foliage and is found in moss on a variety of trees but was only sampled in native oak forests during this research. Both *Orchesia minor* and *Tetratoma ancora* feed on fungi and are associated

with fungi on deciduous trees, but *O. minor* was sampled in both native broadleaved forests and non-native coniferous plantations during this study, whereas *T. ancora* was sampled in native ash forests only. Thus, *O. minor* was sampled from a forest type in Ireland (non-native coniferous tree) which appears to differ from the habitat association of that species in UK forests. However, two other Red-listed species sampled in forest canopies are not woodland-associated species; *Athous campyloides* and *Stenichnus poweri* are more commonly found in open grassland habitats where *A. campyloides* is phytophagous and *S. poweri* is an active hunter (Buckland and Buckland, 2006).

Figure 4.68: *Anobium inexspectatum* (Coleoptera: Anobiidae).

The only nationally rare bird species recorded during the surveys was Garden Warbler (*Sylvia borin*), a summer migrant with an estimated Irish population of less than 400 pairs (Birdlife International, 2004). This species prefers to breed in dense broadleaved woodland and scrub, and was recorded in a native oak woodland Breen Forest, Co. Antrim (BREEN). Most of the other bird species recorded during this project are nationally widespread, and frequent in habitats other than woodland such as parkland, hedgerows, scrub and gardens. However, early successional forests can be important in the conservation of open habitat specialists (Dettmers *et al.*, 1999; Wilson *et al.*, 2006; Burton, 2007). Linnet (*Carduelis cannabina*) and Grasshopper Warbler (*Locustella naevia*) were both found in age class I forests in this study and are on the Amber list in Ireland. Linnet is also a Species of European Concern (SPEC; (Lynas *et al.*, 2007)). Though it occurs at densities too low to have been recorded by this project, one of Ireland's rarest raptors, the Hen Harrier (*Circus cyaneus*), breeds regularly in age class 1 forests (Irwin *et al.*, 2008). No species of conservation concern were recorded in forests in older age classes in this study.

4.10 GIS database

4.10.1 The FORESTBIO database

The Geodatabase contains five tables with non spatial data, which are associated with the spatial datasets within the five File Geodatabase Feature Datasets;

1. Basedata
2. FORESTBIO_Birds
3. FORESTBIO_Canopy_Fogging
4. FORESTBIO_Groundvegetation
5. FORESTBIO_Invertebrates

Each of these Feature Datasets contains several files with spatial data also called File Geodatabase Feature class which number 18 altogether (Fig. 4.69).
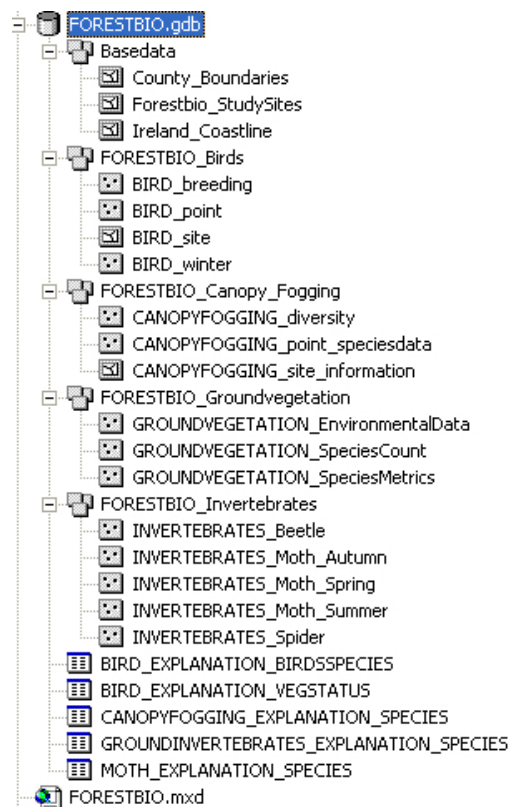
Figure 4.69: Overview of FORESTBIO Geodatabase in ArcCatalogue containing Feature Datasets with Feature Classes and Tables.
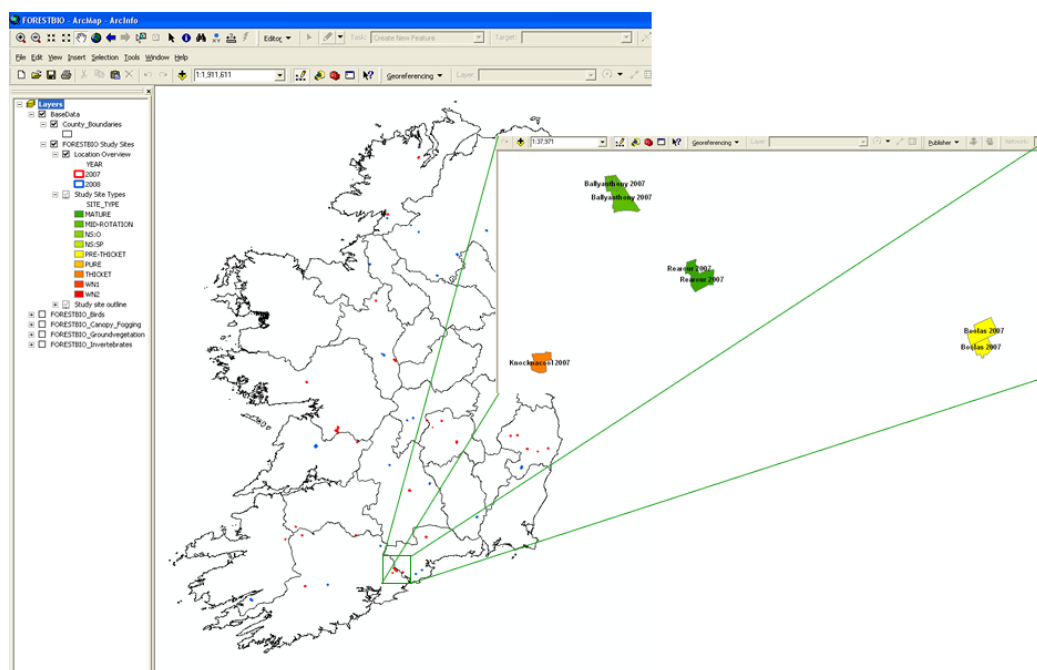
Figure 4.70: ArcMap legend showing individual layers from the Basedata Group Layer switched on and displayed in the Map viewer, which allows an overview of all study sites across the island of Ireland while indicating survey year by colour. A zoom is indicated which reveals further information on study site type as well as labels of the individual study sites.

4.10.2 Visualisation

ArcMap allows a visualisation of the Geodatabase data (Fig. 4.70), where for example the Basedata Group are queries providing an overview and general information on the study sites.

4.10.3 Data Query

ArcMap facilitates data query and analyses via several tools e.g. via the identifier selecting a specific feature or via the attribute table for a specific layer as demonstrated in Fig. 4.71. The Attribute table is opened for the Bird_point data in Fig. 4.68, illustrating that a further amount of information apart from the information that is visualised in ArcMap is stored within the Geodatabase and is also available for investigation via ArcMap for each individual data layer.

The attribute table can be interrogated further in options, for example through selection by attributes (Fig. 4.72). Interrogation of the Geodatabase is also possible via ArcCatalogue, where the GroundVegetation_EnvrionmentalData feature class is selected in the left hand panel and the preview tab shows the location of all study points. Furthermore an enquiry into the attribute table is also possible (Fig. 4.73), when selecting table instead of geography for the preview window.

ArcCatalogue also allows quick and easy access to the non spatial data of the database, as shown in Fig. 4.74 in a species name table which is associated with the spatial canopy fogging data.

4.10.4 Metadata

The Metadata for each spatial dataset can be viewed in ArcCatalogue when selecting the Metadata tab as shown in Fig. 4.75.
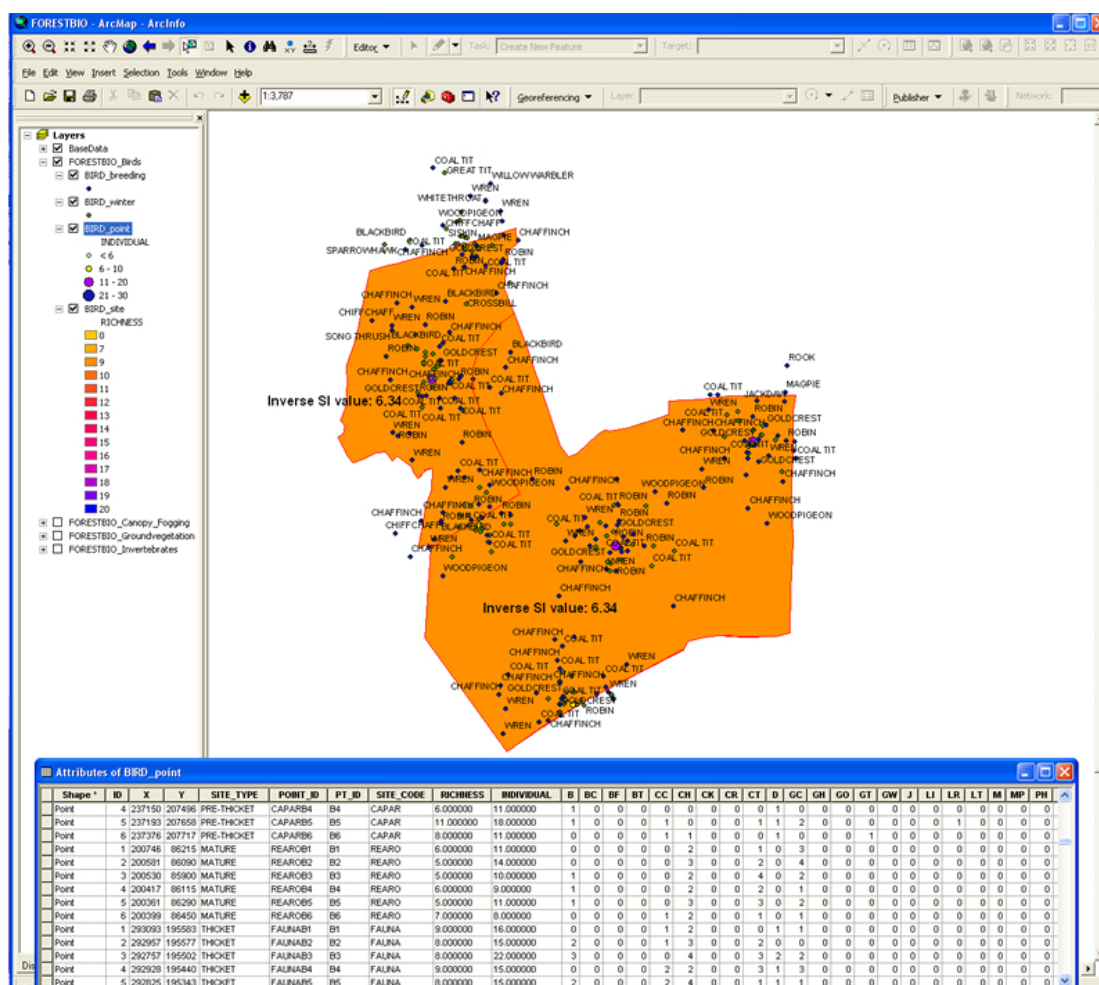
Figure 4.71: ArcMap with all the Bird layers switched on in the legend and displayed for one study site plus open attribute table for one layer, the Bird_point data.
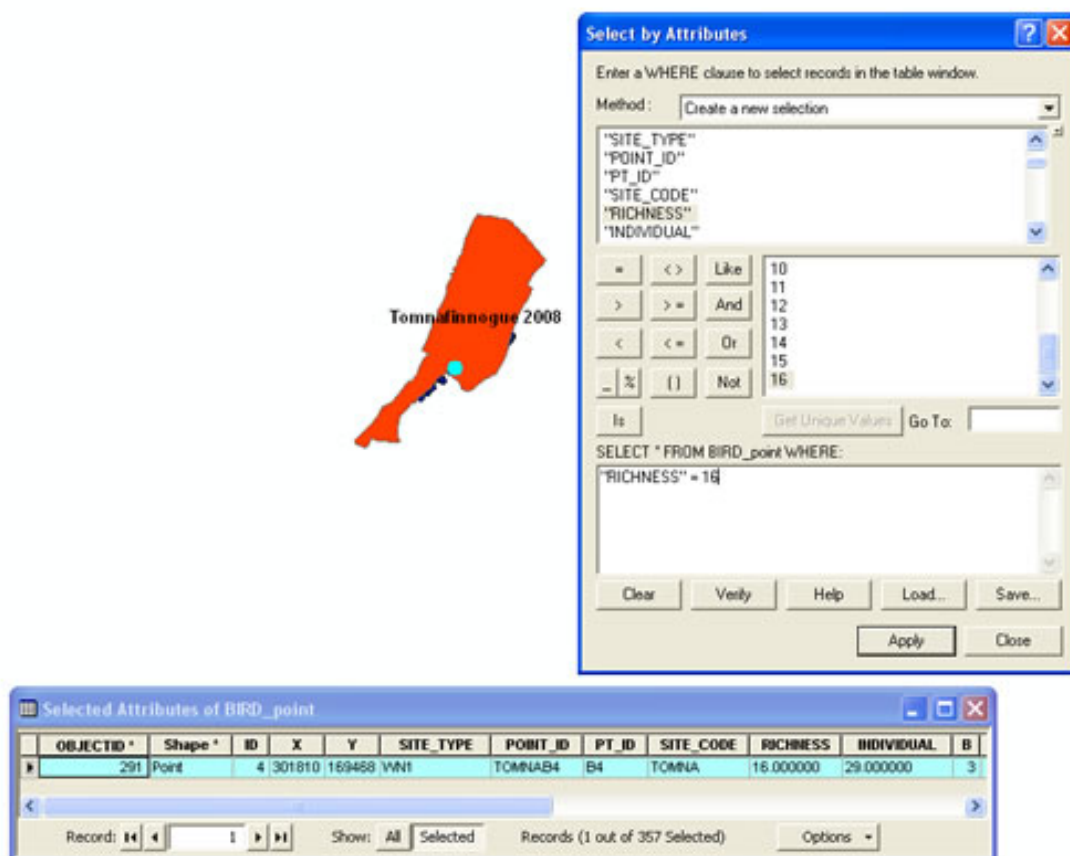
Figure 4.72: Data is further interrogated in the attribute table of the Bird_point layer through the 'Select by Attribute' SQL (Structured Query Language) looking for specific species richness values across all study sites. Selection is highlighting the data point that matches within the attribute table as well as in the Map viewer in bright blue.
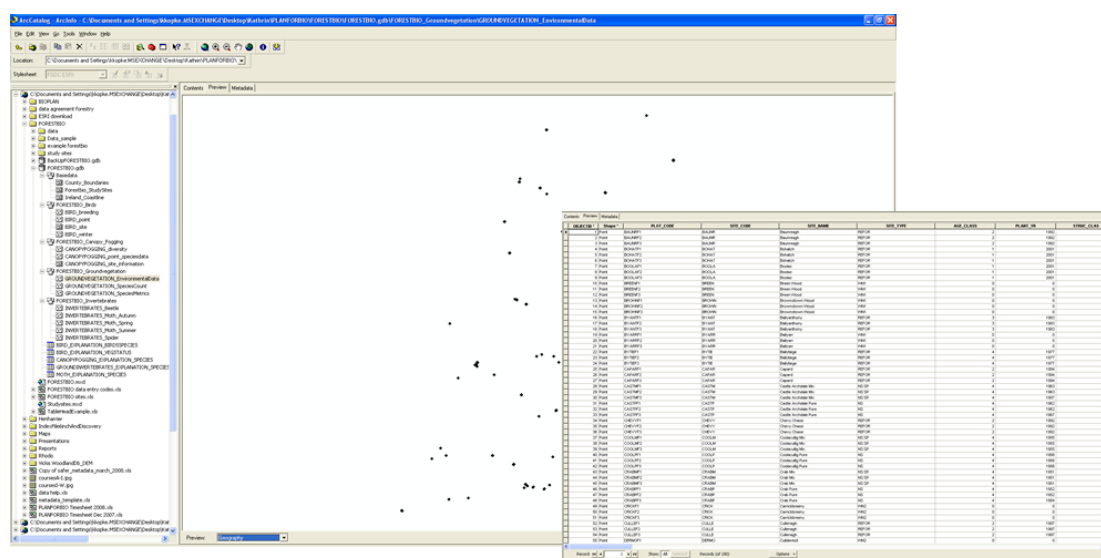
Figure 4.73: ArcCatalogue query of one Ground vegetation feature class and attribute table.

Figure 4.74: CANOPYFOGGING_EXPLANATION_SPECIES table queried in ArcCatalogue.

Figure 4.75: Metadata is displayed for the INVERTEBRATES_Spider Feature data class

5. Discussion

5.1 Epiphytes

5.1.1 Afforestation and reforestation survey

5.1.1.1 Lower trunk epiphyte diversity across the plantation cycle

Age class I sites had the lowest epiphyte species richness overall. The epiphytic communities in these plots largely consisted of pioneer species plus primarily terrestrial species growing upwards onto the tree bases. The low species richness (SR) in these sites was probably due to the fact that epiphytes are slow to colonise (Benzing, 1990; Uliczka and Angelstam, 1999) and sufficient time had not elapsed many epiphyte species to establish, even in the presence of suitable conditions. This is also suggested by the fact that epiphytes were completely absent from three of the plots in this age class. Also, age class I also had the lowest surface area of bark ($76\pm9.2cm^2$ in comparison to $229\pm24.2cm^2$, $292\pm18.3cm^2$ and $206\pm13.5cm^2$ for age class II, III and IV, respectively) due to the small diameter of trees, and number of species found in a survey is positively related to the area sampled (Magurran, 2004).

Age class II sites supported the highest epiphyte SR, presumably because of the high canopy openness and illumination in this age class, as these variables are beneficial to certain epiphytes (Rose, 1993; Coote, 2007). Canopy openness was significantly correlated with epiphyte species richness in age class II - IV. Age class III sites, which had a very dense canopy, also had low species richness, few species being able to survive in the shaded conditions beneath closed canopies (French *et al.*, 2008a). In age class IV plots, the canopy was more open due to thinning, but light levels were still low. These low light conditions seemed to benefit bryophytes, which were most likely favoured by the decreased risk of desiccation in these conditions (Saetre *et al.*, 1997). Lichens, on the other hand, are light-demanding and only a few species can dominate heavily shaded trunks (Rose, 1993), which could explain their low species richness in age class IV plots. The lack of any significant recovery in typical epiphyte species richness in age class IV is also of note. Coote (2007) suggested that the higher lichen species richness in certain commercially over-mature Sitka spruce stands meant that retaining stands beyond commercial maturity could enhance epiphytic lichen diversity.

The positive relationship between total host SR and both total and typical epiphyte species richness in ages classes II – IV may be indirectly related to canopy openness. A more open canopy indicates a decrease in the dominance of the planted trees. This may lead to an increase in the structural diversity and hence an increase in the number of tree and shrub host species (Lindgren and Sullivan, 2001) which provide a wider range of substrates, both physically and chemically (Barkman, 1958), and a greater diversity of microhabitats for epiphytes (Márialigeti *et al.*, 2009).

The area of old woodland within 1km of the sites was also positively correlated with total and typical epiphyte species richness. Old woodlands are known to act as a source of epiphyte propagules, some of which are slow to disperse (Sillett *et al.*, 2000). French (2005) found that proximity to old woodland was related to the number of woodland species that colonised the ground vegetation in first rotation Irish Sitka spruce stands. However, proximity to old woodland was not significantly correlated with any of the species richness variables in the present study. Coote (2007) suggested that, although old woodland can be important as a propagule source, hedgerows and areas of rough pasture with heather (*Calluna* spp.) or areas of gorse (*Ulex* spp.) may also be important. As the plantations studied were in their second rotation,

it is possible that the greater time elapsed meant that epiphytes had successfully colonised from greater distances.

Annual precipitation was also positively correlated with total epiphyte species richness. This factor has been positively associated with total epiphyte and lichen species richness in Sitka spruce plantations by other researchers (Humphrey *et al.*, 2002a; Coote, 2007), who attributed this relationship to variation in moisture deficit (excess of evaporation over precipitation). A low moisture deficit will result in higher humidity, which will favour bryophytes (Saetre *et al.*, 1997). Although epiphytic lichens are adapted to lower and more variable humidity levels than bryophytes (Pearson, 1969; Frahm, 2003), they still require a relatively humidi conditions (Coote, 2007).

Elevation was negatively correlated with epiphyte species richness for all the age classes combined (with and without age class I included) and for age class IV. Coote (2007) found a similar relationship in mature (age class IV) Sitka spruce plantations in Ireland. Price and Hochachka (2001) and Neitlich and McCune (1997) found that cyanolichens typical for mature and old-growth forests (160 yrs and older) were more abundant at elevations above 400 m whereas alectorioids dominated young (50 yrs old) managed forests below 200 m). Showman (1975) suggested that the importance of site elevation in determining lichen distribution in Ohio was related to the fact that high-elevation sites in this hilly region were more exposed to air pollution than sheltered lowland sites.

In terms of epiphyte community composition, age class I plots were the most variable and plots in age class IV the most distinct, having the more indicator species (eight) than any other age class. This convergence in community composition through the forest cycle has also been found for ground vegetation in Sitka spruce plantations (French *et al.*, 2008a). All of the age classes were found to have significantly different species assemblages, suggesting that, as for ground vegetation diversity (French *et al.*, 2008a), epiphyte diversity would be greatest in plantations containing stands of different age classes.

5.1.1.2 Canopy epiphyte diversity in mature afforested and reforested plantations

For the investigated forest stands, afforested and reforested plantations of age class IV did not differ from one another in management regime or tree species composition. iHence, any differences in canopy epiphyte diversity between the two forest types are probably due to either site history or environmental variables, which may influence stand characteristics. Total species richness of canopy epiphytes was higher in reforested sites due to their higher lichen diversity; epiphyte species richness only differed between afforested and reforested sites in the middle and upper plots, which correspond to the optimal habitats for lichens on spruce (Ellyson and Sillett, 2003). Plots in reforested stands were also richer in typical epiphytes and liverworts, whereas moss diversity did not differ between forest types.

Such differences between afforestation and reforestation sites may be due to the interaction between land-use history and life history traits of species in the surveyed taxonomic groups. Pre-plantation habitats of afforestation sites varied from peatland to improved grassland (Iremonger *et al.*, 2007) whereas the previous land use of reforestation stands is, by definition, forest. Many liverworts and lichens, which are known as secondary colonisers owing to their slower dispersal rates (Ratcliffe, 1968; Sillett *et al.*, 2000; Ruchty *et al.*, 2001), may be restricted from colonisation of afforested forests or only establish after a time lag. Although clearfelling of Commercially mature afforested sites disrupts canopy continuity and may result in the loss of most epiphytic lichens that were present in the stand, some epiphytic lichens may survive on remnant trees or deadwood (Nilsson *et al.*, 1995; Sillett *et al.*, 2000). The low species turnover

in ground vegetation (see Section 4.2.1) between afforested age class IV plantations and reforested age class I plantations illustrates the retention of species over successive rotations. Re-colonisation of reforested sites by epiphytic lichens and liverworts may therefore take place more quickly than the colonisation of new plantations, accelerating the development of a diverse canopy epiphyte community.

A change in environmental stand characteristics over the afforestation-reforestation cycle would provide an alternative explanation for the observed differences in diversity between the two plantation types. In Ireland and Britain, reforested plantations have been found to have drier and more acidic soils than afforested plantations due to drainage measures, water uptake by the fast-growing trees and the accumulation of spruce needle litter (Williams *et al.*, 1998; Salmon *et al.*, 2008; Oxbrough *et al.*, 2010). High soil moisture content may help to sustain an evenly humid microclimateic (McCarthy, 1980; Kuusinen, 1996). Faster tree growth and denser canopy cover in reforested sites (Oxbrough *et al.*, 2010) would reduce the proportion of rainfall reaching the soil (Hill, 1979), which may have further reduced air moisture in reforested sites. Lower atmospheric humidity in reforestation sites would have been likely to favour lichens over bryophytes (Pearson, 1969; Ruchty *et al.*, 2001). Distribution of epiphyte species along the vertical gradient may not only have been driven by differences between height zones due to different light and bark conditions (McCune *et al.*, 1997) but also by differences in microclimate.

The cardinal aspect of a plot on the trunk did not influence canopy epiphyte diversity in either afforested or reforested plantations. In forests with a Closed canopy, epiphyte diversity has not been found to be correlated with aspect (Pharo and Beattie, 2002). Aspect seems to be a more important factor for epiphyte communities on trees in more exposed conditions, such as at the edge of the forest (Kivistö and Kuusinen, 2000).

5.1.2 Mixed tree species survey

Plots in Norway spruce/Scots pine mix plantations were significantly richer in lower trunk and canopy epiphytes than plots in pure Norway spruce plantations. Plots on spruce trunks in Scots pine mixes also held more canopy epiphyte species than plots in Norway spruce/oak mix plantations. However, species richness of any of the investigated taxa did not significantly differ between pure Norway spruce and oak mix plantations. One might have expected that enrichment of pure conifer plantations with a broadleaved native tree species would have increased epiphyte diversity, as has been found in other parts of Europe (Felton *et al.*, 2010). Tree diversity in temperate forests has been found to be strongly negatively related to coniferous coverage (Glenn-Lewin, 1977) and, assuming an increase in epiphyte diversity with increasing host tree diversity, epiphyte diversity in oak mix plantations should have been higher than that in pure Norway spruce. However, in our study sites, oak remained below the canopy as an understorey tree and spruce canopy cover remained high. The canopies of both pure Norway spruce and oak mix plantations were significantly less open than those of Scots pine mix plantations. Scots pine has a lower leaf area index than Norway spruce (Lagergren and Lindroth, 2002), resulting in a more open canopy. A previous study found that Scots pine trees appeared to increase overall light penetration when intermingled with spruce trees in the canopy (cf. Beck, 2000). Species richness of lower trunk epiphytes was positively correlated with canopy openness, indicating that light levels may have been an important driver of epiphyte species richness in these plantations. Opening the canopy and decreasing the dominance of the tree layer can increase total structural diversity (Pielou, 1966), which in turn has been shown to positively affect tree species diversity (Lindgren and Sullivan, 2001). The positive relationships between lower trunk

epiphyte SR and both understorey cover and host species richness may, therefore, be indirectly related to canopy openness. The presence of an understorey in plantations, and hence higher host SR, is generally associated with a wider range of physical and chemical bark substrata (Barkman, 1958), which increase the diversity of microhabitats for epiphytes (Márialigeti *et al.*, 2009).

Canopy epiphytes were only investigated on Norway spruce trunks, so differences in bark substratum between plantation types were probably minimal (but see Bates and Brown, 1981 for an example of high variation within tree species bark characteristics). Epiphyte SR in general and typical epiphyte SR in middle and upper plots were significantly lower in pure Norway spruce stands than in Scots pine mixes. These differences were mainly due to positive relationships between species richness and height for liverworts and, to a lesser extent, lichens. As for lower trunk epiphytes, canopy openness was probably the main reason for differences in canopy epiphyte SR between pure and mixed stands, as most lichen and liverwort species are light demanding (Rose, 1993). Species richness of mosses was negatively related to trunk height in all plantation types, reflecting the ability of mosses to tolerate low light levels (Studlar, 1982) and their low tolerance to desiccation (Trynoski and Glime, 1982; Caners *et al.*, 2010).

Elevation and distance to old woodland were both negatively related to typical epiphyte SR, particularly in Scots pine mix plantations. Among recently established forests, isolated stands can harbour a lower diversity of vascular plants and epiphytes than forests located near ancient woodlands (Peterken and Game, 1984; Neitlich, 1993), due to the poor dispersal abilities of many woodland species (Sillett *et al.*, 2000; Dolman and Fuller, 2003; Rackham, 2006). However, although proximity to old woodlands can enhance migration of species into recently-established forests (Bossuyt *et al.*, 1999), such migration processes are only likely to be successful if conditions in these plantations are favourable to potential colonists (Kershaw, 1985; Dzwonko and Gawroński, 1994). This might not have been the case in the densely shaded oak mix and pure Norway spruce plantations.

Although there was a degree of overlap in species assemblages between forest types, pure Norway spruce plantations supported different assemblages of lower trunk epiphytes than did oak mixes, and different assemblages of canopy epiphytes than did either oak mixes or Scots pine mixes. The distinct nature of lower trunk epiphyte assemblages in the oak mixes can be ascribed to the presence of epiphytes on host species additional to the dominant Norway spruce. Many epiphyte species exhibit specificity to particular host species (Aber *et al.*, 2000). Bark propoerties can be particularly important in determining the epiphytic assemblage of a tree species (Fritz *et al.*, 2009a), and oak has a smoother and less acidic bark than Norway spruce (Grodzińska, 1977).

Even if an epiphyte species is associated with a particular tree species, it may still occur on other tree species within an intimately mixed stand. Subordinate trees and shrubs may act as sources of epiphyte propagules, thereby influencing epiphyte communities on neighbouring tree species (Ruchty *et al.*, 2001). For example, *Radula complanata* and all other indicator species for the lower trunk epiphytes of oak mix plantations occurred on lower trunks of both Norway spruce and oak.

As well as differing between forest types, epiphyte assemblages differed according to height zone. Although lower and middle plots were not clearly separated from each other, base and upper plots had unique assemblages of epiphyte species. For spruce trunks, it has already been shown that heights may be positively correlated to lichen diversity and negatively correlated to bryophyte diversity (Ellyson and

Sillett, 2003). Such a zonation is thought to be due to a complex light-moisture gradient, with conditions at different heights favouring different species and growth forms (Kenkel and Bradfield, 1981).

5.1.3 Native woodlands survey

Total SR of lower trunk epiphytes, and of typical epiphytic species in the canopy and on lower trunks, was higher in ash than in oak woodlands. Especially in the lower and middle trunk zones, ash trees hosted more typical epiphyte species than oak trees. Oak woodlands were more open, having a lower understorey cover than ash woodlands, which often had a dense understorey of hazel (*Corylus avellana*) and other species. Higher light levels in oak woodlands should have increased species richness of trunk-dwelling bryophytes and lichens (Rose, 1993; Tinya *et al.*, 2009). Oak has a thick bark with a high water holding capacity (Harris, 1971), characters associated with high bryophyte cover (e.g. at the base of larch trunks (Coote, 2007)). Competition is known to occur between bryophyte and lichen epiphytes (Averis and Coppins, 1998). It is possible that vigorous growth of competitive bryophytes on the lower trunks of oak led to a low species richness of lichen and less competitive bryophyte species at these sites despite the relatively favourable light levels.

Total and typical epiphyte species richness for oak and ash combined were related to a suite of variables that all differed between oak and ash plots. Only one of these variables, total host SR, was correlated with typical epiphyte species richness when the two forest types were examined separately. A decrease in average DBH and an increase in the total tree number and understorey cover are all indications of an increase in the presence of below canopy trees and a greater number of host species. The greater number of host species in ash woodlands may have increased typical epiphyte SR on the lower trunks despite the lower canopy openness. In other European mixed deciduous forests, bryophyte species richness has been found to be related to tree species diversity but not significantly related to differences in light levels (Humphrey *et al.*, 2002a; Márialigeti *et al.*, 2009).

Epiphyte SR on both oak and ash trunks was positively related to height. This was mainly due to a positive relationship between species richness of lichens and (in the case of oak) liverworts and plot height. In contrast, species richness of mosses (on ash trees) was negatively related to height (cf. also section 5.1.2). Epiphyte diversity and biomass are usually higher in the lighter upper canopy than on shady trunk bases (Lang *et al.*, 1980), mainly due to a higher species richness of cyanolichens and alectorioid lichens (McCune *et al.*, 1997), which are light demanding and more adapted to lower and more variable humidity (Pearson, 1969; Rose, 1993)

Host tree species in ash woodlands (mainly ash and hazel) differed from those in oak woodlands (mainly oak, birch and holly), which may at least partly explain the differences in epiphyte species assemblages between oak and ash woodlands. Many epiphyte species are adapted to the characteristic bark surface and bark chemistry of particular host species (Aber *et al.*, 2000) and their characteristic bark surface and bark chemistry (Hauck, 2010). Bark pH and concentrations of Magnesium and Potassium are higher in ash than in oak. However, oak bark has a higher water-holding capacity than that of ash (Bates and Brown, 1981; Bates, 1992), typically being strongly fissured even in young trees, in contrast to ash trees which are smooth barked when young, becoming rough-barked only at maturity (Barkman, 1958).

The cardinal aspect of a plot on the trunk did not influence canopy epiphyte diversity on either oak or ash trees. Such aspect effects on epiphyte communities are more marked for stands where light exposure is

higher, e.g. in solitary trees (Moe and Botnen, 2000). However, in forests with a Closed canopy, aspect has not been found to affect epiphyte diversity (Pharo and Beattie, 2002); any effects may have been concealed by the overwhelming influence of other factors.

5.1.4 Comparison of forest types

5.1.4.1 Canopy epiphytes

Ash woodlands were significantly more species rich in total epiphytes and also in typical epiphytes and lichens than any of the surveyed pure or mixed conifer plantations. This echoes the findings of Watson (1936) that conifer species in Britain host the fewest species of epiphytes among forest trees, probably because of their acid and often flaking bark. In another survey, ash was found to support the highest number of epiphytic bryophyte species among trees in southern Britain (Bates *et al.*, 1997).

Oak woodlands and Norway spruce/Scots pine mix plantations were intermediate in their typical epiphyte, lichen and moss species richness. This is surprising since, although oak trees in Britain showed half of the species richness of ash, they still supported considerably higher numbers of epiphyte species than spruce or pine (Bates *et al.*, 1997). The similarity between oak woodlands and Scots pine mixes revealed here might be more related to environmental conditions within the forest rather than to tree species characteristic. This hypothesis is supported by Humphrey *et al*. (2002a) who found that, whilst dense Scots pine plantations in Britain were poorer in epiphyte species than native oak woodlands, more open native Scots pine woodlands hosted a similar number of epiphyte species to oak woodlands.

Lower epiphyte species richness on trunks of plantation trees than on trees in native stands can often be interpreted as a consequence of reduced light availability in plantations (Humphrey *et al.*, 2002a). More open overstories appear to favour lichens and tuft-forming mosses (Ruchty *et al.*, 2001) whereas very dense stands virtually exclude epiphytes (Coote, 2007). This study revealed an increase of species richness of canopy epiphytes with increasing canopy openness in even-aged plantations (Scots pine mixes, with a mean canopy openness of 7.9%, were considerably richer in epiphytes than pure Norway spruce, where mean canopy openness was only 6.3%). Thinning and retention of open spaces such as rides to increase natural regeneration may be good measures to encourage epiphyte diversity in plantations (Humphrey *et al.*, 2002a; Iremonger *et al.*, 2007). Surprisingly, canopy openness was lower in native oak and ash woodlands than in most of the plantations. This was mainly due to a higher understorey cover, which would not have affected light availability for canopy epiphytes on the middle and upper trunk. Light conditions for canopy epiphytes are generally more favourable in broadleaved woodlands than in conifer plantations.Canopy broadleaves are generally deciduous, permitting substantially greater light penetrationin winter and spring than during the summer. By contrast, all plantation conifers in Ireland, with the exception of larch, are evergreen. In addition, diffuse light useable for photosynthesis penetrates through broadleaved canopies in greater amounts than through conifer canopies (Messier *et al.*, 1998), most likely due to the densely massed foliage of conifer crowns (Kucharic *et al.*, 1999). Such low light levels in spruce plantations explain the lack of an understorey (Alaback, 1982).

The results of the different forest surveys (see Sections 5.1.1, 5.1.2 and 5.1.3) showed that factors such as an increased host tree SR and closer proximity to large old woodland areas were recurring factors for increased epiphyte species richness. While the latter factor is dependent on site availability and ownership

of land, host tree SR is influenced by the management of both native and planted forests. Opening the canopy and increasing light availability stimulates the growth and diversity of ground vegetation (Sakura *et al.*, 1985; Abdy and Mayhead, 1992), hence of host plant diversity in plantation forests. Thinning is one method of opening the canopy in already established forests (Moore and Allen, 1999; Hale, 2003). In native woodlands, canopy openness may be of secondary importance and grazing management may be a priority for promoting host plant diversity (Kirby, 2001; McEvoy, 2006). In plantations, the planting and maintaining of a diverse mixture of canopy species, including species which create a light canopy (e.g. pine Beadle *et al.*, 1982; Gower and Norman, 1991), has been suggested as a way of enhancing ground vegetation diversity (Ramovs and Roberts, 2003; Smith *et al.*, 2005); in this study, we have shown that this would also benefit epiphyte species richness (cf. Scots pine mix plantations).

Besides the differences in species richness, this study has shown that pure and mixed conifer plantations have the potential to support epiphyte communities and some typical epiphyte species. However, these communities show little similarity to the epiphyte communities found in native ash or oak woodlands. Every tree species has a specific biological potential for being a host to different functional groups of plants, animals and fungi. Apart from exotic tree species which have a much lower biological potential than native species (Gosselin, 2004), alder, ash, oak, beech and maple have the potential for a richer epiphytic community than any of the coniferous species native to Europe (Branquart and Dufrêne, 2005). Hence, it is generally assumed that non-native Sitka spruce and Norway spruce plantations will never develop an epiphytic lichen vegetation characteristic of native broadleaved woodlands (Humphrey *et al.*, 2002a). However, this study has shown that, in exceptional cases, conifer stands such as the mature Sitka spruce stand "CHEVY" may support epiphyte communities similar to native (oak) woodlands. Although total and typical canopy epiphyte species richness at this site (29 and 9, respectively) were poorer than the average SR found in native woodlands, CHEVY clustered with other oak woodland sites in the ordination space. This age class IV Sitka spruce reforestation site was subject to considerable light penetration from its edges, which enhanced naturally regenerating broadleaved tree species in its understorey. It was situated on an old woodland site and adjacent to remnants of this old woodland. Old woodlands are known to act as sources of epiphyte propagules (Hilmo and Sastad, 2001), some of which are slow dispersers (Sillett *et al.*, 2000), and can diversify and accelerate re-colonisation of plantations by epiphytes (Neitlich, 1993). The combination of high light levels, diversity of host tree species and a rich local source of propagules may have enabled re-colonisation of a more diverse assemblage of epiphyte species.

Some studies show that diversity of epiphyte communities in plantation forests may increase in late stages of the forest cycle (Holien, 1996; Kuusinen and Siitonen, 1998) and that impoverishment of epiphyte communities in plantations is – amongst other factors – due to a lack of old trees (Humphrey *et al.*, 2002a). Older trees are usually associated with different communities of epiphytic lichens and bryophytes (Fritz *et al.*, 2009b). The retention of remnant trees or stands past commercial maturity provides greater structural diversity and hence encourages epiphyte growth and diversity (Berryman and McCune, 2006). Retention of such features could be an effective management tool for promoting epiphyte diversity in Irish plantation forests (Smith *et al.*, 2005; Coote, 2007).

5.2 Ground vegetation

5.2.1 Afforestation and reforestation survey

5.2.1.1 Differences in ground vegetation diversity and composition across each rotation and between the two rotations

For afforestation, species richness was high during Pre-thicket, before the crop had an impact, was at a minimum during the closed-maturing and re-opening stages and increased again during the commerically mature stage. There were more species in the Commercially mature stage than the Pre-thicket. In the reforestation cycle, species richness was highest during the Pre-thicket and Commercially mature and lowest during the mid stages of Thicket to re-opening. The fluctuation of species richness seen in our research agrees with previous work on the dynamics of plantation ground vegetation diversity (Hill, 1979; Hill, 1986; Franklin, 1988; Kirby, 1988; Fahy and Gormally, 1998; Williams *et al.*, 1998; Humphrey *et al.*, 2003; Smith *et al.*, 2005; French *et al.*, 2008) that report early and late stages are high in SR compared to the mid stages, which are the lowest. In reforestation, the Commercially mature stage was significantly more species rich than all other stages except Pre-thicket. We propose that the high Pre-thicket SR may reflect the presence of large complex brash piles which were positively correlated with species richness. Although at the end of each forest cycle there were no significant differences in species richness and bryophyte SR between the mature stages of the two rotations, these metrics were significantly lower in the Pre-thicket reforestation stage than in the afforestation Commercially mature stage. We propose this may reflect a loss of species during the clearfell and replanting processes.

In reforestation, typical woodland species richness, following an initial decrease, increased significantly over the forest cycle; this was also the case for the afforestation cycle. The initial decrease in typical woodland species richness mirrors the findings of Cooper *et al.* (2008); they reported a decrease in typical woodland species richness in Pre-thicket stages of Sitka spruce reforestation with time from felling of the previous conifer crop. Development of a typical woodland vegetation is considered to be mainly a function of stand age (time to allow typical woodland plants, that are often slow colonizers, to disperse to a site and become established (Brunet and von Oheimb, 1998; Verheyen *et al.*, 2003) and site history (whether the stand was established on a site sufficiently close to semi-natural woodland for woodland species to colonise, or indeed, on a site that was itself previously semi-natural woodland (Peterken and Game, 1984; Brunet and von Oheimb, 1998; Ferris and Simmons, 2000; Peterken, 2001). In support of the influence of stand structural stage this research found a significant increase in typical woodland species richness over both afforestation and reforestation cycles. As for the influence of site history, the results of this study indicate that for these study sites there are other more influential factors impacting typical woodland vegetation development than site history e.g. canopy cover. The model of vegetation development over successive rotations on peatland and heath developed by Peterken (2001) and Hill (1979) proposed that the vegetation will shift away from species of original open habitat to species of woodland in plantation stands and species of open spaces in rides. As the majority of study sites in this research were formerly rough grazing or unimproved grassland this model seems appropriate. However, contrary to the proposed model above, this study found no significant increase in typical woodland species richness over the reforestation cycle in comparison to afforestation; at the end of each forest cycle there was no significant difference in typical woodland SR between the Commercially mature stages of the two rotations. In fact, for several stages there was a trend for higher typical woodland species richness in afforestation. An exception was the significantly higher typical woodland species richness in reforestation Pre-thicket compared to afforestation Pre-thicket, perhaps reflecting the accumulation of typical woodland species

over the proceeding rotation. In our research, the increase in numbers of indicator species with a high affinity for woodland over the forest cycle reflects a shift in vegetation from open habitat species to those of woodland in both rotations. There is a significant increase in typical woodland species richness over the afforestation cycle, and we propose that the significantly higher typical woodland SR in reforestation Pre-thicket compared with afforestation Pre-thicket may reflect the retention of species from the Commercially mature afforestation stage that preceded it. The retention of species between rotations could not be verified on a site by site basis as different afforestation and reforestation sites were studied rather than a direct chronosequence. Notwithstanding the possible retention of some species between successive rotations, there were also indications of species loss. Typical woodland SR was significantly lower in Pre-thicket reforestation stage than in the afforestation Commercially mature stage, perhaps reflecting a loss of species during the clearfell and replanting process.

The change in species composition over successive rotations is illustrated by both the ordination and indicator species analysis and highlighted by the fact that the highest inter-rotational βsim (0.55) was between afforestation Pre-thicket and reforestation Commercially mature. The relatively low βsim (0.35) between afforestation Commercially mature and reforestation Pre-thicket, and the ordination of these two stages close together, also suggest that there may be species retention between rotations. However, there are also significant differences between these stages in species richness (due to the significantly lower bryophyte richness in reforestation Pre-thicket) and in typical woodland species richness, also significantly lower in reforestation Pre-thicket. These differences suggest that a substantial suite of species may be lost between rotations during the clearfell and replanting process. Whether this loss is localized to the stand and whether the species persist in the seed bank or in refuges close by cannot be determined by this study. The higher variability among afforestation Pre-thicket sites is evident from the afforestation Pre-thicket sites having a wider spread in ordination space and significantly higher βsim values than the reforestation Pre-thicket sites. This higher variability may reflect the different starting conditions at afforestation sites in comparison to reforestation sites; pre-plantation habitats can vary from, for example, peatland to improved grassland (Iremonger *et al.*, 2007) whereas land use prior to reforestation stands is, by definition, plantation. That species turnover (βsim) was generally significantly higher in afforestation than reforestation indicates there was a greater change in ground vegetation over the afforestation cycle than over the reforestation cycle. The differences in community dynamics between the two rotations is also evident from the ordination with the reforestation sites relatively clustered in ordination space compared to those of afforestation. These differences may also reflect differing site conditions at the start of each rotation. Despite each rotation having very different starting points there is clear floristic convergence between both rotations as they mature, as indicated by the Commercially mature stages of both rotations ordinating relatively close in space and the lower species turnover (βsim) between rotations in the later stages compared to earlier stages. This floristic convergence between rotations may be driven by similarities (i.e. lack of significant differences) in terms of structural diversity, soil pH and Ellenberg (soil) moisture.

Previous researchers have reported that one of the most important influences on vegetation succession in reforestation following clearfell is whether species can establish before canopy closure, either by having persisted through the forest cycle (vegetatively and/or in the seed bank) or by having migrated to the stand from the surrounding area (Hill, 1986; Eycott *et al.*, 2006). Other influences mentioned include soil type, previous land use, grazing intensity, management intervention and time between clearfell and replanting (Peterken, 1993; Williams *et al.*, 1998; Cooper *et al.*, 2008). Hill (1986) proposed that early

successional vegetation in reforestation would be dominated by species that remained dormant in the soil seed bank during the afforestation rotation and this has been confirmed by Humphrey *et al.* (2003) and Williams *et al.* (1998). Our research also found that many of the indicator species found in the reforestation Pre-thicket stage were species associated with open-ground habitats, for example, heather (*Calluna vulgaris*), seeds of which may remain viable for more than 50 years (Hill, 1986). For species lacking the potential to persist in the seed bank, the survival of a few established individuals, on or near to the stand, may be critical to persistence over successive rotations.

5.2.1.2 Drivers of diversity

Modelling showed that some of the drivers of diversity were similar for species richness and typical woodland species richness i.e. canopy cover and structural diversity. Ground vegetation diversity and community composition in forests is strongly influenced by canopy cover via its influence on temperature, light, water and soil nutrient availability (Saetre, 1999). At high canopy cover in conifer plantations, many ground vegetation species are unable to survive in the low temperature, light, water and soil nutrient limited environment and species that are present often do not have an extensive cover (Kirby, 1988; Wallace, 1998; Ferris *et al.*, 2000a; French *et al.*, 2008). For both species richness and typical woodland species richness, canopy cover was of high relative importance in the MMI model sets but had a non-linear relationship with both metrics. Typical woodland species are adapted to varying light levels in forests (Thomas and Packham, 2007); however, the higher canopy cover levels recorded in reforestation compared to afforestation may have contributed to the relatively low species richness of typical woodland species in reforestation. FWD & needle cover was also negatively related to <u>species richness</u>. Previous research has shown that litter in conifer stands can negatively affect ground vegetation diversity (De Vries, 1995; French, 2005; Eycott *et al.*, 2006); however, it is difficult to separate out the influences of canopy cover and other factors, such as needle litter, that were correlated with it. There is often a combination of adverse influences on ground vegetation; where canopy cover is high, needle litter is also high and less rain can penetrate (Hill, 1979). Canopy cover and FWD & needle litter cover were significantly positively correlated in both rotations, thus the low species richness in the closed-maturing stage is most likely a result of the high canopy cover retarding ground vegetation development through the attenuation of light and rainfall, than the smothering and acidifying effects of FWD & needle cover. The prediction of higher species richness and typical woodland species richness with increasing structural diversity (also reported by Peterken and Game (1984) suggests that structural diversity can be used in the field an indicator for species richness and typical woodland richness across both rotations.
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The positive relationship between species richness and distance to old woodland highlighted by modeling may be due to the confounding effects of differences in age (afforestation Commercially mature sites are up to 10 years older than the oldest reforestation Commercially mature sites) and differing soil types in the chronosequences. These possible confounding effects were not included in the model as age was collinear with canopy cover (r_s = 3.82, P > 0.01) and structural stage (r_s = 9.44, P > 0.01) and soil type information was not included due to issues with soil classification and for some sites it was unknown. That proximity to old woodland for this study's sites was not significant in the model set for typical woodland species richness may reflect the importance of stand management, e.g. thinning, to the development of typical woodland vegetation. This research has shown that, even when a stand is proximate (on/adjacent) to old woodland, typical woodland species richness will be negatively impacted if the canopy reaches high cover (> 60%).

Care should be taken in interpreting averaged model parameters. Structural stage had a high importance value in the set of species richness models but the averaged model parameters are misleading. They predicted higher species richness in Thicket stage than Pre-thicket; however, from mean species richness trends over both rotations it is clear that the Thicket stage had lower species richness. The average model coefficient for Thicket stage was lower than its unconditional standard error (results not shown) indicating that there is large variation in the predicted effect on species richness of the Thicket stage. pH had a high importance value in the set of models for species richness and typical woodland richness, with high species richness predicted at low pH. Significant differences in pH were only recorded between early stages with higher pH in afforestation than reforestation. Previous plantation studies have reported pH as an important influence on ground vegetation composition (Ferris *et al.*, 2000a; French *et al.*, 2008)

CWD volume was significantly higher in reforestation than afforestation (P < 0.01), as expected, due to deadwood being left on site after clearfell and stumps from the sites previous rotation remaining in situ. The canopy cover:CWD volume interaction had a high importance value in the set of models for total species richness and highlighted that the relationship between CWD and species richness changed at different levels of canopy cover. In reforestation, during the closed-maturing stage, canopy cover and CWD volume were at their highest while mean bryophyte species richness was at its lowest. This indicates that deadwood may only become an important habitat for byrophytes in plantations if other environmental conditions are favourable e.g. the light environment is not limiting (Humphrey *et al.*, 2002c). The positive correlation between CWD volume and bryophyte species richness and the higher bryophyte species richness in afforestation compared to reforestation (except in Pre-thicket) was most likely owing to afforestation canopy cover being lower than in reforestation. In fact, in afforestation, bryophyte SR was at its highest when CWD volume was also at its highest and canopy cover as at its second lowest of the cycle. The lack of a positive correlation with CWD volume in Pre-thicket maybe related to the fact that the calculation of CWD volume did not include large complex brash piles, which did in fact contain CWD. We lack comprehensive site histories for this research; however, it appears from the literature (Booth *et al.*, 2007) that deadwood would usually be left on site after felling. The positive relationship found in our research between large complex brash piles and species richness supports the continuation of this practice.

5.2.2 Mixed tree species survey

5.2.2.1 Diversity

In an industry traditionally based on monocultures, the presence of a mix component is expected to play a role in the structure and functioning of a plantation ecosystem (Ferris and Humphrey, 1999). Although this research found no significant enhancement of ground vegetation species richness in mixed stands, the pure sites and the Scots pine mixes had similar-values for all species metrics and both had higher-values of total, vascular plant and typical woodland species richness than the oak mixes. However, non-vascular species richness was higher in the oak mixes than other two forest types. This research found evidence of increasing light availability on the forest floor in Scots pine mixes compared to pure stands e.g. significantly higher canopy openness. Moreover, significant differences in the cover and DBH of Norway spruce and the mix components (Scots pine and oak) found among the different forest types also indicate impacts of the mix component on forest structure in terms of tree size and canopy extent. The extent of the forest canopy strongly influences microclimate conditions on the forest floor that in turn impact non-vascular species (Márialigeti *et al.*, 2009; Raabe *et al.*, 2010). Higher canopy openness often results in

higher temperatures and increased light levels on the forest floor (Raabe *et al.*, 2010) and in these conditions non-vascular species may suffer from desiccation and competition from vascular plants. However, non-vascular species may have a competitive advantage over vascular plants at low light levels as they are mostly shade tolerant and favour high soil moisture and humidity (Simmons and Buckley, 1992; Humphrey *et al.*, 2002a; Coote, 2007). That the pure sites and oak mixes both with significantly lower canopy openness also had significantly lower non-vascular cover than the Scots pine mixes agrees with previous studies that have found that even shade-tolerant non-vascular species will not grow as vigorously in sub-optimum light levels i.e. closed-canopy conditions (Watt, 1931; French, 2005; Felton *et al.*, 2010) and there is an optimum level of incident radiation, above and below which bryophyte richness is negatively affected (Coote, 2007).

That needle litter cover in oak mixes is second to that of pure sites may seem unusual due to its broadleaved component. However, in oak mixes the low canopy openness and was possibly related to these sites having the lowest vascular cover and richness, thus leaving the needle litter highly visible. The higher canopy openness in the Scots pine mixes may be due to the more open canopy structure of the Scots pine tree resulting from the fact that it is a self-pruning species (Anon, 2005b) and the resultant increased light levels are probably related to the significantly higher understorey, vascular and non-vascular covers.

The environmental conditions at the sites surveyed may have been more suitable for the main species, Norway spruce, and less so for the mix component and thus, at least in part, may explain the lack of significant differences in species richness metrics among mixed and pure stands. For mix sites, there was a low ratio of mix to main species trees. Thus, regardless of the planting density of a mixture, the mix species component may be reduced over the forest cycle to a very low representation in the stand due to unsuitable site conditions and so, in ecological terms, it may have no impact on the diversity of the stand. According to the Grime *et al.*'s (2007) CSR classification, all the planted species in this survey are both competitive and stress tolerant and this may suggest ecological compatibility. However, the choice of the mix species, especially that of oak, may have been inappropriate, as mixes should be composed of species that are ecologically compatible with, for example, similar early growth rates (Kerr, 1999). Oak is slow to establish (Anon, 2005a) and the poor growth performance of oak in the mix stands was evident as oak DBH was significantly lower than that of the Norway spruce and it was present as understorey. Scots pine DBH in the mix was also significantly lower than that of Norway spruce, but the difference was not as pronounced as in the oak mixes. Scots pine and European larch (*Larix decidua*) are the only conifer species recommended as compatible with oak and in a non-intimate mixture (Forest Service, 2000a; Anon, 2005a). The Norway spruce may have been originally planted as a nurse species for the oak (Kerr *et al.*, 1992); however, if the oak was severely suppressed by the nurse species, the thinning out of the nurse species may never have happened. Indeed, a British study into mixtures of Norway spruce and oak (Mason and Baldwin, 1995) found that the conifer grew much faster than the oak after the initial establishment phase. They concluded that there are few situations where planting conifers intimately to act as a nurse species for broadleaves is appropriate, since the faster growth of the conifer requires the stands to be specifically managed to favour the broadleaved trees at the expense of conifers. Regardless of whether Norway spruce was planted as a nurse species in our sites, our results agree with previous work on conifer/broadleaved mixes (Mason and Baldwin, 1995) in that, without management to favour broadleaves, the mixes will tend towards conifer dominated stands over time. Current forestry policy in Ireland advises that Norway spruce and Scots pine are compatible in mixture. However, that there is no

significant difference in species metrics for the Scots pine mixes, despite the significantly higher canopy openness, suggests that even intimate mixes between more ecologically compatible species need careful management to open up the canopy and allow light to reach levels that will impact ground vegetation diversity.

Site history may also have been a factor in the lack of significant differences in species metrics among mixed and pure stands. Previous studies have reported that proximity to old woodland is an important factor in the ground vegetation diversity of plantations, especially in terms of typical woodland species (Peterken and Game, 1984; Brunet and von Oheimb, 1998; Ferris and Simmons, 2000; Peterken, 2001; French *et al.*, 2008). There were more pure sites on or adjacent to old woodland than mix sites and many of the sites with high typical woodland species richness were pure Norway spruce sites on or adjacent to old woodland. The influence of site history on the development of a typical woodland vegetation is supported by the fact that the plantation in which two of the 'notable' woodland species of Perrin *et al*. (2008a) occurred were on an area that was previously old woodland. Thus a sites proximity to old woodland may be more important to ground vegetation richness than whether there is a mix component, especially if this component does not alter below canopy conditions significantly from those present in pure plantations.

5.2.2.2 Ground vegetation Composition

The ordination analysis indicated that the presence of a secondary tree species did not have a great influence on the ground flora community composition, as illustrated by the spread of both types of mix and pure sites in the ordination space, i.e. no groups formed of a particular forest type. MRPP analysis at the site level confirmed there were no significant differences in community composition among the forest types. There were no significant differences in vascular plant species numbers of competitors (C), stress-tolerators (S) or ruderals (R) among the three forest types with the majority being C and/or S strategy and a few R strategy. The similar tolerances and adaptations to environmental conditions of the vascular plant communities underline comparable conditions among the different forest types. As reported in Grime *et al.* (1988) this dominance of competitors and stress-tolerators is typical of habitats, such as these Commercially mature plantations, where disturbance is rare. Conversely, ruderals are often found in habitats where disturbance is common and are often weeds with high demands for nutrients and/or are intolerant of competition.

5.2.2.3 Forest structure

The negative correlation between planted tree density and species richness metrics and the positive correlation between canopy openness and species richness metrics are consistent with previous findings that light is a major factor limiting ground vegetation species richness in plantations (Simmons and Buckley, 1992; Liira *et al*., 2007; French *et al*., 2008). Stand structure was impacted by the planting of a mix component with significant differences in tree growth characters observed between the forest types e.g. canopy openness, DBH and cover of Norway spruce and the mix species. Piotto's (2008) review comparing tree growth between mixed and pure plantations reports that, depending on whether interspecific competition is higher than intraspecific or *vice versa,* mixed plantations can have either a negative or positive effect on the growth of the main tree species. He reported that, while mixed plantations did not have higher height growth rates, they had higher diameter growth rates. The trend of an increase in the growth of the main mix species (also reported in other research (Assmann, 1970; Wang

et al., 1995; Bartsch *et al.*, 1996) was found in the present study where Norway spruce had significantly higher DBH in the oak mix than in the other two forest types.

5.2.2.4 Structural indicators

Structural diversity of forests adds potential microhabitats, thus increasing the range of ecological strategies that a forest can support and enhancing biodiversity. Correlation analyses showed positive strong relationships between both total species richness and typical woodland species richness and structural diversity (also reported by Peterken and Game (1984) suggesting that structural diversity can be used in the field as an indicator for ground vegetation diversity in all three forest types. There was no significant association between canopy openness and typical woodland species richness. Typical woodland species are adapted for the varying light levels in forests (Thomas and Packham, 2007) and so can tolerate a certain level of canopy closure but cannot survive below a completely Closed canopy. FWD and needle litter covers are negatively related to most of the species metrics. Low canopy openness may result in the suppression of ground vegetation through the attenuation of light and rainfall, thus leaving FWD and needle litter more visible (Hill, 1979). Previous research has also shown that litter in conifer stands can also directly negatively affect ground vegetation richness (De Vries, 1995; Xiong and Nilsson, 1999; Eycott *et al.*, 2006). The lack of significant correlations with non-vascular richness in this research is noteworthy and perhaps indicative of the fact that the response of non-vascular species to light conditions is unimodal i.e. there is an optimum light level above and below which non-vascular species are negatively affected (Coote, 2007).

5.2.2.5 Functional indicators

Investigations into the potential value of conifer plantations for non-vascular diversity, and how they might be managed to improve habitat quality, have focused on the value of deadwood as a substrate for non-vascular species (Humphrey *et al.*, 2003; Smith *et al.*, 2005; Márialigeti *et al.*, 2009; Raabe *et al.*, 2010). That almost 50% of non-vascular species recorded in this survey were growing on deadwood highlights the importance of this habitat however, there was no significant correlation between total CWD cover and species richness metrics. In general, CWD was present at relatively low covers in the majority of sites, which is likely to have been a limiting factor for the occurrence some deadwood specialist forest species. The positive association between brash pile cover and vascular species richness may be related to opening up of the canopy during thinning operations recently carried out at sites with high brash pile covers, i.e. Scots pine mixes and pure sites.

5.2.3 Native woodlands survey

5.2.3.1 Species richness and vegetation communities

A large range of species was recorded in the woodlands in this survey, including a large proportion of typical woodland species. However, the fact that only two of the 30 'notable' woodland species listed by Perrin *et al* (2008) were recorded suggests either that the woodlands in this study were of relatively poor quality, that the sampling design did not adequately capture the diversity of these woodlands or that these species are rare in Irish native woodlands in general. The latter is suggested by the survey by Perrin *et al*. (2008) of 1320 Irish native woodlands, where only six species were frequently recorded, including *Anemone nemorosa,* the most frequently recorded species, and *Melica uniflora*.

The ash woodlands in this study were found to be significantly more species rich and diverse than the oak woodlands. The National Survey of Native Woodlands (Perrin *et al.*, 2008a) found an average of 29 species in the oak woodlands and 29 in the ash woodlands they studied, both figures from 100m^2 quadrats, suggesting that oak and ash woodlands can have similar species richness values. This is also suggested by other studies which have found an average range of 37 to 52 species in oak woodlands (Kelly and Moore, 1975), and an average range of 38.8 ± 6.2se to 58.1 ± 3.2se in ash woodlands (Kelly and Kirby, 1982) in Ireland; both figures from 200m^2 quadrats. The value of 29 species in oak woodlands recorded in the National Survey of Native Woodlands (Perrin *et al.*, 2008a) is slightly more than the 26.5 ± 1.4 recorded in the present study from the same sized plots, while 29 species in ash woodlands is substantially less than the 41.3 ± 2.3 recorded in the present study. This suggests that the ash woodlands studied were particularly diverse.

A number of the significant differences between the structural and functional variables for oak and ash (number of trees, average DBH, canopy openness) were related to the presence of a dense *C. avellana* understorey in the majority of the ash woodlands. The presence of *C. avellana* may also explain the higher cover of FWD in ash woodlands as this species produces a high proportion of FWD in relation to its basal area (Norden *et al.*, 2004). The lower CWD volume in oak woodland may be related to the fact that a large proportion of the oak woodlands in the present study were previously managed as coppice woodlands which are associated with reduced levels of deadwood compared with natural forests (Kirby, 1992). Leaf litter cover was significantly higher in oak than ash woodlands and it is known that the leaves of *Quercus petraea* and *Ilex aquifolium* decompose slower than those of *Fraxinus excelsior* or *Corylus avellana*, with *Q. petraea* leaves slowest to decompose (Cornelissen, 1996). The slow decomposition of *Q. petraea* leaves may also explain the difference in LOI between the oak and ash woodland soils. Van Oijen *et al.* (2005) found that the higher the proportion of *Q. petraea/robur* in the canopy, the greater the thickness of the litter and fermentation layer and the organic matter content of the mineral soil. The opposite was true for *F. exclesior* and *Populus x canadensis,* both species with base rich, nutrient rich, easily decomposed litter when compared to *Quercus.* The higher cover of bare soil in ash woodlands is an indication of the greater proportion of ash sites grazed by large herbivores, in combination with the greater proportion of poorly drained soils.

The clear difference in vegetation communities and soil pH found between oak and ash woodlands was not surprising given that they were selected to represent contrasting forest types, which occur on strongly acid and base-rich soils respectively. The difference in total nitrogen and phosphorous and carbon/nitrogen ratio between the oak and ash woodlands is also related to the different soils on which they occur; ash woodlands are generally found on limestone buried under glacial deposits which weathers to make fertile, base rich soils while oak woodlands occur over siliceous rocks which weather to poor, acid soils (Kelly, 2005). While there were clear differences in vegetation communities between oak and ash, there was also a great deal of variation in vegetation communities among the plots in each woodland type.

The *Luzula sylvatica* dominated community in Cluster A resembles the *Luzula sylvatica – Dryopteris dilatata* vegetation type of the *Quercus petraea – Luzula sylvatica* group of Perrin *et al.* (2008a), which is characterised by a dominance of *Q. petraea* canopy, the lack of an abundant understorey and a carpet of *L. sylvatica.* Grazing was absent in all of the plots in the group and *L. sylvatica* has been identified as an indicator of ungrazed woods (McEvoy, 2006). It is also resilient to damage, such as that caused by grazing or trampling, increasing its cover rapidly once the cause of the damage has been removed

(Godefroid *et al.*, 2003). It is likely that *L. sylvatica* cover has increased at these sites following the removal of grazing (Minihan and Rushton, 1984) and in the presence of an open canopy (Cross, 1981). Former grazing at the sites may also explain the low structural diversity, as heavy grazing pressure can affect stand structure by inhibiting regeneration of tree species through damage or removal of seedlings and saplings (Perrin *et al.*, 2008a). The dominance of *L. sylvatica* may currently be restricting regeneration at the sites (Cross, 1981; Minihan and Rushton, 1984).

The *Ilex aquifolium* dominated community in cluster C resembles the *Vaccinium myrtillus – Ilex aquifolium* vegetation type of the *Quercus petraea – Luzula sylvatica* group of Perrin *et al.* (2008a), which is characterised by abundant *I. aquifolium* in the understorey and large patches of *V. myrtillus* in the shrub layer. The abundance of *Hedera helix* at some sites in the present study does not fit the description however. *I. aquifolium* is known to cast dense shade which results in a poorly-developed field layer (Bradshaw, 1981; Cross, 1981). *I. aquifolium* is itself shade tolerant (Peterken and Lloyd, 1967) and can regenerate under a closed oak canopy (Perrin *et al.*, 2006a). Despite its spiny leaves, it is palatable to a number of species (Peterken and Lloyd, 1967; Pigott, 1983) and heavy grazing can prevent its regeneration (Perrin *et al.*, 2006a) or indefinitely check height growth (Peterken and Lloyd, 1967). Browsing by sheep and deer is believed to be the cause of its scarcity in many western oak woodlands in Britain (Mitchell and Kirby, 1990). Where grazing is excluded, dense Thickets can quickly form through regeneration and release of pre-established juveniles (Cross, 1981; Kelly, 2000; Perrin *et al.*, 2006a). Competition from species such as *Vaccinium myrtillus* and *L. sylvatica* may restrict its regeneration however (Perrin *et al.*, 2006a). *V. myrtillus* is also known to dominate under low or zero grazing conditions (Kirby *et al.*, 1994). The abundance of *I. aquifolium* and *V. myrtillus* in the plots in cluster C is probably the result of the low or zero grazing at these sites, with *I. aquifolium* dominant where *V. myrtillus* (and *L. sylvatica*) were not. Although grazing was recorded in more than 40% of the plots, the information recorded did not capture differences in grazing levels. The abundance of *Hedera helix* in some of the plots is also likely due grazing levels as it is usually only dominant where grazing is low or absent (Kelly and Kirby, 1982). *H. helix* can also reduce the ground vegetation through competition (Kelly and Kirby, 1982).

The *Rubus fruticosus* dominated community in cluster D resembles the *Rubus fruticosus – Corylus avellana* vegetation type of the *Quercus petraea – Luzula sylvatica* group of Perrin *et al.* (2008a), which is characterised by an abundance of *R. fruticosus*, a dense understorey and the presence of species characteristic of woodland on more base-rich soils. The plots in the current study lacked the dense understorey however. French *et al.* (2008) described a similar community in plantation forests which had a relatively open canopy in common and Harmer *et al.* (2005) found that an oak woodland thinned to 60-70 percent cover became quickly dominated by *Rubus,* which grows vigorously under partial shade. The results from the current study do not suggest a very open canopy, although the levels of diffuse light transmitted through broadleaved canopies can be substantial (Messier *et al.*, 1998). *R.* fruticosus dominated vegetation also tends to develop on more fertile sites (Hill, 1987; Perrin *et al.*, 2008a). The soil results in the present study do not suggest significantly higher fertility; however, total rather than available nitrogen and phosphorus was measured, and the availability of nutrients can be influenced by other factors such as soil water status and pH (Jeffrey, 2003). The lower C/N ratio in this than in the other clusters suggests that nutrients may be more available (Bardgett, 2005), however the difference in C/N ratio is not statistically significant. The presence of *R. fruticosus* is known to have a negative impact on species richness, causing a decline as it becomes dominant, but it is known to be reduced by grazing

(Kirby and Woodell, 1998). Its abundance in the plots in cluster D therefore suggests zero or low levels of grazing. Grazing was present in 50% of the plots but differences in grazing levels were not recorded.

The vegetation communities described above were characterised by the dominance of particular species, namely *Luzula sylvatica*, *Ilex aquifolium, Vaccinium myrtillus, Hedera helix* and *Rubus fruticosus*. Very low or zero levels of grazing are known to produce abundance of the aforementioned species, resulting in uniform conditions of tall growing vegetation (Kirby *et al.*, 1994; Hopkins and Kirby, 2007). This leads to an altered vegetation structure (Kirby *et al.*, 1994) and to conditions which may shade out bryophyte and field layer species (Bradshaw, 1981; Cross, 1981; Mitchell and Kirby, 1990; Kirby and Woodell, 1998).

The remaining oak cluster group (cluster B) had a vegetation type which was not dominated by any one species, resulting in a high diversity and structural diversity. The plots in cluster B had higher cover of *Betula pubescens* and lower cover of *Quercus petraea* and resembled the *Vaccinium myrtillus – Luzula sylvatica* vegetation type of the *Betula pubescens – Molinia caerulea* group rather than any vegetation type in the *Quercus petraea – Luzula sylvatica* group of Perrin *et al.* (2008a). The *Vaccinium myrtillus – Luzula sylvatica* vegetation type is found in birch dominated stands which have several elements of acidic oak forest (*Quercus petraea – Luzula sylvatica* group) and can be viewed as a seral stage in succession towards this forest type (Perrin *et al.*, 2008a). This suggests that the plots in the cluster represented younger areas of woodland formed through woodland expansion, following woodland clearance or in canopy gaps produced by tree falls or tree felling; other plots from the same sites had vegetation types which resembled those in the *Quercus petraea – Luzula sylvatica* group. As mentioned above, many of the oak woodlands studied were previously managed as coppice woodland (Perrin *et al.*, 2008a) and the shift from coppice to high forest will have reduced the proportion of stands with open space or young growth and reduced associated woodland species (Hopkins and Kirby, 2007). The formation of woodland gaps, whether by natural processes or management, will increase plant species richness, but this will decline as canopy cover increases (Hopkins and Kirby, 2007). In the absence of management such as coppicing and felling, these gaps will only be produced by natural events such as storms (Hopkins and Kirby, 2007). The role of grazing is difficult to assess as the proportion of plots grazed was similar to those in clusters B and D, however differences in grazing levels could have existed.

The ash woodland plots in cluster E resemble the *Geum urbanum - Veronica montana* vegetation type of the *Fraxinus excelsior – Hedera helix* group of Perrin *et al.* (2008a), which is a species rich group of moist soils, characterised by abundant *F. excelsior* in the canopy, frequent but not dominant *C. avellana* in the understorey and the presence of *H. helix* and *R. fruticosus* as major elements of the field layer (Perrin *et al.*, 2008a). *C. avellana* dominated in the plots in the current study and *R. fruticosus* and *H. helix* were not major elements of the field layer. The majority of the plots in this cluster, which was the most species rich cluster studied, had moist soils in common, with all but one occurring on gley soil. Hardtle *et al.* (2003) found a positive correlation between species richness and soil moisture in deciduous forests in Germany. They put this down to occurrence of moisture-loving or moisture-tolerant plants, the weakening of the competitiveness of less moisture tolerant species and the release of mineral nutrients with ground water. The evaporation of any persistent ground water and evapotranspiration, combined with the shelter of the surrounding forest, will also lead to high humidity conditions (McCarthy, 1980). These conditions may have permitted the occurrence of a range of bryophytes, which have a low tolerance to desiccation (Saetre *et al.*, 1997). All of the plots were also characterised by grazing, mainly by horses and cattle. This

may explain the absence of *R. fruticosus* and *H. helix* as major elements of the field layer as they are only abundant where grazing is low or absent (Kelly and Kirby, 1982; Kirby and Woodell, 1998).

Cluster F, which contains the *Hedera* dominated plots, also resembles the *Geum urbanum - Veronica montana* vegetation type of the *Fraxinus excelsior – Hedera helix* group of Perrin *et al.* (2008), although the plots had fewer field layer herbs and had better drained soils. They also resembled the *Acer pseudoplatanus – Crataegus monogyna* vegetation types from the same group, which is a group of well drained soils with both *F. excelsior* and *Acer pseudoplatanus* in the canopy, and a well developed understorey; the majority of plots in cluster F contained *A. pseudoplatanus*. These plots were characterised by more freely draining soils than cluster E and the almost complete absence of grazing. Where grazing is low or absent, regeneration of trees and shrubs can be prevented by competition from dense ground vegetation, there can be domination by a few vigorous plant species (as was seen in the oak plot clusters above) and lower plants can be reduced in cover and diversity due to competition (Mitchell and Kirby, 1990). Kelly and Kirby (1982) describe a species poor vegetation community in ash woodlands , which lacks the groups of species found in other ash woodlands and is dominated by *H. helix*. They propose a reduction in field layer and bryophyte diversity through competition as the cause.

The plots in cluster G – just three plots from a single site - also resemble the *Acer pseudoplatanus – Crataegus monogyna* vegetation type of the *Fraxinus excelsior – Hedera helix* group of Perrin *et al* (2008), as *A. pseudoplatanus* is frequent in the canopy, although the understorey is not well developed and *H. helix* does not dominate. These plots were also subject to grazing by cattle; likely the cause of the absence of *H. helix* dominance. It is also possible that grazing levels were higher than in cluster E and damage from trampling by grazing animals may have caused the low non-vascular species richness and browsing the low understorey cover (Mitchell and Kirby, 1990) but this cannot be verified. The significantly more acidic pH of the plots in this cluster matches the *typicum* sub-type of oak-ash-hazel woodland, described by Kelly & Kirby (1982) which is distinguished by species of leached soils. The fact that the three plots from the same site formed a single cluster indicates that this vegetation category was relatively uncommon. The relatively high values of total nitrogen and significantly higher-values for total phosphorus are surprising and may be related to grazing by cattle and deposition of dung (Dahlgren *et al.*, 1997). The fact that the C/N ratio is not significantly different to the other ash clusters suggests that these increased nutrient levels may not be available to the plants (Bardgett, 2005).

5.2.3.2 Relationship between structural and functional variables and diversity measures

The variable identified as being most strongly correlated with the majority of diversity measures in the oak woodlands was leaf litter cover, while this variable was not correlated with any diversity measures for ash. As discussed above, leaf litter cover was significantly higher in oak than ash woodlands. Fewer oak woodland plots were grazed and grazing is known to reduce the abundance of leaf litter (Bromham *et al.*, 1999). Sydes and Grime (1981) found a negative correlation between ground vegetation biomass and amount of leaf litter and noted differences among plant species in their pattern of occurrence at different leaf litter amounts. In a subsequent paper (Sydes and Grime, 1981) they concluded that it is the physical impact of leaf litter on the establishment and growth of plants that is the main determinant of the pattern, species composition and regeneration of woodland herbs. Litter can affect the germination of seeds by preventing them from reaching the soil and can hinder the emergence of seedlings, and therefore also the establishment of different species (Sydes and Grime, 1981; French, 2005). Where thick litter occurs under

a dense evergreen canopy, such as produced by *I. aquifolium* Thickets, the herb layer may be completely eliminated (Sydes and Grime, 1981). While litter may control the distribution of plant species, plants can in turn influence the pattern of litter accumulation (Sydes and Grime, 1981). Robust species such as *L. sylvatica*, *R. fruticosus* and *V. myrtillus* are known to reduce air movement close to the ground so that leaf litter is trapped among the vegetation or in any pockets formed (Cross, 1981; Sydes and Grime, 1981).

Another variable strongly correlated with all of the diversity measures in oak woodlands was the structural diversity of the vegetation; it was also correlated with species diversity in ash woodlands but not with any of the species richness measures. Structural diversity in the tree layers and the field and ground layers has been linked to species diversity (Murdoch *et al.*, 1972; Uuttera *et al.*, 1996). A low structural diversity is indicative of the dominance of particular structural layers (Magurran, 2004). In the plots studied, the dominance of these layers was often related to the dominance of single species, rather than a combination of a group of structurally similar species, i.e. *L. sylvatica* dominance equated to dominance of the field layer, *R. fruticosus, V. myrtillus* or *H. helix* dominance to dominance of the shrub layer, *C. avellana* dominance to dominance of the understorey layer and *Q. petraea* dominance to dominance of the canopy layer. This explains the strong correlation of structural diversity with species diversity (1/D) as the presence of these dominant species led to low values of this measure (Magurran, 2004). Its correlation with the species richness measures in oak but not ash is most likely due to the different effects of the dominance of the structural layers in each forest type. The dominance of the shrub and field layer species mentioned above, which was a common occurrence in oak woodland plots, led to the competitive exclusion of other species and therefore lower species richness, as discussed above. The dominance of *C. avellana* in some ash woodlands, on the other hand, while resulting in lower species diversity (1/D), was not to the detriment of overall plant species richness. Koorem and Moora (2010) found that *C. avellana* canopies supported more species and had higher Ellenberg indicator-values for light than evergreen canopies with the same levels of openness. This may be due to the fact that light intensity is higher in the shade (i.e. diffuse light only) of broadleaved than conifer canopies, most likely due to the even distribution of leaves in broadleaved canopies compared to the dense clumped nature of conifer crowns (Messier *et al.*, 1998; Kucharic *et al.*, 1999). *C. avellana* has thin light leaves which will transmit more radiation than darker thicker leaves such as *I. aquifolium* or conifer needles (Gates *et al.*, 1965).

Presence of grazing and poorly drained soils were also associated with higher-values of various diversity measures in oak and ash woodland, although the differences were more significant in ash woodlands. The relationship between soil moisture and species richness also found by Hardtle *et al* (2003) and their explanation of this relationship has been discussed above. The influence of grazing on species richness has also been discussed, with moderate levels of grazing capable of creating regeneration niches for trees and shrubs, reducing vigorous plant species, increasing plant diversity and increasing the cover of lower plants as competition is reduced (Mitchell and Kirby, 1990). The stronger correlation in ash woodland could be due to higher levels of grazing in these woods as, in order to have a positive influence on diversity, grazing must be above a certain level (Mitchell and Kirby, 1990). The positive correlation of bare soil with all of the species richness measures in ash woodlands may also be related to the association with the presence of grazing, as grazers will create bare ground (Kirby *et al.*, 1994).

Deadwood variables were also correlated with various diversity measures for oak and ash woodlands. Total volume of CWD was negatively correlated with both total and vascular species richness in oak woodlands and positively correlated with species diversity (1/D) in ash woodlands, while cover of FWD was positively correlated with species diversity (1/D) in oak woodlands but negatively correlated with total

and typical woodland species richness in ash woodlands. The negative correlations between the deadwood and diversity measures are counterintuitive, as the importance of deadwood for plant diversity, particularly lower plant diversity, is acknowledged (e.g. by Hodge and Peterken, 1998; Kruys and Jonsson, 1999; Odor and Standovar, 2001; Humphrey *et al.*, 2002c). It is possible that the higher levels of FWD in the plots were related to lower light levels as tree will successively shed lower branches due to low or decreasing light levels (Addicot, 1991). Low light levels in woodlands can decrease species richness, although this will depend on the light requirements of the species found there and may vary with forest type (Hardtle *et al.*, 2003). The fact that cover of FWD was not significantly correlated with non-vascular species richness may be due to the fact that bryophytes, which constituted the majority of non-vascular species, are favoured by low light intensities which decrease the risk of desiccation (Saetre *et al.*, 1997). The fact that canopy openness was not correlated with the species richness measures may be due to the differing light intensities in the shade (diffuse light) of different species, as different leaves will transmit different amounts of light (Gates *et al.*, 1965; Jacquemoud and Baret, 1990). This may mean that ash woodlands with *H. helix* or *I. aquifolium* in the understorey may have lower light levels for the same values of canopy openness than those with *C. avellana*, as darker thicker leaves transmit less light (Gates *et al.*, 1965).

The plots in the most species rich oak cluster (B) contained virtually no CWD. As mentioned above, these plots seemed to be in more recent areas of woodland which are not associated with the high levels of deadwood to be found in older successional stages (Kerr, 1999). It is important to note that CWD volumes in the woodlands studied were very low overall, especially compared with old-growth forests, being more similar to young growth and managed forests elsewhere in Europe (Sweeney *et al.*, 2010b). Green and Peterken (1997) found a relationship between levels of management and volumes of deadwood in forests with managed stands having no more than 30% of natural levels of deadwood, and generally much lower. Many deadwood specialist species need long continuity of suitable deadwood habitats as they are poor colonisers and are highly specific about the size, location and state of decay of deadwood (Kirby, 1992). The measure of CWD volume in the present study did not provide information about deadwood quality; previous research at the same sites found the majority (> 90%) of logs to be less than 20cm diameter and large logs to be scarce (Sweeney *et al.*, 2010b).

Soil chemistry was also found to be important for diversity with soil pH and total phosphorus negatively correlated with non-vascular species richness in oak woodlands and total nitrogen and LOI negatively correlated with species diversity (1/D) in ash woodlands. Saetre *et al.* (1997) also noticed a negative effect of pH on bryophytes in plantations. In that study, as in the study of Dzwonko and Gawronski (2002), high pH was associated with high levels of broadleaved litter; this is also the case in the present study. As well as its effect on bryophytes with low pH optima through increases in soil pH, leaf litter can have a direct negative physical effect on bryophytes (Saetre *et al.*, 1997). The negative correlation of non-vascular species richness with total phosphorus may be due to the increased competitiveness of vascular plants with increased phosphorous levels, which can be to the detriment of non-vascular species (Niinemets and Kull, 2005). The negative association between total nitrogen and LOI and species diversity (1/D) for ash may be related to the presence of *C. avellana* in the understorey. As discussed above, the dominance of *C. avellana* in the understorey of some sites resulted in lower species diversity (1/D) but did not affect species richness. Total nitrogen and organic matter content under a *Corylus* (presumably *C. heterophylla*) understorey were found to be higher than in areas without *Corylus* in China (Chen *et al.*, 2000). *Corylus*

litter is also known to have high nitrogen levels compared to other species (Bocock, 1964; Chen *et al.*, 2000).

5.2.4 Comparison of forest types

The plantations in this study supported a large number of species in total, however a large proportion of these were not typical woodland species. The greater number of species recorded in plantations than native woodlands in total was likely related to the differing sample sizes, as the increase in species richness with increased sampling area is well documented (e.g. Connor and McCoy, 2001). On average, the native woodlands supported a significantly higher number of total and typical woodland species. Previous studies comparing Irish native woodlands and conifer plantations have also found the native woodlands to be significantly more species rich (Magurran, 1988; Fahy and Gormally, 1998; Coroi *et al.*, 2004). Cluster and indicator species analysis have highlighted the fact that plantations and native woodlands can support similar species assemblages, but also can differ quite markedly. This also echoes the findings of previous studies in Britain and Ireland (Kirby, 1988; Wallace *et al.*, 1992; Ferris *et al.*, 2000a; Wallace, 2003; French, 2005).

Structurally, the striking difference between plantations and native woodlands was in their understorey cover, which was significantly lower in plantations, as was shrub cover. The lack of understorey and shrub cover in plantations is a result of shading due to canopy closure (Lindgren and Sullivan, 2001). The more Closed canopy stage in plantations is similar to the 'stem exclusion' phase in a natural forest as described by Oliver and Larson (1996). In natural forests, openings in the canopy can improve conditions for understorey regeneration in the 'understorey reinitiation' phase, while in the 'old growth' phase an all aged structure and irregular canopy are present. Plantations are often clearfelled in the stem exclusion stage (Kerr, 1999) and lack the vertical structure that has been found to be particularly important to birds (MacArthur and MacArthur, 1961).

Forest type has been identified as an important variable in explaining differences in both total and typical woodland species richness and the vegetation communities supported. While native ash woodlands were significantly more species rich and diverse than all other forest types and supported significantly more typical woodland species, oak woodlands did not differ significantly in their total species richness or in their vascular species richness from any of the plantation forest types, and only supported significantly more bryophytes and typical woodland species than some, but not all, of the plantation forest types. In Britain, Kirby (1988) found pine plantations and some conifer/broadleaved mixtures to support similar numbers of vascular plant species to native oak woodlands, while Humphrey *et al.* (2002a), found bryophyte species richness to be similar in native oak and Scots pine woodlands and Sitka spruce and Scots pine plantations in Britain. Ash plantations have been shown by this study to be able to support similar vegetation communities to native ash woodlands, although they support fewer total and typical woodland species. This similarity in vegetation communities had previously been noted by French *et al.* (2008) and appears to derive from a combination of edaphic and site history factors. None of the plantation types resembled the native oak woodland community, echoing the findings of French (2005) that, while Sitka spruce and larch plantations had many similar species to native oak woodland, they lacked the specialist woodland species of this woodland type. However, Kirby (1988) found that a variety of conifer and broadleaved plantations on ancient woodland sites in Britain could support similar vegetation communities to remnants of native oak woodland.

Canopy cover was identified as being important for total species richness, although less important for typical woodland species richness, and was not found to be important for vegetation community composition. For total species richness there was a high importance value for the interaction with forest type, with the relationship with canopy cover appearing negative in Sitka spruce and Norway spruce plantations, while there was no clear relationship in larch, broadleaved plantations or native woodlands. This may be due to the fact that light intensity in the shade (i.e. diffuse light only) of different species can vary, being higher in most broadleaved than conifer canopies, most likely due to the even distribution of leaves in broadleaved canopies compared to the dense clumped nature of conifer crowns (Messier *et al.*, 1998; Kucharic *et al.*, 1999). French *et al.* (2008) noted that many species are unable to survive the shaded conditions beneath closed conifer canopies, and those that do often have low cover. Typical woodland species have many adaptations for the different light levels present in forests (Hardtle *et al.*, 2003; Thomas and Packham, 2007) which may explain the lower importance values for canopy cover and its interaction with forest type for typical woodland species richness. The fact that canopy cover was not found to be important for vegetation community composition may be due to the fact it is not always directly related to understorey light levels; it reflects only the dominance of the site by trees and does not take into account lateral light penetration (French, 2005). The presence of the bramble-dominated community found in native woodlands and plantations may be related to light levels. French *et al*. (2008) noted that plantations with this vegetation type had a relatively open canopy and Harmer *et al.* (2005) found that an oak woodland thinned to 60-70 percent cover became quickly dominated by *Rubus fruticosus* agg.*,* which grows vigorously under partial shade.

A location on or adjacent to historic woodland was identified as an important variable in explaining differences in total and typical woodland species richness and the vegetation communities in the present study. This historic woodland may have acted as a source of propagules for woodland species, which often have very slow dispersal rates (Brunet and von Oheimb, 1998). Brunet and von Oheimb (1998) found that the number and cover of woodland species in recent woods decreased with increasing distance to ancient woods. The high number of typical woodland species supported by the conifer plantations with the T. *tamariscinum*-dominated vegetation community (cluster VI) is likely due to the fact that more than three-quarters of these sites were planted on or adjacent to historic woodland. This is also supported by the fact that the plantations in which two of the 'notable' woodland species of Perrin *et al*. (2008) occurred were on old and historic woodland. Those ash plantations planted on or adjacent to historic woodland developed vegetation communities similar to native ash woodland, while those that were not developed a bramble-dominated community. The ash plantations which developed native woodland communities were also all planted on low elevation sites on base rich soils, habitats typical of native ash woodlands in Ireland (Kelly and Kirby, 1982); elevation and soil pH were both identified as being important factors in separating this community from the rest.

Drainage was another factor identified as being important for both total and typical woodland species richness, with a mainly positive association. Hardtle *et al.* (2003) found a positive correlation between species richness and soil moisture in deciduous forests in Germany. They put this down to occurrence of moisture-loving or moisture-tolerant plants, the weakening of the competitiveness of less moisture tolerant species and the release of mineral nutrients with ground water. Poor drainage will also result in evaporation and evapotranspiration, which, combined with the shelter of the surrounding forest, could lead

to high humidity conditions (McCarthy, 1980). The resulting decreased risk of desiccation may have favoured bryophytes (Saetre *et al.*, 1997).

Grazing was found to have relatively high importance value for total species richness, but a lower importance for typical woodland species richness, although in both cases the association was positive. It was also important in explaining the differences in vegetation community composition. Grazing is a natural feature of woodland ecosystems (Perrin *et al.*, 2008a), but both too high and too low levels can be detrimental to plant diversity (Mitchell and Kirby, 1990). The information collected on grazing at the sites in the current study did not distinguish differences in grazing pressure. The presence of the bramble-dominated community may be related to the presence of low or zero grazing at the sites, as *R. fruticosus* agg. is known to be reduced by grazing (Kirby and Woodell, 1998). Absence of its dominance in other sites may be related to higher grazing levels, in conjunction with light levels. The presence of *R. fruticosus* agg. is known to have a negative impact on species richness, causing a decline as it becomes dominant (Kirby and Woodell, 1998), and few species can survive under dense and extensive *R. fruticosus* agg. layers (French, 2005).

Volume of CWD was found to have low importance in explaining both total and typical woodland species richness and was not found to explain differences in vegetation community composition. This is surprising given that the importance of deadwood for plant diversity, particularly bryophyte diversity, is acknowledged (e.g. Hodge and Peterken, 1998; Kruys and Jonsson, 1999; Odor and Standovar, 2001; Humphrey *et al.*, 2002c). Deadwood volumes were low overall in the sites in the current study and did not differ significantly between native woodlands and plantations. However, the measure of deadwood volume did not take into account the size, type or state of decay of the deadwood, which have been found to be important (Humphrey *et al.*, 2002a). Previous research at some of the same sites as the current study found the majority (> 90%) of logs to be less than 20cm diameter and large logs to be scarce (Sweeney *et al.*, 2010b). With saproxylic organisms being described as being among the most threatened organisms in Europe because of their dependence on deadwood (Ódor *et al.*, 2006) it is important that high quality deadwood is available.

5.3 Ground-dwelling invertebrates and lepidoptera

5.3.1 Afforestation and reforestation survey

5.3.1.1 Spider and beetle diversity across the forest cycle of second rotation plantations

In second rotation plantations, the spider and beetle fauna were influenced by stand structural development, with increasing canopy cover and subsequent changes in vegetation and litter layers affecting species composition and richness. Both taxa are influenced by changes in habitat structure, which can provide hiding places for active hunters, protection from predators, greater prey availability and a more stable microclimate (Thiele, 1977; Uetz, 1991). Such change across the forest cycle is well-documented for these taxa in temperate forests of planted and natural origin (Oxbrough *et al.*, 2005; Buddle *et al.*, 2006; Mullen *et al.*, 2008; Ziesche and Roth, 2008). In this study, the relationship between beetles and forest development was less clear than that for spiders, and may be confounded by geographical location. Jukes (Jukes *et al.*, 2001) found that latitude was an important determinant of assemblage structure in conifer plantations across Britain. In Ireland a longitudinal gradient of wetter and warmer weather in the west to dryer conditions in the east (Met Éireann, 2010b) influences plant species distribution (Poole *et al.*, 2003) and may also be important for Carabid beetles.

For both taxa, the Pre-thicket stands supported the highest number of open habitat species and the lowest number of forest species. This is to be expected at the early stages of the forest cycle where small trees (< 3m) have little impact on the surrounding vegetation. The majority of spider indicator species identified in these stands were associated with open habitats, suggesting a predominately open fauna is supported at the Pre-thicket stage. Total richness of beetles and open species of spiders (richness and abundance) were positively related to lower vegetation layer cover, suggesting this as a potential indicator of species richness for ground-dwelling invertebrates in young second rotation forests as well as those of first rotation (Oxbrough *et al.*, 2005). In contrast to spiders, beetles exhibited relatively low species richness in the Pre-thicket stands. Previous studies of Carabid beetles in plantation forests have shown contrasting results with some reporting highest species richness in the early stages (Mullen *et al.*, 2008; Taboada *et al.*, 2008), some during later stages (Jukes *et al.*, 2001) and some reporting relatively little change across the forest cycle (Day and Carthy, 1988). In the present study only one beetle species was identified as an indicator in the Pre-thicket stands suggesting that they support a generalist fauna that is common across the whole forest cycle. Consequently, this lack of open specialists may contribute to the lower species richness observed at this stage of the forest cycle. Underlying differences in soil conditions influence beetle fauna (Cole *et al.*, 2005), and may reflect major habitat differences such as plant species composition, soil pH and moisture. In this study, since four of the five Pre-thicket stands were on moderate-poorly drained peaty soils with low pH, it is possible that such soils support fewer beetle species than other open habitats.

At the Thicket stage, around the time of canopy closure, richness and relative abundance of spiders associated with forest habitats increased and the assemblages formed an intermediate group between those in the Pre-thicket and the more structurally developed stands. Spider assemblages were directly influenced by tree development: total richness and open species were negatively associated with canopy cover, canopy height and mean DBH whereas forest species were positively related to litter depth. This suggests that the Thicket stage represents a transition from open to Closed canopy habitat which can support both open and forest-associated species (Oxbrough *et al.*, 2005). The beetle assemblages were

characterised by low species richness and little variation between the stands which were dominated by the forest-associated species *A. parallelepipedus* (80% of the captures). However, the lack of indicator species identified at this stage suggests a generalist beetle fauna. Forest beetle species richness was negatively related to upper vegetation layer cover and shrub cover. High cover of these layers may occur in areas with less tree development (as these layers have yet so be shaded out), and provides further evidence for the importance of small scale differences in canopy closure on invertebrate diversity at the Thicket stage.

In the later stages of the forest cycle, spider species richness declined suggesting that fewer species are adapted to the conditions following canopy closure. This is likely related to a corresponding reduction in vegetation complexity, which is important for spider diversity, over the forest cycle (Ferris *et al.*, 2000a). Furthermore, the species composition of stands separated by 100km was relatively similar suggesting that Closed canopy conditions are more important in determining spider assemblages than local factors. By contrast, beetle species richness was greater in stands with a more developed canopy and the assemblages exhibited relatively similar levels of variation at all stages of the forest cycle. Such trends have previously been observed in plantations (Jukes *et al.*, 2001; Mullen *et al.*, 2008; Yu *et al.*, 2008). The presence of relatively high numbers of beetle indicator species in more mature stands suggests a more specialised fauna at the later stages of the forest cycle. Spiders colonise new areas by ground movement and aerially through ballooning, whereas Carabid beetles rely flight or movement along the ground. Consequently, after clear-felling, it may take longer for beetle species associated with undisturbed or forested habitats to colonise, leading to a gradual increase in beetle richness over the forest cycle.

As the canopy developed the numbers of forest-associated species in both taxa increased, along with factors related to structural development (e.g. canopy cover, mean DBH). Following canopy closure, forest species from both taxa are likely to benefit from the structural diversity provided by increased cover of ground layer vegetation and litter layers (Oxbrough *et al.*, 2005; Buddle *et al.*, 2006; Mullen *et al.*, 2008; Taboada *et al.*, 2008). Indeed, in this study beetle species associated with forested habitats were related to cover of the needle litter layer and ground layer vegetation. Oxbrough *et al.* (2005) found that forest-associated spiders were positively related to ground-vegetation in first rotations stands. Although no such relationship was found in this study, ground layer vegetation cover was significantly lower in the second rotation stands, suggesting that cover was not high enough to have a positive influence on the forest spiders present.

Litter depth was negatively associated with overall spider abundance in the Reopening and gommercially mature groups, despite previous reports to the contrary (Uetz, 1979; Wagner *et al.*, 2003). These litter layers were comprised of needles rather than leaves, but as the dominant forest cover in Ireland was historically deciduous broadleaved trees (Mitchell, 1995), these forest spiders may not be adapted to exploiting such litter layers. Overall, there were relatively few significant relationships between spiders associated with forested habitats and the environmental parameters, suggesting that other factors may influence the assemblages. These include small scale parameters such as humidity and temperature (Ziesche and Roth, 2008), as well as those acting at the larger scales such as the shape and distribution of forest cover in the landscape (Barbaro *et al.*, 2005).

5.3.1.2 Does spider diversity differ between rotations of plantation forests?

Spider assemblages were distinguished by rotation as well as structural development, the most distinct being those of first rotation Pre-thicket. By contrast, second rotation Pre-thicket plots were not as clearly distinguished from the more developed stands. First and second rotation Pre-thicket stands supported similar numbers of open associated species, however first rotation stands had twice as many unique species as second rotation. In first rotations, rare or specialist species typical of pre-planting habitats can persist in the early stages of the forest cycle (Oxbrough *et al.*, 2006b), though these species will not remain once the canopy closes (Oxbrough *et al.*, 2005). Therefore, open species sampled in the early stages of second rotation are likely to have colonised from surrounding areas rather than be retained from the pre-afforestation habitat. Open habitat spiders can colonise stands relatively quickly after clearfelling (Buddle *et al.*, 2000; Matveinen-Huju *et al.*, 2009). In this study indicator species associated with second rotation Pre-thicket stands included several species ubiquitous in open habitats, including the active hunting spiders P*. pullata* and P*. amentata* which are known to disperse by ballooning (Richter, 1970). This suggests that, whilst second rotation Pre-thicket stands can support open species, they are more likely to comprise a generalist open fauna, which can exploit newly disturbed open land.

Between rotations the younger stands differed in vegetation and edaphic characteristics. Soil pH was lower in second rotation Pre-thicket and Thicket stands even though both rotations were on similar peaty soils. Over the forest cycle, soils typically grow more acidic (Salmon *et al.*, 2008), and so the early stages of second rotation plantations are likely to reflect those of mature forest from the previous rotation. Second rotation stands may also have had drier soils due to a reduction in soil moisture during the first rotation caused by the canopy and root system (Babel, 1977) but also drainage measures (Forest Service, 2003). Additionally, remnant plant species associated with Commercially mature stands, present at the end of the first rotation, may be retained for several years after clear felling (Cooper *et al.*, 2008). In this study, the early stages of second rotation had a higher ground layer vegetation cover, predominately comprised of mosses, and the Thicket stands had a lower cover of lower vegetation layer. This combination of factors is likely to be important for spiders, particularly for their influence on vegetation complexity.

A greater number of forest-associated species were sampled in second rotation Pre-thicket stands than those of first rotation. Such species may be remnants from the previous rotation. For instance, *Tapinocyba pallens* is typically recorded in mature forests (McFerran, 1997b) and was sampled in second rotation Pre-thicket stands, but not those of first rotation, whereas species shared between rotations included *Lepthyphantes zimmermanni* and *Monocephalus fuscipes*, both of which are commonly found in hedgerows as well as forested habitats, and may have been present prior to afforestation (Oxbrough *et al.*, 2006b). Despite this, the actual difference in forest-associated species richness between rotations was low (1-2 species). The persistence of forest-associated species or their ability to re-colonise after felling, may be influenced by availability of suitable refugia including the amount of forest in the surrounding area and retained forest patches within felled stands (Schowalter, 1995; Siira-Pietikäinen and Haimi, 2009). Current forest biodiversity guidelines recommend the retention of over-mature trees during felling, but make no explicit mention of how they should be selected, in terms of patch size or shape (Forest Service, 2000a). Moreover, although the guidelines recommend a mosaic of various aged stands in larger plantations, further forest planning measures may be required to ensure that clearfelled blocks are located close to mature stands for the purposes of retaining forest species.

In the Thicket stage, forest-associated beetles were negatively related to the cover of brash, which was a notable feature in the early stages of second rotation forests. Previous research has indicated that deadwood can positively influence invertebrate diversity. Castro (2009) has shown that fine woody debris can influence spider species composition, and suggest that its influence on the spider fauna may be more notable in younger forests, whereas Jonsell (2007) found that felling residues of just 1-4cm diameter can support red listed saproxylic beetles species. However, it is possible that the structure of brash piles, which are usually much larger in extent than is typical in natural woodlands, cannot be utilised by forest species. Current forest biodiversity guidelines recommend leaving deadwood in the form of standing or downed logs to benefit saproxylic species (Forest Service, 2000a), but make no mention of the management of brash piles from a biodiversity perspective. Since brash is likely to become a feature of future plantations, further research is required to examine their potential to support biodiversity, particularly with regard to their composition and configuration within a stand.

Spider assemblages between rotations were most similar in the later stages of the forest cycle, emphasizing the importance of canopy cover in shaping the fauna. However, overall species richness was significantly greater in first rotation stands at all stages, with the exception of Pre-thicket. Greater vegetation structure may explain the difference in species richness, as first rotation stands had a greater cover of lower vegetation layer whereas, in second rotation stands, ground layer vegetation cover was greater. In the more Commercially mature stands, these differences may be explained by the much lower canopy cover in first rotation stands, which is probably due to higher thinning levels or a longer time since thinning that has allowed lower vegetation layers to develop. It is also possible that conditions in second rotation plantations are better for tree growth i.e. more suitable soil conditions, leading to larger tree canopies and less potential for the development of structurally diverse vegetation layers.

Ideally, successive rotations would support a greater number of forest species than first rotation; however, as discussed previously, few forest species are retained during the open stages of second rotation forests. A similar trend has also been observed for plants (Cooper *et al.*, 2008). Furthermore, similar numbers of forest species were supported in Commercially mature first and second rotation forests. It is clear that, once a stand is felled, the accumulated forest-associated spider fauna is lost. Although forest policy supports leaving over-mature trees to provide a refuge for such species, it is currently unclear the extent to which consideration is being given to over-mature trees when felling operations are planned. Despite the fact that such considerations may be difficult in regions where plantations are relatively small and productivity may be adversely affected, providing potential refuges for forest species is important to ensure they are retained into the next rotation.

5.3.2 Mixed tree species survey

5.3.2.1 Ground-dwelling invertebrate diversity in mixed and pure plantations

The addition of broadleaves to a conifer stand is likely to create a more open canopy affecting the ground and lower vegetation layers, but also modifying the litter. These factors will influence the availability of potential prey, food availability for phytophagous beetle species, habitat structure and micro-climate conditions, influencing ground-dwelling beetles and spiders (Thiele, 1977; Bultman and Uetz, 1984; Uetz, 1991; Guillemain *et al.*, 1997). Indeed, previous research indicates that spiders respond to variation in litter type within mixed conifer and deciduous stands, which is probably related to small-scale differences in the overhead canopy species (Ziesche and Roth, 2008), whereas differences in Carabid beetle

reproductive success in mixed and pure stands have been linked to variation in micro-climate conditions between forest types (Ziesche and Roth, 2007). Such factors are also important in driving differences in the invertebrate fauna of conifer or deciduous pure plantations in Ireland (Oxbrough *et al.*, 2005). There is evidence for similar patterns in other invertebrate functional groups, for instance higher soil decomposer biomass and abundance has been found in mixes with greater amounts of deciduous trees (Elmer *et al.*, 2004; Laganière *et al.*, 2008) and different collembolan assemblages between mixed and pure stands (Salamon *et al.*, 2008). Furthermore, the addition of deciduous trees to conifer stands may contribute to an increase in soil pH, which benefits soil-dwelling invertebrates (Ammer *et al.*, 2006) and possibly also some plant species. This may be particularly important in Ireland where successive rotations of conifer species can reduce soil pH (Oxbrough *et al.*, 2010).

In the present study, the mixed and pure stands did not show any strong differences in assemblage composition and species richness for either of the taxa. In addition, stand structure, litter and vegetation cover were similar between mixed and pure stands. In the oak mixes this may be due to the smaller size oak trees in comparison with the Norway spruce in the mix stand. This is probably caused by their slower growth rate and lack of competitive fitness, effectively rendering the oak sub-dominant in the canopy. Furthermore, it is possible that the proportion of oak trees in the mix (20-40%) is not high enough to influence the litter, soil and vegetation conditions on the ground. Work *et al.*, (2004) have shown that mixes in which the proportion and size of conifer and deciduous trees are approximately equal, support ground-dwelling invertebrate assemblages more similar to pure coniferous stands than deciduous ones, suggesting that deciduous proportions need to be higher than 50% to support invertebrate species associated with a deciduous forest. In contrast, Pearce (2004) found mixed forests were more similar to deciduous dominated stands, though in this case it is unclear what proportion of the canopy was deciduous. It is likely that the proportion of deciduous trees as well as their distribution within a stand will influence invertebrate assemblages (Laganière *et al.*, 2008; Ziesche and Roth, 2008).

Scots pine trees generally have a more open canopy than other spruce and pine species and therefore support greater plant and invertebrate diversity (Docherty and Leather, 1997; Nilsson *et al.*, 2008). Additionally, the needle litter structure itself is different from spruce forests (individual needles being much longer), and litter cover tends to be much lower than in stands of other conifer species (Docherty and Leather, 1997; Nilsson *et al.*, 2008). Despite this, the Scots pine mixes in this study did not support a different invertebrate fauna from the matching pure stands. Again, this may be attributed to the proportion of the Scots pine in the mix being too low to influence the ground-dwelling invertebrate fauna, although the Scots pine trees were of a similar size to the spruce in the mixes. Additionally, the stands sampled were spread across the island of Ireland and represented a range of situations in terms of soil and elevation. Moreover, management history in terms of thinning frequency differed widely between matching mix and pure stands, which as a measure of canopy openness, is known to influence invertebrates in Irish plantation forests (Oxbrough *et al.*, 2005). Thus, consistent differences in litter and vegetation cover, and any resulting influence on ground-dwelling invertebrates due to the addition of 20-40% Scots pine or oak in a mix may be difficult to detect, being confounded by environmental variation between geographically paired stands.

Despite the lack of an overall strong differentiation between the mixed and pure stand types there is evidence for some subtle differences in assemblages between the site types: the NMS ordinations show a relatively consistent pattern, with plots from mixes having lower axis scores than their geographically

matched pures. For both taxa, these axes were positively correlated with needle litter cover, and for beetles negatively related to ground layer vegetation cover and plant species richness - factors which might be expected to differ between mixed and pure plantations. Indeed, although habitat variables were generally similar between mixed and pure stands, one variable, leaf litter cover was significantly higher in the oak mix stands in comparison with the pure stands. Furthermore, the difference in assemblage composition between oak mixes and pures was approaching significance (P = 0.06). This provides further evidence for a weak effect of the addition of oak to a conifer stand, at least for spiders. Spiders and Carabid beetles are both influenced by differing litter conditions (Bultman and Uetz, 1984; Koivula *et al*., 1999) through its influence on prey availability and microclimate. Nevertheless, it should be noted that, as many litter-dwelling spiders are also web spinners rather than active hunters, differences in litter structure may have a greater influence on their species composition. In the Scots pine mixes, litter cover was lower than in the pures whereas ground vegetation cover was higher. Although these did not differ significantly, this may indicate some presence of the ground conditions more typical under this canopy species (Docherty and Leather, 1997; Nilsson *et al*., 2008).

The indicator species identified also provide evidence for a weak effect of the mix: the Carabid beetle P*. melanarius* was associated with oak mixes which, although a generalist species, has a preference for moister habitats. Drier soil conditions may exist in conifer stands caused by the different root systems and by the canopy, which is intact all year. These may prevent more rain coming into contact with the ground layer than in stands which include deciduous trees. Furthermore, plantations are subject to drainage measures, including ditches established every 8m on sites with wetter soils (Forest Service, 2003). The forest-associated spiders *L. flavipes* and *L. tenebricola* were associated with pure stands. Both species have been previously identified as indicators of Commercially mature Sitka spruce plantations in Ireland (Oxbrough *et al*., 2010) and have a preference for Closed canopy forests (Nolan, 2010), perhaps indicating slightly less open conditions in pure stands.

5.3.2.2 Moth diversity in mixed and pure plantations

Availability of larval food plants is an important determinant of moth species occurrence within a habitat, particularly for species which can utilize only one or two plant species (Lepŝ *et al*., 1998). In forested habitats, moths can be associated with a particular host tree species or the understorey and lower vegetation layers associated with those stand types (Emmet and Heath, 1991). This is supported by previous research showing that moth richness is positively related to tree species diversity (Summerville *et al*., 2004). This suggests that, with the adequate presence of host larval plant species, mixed stands would be able to support a moth fauna typical of both forest types. However, in agreement with the findings for ground-dwelling invertebrates, there was no strong indication of a difference in species composition between the mixed and pure stands in this study. As discussed previously, the secondary mix trees (oak and Scots pine) may not have been present in high enough proportions to facilitate the development of a ground vegetation community typical of oak or Scots pine pure plantations, and hence provide the larval food plants with which specialist moth assemblages are associated. In addition, moth species which are dependent on woody plants are related to patch size of suitable forest area (Summerville *et al*., 2004), which may suggest that the proportion of suitable host plants (i.e. moths specifically associated with oak or Scots pine trees) was too low among our study sites. Although 15 species were collected in this study whose larvae feed on oak, all of these species also feed on a range of other broadleaved trees and vascular plant species and showed no particular preference for the oak mix

forest type. Similarly, four of the nine conifer associated species feed on Scots pine, but also a range of other conifers, and again showed no preference for forest type.

The lack of preference for a particular forest type might also be a reflection of the trapping radius of light traps, which is dependent on the particular moth species and probably surrounding vegetation structure, and can vary between 3m and 135m (Stewart *et al.*, 1969; Baker and Sadovy, 1978; McGeachie, 1988). Thus highly mobile species sampled within smaller forest stands may have been attracted from the surrounding habitat matrix, comprised of various tree species in plantation forest as well as agricultural land interspersed with hedgerows and scrubland. Nevertheless, light traps have been used in numerous studies to show differences in moth diversity between habitat types (Lepŝ *et al.*, 1998; Fiedler and Schulze, 2004; Spalding and Parsons, 2004; Summerville *et al.*, 2004), but perhaps this is more evident when such patterns are clearly delineated.

Although there was no difference in the moth assemblages between mixed and pure stands they displayed a clear separation between Scots pine mixes and their geographically matched pure stands from the oak mixes and their matching pures. This is probably not due to fundamental differences in planting areas between oak and Scots pine mixes, since they were generally established on a similar range of soil types, elevations and management histories. However, there may be some influence of stand and vegetation structure on the moth fauna, through provision of larval host plant or differing micro-climate conditions, as the Scots pine mixes and their matching pures had higher mean canopy openness and cover of lower vegetation than oak mixes and their matching stands. In addition, this group may also be a reflection of the greater conifer species diversity in Scots pine mixes, as Barred red, a species with a larval food preference for conifers, was identified as an indicator. Although there is some evidence that Scots pine may have survived in small remnant patches in Ireland (Roche *et al.*, 2009), it was not widespread. Thus the importance of moths specifically associated with conifers remains questionable in Ireland, particularly when the goal of biodiversity enhancement is to support native species, and the majority of native trees are predominately broadleaved.

5.3.3 Native woodlands survey

5.3.3.1 Ground-dwelling invertebrate diversity in oak and ash native woodlands

Woodland type is an important driver of invertebrate diversity, influencing lower vegetation and litter layers, but also reflecting fundamental differences in environmental conditions between canopy species, such as oak woodlands being on more acidic soils and ash woodlands often at lower elevations. In addition, larger scale factors such as geographical location also have an influence on invertebrate assemblages. For ground-dwelling invertebrates, structural diversity plays a key role in shaping assemblages through the provision of prey, to hiding places for active hunters, web attachment points for spiders, protection from predators and more favourable micro-climate conditions (Thiele, 1977; Uetz, 1991; Guillemain *et al.*, 1997).

In this study, oak and ash woodlands differed in structure, with greater tree DBH (and probably larger canopy extent) in oak woodlands and higher stem densities in ash. This probably results in more 'open' conditions under the canopy of oak, despite similar canopy cover between woodland types. In turn, this influences plant composition, with greater coverage of the lower vegetation layer in areas that are more open under the canopy. This was particularly noticeable for the oak woodlands sampled in 2008. The ash

woodlands had greater cover of ground layer vegetation, which is more typical of habitats with low levels of light penetration due to high stem density and understorey cover, as well as the canopy. Such differences in cover and richness of the ground and lower vegetation layers are related to spider and Carabid beetle diversity in native woodlands and plantations (Molnár *et al.*, 2001; Oxbrough *et al.*, 2005; Ziesche and Roth, 2008; Oxbrough *et al.*, 2010).

Litter layers also make an important contribution to structural complexity on the forest floor influencing prey availability and microclimate to the benefit of ground-dwelling invertebrates (Uetz, 1979; Bultman and Uetz, 1982; Bultman and Uetz, 1984; Loreau, 1987). Both coverage and depth of litter differed between the woodland types, being higher in the oak woodlands. In addition, there was a general trend for a greater number of spider species and forest-associated species to be captured in oak woodlands and more indicator species were identified (9 in oak woodlands, 4 in ash). This suggests that spiders in Irish woodlands have a greater affinity for this woodland type, perhaps being able to better exploit the micro-habitat conditions created by deeper, or more extensive, litter layers. The majority of spider indicator species were from the Linyphiidae family. These small spiders typically build sheet webs on the underside of leaves and other detritus (Harvey *et al*., 2002).

In contrast, beetle richness and that of forest associates was generally higher in the ash woodlands and correspondingly more indicator species were identified for this forest type (9 in ash woodlands, 4 in oak). Previous research has found conflicting results on the influence of litter cover and depth on Carabid beetle diversity: negative relationships have been attributed to the response of habitat generalists which are unable to exploit these layers (Molnár *et al*., 2001) or lower trapping efficiency caused by deep litter restricting beetle movement (Sroka and Finch, 2006); positive relationships have been attributed to a greater incidence of micro-habitats (Magura *et al.*, 2003) and prey availability (Poole *et al*., 2003). In this study it is possible that a difference in habitat generalists, which are not adapted to utilising deeper litter layers, contributed to the apparent greater affinity of beetles for ash woodlands.

The woodland types differed markedly in their soil pH, with oak woodlands typically on more acidic soils. This may indirectly affect ground-dwelling invertebrate diversity through its influence on plant species composition and the likely resulting differences in structural complexity. Additionally, soil pH may influence potential prey living in the litter and soil, such as collembola (Salamon *et al*., 2008), woodlice and millipedes (Topp *et al*., 2006). Several studies in forested habitats have shown a positive relationship between soil pH and Carabid species richness (Magura *et al.*, 2003; Oxbrough *et al.*, 2010) which might suggest that fewer Carabid species are adapted to living in acidic conditions. This may also contribute to the lower number of species sampled in oak woodlands in this study.

Geographic location of the stands played a role in shaping the invertebrate assemblages, with both taxa influenced by an east-west gradient, and, to a lesser extent for beetles, a north-south gradient. A similar effect of latitude on beetle assemblages has been found across the Britain in conifer plantations (Jukes *et al.*, 2001), whereas Oxbrough (2010) found differences with longitude for Carabid beetles in plantation forests, but no such pattern for spiders. Across Ireland, differing climatic conditions occur with the western Atlantic coast usually much wetter than the east: circa 1600 mm of rain /yr compared to 800mm (Met Éireann, 2010b). The more northerly areas are also generally colder, though this difference is less striking than for rainfall. This influences plant community composition (Poole *et al*., 2003) and probably also influences invertebrate species composition, though this is likely confounded by differences in geology,

drainage and mountainous cover across the island (Anderson, 2006). Nevertheless, the island of Ireland supports invertebrate species adapted to both temperate or boreal regions (Anderson *et al.*, 2000; Harvey *et al.*, 2002; Anderson, 2006), although the latter may be at the edge of their range.

The overall proportion of forest-associated spiders species sampled in this study (21%) was relatively low compared to other studies in European semi-/ natural broadleaved woodlands. For instance, Gurdebeke (2003) found that 47% of spiders were forest-associated in Belgian woodlands. Although this may be a reflection of different classification schemes used for determining forest habitat association, it is also likely that historical forest cover in Ireland has an influence, which was reduced to < 1% in the early 1900s (Neeson, 1991). Such low forest cover means that species which have survived are probably forest generalists rather than specialists, able to take advantage of woody features in the dominant agricultural landscape which provide refuge, such as hedgerows (Oxbrough *et al.*, 2007). These species are can probably tolerate fairly open forest conditions typical of small forest patches with greater edge effects (Gaublomme *et al.*, 2008).

In contrast, beetles associated with forests represented 24% of the species sampled in this study. This is relatively comparable to studies in German oak-beech woodlands of around 23% to 34% (Günther and Assmann, 2004; Sroka and Finch, 2006), though at the lower end of this range. However although similar numbers of species are supported, further research is needed to examine which species are present, and whether they are true 'forest interior' species.

5.3.3.2 Potential indicators of ground-dwelling invertebrate diversity and management recommendations

For ground-dwelling spiders and Carabid beetles, woodland type is a primary indicator of invertebrate diversity and the different assemblages supported, particularly forest-associated species, suggest that the conservation of both ash and oak woodlands will be beneficial. This is especially pertinent at larger scales, where the protection and/or rehabilitation of a range of woodland types will enhance overall landscape biodiversity. Other invertebrate groups are also likely to benefit from such an approach, including parasitoid wasps (Fraser *et al.*, 2007), woodlice and millipedes (Topp *et al.*, 2006).

Within the woodlands, richness of spider species was related to cover of vegetation layers, but this relationship differed by forest type: total richness was positively related to cover of ground layer and lower vegetation cover in oak woodland but negatively related to these layers in ash. A similar trend was seen between forest asscoiated spiders and lower vegetation layer cover. This contrasting pattern may be related to finer scale differences in vertical structure within the vegetation layer measured. For instance, the native woodlands differ in plant species composition: oak woodlands were characterised by high cover of wood rush (*Luzula sylvatica*), bilberry (*Vaccinium myrtillus*) and bramble (*Rubus fruticosus* agg.), whereas ash had higher cover of ivy (*Hedera helix*) and ferns, but also mosses (e.g. *Thuidium tamariscinum*). This might suggest that ground and lower vegetation layer plant species present in ash woodlands are not able to support as great a range of spider species as oak woodlands, perhaps through small scale differences in vertical structure, or its influence on available prey or micro-climate. Indeed, Oxbrough *et al.* (Oxbrough *et al.*, 2005) have suggested that lower spider richness in ash plantations in comparison with Sitka spruce plantations may be related to such vertical differences in vegetation structure where, although cover of the lower vegetation layer was similar, plant species composition

differed, with ash plantations having a high cover of ivy. However, further investigation in to the influence of small scale differences in vegetation structure will be needed to examine this fully.

Slope was negatively related to richness for both taxa. It is possible that slope may be a proxy for drainage, where steeper slopes indicate better drained and drier soils and, in Ireland, fewer species may be adapted to living in such conditions. However, further research will be needed to determine if such habitats support unique species (perhaps with specialists of drier forests etc.) and hence may need consideration in conservation plans, or whether such forests only support habitat generalists, in which case they should be given less priority. The finding that species from both taxa responded to within-site differences in vegetation cover and structure highlights the need to conserve forests with a variety of structural diversity within a particular woodland type, especially as overall species richness does not correspond with that of forest-associated species. Variation in habitat structure is also important for other species in Irish woodland such as birds (Sweeney *et al.*, 2010a). Information held in national inventories, such as the National Survey of Native Woodlands in Ireland (Perrin *et al.*, 2008a), could shed light on the structural variation of woodland types within particular landscape settings, so that a full range of woodland habitats are included in conservation management.

Deadwood is an important component of forest ecosystems, providing substrate for saproxylic species which are integral to nutrient cycling. Research also suggests that by adding structural complexity to forested habitats deadwood can be of benefit to spiders (Varady-Szabo and Buddle, 2006). In this study no relationship was found between deadwood cover and invertebrate richness, however Irish woodlands generally have lower amounts of large logs and snags in comparison with forests in other European countries (Sweeney *et al.*, 2010b). Thus, Irish woodlands may not support a large enough range of deadwood to provide structural features in the habitat which are beneficial to spiders.

At a larger scale, the amount of forest area within 200m or 1km of sites was not related to total number of species or forest species in either taxon. For beetles, previous research has shown a negative relationship between total richness and forest area, which is probably related to a lack of open species in larger woodlands (Sroka and Finch, 2006), whereas forest species are positively related (Magura *et al.*, 2001). This suggests that even small woodland patches (10-20ha) have conservation value, and can support equivalent numbers of forest-associated species. Spiders and Carabid beetles are generalist predators by nature and they can exploit a range of prey types in contrast with taxa which are more specific in their dietary requirements. In addition, they have relatively good dispersal abilities, with spiders ballooning and beetles flying, as well as locomotion on the ground enabling them to move between patches more easily than some other invertebrate taxa. This may suggest a lack of forest specialists in Ireland, with forest-associated species being able to withstand greater habitat fragmentation than more specialised invertebrate groups, such as saproxylic beetles, where woodland area is important (Franc *et al.*, 2007). It is logical to target larger woodland areas for conservation; however, smaller patches should not be overlooked by management plans, particularly as they may be important refuges for forest-associated species in intensively managed agricultural landscapes.

5.3.4 Comparison of forest types

Invertebrate species composition was influenced by forest type with distinct assemblages supported between plantations and native woodlands, although for Carabid beetles other factors such as

geographical location were also important. The plantations supported similar numbers of species as native woodlands, but for spiders and moths in particular, a different suite of forest-associated species were captured. This suggests that the planting of non-native conifers is fundamentally altering species composition in Irish forests by enhancing the abundance of forest species that would normally be found in low numbers in natural forests. These forest species are probably able to exploit the unique conditions in conifer plantations, including deep needle litter layers, low vegetation cover (particularly during the Closed canopy Mid-rotation stages) and more acidic soils. Indeed, the spiders *D. latifrons* and *A. paganus* had high indicator-values in the pure plantations in this study, but are most frequently captured in the re-opening phase of the Sitka spruce forest cycle when each stage is examined (Oxbrough *et al.*, 2010). The re-opening phase (after one or two thinnings) is characterised by a high cover of bryophytes and needle litter and low herb layer cover. This suggests that these species can take advantage of the unique Closed canopy conditions in forest plantations. Furthermore, different habitat features influence spider richness between the forest types: in native woodlands ground and lower vegetation layer cover were important, whereas canopy cover and fine woody debris influenced total richness in the plantations and no variables were significant for forest-associated species, suggesting that these suites of forest species are associated with different aspects of the forest habitat in plantations.

The availability of larval food plants is an important determinant of moth species composition. Forest type can directly influence moth fauna through the tree species present, or indirectly through the influence of canopy on lower plant diversity. In this study, there were several species with a larval food preference for broadleaved trees captured exclusively in native woodlands and several conifer associates exclusively found in plantations. The majority of the conifer-associated species (7 out of 9) feed on non-native conifers, but also Scots pine. This species was once widespread across Ireland in bogs and upland areas, however it went extinct naturally around 1600 years ago (Bradshaw and Browne, 1987). This might suggest that moth species associated with Scots pine will not necessarily have a negative impact on Irish forest ecosystems, particularly from the perspective of potential natural predators in existence. However, the two remaining conifer-associated species (*Thera Britannica* and *Eupithecia tantillaria*) constituted 22% of the conifer-associated species catch and feed solely on the non-native species' Norway spruce and Douglas fir. This suggests that large scale planting of conifers may have given rise to a greater prevalence of moths associated with conifer trees which would not otherwise naturally occur, but further research will be needed to determine the impact of this, particularly of those solely associated with non-native species.

Moth species richness was negatively related to ground layer vegetation cover and positively related to plant species richness. Ground layer vegetation cover, particularly in plantations, is likely to represent a cover of bryophytes. In the present study, bryophytes did not constitute the larval food plant of any of the species captured, whereas herbaceous plants accounted for 38%, which may account for the positive relationship with plant species richness, particularly as this was positively correlated with vascular plant richness (Pearson r = 0.83, P ≤ 0.001).

For moths, species richness was related to canopy height, though there was a conflicting pattern between forest types. Overall there was a positive relationship between canopy height and total and forest species richness, but a negative interaction between these metrics and both woodland types. Higher canopies in plantations represent more structurally developed, but also open forests and, in such conditions, the light traps used to sample moths in this study may be more visible and hence sample species from outside of the stand, thus increasing species richness. In contrast, higher canopies in native woodlands may not

equate with more open conditions, as the canopies of oak and ash are broader in extent. The negative relationship in native woodlands may be related to differing micro-climate conditions under canopies of different height or the understorey species present. Further investigation with alternative trapping methods will be required to determine whether these differences are due to trap efficiency or a real effect of tree height on moth diversity among the forest types.

Forest type was less important for the Carabid beetles, with the assemblages being primarily distinguished by geographical location. In addition, only one forest-associated species captured (*C. rotundicollis*) was identified as an indicator and this was of the plantations rather than the native woodlands. This indicates that, in Ireland, the proportion of forest-associated species may be lower for Carabid species than for spiders and moths. These latter groups may be better adapted to landscapes with low forest cover and high levels of fragmentation through their better dispersal capabilities, allowing movement between forest patches and utilisation of habitat corridors such as hedgerows. Furthermore, Carabid richness was negatively related to litter depth in the native woodlands and negatively related to ground layer vegetation cover in the plantations. Although previous research has shown these features to influence forest-dwelling Carabid beetles (Ings and Hartley, 1999; Poole *et al.*, 2003; Mullen *et al.*, 2008), it is possible that they do not create suitable micro-habitat for the large number of habitat generalists sampled in this study.

Neither spider or beetle richness was related to the land cover variables measured, such as amount of conifer or broadleaved forest cover within 200m or 1km of the sites, despite previous research highlighting the importance of forest area and configuration in fragmented landscapes (Barbaro *et al.*, 2005; Gaublomme *et al.*, 2008). This might suggest that patch size or degree of fragmentation is of less importance for these taxa. As suggested previously, spiders are adequate dispersers in this fragmented habitat, and some forest species can utilise hedgerows as habitat corridors (Oxbrough *et al.*, 2007), whereas perhaps the lack of forest Carabid species renders the amount of forested habitat within an area of little importance to their diversity. In contrast, forest-associated moth species were negatively related to amount of Commercially mature plantation within 1km of the sampling sites. Moths are more closely related to particular forest types through their associations with specific larval food plants and, as most of the forest species in this study were broadleaved-associated (76%), it is unsurprising that there are fewer species in areas dominated by plantations, the majority of which are coniferous in Ireland.

5.4 Canopy-dwelling invertebrates

5.4.1 Afforestation and reforestation survey

The total numbers of spider species in both afforested and reforested age class III Sitka spruce plantations were comparable to the canopies of other forest types in Ireland (see sections 5.4.2 and 5.4.4 and Appendix 9). However, in contrast, the total numbers of spider species in age class IV afforested and reforested Sitka spruce plantation canopies, and the total numbers of beetle species sampled in all Sitka spruce forest types, were very low relative to the other forest types (see Appendix 10 and sections 5.4.2 and 5.4.4 for further discussion of this). There are no directly comparable studies on canopy spiders in Sitka spruce, but the mean number of 4.5 canopy beetle species per plot (total beetle species numbers per plot ranged from 0 to 8), is much lower than the average of 15 beetle species found in the canopies of age class III and IV Sitka spruce in the UK (total beetle species ranging from 9 to 22 per plot) (Jukes *et al.*, 2002).Because of such low species numbers, it is very difficult to identify patterns in assemblage composition and/or analyses of guilds, habitat associations and rare species for this study. Accordingly, the results of this research should be interpreted with caution.

Within each of the taxonomic levels examined, the majority of individuals were comprised of only a few relatively abundant groups, e.g., sheet-web spinning spiders, generalist predatory beetles (except for age class III afforested plantations), midges (Diptera: Chironomidae and Ceratopogonidae), aphids (Aphidoidea) and springtails (Collembola), with the latter three taxa comprising 96% of all individuals sampled. Thus, it is clear that there is very low overall diversity in the canopies of age class III and IV Sitka spruce plantations of both first and second rotations. Numbers of phytophagous and broadleaved-associated beetles were lower in the second rotation than in the first rotation.

The low species richness and diversity of canopy invertebrates in Sitka spruce is most likely due to the lack of historical coniferous forest cover in this country (Speight, 1985; Kelly, 1991; Higgins *et al.*, 2004). One of the only native coniferous trees present in Ireland after the last Ice Age was Scots pine (Kelly, 1991; Roche *et al.*, 2009), which became extinct from the Irish landscape scale (at least from an ecologically significant point of view) (Bradshaw and Browne, 1987) between ~4000bp and ~1500bp (Roche *et al.*, 2009), and remained so until its re-introduction by humans ca.300 years ago., This has resulted in the almost complete lack of a specialized conifer invertebrate fauna on this island. This is in stark contrast to the situation in Scotland, where Scots pine has persisted continuously from the early postglacial to the present time and thus has a distinct associated coniferous fauna (Speight, 1985). Thus, non-native conifers are much less likely to provide suitable habitat structure and feeding opportunities for native canopy invertebrate fauna in Ireland than in Britain. The results of this study support the findings of Speight (1985), and suggest that the invertebrate fauna of coniferous trees in Ireland comprises a group of generalist foliage-feeding phytophages, their associated predators, and a few generalist saproxylics/xylophages, but with very few species associated specifically with a particular tree species.

5.4.1.1 Species richness and assemblages

Species richness of both spiders and beetles did not differ significantly between forest rotations or age classes in this study. This is in contrast to the responses of ground spiders and beetles documented in this study. Species richness of ground spiders was higher in afforested than in reforested plantations at all growth stages, but was negatively related to canopy cover, whereas ground beetle (Carabidae) species richness was positively related to canopy cover in reforested plantations (Oxbrough *et al.*, 2010). There

were also no differences in the assemblage composition of canopy spiders and beetles among any of the Sitka spruce forest rotations or age classes in this study. This agrees with analyses of ground spider assemblages in Sitka spruce forests, which found that assemblages of age classes III and IV were relatively similar to one another, both between and within rotationss (Oxbrough *et al.*, 2010). The largest differences in ground spider assemblages in Sitka spruce plantations were found at the earlier growth stages of the plantations (age class I and II, 4-6 years old and 9-16 years old, respectively) (Oxbrough *et al.*, 2010), but those growth stages were not looked at in this study. Thus, it appears that, overall, stand age or rotation does not influence spider or beetle species composition in Sitka spruce plantations to a large extent. This is likely due to the absence of any large-scale structural differences between afforested and reforested plantation canopies at the two age classes investigated.

5.4.1.2 The influence of habitat structure and prey availability on spider guilds

Sheet-web spinning spiders (Family Linyphiidae) were dominant across all forest rotations and stand ages surveyed in this study. This is unsurprising, as almost half the spider fauna in Britain and Ireland belong to the Linyphiidae (Roberts, 1993). They are typically small (ranging in size from 0.95mm to 7.4mm) and thus may be able to take advantage of the small spaces available between needles in the canopy of coniferous trees (Halaj *et al.*, 2000) to construct the small sheet webs they build.

The only significant differences in spider guild composition between forest types were driven by the complete absence of orb-web spinning spiders in age class IV afforested plantations. Sheet-web spinners in age class IV were more dominant at afforested sites than at reforested sites, due to the absence of orb-web spinners. The complete lack of orb-web spinning spiders in age class IV afforested sites is difficult to explain, as this guild was present at all the other forest types sampled. However, habitat structure and prey availability are the two main drivers of spider distribution and abundance (Rypstra, 1983; Halaj *et al.*, 1998), and it is likely that both the lack of this guild and dominance of sheet-web spinners at age class IV afforested sites can be explained by two variables.

5.4.1.3 Beetle guild composition, habitat associations and rare species

Phytophagous beetles were the most dominant guild at age class III afforested plantations, where they comprised approximately 45% of all beetles species. Generalist predators were dominant at the remaining three forest types: comprising approximately 51% of beetles at age class IV afforested, 69% at age class III reforested, and 67% at age class IV reforested sites. There were approximately half the relative number of phytophagous beetles at age class IV afforested sites (approximately 23%) compared to age class III afforested sites, and there were even less than that in reforested plantations at either age class. Interestingly, none of the phytophagous beetles sampled were conifer-associated species, being either broadleaved, mixed-forest or generalist phytophages. The most abundant phytophage, and 2nd most abundant beetle species overall, was *Strophosoma (Strophosoma) melannogrammum*, a weevil (Curculionidae) associated with mixed forests. A lack of conifer-specialist phytophages is due to the lack of historical coniferous forest cover in Ireland (discussed above). Therefore, these results suggest that the high initial proportion of generalist phytophages at age class III afforested plantations were remnant from before afforestation took place, and that this guild are gradually replaced by generalist predators as the forests mature and go through successive rotations.

The first and third most abundant beetle species sampled overall were *Malthodes marginatus* and *Rhagonycha lignosa* (soldier beetles from the Cantharidae family) respectively, both of which are

predominantly aphid predators (Carter, 1973; Parry, 1992). The soldier beetles are one of the most important beetle predators of aphids, along with ladybirds (Coccinellidae) (Straw *et al.*, 2009), and the high abundance of aphids in Sitka spruce canopies is likely to be the reason for the relatively large numbers of these species. Although a negative relationship between soldier beetle and aphid densities in Sitka spruce plantations in the UK has previously been reported (Straw *et al.*, 2009), no such relationship was observed in this study, suggesting that these predators are not numerous enough to exert top-down population control on their prey populations.

There were no significant differences observed between the four forest types in the relative proportions of generalist and forest-associated beetle species, which is in contrast to findings for ground beetles (Carabidae), for which the number of forest-associated species was positively related to structural development (Oxbrough *et al.*, 2010). This provides further support for the theory that forest-associated beetles living in coniferous plantations in Ireland are relatively generalist in their habitat associations, which may be due to the historical lack of coniferous forest cover in this country. However, there were significant differences in the specific habitat associations of beetles within forest-associated species. Notably, broadleaved-associated species were sampled at both afforested site types but not at reforested sites. It is possible that, like phytophagous species, these species may be remnant from before the site was planted with conifers, but are lost during the second forest rotation. Interestingly, age class IV afforested plantations contained no conifer-associated species, although these were present at most age class III afforested sites. However, overall, only five conifer-associated individuals of two species, both of which are predatory species (*Calodromius spilotus* (Carabidae) and *Aphidecta obliterata* (Coccinellidae)) were sampled across all forests. The fact that these species were not collected at age class IV afforested plantations may simply be a consequence of the low numbers of species and individuals found in all Sitka spruce forests.

There were two Red-listed species sampled at Sitka spruce forests overall; the predatory *Malthodes guttifer* (Coleoptera: Cantharidae) (one individual at one forest) and the xylophagous *Athous (Orthathous) campyloides* (Coleoptera: Elateridae) (twenty individuals at six forests) (Appendix 4). Neither of these species is strongly associated with conifers. Reforested age class III sites had a significantly lower mean relative species richness of rare species compared to all other plantation forest types. However, as with the findings for conifer-associated species above, this result should be interpreted with care due to the low species numbers involved.

5.4.1.4 Other taxa

Collembola comprised 48% of the total individuals sampled (106,640 individuals collected in total across all four forest types), making them the most abundant canopy invertebrate in this study. In the UK, Collembola comprise almost a quarter of all canopy fauna in terms of density (Ozanne, 1996; Shaw *et al.*, 2007), contributing significantly to arboreal food webs and being preyed on by a variety of invertebrates, particularly spiders (Turner, 1984; Shaw *et al.*, 2007). Collembolan abundances were negatively correlated with the proportional species richness of both scaffold- and sheet-web spinning spiders. Age class IV afforested plantations contained a lower proportion of Collembola compared to both age class III forest types, and age class IV afforested plantations also contained the highest relative proportion of sheet-web spinning spiders. Thus, there appears to be a top-down effect of spider predation on Collembola, although further research is required to clarify this relationship, which has not previously been reported.

Total and relative abundances of Diptera and Aphididae were not significantly correlated with spider or predatory beetle abundance or species richness but, as mentioned previously, two of the three most abundant beetles are primarily aphid predators. The only other notable trend evident for these taxa was that the proportional abundance of Diptera was lowest at age class III afforested sites compared to both age class IV forest types, but not the reforested age class III sites. However, the vast majority of Diptera were midges (from the families Chironomidae and Ceratopogonidae), which are a highly mobile and opportunist taxa that can utilize a wide variety of habitats, and are generally not associated with a particular tree species. Total Diptera abundance was higher (but not significantly) in both age class IV plantation types, than in either age class III type. It is possible that swarming insects of this order prefer the more open habitat provided by age class IV plantations where they can swarm in greater numbers. However, family-level data is ill-suited to revealing ecological relationships, and more research is required to assess the significance of this finding.

5.4.1.5 Structural variables

The only significant difference in measured structural variables was between the diameter at breast height (DBH) of trees in age class III and IV reforested plantations, but this difference was not observed in afforested plantations. This is in agreement with the findings of Oxbrough *et al.*, (2010), where DBH differed between age class III and IV trees in reforested plantations. However, canopy height and canopy cover was also shown to differ for these stand ages in reforested plantations (Oxbrough *et al*, 2010), but this finding was not observed in this study. This may be explained by the relatively low number of sites studied and the large range in values of the structural variables measured among forests in this study, which are likely to have resulted in tests of low statistical power.

There were no significant correlations between beetle species and Sitka spruce habitat variables, which is in direct agreement with a similar study by Jukes *et al.* (2002), where there was no significant association between spruce tree structural variables, beetle species richness or guild composition. Overstorey tree species appeared to be the greatest driver of canopy beetle community composition in that study. However, for spiders, canopy cover was positively correlated with the sheet-web spinning spider species richness. The relatively more complex canopy structure at age class III sites (less thinned, denser needles, fewer gaps in the canopy etc.) resulted in a higher number of sheet web spinning species, while the relatively more open, less complex canopy at age class IV sites resulted in fewer sheet-web spinning species. This further supports the finding of section 5.4.2 (discussed in more detail in that section) that the numbers of sheet-web spinning species decreased as canopy complexity decreased, from pure conifers of Norway spruce to mixed plantations of Norway spruce/oak, to native oak woodlands.

5.4.2 Mixed tree species survey and comparison of native oak woodlands with mixed and pure plantations

5.4.2.1 The spider and beetle assemblages of native oak woodlands and mixed and pure plantation forest canopies

The results of this study suggest that, while plantations have the ability to support substantial components of invertebrate diversity (in terms of species richness), as has been suggested previously (e.g., Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008), these canopies do not support the same range of

invertebrate guilds and habitat specialists as native oak woodlands. However, this pattern was clearer for beetles than for spiders, as the beetles sampled displayed a range of feeding specializations and habitat associations which are often specific to broadleaves, conifers, or to a particular tree, while spiders are generalist predators more dependent on habitat structure and availability of suitable prey than on the presence of any particular plant species (Rypstra, 1983; Halaj *et al.*, 1998).

Differences in spider assemblages between native oak woodland and pure Norway spruce plantations were driven mainly by differences in the relative abundances of sheet-web spinning spiders (Family Linyphiidae). The number of spider guilds in pure plantations was only half that of the other forest types. Almost 90% of spider species in these forests were sheet-web spinners, while the proportion of scaffold-web spinners was significantly lower than in both oak mixes and native oak woodlands. In contrast, Linyphiids comprised only half of the fauna in native oak woodland and oak mix plantation forests, with active hunters and orb web spinners also present. The proportion of orb-web spinning spiders was significantly lower in oak mix plantations than in native oak woodlands. This finding is similar to that of Halaj *et al*. (1998) who found that relative abundances of sheet-web spinners decreased and orb-web weavers increased as structural complexity of the tree species decreased (from dense needles of Douglas fir (*Pseudotsuga menziesii*) to broadleaves of red alder (*Alnus rubra*)).

Although Linyphiids are the most abundant family of spiders in Britain, Ireland and Northern Europe, accounting for almost half of all spiders in Britain and Ireland, they are typically small (ranging in size from 0.95mm to 7.40mm) (Roberts, 1993). Unlike larger spiders, Linyphiids can use the small spaces available between needles in the canopy of coniferous trees to build their small sheet webs (Halaj *et al.*, 2000). Differences in prey abundance, size and diversity are also likely to be important in determining the composition of spider communities, and pure conifer stands support a different range of potential prey to native oak woodlands. In particular, they support more Aphididae, Collembola and Diptera (comprised predominantly of midges from the families Chironomidae and Ceratopogonidae) (see Section 5.4.1), all of which are relatively small taxa which would be suitable prey items for Linyphiidae (Halaj *et al.*, 1998). Thus, pure conifer canopies may provide more suitable habitat than broadleaved canopies for Linyphiidae. Actively hunting, orb- and scaffold-web spinning spiders appear to prefer the larger spaces between leaves and relative openness of the broadleaved canopy habitat, possibly due to the relatively larger body sizes of spiders in these families. Gunnarsson (1996) found that larger-bodied spiders tended to occupy spruce (*Picea abies*) branches with fewer needles. This may have been due to lack of attachment sites and/or increased predation risk for small spiders on more exposed branches (Gunnarsson, 1996), or it may be that larger-bodied individuals simply require more open space in which to move about.

Additionally, Linyphiid spiders often disperse by ballooning (Roberts, 1993) and so their distributions may not be as constrained by factors such as isolation from existing populations as those of other spider families and beetles. High dispersal ability may explain why forest types did not separate according to spider assemblage in the cluster analysis. A lack of spider indicator species is also unsurprising, as Floren *et al*. (2008) found that there were no distinct spider forest fauna nor strictly arboreal forest fauna for either remnant primeval forest or plantation forests in Poland.

Beetle assemblages as characterised by MRPP differed between native oak woodlands and oak mix plantations, but not between native woodlands and pure spruce plantations. However, both predatory and detritiphagous beetle species were present in higher proportions in pure plantations than in native oak

woodlands, while oak mix plantations had intermediate values for these guilds. The positive relationship between presence of predatory beetles coniferous tree cover along a gradient from native oak woodlands to pure plantations is likely to be due to the relatively large numbers of aphids and Collembola in coniferous plantations, compared to native oak woodlands. Predatory beetles, like spiders are generally more opportunistic and mobile than other beetle guilds, and so are likely to be more generalist in their habitat preferences. Due to the commercial nature of plantation forests, they are more intensively managed than native woodlands. Branch removal and thinning operations create significant amounts of woody debris, both at ground- and canopy-level, which may be one explanation for the higher proportion of detritiphagous beetle species in pure plantations compared to native oak woodlands.

The relative species richness of phytophagous beetles was positively related to the presence of native broadleaves in the canopy, increasing from non-native conifers only in the pure plantations (approximately 8% phytophages), to conifers and broadleaves in the oak mix plantations (approximately 23% phytophages), and finally broadleaves only in the native oak woodlands (approximately 43% phytophages). A similar trend was also found by Southwood *et al*. (1982), who demonstrated that phytophage species richness was much lower on introduced trees in both the UK and South Africa compared to native tree species, although in that study all trees sampled were broadleaves. Southwood *et al*. (1982) speculated that phytophages require time to adapt to new introduced host plant species, particularly if those species are taxonomically isolated in the country of introduction. In Ireland, it is unlikely that many phytophagous species will be adapted to feeding on conifers, as historically coniferous forest cover was low (Cross, 1998), there are very few native coniferous tree species, and Norway spruce is non-native (Kelly, 1991).

Oak mix plantations supported an intermediate number of phytophagous species, perhaps because colonisation of oak trees in the mixes may have been more difficult for phytophagous species than in native oak woodlands due to the intimate mixing of Norway spruce and oak (with relatively low mixing ratios of just 20-40% oak), which may have diluted the apparency (ease with which phytophages could locate their host tree) (Sholes, 2007) of the oaks. Ozanne *et al*., (2000) found that canopy beetle guilds varied between forest patches and single trees, with single trees containing fewer herbivorous species, due in part to the difficulty in colonising isolated trees. Additionally, oak trees in oak mix plantations were almost half the size of Norway spruce in pure plantations, because oaks are slower growing and are shaded out by the faster-growing Norway spruce. Thus, the smaller oak trees in oak mix plantations provided a smaller available canopy habitat for phytophagous beetles, relative to the sampled trees in native oak woodlands and pure plantation forests.

A total of eleven individuals from five oak-associated beetle species were caught across the forest types. However, host tree specialization was higher in native oak woodlands, as the oak-associated species found in plantation forests were both predatory (*Malthinus fasciatus* (Coleoptera: Cantharidae) and *Malthodes fuscus* (Coleoptera: Cantharidae)), whereas phytophagous oak specialists were only sampled in native oak woodlands (*Coeliodes transversealbofasciatus* (Goeze 1777), *Coeliodes rana* (Fabricius 1787), and *Orchestes quercus* (Linnaeus 1758)). Similarly, Magura *et al*. (2003) found that deciduous forest specialist (Coleoptera: Carabidae) abundance was lower in non-native Norway spruce plantations than in native beech forests. The higher number of specialist species on oak may be due to the fact that oak has been present on the island of Ireland for thousands of years. Several studies have shown strong positive relationships between tree colonization history and phytophagous specialists (Southwood *et al*.,

1982; Kennedy and Southwood, 1984; Brändle and Brandl, 2001). Additionally, oak trees are now relatively rare in the Irish landscape (Higgins *et al.*, 2004; Perrin *et al.*, 2006b; Perrin *et al.*, 2008b), and the proportion of phytophagous specialists in the fauna of rare trees than among species found on abundant trees (Brändle and Brandl, 2001).

It is notable that only three phytophagous beetle species specifically associated with oak trees were sampled from native oak canopies in contrast to the 90 or so species reported from oak canopies in the UK (Whitehouse and Smith, 2010). This suggests that the greater numbers of broadleaved-associates at native oak woodland and oak mix plantation forests were due to the presence of broadleaved trees, rather than oak trees specifically. Oak trees at oak mix plantation forests were immature, as they had been planted at the same time as the Norway spruce, and the current rotation time of Irish plantations is insufficient for the slower-growing oaks to have reached commercial maturity (approx. 60 years). For this reason, intimately planted mixes of Norway spruce and oak trees in plantations are typically deemed a "commercial failure" by foresters and are no longer planted due to the stunted nature of the oaks in the mix, which effectively comprise an understorey (Mason, 2007). However, species richness estimates were not biased by the significantly smaller area of canopy available at oak mix plantation forests, as rarefaction explicitly takes variability in number of individuals caught per sample into account (Magurran, 2004).

Whilst oak trees may not 'work' in a mix on a commercial basis, they still have value for biodiversity, under Sustainable Forest Management guidelines, and so could be included for that purpose alone. However, more competitive, faster-growing native broadleaves like ash, rowan (*Sorbus* aucuparia) and birch (*Betula* spp.) may be better suited than oak to providing the habitat for broadleaved forest-associated species in conifer plantations, for several reasons. Firstly, host specialist phytophagous beetles appear to be rare in Irish forests, with most species being relatively generalist in their habitat associations. Secondly, there were no differences between forest types in numbers of mixed-forest-associated species, suggesting that many forest canopy invertebrate species in Ireland are generalists. Thirdly, although native oak woodlands contained the highest proportion of broadleaved-associated species, these species still comprised a considerable proportion of the beetles sampled in both oak mix and pure plantations (29% and 23%, respectively). This lack of specialisation on specific tree species may also explain why there were no differences in relative numbers of xylophagous, mycetophagous and detritiphagous species between forest types. This viewpoint is supported by the findings of Coll *et al.*, (1995), who postulated that the Carabid fauna in two Irish conifer stands may have colonised by dispersal from original forest remnants and hedgerows, suggesting that the canopy fauna is adapted to exploiting any available forest patch. This phenomenon has also been observed for Irish forest bird and vegetation communities (French *et al.*, 2008; Sweeney *et al.*, 2010a; Wilson *et al.*, 2010).

The native oak woodlands surveyed contained no conifer-associated species, whilst both plantation forest types supported broadleaved- and conifer-associated species from various guilds. This suggests that flexibility in habitat associations may only occur in one direction, i.e., broadleaved-associated species may be able to adapt to conditions in coniferous forests, but conifer-associated species may not be able to adapt to conditions in broadleaved forests, perhaps due to the relatively recent introduction of non-native conifer forests to the Irish landscape (Kelly, 1991; Cross, 1998; Higgins *et al.*, 2004). It is interesting to note that although three conifer-associated species were sampled in total, one of them was a predatory species (*Aphidecta obliterata* Linnaeus 1758), and two were xylophagous (*Dryophilus pusillus* Gyllenhall 1808 and *Ernobius mollis* Linnaeus 1758). Thus, there were no conifer-associated phytophagous species

found in plantations in this study. This figure is much lower than the numbers of phytophagous beetles sampled from coniferous plantation canopies in the UK, where between 15 and 30 phytophagous beetle species were collected from Scots pine canopies (Ozanne *et al.*, 2000), and between 5 and 9 phytophagous beetle species were collected from Norway spruce canopies (Jukes *et al.*, 2002). As supported by our results, phytophagous conifer-associated beetles appear to be much rarer in Ireland, which Speight (1985) attributes to the lack of historical coniferous forest cover. Although they are now widespread on a landscape-scale, non-native coniferous plantations in Ireland are not currently providing suitable habitat for this guild.

Similar numbers of Red-listed species occurred in native oak woodlands and pure plantation forests, while oak mix plantations contained lower numbers of Red-listed species. However, there was little overlap among forest types for Red-listed species, with only two out of the seven Red-listed species being sampled in both native oak woodland and pure plantation forests. These were (*Malthodes guttifer* Kiesenwetter 1852, a predator associated with mixed forest, and *Stenichnus (Cyrtoscydmus) poweri* (Fowler 1884), a generalist xylophage), neither of which are phytophagous species. All Red-listed species sampled in native oak woodlands only were phytophagous or xylophagous forest-associated species, while the one species sampled in plantations only was a generalist xylophagous species (*Athous (Orthathous) campyloides* Newman 1833), which is not associated with forests specifically. The lower numbers of Red-listed species in oak mix plantations may have been due to the reduced apparency of oak trees or relatively smaller available canopy habitat in these forests, which was discussed above.

5.4.2.2 The response of spiders and beetles to the inclusion of a broadleaved tree species in a conifer plantation

Spider and beetle communities were affected differently by the presence of native oak trees in the non-native coniferous plantations, due to the different feeding strategies and habitat requirements of these taxa, which are directly related to forest type in the context of comparisons between broadleaves and conifers. The only significant difference in environmental variables between forest types was in diameter at breast height (DBH), which was smaller for oak trees in oak mix plantations than for Norway spruce trees in pure plantations, due to the slower growth rate of the oaks relative to the Norway spruce. Other studies on canopy invertebrate diversity have found that the structural features of trees and/or forest sites were poorly correlated with species metrics of the canopy invertebrate fauna on both native and introduced tree species (Southwood *et al.*, 1982; Jukes *et al.*, 2002). Southwood *et al*. (1982) suggested that variation in canopy invertebrate species richness was more likely to be affected by properties of the particular tree species sampled (such as greater digestibility of leaves), as well as the relative abundance and history of that tree species in the study area, than by forest structure.

The oak mix plantations supported an assemblage and guild composition of spiders more similar to that found in native oak woodlands, and the presence of a native broadleaved tree species in the oak mix plantation doubled the diversity of spider guilds present compared to the pure plantations. Spiders are generalist predators, and are dependent on habitat structure. Actively hunting, scaffold- and orb-web spinning guilds appear to prefer the relative openness and diversity of microhabitat provided by mixed broadleaved and coniferous canopies, or may be unable to utilise the more densely packed and complex needle structure of purely coniferous canopies. Prey availability is also important, however, and it may be that greater diversity of microhabitats in broadleaved canopies has a positive effect on the range and diversity of prey, which in turn results in a more diverse range of predators.

In contrast, beetles have diverse feeding habits, from predators, to phytophages, mycetophages, detritiphages, and xylophages and are thus relatively more dependent on tree species than structure *per se*. The presence of oak trees in the oak mixes had a significant influence on phytophagous beetle species, which were present in significantly higher proportions in oak mix than in pure plantations. Phytophagous beetles in particular can be restricted to specific host tree species, due to the chemical composition of the edible vegetation (Strong *et al.*, 1984), and although relative numbers of phytophagous species were increased in oak mix plantations compared to pure plantations, they were still lower than those in native oak woodlands. This may be due to one or more of several factors, including the small size of the oaks in the oak mixes, their isolation in the coniferous plantation, and the low numbers of oak specialist phytophagous species found overall.

Thus, it appears that the influence of a native tree species on the invertebrate fauna of mix plantations may be affected by factors such as the density of that tree within a mixed forest, its ability to compete successfully with conifers, and the ratio of edge: patch size of that tree species. Mixed plantations may therefore benefit from planting more competitive native broadleaved trees (e.g., ash, rowan, birch) and creating wider gaps around native broadleaves to increase their competitiveness and enhance habitat availability for broadleaved-associated species. This is also likely to enhance the diversity of ground-dwelling invertebrates (Magura *et al* 2002; Oxbrough *et al* 2005). Isolation of single broadleaved trees in a coniferous matrix could also be reduced by planting patches of native broadleaves non-intimately within plantations.

5.4.3 Comparison of forest types

5.4.3.1 Canopy invertebrate diversity and community composition

This study clearly demonstrated that age class IV Sitka spruce plantations do not provide the necessary habitat for a range of canopy spider and beetle species, and other invertebrate taxa, that are found in native ash and oak woodlands. Age class IV Sitka spruce plantations contained approximately two-thirds of the spider species richness and approximately one half of the beetle species richness present in native woodlands. This contrasts with the finding in Section 5.4.2 that there were no significant differences in species richness for these two taxa between native oak woodlands and oak mix and pure Norway spruce plantations. However, because only oak trees were sampled in oak mix plantations, and the invertebrate assemblages found on these trees differed from those in pure Norway spruce plantations, the diversity of invertebrate assemblages in these forests may have been underestimated. Sitka spruce plantations support a higher overall abundance of invertebrates overall than do native woodlands, but the diversity of invertebrates in plantations is much lower across a broad range of taxa at varying taxonomic resolutions.

Even at relatively high taxonomic levels (Family-level and higher), clear differences were evident in the total abundances, richness and mean relative proportions of Diptera, Hemiptera and other taxa between native woodlands and Sitka spruce plantations. Sitka spruce plantations were consistently less diverse at each taxonomic level examined even though total invertebrate abundances were much higher in plantations (Appendices 9, 10 and 11). Additionally, invertebrate assemblages were always dominated by a few relatively abundant groups in Sitka spruce plantations. For example, the Chironomidae (Diptera), Aphididae (Hemiptera) and Collembola all comprised > 50% of all individuals within each taxonomic level examined. In contrast, the relative composition of invertebrates within each taxonomic level was more

even in both native woodland types. Although there were significant differences among Dipteran and Hemipteran families and other invertebrate Orders among forest types, these were mainly driven by the dominance of a few groups in Sitka spruce forests. It is difficult to attribute ecological information to family-level (and higher taxonomic level) data, so differences among those groups not identified to species will not be discussed further. However, it is important to note that the large invertebrate abundances in Sitka spruce plantations could be important for insectivorous birds and mammals, such as bats. In particular, Aphididae and Collembola were present in abundances that were an order of magnitude greater than in both native woodland types. These invertebrate groups are likely to be suitable prey items for small insectivorous birds such as Goldcrests (*Regulus regulus*) and Coal Tits (*Periparus ater*) (Fuller, 1995; Snow and Perrins, 1998a), which are found at high densities in Irish Sitka spruce plantations (Sweeney *et al.*, 2010a). However, further research is required to formally test the relationship between the abundances of invertebrate prey and vertebrate predators in Irish forests.

At species-level, spider assemblages differed markedly between Sitka spruce plantations and native woodlands, but not between ash and oak woodlands. Spiders are unlikely to be influenced by the relatively small-scale structural differences between ash and oak canopies, as both habitat types support a diverse array of prey types, whereas differences in habitat structure and prey availability between coniferous and broadleaved trees are more pronounced, and thus exert a greater influence on spider communities. For example, even though it is a common habitat generalist, *Tetragnatha montana* (Araneae: Tetragnathidae) was not sampled at all in Sitka spruce or Norway spruce forests, though it was present in native woodlands and oak mix plantations. This spider is relatively large-bodied (in comparison to most Linyphiids) and thus may be unable to utilise the small gaps between needles in coniferous plantation canopies, whereas the more open canopies of native woodlands appear to be more suitable to its habitat requirements. The cluster analysis of the canopy spider communities clearly distinguishes Sitka spruce plantations from both native woodland types, while ash and oak woodlands are not clearly separated from one another. Although *Pelecopsis nemoralis* was a significant Indicator species for Sitka spruce forests, this species was present in relatively high numbers across all forest types (Appendix 9), and thus this result is likely to be due to the dominance of this species in Sitka spruce plantations (42% of all individuals). There were no spider Indicator species for either native woodland type.

In contrast, the canopy beetle community data showed a clear separation between all three forest types using species-level assemblage analyses. There were five significant beetle Indicator species each for ash and oak woodlands, even though very few beetle species sampled were associated exclusively with ash or oak trees (Appendix 11), which suggests that ash and oak woodlands have distinct beetle communities. However, the cluster analysis of beetle communities did not distinctly separate Sitka spruce plantations from either of the native woodland types, although oak woodlands were grouped tightly. This may be due to the significantly lower proportion of generalists in oak woodlands compared to both Sitka spruce and ash woodlands, while the relative proportions of generalist species in the latter two forest types was not significantly different (this is discussed further below).

Although total beetle abundance was greater in oak canopies than in ash canopies, overall diversity was similar in both forest types, with ash woodlands holding slightly more beetle species than oak (Appendix 10). This result is in sharp contrast to the findings of several studies on forest canopies in Europe and the UK, where oak canopies are more species-rich than ash and many species are specifically associated with oak trees only. For example, Whitehouse and Smith (2010) found that oak trees supported more than

90 beetle species compared to just 25 on ash trees. However, according to Stork *et al.* (2001) *Quercus* species are among the most intensively studied European deciduous trees, and perhaps the higher numbers of species known to be associated with oak from other studies is partly due to the relative lack of research on other trees species such as ash.

Alternatively, canopy invertebrate communities on oak trees in Ireland may actually be very different to those on UK and European trees, because of differences in the history of forest cover between Ireland and other countries. It is possible that there is relatively high diversity on ash trees in Ireland simply because there are more ash trees remaining in the landscape (Higgins *et al.*, 2004). Host tree abundance in the landscape is one of the best predictors of total invertebrate species richness associated with that tree species (Kennedy and Southwood, 1984). This appears to be borne out by the results of this study, as the habitat variables measured at each forest site were not correlated with abundances or richness of the canopy invertebrate taxa examined. Several other canopy invertebrate studies have also shown that stand-scale variables are relatively unrelated to canopy biodiversity. For example, Jukes *et al.* (2002) demonstrated that latitude and overstorey tree species composition were the two most important factors in determining canopy beetle community composition in several plantation forest types in the UK, while oak-associated saproxylic beetle species richness in Sweden is more closely related to habitat quality and to density of dead oak-wood on a landscape-scale than to large-scale environmental factors or stand-level factors (Franc *et al.*, 2007).

5.4.3.2 Differences in guilds and habitat associations between native oak woodlands and Sitka spruce plantations

Sitka spruce forests entirely lacked actively hunting spiders and had far lower proportions of orb-web spinners than both native woodland types. Sheet-web spinners (Linyphiidae) were highly dominant at Sitka spruce plantations (approximately 82% of all individuals), and it appears that coniferous plantation canopies are unsuitable habitats for the majority of individuals from both the actively hunting and orb-web spinning spider guilds (see Section 5.4.2). Ash woodlands also contained a higher proportion of active hunters and orb-web spinners and a lower proportion of sheet-web spinners than did oak woodlands, which may be due to the relative openness of ash canopies compared to those of oak. As discussed previously, spiders do not actually feed on the tree they inhabit, but only use its structure for web-building and prey capture. Actively hunting and orb-web spinning spiders tend to be larger-bodied than sheet-web spinners, and may prefer the larger gaps between leaves in ash canopies, which would result in increased light availability for active prey capture and increased space available for larger web construction. Scaffold-web spinning spiders (Family Theridiidae) were the only guild to exhibit no significant differences among the three forest types – many of these spiders are also small-bodied like the Linyphiidae, and may be capable of using both the small spaces between coniferous needles and the larger ones in broadleaved forests. However, additional research would be required to further test these hypotheses.

The percentage sampled spider species associated with mixed forest was much higher in Sitka spruce forests than in either native woodland type. This appears to be primarily due to the fact that two of the three most abundant spider species in Sitka spruce forests were classified as mixed forest-associates (*Paidiscura pallens* and *Pelecopsis nemoralis*, which made up approximately 9% and 42% of all individuals respectively, Appendix 9). The proportion of spiders associated with mixed forest was higher in oak woodlands than in ash woodlands. Again, this is likely due to the above two species, which were more abundant in oak than in ash woodlands. Additionally, the habitat generalists *Tetragnatha montana* and

Metellina mengei were relatively more abundant in ash compared to oak woodlands (Appendix 9), all of which may contribute to the relatively low proportions of mixed-forest-associated spider species in ash woodlands.

In contrast to actively hunting spiders, Sitka spruce forests contained the highest proportion of actively hunting beetles, and relatively low proportions of phytophages, mycetophages and detritiphages, compared to both native woodland types. Actively hunting beetles are more generalist in their habitat requirements than species that actually feed on a particular tree species, and the relatively high proportion of actively hunting beetles in Sitka spruce plantations is likely due to the abundance of prey (e.g., Collembola, Aphididae etc.) in these plantations. The relatively low proportions of phytophages and other guilds that feed on tree tissues in Sitka spruce plantations, compared to native woodlands, is likely due to the lack of historical coniferous forest cover in Ireland, which has prevented the development of a specialised canopy invertebrate fauna with the ability to feed on coniferous trees (Speight, 1985).

It is notable that there were relatively high numbers of xylophagous beetle species in ash woodlands and Sitka spruce plantations, relative to oak woodlands, while Sitka spruce plantations also contained significantly higher proportions of deadwood-associated species. This may be due to the different management practices employed in the former two forest types. For example, Sitka spruce plantations are more intensively managed than native woodlands, and there may be more deadwood substrate available in plantations due to thinning and branch-cutting operations for both xylophagous and deadwood-associated species. Coppicing has historically been widely utilised in both semi-natural ash and oak woodlands (Higgins *et al*, 2004), but the high density and small DBH of trees in the ash woodlands sampled in this study suggests that they may have been more heavily coppiced or experienced higher levels of natural regeneration than the oak woodlands. This may have increased the availability of deadwood for xylophagous species. However, the sampling method employed was not directly targeting saproxylic/xylophagous species, and recent research has demonstrated that there are relatively low volumes of large-diameter deadwood in several Irish forest types (Sweeney *et al.*, 2010b). Thus, the creation of high-quality deadwood in Irish forests is something that both plantation and native woodland managers should aim to rectify, as it would likely increase their overall biodiversity value, although this has never been explicitly tested (Davies *et al.*, 2008).

Although the proportion of generalist species is lower in oak woodlands than in either ash woodlands or Sitka spruce plantations, only three of beetle species sampled in oak canopies were specifically associated with oak. Two of these species were also found in ash woodlands, and none of the beetle species sampled were specifically associated with ash (Appendix 11). Unsurprisingly, the proportion of broadleaved-associated species in Sitka spruce plantations was much lower than in either type of native woodland. No obligate conifer specialist species were found in either native ash or oak woodlands, and even in Sitka spruce plantations the proportion of conifer-associated species was low (approximately 8% of individuals), with the proportions of mixed forest-associated species and habitat generalists each being four times greater. Thus, it appears that there are a very low number of species in Ireland which are specifically tied to coniferous forests, even though the majority of Irish forests are now coniferous (Forest Service, 2007), and the majority of species that do utilise coniferous plantations are either habitat generalists or mixed forest-associates. This supports the theory that the ground beetle (Carabidae) fauna in two Irish conifer stands may have colonised by dispersal from original forest remnants and hedgerows

(Coll *et al.*, 1995). Similar findings have been reported for Irish forest birds (Sweeney *et al.*, 2010a; Wilson *et al.*, 2010).

However, even within the native woodlands, there were low levels of tree species specialisation among invertebrates, and the majority of sampled individuals were more generalised broadleaved-associated species. Species that are only associated with oaks in other countries were also found in ash woodlands in this country (*Coeliodes rana*, *Coeliodes transversealbofasciatus* and *Orchestes quercus*). This is likely to be primarily due to the depauperate and fragmented remnant natural forest cover in this country (Higgins *et al.*, 2004; Perrin *et al.*, 2006b; Perrin *et al.*, 2008b).Any forest species that have survived are likely to be highly adaptable and able to exploit any available broadleaved forest patch. Also, the lower numbers of species in Ireland may result in lower levels of inter-specific competition for habitats, resulting in relaxation of the ecological niches for some species whose habitat preferences are more strictly specialist in other countries. However, although the majority of forest canopy invertebrate species in this study were found to be relatively generalist in nature, it appears that many species are still unable to adapt to the relatively alien environment provided by coniferous forests. This suggests that, although high levels of plasticity are evident in the habitat associations of broadleaved-associated species, conifer-associated species do not exhibit the same flexibility.

Sitka spruce forests contained a higher proportion of Red-listed species compared to oak woodlands. However, this result should be interpreted with care, as both the low overall species numbers at Sitka spruce plantations (between 3 and 8 beetle species per site) and the relatively high abundance of the Notable B designated *Athous campyloides* (approximately 7% of all individuals) are contributing factors. Total numbers of Red-listed species were actually much higher in semi-natural woodlands (nine red-listed species) compared to those in Sitka spruce plantations, where two Red-listed species were sampled in total; the above-mentioned *A. campyloides*, and one other individual of *Malthodes guttifer*.

5.5 Birds

5.5.1 Afforestation and reforestation survey

5.5.1.1 Bird communities in second-rotation forests

Prior to canopy closure, plantations are occupied by species characteristic of open habitats (Askins *et al.*, 2007) which are replaced by generalist and forest adapted species as canopy closure progresses (Humphrey *et al.*, 2003b; Wilson *et al.*, 2006). In this study, Redpoll and Whitethroat, both species that are closely associated with open habitats, were identified as indicators for Pre-thicket. Coal Tit, Chaffinch, Dunnock, Song Thrush and Robin, indicators for Thicket, are all typical of wooded habitats. Coal Tit was also an indicator for Closed canopy, and the fact that Coal Tit had a higher indicator-value for this stage reflects the fact that this species, as well as Goldcrest, favours mature coniferous forests (Snow and Perrins, 1998). The results of this study are therefore consistent with those of previous research that has identified changes in bird assemblages as plantations mature.

Early successional forests can be important in the conservation of open habitat specialists (Dettmers, 2003; Wilson *et al.*, 2006; Burton, 2007). Some of the species, including some long distance migrants, that were found predominantly in Pre-thicket in this study, have undergone recent population declines elsewhere in their ranges (Hewson and Noble, 2009). Our results therefore support the suggestion that young forests provide important breeding sites for open habitat birds. Linnet (*Carduelis cannabina*) and Grasshopper Warbler (*Locustella naevia*) were both found in Pre-thicket in this study and are on the Amber list in Ireland. Linnet is also a Species of European Concern SPEC; (Lynas *et al.*, 2007). No species of conservation concern were recorded in forests in older age classes in this study.

Thicket supported the highest bird density, similar to the findings of a previous study that used broader age classes (Patterson *et al.*, 1995). This may be due to the fact that, unlike other stages, Thicket held relatively high densities of both migrants and resident species. In contrast, migrant density was lower in Closed canopy. Bird species richness was similar between the different stages despite some turnover in species as plantations matured. Twenty-four species were recorded in Pre-thicket and 21 in Closed canopy, with 13 species common to both stages. This species turnover is illustrated by the ordination, where Pre-thicket separated clearly from the other stages. This pattern has also been shown for plantation forests in Britain (Fuller and Browne, 2003). These authors point out that the separation of Pre-thicket highlights the importance of this stage to the diversity of the coniferous forest cycle as the bird assemblage is markedly distinct, whereas those of the other stages more closely resemble each other.

Closed canopy tended to be occupied by a suite of generalist and forest adapted species while Pre-thicket was occupied by less common open habitat specialists, as well as some species found in other stages. This overlap may be due to the lack of forest bird specialists in Ireland. Island biogeographical factors (Kelly, 2008), an east to west decrease in bird species richness within Europe (Fuller *et al.*, 2007a) and historical loss of species due to extensive deforestation (Yalden and Carthy, 2004; Rackham, 2006) are possible explanations for this pattern. The generalist nature of the Irish avifauna means that plantation forests support a significant proportion of the terrestrial bird fauna (O'Halloran *et al.*, 1998).

Although their slopes were not significantly different, the rank-abundance curves suggest a change in community structure between Pre-thicket and Thicket and the Closed canopy stage. The steep curve in the Closed canopy stage shows that, as plantations mature, the bird community becomes dominated by a

small number of common species, despite the fact that species richness remains similar throughout the remainder of the forest cycle.

Migrant bird densities in Closed canopy forests were lower than in other stages because most migrant passerines to Ireland are typical of non-forest habitats (Fuller, 1995; Snow and Perrins, 1998; Robinson, 2005). In Great Britain, the proportion of migrants in first-rotation plantations is greatest in young and mature forests, with lower numbers present in intermediate stages (Donald *et al.*, 1998b). The mature forests with high migrant densities in that study were between 50 and 90 years old, whereas the maximum age of Closed canopy forests in our study was 50 years. Most commercial plantations in Ireland are felled at or before this age. However, the forest migrants such as Redstart (*Phoenicurus phoenicurus*), Wood Warbler, (*Phylloscopus sibilatrix*), and Pied Flycatcher (*Ficedula hypoleuca*), typical of forest habitats and partially responsible for the observed increase in migrants in later growth stages in Great Britain, are all but absent from Ireland. It is not completely clear as to whether this pattern is due to biogeographical factors such as Ireland's distance from migration pathways, or to historical deforestation. The fact that the aforementioned migrants breed in large numbers on the Eastern seaboard of Britain (Robinson, 2005), but are almost entirely absent in eastern counties of Ireland, such as Wicklow, that possess some apparently suitable habitat, suggests that deforestation alone cannot account for their absence. The absence of these species may limit the potential for increases in migrant density in later stages, even if Irish plantations were allowed to develop beyond commercial maturity, but this could be tested by allowing some plantations to over-mature.

5.5.1.2 Vegetation structure and differences between rotations

The ordination represents a gradient from immature, structurally diverse age class I (Pre-thicket) forests characterised by high shrub cover and a low, open canopy on the right, through to age class IV plantations characterised by high needle and moss cover and low shrub cover on the left. There is relatively little difference in these structural variables between age class III and IV forests and therefore little change in bird habitat in the last 20 years of a forests' rotation, which helps to explain the overlap in the bird communities of these age classes.

Shrubs benefit birds by increasing habitat heterogeneity (Berg, 2002; Diaz, 2006) and providing nest sites and invertebrate prey (Quine *et al.*, 2007). In light of this, the fact that the forests with the highest levels of shrub cover, Pre-thicket, also had the lowest total bird density in both rotations initially appears counter-intuitive. Low bird density has previously been noted in young plantations (Donald *et al.*, 1998; Bibby *et al.*, 2000) and may be due to the lower surface area of the crowns and trunks of small trees for foraging and nesting.

Despite there being no significant difference in total bird density between rotations in Pre-thicket after correcting for natural population increase, second-rotation Pre-thicket did support significantly higher migrant bird density than first-rotation Pre-thicket. This likely reflects the fact that many migrant passerines to Ireland utilise shrubs for nesting or foraging (Fuller, 1995; Snow and Perrins, 1998; Robinson, 2005), and the higher shrub cover in the second rotation increased the carrying capacity of this age class for such migrant species. However, some resident species, notably Skylark which is a species of conservation concern (Lynas *et al.*, 2007), were recorded at lower density in second-rotation Pre-thicket than in the first rotation. Skylark requires open ground for nesting (Snow and Perrins, 1998) and the increase in shrub cover may render second-rotation Pre-thicket less suitable than first-rotations for this

species. A similar mechanism may explain the lower densities of Meadow Pipit and Reed Bunting in second-rotation Pre-thicket.

The indicator species for the three stages in this study differed slightly to those of the three stages in the first rotation (Wilson *et al.*, 2006), but there was considerable overlap. This suggests that, although differences exist in both vegetation structure and the bird communities of a particular stage in different rotations, these differences are not fundamental enough to change their suitability to particular species. For example, Chaffinch was an indicator of Closed canopy forest in the first rotation and Thicket in the second, but it seems unlikely that this pattern is driven by fundamental differences in second-rotation forests. Chaffinch is a widespread generalist species and was also present at relatively high density in second-rotation Closed canopy.

Second-rotation forests differ from those of the first-rotation in their pre-planting state. While afforestation typically involves a change from open habitat to forest, second-rotation plantations replace recently harvested forests. Forestry activities can affect soils (Worrell and Hampson, 1997), and the productivity of a site may increase in later rotations as a result of deposited organic matter (Fox, 2000). Additionally, young stands of second-rotation forests may differ structurally from first-rotation stands because non-crop tree species have had more time to colonise both prior to and following clear felling. (Cooper *et al.*, 2008). Because changes in bird communities are often related to changes in vegetation (Cherkaoui *et al.*, 2009; Nikolov, 2009) we may therefore expect young second-rotation plantations to have a higher carrying capacity for birds than similar aged first rotation plantations.

However, the greatest differences between rotations existed in later stages when structural complexity was low in second rotation forests, and differences in vegetation between rotations was small. In Closed canopy, differences between rotations were largely due to increases in two species, Coal Tit and Goldcrest, and, when these species were removed, the difference in total density between rotations in Closed canopy was no longer significant. Work is ongoing to test whether invertebrate abundance is different between rotations, and whether this can explain the difference in Coal Tit and Goldcrest density. Populations of both Coal Tit and Goldcrest are increasing in Ireland, perhaps as a consequence of increasing forest cover, and so natural population increase in the time period between the first and second rotation fieldwork may also account for some of the difference. Finally, because different observers were used in the first and second rotation fieldwork and density estimations of Coal Tit and Goldcrest are particularly prone to observer differences, it is difficult to completely exclude an effect of observer on the densities of these species.

Bird density remained higher in second rotation Thicket after the removal of Coal Tit and Goldcrest, despite a reduction in shrub and field layer cover in the second rotation. Some birds may utilise young plantation trees as tall shrubs (Loyn *et al.*, 2007), and the slightly taller trees and higher canopy cover in the second rotation may therefore have provided more nesting and foraging opportunities. The increase in canopy cover in second rotation Thicket may reflect a slight improvement in growth rates of the crop species in the second rotation. The higher densities of Robin and Chaffinch in second-rotation Thicket are difficult to explain, as shrub and canopy cover were similar between rotations. Both are generalist species that thrive in a range of habitats, although Robin may benefit from brash piles in second-rotation forests left over after clearfelling (Snow and Perrins, 1998).

Migrant birds are typically more vulnerable to decline than sedentary species (Heldbjerg and Fox, 2008; Kirby *et al.*, 2008). The higher density of migrants in second-rotation Pre-thicket therefore suggests that the increasing extent of second-rotation Pre-thicket in the landscape may be a positive development for such species, especially as some of the migrant species in this study have declined in other parts of their ranges (Hewson and Noble, 2009). However, comparisons of densities recorded in different years must be interpreted with caution as breeding numbers of species such as Grasshopper Warbler are known to fluctuate from year to year (Snow and Perrins, 1998).

5.5.2 Mixed tree species survey

We found no consistent differences in bird assemblages between mixed and pure plantations, although the trend was for both Scots pine and oak mixes to have higher species richness, Simpson's diversity and total bird density than pure Norway spruce plantations. Finding mixed plantations proved to be very difficult, and the power of the study to detect differences between the sites types is restricted by the heterogeneity between the sites and by the small sample size. It should also be noted that the ability to translate these findings into recommendations for future plantation forest management depends on the observed patterns in Norway spruce being a good model for Sitka spruce, as the latter is by some distance the most abundant plantation forest tree species in Ireland. The composition of the bird assemblages of Norway and Sitka spruce have been shown to be broadly similar (O'Halloran *et al.*, 1998), and Norway spruce may even support more bird species than Sitka spruce, which allows less light penetration (Batten, 1976). The higher species diversity in Norway spruce could be due to its status as a native species over much of Europe, where many of the bird species considered in this study are also commonly found. Sitka spruce, by contrast, is a native of North America. The impact of a native tree mix component on bird assemblages may therefore be even more pronounced in Sitka spruce plantations than in those composed of Norway spruce.

The relationship between shrub cover and bird density, species richness and Simpson's diversity suggests that the ecological state of the forest rather than the tree species *per se* probably exerts the greatest influence on the bird communities of plantations. It is well documented that structural attributes affect populations of various bird species in forests (e.g. Quine *et al.*, 2007). Shrubs provide both nesting and foraging sites for many forest breeding birds, both native and plantation (Fuller, 1995), and a covering of shrubs under the canopy therefore increases the carrying capacity of a stand for a wider range of birds, increasing density, species richness and diversity. The population densities of species that are highly arboreal, such as Coal Tit and Goldcrest, varied less between the forest types as shrubby vegetation is not as important to their life-histories. The presence of rides in a stand was also significantly associated with bird density. Rides act as elongated clearings in forests and, like roads and glades, allow increased light penetration and enhance non-crop plant diversity (Smith *et al.*, 2007), which may in turn result in higher numbers of birds using such areas for foraging. We did not find a significant influence of the area of open space on birds, but this may be due to the fact that most forests possessed very little open space, with only a small number of stands having a large amount of open space due to the presence of areas of windthrow or parking bays. Although it is recommended to leave some open space for biodiversity considerations (Forest Service, 2000a), plantations are managed primarily for timber production and therefore open space is probably minimised. It is not immediately obvious why field layer cover should negatively influence bird density, and this result may be due to the relationship between shrub and field layer cover: in forests where shrub cover was high, field layer cover tended to be low and vice versa.

Understorey vegetation, including shrub cover, is affected by light intensity which is in turn influenced by canopy openness (Smith *et al.*, 2008). Although we found no current difference in canopy openness between Scots pine mixes and pure Norway spruce, the higher levels of shrub and understorey vegetation in the Scots pine mixes suggest that historical differences in growth rates of the crop trees may have previously allowed greater light penetration. Initially, the fact that pure Norway spruce canopies were slightly more open than those in oak mixes appears difficult to explain. However, this can probably be explained by sampling technique: the camera was mounted on a tripod which was situated 1.3metres above the ground. Therefore understorey vegetation (which included most of the oak trees that had become out-competed by the surrounding Norway Spruce and was significantly higher in oak mixes than in pure Norway spruce) also influenced the measure of openness.

That openness may affect non-crop vegetation, which in turn influences bird communities (Wilson *et al.*, 2010), suggests that forest management has an important role to play in maximising the utility of plantations for birds, as thinning increases light transmittance through a coniferous canopy (Hale, 2003a). However this runs contrary to the findings of a study in Scotland where management, in the form of thinning, had little effect on breeding bird communities (Calladine *et al.*, 2009). It may be that variation in thinning intensity between treatments in this study was too low to exert a strong influence on light penetration and thus understorey vegetation, a result of forest managers wishing to maximise crop tree growth for pulp production and minimise growth of competitive non-crop understorey species (J. Calladine, *pers. comm.*).

We controlled for the influence of management where possible by selecting forests that were structurally similar, thus indicating a similar management history. Some structural variation did exist among the sites but, as neither stem density, DBH nor basal area differed significantly between the forest types, observed differences are unlikely to be driven by differences in thinning regimes. A study of British forests has shown that mixed plantations possess bird communities intermediate between those of pure coniferous and pure broadleaved stands (Donald *et al.*, 1998b). This pattern was not evident in this study where differences between the pure Norway spruce and the mixed plantations were small. This could be partially due to the paucity of specialist woodland bird species in Ireland, which results in much of the breeding bird fauna utilising a variety of habitats, including coniferous plantations. In contrast, several species that are not part of the Irish breeding bird fauna exhibited close associations with broadleaved stands in Britain (Donald *et al.*, 1998b).

Several species have been identified that occur in Irish coniferous plantations but that are more closely associated with broadleaved vegetation: Blackcap, Blue Tit, Bullfinch, Chiffchaff, Great Tit, Long-tailed Tit, Treecreeper and Willow Warbler (Wilson *et al.*, 2010). To this list Garden Warbler and Spotted Flycatcher may be added (Fuller, 1995). We found that all of these species, except Willow Warbler and Garden Warbler, achieved their highest population densities in mixed plantations, with some (e.g. Blackcap, Blue Tit and Treecreeper) two to three times as abundant in mixed plantations as they were in pure Norway spruce. Garden Warbler was only recorded once in dense shrubs in an area of windthrow at the edge of a pure Norway spruce plantation which was situated close to Lough Erne, the Irish breeding stronghold of the species (Herbert, 1991). Bibby *et al.* (2000) suggest that one method of judging the success of conifer plantation management could be the presence of broadleaved-associated birds in such plantations. In this regard, oak and Scots pine mixes were superior to pure Norway spruce. In the case of the oak mixes the

obvious explanation for the higher population densities of broadleaved-associated species is the presence of broadleaved trees. However, Scots pine is a conifer and therefore another mechanism is likely to explain the increase in these species in the Scots pine mixes. Enhanced growth of non-crop vegetation due to increased light penetration associated with a more open canopy may have resulted in the higher understorey and shrub cover that was recorded. The habitat provided by such non-crop vegetation is probably responsible for the increase in population density of broadleaved-associated birds in Scots pine mixes ((Bibby *et al.*, 2000); Wilson *et al.*, 2010). This explanation is supported by the fact that the highest population densities of most recorded species (16 of the 25 species analysed), not just those that prefer broadleaved trees, were found in the Scots pine mixes. Grazing also affects bird communities through altering vegetation structure (Donald *et al.*, 1998b; Fuller *et al.*, 2007b) but, as no grazing animals were observed in any of the study sites, this is unlikely to have been a contributing factor to the differences among the forest types.

Some of the differences between the oak and Scots pine mixes may be due to the different growth rates of the secondary tree species. In the Scots pine mixes the Scots pine was a component of the canopy, while frequently in the oak mixes the oak acted as an understorey. It is not recommended to grow oak and Norway spruce in the same plantation due to the possibility of suppressing the oak component (Joyce, 2002), and this has occurred in all of our study sites. Management to encourage more vigorous growth of the oak component, either by thinning or planting oak in clumps where individual trees are not in direct competition with the primary plantation species, may increase the utility of oak mixes to birds. Another possible solution, which may be preferable from a commercial point of view, is to mix conifers and broadleaves at a larger scale by planting pure stands adjacent to each other (Archaux and Bakkaus, 2007).

Because of the longer rotation time of oaks, the oak component of our study sites would be left after felling the conifers. Any subsequent rotation may therefore contain a secondary oak component that is much more similar in size to the surrounding conifers. Unfortunately few, if any, such stands currently exist in the Irish landscape, and testing the potential influence of such stands on birds is therefore not yet possible.

5.5.3 Comparison of plantations and native woodlands

The clear separation of oak and ash native woodlands from Sitka spruce plantations via ordination illustrates distinct structuring of the bird communities of native woodlands and plantation forests. This provides support for the idea that plantations are complementary habitats (Donald *et al.*, 1998b; Barlow *et al.*, 2007). The difference in species richness and Simpson's diversity suggests that the carrying capacity of plantations is lower than that of native woodlands for most bird species. That much of the generalist terrestrial bird fauna that characterises Ireland is present at low densities in plantations is an important finding and suggests that differences between plantations and native woodlands will be more pronounced in areas with a specialised woodland bird fauna.

The Simpson's diversity index is a function of both the number of species and their abundance, and the significantly lower Simpson's diversity in plantations reflects the fact that a few species (primarily Coal Tit and Goldcrest) dominate the bird fauna of plantations in these age classes. Similar patterns of low diversity and dominance of a few species in coniferous plantations have been observed previously ((Bibby

et al., 2000); Fuller and Browne, 2003), but not in as pronounced a way as reported in this study where Coal Tit and Goldcrest accounted for approximately 60% of the total bird density in plantations.

Other species common to plantations, such as Chaffinch and Robin, achieved similar densities in native woodlands whereas densities of Coal Tit and Goldcrest were much lower in native woodlands than in plantations. Both Coal Tit and Goldcrest are largely arboreal and small-bodied and Goldcrests feed on very small invertebrates of the orders Hemiptera and Collembola (Fuller, 1995; Snow and Perrins, 1998) which are abundant in Sitka spruce plantations (Straw *et al.*, 2006). Besides also feeding on invertebrates, Coal Tits utilise spruce seeds taken from cones (Snow and Perrins, 1998). Such diet preferences may render plantations more suitable for these small bodied species, rather than larger species which may not utilise the smallest prey items. This may help to explain the high population densities of Coal Tit and Goldcrest in plantations.

Several species recorded in this study have been identified as occurring in Irish Sitka spruce plantations but being closely associated with non-crop broadleaved elements (Wilson *et al.*, 2010). Each of these species (Blackcap, Blue Tit, Bullfinch, Chiffchaff, Great Tit, Long-tailed Tit, Treecreeper and Willow Warbler) was at highest density in either oak or ash woodlands, in some cases being several times as abundant as in plantations. Garden Warbler and Spotted Flycatcher can be added to this list of species that prefer broadleaved vegetation (Snow and Perrins, 1998). The occurrence of broadleaved-associated species may be one way in which the quality of plantations can be evaluated (Bibby *et al.*, 2000), and by this measure plantations are currently lower quality habitat for birds than native woodlands. This offers a solid method by with which the effectiveness of future plantation management can be evaluated in terms of its success in bird conservation.

Two species of conservation concern were detected in this study, the Spotted Flycatcher and the Stock Dove. Both are on the Amber list of birds of conservation concern in Ireland and the Spotted Flycatcher is also a Species of European Concern (Lynas *et al.*, 2007). The Spotted Flycatcher was found in both oak and ash woodlands but not in Sitka spruce plantations, while the Stock Dove was found in only one oak woodland. The Spotted Flycatcher requires open areas and perches for foraging so the typically uniform nature of Sitka spruce plantation canopies may be less suitable. In the case of Stock Dove, native woodlands probably offer tree hollows for nesting (Snow and Perrins, 1998).

5.5.3.1 Vegetation structure and bird communities

Species richness and Simpson's diversity were both significantly related to vegetation structure; in particular understorey cover and shrub cover. Bird species richness is associated with vegetation structure (Cherkaoui *et al.*, 2009; Nikolov, 2009), and changes in the structural diversity of woodland is one possible contributing factor to observed declines in British woodland bird populations (Fuller *et al.*, 2007b; Gill and Fuller, 2007; Hopkins and Kirby, 2007b).

Canopy cover is negatively associated with understorey vegetation in plantation forests (Smith *et al.*, 2008), which suggests that measures to reduce canopy cover and allow more light penetration could benefit bird diversity and species richness through the promotion of heterogeneous vegetation layers (Ding *et al.*, 2008) which, in turn, provide nesting and foraging opportunities for a wide range of bird species (Quine *et al.*, 2007). The positive relationship between Simpson's diversity and stem number is likely a consequence of the more uneven canopy cover in native woodlands permitting the growth of

understorey vegetation and saplings, thus providing more structural diversity. Invertebrate species richness may increase with field layer cover (Oxbrough *et al.*, 2005), and higher levels of field layer cover may thus result in the provision of more invertebrate prey for birds which helps to explain the association between Simpson's diversity and field layer cover. Mature coniferous plantations may have low structural diversity in the field and shrub layers (Ferris *et al.*, 2000a) and so may represent a lower quality habitat for birds than unmanaged, structurally heterogeneous native woodlands.

The negative association between understorey cover and total bird density initially appears paradoxical when viewed in light of the positive influence of understorey vegetation on Simpson's diversity and species richness. However, understorey vegetation tended to be sparse in Sitka spruce plantations (the maximum value was 8%) yet total bird density was slightly higher than in oak and ash native woodlands where understorey vegetation was abundant (maximum value 67%). The model thus negatively associated understorey vegetation with bird density.

Blue Tit, Great Tit and Treecreeper, indicator species identified for oak and ash woodlands, are all associated with structural aspects of woodlands. Blue Tit and Great Tit are hole nesting species (Fuller, 1995) and it is likely that populations of cavity nesting species are limited in plantations as a result of short rotation times and a lack of old, cavity rich trees (Newton, 1994). Treecreepers do not require holes but utilise loose bark and fissures (Fuller, 1995), which are also likely to be more common on older trees. The herbivorous diet of Woodpigeons means that native woodlands, with more shrub and understorey vegetation, likely provide higher quality foraging opportunities, hence the identification of this species as an indicator of native woodlands. The occurrence of Robin as an indicator for both native woodlands and age class III plantations reflects this species' ability to utilise a wide range of habitats (Fennessy and Kelly, 2006). Dunnock, common in the age class I and II (4-16 years) of plantations (Wilson *et al.*, 2006), was also an indicator of age class III Sitka spruce plantations. This was surprising as it is a species more associated with scrub (Fuller, 1995). It may be that the species manages to persist from early age classes into age class III, but the oldest plantations become unsuitable, hence the species absence from age class IV of the plantation forest cycle.

The oak and ash woodlands that were used in this study are all considerably older than any of the plantations. Commercially over-mature (90-150 years) stands of conifers in Britain are utilised by birds that are associated with broadleaves ((Bibby *et al.*, 2000); Donald *et al.*, 1998b). Were Irish plantations allowed to mature to a similar age as native woodlands, bird communities of Sitka spruce plantations may eventually come to resemble those of native woodlands as structural diversity increases. Currently, some plantations are being left to mature beyond commercial felling age to provide seed for stock and for recreation purposes, and it would be interesting to survey the bird communities of such plantations in the future. However, current typical forestry practice involves clearfelling and replanting, and over-mature stands are therefore only likely to occur in areas that are inaccessible or no longer economically viable to harvest.

5.5.4 Comparison of forest types in winter and breeding season

5.5.4.1 Winter bird assemblages

The extensive overlap in the composition of the bird assemblages between the native woodlands and plantations in winter indicates greater mobility of birds in winter compared to the territorial behaviour

exhibited by many breeding birds (Bibby *et al.*, 2000). Many species recorded in this study are known to change their distributions and to diversify their food sources between seasons (Simms, 1971; Perrins, 1979; Fuller, 1982; O'Halloran *et al.*, 1998). In English forests, bird assemblages are distinct between coniferous, mixed and broadleaved forests in winter (Donald *et al.*, 1997), but this partitioning is not as evident in Irish forests. Breeding individuals may choose a preferred nest site (Goodenough *et al.*, 2009) and, where several species exhibit this behaviour, distinct structuring of bird assemblages will occur as a result of differing habitat preferences between species. By contrast, because resources are scarcer in winter than the breeding season (Newton, 1998), the priority for birds in winter is obtaining food. Much of their daily energy expenditure may be used in metabolism (Alatalo, 1978), and Long-tailed Tits may spend as much as 90% of the day feeding (Perrins, 1979). The need to accumulate energy reserves, in the form of fat, is balanced against increased predation risk of heavier birds (Gosler *et al.*, 1995). Because the Irish songbird fauna is largely composed of generalists, individual species may be less restricted to a particular habitat. This could result in many species utilising a variety of habitats to meet their winter resource requirements, which would be consistent with the indistinct patterns of winter bird assemblages found in this study. The fact that the bird assemblages of both native woodlands and plantation forests changed markedly across seasons suggests that the bird assemblages of both forest types respond to seasonal changes in a similar manner.

In winter, species richness and Simpson's diversity were higher in oak and ash woodlands than in age class III and IV Sitka spruce, but no differences were found between the other plantation forests and native woodlands. In English forests, broadleaved stands have higher species richness than coniferous stands in winter (Hill *et al.*, 1991; Donald *et al.*, 1997), and the differences between the native woodlands and plantations detected in this study are smaller than might have been expected from these studies. This may also be attributable to the highly generalist nature of the Irish songbird fauna.

The high density of birds in all forests in winter when compared to breeding season densities is a particularly interesting result. Winter populations of species are augmented by an influx of European birds (Lack, 1986), and winter bird populations, of both resident and migratory species, have been shown to be large in Ireland in respect to British populations. This is likely due to Ireland's mild climate (Rohan, 1975). High overwinter survival, leading to high resident bird populations early in the breeding season, is a potential explanation for low breeding migrant density. Migrants arriving to an area may be unable to compete with resident birds that have had a head start in breeding (O'Connor *et al.*, 1986). The lower winter density of resident birds in age class I may therefore be one reason why breeding migrant density is higher in this age class than the other studied forests. On the other hand, the high breeding densities of resident birds in mature woodland may help to explain why Ireland lacks migrant species such as Redstart (*Phoenicurus phoenicurus*), Pied Flycatcher (*Ficedula hypoleuca*) and Wood Warbler (*Phylloscopus sibilatrix*) that breed in mature British forests (Donald *et al.*, 1998; Robinson, 2005).

Another notable finding of this study was the high densities of Goldcrest in all forests. High densities of Goldcrest in the age class III and IV Sitka spruce plantations were found in the breeding season, but winter densities were approximately 30% higher. In the case of native woodlands, winter Goldcrest density was three times higher than in the breeding season. Individuals of this species that breed in other European countries are known to overwinter in Ireland (Lack, 1986) which helps to explain the higher densities recorded in winter, but the winter densities in native broadleaved woodland are surprising. It is possible that native woodlands are sub-optimal habitat for Goldcrest, a species associated with coniferous

forests (Snow and Perrins, 1998b), and that the high density of resident Goldcrest requires winter arrivals to occupy this sub-optimal habitat. Targeted research is required to further explore this hypothesis.

5.5.4.2 Vegetation and birds in winter

The negative relationship between bird density and evergreen shrub cover can be explained by the abundance of Gorse in age class I, the age-class that held the lowest density of birds. Bird abundance has previously been shown to be higher in older forests than in younger forests in winter (Patterson *et al.*, 1995; Donald *et al.*, 1997) and this study supports these findings. However, in contrast to those studies, there was no influence of forest age on species richness in this study. Understorey vegetation and ivy were found to be positively related to bird species richness, Simpson's diversity and density in winter.

Because holly and ivy were large constituents of shrub and understorey vegetation in the studied forests, it is likely that berries, and perhaps shelter, provided by these two plant species is a driver behind the observed patterns. Ivy berries are very nutritious due to their high fat content (Snow and Snow, 1988). Blackbird, Redwing and Song Thrush all eat berries in winter (Snow and Snow, 1988) and were all indicator species for ash woodland. Leaf litter is also abundant in native woodlands in winter, and all three species may forage in leaf litter for ground-dwelling invertebrates (Fuller, 1995; Snow and Perrins, 1998b). Such ground-foraging habits may help to explain why Song Thrush was also an indicator for age class III. Other common understorey plant species in Irish forests include hazel (*Corylus avellana*), birch (*Betula* spp.) and willow (*Salix* spp.) which provide catkins and, in the case of birch and hazel, seeds that are eaten by species such as Blue Tit, Great Tit, Redpoll and Siskin (Perrins, 1979; Fuller, 1995). Blue Tit was an indicator species for oak and ash woodland in winter, likely reflecting their use of deciduous leaf buds for feeding (Perrins, 1979).

Higher levels of understorey vegetation in native woodlands are also likely to explain the positive relationship between density of stems and bird density, which supports research in England forests that found winter species richness and bird abundance to be positively associated with sapling density (Donald *et al.*, 1997). However, that study also found a positive influence of shrub cover on bird assemblages, which was not evident in this study. One possible explanation for this is that bramble (*Rubus fructicossus* agg.), which was a large component of the shrub layer in this study, does not produce fruit in winter. This may reduce its importance to birds in winter relative to species such as holly and ivy. However, shrub cover is likely to have been important to some individual species. The identification of Wren as an indicator species in age class and the oak mix plantations is likely due to the high shrub cover which was typical of both these forest types, and with which high densities of Wren are associated (Hill *et al.*, 1991; Fuller, 1995).

5.5.4.3 Comparisons with the breeding season

Although a weak gradient in winter bird communities was identified from pure Sitka and Norway spruce plantations through, to mixed plantations and native woodlands, assemblages were much less distinct than during the breeding season. Especially notable in this regard is age class I. Because age class I more closely resembles scrub than a forest habitat, the breeding bird assemblage of this age class includes migrant warbler species that prefer open habitats for breeding (Snow and Perrins, 1998b), some of which were identified as indicator species in age class I in the breeding season. These species are absent from Ireland in winter, with the result that the winter bird assemblage of age class I is less distinct from the other forest types. Interestingly, the winter assemblages of age clas I forests were grouped more

closely to the native woodlands than the other plantations. This may have been due to the occurrence of Bullfinch and Redpoll in both age class I and native woodlands. One species of conservation concern, Linnet, was also recorded in age class I in winter, the only time a species of conservation concern was recorded in the study in winter.

Approximately one third of the variation in winter species richness and Simpson's diversity was explained by the breeding season values for these variables (35% and 28% respectively). The correlations between breeding season and winter bird diversity may be due to certain aspects of forest vegetation and structure, such as understorey cover and stem density that exerted similar influences on the bird community in both seasons. The explained variation was lower for bird density (20%) and the correlation significant only after excluding Coal Tit and Goldcrest from analysis. However, 20% is a stronger relationship than that shown for coniferous plantations in Britain (Patterson *et al.*, 1995), which may be due to the inclusion of native woodlands in this study. The absence of several migrant species from Ireland in winter, and an influx of birds from Europe to overwinter in Ireland, may explain the relatively low amount of winter variation in bird density explained by breeding season patterns in this study.

The correlations between seasons show that forests that provide the best quality habitat in the breeding season also provide the highest quality habitat in winter. Greater structural diversity may provide more food in winter, and both food and nest sites in the breeding season (Quine *et al.*, 2007). Some tit species may also store food in the breeding season for use in winter (Perrins, 1979), and such individuals would therefore tend to occupy or return to the same areas in both seasons. That bird density did not correlate between seasons prior to the removal of Goldcrest and Coal Tit may be due to the arboreal habits of these species. Both obtain insects and, in the case of Coal Tits, spruce seeds in winter from the canopies of coniferous forests (Snow and Perrins, 1998b). Therefore, they may not be as responsive to differences in shrub and understorey vegetation as those species that primarily utilise these layers for foraging.

5.5.4.4 Forest area

Bird species richness of small woodlands in England is positively related to forest area in the breeding season and in winter (Bellamy *et al.*, 1996; Vanhinsbergh *et al.*, 2002), but individual species may change their responses to forest area between seasons (Yamaura *et al.*, 2009). However, no relationship between forest area and either species richness or Simpson's diversity was evident for birds in Irish forests in either the breeding season or winter. This is likely a consequence of the lack of forest specialist bird species in Ireland which may be restricted to forest habitats in both seasons. In this study, total bird density was negatively correlated with forest area in the breeding season, but there was no relationship between forest area and bird density in winter, although the sample size was small (14 forests). Winter bird abundance in England is not related to stand size either (Donald *et al.*, 1997). Flocking may decrease the similarity of bird distributions between the breeding season and winter (Møller, 1984), perhaps through increasing the variability of bird density estimates, as estimates will depend on both the successful detection of flocks and the size of the detected flocks. This variability in winter density is evident for the native woodlands in this study and may reflect both the more seasonal nature of deciduous woodlands as opposed to coniferous plantations, and resource depletion of woodlands as winter progresses.

5.5.4.5 Conclusions and management implications

The breakdown in distinction between the bird assemblages of native woodlands and plantation forests in winter when compared to the breeding season indicates that birds in both forest types respond to seasonal changes in a similar manner. Understorey and ivy cover, as well as the stem density, are important influences on winter bird assemblages. Plantation forest managers should seek, therefore, to maximise understorey vegetation cover, particularly of those plant species that provide winter food such as holly and ivy, for the benefit of birds in winter. There is overlap between the vegetation and structural components of Irish forests that are important for breeding birds and that are important for birds in winter. Such similarity helps to explain why winter species richness and Simpson's diversity correlated with breeding season patterns, and means that managing forests for the benefit of winter birds will benefit birds in the breeding season and vice versa. Winter bird densities were high in all forests compared to the breeding season, which may be due in part to an influx of birds from continental Europe. This raises interesting questions about the species richness and breeding densities of spring migrant species in Ireland.

5.6 Deadwood

The size distribution of logs in native woodlands resembled that of young-growth (Green and Peterken, 1997) and managed forests (Siitonen *et al.*, 2000) elsewhere in Europe, with only two large logs (> 40 cm diameter) recorded in this study study. Large living trees are a prerequisite for large logs and snags, and these are scarce in Irish forests (Coote *et al.* unpublished data). In terms of CWD volume, Irish forests also fall well below old-growth forests. This is partly a consequence of the low numbers of large-diameter dead logs which contain large volumes of deadwood, but may also be a consequence of Ireland's mild, damp climate which likely results in rapid decomposition of deadwood. The high density of small snags that we recorded may be the result of stem mortality due to competition. Old-growth forests are characterised by having fewer snags with larger DBH (Nilsson *et al.*, 2002) with one study finding 60% of snags to be over 30cm DBH (Jonsson, 2000). The prevalence of such snags in Irish forests is just 1%.

We found that log volume in forest plantations decreased considerably when we used a larger (> = 10 cm) minimum log diameter than the standard 5cm, which indicates that deadwood in plantations is largely composed of small diameter timber. Current forestry guidelines (Forest Service, 2000b) state that some deadwood should be left *in situ* after thinning and harvesting. Thinning is routinely carried out in plantations in the Republic of Ireland (where all second rotation Sitka spruce plantation forests were located) to promote the growth of remaining trees, and some of the smaller diameter thinnings may be left through biodiversity considerations. Such timber accounted for a large proportion of logs in some plantations. According to our results, many Irish plantations may exceed the deadwood volume guidelines, but the guidelines are low and more ambitions targets would be desirable. Plantations in this study contained a greater amount of deadwood in stumps than in logs. The higher stump volume in our study is probably due to the fact that all forests were in their second rotation and some stumps still persist from when the sites were last harvested. The large number of intact stumps recorded suggests that recent thinning has further increased stump density. Our findings suggest that stumps are an important source of deadwood in plantations and that the value of this resource for some saproxylic species may increase as sites enter later rotations and more stumps become part or well rotted.

5.7 Terrestrial laser scanning

Investigation of the potential for using ground based Lidar to provide an alternative to manual surveys of forest biodiversity measurement was an interesting addition to the FORESTBIO project. We looked at a novel approach to predicting biodiversity in forests by reasoning about their physical structure. This approach is based on terrestrial scans of forests from which a rich physical description of a forest can be obtained. Based on such a description, we have shown how several standard data-mining techniques can accurately predict five biodiversity measures of the species richness and abundance of birds, spiders and beetles. This study presents a first step in assessing the potential to automate the development of a world inventory of forests rich with environmental concerns. In our future work we plan to significantly expand the set of features that can be extracted from the laser scans. Of particular interest will be the measurement of standing deadwood in a clear and user-friendly manner. The results attained on application of Multilayer Perceptron, REP Tree and Linear Regression are very strong, most significant at the 99% level. Multilayer Perceptron was the best performing function regardless of execution time. Linear Regression as facilitated by the environment for knowledge analysis that was used for data-mining (WEKA) was the most transparent, user-friendly function of the 5 that also performed well. The results

attained via the methodology required just basic programming experience, and once automated the required tasks could be carried out by users with knowledge of Microsoft Excel. However, extensive use was made of Faro Scene scan point cloud manipulation software and TreeMetrics AutoStem tree profiling software.

5.8 Cross-taxon analysis

5.8.1 Limitations of this study

This study has documented the ground vegetation, ground-dwelling spider and beetle, Lepidoptera, canopy-invertebrate, epiphyte and bird diversity of (i) Sitka spruce plantations over the second rotation forest cycle; (ii) Norway spruce plantations in monoculture and in a mix with either Scots pine or oak; and (iii) native oak and ash woodlands. However, when interpreting the results of this study, the caveats discussed below should be borne in mind.

This study has been limited to the forest types mentioned above, therefore there may be factors that affect biodiversity in forests of other coniferous or broadleaved species, planted in monoculture or in mixture, or in other native woodland types that we did not identify in our study. This study also does not address the relative biodiversity of other plantation forest or native woodland types. The examination of other conifer and broadleaved species across the forest cycle would be interesting, particularly for those conifer species that allow greater light penetration, such as pine and larch, and which may prevent the development of Closed canopy conditions during the middle of the forest cycle (Hill, 1979; Ferris *et al.*, 2000a). While the BIOFOREST project found no difference in species richness or diversity measures between ash and Sitka spruce plantations across the forest cycle (Smith *et al.*, 2005), the examination of plantations of other broadleaved species such as oak and birch (*Betula* spp), which support many phytophagous invertebrate species (Jones, 1959; Atkinson, 1992; Key, 1995) may show greater differences. A comparison between plantations of these broadleaved species and native woodlands incorporating the same species would also be informative. Other conifer/conifer and conifer/broadleaved mixes, planted in varying proportions and configurations, would also be interesting to examine, particularly species combinations that are better suited to growing together (such as birch and spruce), as these may produce greater contrasts in biodiversity between pure and mixed stands than those we found.

Although this study covered a wide range of taxonomic and functional groups, there were inevitably some important components of forest biodiversity that have not been sampled. We did not study fungi, many species of which are forest specialists, being associated with deadwood, forest litter or the mycorrhizae of particular tree species. As well as contributing to the compositional diversity of forests, fungi play a crucial role in nutrient cycling in forests, through which they can affect a wide range of other taxa (Ferris *et al.*, 2000b; Humphrey *et al.*, 2000). While a diverse range of invertebrate groups was studied, there are inevitably many taxa that were not studied, whose life histories, mobility, habitat and feeding requirements, differ in many respects from those we surveyed. It is important to bear in mind that the groups studied do not cover the entire range of invertebrate diversity within forest ecosystems. A study focussing on forest specialist groups of invertebrates, particularly those of functional importance, such as saproxylics and other decomposers, would be particularly valuable. The only vertebrate group studied was birds and, although other Irish vertebrate groups are generally species poor and lacking in forest specialists, forests may provide important habitat for bats, while mammals such as Red Squirrel and Pine Marten are forest specialists.

Our sampling design attempted to provide adequate levels of replication, and to counterbalance the confounding effects of environmental variation in data analysis, but this could not always be achieved. Due to the time-intensive nature of sampling, particularly of canopy-based fauna and flora, the levels of replication, levels of replication may not have been adequate to detect trends in biodiversity among

taxonomic groups. This applies especially to forest types for which only five sites were studied, which include the individual age classes in the reforestation survey, and the mixed Norway spruce plantations. While we attempted to match afforestation and reforestation sites as closely as possible in terms of location and soil type, both within geographical clusters and between rotations, this was not always possible. Matching for location and soil type was particularly difficult for the mixed and pure Norway spruce plantations due to the limited number of existing mixed plantations at commercial maturity. The selection of mix types was also constrained by the availability of Commercially mature mixed stands at the time of the study and they are therefore not representative of recent planting practice at the time of this study. Our criteria for selection of native woodlands, including minimum size, tree species composition and management history, greatly limited the number of woodlands available to us as study sites, so that the woodlands we studied are not fully representative of the range of biodiversity in Irish native woodlands.

5.8.2 Trends across the forest cycle and between afforestation and reforestation

Across the reforestation cycle, the different taxonomic groups displayed a similar pattern in their species richness with values generally high at the beginning and/or end of the cycle and low in the middle. Trends were also broadly similar between afforestation and reforestation, with the main differences related to retention of species between rotations, the presence of large, complex brash piles in Pre-thicket (age class I) reforestation sites and the higher canopy cover in reforestation. The different taxonomic groups also displayed a similar pattern in their community composition, with the early stages generally the most distinct, both between and within rotations, and composition converging towards the end of the cycle. In Pre-thicket (age class I) reforestation, the high species richness was probably due to a combination of germination of plant species from the seed/spore bank, colonisation of species from surrounding habitats and retention of species from the previous rotation. Therefore, the pre-planting habitat and the diversity of the surrounding landscape are likely to be important influences on the diversity of this stage and may explain the large variation in community composition. Increased afforestation in improved grassland landscapes is therefore unlikely to produce the same levels of biodiversity in Pre-thicket (age class I) forests. The fact that the number of species supported in Commercially mature forests was generally high number of species, and (for most of the groups investigated) included a higher number of forest-associated species than any other age class, suggests that measures aimed at enhancing the biodiversity of plantations in the later stages of the commercial cycle could have a positive impact on forest biodiversity. Measures focussed on forest-associated species and on improving the retention of these species between rotations would be particularly beneficial. The generally lower species richness of reforestation compared to afforestation plantations, and the fact that an increasing proportion of the forest estate has completed one or more commercial rotations, suggests that the potential of such measures to benefit biodiversity may be particularly great in second rotation forests. Despite the fact that groups followed the same general trends across the cycle, finer scale variation meant that there were few significant correlations across all age classes combined for species richness or forest-associated species richness, suggesting that the potential for surrogacy among the taxonomic group we looked at is low. Only canopy and lower trunk epiphytes had a correlation coefficient greater than 0.7, which is the level suggested for the diversity of one group to act as a surrogate for the other (see section 3.3.6.1.2). These

two groups are distinguished by their location on the tree rather than by taxonomic grouping, so it is not surprising that they are strongly correlated.

5.8.3 The effect of planting Scots pine or oak with Norway spruce

In our study sites, the presence of oak or Scots pine in an intimate mixture with Norway spruce appeared to have little effect on diversity and community composition of the taxa we studied, with the important exception of those groups specifically adapted to living or feeding on native broadleaved trees. Therefore, our results suggest that the inclusion of a light canopied conifer or a broadleaved species does not always increase light penetration to a point where the biodiversity of Norway spruce plantations is enhanced. Since Sitka spruce is the predominant plantation tree in Ireland and allows less light penetration through its canopy than Norway spruce (Hale, 2001), a mix component which succeeds in increasing light penetration will likely have a greater effect than for Norway spruce. The reason for the limited effect of the mix species on biodiversity may be due to the fact that the proportion of Scots pine in the mixtures studied was low and that the position of oak as an understorey tree was insufficient to have an effect, particularly on light penetration. Norway spruce and Scots pine are recommended as being compatible in mixture, while the only conifer species recommended as being compatible with oak are Scots pine and European larch (*Larix decidua*), with large blocks rather than small groups of oak recommended (Forest Service, 2000a). The Norway spruce/oak mixes studied were planted with the intention of the Norway spruce acting as a nurse species for the oak and being subsequently removed. In the continued presence of the Norway spruce, which was not removed after canopy closure, it is unsurprising that oak was outcompeted in the canopy and relegated to being an understorey tree. Sitka spruce is not recommended for planting in an intimate mix with Scots pine or with any broadleaved species, suggesting that mixtures of this kind would require planning or management to favour the less vigorous species, if outcompetition by spruce was to be avoided. Previous research on non-intimate Sitka spruce/ash mixes found little difference in the diversity of the conifer and broadleaved component, but differences in community composition indicated that the addition of the broadleaved component increased biodiversity at the plantation scale (Smith *et al.*, 2005). This suggests that the proportions and configurations of the mix components play important roles in the effect that a tree species mixture will have.

The formal analysis identified a number of significant correlations between the total species richness of the different taxonomic groups across all sites combined, suggesting that some of the species groups respond in a similar way within Commercially mature Norway spruce plantations, particularly Scots pine mixes, although these responses may not be proximally due to the same variable. For instance, while light penetration within the stand is important to plants, this in turn will influence the compositional and structural diversity of vegetation, which are important to several other taxonomic groups. Only the correlation between canopy-dwelling invertebrates and canopy epiphytes was greater than 0.7, suggesting that the potential for surrogacy among the taxonomic group we looked at is low. Some of the groups, particularly the ground-dwelling beetles, showed markedly differing responses to other taxonomic groups. There were fewer significant correlations for forest-associated species richness and none were greater than 0.7, suggesting that forest-associated species are more exacting in their requirements and that these requirements differ more among taxonomic groups than for more generalist species.

5.8.4 Differences between oak and ash native woodlands

Native woodland type did not generally have a major effect on biodiversity, other than for the ground vegetation and epiphytes, and for the ground vegetation this difference does not seem to hold for other oak and ash native woodlands in Ireland (Perrin *et al.*, 2008a). There were more differences in community composition between the two woodland types, suggesting that, as well as their pre-defined difference in vegetation type, they also support relatively different invertebrate communities. This suggests that conserving both oak and ash woodlands will increase biodiversity at the landscape scale, and it is probable that other woodland types in Ireland may also support distinct biodiversity, although this requires further investigation. The formal analysis showed some significant correlations for both species richness and forest-associated species richness for both woodland types combined but few had correlation coefficients greater than 0.7. Those that were greater than 0.7 were mainly between different plant groupings. There was little consistency in the groups that were correlated for both woodland types combined and when oak and ash woodlands were examined separately, other than for the vascular and non-vascular ground vegetation species richness. Most animal groups responded quite differently to the other groups and to each other.

5.8.5 Comparison of native woodlands and plantations

The general trend was for native woodlands to be more species rich and to support different communities to plantations. Since forestry plantations are the predominant forest cover in Ireland, this indicates that the species composition of forests is being altered. Where similar or greater numbers of species were supported in plantations, the communities differed from those in native woodlands, and where communities were similar, more species were supported in native woodlands. Ground-dwelling beetles did not follow this pattern, having similar numbers of species in spruce plantations and native woodlands, more forest-associated species in spruce than in oak woodlands, and a lack of distinct communities in plantations and native woodlands. The same pattern was also apparent from the Procrustes analysis, where ground-dwelling beetles stood out as having the fewest significant correlations with the other groups. This group is composed of generalist species and so its diversity is more influenced by geographic location than by forest type. Virtually all combinations of the other groups were significantly correlated, indicating a broad similarity in their responses at the coarse scale of all forest types combined. However, none of the groups had correlation coefficients greater than 0.7, which is the level above which one taxonomic group may be considered a potential surrogate for another. The closest groups to this level were the lower trunk and canopy epiphytes. These two groups are distinguished by their location on the tree rather than by taxonomic grouping, so it is not surprising that they are strongly correlated. The mean Procrustes residuals from the different forest types suggest that the taxonomic groups mirrored each other's community composition and abundance least in age class I (Pre-thicket) Sitka spruce plantations.This is probably due to the different levels of specialisation and mobility among the different taxonomic groups.

5.8.6 Cross-taxon surrogacy

Whether it is carried out for scientific, conservation or management purposes, the scope of a biodiversity survey is inevitably constrained by the resources available. In cases where not all taxa of interest can be included in a survey, information about unsurveyed taxa can be inferred from known relationships with

environmental variables (indicators) or other taxonomic groups (surrogate taxa). The latter approach has been advocated by several recent studies (e.g. Rodrigues and Brooks, 2007; Gioria *et al.*, 2010) and has a number of possible benefits. These benefits are most obvious when the status of one or more relatively cryptic, inaccessible or hard-to-identify groups can be effectively estimated using survey results from a different group that it is relatively easy to gather information from. For instance, epiphytes on the lower trunks of trees are much easier and safer to survey than canopy epiphyte assemblages in the same site. If this study had shown that the epiphyte assemblage in one situation could be used to predict that in the other, then using lower trunk epiphytes as a surrogate of those in the canopy would enable a substantial saving in survey resources compared to conducting a survey that comprehensively covered both vegetation layers.

The presence, abundance or diversity of a species or higher taxon depends on not one, but many environmental variables. In situations where two different taxa respond in a similar way to a broad suite of variables, estimating the status of one using survey data derived from the other may be easier than using environmental information to estimate the status of both taxa. If, as is often the case, the relationships between a taxon and its environment are poorly understood, using an ecologically similar surrogate taxon may result in better estimates than would be obtained using environmental variables. However, incomplete understanding of the ecology of either taxon in a surrogate pair may lead to unanticipated differences in their variation between sites – especially in ecological situations where they have not been studied before. Even ecologically and taxonomically similar groups can vary quite differently across a given spectrum of environmental variation (Ricketts *et al.*, 2002; Davis *et al.*, 2008). It is therefore safest to use surrogate taxa in situations where both groups have been studied before. However, the need for surrogates and indicators is necessarily greatest where prior knowledge is scant.

While the Procrustes analyses across all sites show that community composition of most of the taxa varies in a broadly similar way between sites, comparisons of the variation in species richness and forest-associated species richness between the different taxonomic groups revealed few significant correlations, and even fewer with a correlation coefficient greater than 0.7. Correlations between different groups within site types show even lower levels of congruence. In part this may be due to the reduced number of sites available for comparisons within subsets of the site types used in the procrustes analysis. However, the proportion of correlations that are significant (less than 10%) is smaller in comparisons of 7-10 sites than in comparisons using data from 6 sites or less. This suggests that small sample sizes are not the only reason for the low levels of congruence. Another likely reason is that, as the group of sites under consideration becomes more homogenous, the range of variation in taxon diversity and assemblage also decreases. Across all study sites, a correlation between two taxa might be due to the species richness and assemblage of the taxa responding to some of the same, broad differences in habitat between the sites. Sites of the same type will be much more similar to one another, and the more subtle differences between them may be more likely to affect different taxa in different ways. This is suggested by the fact that previous studies have found cross-taxon surrogacy to work best across large geographic scales, where the range of environmental variation is likely to be greater (Lewandowski *et al.*, 2010). Especially at small scales, animal and plant distributions are influenced by unmeasurable (stochastic) as well as measurable factors. Predicting the status or distribution of one taxon using another as a surrogate introduces the potential for twice as much stochastically-derived error in one's estimates as would relying on a suite of environmental variables that have a direct effect on the taxon under investigation.

Our data show that, although some relatively easily surveyed groups, such as vascular plants and birds, are congruent with many of the other taxa when looking across all study sites, the similarities in response are not strong enough to warrant use of these taxa as surrogates. Moreover, the usefulness of surrogates across all sites is questionable if the patterns they are based on can also be explained more simply in terms of site types. Taxon surrogacy would only be very useful if it could predict diversity and assemblage of hard-to-survey taxa with groupings of sites of a similar habitat. However, congruence within site-types, as measured by inter-taxon species richness correlations, was even lower. This strongly suggests that the taxa we studied cannot be used as surrogates of one another at the scales we studied. In order to capture a wide range of biotic variation, assessments of biodiversity in Irish forests must encompass several taxonomic groups, and/or rely on the use of non biotic (structural or functional) indicators of diversity.

5.8.7 Non-biotic indicators of biodiversity

We identified indicators of biodiversity value for afforestation and reforestation Sitka spruce plantations, for pure Norway spruce plantations and Norway spruce mixed with either Scots pine or oak, and for native woodlands dominated by oak and ash. There is broad overlap between taxa for several of these indicators, increasing our confidence that they might enable managers and operators to get an impression of a site's biodiversity value. This confidence is further increased by substantial overlaps between some of the indicators identified during the previous BIOFOREST project and those arising from the current project.

Indicators are not substitutes for surveys of fauna and flora in terms of providing detailed information about a site's biodiversity. However, they can serve as a means of assessing the effectiveness of management for biodiversity, or enable identification of sites with potential biodiversity interest without having to conduct labour- and time-intensive surveys. Indicators of specialist components of forest biodiversity should be given particular weight in assessments of forest habitats utilising the indicators proposed below. Rare specialists may make a greater contribution to the biodiversity of a site than do common generalists, the discrepancy between them increasing with the biogeographic scale being considered.

The results from this project suggest that certain environmental variables might serve as indicators of biodiversity. Using the taxon abbreviations listed below, each taxon from which the data supporting an indicator are derived, as well as the direction of the relationship between taxon diversity and the environmental variable is listed in bold font and placed in parentheses. Following this, all other taxa for which the environmental variable in question was investigated but no relationship was found are listed in italics and placed in square brackets. After this is a list of the study or studies from which the relevant data were derived (Afforestation and reforestation survey comparison = "Refor", Mixed tree species survey = "Mixes" or Native woodlands survey = "Natives"). Indicators labelled "Refor" are derived not only from biodiversity trends across the forest cycle within reforestation plots, but also from comparisons between first and second rotation forests. For indicators that overlap with indicators previously identified by the BIOFOREST project, a summary of the indicator description from the BIOFOREST project is given.

Abbreviations

B = Birds

CB = Canopy-dwelling beetles

CE = Canopy epiphytes

CI = Canopy-dwelling invertebrates

CS = Canopy-dwelling spiders

E = Epiphytes

GB = Ground-dwelling beetles

GV = Ground vegetation

GI = Ground-dwelling invertebrates

GS = Ground-dwelling spiders

I = Invertebrates

L = Lepidoptera

LE = Lower trunk epiphytes

Forest type (**B, E, GV, I**) Comparing native and plantations

The general trend was for native woodlands to be more species rich and support different communities to plantations. Where similar or greater numbers of species were supported in plantations, the communities differed from those in native woodlands, and where communities were similar, more species were supported in native woodlands. Since forestry plantations are the predominant forest type in Ireland, the preservation or extension of existing native woodlands, or management of plantations to encourage native-woodland characteristics, would typically act to enhance biodiversity at both the forest and landscape scales.

Canopy cover (**-E, +sheet web CS, -GS, -B, -GV**) [*CB, GB, L*] Refor, Mixes

BIOFOREST: Canopy cover negatively related to diversity of spiders and ground vegetation from Thicket stage onwards, while thinning was positively related

This was negatively associated with diversity of most taxa in conifer plantations. Increased light penetration allows the development of sub-canopy vegetation layers which are directly associated with plant species diversity, and provide habitat for many species of invertebrates and birds (see below). This relationship was reflected by an inverse parabolic relationship between diversity and forest age for several taxa, with the highest levels of species richness at the start and end of the commercial forest cycle.

Understorey and shrubs (**+B, +E**) Mixes, Natives

BIOFOREST: shrub cover positively related to bird diversity from Thicket onwards and, in study of open space, non-crop broadleaves positively related to bird diversity

As well as being associated with canopy openness and vertical diversity of forests, presence of understorey trees and shrubs can directly enhance bird and epiphyte diversity, by providing a more diverse range of bark texture and chemistry for plants to grow on, as well as increased foraging and nesting opportunities for insectivorous, berry-eating and hole-nesting birds. A comparison of trends across all study sites suggests that native broadleaved trees are associated with increased bird diversity, and shrub cover was positively associated with bird species richness in pure and mixed plantations.

Structural diversity (**+GV, +GI**) Refor, Mixes, Natives
BIOFOREST: shrub cover positively related to bird diversity from Thicket onwards, as well as in grasslands; cover of 10-50cm tall vegetation positively related to spider diversity from Thicket onwards

Both positive and negative relationships with species richness of different invertebrate taxa indicate that diversity of ground invertebrates within a stand will be favoured by a mosaic of different vegetation types. Vertical and horizontal variation in vegetation structure provides a variety of niches and microhabitats that increases the range of ecological strategies (and therefore species) that a forest can cater for. In plantations, structural diversity is typically predicted by canopy openness. In native woodland, however, canopy openness and structural diversity were not as closely related. It is likely that canopy openness in these woodlands was a much less limiting factor than in conifer plantations, partly because of the greater diffuse light penetration through the canopy and partly because of the seasonal variation in light penetration in deciduous woodlands.

Leaf and needle litter (-GV, -GB, +GS)

Conifer needle litter cover was positively related to diversity of ground spiders, probably due to this element of ground cover increasing the variety of habitat structures available to species in this taxon. This variable also appears to be negatively related to diversity of ground vegetation in conifer plantations, possibly due to its suppressing effect on plant establishment and growth. However, since needle litter is positively correlated with canopy cover, it is hard to distinguish between the potentially suppressing effects of both of these variables on ground vegetation. Broadleaved leaf litter in oak woodlands was also negatively related to diversity of ground vegetation. This relationship is much less likely to be due to a relationship between leaf litter and canopy cover, as the broadleaved canopy of oak woodlands is a much less effective barrier to light penetration than the canopy in conifer plantations. This suggests that leaf litter can actively suppress plant diversity in some oak woodlands. Leaf litter was also negatively related to the diversity of ground beetles, probably due to the generalist nature of this group, making them unsuited to exploiting deep litter layers.

Old woodland influence (**+E, +GV**) Refor, Mixes
BIOFOREST: distance to old woodland positively related to woodland vascular plant diversity

Both the epiphytic and ground vegetation of plantations can be positively influenced by sources from which forest species can colonise. Both proximity to old woodlands and area of old woodland within a 1 km radius were positively associated with plant diversity in pure and mixed plantations.

Deadwood (**+/-GV, -GI**) [*E*] Refor, Natives
BIOFOREST: CWD positively related to bryophyte diversity in Thicket to Commercially mature forests

Deadwood has been identified as one of the most important components of forest ecosystems, and abundance of deadwood is one of the factors that most clearly separates woodlands with natural characteristics from more intensively managed forests. It is not surprising therefore that deadwood was positively related to diversity of a range of taxa and in all three types of study site. In reforestation and afforestation plantations, CWD was positively related to non-vascular (bryophyte) diversity, though the relationship appeared to be contingent on deadwood being present in situations were the light environment is not limiting. Large, complex brash piles of wood left over from clearfelling, and only found

in reforestation Pre-thicket stages, were positively associated with ground vegetation and non-vascular (bryophyte) species richness for reforestation. In the mixes fine woody debris was negatively related to ground spider diversity. Coarse and fine woody debris were related to diversity and richness of ground vegetation in oak and ash woodlands in a number of ways, both positively and negatively. However, it is important to bear in mind that deadwood of all sizes, and especially deadwood in an advanced state of decomposition, was present at relatively low volumes in the majority of our study sites. This is likely to have been a limiting factor for occurrence and abundance of many specialist forest species.

Grazing (**+GV at moderate levels**) Natives
BIOFOREST: Grazing intensity negatively associated with diversity in grasslands – some sites lacking structural diversity and with poor natural regeneration may have been heavily grazed in the past.
Herbivory has a direct effect on under-canopy vegetation. At high levels of grazing pressure, ground vegetation and regeneration of trees and shrubs can be suppressed, while at low levels and in the absence of grazing, competitive species can dominate. At moderate levels, however, grazing can have a positive effect on diversity of vegetation, as in ash woodlands where it prevented competitive plant species such as *Hedera helix* and *Rubus fruticosus* from becoming dominant to the extent where most other species are excluded.

Drainage (**-GV**) Natives
Moist forest soils were associated with higher species richness in native woodlands, possibly due to the presence of more moisture-loving or -tolerant species in conjunction with a reduction in the competitiveness of less moisture-tolerant species compared to well-drained soils.

6. Implications for policy and practice

6.1 Epiphytes

6.1.1 Afforestation and reforestation survey

Reforestation plantations have been found to be richer in epiphyte species than afforestation plantations. This is encouraging given the increasing proportion of the forest estate that is being reforested. However, although more typical epiphyte species were recorded in reforestation sites, the number of species in each site was low. The role that plantations can play in supporting these species may be particularly important given the low native woodland cover in Ireland (MCPFE Liaison Unit Warsaw, 2007), therefore it is important that the potential of plantations to support these species is maximised. Because of their more specialised ecology, typical epiphyte species are more affected by clearfelling than species with a medium or low affinity for epiphytism (Caners *et al.*, 2010). Continuous cover forestry, where the forest canopy is maintained without clearfelling (Farmer and Nisbet, 2004), has been suggested as a method of increasing epiphyte diversity (Humphrey *et al.*, 2002a). In the absence of this, retention of patches of intact forest after clearfelling has also been suggested to mitigate the negative effects (Perhans *et al.*, 2009), as species may survive there and subsequently colonise the newly planted stands in their vicinity (Muir *et al.*, 2006). The size of the patch retained will be positively correlated with the number of species surviving (Caners *et al.*, 2010); further research is required to determine minimal and optimal patch sizes.

While the measures suggested above will assist with the retention of species between rotations and thereby increase epiphyte species richness, the management of the plantation during the forest cycle will also be important. Canopy openness was identified as an important driver of epiphyte species richness, with the high epiphyte diversity of age class II plantations being lost once the canopy closed. The thinning of conifer plantations to prevent the closure of the canopy will therefore increase epiphyte diversity. However, heavy thinning has economic implications as it can decrease the quality of the timber due to the production of large lower branches which, unless they are pruned, lead to large knots (O'Carroll, 1983). In stands on unstable sites, the risk of windthrow may also be too great for heavy thinning to be possible (Joyce and O'Carroll, 2002). However, Coote (2007) has found that poorly drained, unthinned spruce plantations can be rich in epiphytic bryophytes.

The retention of a plantation beyond commercial maturity may also lead to increased light levels (Williams *et al.*, 1998). Retaining stands beyond commercial maturity could enhance epiphytic lichen diversity, as has previously been shown for commercially over-mature Irish Sitka spruce stands (Coote, 2007). Both thinning and the retention of plantations beyond commercial maturity can enhance natural regeneration of trees and shrubs. Such an increase in understorey diversity means providing a more diverse range of host species for epiphytes, especially for species that show host specificity (Aber *et al.*, 2000), and thus has the effect of increasing epiphyte species richness. However, heavy grazing could prevent regeneration (Mitchell and Kirby, 1990), i.e. plantations may require management to provide the optimal grazing regime.

Sites close to a larger area of old woodland were found to be richer in epiphytes. A higher diversity of epiphytes is thought to be related to the area and relative abundance of suitable substrate trees (Bates *et al.*, 1997). Larger old woodlands, which act as a source of re-colonising epiphyte species for plantations (Hilmo and Sastad, 2001), may therefore provide a higher diversity and therefore a better source of

epiphytes. Establishing plantations close to old woodlands of a large size can enhance epiphyte diversity in these plantations (Humphrey *et al.*, 2004) as long as epiphytes encounter favourable conditions such as high host species richness and a relatively open canopy (Uliczka and Angelstam, 1999; Vellak and Paul, 1999). Since native forest-associated epiphytes are more likely to colonise where native tree species exist, planting of native species and the encouragement of natural regeneration of native tree species may also be expected to increase epiphyte diversity. However, to promote epiphyte diversity, sites will require careful management.

All of the four age classes in the present study were found to have significantly different species assemblages suggesting that, as for ground vegetation diversity (French *et al.*, 2008), epiphyte diversity would be greatest in plantations containing stands of different age classes. Structural diversity, which is correlated to epiphyte diversity (Hauck, 2010), increases with an increase in age diversity, because tree individuals undergo successional change e.g. in bark characteristics (Fritz *et al.*, 2009b) and provide substrates for different epiphyte species at different age stages (Hilmo, 1994; Ruchty *et al.*, 2001). Maintaining stands of different ages within a plantation and retaining patches of mature trees after clearfelling can therefore increase epiphyte diversity in plantation forests.

6.1.2 Mixed tree species survey

The choice of species to be used in mixture with Norway spruce has been shown to affect the influence of the mixture on epiphyte diversity. The addition of Scots pine to Norway spruce plantations resulted in a significantly higher epiphyte species richness compared to pure Norway spruce plantations, while the addition of oak did not affect species richness. Ecological compatibility of mixed tree species is essential if diversity is to be enhanced (Kerr, 1999). Norway spruce and Scots pine are recommended as being compatible when grown in mixtures (Code of Best Forest Practice; (Forest Service, 2000a), while only Scots pine and European larch (*Larix decidua*) are recommended as being compatible with oak. These conifers are recommended for mixture with oak due to the fact that they are slow growing in the early stages and, even then, it is recommended that oak is planted in large blocks (Forest Service, 2000a). Mason (2006) has suggested that the faster growth rate of conifers means that intimate mixes of conifers and broadleaves will only be sustainable if they are managed to favour broadleaved trees at the expense of conifers. No such management had taken place in the Norway spruce/oak mixes in the present study and the oak trees were present as an understorey beneath a spruce canopy. Any management which favours broadleaves may be costly and result in reduced stem quality in conifers, due to the presence of large branches on the lower stem and the resulting high incidence of knots (Mason, 2006). Mason (2006) suggests that a more realistic strategy would be to produce a mosaic where pure broadleaves alternate with pure conifers. Although the addition of oak to Norway spruce plantations did not increase species richness, these mixed plantations supported a different epiphyte assemblage to pure Norway spruce plantations. This suggests that conifer/broadleaved mixes will increase epiphyte diversity at the landscape scale and should be encouraged.

One of the drivers of diversity in all of the plantations studied was canopy openness. The presence of Scots pine in the canopy at the sites increased light penetration and therefore epiphyte species richness. The dense canopy of spruce plantations in the present study supported few epiphyte species. The thinning of conifer plantations to prevent the closure of the canopy will increase epiphyte diversity; however, heavy thinning has economic implications as it can decrease the quality of the timber due to the

production of large lower branches which, unless they are pruned, lead to large knots (O'Carroll, 1983). In stands on unstable sites, the risk of windthrow may also be too great for heavy thinning to be possible (Joyce and O'Carroll, 2002). However, Coote (2007) has found that poorly-drained, unthinned spruce plantations can be rich in epiphytic bryophytes. One of the benefits of a more open canopy was the presence of naturally regenerated trees and shrubs. These had the effect of increasing epiphyte species richness by providing a greater range of host species. However,natural regeneration could be prevented in heavily grazed sites (Mitchell and Kirby, 1990) and management intervention may be required.

Sites closer to old woodland were also found to be richer in epiphytes, as the migration of species into the plantation was enhanced (Bossuyt *et al.*, 1999). However, in the more Closed canopy plantations, the development of a richer epiphyte community may be restricted by low light levels, even when old woodland was in close proximity. This suggests that, in order to promote epiphyte diversity, sites on or in close proximity to old woodland require careful management, for example to prevent canopy closure. The provision of suitable substrates for epiphyte colonisation will also be important, as epiphyte species and communities show a degree of host specificity (Aber *et al.*, 2000). The planting of native tree species and the encouragement of natural regeneration of suitable host tree species same may be expected to increase epiphyte diversity. Further research on the epiphytes of plantations of native trees is also required.

6.1.3 Native woodlands survey

While the ash woodlands in the current study were more species rich and supported more typical epiphyte species, oak and ash woodlands were found to support different species assemblages. Therefore it is important that management is targeted towards both forest types, but oak woodlands in particular, in order to retain the epiphyte diversity of these woodlands.

The presence of an understorey and its effects on microclimatic conditions and on the variety of bark substrates available for epiphyte colonisation appeared to be the most important factor in determining the epiphyte diversity of the woodlands studied. The management of the woodlands in relation to grazing may explain the differences in understorey cover and number of host species present. Heavy grazing pressure can affect stand structure by inhibiting regeneration of tree species through damage to or removal of seedlings and saplings (Perrin *et al.*, 2008a). This may explain the low understorey cover in the oak woodlands sampled. Moderate levels of grazing, on the other hand, are capable of creating regeneration niches for trees and shrubs (Mitchell and Kirby, 1990). Further research on the interactions among grazing level, understorey development and epiphyte diversity is required.

6.1.4 Comparison of forest types

6.1.4.1 Canopy epiphytes

Native woodlands have been shown to be the most favourable habitat for forest epiphyte species in Ireland. Not only did they contain the greatest numbers of epiphyte species but they also supported very different epiphyte communities depending on the dominant tree species within the woodland. Planting, expanding or (re-)establishing mosaics of different types of native broadleaved species, which then develop into old-growth native woodlands, is therefore the best method to increase diversity on a

landscape level (Thompson *et al.*, 2003). These woodlands will require a certain amount of management, e.g. to ensure the development of a diverse understorey by optimising the level of grazing (Putman, 1996; McEvoy, 2006) or to enhance structural diversity by encouraging the development of trees of different age classes (Márialigeti *et al.*, 2009).

While native woodlands have been shown to be the most favourable epiphyte habitat, this study has also demonstrated that plantations have the potential to develop communities similar to native woodlands, although less species rich. Plantation sites close to old woodland areas, which act as a source for epiphyte propagules (Hilmo and Sastad, 2001), were (re-)colonised by a wider range of species (e.g. CHEVY). Such sites should be managed with extra care to secure a rich diversity of epiphytes by providing suitable substrata (naturally regenerating understorey) and abiotic conditions (light penetration) for (re-)colonising species (Kershaw, 1985). Species richness in these plantation stands would have been even greater if migrating epiphyte propagules had met more favourable conditions - such as those in native woodlands. Therefore, former woodland sites or sites close to old woodlands should be considered for replanting with a mixture of native broadleaved species in order to re-expand the area of native woodlands (Thompson *et al.*, 2003). It is clear that the conservation of old stands of native woodland is of the highest importance for the conservation of Irish epiphyte diversity.

As a fallback, native broadleaved plantations should be established, as light conditions in such plantations will be more favourable for epiphytic growth than in plantations of conifers or of exotic broadleaves such as beech, a species which casts a heavy shade intolerable for many vascular plants and bryophytes (Watt, 1931; French, 2005). This study did not investigate mixed native broadleaved plantations; further research on the epiphytes of these is required.

From an economic point of view, broadleaved forestry may be at a disadvantage in comparison with coniferous plantations. In light of this study, mixed conifer plantations should be preferred over pure stands. The choice of species to be used in a mixture with spruce has been shown to affect the influence of the mixture on epiphyte diversity. In particular, the planting of species which create a light canopy (Beadle *et al.*, 1982; Gower and Norman, 1991), can create light environments suitable for epiphytes. Ecological compatibility of mixed tree species is essential if diversity is to be enhanced (Kerr, 1999): Scots pine and European larch (*Larix decidua*) are recommended by the Code of Best Forest Practice (Forest Service, 2000a) as being compatible with oak while Norway spruce is not; Norway spruce and Scots pine are recommended as being compatible with each other. Plantations of intimate mixes require specific management regimes; to maintain a mixed canopy in cases where growth rates of intimately mixed species differ, plantations have to be managed in favour of the slower growing species (Mason, 2006). In case of broadleaved-conifer mixes, plantations will generally require management to favour the slower growing broadleaved component (Mason and Baldwin, 1995).

One of the drivers of diversity in all of the plantations studied was canopy openness. In the absence of a mix species, which increases light penetration, the thinning of conifer plantations to prevent the closure of the canopy and retention of open spaces can increase epiphyte diversity (Humphrey *et al.*, 2002a; Iremonger *et al.*, 2007). Although opening up the stand could compromise the stand stability and economic value of the timber (O'Carroll, 1983; Mason and Kerr, 2001), a benefit of a more open canopy could be the presence of naturally regenerated trees and hence a more diverse range of host species. Open spaces may also promote natural tree regeneration. Epiphyte species and communities show a

degree of host specificity (Aber *et al.*, 2000), and it is more likely that native epiphyte species will colonise where native tree species exist as suitable substrates. Hence the encouragement of natural regeneration of native tree species will most likely increase epiphyte diversity. However, regeneration could be prevented in heavily grazed sites (Mitchell and Kirby, 1990) and management intervention may be required.

Retention of forest patches or stands beyond commercial maturity, which results in maintaining a structure of different age classes within a plantation, has been recommended as another approach to enhance epiphytic diversity (Muir *et al.*, 2006). Retaining older trees will increase the structural diversity of epiphyte microhabitats within a forest and will especially enhance late-successional epiphyte species (Fritz *et al.*, 2009b).

6.2 Ground vegetation

6.2.1 Afforestation and reforestation survey

As highlighted in previous work, no one indicator should be used in isolation; rather, variables found to be influential and appropriate as indicators of diversity should be used in combination (Ferris and Humphrey, 1999). Although several soil variables (pH, Ellenberg nitrogen (N) and moisture (F)) were in the set of models for species richness and mean typical woodland species richness there is more scope for manipulating forest structure and deadwood (which were also in the model sets) to enhance diversity over successive rotations.

As seen in this research manipulating forest structure, namely canopy cover, by thinning increases the quality and size of the remaining trees and promotes ground vegetation development for both species richness and typical woodland richness. The impact of thinning on vegetation has been attributed by Williams *et al.* (1998) to increased light availability and moisture and temperature conditions which in turn stimulate soil fauna productivity, the decomposition process and increase nutrient availability. Once initiated, thinning is carried out on a 3 or 5 year cycle depending on growth rate, with three to four thinnings taking place over the forest cycle (Anon, 2002a). Line thinning (e.g. 1 row of trees in 7 removed) is typically followed by selective thinning (removal of dead, suppressed or poorly formed trees). The recommended age for first thinning for normal production conifer sites in Ireland is nineteen years or a top height of 12 m although it is acknowledged that canopy closure (indicated by branches dead up to 2 m and suppression of ground vegetation) occurs at 7-9 m (Booth *et al.*, 2007). In this study, the values for these stand characters of age and canopy height are typical of the closed-maturing stage in both rotations i.e. thinning is presently recommended *at* closed-maturing stage. One reforestation site and several afforestation sites had been thinned 2 years prior to survey, yet structurally they are classified as closed-maturing stage, suggesting that the thinning carried out was not sufficient to reopen the canopy. Management policy for earlier and more vigorous thinning to prevent canopy closure should be implemented where appropriate. However, caution should be applied in areas susceptible to wind throw as thinning can significantly increase the risk in some areas (Dhubhain *et al.*, 2001; Joyce and O'Carroll, 2002). Retention of the biodiversity gains of afforestation may be facilitated by maintaining canopy openness throughout reforestation, as suggested by Cooper *et al.* (2008). Thinning may require to be carried out earlier and more often in reforestation as compared to afforestation as, throughout the forest cycle, reforestation had a higher canopy cover than afforestation.

The interaction of canopy openness and CWD volume on species richness highlights the importance of strategic planning to enhance ground vegetation diversity in plantations i.e. deadwood resource required in conjunction with management of structure for adequate light levels. Also, it is important that continuity of deadwood supply is maintained during the forest cycle so that there is no local loss of species dependent on deadwood (Humphrey *et al.*, 2002c). In Ireland, deadwood is usually left on site after felling but occasionally some of the larger waste wood may removed for domestic use, however, thinning residues are rarely left on site and instead are removed for sale (Booth *et al.*, 2007). However, as Sweeney *et al.* (2010b) report, there is a lack of large diameter logs and snags in Irish plantations so there is potential for management to increase the availability of this resource by leaving as much deadwood on site as possible, both after felling and after thinning. It should be noted that, if there is infection by fungal pathogens e.g. *Heterobasidion annosum,* at a clearfell site and if control methods (Pratt and Redfern, 2001) are not successful, the removal of deadwood after clearfell may be required in order to protect the health of future forests in that area, as recommended by Eycott *et al.* (2006). The removal of wood residues after clearfell for use as a commercial fuel is common in Sweden and other Scandanavian countries. In Ireland, this practice is gaining support as a contribution to meeting government targets for renewable energy (Hoyne and Thomas, 2001; Whelan, 2010) highlighting potential for conflict among forestry management policies that focus on different outcomes.

Structural stage had a high importance value in the set of models for species richness and is suitable for manipulation through forest planning. Pre-thicket stages of both rotations had species not found through the rest of forest cycle i.e. heath and grassland species. Planning for structural stage diversity at the plantation scale will ensure representation of the Pre-thicket stage, mitigate the negative impact of a Closed canopy on overall ground vegetation diversity, retain areas that may act as sources for recolonisation of woodland vegetation and lessen the visual impacts of even aged, abruptly edged plantations (Williams *et al.*, 1998; Peterken, 2001; Kerr, 2002; French *et al.*, 2008).

Peterken *et al.* (1992) proposed the enhancement of structural diversity by the retention of stands beyond commercial maturity which would in turn improve the ground vegetation diversity of plantations. In our study the Commercially mature stages had significantly greater typical woodland SR than the younger stages for both rotations. It is recommended that consideration should be given to retaining stands beyond commercial maturity, especially in areas that are exhibiting the potential to develop, or have developed, vegetation of conservation interest e.g. typical woodland vegetation as this can result in increased light and nutrient levels (Williams *et al.*, 1998). Conversion by 'gradual replacement' (Pryor *et al.*, 2002) to semi-natural woodland, especially of those stands that have vegetation of conservation interest, should also be considered.

There is increased awareness of the potential damage that conifer planting can cause to open-ground and wetland communities such as heath and peatlands (Hill and Jones, 1978; Wallace and Good, 1995; Peterken, 2001). The conservation of early successional species of these open habitats should be encouraged especially in areas where a plantation is unlikely to recruit a well developed woodland vegetation and the pre-afforestation habitats were heath or peatland (Eycott *et al.*, 2006; French *et al.*, 2008). The negative impacts of clearfell management on ground vegetation include a reduction in light at the forest floor during the Closed canopy stage of plantation, disturbance during thinning and intensive disturbance during clearfelling (Eycott *et al.*, 2006). These impacts on ground vegetation may be mitigated by leaving uncut areas containing species that are sensitive to harvesting and of conservation interest

(Hannerz and Hånell, 1997). Continuous cover forestry, where the forest is maintained at one or more levels without clearfelling (Farmer and Nisbet, 2004; Mason and Kerr, 2004) would also allow for species refuges (Mason *et al.*, 1999).

6.2.2 Mixed tree species survey

The results indicate that future forest policy in Ireland should aim to further promote the planting of native species where a mix is considered appropriate. However, to derive the most benefit in terms of biodiversity value these species need to form the dominant component of the mix. This may be in conflict with the broad forest policy in Ireland for planting non-native conifers and so further consideration must be given to how mixes of native species can be incorporated more extensively into forest management plans.

6.2.3 Native woodlands survey

A number of vegetation communities have been identified in oak and ash woodland and some drivers of the differences in diversity among plots have been identified. While edaphic factors account for some of the differences, the main driver appears to be past and present management. This means that considerable scope exists for improving the diversity of these woodlands, particularly as many of them are designated as SACs or Nature Reserves.

Management in relation to grazing appeared to have one of the biggest impacts. It is recognised that a certain level of grazing provides greater diversity in structural and species composition than either zero or high grazing levels (Mitchell and Kirby, 1990). Former heavy grazing at a number of the oak woodland sites appears to have decreased structural diversity, while more recent reduction or cessation of grazing has resulted in dominance in the field or shrub layer by competitive species (Mitchell and Kirby, 1990). Low levels of grazing may also account both directly and indirectly for the high cover of leaf litter, which is having a detrimental effect on oak woodland diversity. In the ash woodlands, on the other hand, the presence of grazing appears to result in increased diversity. Further research is required to determine the optimum grazing levels for different types of native woodland.

The low volume of CWD in the sites studied is worrying and is probably related to past and present management for timber production. The lack of large diameter logs, which are believed to be important for many species groups, is of particular concern, but the importance of FWD should not be overlooked (Norden *et al.*, 2004). Increasing volumes of CWD in the short term can be achieved by inducing premature death in younger trees, killing of unwanted non-native trees, removing large branches from live trees, transporting deadwood into a site, and ensuring deadwood is not removed (Speight,1989). In the longer term, natural processes should ensure a continuous supply of large, deadwood at different stages of decomposition (Fries *et al.*, 1997).

6.2.4 Comparison of forest types

The results presented above suggest that plantations of both broadleaves and conifers have the potential to support a high number of typical woodland species and vegetation communities similar to native woodland. This echoes the findings of Humphrey *et al.* (2002b) for Britain and French *et al.* (2008) for Ireland. A range of silvicultural, geographic and edaphic factors have been identified as being responsible for the differences in the typical woodland species richness and the ground vegetation communities of the

plantations studied. While it is impossible to control geographic and edaphic factors, changes in forest planning and management could increase the number of typical woodland species supported by plantations and allow them to support vegetation communities more similar to those of native woodlands.

The importance of forest type, proximity to historic woodland and edaphic factors identified by this study for the species and vegetation communities supported by plantations has implications for the selection of sites and species for afforestation. Plantations on or adjacent to historic woodland supported the largest numbers of typical woodland species. This echoes the findings of French *et al.* (2008) and previous studies in Britain and mainland Europe (Grashof-Bodkam and Geertsema, 1998; Ferris and Simmons, 2000; Humphrey *et al.*, 2002b; Verheyen *et al.*, 2003). While ash plantations on base rich soils developed vegetation communities similar to native ash woodland, those planted on poor soils away from historic woodland did not, nor did conifer plantations develop vegetation communities similar to either native oak or ash woodlands. This has implications for species selection on sites adjacent to native woodland or in areas with historic woodland cover. Broadleaved species, preferably native broadleaves suited to the soil type, should be favoured for planting in these areas, since conifers and non-native broadleaves such as beech, as well as not developing a native vegetation community, could also compromise the native status and conservation importance of the adjacent native woodlands (French *et al.*, 2008). The investigation of the vegetation communities of oak and other broadleaved plantations adjacent to native oak woodlands would be informative. Those plantations on or adjacent to historic woodland will require sensitive management to enhance the development of native vegetation communities and should be considered for conversion to continuous cover forestry and/or non-intervention natural reserves (Humphrey *et al.*, 2002b). Those conifer plantations already on or adjacent to historic woodland should be considered for conversion to a native tree species or a native/non-native mix (Humphrey *et al.*, 2002b).

Canopy cover has been identified as an important factor in determining the species richness and vegetation communities of conifer plantations. The early and regular thinning of conifer plantations to prevent the closure of the canopy, will prevent the development of the species poor Closed canopy conifer forest community and promote the development of one of the more species rich bryophyte-dominated, bramble dominated or *Thuidium*-dominated communities. However, heavy thinning has economic implications as it can lead to the production of large lower branches which, unless they are pruned, lead to large knots which decrease the quality of the timber (O'Carroll, 1983). In stands on unstable sites, the risk of windthrow may also be too great for heavy thinning to be possible (Joyce and O'Carroll, 2002). The absence of an understorey and reduced shrub layer in plantations is also related to canopy cover. Since most plantations are clearfelled in the 'stem exclusion' phase, increasing rotation length so that they move into the 'understorey reinitiation' and even the 'old growth' phase (see above) has been suggested as a method of improving the diversity of habitat structure and therefore biodiversity (Kerr, 1999). Deadwood volume would also be enhanced by maintaining plantations beyond the stem exclusion stage (Kerr, 1999). Humphrey *et al*. (2002c) suggest that the focus should be on creating quality deadwood habitats in networks of old-growth natural reserves of 5ha or greater, which would require minimal management inputs. However, the retention of harvesting residues on clearfells, thinnings in stands, patches of windthrow, groups of trees of poorer form or groups of broadleaves can maintain the continuity of habitat for deadwood species throughout the normal forest rotations (Humphrey *et al.*, 2002c).

Grazing has also been identified as an important factor in determining the different communities present and therefore also the number of typical woodland species supported. Low or zero grazing may account

for the abundance of *R. fruticosus* agg. at some sites, while higher grazing levels may explain its lack of abundance in others. In native woodlands, the complete absence of grazing is undesirable for the maintenance of biodiversity (Mitchell and Kirby, 1990; Perrin *et al.*, 2006a). In commercial plantations, as well as having an effect on the vegetation communities, grazing animals can damage the maturing crop, sometimes causing checking of growth, making trees more susceptible to disease and even reducing the economic value of the crop (Putman, 1996). However, there is little information on the threshold densities above which damage becomes significant and below which the impact is acceptable (Putman, 1996). Further research is required in this area.

6.3 Ground-dwelling invertebrates and Lepidoptera

6.3.1 Afforestation and reforestation survey

Forest-associated species which accumulate over the plantation cycle are not supported after felling or during the early stages of the second rotation. However, mature forest areas directly adjacent to felled stands may act as refuges for these species. Forest policy should allow for a flexible, long-term, approach to forest planning which facilitates the felling of stands only when there is an adjacent closed-canopy stand in the landscape matrix. These adjacent closed-canopy stands should be a minimum of 25 years or well developed structurally. Current recommendations mention a mosaic of structural stages on the landscape but make no mention of their spatial arrangement and further exploration is needed.

Habitat heterogeneity promotes the diversity of both open and forest species at a small scale within a stand. This is particularly important as plantation forests become more homogenous with successive rotations. This reiterates the findings of BIOFOREST which suggests small canopy gaps to promote the growth and maintenance of a more diverse ground vegetation. Greater habitat heterogeneity can be achieved in plantations through creation of canopy gaps or earlier thinning to enhance structural diversity of the lower vegetation layers. Future forest policy should aim to focus these measures in monoculture stands, where there is a lack of canopy species diversity, and at the closed-canopy stages of conifer plantations where diversity is lowest. This will give a greater focus to within-stand structural diversity in forest management.

6.3.2 Mixed tree species survey

The results indicate that future forest policy in Ireland should aim to further promote the planting of native species where a mix is considered appropriate. However, to derive the most benefit in terms of biodiversity value these species need to form the dominant component of the mix. This may be in conflict with the broad forest policy in Ireland for planting non-native conifers and so further consideration must be given to how mixes of native species can be incorporated more extensively into forest management plans.

6.3.3 Native woodlands survey

These findings support current forest policy of native woodland rehabilitation and expansion (e.g. the Native woodland scheme).

6.3.4 Comparison of forest types

The findings indicate that large scale planting of non-native conifers has caused a fundamental change in the common forest species across Ireland. In addition, rarer species associated with native woodlands are not supported in conifer plantations. This would suggest that Irish forest policy should seek to enhance the proportion of broadleaved woodland in the national forest estate through plantation establishment and natural woodland expansion (e.g. the native woodland scheme). Although current forest policy recommends establishing broadleaves where site conditions allow, it is unclear to what extent this practice being carried out. A review of current planting trends (both in terms of species selection and areas being planted) may be necessary to examine how to further the planting of broadleaves in Ireland, given the current large scale planting of non-native conifers. In addition, the aim of such a review would be to propose minimum acheiveable targets for broadleaved forest cover in Ireland.

6.4 Canopy-dwelling invertebrates

The results of this study are important in terms of the conservation of native canopy invertebrate fauna in native woodlands and the future management of mixed and pure plantation forests containing native and non-native tree species. It is notable that the patterns observed when comparing native woodland and plantation forest canopies were often similar to those found in the UK and continental European countries with different forest cover and forestation histories. Although plantations form a large part of the future forest estate in Ireland, this study has demonstrated that plantation canopies do not support the same range of invertebrate guilds and habitat specialists as native woodlands. Some components of invertebrate diversity (in terms of species richness) were supported by plantation forests, as has been suggested previously (e.g., Hartley, 2002; Berndt *et al.*, 2008; Brockerhoff *et al.*, 2008), although this was only evident in Norway spruce plantations. In contrast, as well as supporting different canopy and spider guilds, Sitka spruce plantations contained lower invertebrate diversity overall, across a range of invertebrate taxa identified to varying taxonomic levels.

Remnant forest-associated species in Ireland have had to be highly adaptive in their exploitation of any remaining forest patches, due to the extensive historical degradation and destruction of native woodlands (Higgins *et al.*, 2004) and many forest species that are relatively common in other parts of Europe are rare or absent in Ireland (Davenport *et al.*, 2008; Sweeney *et al.*, 2010a). Therefore, many of the canopy invertebrate species identified in this study are relatively generalist in their habitat associations in Irish forests, compared to the UK and other European countries. Even so, native phytophagous Irish canopy invertebrates are not adapted to feeding on the relatively recently introduced non-native conifers which are widely planted in many plantations and dominate the forest estate. Thus, these plantations cannot support the same range of canopy invertebrates found in nataive woodlands. Increased planting of native trees or increased inclusion of native tree species in mixed plantations would help to address this issue. In particular, the planting of fast-growing native tree species such as ash or rowan, which can compete with non-native conifers, would be beneficial to forest invertebrate biodiversity.

Canopy spiders and beetles responded differently to the various forest types surveyed in this study. This was driven by the different habitat constraints and environmental requirements of both taxa. For example, spiders are generalist predators more dependent on habitat structure and prey availability than the actual tree species they inhabit (Halaj *et al.*, 1998; Halaj *et al.*, 2000). Beetles are more diverse in their foraging

strategies and, along with predatory species, many species feed solely on elements of their habitat (i.e., as phytophages, mycetophages, detritiphages, and xylophages), and are thus constrained by the chemical composition of the tree species on which they live, as well as being influenced by its structural elements (Moore *et al.*, 1991). Phytophagous beetles in particular are generally adapted to inhabiting a specific host tree species, due to the chemical composition of the edible vegetation and the defensive compounds produced by plants (Strong *et al.*, 1984). However, the overall patterns observed across these two taxa, which possess a variety of lifestyles, mobility, habitat and feeding requirements suggests that plantation forests have much room for improvement if they are to provide habitat for native canopy invertebrate fauna present in native woodlands.

6.5 Birds

6.5.1 Afforestation and reforestation survey

Although species richness is similar between stages, bird assemblages of Pre-thicket and Thicket forests are more even than those of Closed canopy forests which are dominated by two or three common species. Migrant densities are low in Closed canopy forests, likely due to the habitat preferences of these species. Pre-thicket, and to a lesser extent Thicket, support species that are declining elsewhere. This study supports findings elsewhere in illustrating the importance of Pre-thicket to the diversity of coniferous forests.

Higher migrant bird density in second-rotation Pre-thicket is likely linked to increased shrub cover, while differences in other stages between rotations may be due to differences in crop vegetation structure. Differences between Closed canopy forests may also have been partially affected by observer differences, but this is unlikely to have been the case in Pre-thicket or Thicket. The species present at higher densities in the second rotation tended to be common species which suggests that the future expansion of second-rotation forests will not affect all species equally. Notably, some species of conservation concern were also present at higher density in young second-rotation forests than in first-rotation forests, although one was present at lower density.

The future increase of second-rotation plantations may benefit bird communities up to the point of canopy closure. However, bird assemblages in the second rotation were broadly similar to the first rotation, and became more so as the forest cycle progressed. Management, targeted at the Closed canopy stage of the forest cycle and aiming to increase habitat heterogeneity, may help to decrease the dominance of a small number of species and enable plantations to benefit a wider range of species.

6.5.2 Mixed tree species survey

We found no significant difference in species richness or Simpson's diversity between the oak and Scots pine mixes and pure Norway spruce. However, Scots pine mixes supported a higher density of birds than either oak mixes or pure plantations. The mixes and pure Norway spruce sites differed from one another in respect of several structural variables, of which the most important was shrub cover, which had a positive influence on bird density, species richness and Simpson's diversity. This suggests plantation managers aiming to improve the quality of forest habitat for breeding birds can do so by increasing shrub cover within their forests. Because the bird assemblages supported by mixes are slightly more diverse

than those in monocultures, we recommend the establishment of mixed plantations (with a native tree component) where possible. In the case of oak mixes, current management regimes do not allow effective development of the oak component. Such plantations could be improved for birds either by more intensive thinning of the conifer component, or by planting oaks in clumps in order to reduce shading from surrounding conifers.

6.5.3 Comparison of forest types

We have demonstrated that the bird communities of native woodlands and those of older Sitka spruce plantations are distinct, even in a country with a highly generalised bird fauna. The differences are most likely due to differences in vegetation structure between the woodland types. However, because of the generalist bird fauna typical of Ireland, it is likely that relatively small measures (e.g. carrying out thinning in the age class II phase) could improve the utility of plantations to birds, and allow more broadleaved-associated species to achieve higher population densities. A striking feature of these results is the similarity of the bird communities of the age class III and IV Sitka spruce age classes. Species richness and Simpson's diversity are low by the time plantations are 20 years old and remain low until felling, which may be 20-30 years later. Age class III therefore provides a management target to increase the utility of plantations to birds.

We have demonstrated the importance of structural components of woodlands, particularly understorey and shrub cover, on bird species richness and Simpson's diversity. Thus, management to promote these features, and therefore increase the carrying capacity of plantations, will likely increase the utility of plantations for bird conservation. Because few woodland specialist species occur in Ireland, and because many of the species in the study occurred in both native woodlands and plantation forests, there is potential for plantations to host a large proportion of Ireland's terrestrial bird fauna. To achieve this in the relatively short lifetime of a plantation, stands entering age class III should be targeted for thinning in wide lines or patches to allow light penetration and encourage the establishment of pioneer species such as birch (*Betula* spp) and bramble (*Rubus fructicosus*) and climbers such as ivy (*Hedera helix*). This would mirror more closely the structure of native woodlands and provide both nesting and foraging opportunities for birds, including species of conservation concern such as the Spotted Flycatcher. The effectiveness of management may then be judged by the population densities of bird species associated with broadleaved vegetation.

Allowing some individual trees or stands of trees to remain and senesce following harvesting may increase nest site availability for cavity nesting species in the long term. The excavation of nest holes by the Great Spotted Woodpecker (*Dendrocopos major*) which appears to be re-colonising Ireland (Hillis, 2007) may also increase cavities in such trees in the long term. In the short term, the provision of nest boxes which both Blue Tit and Great Tit are known to readily use (Fuller, 1995; Mänd *et al.*, 2009), would likely increase the utility of plantations to cavity nesting species.

6.6 Deadwood

Because domestic demand for wood has dropped with the availability of different fuels and building materials, most native woodlands are probably currently subject to little timber exploitation. An opportunity therefore exists to increase deadwood levels for the benefit of biodiversity, particularly in those forests that are owned and managed by the state. One of our study sites is subject to a management plan which

involves resuming coppicing in the forest. This site was one of the few in which large-diameter deadwood was encountered, and because the large oak standards present are not included in the management plan, they may continue to deposit large diameter deadwood following branch death or storm damage.

Deadwood levels in Irish forests are low even compared to those in Great Britain which has also experienced extensive forest clearance (Rackham, 2006). According to the deadwood categories proposed by Kirby *et al*. (1998) for use in British forests, most Irish native woodlands and plantations would be classed as low or medium in terms of CWD levels, snag density and snag size. However, these proposed categories do not take account of the requirements of deadwood flora and fauna and are based on existing deadwood levels.

Despite a lack of published research on saproxylic flora and fauna in Ireland, at least 600 species of invertebrates are known to utilise deadwood and many are rare or localised in the country, particularly some Staphylinidae species (Alexander, 2002). Historical forest clearance and loss of CWD and mature trees; a decrease in pine in the landscape; changes to forest disturbance regimes and climate change may all have contributed to the extinction of several species of forest beetle in Ireland, even some that are presently relatively common in Britain (Whitehouse, 2006). It is therefore unlikely that Ireland currently possesses a specialised saproxylic beetle fauna. Furthermore, because such beetles may often be poor dispersers (Grove, 2002), recolonisation will likely be difficult but, given the potential involvement of long-distance dispersal in the original post-glacial colonisation of Ireland by such species, perhaps not impossible (Whitehouse, 2006). In any case, a diverse range of deadwood habitats are utilised by current saproxylic fauna (Alexander, 2002) and so management should aim to ensure a mix of deadwood types and to ensure that some deadwood is sun-exposed (Lindhe *et al.*, 2005).

Due to the lack of knowledge of the saproxylic flora and fauna of either native woodlands or plantation forests, it is difficult to suggest meaningful deadwood targets. However, large logs host many saproxylic insects (Lindhe *et al.*, 2004) due to the variety of microhabitats and slow decomposition rates (Grove, 2002), and increasing the prevalence of such logs should therefore be one of the primary targets for management of deadwood in Irish forests. Snags are also important nesting and foraging sites for woodpeckers (Smith, 1997), and the lack of large diameter snags in Irish forests may have implications for the colonisation of Ireland by the great spotted woodpecker (*Dendrocopos major*), which is known to have bred successfully in several locations in Ireland in 2009 (Coombes, 2009). Felling unwanted non-native tree species and importing large logs grown elsewhere are two other methods to increase large diameter deadwood in a forest in a short space of time (Speight, 1989). In the absence of timber extraction, this would be augmented over time by natural processes which would ensure the deposition of deadwood in a variety of decay states (Similä *et al.*, 2003).

Plantation forests currently meet the forestry guidelines in terms of recommended deadwood volumes. However, most of this deadwood is in the form of small diameter timber, and large logs and snags are even scarcer in plantations than in native woodlands. Forestry guidelines state that over-mature trees should be retained following harvesting (Forest Service, 2000b), but such trees remain rare in plantations. Stricter adherence to these guidelines would help to ensure the long-term development of large-diameter deadwood. These trees should be as large as possible to increase the potential for deposition of large diameter CWD (Similä *et al.*, 2003). Ideally, some large-diameter logs should also be left post harvesting to complement the large amounts of brash typically left following clearfelling.

7. Conclusions and recommendations

Abbreviations

B = Birds

CB = Canopy-dwelling beetles

CE = Canopy epiphytes

CI = Canopy-dwelling invertebrates

CS = Canopy-dwelling spiders

E = Epiphytes

GB = Ground-dwelling beetles

GV = Ground vegetation

GI = Ground-dwelling invertebrates

GS = Ground-dwelling spiders

I = Invertebrates

L = Lepidoptera

LE = Lower trunk epiphytes

7.1 Plantations

1. **Maintenance/retention of forest cover (E, GV, GI)**: continuous cover forestry, where a canopy is maintained throughout the lifetime of commercial forests, with ongoing and small scale harvesting of individual trees and groups of trees, should be practiced more widely in Ireland, in order to accommodate forest specialist species that may take a long time to become established in a site, or do not colonise efficiently. Where this is not possible or practical, patches of mature trees retained after clearfelling may serve as reservoirs for such species, ensuring that they do not go entirely extinct on a site. In addition, retaining trees in stands, patches or even as individuals will result in the development of overmature trees that may provide microhabitats for canopy-dwelling fauna and flora that are scarce in the rest of the plantation.

2. **Diversity of age structure (B, E, GV, GI)**: in areas being managed by clearfelling, staggering harvesting of large, contiguous blocks so that a mosaic of widely different age classes develops will maximize the diversity of forest blocks

3. **Diversity of vegetation structure (B, E, GV, GI)**: the structural requirements of different species and groups are diverse, so providing a wide range of vegetation structures within a stand will tend to maximize the number of species it can support. Particularly during the later stages of a commercial rotation, after canopy closure, vertical diversity of structure in conifer plantations is typically low. Where feasible, increasing light penetration in post-Thicket plantations by early and frequent thinning, or by the creation of open spaces within the forest, will encourage the development of ground, field, shrub and understorey vegetation, all of which can benefit species in a wide range of taxa.

4. **Native broadleaved species (B, E, GV, I)**: Diversity and abundance of broadleaved species in the canopy, understorey and shrub layer, whether derived from planted stock or from natural regeneration, were found to benefit several taxa including epiphytes, canopy-dwelling

phytophages and birds. In addition, the encouragement of berry-bearing species such as holly and ivy will be particularly valuable to wintering bird populations through provision of food.

5. **Grazing management (B, LE, GV)**: although the relationship between grazing levels and biodiversity in Irish plantations is not well understood, it is very high in some forested areas, predominantly through grazing by deer. It is likely that, in such forests, increasing light penetration will not be enough to ensure establishment of native trees and shrubs, and an increase in field layer cover. Ways of moderating grazing pressure should be investigated further before a strategy for grazing management is decided upon.

6. **Proximity to old woodland and conversion to native species (GF, E)**: where plantations have been established on or in close proximity to historical or existing areas of old woodland, this may provide an increased chance for some forest specialists with limited distributions or poor dispersal abilities to colonise. Plantations of non-native trees in such situations may also present a threat to the ecological integrity of existing patches of old and native woodlands, through colonization by non-native trees and associated species. Such plantations should therefore be managed sensitively. Particularly where the ground vegetation indicates that there is potential for a woodland flora of high conservation value to develop, or where non-native plantations pose a threat to the integrity of nearby native woodlands, conversion to native tree species should be considered.

7. **Deadwood (GV)**: deadwood is important for many forest species, particularly non-vascular plants and fungi, which use it as a substrate. The positive effect of deadwood on ground vegetation depends to a large extent on this resource being available in conjunction with optimal light levels, so measures to increase availability of deadwood should try to ensure that it is provided in a range of conditions from light-exposed to shaded.

8. **Nest sites (B)**: In plantations lacking ecologically mature (i.e. commercially over-mature) or standing dead trees, lack of nest sites for hole-nesting birds can be addressed in the short term by providing nest boxes, longer term by letting oerv mature trees be retained.

7.2 Mixed species plantations

The above recommendations apply to mixed species plantations as well as monocultures. However, some additional recommendations can be made specifically in relation to management of plantations with a mixed canopy of native and non-native species.

1. **Native species (B, E, GI):** mixes planted for biodiversity should, wherever possible, include at least one native tree species.

2. **Ecologically compatibility (E, GV, GI):** if mixes are to be used as part of a biodiversity enhancement strategy, they should be comprised of species that are compatible with one another (i.e. with similar growth rates and/or ecological strategies in terms of competitive and stress-tolerating tendencies), to increase the chance of the native element successfully exerting an influence on the commercial conifer element.

3. **Favour native element (B, E, GI):** wherever the native element of a mix is at a competitive disadvantage to the more commercial element, mixes should be managed to prevent the native element being excluded from the canopy and eventually shaded out altogether. Such management might incorporate strategies such as strategic thinning around native trees, aggregated planting of

natives to reduce competition with surrounding commercial species (at an extreme, such segregation would result in non-intimate mixes, where two species are planted in adjacent but separate blocks).

7.3 Native woodlands

Management of native woodlands, though it has been intensive in the past, is now typically less interventionist than management of commercial plantations. Nevertheless, some measures can be put forward to help native woodlands to maximize their biodiversity value.

1. **Grazing and vegetation structure (B, E, GV, GI):** because light is a much less limiting factor in native woodlands than in plantations, grazing is likely to be even more important in terms of the influence it has on understorey canopy, shrubs and other vegetation layers. As in plantations, heavy grazing may limit the development of understorey vegetation, but the more open canopy in native woodlands means that, in the absence of grazing, one or more understorey vegetation layers may become dominant. This will tend to result in native woodlands become less diverse in structure and tree and shrub species, with conditions suited to a narrower range of species than they might otherwise support.

2. **Deadwood (B, E, GV, I):** this has been found to be one of the most important factors influencing temperate forest biodiversity, with more forest specialist species depending on deadwood than any other forest-related resource. Because of their long history of timber extraction, most native woodlands have very depleted deadwood resources compared to long-established forests in Europe. Management to improve deadwood resources in native woodlands should aim to increase the abundance and diversity of deadwood, particularly of large diameter classes of deadwood in a variety of decay states. Standing deadwood on old trees and in snags can provide habitat for epiphytes and hole-nesting birds (Anderson, 2001).

3. **Conservation and restoration of native woodland (B, E, GV, I):** we found that native woodlands were generally more biodiverse habitats than plantation forests. However, native woodlands account for less than a tenth of Ireland's forest estate. All native woodland patches should be considered potentially worthy of conservation, regardless of their size. Wherever possible existing native woodlands should be extended and, where appropriate, improved. Conversion and modification of existing plantations to become more similar in composition and character to native woodlands will also enhance Ireland's forest biodiversity.

4. **Native woodland diversity (E, GV, I):** we found that the species assemblages supported by ash and oak dominated woodlands were different for several taxa. In order to ensure the effective conservation of native woodland biodiversity in Ireland, all types of woodland native to Ireland should be conserved and, especially for rarer woodland types, extended.

7.4 Further research

1. **Continuous cover forestry:** this system is practiced rarely in Ireland, and there is consequently a lack of information regarding its effect on fauna and flora and how it compares to the plantations managed for clearfell harvest that were investigated in this and previous projects.

2. **Retention of over mature trees:** as a more practical option in many situations than large-scale conversion of clearfell to continuous cover forestry systems, retention of trees beyond their age of commercial maturity deserves further investigation. Topics for future research include the effects of

size, shape and frequency of retained patches, the biodiversity they support and effects on surrounding forest.

3. **Mixed species plantations:** management of mixed species plantations for biodiversity would benefit greatly from future research in a number of areas. Different combinations and configurations of tree species should be tested in order to identify mixed planting regimes that successfully increase light penetration through the canopies of commercial conifer plantations, and allow participation of native and broadleaved tree species in these canopies. For some mix types the effect of increased or more focused thinning programmes should be investigated, as successful integration of a mixed stand may rely on interventionist management. Finally, the effects of mixed planting on the younger stages of the growth cycle should be investigated, in order to identify whether a secondary species exerts a positive influence on biodiversity before or shortly after canopy closure.

4. **Native woodland size:** further research should be carried out to investigate whether and to what extent patch size of native woodlands is a limiting factor in the occurrence and abundance of specialist woodland taxa.

5. **Brash:** currently by far the most abundant deadwood resource in plantations, management of brash for biodiversity would benefit from research on optimal configurations of brash for the species that make use of it, including saproxyles and non-vascular plants.

6. **Saproxylic species:** these are now among the least well-studied taxa in woodlands, though they are functionally of great importance and are likely to have a greater proportion of forest habitat specialists than most other groups. They are an obvious candidate for further research on forest biodiversity, which should focus on the contribution of different decay states and size classes, and the requirements of different saproxylic species in terms of temporal and spatial distribution of deadwood in Irish woodlands and plantations.

7. **Other taxa:** other invertebrate taxa would also benefit from further study, including phytophagous specialists of native broadleaved trees, and less mobile groups based close to the ground or in the soil which are unlikely to have been sampled effectively by the methods we used. Fungi were not included in this study but are among the groups most likely to display close relationships with forest habitats and deadwood resources, and have huge potential to affect other taxa through the role they play in nutrient cycling.

8. **Grazing:** more detailed research on the effects of different grazing regimes on biodiversity of woodlands and plantations, as well as the influence of landscape-scale configuration of forests, is needed in order to give better guidance to forest managers about the effects that management for grazers is likely to have.

9. **Extension of native woodlands:** the possibility of extending woodland habitat by planting native broadleaved species adjacent to existing native woodlands is one way in which the conservation status of existing native woodlands, which are typically small and fragmented, could be enhanced. However, more information is needed on the extent to which the ground vegetation and other biota of native broadleaved plantations can be made to approximate that of a native woodland.

8. References

Abdy, E. M. and Mayhead, G. J. 1992. The ground vegetation in upland Spruce plantation in North Wales. Aspects of Applied Biology. Vol. (29): 73 81

Aber, J., Christensen, N., Fernandez, I., Franklin, J., Hidinger, L., Hunter, M., MacMahon, J., Mladenoff, D., Pastor, J., Perry, D., Slangen, R. and van Miegroet, H. 2000. Applying Ecological Principles to Management of the U.S. National Forests. Issues in Ecology. Washington, D.C., USA, Ecological Society of America. 6. 20.

Addicot, F. T. 1991. Abscission: Shedding of Parts. *In*: Physiology of Trees. Raghavendra, A. S. (Eds). New York, John Wiley & Sons Inc.

Agresti, A. 2007. An Introduction to Categorical Data Analysis. Hoboken, New Jersey, USA, John Wiley & Sons.

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce - western hemlock forests of southeast Alaska. Ecology. Vol. 63 (6): 1932-1948.

Alatalo, R. V. 1978. Bird community energetics in a boreal coniferous forest. Holarctic Ecology. Vol. 1: 367-376.

Alexander, K. N. A. 2002. Research Report number 467: The invertebrates of living and decaying timber in Britain & Ireland. A provisional annotated checklist. Peterborough, English Nature.

Alldredge, M. W., Simons, T. R. and Pollock, K. H. 2007. Factors affecting aural detections of songbirds. Ecological Applications. Vol. 17 (3): 948-955.

Ammer, S., Weber, K., Abs, C., Ammer, C. and Prietzel, J. 2006. Factors influencing the distribution and abundance of earthworm communities in pure and converted Scots pine stands. Applied Soil Ecology. Vol. 33 (1): 10-21.

Andelman, S. J. and Fagan, W. F. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? PNAS. Vol. 97: 5954-5959.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology. Vol. 26: 32-46.

Anderson, M. J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics. Auckland, New Zealand, University of Auckland.

Anderson, M. J. and Ter Braak, C. J. F. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computation and Simulation. Vol. 73 (2): 85-113.

Anderson, R. 2006. Ground Beetles of Ireland. Belfast, National Museum of Northern Ireland.

Anderson, R., McFerran, D. and Cameron, A. 2000. The Ground Beetles of Northern Ireland (Coleoptera-Carabidae). Belfast.

Anon 2000a. Code of Best Forest Practice – Ireland, Forest Service, Department of the Marine and Natural Resources, Leeson Lane, Dublin 2. 97.

Anon 1999. Flora Protection Order.

Anon 2000b. Forest Biodiversity Guidelines, Forest Service, Department of the Marine and Natural Resources, Leeson Lane, Dublin 2.

Anon 2002a. Forestry Yearbook Irish Timber Growers Association.

Anon 1996. Growing for the future - A strategic plan for the development of the forestry sector in Ireland, Department of Art, Heritage, Gaeltacht and the Islands. 98.

Anon 2002b. National Biodiversity Plan, Department of Art, Heritage, Gaeltacht and the Islands. 49.

Anon 2005a. Oak (*Quercus robur* L. & *Quercus petraea* (Mattuschka) Lieblein), Forest Service. 2005.

Anon 2005b. Scots Pine (*Pinus sylvestris* L.), Forest Service. 2005.

Anon. 1995. Red Data Book of European bryophytes. European Committee for the Conservation of Bryophytes, Trondheim.

Assmann, E. 1970. The Principals of Forest Yield Study. New York, Pergamon Press.

Atkinson, M. D. 1992. *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. Journal of Ecology. Vol. 80 (4): 837-870.

Averis, A. B. G. and Coppins, A. M. 1998. Bryophytes, lichens and woodland management in the western highlands. Report to Scottish Natural Heritage, Scottish Natural Heritage. 41.

Babel, U. 1977. Influence of High Densities of Fine Roots of Norway Spruce on Processes in Humus Covers. Ecological Bulletins. Vol. 25: 584-586.

Baker, R. and Sadovy, Y. 1978. The distance and nature of the light trap response of moths. Nature. Vol. 276: 818-821.

Barbaro, L., Pontcharraud, L., Vetillard, F., Guyon, D. and Jactel, H. 2005. Comparative responses of bird, carabid, and spider assemblages to stand and landscape diversity in maritime pine plantation forests. Ecoscience. Vol. 12 (1): 110-121.

Bardgett, R. 2005. The biology of soil: a community and ecosystem approach. New York, Oxford University Press.

Barker, M. G. and Pinard, M. A. 2001. Forest canopy research: sampling problems, and some solutions. Plant Ecology. Vol. 153: 23-38.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes. Assen, Van Gorcum. 628

Barton, K. 2009. MuMIn: Multi-model inference. R package version 0.12.2/r18. http://R-Forge.R-project.org/projects/mumin/.

Bartsch, N., Petercord, R. and Von Lupke, B. 1996. Growth of sessile oak in a mixture with Scots pine. Forst und Holz. Vol. (51): 195-200.

Baselga, A. 2009. beta.sim. Boston, USA, Free Software Foundation, Inc.

Bates, D. and Maechler, M. 2010. lme4: Linear mixed-effects models using S4 classes.

Bates, D. and Sarkar, D. 2006. lme4: Linear mixed-effects models using S4 classes. R package version 0.9975–10.

Bates, J. W. 1992. Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. Journal of Ecology. Vol. 80 (1): 163-179.

Bates, J. W. and Brown, D. H. 1981. Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* in a maritime area of South West England. Vegetatio. Vol. 48: 61-70.

Bates, J. W., Proctor, M. C. F., Preston, C. D., Hodgetts, N. G. and Perry, A. R. 1997. Occurence of epiphytic bryophytes in a 'tetrad' transect across southern Britain 1. Geographical trends in abundance and evidence of recent change. Journal of Bryology. Vol. 19 (4): 685-714.

Beadle, C. L., Talbot, H. and Jarvis, P. G. 1982. Canopy structure and leaf area index in a mature Scots pine forest. Forestry. Vol. 55 (2): 105-123.

Beck, W. 2000. Silviculture and stand dynamics of Scots pine in Germany. Investigacion agravia: Sistemas y recursos Forestales: Fuera de Serie. Vol. 1: 199-212.

Beers, T. W., Dress, P. E. and Wensel, L. C. 1966. Aspect transformation in site productivity research. Journal of Forestry. Vol. 64: 691-692.

Bellamy, P. E., Hinsley, S. A. and Newton, I. 1996. Factors influencing bird species numbers in small woods in south-east England. Journal of Applied Ecology. Vol. 33 (2): 249-262.

Benzing, D. H. 1990. Vascular Epiphytes. Cambridge, UK, Cambridge University Press. 354

Berndt, L. A., Brockerhoff, E. G. and Jactel, H. 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodiversity and Conservation. Vol. 17: 1171-1185.

Berryman, S. and McCune, B. 2006. Estimating epiphytic macrolichen biomass from topography, stand structure and lichen community data. Journal of Vegetation Science. Vol. 17 (2): 157-170.

Bibby, C. J., Aston, N. and Bellamy, P. E. 1989. Effects of broadleaved trees on birds of upland conifer plantations in North Wales. Biological Conservation. Vol. 49 (1): 17-29.

Bibby, C. J., Burgess, N. D. and Hill, D. A. 2000. Bird Census Techniques. London, Academic Press.

Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? Ecological Applications Vol. 9: 164–170.

Bloomfield, P. and Davis, J. M. 1994. Orthogonal rotation of complex principal components. International Journal of Climatology. Vol. 14 (7): 759–775.

Bobiec, A. 2002. Living stands and dead wood in the Bialowieza forest: suggestions for restoration management. Forest Ecology and Management. Vol. 165: 125–140.

Bocock, K. L. 1964. Changes in the Amounts of Dry Matter, Nitrogen, Carbon and Energy in Decomposing Woodland Leaf Litter in Relation to the Activities of the Soil Fauna. Journal of Ecology. Vol. 52 (2): 273-284.

Bohan, R. 1997. The historical ecology of the woodlands of Ireland, Western Scotland and the Isle of Man. Dublin, Trinity College Dublin. PhD.

Booth, A., Ryan, T. and Whelan, D. P. 2007. Irish Thinning Protocol:A complete step by step guide to the requirements and implementation of thinning systems in Ireland, Forestry Development Association and Irish Timber Growers Association.

Bossuyt, B., Hermy, M. and Deckers, J. 1999. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. Journal of Ecology. Vol. 87 (4): 629-638.

Boston, K. and Murphy, G. 2003. Value recovery from two mechanized bucking operations in the Southeastern United States. Southern Journal of Applied Forestry. Vol. 27: 259-263.

Bowden, J. 1973. The influence of moonlight on catches of insects in light-traps in Africa. Part I. The moon and moonlight, Cambridge Journals Online. 63. 113-128.

Bradshaw, R. H. W. 1981. Modern Pollen-Representation Factors for Woods in South-East England. Journal of Ecology. Vol. 69 (1): 45-70.

Bradshaw, R. H. W. and Browne, P. 1987. Changing Patterns in the Post-Glacial Distribution of Pinus sylvestris in Ireland. Journal of Biogeography. Vol. 14 (3): 237-248.

Brändle, M. and Brandl, R. 2001. Species richness of insects and mites on trees: expanding Southwood. Journal of Animal Ecology. Vol. 70 (3): 491-504.

Brandtberg, P. O., Lundkvist, H. and Bengtsson, J. 2000. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. Forest Ecology and Management. Vol. (130): 253–264.

Branquart, E. and Dufrêne, M. 2005. Les arbres, de puissants révélateurs de la biodiversité forestière. *In*: Résumé des interventions de la journée d'étude "Gestion forestière et biodiversité", 23/03/2005, Gembloux, Belgium. E., B., Direction générale des Ressources naturelles et de l'Environnement, Ministère de la Région Wallonne. pp. 8-10.

Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P. and Sayer, J. 2008. Plantation forests and biodiversity: Oxymoron or opportunity? Biodiversity and Conservation. Vol. 17: 925-921.

Bromham, L., Cardillo, M., Bennett, A. F. and Elgar, M. A. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Australian Journal of Ecology. Vol. 24: 199-207.

Brunet, J. and von Oheimb, G. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology. Vol. 86: 428-438.

Buckland, P. I. and Buckland, P. C. 2006. Bugs Coleopteran Ecology Package (BugsCEP), Downloaded from http://www.bugscep.com/.

Buddle, C. M., Langor, D. W., Pohl, G. R. and Spence, J. R. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation. Vol. 128 (3): 346-357.

Buddle, C. M., Spence, J. R. and Langor, D. W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography. Vol. 23 (4): 424-436.

Bultman, T. L. and Uetz, G. W. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia. Vol. 55 (1): 34-41.

Bultman, T. L. and Uetz, G. W. 1984. Effect of Structure and Nutritional Quality of Litter on Abundances of Litter-Dwelling Arthropods. American Midland Naturalist. Vol. 111 (1): 165-172.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. New York, Springer. 488

Burnham, K. P. and Anderson, D. R. 2004. Multimodel inference - understanding AIC and BIC in model selection. Sociological Methods & Research. Vol. 33 (2): 261-304.

Burton, N. H. K. 2007. Influences of restock age and habitat patchiness on Tree Pipits *Anthus trivialis* breeding in Breckland pine plantations. Ibis. Vol. 149 (s2): 193-204.

Buse, A. and Good, J. E. G. 1993. The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): implications for conservation. Biological Conservation. Vol. 64 (1): 67-76.

Caners, R. T., Macdonald, S. E. and Belland, R. J. 2010. Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. Botany. Vol. 88 (4): 315-328.

Carey, A. B. and Harrington, C. A. 2001. Small mammals in young forests: implications for management and sustainability. Forest Ecology and Management. Vol. 154: 289-309.

Carmel, Y. and Stoller-Cavari, L. 2006. Comparing environmental and biological surrogates for biodiversity at a local scale. Israel Journal of Ecology & Evolution. Vol. 52 (1): 11-27.

Carter, C. I. 1973. Green spruce aphid, *Elatobium abietinum*. Report on Forest Research, H. London. 104-105.

Casida, J. E. 1980. Pyrethrum flowers and pyrethroid insecticides. Environmental Health Perspectives. Vol. 34: 189-202.

Castro, A. and Wise, D. 2009. Influence of fine woody debris on spider diversity and community structure in forest leaf litter. Biodiversity and Conservation. Vol. 18 (14): 3705-3731.

Chen, Y.-L., Cheng, G.-L. and Han, S.-J. 2000. Effect of corylus clusters on the physicochemical properties of soil. Journal of Forestry Research. Vol. 11 (3): 173-176.

Chinery, M. 1993. Collins Field Guide to the Insects of Britain and Northern Europe, Harper Collins Publishers, London.

Church, J, M, Hodgetts, N. G., Preston, C. D. and Stewart, N. F. 2001. British Red Data Books mosses and liverworts. JNCC, Peterborough.

Clapham, A. R., Tutin, T. G. and Moore, D. M. 1987. Flora of the British Isles. Cambridge, Cambridge University Press. 688

COFORD 2009. Forestry 2030 - http://www.coford.ie/iopen24/-t-127_525.html.

Cole, L. J., McCracken, D. I., Downie, I. S., Dennis, P., Foster, G. N., Waterhouse, T., Murphy, K. J., Griffin, A. L. and Kennedy, M. P. 2005. Comparing the effects of farming practices on ground beetle

(Coleoptera: Carabidae) and spider (Araneae) assemblages of Scottish farmland. Biodiversity and Conservation. Vol. 14 (2): 441-460.

Coll, M. T., Heneghan, L. and Bolger, T. 1995. Carabidae fauna in two Irish conifer stands: a comparison with those of some other European forests. Biology and Environment. Proceedings of the Royal Irish Academy. Vol. 94B (3): 171 - 177.

Connolly, N. 1992. The phenology of canopy arthropod assemblages in *Picea sitchnesis* and *Pinus contorta*, with an assessment of the canopy fogging method. Department of Zoology and Animal Ecology. Cork, University College Cork.

Connor, E. F. and McCoy, E. D. 2001. Species-area relationships. *In*: Encycolpedia of Biodiversity. Levin, S. A. (Eds). New York, Academic Press. 5. pp. 791-833.

Coombes, R. H. 2009. Woodpeckers move in. Wings. 55.

Coombes, R. H., Crowe, O., Lauder, A., Lysaght, L., O'Brien, C., O'Halloran, J., O'Sullivan, O. and Tierney, T. D. 2009. Countryside Bird Survey Report 1998-2007, BirdWatch Ireland, Wicklow.

Cooper, A., McCann, T. and Ridge, D. 2008. Vegetation development in second rotation Irish conifer plantations. Forest Ecology and Management. Vol. 255: 962-972.

Coote, L. 2007. Epiphyte diversity in Irish conifer plantations. Botany. Dublin, Ireland, University of Dublin, Trinity College. PhD.

Coote, L., Smith, G. F., Kelly, D. L., O'Donoghue, S., Dowding, P., Iremonger, S. and Mitchell, F. J. G. 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. Biodiversity and Conservation. Vol. 17: 953-968.

Coppins, B. J. 2002. Checklist of lichens of Great Britain and Ireland. London, British Lichen Society.

Cornelissen, J. H. C. 1996. An Experimental Comparison of Leaf Decomposition Rates in a Wide Range of Temperate Plant Species and Types. Journal of Ecology. Vol. 84 (4): 573-582.

Coroi, M., Skeffington, M. S., Giller, P., Smith, C., Gormally, M. and O'Donovan, G. 2004. Vegetation diversity and stand structure in streamside forests in the south of Ireland. Forest Ecology and Management. Vol. 202 (1): 39-57.

Cross, J. R. 1981. The Establishment of *Rhododendron ponticum* in the Killarney Oakwoods, S. W. Ireland. Journal of Ecology. Vol. 69 (3): 807-824.

Cross, J. R. 1998. An outline and map of the potential natural vegetation of Ireland. Applied Vegetation Science. Vol. 1: 241-252.

Curtis, D. J. 1980. Pitfalls in spider community studies (Arachnida, Araneae). Journal of Arachnology. Vol. 8 (3): 271-280.

Curtis, T. G. F. and McGough, H. N. 1988. The Irish Red Data Book. 1. Vascular plants. Dublin, The Stationery Office. 168

Dahlgren, R. A., Singer, M. J. and Huang, X. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. Biogeochemistry. Vol. 39: 45-64.

Davenport, J. L., Sleeman, D. P. and Woodman, P. C. 2008. Mind the Gap - Post glacial colonization of Ireland. Irish Naturalists Journal. Vol. Special Supplement.

Davies, Z., Tyler, C., Stewart, G. and Pullin, A. 2008. Are current management recommendations for saproxylic invertebrates effective? A systematic review. Biodiversity and Conservation. Vol. 17: 209-234.

Davis, J. D., Hendrix, S. D., Debinski, D. M. and Hemsley, C. J. 2008. Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. Journal of Insect Conservation. Vol. 12 (1): 69-79.

Day, K. R. and Carthy, J. 1988. Changes in carabid beetle communities accompanying a rotation of sitka spruce. Agriculture, Ecosystems & Environment. Vol. 24 (4): 407-415.

Day, R. W. and Quinn, G. P. 1989. Comparisons of treatments after an anlysis of variance in ecology Ecological Monographs. Vol. 59 (4): 433-463.

De Bakker, D., Maelfait, J. P., Hendrickx, F., Van Waesberghe, D., De Vos, B., Thys, S. and De Bruyn, L. 2000. A first analysis on the relationship between forest soil quality and spider (Araneae) communities of Flemish forest stands. Ekologia-Bratislava. Vol. 19: 45-58.

De Vries, B. W. L. 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. Biodiversity and Conservation. Vol. 4: 156-164.

Department of Agriculture and Food 2003. National report to the fourth session of the United Nations forum on forests: Ireland. Dublin.

Department of Agriculture, F. a. F. 1996. Growing for the future: a strategic plan for the development of the forestry sector in Ireland. Dublin.

Dettki, H. and Esseen, P.-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. Ecography. Vol. 21 (6): 613-624.

Dettki, H. and Esseen, P.-A. 2003. Modelling long term effects of forest managment on epiphytic lichens in northern Sweden. Forest Ecology and Management. Vol. 175: 223-238.

Dettmers, R., Buehler, D. A., Bartlett, J. G. and Klaus, N. A. 1999. Influence of point count length and repeated visits on habitat model performance. Journal of Wildlife Management. Vol. 63: 815-823.

Dhubhain, A. N., Walshe, J., Bulfin, M., Keane, M. and Mills, P. 2001. The initial development of a windthrow risk model for Sitka spruce in Ireland. Forestry. Vol. 74 (2): 161-170.

Dobson, F. S. 2000. Lichens: An Illustrated Guide to the British and Irish Species. Slough, UK, Richmond. 431

Docherty, M. and Leather, S. R. 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. Forest Ecology and Management. Vol. 95 (3): 197-207.

Dolman, P. M. and Fuller, R. J. 2003. The processes of species colonisation in wooded landscapes: a review of principles. In: The Restoration of Wooded Landscapes. Humphrey, J., Newton, A., Latham, J.et al (Eds). Edinburgh, UK, Forestry Commission. pp. 25-36.

Donald, P. F., Fuller, R. J., Evans, A. D. and Gough, S. J. 1998. Effects of forest management and grazing on breeding bird communities in plantations of broadleaved and coniferous trees in western England. Biological Conservation. Vol. 85: 183-197.

Donald, P. F., Haycock, D. and Fuller, R. J. 1997. Winter bird communities in forest plantations in western England and their response to vegetation, growth stage and grazing. Bird Study. Vol. 44: 206-219.

Dufrene, M. and Legendre, P. 1997a. Species assemblages and indicator species: the need for a flexible assymetric approach. Ecological Monographs. Vol. 67: 345-366.

Dytham, C. 2003. Choosing and using statistics: a biologists guide, Blackwell Science.

Dzwonko, Z. and Gawronski, S. 2002. Effect of litter removal on species richness and acidification of a mixed oak-pine woodland. Biological Conservation. Vol. 106: 389-398.

Dzwonko, Z. and Gawroński, S. 1994. The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. Plant Ecology. Vol. 111 (2): 149-160.

Ellyson, W. J. T. and Sillett, S. C. 2003. Epiphyte communities on Sitka spruce in an old-growth redwood forest. The Bryologist. Vol. 106 (2): 197-211.

Elmer, M., La France, M., Forster, G. and Roth, M. 2004. Changes in the decomposer community when converting spruce monocultures to mixed spruce/beech stands. Plant and Soil. Vol. 264 (1-2): 97-109.

Emmet, A. and Heath, J., Eds. 1991. The Moths and Butterflies of Great Britain and Ireland.

Volume 7 part 2 Lasciocampidae to Thyatiridae, with Life History Chart of the British Lepidoptera. Colchester, Harley Books.

EPA 2008. State of the Environment Report. Wexford, Ireland, Environmental Protection Agency.

Esseen, P.-A., Renhorn, K.-E. and Pettersson, R. B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications. Vol. 6 (1): 228-238.

Eycott, A. E., Watkinson, A. R. and Dolman, P. M. 2006. Ecological patterns of plant diversity in a plantation forest managed by clearfelling. Journal of Applied Ecology. Vol. 43 (6): 1160-1171.

Fahy, O. and Gormally, M. 1998. A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. Forest Ecology and Management. Vol. 110: 263-273.

FAO 2001. State of the World's forests, Food and Agriculture Organisation of the United Nations, Rome.

Farmer, A. M., Bates, J. W. and Bell, J. N. B. 1991. Comparisons of three woodland sites in NW Britain differing in richness of the epiphytic Lobarion pulmonariae community and levels of wet acidic deposition. Ecography. Vol. 14 (2): 85-91.

Farmer, R. A. and Nisbet, T. R. 2004. An overview of forest management and change with respect to environmental protection in the UK. Hydrology and Earth System Sciences. Vol. 8 (3): 279-285.

Fauna Europaea Web Service 2004. Fauna Europaea Version 1.1, Downloaded from http://www.faunaeur.org.

Felton, A., Lindbladh, M., Brunet, J. and Fritz, Ö. 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management. Vol. 260 (6): 939-947.

Ferris, R. and Humphrey, J. W. 1999. A review of potential biodiversity indicators for application in British forests. Forestry. Vol. 72 (4): 313-328.

Ferris, R., Peace, A. J., Humphrey, J. W. and Broome, A. C. 2000a. Relationships between vegetation, site type and stand structure in coniferous plantations in Britain. Forest Ecology and Management. Vol. 136: 35-51.

Ferris, R., Peace, A. J. and Newton, A. C. 2000b. Macrofungal communities of lowland Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karsten.) plantations in England: relationships with site factors and stand structure. Forest Ecology and Management. Vol. 131: 255-267.

Ferris, R. and Simmons, E. 2000. Plant Communities and Soil Seedbanks in Broadleaved-Conifer Mixtures on Ancient Woodland Sites in Lowland Britain. Forestry Comission Information Note Edinburgh, Forestery Commission.

Fiedler, K. and Schulze, C. H. 2004. Forest Modification Affects Diversity (But Not Dynamics) of Speciose Tropical Pyraloid Moth Communities. Biotropica. Vol. 36 (4): 615-627.

Fitter, A. H. and Peat, H. J. 1994. The ecological flora database. Journal of Ecology. Vol. 82: 415-425.

Floren, A., Otto, S. and Linsenmair, K. E. 2008. Do spider communities in primeval forests differ from those in forest plantations? A canopy study in the Bialowieza Forest (Poland). *In*: Canopy arthropod research in Europe. Floren, A. and Schmidl, J. (Eds). Nuremberg, Germany, Bioform Entomology. pp. 489-506.

Folan, A. C. M. and Mitchell, M. E. 1970. The lichens and lichen parasites of Derryclare wood Connemara. Proceeding of the Royal Irish Academy. Vol. 70(B) (7): 163-170.

Ford, E. D. and Newbould, P. J. 1977. The biomass and production of ground vegetation and its relation to tree cover through a deciduous woodland cycle. Journal of Ecology. Vol. 65: 201-212.

Forest Service 2000a. Code of Best Forest Practice, Forest Service, Johnstown Castle Estate, Co. Wexford.

Forest Service 2000b. Forest Biodiversity Guidelines, Forest Service, Johnstown Castle Estate, Co. Wexford.

Forest Service 2003. Forestry Schemes Manual. Dublin, Department of the Marine and Natural Resources.

Forest Service 2000c. Forestry schemes procedures and standards manual. Dublin, Department of the Marine and Natural Resources.

Forest Service 2004. Forestry statistics. http://www.agriculture.gov.ie/forestry/files/standard.xls. Dublin, Department of Agriculture and Food.

Forest Service 2007. National Forest Inventory: Republic of Ireland Results. Wexford, Ireland, Department of Agriculture, Fisheries and Food.

Forest Service 2001. Native Woodland Scheme, Forest Service, Johnstown Castle Estate, Co. Wexford, Ireland.

Fossitt, J. 2000. A Guide to Habitats in Ireland. Dublin, The Heritage Council.

Fox, H., Cullen, M., D.J., L., M., R., Ciarruiz, P., Dwyer, R. and Boyle, G. M. 2001. Vegetation monitoring and botanical survey of Brackloon Wood, Westport, Co. Mayo. Dublin, Ireland, Forest Ecosystem Research Group, Department of Environmental Resource Management, University College Dublin. 31. 91.

Frahm, J.-P. 2003. Climatic habitat differences of epiphytic lichens and bryophytes. Crypotgamie, Bryologie. Vol. 24 (1): 3-14.

Franc, N., Gotmark, F., Okland, B., Norden, B. and Paltto, H. 2007. Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biological Conservation. Vol. 135 (1): 86-98.

Franklin, J. F. 1988. Structural and functional diversity in temperate forests. *In*: Biodiversity. Wilson, E. O. and Peter, F. M. (Eds). Washington, National Academy Press.

Fraser, S. E. M., Dytham, C. and Mayhew, P. J. 2007. Determinants of parasitoid abundance and diversity in woodland habitats. Journal of Applied Ecology. Vol. 44: 352-361.

Frazer, G. W., Canham, C. D. and Lertzman, K. P. 1999a. Gap Light Analyzer, Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

French, L. 2005. Ground flora communities in Ireland's plantation forests: their diversity, structure and composition. Botany. Dublin, University of Dublin, Trinity College. PhD. 244.

French, L. J., Smith, G. F., Kelly, D. L., Mitchell, F. J. G., O'Donoghue, S., Iremonger, S. and McKee, A.-M. 2008. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. Forest Ecology and Management. Vol. 255: 476-494.

Fries, C., Johansson, O., Petterson, B. and Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. Forest Ecology and Management. Vol. 94: 89-103.

Fritz, Ö., Caldiz, M. S. and Brunet, J. 2009a. Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. The Bryologist. Vol. 112: 488-505.

Fritz, Ö., Niklasson, M. and Churski, M. 2009b. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Applied Vegetation Science. Vol. 12 (1): 93-106.

Fry, R. and Waring, P. 2001. A Guide To Moth Traps and Their Use, Orpington, Kent, England.

Fuller, R. J. 1995. Bird life of woodland and forest. Cambridge, Cambridge University Press.

Fuller, R. J. 1982. Habitats in Britain T & A D Poyser, Calton.

Fuller, R. J. and Browne, S. 2003. Effects of plantation structure and management on birds. *In*: Biodiversity in Britain's Planted Forests. Results from the Forestry Commission's Biodiversity Assessment Project: 93-99. Humphrey, J., Ferris, R. and Quine, C., Forestry Commission, Edinburgh.

Fuller, R. J., Noble, D. G., Smith, K. W. and Vanhinsbergh, D. 2005. Recent declines in populations of woodland birds in Britain: a review of possible causes. British Birds. Vol. 98: 116-143.

Gardiner, M. J. and Radford, T. 1980. Soil associations of Ireland and their land use potential. Dublin, An Foras Taluntais.

Gates, D. M., Keegan, H. J., Schleter, J. C. and Weidner, V. R. 1965. Spectral Properties of Plants. Applied Optics. Vol. 4 (1): 11-20.

Gaublomme, E., Hendrickx, F., Dhuyvetter, H. and Desender, K. 2008. The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biological Conservation. Vol. 141 (10): 2585-2596.

Gerson, U. and Seaward, M. R. D. 1977. Lichen-Invertebrate Associations. *In*: Lichen Ecology. Seaward, M. R. D. (Eds). London, Academic Press.

Gioria, M., Schaffers, A., Bacaro, G. and Feehan, J. 2010. The conservation value of farmland ponds: predicting water beetle assemblages using vascular plants as a surrogate group. Biological Conservation. Vol. 143 (5): 1125-1133.

Gittings, T. and Bond, K. 2008. Database of Irish Lepidoptera. 1 – Macrohabitats, microsites and traits of Noctuidae and butterflies. Irish Wildlife Manuals No. 35. Department of Environment, Heritage and Local Government, Dublin.

Gittings, T., O'Halloran, J., Kelly, T. and Giller, P. S. 2006. The contribution of open spaces to the maintenance of hoverfly (Diptera, Syrphidae) biodiversity in Irish plantation forests. Forest Ecology and Management. Vol. 237 (1-3): 290-300.

Glenn-Lewin, D. C. 1977. Species diversity in North American temperate forests. Plant Ecology. Vol. 33 (2): 153-162.

Godefroid, S., Massant, W., Weyembergh, G. and Koedam, N. 2003. Impact of Fencing on the Recovery of the Ground Flora on Heavily Eroded Slopes of a Deciduous Forest. Environmental Management. Vol. 32 (1): 62-76.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography. Vol. 26 (5): 573-584.

Goodenough, A. E., Elliot, S. L. and Hart, A. G. 2009. Are nest sites actively chosen? Testing a common assumption for three non-resource limited birds Acta Oegologica. Vol. 35: 598-602.

Gosler, A. G., Greenwood, J. J. D. and Perrins, C. 1995. Predation risk and the cost of being fat. Nature. Vol. 377 (6550): 621-623.

Gosselin, F. 2004. Imiter la nature, hâter son oeuvre? Quelques réflexions sur les éléments et stades tronqués par la sylviculture. *In*: Biodiversité et gestion forestière. Connaître pour préserver. Gosselin, M. and Laroussinie, O. (Eds). Antony, France, Coédition Groupement d'Intérêt Public Ecosystèmes Forestiers (GIPECOFOR) - Cemagref Editions. pp. 217-256.

Gotelli, N. J. and Colwell, R. K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters. Vol. 4 (4): 379-391.

Gotelli, N. J. and Entsminger, G. L. 2001. Ecosim null model software for ecology, Version 6.0., Acquired Intelligence Inc. & Keysey-Bear.

Gower, J. C. 1971. Statistical methods of comparing different multivariate analyses of the same data. *In*: Mathematics in the Archaeological and Historical Sciences. Hodson, F. R., Kendall, D. G. and Tautu, P. (Eds). Edinburgh, UK, Edinburgh University Press. pp. 138-149.

Gower, S. T. and Norman, J. M. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. Ecology. Vol. 72 (5): 1896-1900.

Gradstein, S. R., Hietz, P., Lucking, R., Lucking, A., Sipman, H. J. M., Vester, H. F. M., Wolf, J. H. D. and Gardette, E. 1996. How to sample the epiphytic diversity of tropical rain forests. Ecotropica. Vol. 2: 59-72.

Grashof-Bodkam, C. J. and Geertsema, W. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. Journal of Biogeography. Vol. 25 (5): 837-846.

Green, P. and Peterken, G. F. 1997. Variation in the amount of dead wood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. Forest Ecology and Management. Vol. 98: 229–238.

Gregory, R. D., Vorisek, P., Van Strien, A., Gmelig Meyling, A. W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. and Burfield, I. J. 2007. Population trends of widespread woodland birds in Europe. Ibis. Vol. 149 (s2): 78-97.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative Plant Ecology: A Functional Approach to Common British Species. London, UK, Chapman & Hall. 742

Grime, J. P., Hodgson, J. G. and Hunt, R. 2007. Comparative plant ecology: a functional approach to common British species. London, Castlepoint Press.

Grodzińska, K. 1977. Acidity of tree bark as a bioindicator of forest pollution in Southern Poland. Water, Air, & Soil Pollution. Vol. 8 (1): 3-7.

Grove, S., J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics. Vol. 33: 1-23.

Guillemain, M., Loreau, M. and Daufresne, T. 1997. Relationships beetween the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. Acta Oecologica. Vol. 18 (4): 465-483.

Gunnarsson, B. 1996. Bird predation and vegetation structure affecting spruce-living arthropds in a temperate forest. Journal of Animal Ecology. Vol. 65: 389 - 397.

Gunnarsson, B., Heyman, E. and Vowles, T. 2009. Bird predation effects on bush canopy arthropods in suburban forests. Forest Ecology and Management. Vol. 257 (2): 619-627.

Günther, J. and Assmann, T. 2004. Fluctuations of carabid populations inhabiting an ancient woodland (Coleoptera, Carabidae). Pedobiologia. Vol. 48 (2): 159-164.

Gurdebeke, S., De Bakker, D., Vanlanduyt, N. and Maelfait, J. P. 2003. Plans for a large regional forest in eastern Flanders (Belgium): assessment of spider diversity and community structure in the current forest remnants. Biodiversity and Conservation. Vol. 12 (9): 1883-1900.

Hafner, S. D. and Groffman, P. M. 2005. Soil nitrogen cycling under litter and coarse woody debris in a mixed forest in New York State. Soil Biology and Biochemistry. Vol. 37 (11): 2159-2162.

Haila, Y., Hanski, I., Niemelä , J., Punttila, P., Raivio, S. and Tukia, H. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Ann. Zool. Fennici. Vol. 31: 187-202.

Halaj, J., Ross, D. W. and Moldenke, A. R. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. Journal of Arachnology. Vol. 26 (2): 203-220.

Halaj, J., Ross, R. and Moldenke, R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos. Vol. 90: 139 - 152.

Hale, S. 2001. Light regime beneath Sitka spruce plantations in northern Britain: preliminary results. Forest Ecology and Management. Vol. 51: 61-66.

Hale, S. E. 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management. Vol. 179: 341-349.

Halonen, P., Hyvarinen, M. and Kauppi, M. 1991. The epiphytic lichen flora on conifers in relation to climate in the Finnish middle boreal subzone. The Lichenologist. Vol. 23 (1): 61-72.

Hannerz, M. and Hånell, B. 1997. Effects on the flora in Norway spruce forests following clearcutting and shelterwood cutting. Forest Ecology and Management. Vol. 90 (1): 29-49.

Hardtle, W., von Oheimb, G. and Westphal, C. 2003. The effects of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). Forest Ecology and Management. Vol. 182: 327-338.

Harmer, R., Boswell, R. and Robertson, M. 2005. Survival and growth of tree seedlings in relation to changes in the ground flora during natural regeneration of an oak shelterwood. Forestry. Vol. 78 (1): 21-32.

Harris, G. P. 1971. The ecology of corticolous lichens. I. The zonation on oak and birch in south Devon. Journal of Ecology. Vol. 59 (2): 431-439.

Hartley, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. Forest Ecology & Management. Vol. 155: 81-95.

Harvey, P., Nellist, D. and Telfer, M. 2002. Provisional Atlas of British spiders (Arachnida, Araneae), Volume 1 & 2. Huntingdon, Biological Records Centre.

Hassan, R. M., Scholes, R. and Ash, N. 2006. Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment. Washington D.C., Island Press.

Hauck, M. 2010. Site factors controlling epiphytic lichen abundance in northern coniferous forests. Flora - Morphology, Distribution, Functional Ecology of Plants. Vol.: doi:10.1016/j.flora.2010.02.001.

Heino, J. 2010. Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? Ecological Indicators. Vol. 10 (2): 112-117.

Higgins, G. T., Martin, J. R. and Perrin, P. M. 2004. National survey of native woodland in Ireland, Dept. of the Environment, Heritage and Local Government.

Highland Statistics LTD 2007. Brodgar. Software package for data exploration, univariate analysis, multivariate analysis and time series analysis. Aberdeenshire, Scotland.

Hill, D. A., Lambton, S., Proctor, I. and Bullock, I. 1991a. Winter bird communities in woodland in the Forest of Dean, England, and some implications of livestock grazing. Bird Study. Vol. 38: 57-70.

Hill, M. O. 1979. The development of flora in even-aged plantations. *In*: The Ecology Of Even Aged Plantations. Ford, E. D., Malcolm, D. C. and Atterson, J. (Eds). Cambridge, Institute for Terrrestrial Ecology. pp. 175-192.

Hill, M. O. 1986. Ground flora and succession in commercial forests. *In*: Trees and Wildlife in the Scottish Uplands. Jenkins, D., NERC/ITE. pp. 8.

Hill, M. O. 1987. Opportunities for vegetation management in plantation forests. *In*: Environmental Aspects of Plantation Forestry in Wales. Good, J. E. G. (Eds). Grange-over-Sands, NERC/ITE. pp. 64-69.

Hill, M. O. and Jones, E. W. 1978. Vegetation changes resulting from afforestation of rough grazing in Caeo Forest, South Wales. Journal of Ecology. Vol. 66: 433-456.

Hill, M. O., Preston, C. D., Bosanquet, S. D. S. and Roy, D. B. 2007. BRYOATT: Attributes of British and Irish Mosses, Liverworts and Hornworts with information on Native status, size, life form, life history, geography and habitat. Cambridgeshire, Centre for Ecology and Hydrology.

Hill, M. O., Preston, C. D. and Roy, D. B. 2004. PLANTATT - Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats. Peterborough, Centre for Ecology and Hydrology.

Hill, M. O., Preston, C. D. and Smith, A. J. E. 1991. Atlas of the Bryophytes of Britain and Ireland. Volume 1. Liverworts (Hepaticae and Anthocerotae). Colchester, Harley Books.

Hill, M. O., Preston, C. D. and Smith, A. J. E. 1992. Atlas of the Bryophytes of Britain and Ireland. Volume 2. Mosses (except Diplolepideae). Colchester, Harley Books.

Hill, M. O., Preston, C. D. and Smith, A. J. E. 1994. Atlas of the Bryophytes of Britain and Ireland. Volume 3. Mosses (Diplolepideae). Colchester, Harley Books.

Hillis, J. P. 2007. Rare Irish breeding birds 2007. The seventh annual report of the Irish rare breeding birds panel. Irish Birds. Vol. 8 (3): 365-372.

Hilmo, O. 1994. Distibution and succession of epiphytic lichens in *Picea abies* branches in a boreal forest, central Norway. The Lichenologist. Vol. 26 (2): 149-169.

Hilmo, O. 2002. Growth and morphological response of old-forest lichens transplanted into a young and an old *Picea abies* forest. Ecography. Vol. 25: 329-335.

Hilmo, O. and Holien, H. 2002. Epiphytic lichen response to the edge environment in a boreal *Picea abies* forest in central Norway. The Bryologist. Vol. 105 (1): 48-56.

Hilmo, O. and Sastad, S. M. 2001. Colonization of old-forest lichens in a young and an old boreal *Picea abies* forest: an experimental approach. Biological Conservation. Vol. 102: 251-259.

Hodge, S. J. and Peterken, G. F. 1998. Deadwood in British forests: priorities and a strategy. Forestry. Vol. 71 (2): 99-112.

Holien, H. 1996. The influence of site and stand factors on the distribution of crustose lichens of the Calciales in a suboceanic spruce forest are in Central Norway. Lichenologist. Vol. 28: 315-330.

Holyoak, D. 2003. The distribution of bryophytes in Ireland. Dinas Powys, Broadleaf Books.

Hopkins, J. J. and Kirby, K. J. 2007. Ecological change in British broadleaved woodland since 1947. Ibis. Vol. 149 (2): 29-40.

Hothorn, T. and Hornik, K. 2010. exactRankTests: Exact Distributions for Rank and Permutation Tests.

Hottola, J. and Siitonen, J. 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodiversity and Conservation. Vol. 17: 2559–2577.

Howard, P. J. A. and Howard, D. M. 1990. Use of organic carbon and loss-on-ignition to estimate soil organic matter in different soil types and horizons. Biology and Fertility of Soils. Vol. 9: 306-310.

Hoyne, S. and Thomas, A. 2001. Forest residues:Harvesting, storage and fuel value, COFORD.

Hubbard, C. E. 1984. Grasses: A Guide to Their Structure, Identification, Uses and Distribution in the British Isles. London, UK, Penguin Books.

Humphrey, J., Ferris, R. and Quine, C. 2003. Biodiversity in Britain's Planted Forests: Results from the Forestry Commission's Biodiversity Assessment Project. Edinburgh, Forestry Comission.

Humphrey, J. W., Davey, S., Peace, A. J., Ferris, R. and Harding, K. 2002a. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biological Conservation. Vol. 107: 165-180.

Humphrey, J. W., Ferris, R., Jukes, M. R. and Peace, A. J. 2002b. The potential contribution of conifer plantations to the UK Biodiversity Action Plan Botanical Journal of Scotland. Vol. 54 (1): 49-62.

Humphrey, J. W., Hawes, C., Peace, A. J., Ferris-Kaan, R. and Jukes, M. R. 1999. Relationships between insect diversity and habitat characteristics in plantation forests. Forest Ecology and Management. Vol. 113: 11-21.

Humphrey, J. W., Newton, A. C., Peace, A. J. and Holden, E. 2000. The importance of conifer plantations in northern Britain as a habitat for native fungi. Biological Conservation. Vol. 96: 241-252.

Humphrey, J. W., Peace, A. J., Jukes, M. R. and Poulsom, E. L. 2004. Multiple-scale factors affecting the development of biodiversity in UK plantations. *In*: Forest Biodiversity: Lessons from History for Conservation. Honnay, O., Verheyen, K., Bossuyt, B. and Hermy, M. (Eds). Oxford, UK, CABI. CABI/IUFRO Research Series. pp. 143-162.

Humphrey, J. W., Stevenson, A., Whitfield, P. and Swailes, J. 2002c. Life in the deadwood: a guide to managing deadwood in Forestry Commission forests. Edinburgh, Forestry Commission.

Hunter, M. L. 1999. Maintaining biodiversity in forest ecosystems, Cambridge University Press. 714

Hyvärinen, M., Halonen, P. and Kauppi, M. 1992. Influence of stand age and structure on the epiphytic lichen vegetation in the middle-boreal forests of Finland. The Lichenologist. Vol. 24 (2): 165-180.

Ings, T. and Hartley, S. 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. Forest Ecology and Management. Vol. 119: 123 - 136.

Innes, J. L. and Kock, B. 1998. Forest biodiversity and its assessment by remote sensing. Global Ecology and Biogeography Letters. Vol. 7: 397-419.

Iremonger, S., Gittings, T., Smith, G. F., Wilson, M., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D. L., Giller, P. S., O'Sullivan, A., Neville, P., Mitchell, F. J. G., O'Donnell, V., Kelly, T. and Dowding, P. 2006a. Investigation of experimental methods to enhance biodiversity in plantation forests.

Iremonger, S., Gittings, T., Smith, G. F., Wilson, M., Oxbrough, A., Coote, L., Pithon, J., O'Donoghue, S., McKee, A.-M., O'Halloran, J., Kelly, D. L., Giller, P. S., O'Sullivan, A., Neville, P., Mitchell, F. J. G., O'Donnell, V., Kelly, T. and Dowding, P. 2007. Investigation of experimental methods to enhance biodiversity in plantation forests. Dublin, Ireland, COFORD and EPA. 190.

Irwin, S., Wilson, M., Kelly, T. C., O'Donoghue, B., O'Mahony, B., Oliver, G., Cullen, C., O'Donoghue, T. and O'Halloran, J. 2008. Aspects of the breeding biology of Hen Harriers *Circus cyaneus* in Ireland. Irish Birds. Vol. 8: 331-334.

Jackson, D. A. 1995. PROTEST: a PROcrustean randomization TEST of community environment concordance. Ecoscience. Vol. 2 (3): 297-303.

Jacquemoud, S. and Baret, F. 1990. PROSPECT: A Model of Leaf Optical Properties Spectra. Remote Sensing of Environment. Vol. 34: 75-91.

James, P. W., Hawksworth, D. L. and Rose, F. 1977. Lichen communities in the British Isles: a preliminary conspectus. *In*: Lichen Ecology. Seaward, M. R. D. (Eds). London, UK, Academic Press. pp. 295-413.

Jarvis, A. 1999. Quantifying the hydrological role of cloud deposition onto epiphytes in a tropical montane. London, Kings College London. 250.

Jeffrey, D. W. 2003. Grasslands and Heath: a Review and hypothesis to Explain the Distribution of Burren Plant Communities. Biology and Environment: Proceedings of the Royal Irish Academy. Vol. 103B (3): 111-123.

Jeffrey, D. W. 1970. A note on the use of ignition loss as a means for the approximate estimation of soil bulk density. Journal of Ecology. Vol. 58: 297-299.

Jermy, A. C., Chater, A. O. and David, R. W. 1982. Sedges of the British Isles. BSBI Handbook No. 1. London, UK, Botanical Society of the British Isles. 268.

JNCC 2010. Invertebrate Red Data Books, Joint Nature Conservation Committee. Downloaded from http://www.jncc.gov.uk/page-2133.

Joint Nature Conservation Committee 2010. Invertebrate Red Data Books.

Jones, E. W. 1959. Biological Flora of the British Isles. *Quercus* L. Journal of Ecology. Vol. 47: 169-222.

Jonsell, M., Hansson, J. and Wedmo, L. 2007. Diversity of saproxylic beetle species in logging residues in Sweden - Comparisons between tree species and diameters. Biological Conservation. Vol. 138 (1-2): 89-99.

Jonsson, B. G. 2000. Availability of coarse woody debris in a Boreal old-growth *Picea abies* forest. Journal of Vegetation Science. Vol. 11 (1): 51-56.

Joy, N. H. 1932. A practical handbook of British beetles, Vol. I and II, H. F. & G. Witherby, UK.

Joyce, P. M. and O'Carroll, N. 2002. Sitka Spruce in Ireland. Dublin, Ireland, COFORD.

Jukes, M. R., Ferris, R. and Peace, A. J. 2002. The influence of stand structure and composition on diversity of canopy Coleoptera in coniferous plantations in Britain. Forest Ecology and Management. Vol. 163 (1-3): 27-41.

Jukes, M. R., Peace, A. J. and Ferris, R. 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. Forest Ecology and Management. Vol. 148 (1-3): 271-286.

Kaiser, H. F. 1958. The varimax criterion for analytic rotation in factor analysis. Psychometrika. Vol. 23: 187-200.

Kappes, H. 2006. Relations between forest management and slug assemblages (Gastropoda) of deciduous regrowth forests. Forest Ecology and Management. Vol. 237 (1-3): 450-457.

Kelly, D. L. 2000. Charting diversity in a Killarney oakwood: levels of resolution in floristic recording, and the effects of fencing and felling. *In*: Biodiversity: The Irish Dimension. Rushton, B. S. (Eds). Dublin, Royal Irish Academy. pp. 76-94.

Kelly, D. L. 1975. Native woodland vegetation in western Ireland with especial reference to the region of Killarney. Department of Botany. Dublin, University of Dublin, Trinity College. PhD. 337.

Kelly, D. L. 1991. Trees, Irish Biogeographical Society, Dublin.

Kelly, D. L. 2005. Woodland on the Western fringe: Irish oakwood diversity and the challenges of conservation. Botanical Journal of Scotland. Vol. 57: 21-40.

Kelly, D. L. and Kirby, E. N. 1982. Irish native woodlands over limestone. Journal of Life Sciences, Royal Dublin Society. Vol. 3: 181-198.

Kelly, D. L. and Moore, J. J. 1975. A preliminary sketch of the Irish acidophilous oakwoods. *In*: La Vegetation des Forets Caducifoliees Acidophiles. Gehu, J. M. (Eds). Vaduz, J. Cramer. pp. 375-387.

Kenkel, C. and Bradfield, G. E. 1981. Ordination of epiphytic bryophyte communities in a wet-temperate coniferous forest, South-Coastal British Columbia. Vegetatio. Vol. 45: 147-154.

Kennedy, C. E. J. and Southwood, T. R. E. 1984. The number of species of insects associated with British trees: A re-analysis. The Journal of Animal Ecology. Vol. 53 (2): 455-478.

Kennedy, P. G. and Quinn, T. 2001. Understory plant establishment on old-growth stumps and the forest floor in western Washington. Forest Ecology and Management. Vol. 154 (1-2): 193-200.

Kerr, G. 2002. Uneven-aged silviculture: putting ideas into practice. Quarterly Journal of Forestry. Vol. 96 (2): 111-116.

Kerr, G. 1999. The uses of silvicultural sytems to enhance the biological diversity of plantation forests in Britain. Forestry. Vol. 72 (3): 191-205.

Kerr, G., Nixon, C. J. and Matthews, R. W. 1992. Silviculture and yield of mixed-species stands: the UK experience. *In*: The Ecology of Mixed-Species Stands of Trees. Cannell, M. G. R., Malcolm, D. C. and Robertson, P. A. (Eds). London, Blackwell. pp. 35–51.

Kershaw, K. A. 1985. Physiological Ecology of Lichens. Cambridge, UK, Cambridge University Press.

Kevan, P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture, Ecosystems & Environment. Vol. 74 (1-3): 373-393.

Key, R. S. 1995. Invertebrate conservation and new woodland in Britain. *In*: The Ecology of Woodland Creation. Ferris-Kaan, R. (Eds). Chichester, UK, John Wiley and Sons Ltd. pp. 149-162.

Kirby, E. N. and O'Connell, M. 1982. Shannawoneen Wood, County Galway, Ireland: the woodland and saxicolous communities and the epiphytic flora. Journal of Life Sciences of the Royal Dublin Society. Vol. 4: 73-96.

Kirby, K. J. 1992. Accumulation of dead wood - a missing ingredient in coppicing. *In*: Coppicing and natural disturbance in temperate woodlands–a review. Buckley, G. P. (Eds). London, Chapman & Hall.

Kirby, K. J. 1988. Changes in the ground flora under plantations on ancient woodland sites. Forestry. Vol. 61: 317-338.

Kirby, K. J. 2001. The impact of deer on the ground flora of British broadleaved woodland. Forestry. Vol. 74 (3): 219-229.

Kirby, K. J., Mitchell, F. J. and Hester, A. J. 1994. A role for large herbivores (deer and domestic stock) in nature conservation management in British semi-natural woods. Arboricultural Journal. Vol. 18 (4): 381-399.

Kirby, K. J., Reid, C. M., Thomas, R. C. and Goldsmith, F. B. 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. Journal of Applied Ecology. Vol. 35: 148-155.

Kirby, K. J. and Woodell, S. R. J. 1998. The distribution and growth of bramble (*Rubus fruticosus*) in British semi-natural woodland and the implications for nature conservation. Journal of Practical Ecology. Vol. 2 (1): 31-41.

Kivistö, L. and Kuusinen, M. 2000. Edge effects on the epiphytic lichen flora of *Picea abies* in middle boreal Finland. Lichenologist. Vol. 32 (4): 387-398.

Koivula, M., Punttila, P., Haila, Y. and Niemelä, J. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography. Vol. 22 (4): 424-435.

Koorem, K. and Moora, M. 2010. Positive association between understory species richness and a dominant shrub species (Corylus avellana) in a boreonemoral spruce forest. Forest Ecology and Management. Vol. 260: 1407-1413.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecological Applications. Vol. 2: 203-217.

Kruys, N. and Jonsson, B. G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research. Vol. 29 (8): 1295-1299.

Kucharic, C. J., Norman, J. M. and Gower, S. T. 1999. Characterization of radiation regimes in nonrandom forest canopies: theory, measurements, and a simplified modeling approach. Tree Physiology. Vol. 19: 695-706.

Kuusinen, M. 1996. Importance of swamp-forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. Ecography. Vol. 19: 41-51.

Kuusinen, M. and Siitonen, J. 1998. Epiphytic lichen diversity in oldgrowth and managed Picea abies stands in southern Finland. Journal of Vegetation Science. Vol. 9: 283–292.

Lack, P. 1986. The Atlas of Wintering Birds in Britain and Ireland. Calton, T & AD Poyser.

Laganière, J., Paré, D. and Bradley, R. L. 2008. Linking the abundance of aspen with soil faunal communities and rates of belowground processes within single stands of mixed aspen-black spruce. Applied Soil Ecology. Vol. In Press, Corrected Proof.

Lagergren, F. and Lindroth, A. 2002. Transpiration response to soil moisture in pine and spruce trees in Sweden. Agricultural and Forest Meteorology Vol. 112: 67-85.

Lande, R., DeVries, P. J. and Walla, T. 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. Oikos. Vol. 89: 601-605.

Lang, G. E., Reiners, W. A. and Pike, L. H. 1980. Structure and biomass dynamics of epiphytic lichen communities of balsam fir forests in New Hampshire. Ecology. Vol. 61 (3): 541-550.

Larsen, J. B. 1995. Ecological stability of forests and sustainable silviculture. Forest Ecology and Management. Vol. 73: 85-96.

Larsson, T.-B. 2001. Ecological Bulletins, 50, Biodiversity evaluation tools for European forests, Wiley. 242

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Amsterdam, Elsevier. 853

Lepŝ, J., Spitzer, K. and Jaroŝ, J. 1998. Food Plants, Species Composition and Variability of the Moth Community in Undisturbed Forest. Oikos. Vol. 81 (3): 538-548.

Lewandowski, A. S., Noss, R. F. and Parsons, D. R. 2010. The effectiveness of surrogate taxa for the representation of biodiversity. Conservation Biology. Vol. 24: 1367-1377.

Liira, J., Sepp, T. and Parrest, O. 2007. The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. Forest Ecology and Management. Vol. 250 (1-2): 34-46.

Lindenmayer, D. B., Incoll, R. D., Cunningham, R. B. and Donnelly, C. F. 1999. Attributes of logs on the floor of Australian Mountain Ash (*Eucalyptus regnans*) forests of different ages. Forest Ecology and Management. Vol. 123: 195–203.

Lindgren, P. M. F. and Sullivan, T. P. 2001. Influence of alternative vegetation management treatments on conifer plantation attributes: abundance, species diversity, and structural diversity. Forest Ecology and Managament. Vol. 142: 163-182.

Lindhe, A., Åsenblad, N. and Toresson, H.-G. 2004. Cut logs and high stumps of spruce, birch, aspen and oak - nine years of saproxylic fungi succession. Biological Conservation. Vol. 119 (4): 443-454.

Lindhe, A., Lindelöw, Å. and Åsenblad, N. 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodiversity and Conservation. Vol. 14 (12): 3033-3053.

Lomov, B., Keith, D. A., Britton, D. R. and Hochuli, D. F. 2006. Are butterflies and moths useful indicators for restoration monitoring? A pilot study in Sydney's Cumberland Plain Woodland. Ecological Management & Restoration. Vol. 7 (3): 204-210.

Loreau, M. 1987. Vertical distribution of activity of carabid beetles in a beech forest floor. Pedobiologia. Vol. 30: 173-178.

Lowman, M. D. and Wittman, P. K. 1996. Forest canopies: methods, hypotheses and future directions. Annual Review of Ecology and Systematics. Vol. 27: 55-81.

Luff, M. 2007. RES Handbook Volume 4 Part 2: The Carabidae (Ground Beetles) of Britain and Ireland, Field Studies Council, Shropshire, UK.

Shropshire, UK, Field Studies Council.

Lynas, P., Newton, S. F. and Robinson, J. A. 2007. The status of birds in Ireland: an analysis of conservation concern 2008-2013. Irish Birds. Vol. 8: 149-167.

MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. Ecology. Vol. 42 (3): 594-598.

Magura, T., Ködöböcz, V. and Tóthmérész, B. 2001. Effects of habitat fragmentation on carabids in forest patches. Journal of Biogeography. Vol. 28 (1): 129-138.

Magura, T., Tóthmérész, B. and Elek, Z. 2003b. Diversity and composition of carabids during a forestry cycle. Biodiversity and Conservation. Vol. 12 (1): 73-85.

Magurran, A. 1985. The diversity of Macrolepidoptera in two contrasting woodland habitats at Banagher, Northern Ireland. Proceedings of the Royal Irish Academy B. Vol. 85 (10): 121-132.

Magurran, A. E. 1988. Ecological Diversity and Its Measurement, Chapman and Hall.

Magurran, A. E. 2004. Measuring Biological Diversity, Blackwell Publishing. 256

Majerus, M. and Kearns, P. 1989. Naturalists' Handbooks 10: Ladybirds, The Richmond Publishing Co. Ltd.

Mänd, R., Leivits, A., Leivits, M. and Rodenhouse, N. L. 2009. Provision of nestboxes raises the breeding density of Great Tits *Parus major* equally in coniferous and deciduous woodland. Ibis. Vol. 151 (3): 487-492.

Marage, D. and Lemperiere, G. 2005. The management of snags: a comparison in managed and unmanaged ancient forests of the Southern French Alps. Annals of Forest Science. Vol. 62: 135–142.

Márialigeti, S., Németh, B., Tinya, F. and Ódor, P. 2009. The effects of stand structure on ground-floor bryophyte assemblages in temperate mixed forests. Biodiversity and Conservation. Vol. 18 (8): 2223-2241.

Martin, N. M. 1938. Some observations on the epiphytic moss flora of trees in Argyll. Journal of Ecology. Vol. 26 (1): 82-95.

Martin, R. D. In Press. *Anobium inexspectatum* Lohse (Coleoptera: Anobiidae) at Drummin Wood, Co. Galway, and Uragh Wood, Co. Kerry, a new record for Ireland. Irish Naturalists Journal. Vol.

Martin, R. D. 2009. *Entelecara acuminata* (Wider, 1834) at Brownstown Wood, Co Kilkenny (Araneae: Linyphiidae), a new record to Ireland. Irish Naturalist's Journal. Vol. 30 (1): 65-66.

Mason, B. 2006. Managing Mixed Stands of Conifers and Broadleaves in Upland Forests in Britain. Edinburgh, Forest Commission.

Mason, B. and Kerr, G. 2004. Transforming even-aged conifer stands to continuous cover management. Edinburgh, Forestry Comission.

Mason, W. L. 2007. Changes in the management of British forests between 1945 and 2000 and possible future trends. 149. 41-52.

Mason, W. L. and Baldwin, E. 1995. Performance of pedunculate oak after 40 years in mixture with European larch and Norway spruce in Southern Scotland. Scottish Forestry. Vol. 49 (1): 5-13.

Mason, W. L. and Kerr, G. 2001. Transforming even-aged conifer stands to continuous cover management. Edinburgh, UK, Information Note 40. Forestry Commission.

Mason, W. L., Kerr, G. and Simpson, J. 1999. What is continuous cover forestry? Commission, F. Edinburgh.

Mather, P. M. 1976. Computational Methods of Multivariate Analysis in Physical Geography. London, UK, J.Wiley & Sons.

Matveinen-Huju, K., Koivula, M., Niemelä, J. and Rauha, A. M. 2009. Short-term effects of retention felling at mire sites on boreal spiders and carabid beetles. Forest Ecology and Management. Vol. 258 (11): 2388-2398.

Mayer, P. M. 2008. Ecosystem and decomposer effects on litter dynamics along an old field to old-growth forest successional gradient. Acta Oecologica. Vol. 33 (2): 222-230.

McAree, D. 2002. The forest service biodiversity plan. Biology and Environment: Proceedings of the Royal Irish Academy. Vol. 102B (3): 183-184.

McCarthy, P. M. 1980. Vertical zonation of lichens on alder (*Alnus glutinosa* (L.) Gaertn.) near Cork, Ireland. Scientific Proceedings, Royal Dublin Society, Series A. Vol. 6: 397-405.

McCarthy, P. M., Mitchell, M. E. and Schouten, M. G. C. 1986. Lichens epiphytic on *Calluna vulgaris* (L) Hull in Ireland. Nova Hedwigia. Vol. 42 (1): 91-98.

McCune, B., Amsberry, K. A., et al. 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. Northwest Science. Vol. 71 (2): 145-152.

McCune, B. and Grace, J. 2002b. Analysis of Ecological Communities. Oregon, MjM software Design.

McCune, B. and Mefford, M. 1997. PC-ORD for Windows. Glenedon Beach, Oregon, MjM Software.

McCune, B. and Mefford, M. J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Gleneden Beach, Oregon, USA, MjM Software

McEvoy, P. M. 2006. The effects of livestock grazing on ground flora in broadleaf woodlands in Northern Ireland. Forest Ecology and Management. Vol. 225: 39-50.

McFerran, D. 1997a. Environment and Heritage Research and Developement Series. No. 97/10, Evironment and Heritage Service.

McFerran, D. 1997b. Northern Ireland Species Inventory: spiders (Arachnida). Environment and Heritage Research and Development Series. No. 97/10. Belfast, Environment and Heritage Service. 58.

McGeachie, W. J. 1988. A remote sensing method for the estimation of light-trap efficiency, Cambridge Journals Online. 78. 379-385.

MCPFE Liaison Unit Warsaw 2007. State of Europe's Forests 2007: The MCPFE Report on Sustainable Forest Management in Europe. Warsaw, Poland, United Nations Economic Commission for Europe & Food and Agriculture Organization of the United Nations.

Melbourne, B. 1999. Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. Australian Journal of Ecology. Vol. 24: 228 - 239.

Messier, C., Parent, S. and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science. Vol. 9 (4): 511-520.

Met Éireann 2010a. Monthly weather data reports, Met Éireann.

Met Éireann 2010b. Rainfall in Ireland. Dublin.

Minihan, V. B. and Rushton, B. S. 1984. The taxonomic status of oaks (*Quercus* spp.) in Breen Wood, Co. Antrim, Northern Ireland Watsonia. Vol. 15: 27-32.

MINITAB 2007. MINITAB 15 for Windows, Minitab Inc.

Minitab 2000. MINITABTM Statistical Software for Windows version 13. State College, State College, Pensylvania.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species - a literature review. General Technical Report PNW-GTR-087. Portland, OR, USA, Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service. 72.

Mitchell, F. 1995. The dynamics of Irish post-glacial forests. *In*: Woods, trees and forests in Ireland. Pilcher, R. and Mac an tSaoir, S. (Eds). Dublin, Royal Irish Academy.

Mitchell, F. J. G. and Kirby, K. J. 1990. The impact of large herbivores on the conservation of semi-natural woods in the British uplands. Forestry. Vol. 63: 333-353.

Mitchell, M. E. 1964. Lichens occurring on *Arbutus* at Killarney. Irish Naturalists Journal. Vol. 14: 277-278.

Moe, B. and Botnen, A. 2000. Epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* in four different habitats at Grinde, Leikanger, western Norway. Plant Ecology. Vol. 151: 143-159.

Møller, A. P. 1984. Community structure of birds in agricultural areas in summer and winter in Denmark. 7. 413-418.

Molnár, T., Magura, T., Tóthmérész, B. and Elek, Z. 2001. Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. European Journal of Soil Biology. Vol. 37 (4): 297-300.

Moore, R., Warrington, S. and Whittaker, J. B. 1991. Herbivory by insects on oak trees in pure stands compared with paired mixtures. Journal of Applied Ecology. Vol. 28 (1): 290-304.

Moore, S. E. and Allen, H. L. 1999. Plantation forestry. *In*: Maintaining Biodiversity in Forest Ecosystems. Malcolm, L. and Hunter, J. R. (Eds). Cambridge, UK, Cambridge University Press. pp. 400-433.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos. Vol. 100 (2): 403-405.

Morris, M. G. 1990. Handbooks for the identification of British insects, Volume 5 (Part 16): Orthocerous weevils, The Royal Entomological Society, UK.

Morris, M. G. 1991. Handbooks for the identification of British insects: Weevils, Richmond Publishing, UK.

Muir, P. S., Rambo, T. R., Kimmerer, R. W. and Keon, D. B. 2006. Influence of overstory removal on growth of epiphytic mosses and lichens in western Oregon. Ecological Applications. Vol. 16 (3): 1207-1221.

Mullen, K., O'Halloran, J., Breen, J., Giller, P., Pithon, J. and Kelly, T. 2008. Distribution and composition of carabid beetle (Coleoptera, Carabidae) communities across the plantation forest cycle - Implications for management. Forest Ecology and Management. Vol. 256 (4): 624-632.

Murdoch, W. W., Evans, F. C. and Peterson, C. H. 1972. Diversity and Pattern in Plants and Insects. Ecology. Vol. 53 (5): 819-829.

Nadkarni, N. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. American Zoologist. Vol. 34: 70-78.

Nascimbene, J., Marini, L. and Nimis, P. L. 2010. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in Alpine spruce forests. Forest Ecology and Management. Vol. 260 (5): 603-609.

Neeson, E. 1991. A history of Irish forestry. Dublin, Lilliput press.

Neitlich, P. N. 1993. Lichen abundance and biodiversity along a chronosequence from young managed stands to ancient forest. Burlington, Vermont, USA, University of Vermont.

Neitlich, P. N. and McCune, B. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. Conservation Biology. Vol. 11 (1): 172-182.

New, T. 2004. Moths (Insecta: Lepidoptera) and conservation: background and perspective. Journal of Insect Conservation. Vol. 8: 79-94.

Newson, S. E., Woodburn, R. J. W., Noble, D. G., Baillie, S. R. and Gregory, R. D. 2005. Evaluating the Breeding Bird Survey for producing national population size and density estimates. Bird Study. Vol. 52: 42-54.

Newton, I. 1998. Population limitation in birds Academic Press, London.

Niemelä, J. and Spence, J. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. Ecography. Vol. 17: 166 - 175.

Niinemets, U. and Kull, K. 2005. Co-limitation of plant primary productivity by nitrogen and phosphorus in a species-rich wooded meadow on calcareous soils. Acta Oecologica. Vol. 28: 345-356.

Nilsson, C., Engelmark, O., Cory, J., Forsslund, A. and Carlborg, E. 2008. Differences in litter cover and understorey flora between stands of introduced lodgepole pine and native Scots pine in Sweden. Forest Ecology and Management. Vol. 255 (5-6): 1900-1905.

Nilsson, S. G., Arup, U. L. F., Baranowski, R. and Ekman, S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. Conservation Biology. Vol. 9 (5): 1208-1215.

Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., Ljungberg, H., Mikusinski, G. and Ranius, T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management. Vol. 161 (1-3): 189-204.

Nolan, M. 2010. Database of Irish spiders. Irish Wildlife Manual No. XX. Dublin, Ireland, National Parks and Wildlife Service, Department of Environment, Heritage and Local Government.

Norden, B., Gotmark, F., Tonnberg, M. and Ryberg, M. 2004. Dead wood in semi-natural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. Forest Ecology and Management. Vol. 194: 235-248.

Nordén, B., Ryberg, M., Gotmark, F. and Olausson, B. 2004b. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation. Vol. 117 (1): 1-10.

Norris, K. 1999. Quantifying change through time in spider assemblages: sampling methods, indices and sources of error. Journal of Insect Conservation. Vol. 3: 309 - 325.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology. Vol. 4 (4): 355-364.

O'Carroll, N. 1983. The Forests of Ireland: history, distribution and silviculture. Dublin, Turoe Press.

O'Connor, R. J., Usher, M. B., Gibbs, A. and Brown, K. C. 1986. Biological characteristics of invaders among bird species in Britain. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences. Vol. 314 (1167): 583-598.

O'Halloran, J., Walsh, P. M., Giller, P. S., Kelly, T. C. and Duffy, B. 1998. An assessment of avian biodiversity and opportunities for enhancement in Ireland's forests: prelimina ry results. Irish Forestry. Vol. 55: 2-14.

Ódor, P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K. W., Piltaver, A., Siller, I., Veerkamp, M. T., Walleyn, R., Standovár, T., van Hees, A. F. M., Kosec, J., Matocec, N., Kraigher, H. and Grebenc, T. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation. Vol. 131: 58-71.

Odor, P. and Standovar, T. 2001. Richness of bryophyte vegetation in near-natural and managed beech stands: the effects of management-induced differences in dead wood. Ecological Bulletins. Vol. 49: 219-229.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. 2010. vegan: Community Ecology Package.

Oliver, C. D. and Larson, B. C. 1996. Forest Stand Dynamics. New York, John Wiley.

Oosterbroek, P. 2006. The European families of the Diptera: Identification, diagnosis, biology, KNNV Publishing, Utrecht, Holland.

Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P. S. and Kelly, T. 2006a. The influence of open space on ground-dwelling spider assemblages within forest plantations. Forest Ecology and Management. Vol. 237: 404-417.

Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P. S. and Smith, G. F. 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecology and Management. Vol. 212: 171 - 183.

Oxbrough, A., Irwin, S., Kelly, T. C. and O'Halloran, J. 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management. Vol. 259 (10): 2111-2121.

Oxbrough, A. G., Gittings, T., O'Halloran, J., Giller, P. S. and Kelly, T. C. 2007. Biodiversity of the ground-dwelling spider fauna of afforestation habitats. Agriculture, Ecosystems & Environment. Vol. 120 (2-4): 433-441.

Oxbrough, A. G., Gittings, T., O'Halloran, J., Giller, P. S. and Kelly, T. C. 2006b. The initial effects of afforestation on the ground-dwelling spider fauna of Irish peatlands and grasslands. Forest Ecology and Management. Vol. 237 (1-3): 478-491.

Ozanne, C., Speight, M., Hambler, C. and al, e. 2000. Isolated trees and forest patches: Patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots pine). Forest Ecology and Management. Vol. 137 (1 - 3): 53 - 63.

Ozanne, C. M. P. 1996. The arthropod communities of coniferous forest trees. Selbyana. Vol. 17: 43-49.

Ozanne, C. M. P., Hambler, C., Foggo, A. and Speight, M. R. 1997. The signficance of edge effects in the management of forests for invertebrate biodiversity. *In*: Canopy Arthropods. Stork, N. E., Adis, J. and Didham, R. K., Chapman & Hall, London. pp. xvi + 567.

Paritsis, J. and Aizen, M. A. 2008. Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in *Nothofagus dombeyi* forests. Forest Ecology and Management. Vol. 255 (5-6): 1575-1583.

Parry, W. H. 1992. A comparison of *Aphidecta obliterata* L. (Col., Coccinellidae) populations feeding on *Elatobium abietinum* (Walker) and on *Adelges cooleyi* (Gillette). Journal of Applied Entomology. Vol. 114: 280-288.

Paton, J. A. 1999. The Liverwort Flora of the British Isles. Colchester, Harley Books.

Patterson, I. J., Ollason, J. G. and Doyle, P. 1995. Bird populations in upland spruce plantations in northern Britain. Forest Ecology and Management. Vol. 79 (1-2): 107-131.

Pearce, J. L. and Venier, L. A. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators. Vol. 6 (4): 780-793.

Pearce, J. L., Venier, L. A., Eccles, G., Pedlar, J. and McKenney, D. 2004. Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. Biodiversity & Conservation. Vol. 13 (7): 1305-1334.

Pearson, L. C. 1969. Influence of temperature and humidity on distribution of lichens in a Minnesota bog. Ecology. Vol. 50 (4): 740-746.

Peres-Neto, P. R. and Jackson, D. A. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia. Vol. 129 (2): 169-178.

Perhans, K., Appelgren, L., Jonsson, F., Nordin, U., Soderstrom, B. and Gustafsson, L. 2009. Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. Biological Conservation. Vol. 142: 1125-1133.

Perrin, P., Kelly, D. L. and Mitchell, F. J. G. 2006a. Long-term deer exclusion in yew-wood and oakwood habitats in southwest Ireland: Natural regeneration and stand dynamics. Forest Ecology and Management. Vol. 236: 356-357.

Perrin, P., Martin, J. R., Barron, S. J., O'Neill, F., McNutt, K. and Delaney, A. 2008a. National Survey of Native Woodlands 2003-2008, National Parks and Wildlife, Dublin.

Perrin, P. M., Barron, S. J. and Martin, J. R. 2006b. National survey of native woodland in Ireland; Second Phase Report, Dept. of the Environment, Heritage and Local Government.

Perrin, P. M., Martin, J. R., Barron, S. J., O' Neill, F., McNutt, K. and Delaney, A. 2008b. National survey of native woodlands 2003-2008. A report submitted to the NPWS. Botanical, E. C. C. L.

Perrins, C. 1979. British Tits. London, Collins.

Peterken, G. F. 1986. Commercial forests and woods: the nature conservation opportunites. *In*: Forestry's Social and Environmental Benefits and Responsibilites. Davies, R. J. (Eds). Oxford, Institute of Chartered Foresters. pp. 53-62.

Peterken, G. F. 2001. Ecological effects of introduced tree species in Britain. Forest Ecology and Management. Vol. 141 (1-2): 31-42.

Peterken, G. F. 1993. Woodland Conservation and Management. London, Chapman and Hall. 374

Peterken, G. F., Ausherman, D., Buchenau, M. and Forman, R. T. T. 1992. Old-growth conservation within British upland conifer plantations. Forestry. Vol. 65 (2): 127-144.

Peterken, G. F. and Game, M. 1984. Historical factors affecting the number and distribution of vasculat plant species in the woodlands of central Lincolnshire. Journal of Ecology. Vol. 72: 155-182.

Peterken, G. F. and Lloyd, P. S. 1967. Biological flora of the British Isles: *Ilex aquifolium* L. Journal of Ecology. Vol. 55: 841-858.

Pettersson, R. B., Ball, J. P., Renhorn, K.-E., Esseen, P.-E. and Sjoberg, K. 1995. Invertebrate communities in Boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. Biological Conservation. Vol. 74 (1): 57-63.

Pharo, E. J. and Beattie, A. J. 2002. The association between substrate variability and bryophyte and lichen diversity in eastern Australian forests. The Bryologist. Vol. 105 (1): 11-26.

Phillips, E. A. 1959. Bark bryophyte unions in southern Ireland. The Bryologist. Vol. 62: 24-31.

Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. Journal of Theoretical Biology. Vol. 10 (2): 370-383.

Pigott, C. D. 1983. Regeneration of oak-birch woodland following exclusion of sheep. Journal of Ecology. Vol. 71 (2): 629-646.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core team 2009. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-96.

Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management. Vol. 255 (3-4): 781-786.

Pócs, T. 1982. Tropical forest bryophytes. *In*: Bryophyte ecology. Smith, A. J. E. (Eds). London, Chapman and Hall.

Poole, A., Gormally, M. and Sheehy Skeffington, M. 2003. The flora and carabid beetle fauna of a mature and regenerating semi-natural oak woodland in south-east Ireland. Forest Ecology and Management. Vol. 177 (1-3): 207-220.

Pratt, E. and Redfern, B. 2001. Infection of Sitka spruce stumps by spores of Heterobasidion annosum: control by means of urea. Forestry. Vol. 74 (1): 73-78.

Preston, C. D., Pearman, D. A. and Dines, T. D., Eds. 2002. New Atlas of the British and Irish Flora. Oxford, UK, Oxford University Press.

Price, K. and Hochachka, G. 2001. Epiphytic lichen abundance: effects of stand age and composition in coastal British Columbia. Ecological Applications. Vol. 11 (3): 904-913.

Primer-E Ltd 2006. Primer 6. Plymouth, U.K.

Pryor, S. N., Curtis, T. A. and Peterkin, G. F. 2002. Restoring plantations on ancient woodland sites, The Woodland Trust.

Purvis, O. W., Coppins, B. J., Hawksworth, D. L., James, P. W. and Moore, D. M. 1992. The Lichen Flora of Great Britain and Ireland. London, Natural History Publications and The British Lichen Society.

Putman, R. J. 1996. Ungulates in temperate forest ecosystems: perspectives and recommendations for future research. Forest Ecology and Managament. Vol. 88: 205-214.

Quine, C. P., Fuller, R. J., Smith, K. W. and Grice, P. V. 2007. Stand management: a threat or opportunity for birds in British woodland? Ibis. Vol. 149: 161-174.

R Development Core Team 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria, http://www.R-project.org.

Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U., Göttlein, A., Förster, B., Brandl, R. and Bässler, C. 2010. Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. Forest Ecology and Management. Vol. 260 (11): 1956-1964.

Rackham, O. 2006. Woodlands. London, Harper Collins.

Rainio, J. and Niemelä , J. 2003. Ground beetles (Coleoptera: Carabidaae) as bioindicators. Biodiversity and Conservation. Vol. 12: 487 - 506.

Ramovs, B. V. and Roberts, M. R. 2003. Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecological Applications. Vol. 13 (6): 1682-1700.

Ratcliffe, D. A. 1968. An ecological account of Atlantic bryophytes in the British Isles. New Phytologist. Vol. 67: 365-439.

Ratcliffe, P. R. and Peterken, G. F. 1995. The potential for biodiversity in British upland spruce forests. Forest Ecology and Management. Vol. 79 (2): 153-160.

Reid, W. V. C., McNeely, J. A., Tunstall, D. B., Bryant, D. A. and Winograd, M. 1993. Biodiversity Indicators for Policy-Makers. Washington, D.C., World Resources Institute.

Relys, V., Koponen, S. and Dapkus, D. 2002. Annual differences in species turnover in peat bog spider communities. Journal of Arachnology. Vol. 30: 416-424.

Richards, P. W. 1938. The bryophyte communities of a Killarney oakwood. Annales Bryologici. Vol. 11: 108-130.

Richardson, D. H. S., Ed. 1987. Biological indicators of pollution. Dublin, Royal Irish Academy.

Richardson, D. H. S. and Young, C. M. 1977. Lichens and Vertebrates. *In*: Lichen Ecology. Seaward, M. R. D. (Eds). London, Academic Press.

Richter, C. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa: Araneae: Lycosidae). Oecologia. Vol. 5: 200-214.

Ricketts, T. H., Daily, G. C. and Ehrlich, P. R. 2002. Does butterfly diversity predict moth diversity? Testing a popular indicator taxon at local scales. Biological Conservation. Vol. 103: 361-370.

Ringvall, A. and Ståhl, G. 1999. Field aspects of line intersect sampling for assessing coarse woody debris. Forest Ecology and Management. Vol. 119: 163-170.

Roberts, M. 1993. The Spiders of Great Britain and Ireland (compact edition). Part One. Colchester, Harley Books.

Robinson, R. A. 2005. Birdfacts: species profiles of birds occurring in Britain and Ireland, British Trust for Ornithology, Thetford.

Roche, J., Mitchell, F. and Waldren, S. 2009a. Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland. Biodiversity and Conservation. Vol. 18 (8): 2185-2203.

Rodrigues, A. S. L. and Brooks, T. M. 2007. Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annual Review of Ecology Evolution and Systematics. Vol. 38: 713-737.

Rohan, P. K. 1975. The climate of Ireland. Dublin, The Stationary Office.

Rose, F. 1993. Ancient british woodland and their epiphytes. British Wildlife. Vol. 5: 83-93.

Ruchty, A., Rosso, A. L. and McCune, B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. The Bryologist. Vol. 104 (2): 274 281.

Rypstra, A. L. 1983. The Importance of Food and Space in Limiting Web-Spider Densities; A Test Using Field Enclosures. Oecologia. Vol. 59 (2/3): 312-316.

Saetersdal, M., Gjerde, I., Blom, H. H., Ihlen, P. G., Myrseth, E. W., Pommeresche, R., Skartveit, J., Solhoy, T. and Aas, O. 2003. Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. Biological Conservation. Vol. 115 (1): 21-31.

Saetre, P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. Ecography. Vol. 22: 183-192.

Saetre, P., Saetre, L. S., Brandtberg, P.-O., Lundkvist, H. and Bengtsson, J. 1997. Ground vegetation composition and heterogeneity in pure Norway spruce and mixed Norway spruce - birch stands. Canadian Journal of Forest Research. Vol. 27: 2034-2042.

Sakura, T., Gimingham, C. H. and Millar, C. S. 1985. Effect of tree density on gournd vegetation in a Japanese larch population. Scottish Forestry. Vol. 39: 191-198.

Salamon, J.-A., Scheu, S. and Schaefer, M. 2008. The Collembola community of pure and mixed stands of beech (Fagus sylvatica) and spruce (Picea abies) of different age. Pedobiologia. Vol. 51 (5-6): 385-396.

Salmon, S., Artuso, N., Frizzera, L. and Zampedri, R. 2008. Relationships between soil fauna communities and humus forms: response to forest dynamics and solar radiation. Soil Biology and Biochemistry. Vol. 40 (7): 1707-1715.

Sanders, D., Nickel, H., Grützner, T. and Platner, C. 2008. Habitat structure mediates top-down effects of spiders and ants on herbivores. Basic and Applied Ecology. Vol. 9 (2): 152-160.

Sax, D. F. 2002. Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. Global Ecology and Biogeography. Vol. 11 (1): 49-57.

Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. The Condor. Vol. 99 (1): 179-190.

Schowalter, T. D. 1995. Canopy arthropod communities in relation to forest age and alternative harvest practices in western Oregon. Forest Ecology and Management. Vol. 78 (1-3): 115-125.

Selva, N., Jedrzejewska, B. and Jedrzejewski, W. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology. Vol. 83 (12): 1590-1601.

Shaw, P., Ozanne, C., Speight, M. and Palmer, I. 2007. Edge effects and arboreal Collembola in coniferous plantations. Pedobiologia. Vol. 51 (4): 287-293.

Sholes, O. D. V. 2007. Effects of associational resistance and host density on woodland insect herbivores. Journal of Animal Ecology. Vol. 77 (1): 16-23.

Showman, R. E. 1975. Lichens as indicators of air quality around a coal-fired power generating plant. Bryologist. Vol. 78: 1-6.

Siira-Pietikäinen, A. and Haimi, J. 2009. Changes in soil fauna 10 years after forest harvestings: Comparison between clear felling and green-tree retention methods. Forest Ecology and Management. Vol. 258 (3): 332-338.

Siitonen, J., Martikainen, P., Punttila, P. and Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. Forest Ecology and Management. Vol. 128 (3): 211-225.

Sillett, S. C., McCune, B., Peck, J. E., Rambo, T. R. and Ruchty, A. 2000. Dispersal limitations of epiphytic lichens result in species dependent on old-growth forests. Ecological Applications. Vol. 10: 789-799.

Similä, M., Kouki, J. and Martikainen, P. 2003. Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. Forest Ecology and Management. Vol. 174 (1-3): 365-381.

Simmons, E. A. and Buckley, E. A. 1992. Ground vegetation under planted mixtures. *In*: The Ecology of Mixed Species Stands of Trees. Fennell, M. G. R., Malcolm, D. C. and Robertson, P. A., Blackwell. pp. 211-232.

Simms, E. 1971. Woodland Birds. Collins, London.

Skoczylas, D. R., Muth, N. Z. and Niesenbaum, R. A. 2007. Contribution of insectivorous avifauna to top down control of *Lindera benzoin* herbivores at forest edge and interior habitats. Acta Oecologica. Vol. 32 (3): 337-342.

Smith, A. J. E. 1990. The liverworts of Britain and Ireland. Cambridge, Cambridge University Press.

Smith, A. J. E. 2004. The Moss Flora of Britain and Ireland. Cambridge, UK, Cambridge University Press. 1012

Smith, G., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., Pithon, J., O'Donnell, V., McKee, A.-M., Iremonger, S., O'Halloran, J., Kelly, D., Mitchell, F., Giller, P. and Kelly, T. 2005. Assessment of biodiversity at different stages of the forest cycle. Dublin, Ireland, COFORD and EPA. 195.

Smith, K. W. 1997. Nest site selection of the great spotted woodpecker *Dendrocopus major* in two oak woods in southern England and its implications for woodland management. Biological Conservation. Vol. 80 (3): 283-288.

Smith, K. W. 2007. The utilization of dead wood resources by woodpeckers in Britain. Ibis. Vol. 149 (s2): 183-192.

Snow, B. and Snow, D. 1988. Birds and Berries. London, T & AD Poyser.

Snow, D. W. and Perrins, C. M. 1998a. The birds of the Western Palearctic: concise edition, Oxford University Press, Oxford, UK.

Snow, D. W. and Perrins, C. M. 1998b. The Birds of the Western Palearctic: concise edition. Oxford, Oxford University Press.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry. New York, W.H. Freeman and Co.

Southwood, T., Moran, V. and Kennedy, T. 1982. The richness, abundance and biomass of the arthropod communities on trees. Journal of Animal Ecology. Vol. 51: 635 - 649.

Southwood, T. R. E., Wint, G. R. W., Kennedy, C. E. J. and Greenwood, S. R. 2005. The composition of the arthropod fauna of the canopies of some species of oak (Quercus). European Journal of Entomology. Vol. 102 (1): 65-72.

Spalding, A. and Parsons, M. 2004. Light trap transects-a field method for ascertaining the habitat preferences of night-flying Lepidoptera, using *Mythimna turca* (Linnaeus 1761) (Lepidoptera: Noctuidae) as an example. Journal of Insect Conservation. Vol. 8: 185-190.

Speight, M. C. D. 1985. The extinction of indigenous *Pinus sylvestris* in Ireland: relevant faunal data. Irish Naturalists Journal. Vol. 21 (10): 449-453.

Speight, M. C. D. 1989. Saproxylic Invertebrates and their Conservation. Strasbourg, Council of Europe.

SPSS 2007. SPSS for Windows. Chicago, SPSS.

SPSS 2002. SPSS for Windows. Chicago, SPSS.

SPSS Inc. 2006. SPSS V12.0.1.

Sroka, K. and Finch, O. D. 2006. Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). Journal of Insect Conservation. Vol. 10 (4): 335-350.

Stace, C. 1997. New Flora of the British Isles. Cambridge, Cambridge University Press. 1130

Stewart, P., Lam, J., Jesse, J. and Blythe, J. 1969. Influence of Distance on Attraction of Tobacco Horn worm and Corn Ear worm Moths to Radiations of a Blacklight Lamp. Journal of Economic Entomology. Vol. 62: 58-60.

Stork, N. and Hammond, P. 1997. Sampling arthropods from tree crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (UK). *In*: Canopy Arthropods. Stork, N., Adis, J. and Didham, R. (Eds). London, Chapman and Hall. pp. 3 - 26.

Stork, N., Hammond, P., Russell, B. and Hadwen, W. 2001. The spatial distribution of beetles within the canopies of oak trees in Richmond Park, UK. Ecological Entomology. Vol. 26: 302-311.

Straw, N. A., Fielding, N. J. and Waters, A. 1996. Phytotoxicity of insecticides used to control aphids on Sitka spruce, *Picea sitchensis* (Bong.) Carr. Crop Protection. Vol. 15: 451-459.

Straw, N. A., Timms, J. E. L. and Leather, S. R. 2009. Variation in the abundance of invertebrate predators of the green spruce aphid Elatobium abietinum (Walker) (Homoptera: Aphididae) along an altitudinal transect. Forest Ecology and Management. Vol. 258 (1): 1-10.

Strong, D. R., Lawton, J. H. and Southwood, T. R. E. 1984. Insects on plants. Community patterns and mechanisms., Blackwell Scientific Publications, Oxford.

Studlar, S. M. 1982. Succession of epiphytic bryophytes near Mountain Lake, Virginia. The Bryologist. Vol. 85 (1): 51-63.

Summerville, K. S., Ritter, L. M. and Crist, T. O. 2004. Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. Biological Conservation. Vol. 116 (1): 9-18.

Sweeney, J., Wilson, J., Mayes, E., Minchin, D., Emblow, C., Wilson, J., Donnelly, A., Jones, M. B., Byrne, C., Farrell, E. P., Byrne, K. A., Purser, P. M., Moore, S., Charlton, R. A., Brereton, J. A., Holden, N. M. and Fealy, R. 2003. Climate Change: Scenarios and Impacts for Ireland: Final Report. Environmental RTDI Programme. Report 15.

Sweeney, O., Wilson, M., Irwin, S., Kelly, T. and O'Halloran, J. 2010a. Are bird density, species richness and community structure similar between native woodlands and non-native plantations in an area with a generalist bird fauna? Biodiversity and Conservation. Vol. 19 (8): 2329-2342.

Sweeney, O. F. M., Martin, R. D., Irwin, S., Kelly, T. C., O'Halloran, J. and McEvoy, P. M. 2010b. A lack of large-diameter logs and snags characterises dead wood patterns in Irish forests. Forest Ecology and Managament. Vol. 259 (10): 2056-2064.

Sydes, C. and Grime, J. P. 1981. Effects of Tree Leaf Litter on Herbaceous Vegetation in Deciduous Woodland: II. An Experimental Investigation. Journal of Ecology. Vol. 69 (1): 249-262.

Taboada, A., Kotze, D. J., Tárrega, R. and Salgado, J. M. 2008. Carabids of differently aged reforested pinewoods and a natural pine forest in a historically modified landscape. Basic and Applied Ecology. Vol. 9 (2): 161-171.

Teagasc: Irish Agriculture and Food Development authority 2005. http://teagasc.ie/. Carlow, Teagasc.

ter Braak, C. J. F. and Smilauer, P. 1998. CANOCO Reference Manual and User's Guide to CANOCO for Windows: Software for Canonical Community Ordination (Version 4). New York, Microcomputer Power.

The Woodland Trust 2007a. Back on the Map: An inventory of ancient and long-established woodland for Northern Ireland. Preliminary report. Bangor, The Woodland Trust.

The Woodland Trust 2007b. Back on the Map: An Inventory of Ancient and Long Established Woodland for Northern Ireland - Preliminary Report. Bangor, The Woodland Trust.

Thiele, H. 1977. Carabid Beetles in their Environments. A study on Habitat Selection by Adaptations in Physiology and Behaviour, Springer Verlag.

Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Hedley, S. L., Pollard, J. H., Bishop, J. R. B. and Marques, T. A. 2006. Distance 5.0. Release 2. University of St. Andrews, UK, Research Unit for Wildlife Population Assessment.

Thomas, P. A. and Packham, J. R. 2007. Ecology of woodlands and forests: description, dynamics and diversity. Cambridge, Cambridge Univeristy Press.

Thompson, R. N., Humphrey, J. W., Harmer, R. and Ferris, R. 2003. Restoration of native woodland on ancient woodland sites. Forestry Commission Practice Guide. Edinburgh, UK, Forestry Commission.

Tinya, F., Márialigeti, S., Király, I., Németh, B. and Ódor, P. 2009. The effect of light conditions on herbs, bryophytes and seedlings of temperate mixed forests in Őrség, Western Hungary. Plant Ecology. Vol. 204 (1): 69-81.

Topp, W., Kappes, H., Kulfan, J. and Zach, P. 2006. Distribution pattern of woodlice (Isopoda) and millipedes (Diplopoda) in four primeval forests of the Western Carpathians (Central Slovakia). Soil Biology and Biochemistry. Vol. 38 (1): 43-50.

Trynoski, S. E. and Glime, J. M. 1982. Direction and height of bryophytes on four species of northern trees. The Bryologist. Vol. 85 (3): 281-300.

Turner, B. D. 1984. Predation pressure on the arboreal epiphytic herbivores of larch trees in southern England. Ecological Entomology. Vol. 9: 91-100.

Tyner, A. 2010. Moths Ireland. http://www.mothsireland.com/index.htm.

Uetz, G. 1991. Habitat structure and spider foraging. *In*: Habitat structure. The physical arrangement of objects in space. Bell, S., McCoy, E. and Mushinsky, H. (Eds). London, Chapman and Hall.

Uetz, G. 1979. The influence of variation in litter habitats on spider communities. Oecologia. Vol. 40: 29-42.

Uliczka, H. and Angelstam, P. 1999. Occurence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography. Vol. 22 (4): 396-405.

Unwin, D. 2001. A key to the families of British bugs (Insecta, Hemiptera), Field Studies Council, UK.

Uuttera, J., Maltamo, M. and Kuusela, K. 1996. Impact of forest management history on the state of forests in relation to natural forest succession Comparative study, North Karelia, Finland vs. Republic of Karelia, Russian Federation. Forest Ecology and Management. Vol. 83: 71-85.

van Oijen, D., Markus, F., Hommel, P., den Ouden, J. and de Waal, R. 2005. Effects of tree species composition on within-forest distribution of understorey species. Applied Vegetation Science. Vol. 8: 155-166.

van Weerd, M. and de Haes, H. A. U. 2010. Cross-taxon congruence in tree, bird and bat species distributions at a moderate spatial scale across four tropical forest types in the Philippines. Biodiversity and Conservation. Vol. 19 (12): 3393-3411.

Vanhinsbergh, D., Gough, S., Fuller, R. J. and Brierley, E. D. R. 2002. Summer and winter bird communities in recently established farm woodlands in lowland England. Agriculture Ecosystems & Environment. Vol. 92 (2-3): 123-136.

Varady-Szabo, H. and Buddle, C. M. 2006. On the relationships between ground-dwelling spider (Araneae) assemblages and dead wood in a northern sugar maple forest. Biodiversity and Conservation. Vol. 15: 4119-4141.

Vellak, K. and Paul, J. 1999. Diversity of bryophyte vegetation in some forest types in Estonia: a comparison of old unmamaged and managed forests. Biodiversity and Conservation. Vol. 8: 1595-1620.

Verheyen, K., Guntenspergen, G. R., Biesbrouck, B. and Hermy, M. 2003. An integrated analysis of the effects of past land use on forest herb colonizationat the landscape scale. Journal of Ecology. Vol. 91: 731-742.

Wagner, J. D., Toft, S. and Wise, D. H. 2003. Spatial stratification in litter depth by forest-floor spiders. Journal of Arachnology. Vol. 31 (1): 28-39.

Wallace, H. 2003. NVC use in plantations. *In*: National Vegetation Classification - Ten years' Experience Using the Woodland Section. JNCC Report, No. 335. Goldberg, E. (Eds). Peterborough, JNCC.

Wallace, H. L. 1998. Ground flora associated with birch in spruce plantations. *In*: Birch in Spruce Plantations – Management for Biodiversity. Humphrey, J., Holl, K. and Broome, A. (Eds). Edinburgh, Forestry Commission.

Wallace, H. L. and Good, J. E. G. 1995. Effects of afforestation on upland plant communities and implications for vegetation management. Forest Ecology and Management. Vol. 79: 29-46.

Wallace, H. L., Good, J. E. G. and Williams, T. G. 1992. The effects of afforestation on upland plant communities: an application of the British National Vegetation Classification. Journal of Applied Ecology. Vol. 29: 180-194.

Wang, J. R., Comeau, P. and Kimmins, J. P. 1995. Simulation of mixed wood management of aspen and white spruce in northeastern British Columbia. Water, Air & Soil Pollution. Vol. (82): 171-178.

Wannebo-Nilsen, K., W., B. J., Beck, P. S. A. and Tømmervik, H. 2010. Epiphytic macrolichens in spruce plantations and native birch forests along a coast-inland gradient in North Norway. Boreal Environment Research. Vol. 15: 43-57.

Watson, E. V. 1981. British Mosses and Liverworts. Cambridge, Cambridge University Press.

Watson, W. 1936. The bryophytes and lichens of british woods. Part II, Other Woodland. Journal of Ecology. Vol. 24 (2): 446-478.

Watt, A. S. 1931. Preliminary observations on Scottish beechwoods (Continued). Journal of Ecology. Vol. 19 (2): 321-359.

Webb, D. A., Parnell, J. and Doogue, D. 1996. An Irish Flora. Dundalk, Ireland, Dundalgan Press. 337

Weltz, M. A., Ritchie, J. C. and Fox, H. D. 1994. Comparison of laser and field measurements of vegetation height and canopy cover. Water Resources Research. Vol. 30: 1311-1319.

Whelan, D. 2010. World Bioenergy 2010 Jonkoping, Sweden. Irish Timber Growers Association Newsletter. Dublin, Irish Timber Growers Association.

Whitehouse, N. J. 2006. The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. Quaternary Science Reviews. Vol. 25 (15-16): 1755-1789.

Whitehouse, N. J. and Smith, D. 2010. How fragmented was the British Holocene wildwood? Perspectives on the "Vera" grazing debate from the fossil beetle record. Quaternary Science Reviews. Vol. 29: 539-553.

Whittaker, R. H. 1977. Evolution of species diversity in land communities. *In*: Evolutionary Biology, Volume 10. Hecht, M. K., Steere, W. C. and Wallace, B. (Eds). New York, Plenum Press. pp. 1-67.

Williams, A., Essex, S. and Pollard, A. 1998. Ecological and landscape effects of afforestation at a second rotation plantation: a case study of Fernworthy, Dartmoor. Landscape Research. Vol. 23 (2): 101-118.

Williams, C. B. 1961. Studies in the Effect of Weather Conditions on the Activity and Abundance of Insect Populations. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences. Vol. 244 (713): 331-378.

Williams, P. H. and Gaston, K. J. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biological Conservation. Vol. 67: 211-217.

Wilson, E. O. 1988. Biodiversity. Washington D.C., National Academy Press.

Wilson, J. D., Morris, A. J., Arroyo, B. E., Clark, S. C. and Bradbury, R. B. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agriculture, Ecosystems & Environment. Vol. 75 (1-2): 13-30.

Wilson, M. W., Gittings, T., Kelly, T. C. and O' Halloran, J. 2010. The importance of non-crop vegetation for bird diversity in Sitka spruce plantations in Ireland. Bird Study. Vol. 57 (1): 116 - 120.

Wilson, M. W., Pithon, J., Gittings, T., Kelly, T. C., Giller, P. S. and O'Halloran, J. 2006. Effects of growth stage and tree species composition on breeding bird assemblages of plantation forests. Bird Study. Vol. 53: 225-236.

Wood, S. N. 2008. mgcv package: Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical: Society (B) 70(3):495-518.

Work, T. T., Shorthouse, D. P., Spence, J. R., Volney, W. J. A. and Langor, D. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research. Vol. 34 (2): 417-430.

Xiong, S. and Nilsson, C. 1999. The effects of plant litter on vegetation: a meta-analysis. Journal of Ecology. Vol. 87 (6): 984-994.

Yamaura, Y., Ikeno, S., Sano, M., Okabe, K. and Ozaki, K. 2009. Bird responses to broad-leaved forest patch area in a plantation landscape across seasons. Biological Conservation. Vol. 142 (10): 2155-2165.

Yu, X.-D., Luo, T.-H. and Zhou, H.-Z. 2008. Distribution of carabid beetles among 40-year-old regenerating plantations and 100-year-old naturally regenerated forests in Southwestern China. Forest Ecology and Management. Vol. 255 (7): 2617-2625.

Zar, J. 1996. Biostatistical Analysis. New Jersey, Prentice-Hall.

Ziesche, T. and Roth, A. 2007. Is the age of forest habitats affecting the reproductive rate of generalist predatory ground beetle species? Community Ecology. Vol. 8: 183-194.

Ziesche, T. M. and Roth, M. 2008. Influence of environmental parameters on small-scale distribution of soil-dwelling spiders in forests: What makes the difference, tree species or microhabitat? Forest Ecology and Management. Vol. 255 (3-4): 738-752.

Zurita, G. A., Rey, N., Varela, D. M., Villagra, M. and Bellocq, M. I. 2006. Conversion of the Atlantic Forest into native and exotic tree plantations: effects on bird communities from the local and regional perspectives. Forest Ecology and Management. Vol. 235 (1-3): 164-173.

Zuur, A., Ieno, E., Walker, N., Savaliev, A. and Smith, G. 2009. Mixed Effects Models and Extension in Ecology with R. New York, Springer.

9. Full list of outputs from the project

9.1 Popular articles

Irwin, S. 2007. Management for biodiversity in Ireland's contemporary forests. Science Spin, Issue 24.

Irwin, S. 2007. Woodland biodiversity v forest industry: Is there an answer? UCC News, September 2007.

Irwin, S. 2009. A novel approach to forest biodiversity assessment. Science Spin, Issue 37.

Irwin, S. and O'Halloran, J. 2009. The Biodiversity of Ireland's forests. Biodiversity, Issue 3.

Irwin, S. 2009. Afforestation – enhancing biodiversity in the Irish countryside. In Forestry 2030, COFORD Council, October 2009.

Martin, R., Oxbrough, A., Irwin, S., Kelly, T. and O'Halloran, J. 2010. New records and rare invertebrate specimens recorded during a decade of forest biodiversity research in Ireland. *Antenna*, Quarterly Bulletin of the Royal Entemological Society. 34: 111-118.

Moore, K. 2008. Plant communities after clearfelling. Irish Tree Society Winter Newsletter.

In addition to these articles regular contributions were made to the newsletters of COFORD, Coillte, UCC and TCD to promote the project. The FORESTBIO project also featured in all issues of the PLANFORBIO Research Programme newsletter which was circulated twice yearly to all stakeholders.

9.2 Peer-reviewed papers

Martin, R. 2009. *Entelecara acuminata* (Wider, 1834) at Brownstown Wood, Co Kilkenny (Araneae: Linyphiidae), a new record to Ireland. Irish Naturalist's Journal, 30: 65-66.

Martin, R. 2010. *Anobium inexspectatum* Lohse (Coleoptera: Anobiidae) at Drummin Wood, Co. Galway, and Uragh Wood, Co. Kerry, a new record for Ireland. Irish Naturalist's Journal.

Oxbrough, A., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. Ground dwelling invertebrates in reforested conifer plantations. Forest Ecology and Management, 259: 2111-2121.

Sweeney, O.F.McD., Martin, R., O'Halloran, J., Irwin, S., Kelly, T.C., Wilson, M. and McEvoy, P.M. 2010. A lack of large diameter logs and snags characterises deadwood forests in Irish forests. Forest Ecology and Management, 259: 2056-2064.

Sweeney, O.F.McD., Wilson, M.W., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. Breeding bird communities of second rotation plantations at different stages of the forest cycle. Bird Study, 57: 301-314.

Sweeney, O.F.McD., Wilson, M.W., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. Are bird density, species richness and community structure similar between native woodlands and non-native plantations in an area with a generalist bird fauna? Biodiversity & Conservation, 19: 2329-2342.

Sweeney, O.F.McD., Wilson, M.W., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. The influence of a native tree species mix component on bird communities in non-native coniferous plantations in Ireland. Bird Study, 57: 483-494.

9.3 Presentations at workshops and conferences (including posters)

Coote, L., Kelly, D. L., Kelly, T., Mitchell, F., Irwin, S., Oxbrough, A., Wilson, M. W., Martin, R., French, V., Fox, H., Sweeney, O., Moore, K., Neville, P., Keane, M. and O'Halloran, J. 2008. FORESTBIO. Irish Plant Scientists Association meeting 2008. NUI Maynooth.

Coote, L. French, L.J. Moore, K. Mitchell, F.J.G. and Kelly, D.L. 2010. Can plantation forests support species and vegetation communities typical of semi-natural woodlands? British Ecological Society Annual Meeting, September 2010.

Fox, H. and Kelly, D. L. 2008. Epiphyte diversity in native and plantation forests. ENVIRON 2008, Dundalk Institute of Technology.

French, V., Oxbrough, A., Irwin, S., Kelly, T.C. and O'Halloran, J. 2009. Moth diversity in native woodlands and plantation forests. ENVIRON 2009. Waterford Institute of Technology.

Irwin, S., Kelly, D. L., Kelly, T., McCarthy, N., Mitchell, F., Coote, L., Oxbrough, A., Wilson, M., Martin, R., French, V., Fox, H., Sweeney, O., Moore, K. and O'Halloran, J. 2008. Planning and management tools for biodiversity in a range of Irish forests. ENVIRON 2008, Dundalk Institute of Technology.

Irwin, S., Kelly, D. L., Kelly, T., McCarthy, N., Mitchell, F., Coote, L., Oxbrough, A., Wilson, M., Martin, R., French, V., Fox, H., Sweeney, O., Moore, K. and O'Halloran, J. 2008. Planning and management tools for biodiversity in a range of Irish forests. Scientific Seminar in the connection to the European Forest Institute Annual Conference: Forest Ecosystem Management in the 21st Century, Dublin, Ireland.

Irwin, S., Kelly, D. L., Kelly, T., McCarthy, N., Mitchell, F., Coote, L., Oxbrough, A., Wilson, M., Martin, R., French, V., Fox, H., Sweeney, O., Moore, K. and O'Halloran, J. 2008. Planning and management tools for biodiversity in a range of Irish forests. Scientific Seminar in the connection to the European Forest Institute Annual Conference: Forest Ecosystem Management in the 21st Century, Dublin, Ireland.

Keady, S., O'Sullivan, B., Irwin, S. and O'Halloran, J. 2010. LAseRBIO: The Applicability of Terrestrial Laser Scanning in Forest Biodiversity Assessment. EPA National Research Conference, 23 June 2010, Croke Park Conference Centre, Dublin. Poster Presentation

Kelly, T. 2010. Monitoring biodiversity in Irish forests. Meeting of Heads of European National Forest Research Institutes, The Royal College of Physicians, Dublin, 5–7 July 2010.

O'Sullivan, B., Keady, S., Keane, E., Irwin, S. and O'Halloran, J. 2010. Data Mining for Biodiversity Prediction in Forests. Proceedings of the 2010 conference on ECAI 2010: 19th European Conference on Artificial Intelligence. 289-294.

Martin, R., Kelly, T., Oxbrough, A., Wilson, M., Irwin, S. and O'Halloran, J. 2007. Assessing the biodiversity of canopy arthropods in a range of forest types. Forest Task Force Annual Workshop, Białowieża, Poland.

Martin, R., Kelly, T. C., Oxbrough, A., Wilson , M., Irwin, S. and O'Halloran, J. 2008. Assessing the biodiversity of canopy invertebrates in a range of forest types. ENVIRON 2008, DkIT and PEF 2008, TCD.

Martin, R., Oxbrough, A., Irwin, S., Kelly, T.C. and O' Halloran, J. 2009. Assessing the biodiversity of canopy arthropods in a range of forest types throughout Ireland. 2nd European Congress of Conservation Biology: Conservation biology and beyond: from science to practice, Prague.

Martin, R., Oxbrough, A., Irwin, S., Kelly, T., and O'Halloran, J. 2010. Canopy invertebrate biodiversity in various Irish forest types. 24th International Congress for Conservation Biology (ICCB) - 'Conservation for a Changing Planet', Edmonton, Canada.

Moore, K., Coote, L., Fox, H., Vézeau, C., Mitchell, F. and Kelly, D. L. 2008. Ground flora diversity of Sitka spruce reforestation plantations in comparison with afforestation plantations in Ireland. ENVIRON 2008 DkIT, Postgraduate Ecology Forum 2008 TCD & Irish Plant Scientists Association Meeting 2008 NUI Maynooth.

Moore, K. A. 2009. Bryophyte Identification. Dublin Naturalists Field Club, March 2009.

Moore, K. Coote, L. Mitchell, F.J.G. and Kelly, D.K. 2010. Factors influencing the ground-flora diversity of successive rotations of non-native conifer plantations. British Ecological Society Annual Meeting, September 2010.

O'Halloran, J. 2008. Biodiversity of birds in Irish woodlands. Seminar Series Hilary Term, Trinity College Dublin.

O'Halloran, J., Kelly, D. K., Kelly, T., Mitchell, F., Giller, P. S., Iremonger, S. and Irwin, S. 2008. BIOFOREST and PLANFORBIO. Environmental Research Conference 2008, Royal Hospital Kilmainham, Environmental Protection Agency.

O'Halloran, J. 2009. PLANFORBIO. Presentation to COFORD Council. Cork, March 2009.

O'Sullivan, B., Keady, S., Irwin, S. and O'Halloran, J. 2010. Data-mining for biodiversity prediction in forests. 6th Conference on Prestigious Applications of Intelligent Systems, Lisbon, Portugal.

Oxbrough, A., French, V., Irwin, S., Kelly, T.C. and O'Halloran, J. 2010. Spiders, beetles and moths in exotic plantations and native woodlands: indicators of forest biodiversity at stand and landscape scales. XXII IUFRO World Congress "Forests for the Future: Sustaining Society and The Environment", Seoul, Korea.

Oxbrough, A., Kelly, T., Irwin, S., and O;Halloran, J. 2008. Biodiversity indicators of ground-dwelling spiders in Irish plantation forests and native woodlands. Biodiversity in Forest Ecosystems and Landscapes' (IUFRO) conference, Thompson Rivers University, Canada.

Oxbrough, A. 2009. Biodiversity indicators of ground-dwelling spiders in Irish plantation forsts and native woodlands. ERI Research Open Day, UCC, May 2009.

Sweeney, O., Kelly, T., Wilson, M., Irwin, S. and O'Halloran, J. 2007. What affects bird diversity in native and plantation woodlands? Institute of Ecology and Environment Management Irish Section Conference, Dublin.

Sweeney, O., Kelly, T., Wilson, M.W., Irwin, S. and O'Halloran, J. 2007. What affects bird diversity in native and plantation woodlands? Forest Task Force Annual Workshop, Białowieża, Poland.

Sweeney, O.F.McD., Kelly, T., Wilson, M.W., Irwin, S. and O'Halloran, J. 2008. Bird diversity in native and plantation woodlands. ENVIRON 2008, Dundalk Institute of Technology.

Sweeney, O.F.McD., Wilson, M.W., Irwin, S., Kelly, T. C. and O'Halloran, J. 2008. Bird diversity of Irish Woodlands. Postgraduate Ecology Forum 2008, Trinity College Dublin.

Sweeney, O.F.McD., Wilson, M.W., Kelly, T.C., Irwin, S. and O'Halloran, J. 2008. Bird diversity and abundance in different stages of the forest cycle in first and second rotation plantation forests. Current Ornithological Research in Ireland: 5th Ornithological Research Conference, University College Cork, November 2008.

Sweeney, O.F.McD. 2009. Woodland and Forest Biodiversity. Trees - why we need them. Dunmanway, October 2009.

Sweeney, O.F.McD., Wilson, M.W., Kelly, T.C., Irwin, S. and O'Halloran, J. 2009. What differences exist between the bird communities of first and second rotation plantation forests? *In*: Keller, V. and O'Halloran, J. (eds) 7th Conference of the European Ornithologists' Union Abstracts, Swiss Ornithological Institute, 152pp.

Sweeney, O.F.McD., Wilson, M.W., Kelly, T.C., Irwin, S. and O'Halloran, J. 2009. Bird density and species richness in native and plantation woodlands in Ireland: what differences exist and why? 2nd European Congress of Conservation Biology: Conservation biology and beyond: from science to practice, Prague.

Wilson, M.W. and Oxbrough, A. 2008. Forest Biodiversity Research in Ireland. Workshop presented to the Forest Service of Northern Ireland. December 6th 2008.

9.4 Theses

Chauvigne, C. 2008. The ground-dwelling invertebrate communities of native Oak woodlands (Quercus sp.), pure plantation forests (Norway spruce (Picea abies)) and mixed plantation forests (Norway spruce and oak). MSc Thesis, Ecole Superieure d'Agriculture d'Angers (data collection and analysis carried out at UCC).

Daly, O.H. 2008. An investigation of the ground flora diversity of mixed forests. MSc Thesis, Trinity College Dublin.

Martin, R. 2011. Canopy invertebrate biodiversity in a range of forest types. PhD Thesis, University College Cork.

Moore, K. 2007. Ground flora biodiversity of Sitka spruce reforestation plantations in comparison with afforestation plantations in Ireland. MSc Thesis, Trinity College Dublin.

Moore, K. A. 2011. Successional change in ground flora diversity in a range of Irish forest types. PhD Thesis, Trinity College Dublin.

Palmu, E. 2009. Initial effects of afforestation on ground beetles (Coleoptera: carbidae) in Irish grasslands and peatlands. MSc Thesis, Lunds University, Sweden (data collection and analysis carried out at UCC).

Sweeney, O.F.McD. 2010. Bird assemblages of native woodlands and non-native plantations in Ireland. PhD Thesis, University College Cork.

Vézeau, C. 2007. Investigating the light regime over the forest development stages in second rotation Sitka spruce plantations in Ireland. Project from UREKA site Integrating Ecology and Evolution in a Changing World, Trinity College Dublin.

9.5 Inputs to curriculum development and teaching

John O'Halloran presented a lecture entitled 'Biodiversity of birds in Irish woodlands' as part of the Hilary Term Seminar Series at TCD. Anne Oxbrough has lectured to the MSc Ecosystem Conservation and Landscape Management run by the ZEPS department, University College Cork. In addition she has presented two lectures at the University of Alberta, for the Department of Renewable Resources Seminar Series (April 2010) and the Entomology seminar series (December 2010). These focused on the invertebrate research carried out during the FORESTBIO project. A number of staff members have given lectures to on forest biodiversity to the Biodiversity Components of Forestry course at UCC as follows.

Oxbrough, A. 2007. Spiders as biodiversity indicators in Irish plantation forests. Biodiversity Components of Forestry Certificate Course, UCC.

O'Halloran, J. 2007. Introduction to biodiversity with particular reference to forests. Biodiversity Components of Forestry Certificate Course, UCC.

O'Halloran, J. 2007. Assessing biodiversity in forest: some approaches. Biodiversity Components of Forestry Certificate Course, UCC.

Sweeney, O.F.McD. 2008. Ongoing Forestry Research in Ireland. Biodiversity Components of Forestry Certificate Course, UCC.

9.6 Databases and data management

A GIS database of all data collected on this project has been compiled.

9.7 Internet presence

http://www.ucc.ie/en/planforbio/FORESTBIO

This dedicated project website provides information on the project including staff members and details of project outputs.

9.8 Any other technology transfer activities

The PLANFORBIO research programme featured in Series 6 of RTE's EcoEye in January 2008. Filming for this programme was undertaken in autumn 2007 during canopy fogging fieldwork and an interview with Rebecca Martin was filmed. The program comprised shots of canopy fogging, laboratory identification of invertebrates, an interview about the general aims of the PLANFORBIO research program, and an overview of fogging as a technique for canopy arthropod collection.

A workshop dealing with the interaction between mammals and forests was organised by Fidelma Butler (UCC), the FORESTBIO Mammal expert. This was held on Sunday 8th November 2009 as part of the All Ireland Mammal Symposium hosted by Waterford Institute of Technology and The National Biodiversity Data Centre and took place at Waterford Institute of Technology. This workshop brought together those whose work or interests involve mammals and forests, either through a regulatory, research, conservation or practitioner role and provided a forum to discuss the priorities for future work. The workshop included a number of oral presentations (detailed below) followed by a public discussion and a summation.

- **Colin Lawton**: Squirrels in forests.
- **Tim Burkitt**: Deer in forests.
- **Peter Turner**: Pine marten in forests.
- **Conor Kelleher**: Bats in forests.

A PLANFORBIO Extension Day took place on the 31st March 2010 at the Environmental Research Institute Building, UCC followed by a visit to the field site at Garrynagree, Co. Waterford (Appendix 33). The aim of this meeting was to share some of the findings of the FORESTBIO research project as they relate to biodiversity of plantation forests and to provide an opportunity for researchers and practitioners to gain improved understanding of forest biodiversity. The audience included stakeholders from UCC, TCD, WIT, Forest Service, Coillte, NPWS and the Heritage Council. The morning session consisted of a series of short, informative seminars presented by FORESTBIO researchers from UCC and TCD and representatives from the Forest Service and Coillte. In the afternoon Dr. Mark Wilson and Dr. Linda Coote led delegates through the field site at Garrynagree, Co. Waterford which is a Norway Spruce/oak Mix

Forest. The informal structure to the day facilitated communication between FORESTBIO researchers and a very wide range of stakeholders. Presentations made on the day were as follows:

- **Orla Fahy**, Forest Service: Approvals and licences – biodiversity implications.
- **Pat Neville**, Coillte Teoranta: Coillte's work on biodiversity – challenges and opportunities.
- **John O'Halloran,** UCC: PLANFORBIO Research Programme.
- **Linda Coote**, TCD: Forestry and plant diversity.
- **Rebecca Martin**, UCC: Invertebrate biodiversity in various planted forest types.
- **Oisín Sweeney**, UCC: Bird assemblages of native and plantation forests: importance of vegetation structure and management recommendations for bird conservation.

Following the event, a press release was published on the UCC website homepage (www.ucc.ie) which brought the attention of the event to a wider audience.

Regular updates on the FORESTBIO project were included in the biannual newsletter of the PLANFORBIO research programme. This was circulated to all stakeholders and provided an informal means of communicating project progress and findings.

10. Appendices

Appendix 1: Details of sites where different biodiversity surveys were conducted. NS = Norway spruce, NS/SP = Scots pine mix, NS/oak = oak mix; an * indicates sites used in the comparison of forest types. For full site names and location see Table 3.1, Table 3.2 & Table 3.3.

REFORESTATION SURVEY (n = 20 sites)

	E'phyt Lower trunk	E'phyt Canopy	Ground vegetation	Ground Inverts	Lepid Winter Spring	Lepid Sum	Canopy Inverts	Birds Summ	Birds Winter	Dead wood	Laser Scan
Age class I											
REYRA	X	n/a	X	X	n/a	n/a	n/a	X	n/a	n/a	n/a
GLENG	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
BOOLA	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
CAPAR	X	n/a	X	X	n/a	n/a	n/a	X	n/a	n/a	n/a
THREE	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
Age class II											
DYKEE	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
TARTY	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
KKCOO	X	n/a	X	X	n/a	n/a	n/a	X	n/a	n/a	n/a
SHKIN	X	n/a	X	X	n/a	n/a	n/a	X	n/a	n/a	n/a
FAUNA	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
Age class III											
BOHAT	X	n/a	X	X	n/a	n/a	n/a	X		n/a	n/a
MEENY	X	n/a	X	X	n/a	n/a	X	X	X	n/a	X
BYANT	X	n/a	X	X	n/a	n/a	X	X	X	n/a	X
CULLE	X	n/a	X	X	n/a	n/a	X	X		n/a	X
SWMID	X	n/a	X	X	n/a	n/a	n/a	X	X	n/a	n/a
Age class IV											
CHEVY	X	X*	X*	X*	n/a	n/a	n/a	X	X	X	n/a
QUITR	X	X*	X*	X*	n/a	n/a	X*	X		X	X
REARO	X	X*	X*	X*	n/a	n/a	X*	X	X	X	X
BAUNR	X	X*	X*	X*	n/a	n/a	X*	X		X	X
BYTIE	X	X*	X*	X*	n/a	n/a	n/a	X	X	X	n/a
TOTAL	**20**	**5**	**20**	**20**	**n/a**	**n/a**	**6**	**20**	**12**	**5**	**6**

MIXED TREE SPECIES SURVEY (n = 20 sites)

	E′phyt Lower trunk	E′phyt Canopy	Ground vegetation	Ground Inverts	Lepid Winter Spring	Lepid Sum	Canopy Inverts	Birds Summ	Birds Winter	Dead wood	Laser Scan
NS / oak											
THOMM	X	X*	X*	X*	n/a	X*	X	X	n/a	n/a	n/a
GARRM	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
GOSFM	X	X	X*	X*	n/a	X*	n/a	X	X	n/a	n/a
WOODM	X	X*	X*	X*	X	X*	X	X	n/a	n/a	n/a
PARKM	X	X*	X*	X*	X	X*	n/a	X	X	n/a	n/a
NS / SP											
MOTEM	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
CRABM	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
CASTM	X	X*	X*	X*	n/a	X*	X	X	n/a	n/a	n/a
JENKM	X	X*	X*	X*	n/a	X*	n/a	X	n/a	n/a	n/a
COOLM	X	X*	X*	X*	X	X*	n/a	X	X	n/a	n/a
Pure NS											
THOMP	X	X*	X*	X*	n/a	X*	X	X	n/a	n/a	n/a
GARRP	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
GOSFP	X	X*	X*	X*	n/a	X*	n/a	X	X	n/a	n/a
WOODP	X	X*	X*	X*	X	X*	X	X	n/a	n/a	n/a
PARKP	X	X*	X*	X*	X	X*	n/a	X	X	n/a	n/a
MOTEP	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
CRABP	X	X*	X*	X*	X	X*	X	X	X	n/a	n/a
CASTP	X	X*	X*	X*	n/a	X*	X	X	n/a	n/a	n/a
JENKP	X	X*	X*	X*	n/a	X*	n/a	X	n/a	n/a	n/a
COOLP	X	X	X*	X*	X	X*	n/a	X	X	n/a	n/a
TOTAL	**20**	**18**	**20**	**20**	**12**	**20**	**12**	**20**	**12**	**0**	**0**

NATIVE WOODLANDS SURVEY (n = 20 sites)

	E'phyt Lower trunk	E'phyt Canopy	Ground vegetation	Ground Inverts	Lepid Winter Spring	Lepid Sum	Canopy Inverts	Birds Summ	Birds Winter	Dead wood	Laser Scan
Oak											
BYARR	X	X*	X*	X*	n/a	n/a	n/a	X	X	X	n/a
DRUMM	X	X*	X*	X*	n/a	n/a	X*	X	X	X	X
KCREA	X	X	X*	X*	n/a	n/a	X*	X	n/a	X	X
KKBRA	X	X	X*	X*	n/a	n/a	n/a	X	n/a	X	n/a
PROHU	X	X*	X*	X*	n/a	n/a	X*	X	X	X	X
URAGH	X	X*	X*	X*	X	X*	X*	X	X	X	n/a
TOMNA	X	X*	X*	X*	X	X*	n/a	X	n/a	X	n/a
BROWN	X	X*	X*	X*	n/a	X*	X*	X	n/a	X	X
BREEN	X	X	X*	X*	n/a	X*	X*	X	X	X	n/a
ROSTR	X	X*	X*	X*	X	X*	n/a	X	X	X	n/a
Ash											
DERMO	X	X*	X*	X*	n/a	n/a	n/a	X	X	X	n/a
DRISL	X	X*	X*	X*	n/a	n/a	n/a	X	n/a	X	n/a
KILLO	X	X*	X*	X*	n/a	n/a	n/a	X	n/a	X	n/a
OUGHT	X	X*	X*	X*	n/a	n/a	n/a	X	X	X	n/a
STJON	X	X*	X*	X*	n/a	n/a	X	X	X	X	n/a
KILLA	X	X*	X*	X*	X	X*	X	X	X	X	n/a
GOLEW	X	X	X*	X*	n/a	X*	X	X	n/a	X	n/a
GREEN	X	X	X*	X*	X	X*	X	X	X	X	n/a
CRICK	X	X*	X*	X*	n/a	X*	X	X	n/a	X	n/a
DROMO	X	X*	X*	X*	X	X*	X	X	X	X	n/a
TOTAL	**20**	**20**	**20**	**20**	**6**	**10**	**12**	**20**	**12**	**20**	**4**

AFFORESTATION CANOPY FOGGING SITES

SITE NAME	SITE CODE	CLUSTER	DETAILS
Blackcurragh	BAAFO	Midlands	Age class IV
Ballyguyroe	QUAFO	Southwest	Age class IV
Ballinteosig	REAFO	South	Age class IV
Cullenagh	CUAFO	Midlands	Age class III
Cummery_Connell	MEAFO	Southwest	Age class III
Ballyknockane	BYAFO	South	Age class iii

Appendix 2: Habitat associations of the spider species sampled within a particular survey (1 = present in that survey; 0 = not present).

Species name and authority	Family	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Agelena labyrinthica (Clerck, 1757)	Agelenidae	Generalist	Generalist	0	1	0
Amaurobis fenestralis (Ström, 1768)	Amaurobiidae	Forest	Generalist	1	0	0
Anyphaena accentuata (Walckenaer, 1802)	Anyphaenidae	Forest	Generalist	0	0	1
Cyclosa conica (Pallas 1772)	Araneidae	Forest	Generalist	1	0	0
Clubiona comta (C.L. Koch, 1839)	Clubionidae	Forest	Generalist	1	0	1
Clubiona lutescens (Westring, 1851)	Clubionidae	Generalist	Generalist	0	0	1
Clubiona pallidula (Clerk, 1757)	Clubionidae	Generalist	Generalist	0	0	1
Clubiona reclusa (O.P.-Cambridge, 1863)	Clubionidae	Generalist	Generalist	0	1	0
Cryphoeca sylvicola (C.L.Koch, 1834)	Dictynidae	Forest	Generalist	1	1	1
Drassodes cupreus (Blackwall, 1834)	Gnaphosidae	Open	Generalist	0	1	0
Haplodrassus signifer (C.L. Koch, 1839)	Gnaphosidae	Open	Generalist	0	1	0
Micaria pulicaria (Sundevall, 1831)	Gnaphosidae	Open	Generalist	0	1	0
Antistea elegans (Blackwall, 1841)	Hahniidae	Generalist	Moist	1	1	0
Hahnia helveola (Simon, 1875)	Hahniidae	Forest	Generalist	1	0	1
Agyneta cauta (O.P.-Cambridge, 1902)	Linyphiidae	Generalist	Generalist	1	0	0
Agyneta conigera (O.P.-Cambridge, 1863)	Linyphiidae	Generalist	Generalist	1	1	1
Agyneta olivacea (Emerton, 1882)	Linyphiidae	Generalist	Moist	0	1	0
Agyneta ramosa (Jackson, 1912)	Linyphiidae	Forest	Generalist	1	1	1
Agyneta subtilis (O.P.-Cambridge, 1863)	Linyphiidae	Generalist	Generalist	1	1	1
Asthenargus paganus (Simon, 1884)	Linyphiidae	Forest	Generalist	1	1	1
Bathyphantes gracilis (Blackwall, 1841)	Linyphiidae	Generalist	Generalist	1	1	1
Bathyphantes nigrinus (Westring, 1851)	Linyphiidae	Generalist	Generalist	1	1	1
Bathyphantes parvulus (Westring, 1851)	Linyphiidae	Open	Generalist	0	1	1
Centromerus arcanus (OP -Cambridge, 1873)	Linyphiidae	Generalist	Generalist	0	1	0

Species name and authority	Family	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Centromerus dilutus (O.P.-Cambridge, 1875)	Linyphiidae	Generalist	Generalist	1	1	1
Centromerus prudens (OP -Cambridge, 1873)	Linyphiidae	Open	Generalist	1	0	0
Centromerus sylvaticus (Blackwall, 1841)	Linyphiidae	Generalist	Generalist	0	1	1
Ceratinella brevipes (Westring, 1851)	Linyphiidae	Generalist	Generalist	1	1	1
Ceratinella brevis (Wider, 1834)	Linyphiidae	Generalist	Generalist	0	0	1
Ceratinella scabrosa (O.P.-Cambridge, 1871)	Linyphiidae	Generalist	Generalist	1	1	1
Cnephalocotes obscurus (Simon, 1884)	Linyphiidae	Generalist	Generalist	0	1	0
Dicymbium nigrum (Blackwall, 1834)	Linyphiidae	Generalist	Generalist	0	0	1
Dicymbium tibiale (Blackwall, 1836)	Linyphiidae	Forest	Generalist	1	1	1
Diplocephalus latifrons (O.P.-Cambridge, 1863)	Linyphiidae	Forest	Generalist	1	1	1
Diplocephalus permixtus (O.P.-Cambridge, 1871)	Linyphiidae	Generalist	Moist	1	1	1
Diplocephalus picinus (Blackwall, 1831)	Linyphiidae	Forest	Generalist	1	0	1
Diplostylor concolor (Wider, 1834)	Linyphiidae	Forest	Generalist	1	0	1
Dismodicus bifrons (Blackwall, 1841)	Linyphiidae	Generalist	Generalist	1	1	1
Drapetisca socialis (Sundevall, 1833)	Linyphiidae	Generalist	Generalist	1	0	0
Erigone atra (Blackwall, 1833)	Linyphiidae	Open	Generalist	1	1	1
Erigone dentipalpis (Wider, 1843)	Linyphiidae	Open	Generalist	1	1	1
Erigonella hiemalis (Blackwall, 1841)	Linyphiidae	Forest	Generalist	1	1	1
Gnathonarium dentatum (Wider, 1834)	Linyphiidae	Open	Moist	0	1	0
Gonatium rubellum (Blackwall, 1841)	Linyphiidae	Forest	Generalist	1	0	1
Gongylidiellum vivum (O.P.-Cambridge, 1875)	Linyphiidae	Generalist	Moist	1	1	1
Gongylidum rufipes (Linnaeus, 1758)	Linyphiidae	Forest	Moist	1	1	1
Hilaira excisa (O. P.-Cambridge, 1870)	Linyphiidae	Generalist	Moist	0	1	1
Hypomma cornutum (Blackwall, 1833)	Linyphiidae	Generalist	Generalist	1	1	0
Jacksonella falconeri (Jackson, 1908)	Linyphiidae	Generalist	Generalist	0	0	1
Lepthyphantes alacris (Blackwall, 1853)	Linyphiidae	Forest	Generalist	1	1	1
Lepthyphantes cristatus (Menge, 1866)	Linyphiidae	Forest	Generalist	1	1	1
Lepthyphantes ericaeus (Blackwall, 1853)	Linyphiidae	Generalist	Generalist	1	1	1
Lepthyphantes flavipes (Blackwall, 1854)	Linyphiidae	Forest	Generalist	1	1	1

Species name and authority	Family	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Lepthyphantes mengei (Kulczynski, 1887)	Linyphiidae	Generalist	Generalist	0	1	1
Lepthyphantes obscurus (Blackwall, 1841*)*	Linyphiidae	Forest	Generalist	1	1	1
Lepthyphantes pallidus (O.P.-Cambridge, 1871)	Linyphiidae	Generalist	Generalist	1	1	1
Lepthyphantes tenebricola (Wider, 1834)	Linyphiidae	Forest	Generalist	1	1	1
Lepthyphantes tenuis (Blackwall, 1852)	Linyphiidae	Generalist	Generalist	1	1	1
Lepthyphantes zimmermanni (Bertkau, 1890)	Linyphiidae	Generalist	Generalist	1	1	1
Leptorhoptrum robustum (Westring, 1851)	Linyphiidae	Generalist	Moist	1	1	1
Linyphia hortensis (Sundevall, 1830)	Linyphiidae	Forest	Generalist	0	0	1
Lophomma punctatum (Blackwall, 1841)	Linyphiidae	Generalist	Moist	0	0	1
Macrargus rufus (Wider, 1834)	Linyphiidae	Forest	Generalist	0	1	0
Maro minutus (O.P.-Cambridge, 1906)	Linyphiidae	Generalist	Generalist	1	1	1
Maso sundervalli (Westring, 1851)	Linyphiidae	Generalist	Generalist	1	0	1
Meioneta saxatilis (Blackwall, 1844)	Linyphiidae	Generalist	Generalist	0	1	0
Metopobactrus prominulus (O.P.-Cambridge, 1872)	Linyphiidae	Generalist	Generalist	0	1	1
Micrargus herbigradus (Blackwall, 1854)	Linyphiidae	Generalist	Generalist	1	1	1
Micrargus subaequalis (Westring, 1851)	Linyphiidae	Generalist	Generalist	0	0	1
Microlinyphia pusilla (Sundevall, 1830)	Linyphiidae	Generalist	Generalist	0	1	1
Microneta viaria (Blackwall, 1841)	Linyphiidae	Forest	Generalist	1	1	1
Minyriolus pusillus (Wider, 1834)	Linyphiidae	Generalist	Generalist	1	1	1
Monocephalus castaneipes (Blackwall, 1836)	Linyphiidae	Forest	Generalist	1	0	0
Monocephalus fuscipes (Blackwall, 1836)	Linyphiidae	Forest	Generalist	1	1	1
Nereine clathrata (Sundevall, 1830)	Linyphiidae	Generalist	Generalist	1	1	1
Neriene peltata (Wider, 1834)	Linyphiidae	Generalist	Generalist	1	1	1
Oedothorax fuscus (Blackwall, 1834)	Linyphiidae	Generalist	Generalist	1	1	1
Oedothorax gibbosus (Blackwall, 1841)	Linyphiidae	Generalist	Moist	1	1	1
Oedothorax retusus (Blackwall, 1851)	Linyphiidae	Generalist	Generalist	0	0	1
Pelecopsis nemoralis (Blackwall, 1841)	Linyphiidae	Forest	Generalist	1	1	1
Pepnocranium ludicrum (O.P.-Cambridge, 1861)	Linyphiidae	Generalist	Generalist	0	1	1
Pocadicnemis juncea (Locket & Millidge, 1953)	Linyphiidae	Open*	Generalist	1	1	1

Species name and authority	Family	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Pocadicnemis pumila (Blackwall, 1841)	Linyphiidae	Open	Generalist	0	1	1
Poeciloneta globosa (Blackwall, 1841)	Linyphiidae	Open	Generalist	0	1	0
Porrhomma egeria (Simon, 1884)	Linyphiidae	Cryptic	n/a	1	0	0
Porrhomma montanum (Jackson, 1913)	Linyphiidae	Generalist	Generalist	1	0	0
Porrhomma oblitum (O.P.-Cambridge, 1871)	Linyphiidae	Forest	moist	0	0	1
Porrhomma pallidum (Jackson, 1913)	Linyphiidae	Generalist	Generalist	1	1	1
Saaristoa abnormis (Blackwall, 1841)	Linyphiidae	Generalist	Generalist	1	1	1
Saaristoa firma (O.P.-Cambridge, 1905)	Linyphiidae	Generalist	Generalist	1	1	1
Savignya frontata (Blackwall, 1833)	Linyphiidae	Generalist	Generalist	1	0	0
Silometopus elegans (O.P.-Cambridge, 1872)	Linyphiidae	Open	Moist	0	1	1
Tapinoba longidens (Wider, 1834)	Linyphiidae	Generalist	Generalist	0	0	1
Tapinocyba insecta (L. Koch, 1869)	Linyphiidae	Forest	Generalist	1	0	1
Tapinocyba pallens (O.P.-Cambridge, 1872)	Linyphiidae	Forest	Generalist	1	1	1
Taranucnus setosus (Simon, 1884)	Linyphiidae	Open	Moist	0	1	0
Walckenaeria acuminata (Blackwall,1833)	Linyphiidae	Generalist	Generalist	1	1	1
Walckenaeria atrobtibialis (O. P.-Cambridge, 1878)	Linyphiidae	Generalist	Generalist	1	1	1
Walckenaeria cucullata (C.L.Koch, 1836)	Linyphiidae	Forest	Generalist	0	0	1
Walckenaeria cuspidata (Blackwall, 1833)	Linyphiidae	Generalist	Generalist	0	1	1
Walckenaeria dysderoides (Wider, 1843)	Linyphiidae	Shade	Generalist	1	1	1
Walckenaeria nudipalpis (Westring, 1851)	Linyphiidae	Generalist	Generalist	1	1	1
Walckenaeria unicornis (O.P.-Cambridge, 1861)	Linyphiidae	Generalist	Generalist	0	1	0
Walckenaeria vigilax (Blackwall, 1851)	Linyphiidae	Generalist	Moist	1	1	1
Alopecosa pulverulenta (Clerck, 1757)	Lycosidae	Open	Generalist	0	1	0
Pardosa amentata (Clerck, 1757)	Lycosidae	Open	Generalist	0	1	1
Pardosa lugubris (Walckenaer, 1802)	Lycosidae	Forest	Generalist	0	0	1
Pardosa nigriceps (Thorell, 1856)	Lycosidae	Open	Generalist	0	1	0
Pardosa palustris (Linnaeus, 1758)	Lycosidae	Open	Generalist	0	0	1
Pardosa pullata (Clerck, 1757)	Lycosidae	Open	Generalist	0	1	1
Pirata hygrophilus (Thorell, 1872)	Lycosidae	Generalist	Moist	1	1	1

Species name and authority	Family	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Pirata piraticus (Clerck, 1757)	Lycosidae	Open	Moist	0	1	0
Pirata uliginosus (Thorell, 1856)	Lycosidae	Open	Generalist	0	1	1
Trochosa spinipalpis (O.P.-Cambridge, 1895)	Lycosidae	Open	Moist	0	1	0
Trochosa terricola (Thorell, 1836)	Lycosidae	Open	Generalist	0	1	0
Ero cambridgei (Kulczynski, 1911)	Mimetidae	Generalist	Generalist	0	1	0
Pisaura mirabilis (Clerck, 1757)	Pisauridae	Generalist	Generalist	0	1	0
Neon reticulatus (Blackwall, 1853)	Salticidae	Generalist	Generalist	0	0	1
Segestria senoculata (Linnaeus, 1758)	Segestriidae	Generalist	Generalist	1	0	1
Meta mengei (Blackwall, 1869)	Tetragnathidae	Generalist	Generalist	1	0	1
Meta merianae (Scopli, 1763)	Tetragnathidae	Cryptic	Moist	1	0	1
Pachygnatha clercki (Sundevall, 1823)	Tetragnathidae	Generalist	Moist	0	1	0
Pachygnatha degeeri (Sundevall, 1830)	Tetragnathidae	Generalist	Generalist	0	1	0
Pachygnatha listeri (Sundevall, 1830)	Tetragnathidae	Forest	Generalist	0	0	1
Enoplognatha ovata (Clerck, 1757)	Theridiidae	Open	Generalist	0	0	1
Pholcomma gibbum (Westring, 1851)	Theridiidae	Generalist	Generalist	0	1	0
Robertus lividus (Blackwall, 1836)	Theridiidae	Generalist	Generalist	1	1	1
Theonoe minutissima (O.P.-Cambridge, 1879)	Theridiidae	Generalist	Generalist	1	1	1
Theridion bimaculatum (Linnaeus, 1767)	Theridiidae	Generalist	Generalist	0	1	0
Theridion instabile (O.P.-Cambridge, 1870)	Theridiidae	Generalist	Generalist	1	0	1
Theridion pallens (Blackwall, 1834)	Theridiidae	Generalist	Generalist	0	0	1
Theridion sisyphium (Clerck, 1757)	Theridiidae	Generalist	Generalist	0	1	0
Theridiosoma gemnosum (Koch, 1877)	Theridiidae	Generalist	Moist	1	0	1
Ozyptila trux (Blackwall, 1846)	Thomisidae	Generalist	Generalist	1	1	1
Xysticus cristatus (Clerck, 1757)	Thomisidae	Open	Generalist	0	1	0
Zora spinimana (Sundevall, 1833)	Zoridae	Generalist	Generalist	1	1	0

Appendix 3: Habitat associations of the Carabid beetle species sampled within a particular survey (1 = present in that survey; 0 = not present).

Species name and authority	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Abax parallelepipedus (Piller & Mitterpacher, 1783)	Forest	Generalist	1	1	1
Agonum emarginatum (Gyllenhal 1827)	Open	Moist	0	0	1
Agonum fuliginosum (Panzer, 1809)	Generalist	Moist	1	1	1
Agonum thoreyi Dejean, 1828	Open	Moist	0	1	0
Agonum viduum (Panzer, 1796)	Open	Moist	0	0	1
Amara aenea (Degeer, 1774)	Open	Dry	0	1	0
Amara communis (Panzer, 1797)	Generalist	Generalist	0	1	0
Amara familiaris (Duftschmid, 1812)	Open	Generalist	0	1	0
Amara lunicollis Schioedte, 1837	Open	Generalist	0	1	0
Amara ovata (Fabricius, 1792)	Open	Dry	0	1	0
Amara plebeja (Gyllenhal, 1810)	Generalist	Generalist	1	1	0
Amara similata (Gyllenhal, 1810)	Open	Moist	0	0	1
Anchomenus dorsalis (Pontoppidan, 1763)	Generalist	Dry	0	1	0
Asaphidion curtum (Heyden, 1870)	Generalist	Generalist	0	0	1
Asaphidion flavipes (Linnaeus, 1761)	Generalist	Moist	0	1	1
Badister bullatus (Schrank, 1798)	Generalist	Generalist	1	0	1
Badister sodalis (Duftschmid, 1812)	Forest	Moist	1	1	1
Bembidion aeneum Germar, 1824	Generalist	Moist	1	1	0
Bembidion lampros (Herbst, 1784)	Open	Dry	0	1	1
Bembidion mannerheimii Sahlberg, 1827	Generalist	Moist	0	1	1
Blethisa multipunctata (Linnaeus, 1758)	Generalist	Moist	0	0	1
Bradycellus harpalinus (Serville, 1821)	Generalist	Generalist	0	1	0
Bradycellus verbasci (Duftschmid, 1812)	Generalist	Dry	0	1	0
Calathus melanocephalus agg. (Linnaeus, 1758)	Open	Dry	1	1	1
Calathus rotundicollis Dejean, 1828	Forest	Generalist	1	1	1
Carabus arvensis Herbst, 1784	Generalist	Generalist	0	1	1
Carabus glabratus Paykull, 1790	Generalist	Generalist	1	0	1
Carabus granulatus Linnaeus, 1758	Generalist	Moist	1	1	1
Carabus nemoralis Mueller, 1764	Generalist	Generalist	1	1	1
Carabus problematicus Herbst, 1786	Forest	Generalist	1	1	1
Clivina fossor (Linnaeus, 1758)	Open	Generalist	1	1	1
Cychrus caraboides (Linnaeus, 1758)	Forest	Generalist	1	1	1

Species name and authority	Habitat association	Moisture association	Mixed tree species survey	Reforestation survey	Native woodlands survey
Dromius quadrimaculatus (Linnaeus, 1758)	Forest	Generalist	1	0	0
Dyschirius globosus (Herbst, 1784)	Open	Generalist	0	0	1
Elaphrus cupreus Duftschmidt, 1812	Generalist	Moist	1	0	1
Harpalus latus (Linnaeus, 1758)	Generalist	Generalist	1	1	1
Harpalus rufipes (Degeer, 1774)	Open	Generalist	0	0	1
Leistus fulvibarbis Dejean, 1826	Forest	Generalist	1	1	1
Leistus terminatus (Hellwig, 1793)	Generalist	Moist	1	1	1
Loricera pilicornis (Fabricius, 1775)	Generalist	Generalist	1	1	1
Nebria brevicollis (Fabricius, 1792)	Forest	Generalist	1	1	1
Notiophilus biguttatus (Fabricius, 1779)	Generalist	Generalist	1	1	1
Notiophilus palustris (Duftschmid, 1812)	Generalist	Generalist	0	1	0
Ocys harpaloides Serville, 1821	Forest	Moist	1	1	1
Olisthopus rotundatus (Paykull, 1790)	Open	Dry	1	0	0
Oxyselaphus obscurus (Herbst, 1784)	Forest	Moist	0	0	1
Paradromius linearis (Olivier, 1795)	Open	Generalist	0	1	0
Paranchus albipes (Fabricius, 1796)	Generalist	Moist	0	1	0
Platynus assimilis (Limodromus assimilis, Paykull, 1790)	Forest	Moist	1	1	1
Poecilus versicolor (Sturm, 1824)	Open	Generalist	0	1	0
Pterostichus adstrictus Eschscholtz, 1823	Open	Generalist	0	0	1
Pterostichus diligens (Sturm, 1824)	Generalist	Moist	1	1	1
Pterostichus madidus (Fabricius, 1775)	Generalist	Generalist	1	1	1
Pterostichus melanarius (Illiger, 1798)	Generalist	Moist	1	1	1
Pterostichus niger (Schaller, 1783)	Generalist	Generalist	1	1	1
Pterostichus nigrita (Paykull, 1790)	Generalist	Moist	1	1	0
Pterostichus oblongopunctatus (Fabricius, 1787)	Forest	Generalist	0	0	1
Pterostichus rhaeticus Heer	Generalist	Moist	1	1	1
Pterostichus strenuus (Panzer, 1796)	Generalist	Generalist	1	1	1
Pterostichus vernalis (Panzer, 1795)	Generalist	Moist	1	1	1
Stomis pumicatus (Panzer, 1795)	Generalist	Generalist	1	0	1
Synuchus vivalis (Illiger, 1798)	Generalist	Generalist	1	0	1
Trechus obtusus Erichson, 1837	Generalist	Generalist	1	1	1
Trechus quadristriatus (Schrank, 1781)	Open	Dry	0	1	0

Appendix 4: Habitat associations of the Moth species sampled within a particular survey (1 = present in that survey; 0 = not present).

Species name and authority	Common name	Family	Habitat association	Larval food plant preference	Mixed tree species survey	Native woodlands survey
Abraxas grossulariata (Linnaeus, 1758)	Magpie	Geometridae	Generalist	Woody shrub/Broadleaved	1	0
Abraxas sylvata (Scopoli, 1763)	Clouded Magpie	Geometridae	Forests/scattered trees	Broadleaved	0	1
Abrostola tripartita (Hufnagel, 1766)	Spectacle	Noctuidae	Generalist	Herbaceous plants	1	1
Abrostola triplasia (Linnaeus, 1758)	Dark Spectacle	Noctuidae	Generalist	Herbaceous plants	1	0
Acasis viretata (Hübner, 1799)	Yellow-barred Brindle	Geometridae	Generalist	Woody shrub	1	1
Acronicta megacephala (Denis & Schiffermüller, 1775)	Poplar Grey	Noctuidae	Forests/scattered trees	Broadleaved	1	1
Acronicta psi (Linnaeus, 1758)	Grey Dagger	Noctuidae	Forests/scattered trees	Broadleaved	0	1
Agrotis exclamationis (Linnaeus, 1758)	Heart and Dart	Noctuidae	Generalist	Herbaceous plants	1	1
Alcis repandata (Linnaeus, 1758)	Mottled Beauty	Geometridae	Generalist	Herb/Broadleaved	0	1
Anaplectoides prasina (Denis & Schiffermüller, 1775)	Green Arches	Noctuidae	Generalist	Woody shrub	1	0
Apamea monoglypha (Hufnagel, 1766)	Dark Arches	Noctuidae	Generalist	Herbaceous plants	1	1
Apamea remissa (Hübner, 1809)	Dusky Brocade	Noctuidae	Generalist	Herbaceous plants	1	0
Apeira syringaria (Linnaeus, 1758)	Lilac Beauty	Geometridae	Generalist	Woody shrub	1	1
Atolmis rubricolis (Linnaeus, 1758)	Red-necked Footman	Arctiidae	Forests/scattered trees	Lichen	1	1
Autographa pulchrina (Haworth, 1809)	Beautiful Golden Y	Noctuidae	Generalist	Herb/Broadleaved	1	1
Axylia putris (Linnaeus, 1761)	Flame	Noctuidae	Generalist	Herbaceous plants	1	0
Biston betularia (Linnaeus, 1758)	Peppered Moth	Geometridae	Forests/scattered trees	Broadleaved	1	1
Blepharita adusta (Esper, 1790)	Dark Brocade	Noctuidae	Open habitats	Herb/Broadleaved	0	1
Bupalus piniaria (Linnaeus, 1758)	Bordered White	Geometridae	Forests/scattered trees	Conifer	1	0
Cabera exanthemata (Scopoli, 1763)	Common Wave	Geometridae	Forests/scattered trees	Broadleaved	1	1
Cabera pusaria (Linnaeus, 1758)	Common White Wave	Geometridae	Forests/scattered trees	Broadleaved	1	1
Calliteara pudibunda (Linnaeus, 1758)	Pale Tussock	Lymantriidae	Forests/scattered trees	Broadleaved	1	1
Campaea margaritata (Linnaeus, 1767)	Light Emerald	Geometridae	Forests/scattered trees	Broadleaved	0	1
Chlorclysta truncata (Hufnagel, 1767)	Common Marbled Carpet	Geometridae	Generalist	Woody shrub	1	1
Chloroclystis v-ata (Haworth, 1809)	V-Pug	Geometridae	Generalist	Herb/Broadleaved	1	1
Cleorodes lichenaria (Hufnagel, 1767)	Brussels Lace	Geometridae	Generalist	Lichen	1	1
Colocasia coryli (Linnaeus, 1758)	Nut-tree Tussock	Noctuidae	Forests/scattered trees	Broadleaved	1	1
Colostygia pectinataria (Knoch, 1781)	Green Carpet	Geometridae	Generalist	Herbaceous plants	1	1
Cosmia trapezina (Linnaeus, 1758)	Dun-bar	Noctuidae	Forests/scattered trees	Broadleaved	0	1
Crocallis elinguaria (Linnaeus, 1758)	Scalloped Oak	Geometridae	Forests/scattered trees	Broadleaved	0	1

Species name and authority	Common name	Family	Habitat association	Larval food plant preference	Mixed tree species survey	Native woodlands survey
Cyclophora linearia (Hübner, 1799)	Clay Triple-lines	Geometridae	Forests/scattered trees	Broadleaved	1	1
Deilephila elpenor (Linnaeus, 1758)	Elephant Hawkmoth	Sphingidae	Generalist	Herbaceous plants	0	1
Deileptenia ribeata (Clerck, 1759)	Satin Beauty	Geometridae	Forests/scattered trees	Conifer	1	0
Diachrysia chrysitis (Linnaeus, 1758)	Burnished Brass	Noctuidae	Open habitats	Herbaceous plants	1	0
Diaphora mendica (Clerck, 1759)	Muslin Moth	Arctiidae	Generalist	Herbaceous plants	1	0
Diarsia brunnea (Denis & Schiffermüller, 1775)	Purple Clay	Noctuidae	Habitat association	Herb/shrub	1	1
Diarsia mendica (Fabricius, 1775)	Ingrailed Clay	Noctuidae	Generalist	Woody shrub	1	1
Ecliptopera silaceata (Denis & Schiffermüller, 1775)	Small Phoenix	Geometridae	Generalist	Herbaceous plants	1	1
Ectropis spp. (Goeze, 1781)	Engrailed/Small Engrailed	Geometridae	Forests/scattered trees	Broadleaved	1	1
Eilema depressa (Esper, 1787)	Buff Footman	Arctiidae	Generalist	Lichen	0	1
Electrophaes corylata (Thunberg, 1792)	Broken-barred Carpet	Geometridae	Forests/scattered trees	Broadleaved	1	1
Epirrhoe alternata (Müller, 1764)	Common Carpet	Geometridae	Generalist	Herbaceous plants	1	0
Eulithis populata (Linnaeus, 1758)	Northern Spinach	Geometridae	Generalist	Woody shrub	0	1
Euphyia unangulata (Haworth, 1809)	Sharp-angled Carpet	Geometridae	Generalist	Herbaceous plants	1	1
Eupithecia abietaria (Goeze, 1781)	Cloaked Pug	Geometridae	Forests/scattered trees	Conifer	1	0
Eupithecia absinthiata (Clerck, 1759)	Wormwood Pug	Geometridae	Generalist	Herbaceous plants	1	0
Eupithecia exiguata (Hübner, 1809-13)	Mottled Pug	Geometridae	Forests/scattered trees	Broadleaved	1	1
Eupithecia indigata (Hübner, 1813)	Ochreous Pug	Geometridae	Forests/scattered trees	Conifer	1	0
Eupithecia pulchellata (Stephens, 1831)	Foxglove Pug	Geometridae	Generalist	Herbaceous plants	1	1
Eupithecia subfuscata (Haworth, 1809)	Grey Pug	Geometridae	Generalist	Herbaceous plants	1	1
Eupithecia tantillaria (Boisduval, 1840)	Dwarf Pug	Geometridae	Forests/scattered trees	Conifer	1	0
Eupithecia vulgata (Haworth, 1809)	Common Pug	Geometridae	Generalist	Herb/Broadleaved	1	1
Euplexia lucipara (Linnaeus, 1758)	Small Angle Shades	Noctuidae	Generalist	Herb/Broadleaved	1	1
Euthrix potatoria (Linnaeus, 1758)	Drinker	Lasiocampidae	Generalist	Herbaceous plants	1	0
Falcaria lacertinaria (Linnaeus, 1758)	Scalloped Hook-tip	Drepanidae	Forests/scattered trees	Broadleaved	0	1
Geometra papilionaria (Linnaeus, 1758)	Large Emerald	Geometridae	Forests/scattered trees	Broadleaved	1	1
Graphiphora augur (Fabricius, 1775)	Double Dart	Noctuidae	Forests/scattered trees	Broadleaved	0	1
Gymnoscelis rufifasciata (Haworth, 1809)	Double-striped Pug	Geometridae	Generalist	Herb/Broadleaved	0	1
Habrosyne pyritoides (Hufnagel, 1766)	Buff Arches	Thyatiridae	Generalist	Woody shrub	1	1
Hadena rivularis (Fabricius, 1775)	Campion	Noctuidae	Open habitats	Herbaceous plants	1	0
Hepialus fusconebulosa (DeGeer, 1778)	Map-winged Swift	Hepialidae	Generalist	Herbaceous plants	1	1
Hepialus hecta (Linnaeus, 1758)	Gold Swift	Hepialidae	Generalist	Herbaceous plants	1	1

Species name and authority	Common name	Family	Habitat association	Larval food plant preference	Mixed tree species survey	Native woodlands survey
Hepialus humuli (Linnaeus, 1758)	Ghost Moth	Hepialidae	Generalist	Herbaceous plants	1	0
Herminia grisealis (Denis & Schiffermüller, 1775)	Small Fan-foot	Noctuidae	Forests/scattered trees	Broadleaved	1	0
Hydriomena furcata (Thunberg, 1784)	July Highflyer	Geometridae	Generalist	Woody shrub/Broadleaved	0	1
Hydriomena impulviata (Denis & Schiffermüller, 1775)	May Highflyer	Geometridae	Forests/scattered trees	Broadleaved	1	1
Hylaea fasciaria (Linnaeus, 1758)	Barred Red	Geometridae	Forests/scattered trees	Conifer	1	0
Hypena crassalis (Fabricius, 1787)	Beautiful Snout	Noctuidae	Generalist	Woody shrub	1	0
Hypena proboscidalis (Linnaeus, 1758)	Snout	Noctuidae	Generalist	Herbaceous plants	0	1
Idaea aversata (Linnaeus, 1758)	Riband Wave	Geometridae	Generalist	Herbaceous plants	1	1
Jodis lactearia (Linnaeus, 1758)	Little Emerald	Geometridae	Forests/scattered trees	Broadleaved	1	1
Lacanobia thalassina (Hufnagel, 1766)	Pale-shouldered Brocade	Noctuidae	Generalist	Herb/Broadleaved	1	1
Laothoe populi (Linnaeus, 1758)	Poplar Hawkmoth	Sphingidae	Forests/scattered trees	Broadleaved	1	1
Lomaspilis marginata (Linnaeus, 1758)	Clouded Border	Geometridae	Forests/scattered trees	Broadleaved	1	1
Lomographa temerata (Denis & Schiffermüller, 1775)	Clouded Silver	Geometridae	Forests/scattered trees	Broadleaved	1	1
Lycophotia porphyrea (Denis & Schiffermüller, 1775)	True Lover's Knot	Noctuidae	Generalist	Woody shrub	1	1
Macaria liturata (Clerck, 1759)	Tawny-barred Angle	Geometridae	Forests/scattered trees	Conifer	1	1
Melanchra persicariae (Linnaeus, 1761)	Dot Moth	Noctuidae	Generalist	Herb/Broadleaved	0	1
Melanchra pisi (Linnaeus, 1758)	Broom Moth	Noctuidae	Generalist	Herb/Broadleaved	0	1
Mesapamea spp. (Linnaeus, 1758)	Common Rustic agg.	Noctuidae	Generalist	Herbaceous plants	1	1
Mesoleuca albicillata (Linnaeus, 1758)	Beautiful Carpet	Geometridae	Generalist	Herbaceous plants	1	1
Noctua pronuba (Linnaeus, 1758)	Large Yellow Underwing	Noctuidae	Generalist	Herbaceous plants	1	1
Notodonta ziczac (Linnaeus, 1758)	Pebble Prominent	Notodontidae	Forests/scattered trees	Broadleaved	1	0
Nudaria mundana (Linnaeus, 1761)	Muslin Footman	Arctiidae	Generalist	Lichen	1	0
Ochropacha duplaris (Linnaeus, 1761)	Common Lutestring	Thyatiridae	Forests/scattered trees	Broadleaved	1	1
Ochropleura plecta (Linnaeus, 1761)	Flame Shoulder	Noctuidae	Generalist	Herbaceous plants	1	1
Odontopera bidentata (Clerck, 1759)	Scalloped Hazel	Geometridae	Forests/scattered trees	Broadleaved/Conifer	1	1
Oligia fasciuncula (Haworth, 1809)	Middle-barred Minor	Noctuidae	Generalist	Herbaceous plants	1	0
Opisthograptis luteolata (Linnaeus, 1758)	Brimstone	Geometridae	Forests/scattered trees	Broadleaved	1	1
Ourapteryx sambucaria (Linnaeus, 1758)	Swallow-tailed Moth	Geometridae	Generalist	Woody shrub/broadleaved	0	1
Pasiphila debiliata (Hübner, 1817)	Bilberry Pug	Geometridae	Generalist	Woody shrub	1	0
Pasiphila rectangulata (Linnaeus, 1758)	Green Pug	Geometridae	Forests/scattered trees	Broadleaved	1	1
Peribatodes rhomboidaria (Denis & Schiffermüller, 1775)	Willow Beauty	Geometridae	Generalist	Woody shrub/broadleaved	1	0

Species name and authority	Common name	Family	Habitat association	Larval food plant preference	Mixed tree species survey	Native woodlands survey
Phalera bucephala (Linnaeus, 1758)	Buff-tip	Notodontidae	Forests/scattered trees	Broadleaved	1	1
Pheosia tremula (Clerck, 1759)	Swallow Prominent	Notodontidae	Forests/scattered trees	Broadleaved	0	1
Photedes minima (Haworth, 1809)	Small Dotted Buff	Noctuidae	Generalist	Herbaceous plants	1	0
Plagodis dolabraria (Linnaeus, 1767)	Scorched Wing	Geometridae	Forests/scattered trees	Broadleaved	0	1
Plagodis pulveraria (Linnaeus, 1758)	Barred Umber	Geometridae	Forests/scattered trees	Broadleaved	0	1
Polia nebulosa (Hufnagel, 1766)	Grey Arches	Noctuidae	Generalist	Herb/shrub	1	1
Protodeltote pygarga (Hufnagel, 1766)	Marbled White Spot	Noctuidae	Generalist	Herbaceous plants	1	1
Pseudoips prasinana (Warren, 1913)	Green Silver-lines	Noctuidae	Forests/scattered trees	Broadleaved	1	1
Pterostoma palpina (Clerck, 1759)	Pale Prominent	Notodontidae	Forests/scattered trees	Broadleaved	1	1
Ptilodon capucina (Linnaeus, 1758)	Coxcomb Prominent	Notodontidae	Forests/scattered trees	Broadleaved	0	1
Scoliopteryx libatrix (Linnaeus, 1758)	Herald	Noctuidae	Generalist	Herb/Broadleaved	1	0
Scopula floslactata (Haworth, 1809)	Cream Wave	Geometridae	Generalist	Herbaceous plants	1	0
Scotopteryx chenopodiata (Linnaeus, 1758)	Shaded Broad-bar	Geometridae	Open habitats	Herbaceous plants	1	0
Scotopteryx luridata ssp.plumbaria (Hufnagel, 1767)	July Belle	Geometridae	Generalist	Woody shrub	1	0
Scotopteryx mucronata (Scopoli, 1763)	Lead Belle	Geometridae	Generalist	Woody shrub	0	1
Spilosoma lubricipeda (Linnaeus, 1758)	White Ermine	Arctiidae	Generalist	Herbaceous plants	1	1
Spilosoma luteum (Hufnagel, 1766)	Buff Ermine	Arctiidae	Generalist	Herb/Broadleaved	1	1
Syngrapha interrogationis (Linnaeus, 1758)	Scarce Silver Y	Noctuidae	Generalist	Woody shrub	0	1
Thera britannica (Turner)	Spruce Carpet	Geometridae	Forests/scattered trees	Conifer	1	0
Thera obeliscata (Hübner, 1787)	Grey Pine Carpet	Geometridae	Forests/scattered trees	Conifer	1	1
Thyatira batis (Linnaeus, 1758)	Peach Blossom	Thyatiridae	Generalist	Woody shrub	1	1
Tyria jacobaeae (Linnaeus, 1758)	Cinnabar	Arctiidae	Generalist	Herbaceous plants	1	1
Xanthorhoe designata (Hufnagel, 1767)	Flame Carpet	Geometridae	Generalist	Herbaceous plants	0	1
Xanthorhoe fluctuata (Linnaeus, 1758)	Garden Carpet	Geometridae	Generalist	Herbaceous plants	1	0
Xanthorhoe montanata (Denis & Schiffermüller, 1775)	Silver-ground Carpet	Geometridae	Generalist	Herbaceous plants	1	1
Xestia baja (Denis & Schiffermüller, 1775)	Dotted Clay	Noctuidae	Generalist	Herb/Broadleaved	1	1
Xestia c-nigrum (Clerck, 1759)	Setaceous Hebrew Character	Noctuidae	Generalist	Herbaceous plants	0	1
Xestia ditrapezium (Denis & Schiffermüller, 1775)	Triple-spotted Clay	Noctuidae	Generalist	Herb/Broadleaved	1	1
Xestia triangulum (Hufnagel, 1766)	Double Square-spot	Noctuidae	Generalist	Herb/Broadleaved	1	1
Zanclognatha tarsipennalis (Treitschke, 1835)	Fan-foot	Noctuidae	Generalist	Herb/Broadleaved	0	1

Appendix 5: Forest types, locations and dates sampled for the canopy fogging study.

Site Name	County	Site Type	Date Fogged
Thomastown	Offaly	Norway spruce/oak mix	04/07/2008
Garrynagree	Waterford	Norway spruce/oak mix	02/06/2008
Woodburn	Antrim	Norway spruce/oak mix	27/07/2008
Thomastown	Offaly	Pure Norway spruce	04/07/2008
Garrynagree	Waterford	Pure Norway spruce	02/06/2008
Woodburn	Antrim	Pure Norway spruce	27/07/2008
Uragh	Kerry	Oak woodland	08/08/2008
Brownstown Wood	Kilkenny	Oak woodland	10/06/2008
Breen Wood	Antrim	Oak woodland	14/07/2008
Gole Wood	Fermanagh	Ash woodland	13/07/2008
Carrickbreeny	Donegal	Ash woodland	21/06/2008
Dromore Nature Reserve	Clare	Ash woodland	23/07/2008
Drummin	Galway	Oak woodland	09/07/2009
Kilmacrea	Wicklow	Oak woodland	10/07/2009
Prohus	Cork	Oak woodland	22/06/2009
St Johns Wood	Roscommon	Ash woodland	23/06/2009
Greenaun	Leitrim	Ash woodland	24/06/2009
Killavalla	Tipperary	Ash woodland	13/06/2009
Baunreagh	Laois	Age class IV reforested Sitka spruce	16/06/2009
Blackcurragh	Laois	Age class IV afforested Sitka spruce	16/06/2009
Quitrent	Cork	Age class IV reforested Sitka spruce	02/05/2009
Ballyguyroe	Cork	Age class IV afforested Sitka spruce	24/05/2009
Rearour	Waterford	Age class IV reforested Sitka spruce	25/05/2009
Ballinteosig	Waterford	Age class IV afforested Sitka spruce	03/06/2009
Cullenagh	Laois	Age class III reforested Sitka spruce	11/06/2009
Cullenagh	Laois	Age class III afforested Sitka spruce	05/06/2009
Meentinny	Kerry	Age class III reforested Sitka spruce	20/04/2009
Cummery Connell	Kerry	Age class III afforested Sitka spruce	20/04/2009
Ballyanthony	Waterford	Age class III reforested Sitka spruce	02/06/2009
Ballyknockane	Waterford	Age class IIIafforested Sitka spruce	03/06/2009

Appendix 6: Total abundances and mean relative proportions of all taxa (excluding spiders, beetles, true flies and true bugs) sampled in the canopies ofnative ash and oak woodlands and age class IV Sitka spruce plantations.

Order/Class/Group	Total			Mean Proportion of Total		
	Ash	Oak	Age class IVSitka spruce	Ash	Oak	Age class IV Sitka spruce
Acari	470	1194	240	0.10	0.11	0.05
Aranae (Immature)	1073	1608	67	0.28	0.28	0.02
Archaeognatha	12	0	0	0.00	0.00	0.00
Coleoptera (Larvae)	266	148	302	0.07	0.07	0.06
Collembola	135	208	18992	0.03	0.02	0.51
Dermaptera	12	7	0	0.00	0.00	0.00
Diplopoda	6	6	0	0.00	0.00	0.00
Diptera (Larvae)	15	5	3	0.00	0.00	0.00
Ephemeroptera	5	4	0	0.00	0.00	0.00
Hymenoptera	1613	2351	384	0.37	0.29	0.09
Isopoda	31	16	0	0.01	0.00	0.00
Lepidoptera	18	32	7	0.00	0.00	0.00
Lepidoptera (Larvae)	132	114	21	0.04	0.01	0.01
Lithobiomorpha	4	9	0	0.00	0.00	0.00
Megaloptera	5	12	0	0.00	0.00	0.00
Nematoda	1	1	0	0.00	0.00	0.00
Neuroptera	5	6	1	0.00	0.00	0.00
Oligochaeta	0	1	0	0.00	0.00	0.00
Opiliones (Immature)	0	1	1	0.00	0.00	0.00
Phthiraptera	0	1	0	0.00	0.00	0.00
Plecoptera	0	0	40	0.00	0.00	0.00
Protura	0	3	4	0.00	0.00	0.00
Psocoptera	284	1548	1251	0.06	0.21	0.25
Pulmonata	4	4	5	0.00	0.00	0.00
Thysanoptera	97	99	7	0.02	0.01	0.00
Trichoptera	11	20	1	0.00	0.00	0.00
Total abundance	**4199**	**7398**	**21326**			
Total taxa	**22**	**25**	**17**			

Appendix 7: Summary of BIOFOREST project study sites used in the comparison of forest types for the ground vegetation, including the code for each site, forest name, location (county and grid reference) and stand age.

BIOFOREST Code	Site	County	Grid Ref.	Age (yrs)
Plantations				
Sitka Spruce (*Picea sitchensis*)				
COON	Cooneen Hill	Tipperary	R916 687	36
DERR	Derrybrien East	Galway	M623 010	39
FURY	Fuhiry	Cork	W144 733	38
KILASS	Killalongford	Carlow	S996 742	43
MSOP	Monasop	Laois	S279 997	37
MONT	Moneyteige	Wicklow	T139 751	43
MUNG	Mungacullin	Wicklow	S954 686	39
RATHSS	Rathcarrick	Sligo	G638 349	47
SINBSS	Sinnotts Bog	Wexford	T062 664	37
SUNSSS	Sunderlands	Wicklow	T251 811	44
UNIO	Union	Sligo	G689 729	47
Larch (*Larix kaempferi*)				
BALL	Ballintombay	Wicklow	T140 900	40
CARR	Carriglinneen	Wicklow	T114 914	31
BEGG	Coolbeggan	Waterford	X043 883	39
CRUA	Cruagh	Dublin	O128 226	64
CURT	Curtlestown	Wicklow	O181 172	66
DONN	Derrydonnell	Galway	M451 273	42
SCAG	Scaragh	Tipperary	S016 250	32
SCAR	Scaragh	Tipperary	S003 242	37
Ash (*Fraxinus excelsior*)				
BALY	Ballygiblin[BE]	Cork	R462 028	52
BARN	Barnadown	Wexford	T140 543	62
CAST	Castletown	Kildare	N986 343	31
DEME	Demesne	Kildare	N832 324	62
DESM	Demesne	Galway	M849 031	38
DROM	Dromoland[BE]	Clare	R397 705	39
KILAASH	Killalongford	Carlow	S967 743	45
RATHASH	Rathcarrick[SY]	Sligo	G637 350	47
RINC	Rincrew[SY]	Waterford	X082 818	81
SINBASH	Sinnott's Bog	Wexford	T061 662	37
SUNSASH	Sunderlands[BE,SC]	Wicklow	T250 809	44

[BE] beech (*Fagus sylvatica*), [SY] sycamore (*Acer pseudoplatanus*) & [SC] sweet chestnut (*Castanea sativa*) formed substantial components of the canopy at these sites.

Appendix 8: The ground vegetation species recorded during the study in the four age classes of reforestation Sitka spruce plantations, in pure Norway spruce (NS),Norway spruce/oak mix (Oak mix) and Norway spruce/Scots pine mix (Scots pine mix) plantations and native oak and ash woodlands. Nomenclature follows Stace (1997) for vascular plants, (Smith, 2004) for mosses, (Paton, 1999) for liverworts and (Coppins, 2002) for lichens.

| Species name | Reforestation Sitka spruce | | | | Pure and mixed NS | | | Native | |
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Abies alba					x				x
Acer campestre									x
Acer platanoides						x			
Acer pseudoplatanus				x	x	x	x	x	x
Agrostis canina s.l.	x	x		x	x	x		x	x
Agrostis capillaris	x	x	x	x	x	x	x	x	x
Agrostis gigantea	x								x
Agrostis species							x		
Agrostis stolonifera	x			x	x	x	x	x	x
Ajuga reptans				x	x	x	x		x
Allium ursinum				x					x
Alnus glutinosa									x
Alnus incana (planted)	x								
Amblystegium serpens									x
Anemone nemorosa									x
Anthoxanthum odoratum	x			x	x			x	
Arctium species									x
Arrhenatherum elatius	x								x
Arum maculatum					x				x
Asplenium trichomanes									x
Athyrium filix-femina	x	x	x	x	x	x	x	x	x
Atrichum undulatum				x	x	x	x		x
Bazzania trilobata								x	
Betula pendula		x			x		x	x	x
Betula pubescens	x	x	x	x	x		x	x	x
Blechnum spicant	x	x	x	x	x	x	x	x	x
Brachythecium rutabulum	x				x	x		x	x
Brachypodium sylvaticum				x	x		x		x
Bryoerythrophyllum recurvirostrum									x
Bryum species									x
Calliergonella cuspidata									x

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Calluna vulgaris	x	x		x	x			x	
Calypogeia fissa					x	x	x	x	x
Calypogeia muelleriana	x		x	x	x	x	x	x	x
Campylopus flexuosus	x	x		x	x			x	
Campylopus introflexus	x		x					x	
Campylopus pyriformis			x	x				x	
Campylopus species									x
Cardamine flexuosa				x	x	x	x		x
Cardamine hirsuta					x				
Cardamine pratensis	x					x			x
Carex binervis	x			x					
Carex echinata	x	x	x	x				x	
Carex elata	x								
Carex flacca					x	x			x
Carex nigra	x	x							
Carex ovalis						x			
Carex pendula							x		
Carex pilulifera	x	x							
Carex remota				x	x	x	x		x
Carex species	x	x	x	x	x	x			
Carex strigosa							x		
Carex sylvatica				x	x		x		x
Cephalozia bicuspidata				x	x				
Cerastium fontanum					x				
Ceratodon purpureus	x								
Chamerion angustifolium	x			x	x	x	x		
Chiloscyphus pallescens									x
Chrysosplenium oppositifolium				x	x	x	x		x
Circaea lutetiana					x	x	x		x
Cirriphyllum piliferum									x
Cirsium palustre					x		x		x
Cladonia chlorophaea								x	
Cladonia coniocraea						x		x	x
Cladonia fimbriata	x	x							

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Cladonia macilenta								x	x
Cladonia parasitica								x	
Cladonia polydactyla		x							
Cladonia portentosa	x	x							
Cladonia species		x		x					
Cladonis subulata	x	x							
Climacium dendroides							x		
Conopodium majus									x
Corylus avellana					x		x	x	x
Cotoneaster species							x		
Cotoneaster x watereri							x		
Crataegus monogyna			x	x	x	x	x	x	x
Ctenidium molluscum								x	x
Cynosurus cristatus				x					
Dactylorhiza fuchsii									x
Dactylis glomerata					x				x
Daltonia splachnoides	x								
Deschampsia cespitosa	x	x		x		x	x		x
Deschampsia flexuosa		x							
Dichodontium pellucidum									x
Dicranum bonjeanii								x	
Dicranodontium denudatum								x	
Dicranella heteromalla	x	x	x	x	x	x		x	
Dicranum majus								x	x
Dicranum scoparium	x	x	x	x	x			x	x
Digitalis purpurea		x		x	x	x			
Diplophyllum albicans	x	x		x				x	
Dryopteris aemula	x				x	x		x	
Dryopteris affinis	x	x	x	x	x	x	x	x	x
Dryopteris carthusiana		x							
Dryopteris x complexa					x				
Dryopteris dilitata	x	x	x	x	x	x	x	x	x
Dryopteris filix-mas					x	x	x	x	x
Dryopteris species	x	x	x	x				x	x

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Enterographa zonata								x	
Epilobium brunnescens					x				
Epilobium montanum				x	x	x	x		x
Epilobium obscurum					x				
Epilobium species	x	x			x		x		
Epipactis helleborine					x	x			x
Equisetum arvense									x
Equisetum species						x			
Equisetum sylvaticum							x		x
Erica cinerea	x	x							
Erica tetralix	x		x						
Euonymus europaeus							x		x
Eurhynchium striatum				x	x	x	x	x	x
Fagus sylvatica			x	x	x	x	x	x	x
Festuca gigantea									x
Festuca ovina		x						x	x
Festuca rubra	x								
Filipendula ulmaria									x
Fissidens adianthoides							x		
Fissidens bryoides						x			
Fissidens dubius									x
Fissidens osmundoides									x
Fissidens taxifolius				x	x		x	x	x
Fragaria vesca					x		x		x
Fraxinus excelsior				x	x	x	x		x
Frullania dilatata	x							x	x
Frullania tamarisci	x			x	x			x	x
Fuchsia magellanica					x				
Galium aparine					x	x			x
Galium palustre					x		x		x
Galium saxatile	x	x		x				x	
Galium uliginosum						x			x
Geranium robertianum				x	x	x	x		x
Geum urbanum					x				x

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Glechoma hederacea									x
Glyceria fluitans					x				
Hedera helix		x	x	x	x	x	x	x	x
Heterocladium heteropterum					x			x	
Holcus lanatus	x			x	x		x	x	x
Holcus mollis								x	
Homalothecium sericeum								x	x
Homalia trichomanoides									x
Hookeria lucens					x	x	x	x	x
Hyacinthoides non-scripta					x		x	x	x
Hylocomium splendens	x	x	x					x	x
Hymenophyllum tunbrigense								x	
Hypericum androsaemum					x				x
Hypericum pulchrum	x			x	x		x		
Hypnum andoi				x	x	x	x	x	
Hypnum jutlandicum	x	x	x	x	x	x	x	x	x
Hypnum resupinatum	x		x		x	x	x		x
Ilex aquifolium	x		x	x	x	x	x	x	x
Iris pseudacorus									x
Isothecium alopecuroides					x			x	x
Isothecium myosuroides				x	x	x	x	x	x
Juncus acutiflorus	x								
Juncus articulatus				x					
Juncus bulbosus	x			x					
Juncus comglomeratus	x								x
Juncus effusus	x	x		x	x	x	x		x
Juncus squarrosus	x								
Juncus tenuis				x					
Kindbergia praelonga	x	x	x	x	x	x	x	x	x
Kurzia pauciflora	x								
Lapsana communis									x
Larix kaempferi	x								
Lathyrus linifolius	x				x				
Lathyrus pratensis									x

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Lejeunea cavifolia								x	x
Lejeunea lamacerina				x	x	x	x		
Lejeunea patens									x
Leontodon autumnalis					x				x
Lepidozia cupressina								x	
Lepidozia reptans			x	x				x	x
Lepraria incana					x			x	
Leproloma vouauxii									x
Leptogium cyanescens									x
Listera cordata						x			
Listera ovata				x					x
Lobaria pulmonaria									x
Loeskeobryum brevirostre					x			x	x
Lolium perenne					x				
Lonicera periclymenum					x	x	x	x	x
Lophocolea bidentata	x	x	x	x	x	x	x	x	x
Lophocolea heterophylla					x	x	x		
Lophozia incisa	x								
Lophozia ventricosa	x		x						
Lotus corniculatus	x								
Lotus pedunculatus				x					
Luzula multiflora	x			x	x		x		
Luzula species	x			x	x		x	x	x
Luzula sylvatica			x	x		x		x	
Lysimachia nemorum					x		x		x
Malus sylvestris									x
Melampyrum pratense								x	
Melica uniflora									x
Metzgeria furcata			x		x	x	x	x	x
Metzgeria temperata		x		x	x	x	x	x	
Micarea denigrata	x								
Micarea prasina			x						
Micarea species			x	x					
Microlejeunea ulicina				x			x	x	

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Mnium hornum				x	x	x	x	x	x
Molinia caerulea	x	x	x			x		x	
Neckera complanata					x	x	x		x
Neckera crispa							x		x
Neckera pumila				x	x				
Nowellia curvifolia							x		x
Opegrapha gyrocarpa								x	
Orchis mascula									x
Oxalis acetosella	x		x	x	x	x	x	x	x
Oxyrrhynchium hians									x
Pellia endivifolia				x	x				x
Pellia epiphylla			x					x	
Pellia neesiana	x								
Pellia species				x					x
Peltigera hymenina	x	x							
Peltigera praetextata									x
Phyllitis scolopendrium					x		x		x
Picea abies					x	x	x		x
Picea abies (planted)					x	x	x		
Picea sitchensis (unplanted)		x	x	x					
Picea sitchensis (planted)	x	x	x	x					
Pinus contorta (planted)	x	x	x						
Pinus contorta (unplanted)	x	x							
Pinus sylvestris (planted)							x		
Plagiochila asplenioides					x		x		x
Plagiochila porelloides								x	x
Plagiochila punctata									x
Plagiomnium rostratum					x		x		x
Plagiochila spinulosa								x	
Plagiomnium undulatum				x	x	x	x	x	x
Plagiothecium laetum		x							
Plagiothecium succulentum									x
Plagiothecium undulatum	x	x	x	x	x	x	x	x	x
Pleurozium schreberi	x								

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Poa annua									x
Poa nemoralis									x
Poa trivialis				x					x
Polystichum aculeatum					x		x	x	x
Polytrichum commune	x	x	x	x	x		x		
Polytrichastrum formosum	x	x	x	x	x	x	x	x	x
Polytrichum juniperinum	x								
Polystichum setiferum					x	x			x
Polypodium vulgare s.l.					x	x	x	x	x
Populus tremula								x	
Porella arboris-vitae									x
Potentilla anglica					x				
Potentilla erecta	x	x		x	x	x		x	x
Potentilla reptans							x		
Potentilla sterilis	x			x	x				x
Primula vulgaris					x		x		x
Prunus avium						x			x
Prunus padus							x		
Prunus spinosa							x		x
Prunella vulgaris									x
Pseudotaxiphyllum elegans		x	x	x	x	x	x	x	
Pseudoscleropodium purum	x	x		x	x	x	x	x	x
Pteridium aquilinum	x	x						x	
Pyrenula macrospora									x
Quercus petraea (planted)						x			
Quercus petraea (unplanted)								x	x
Quercus robur (planted)						x			
Quercus robur (unplanted)					x	x	x		x
Quercus species (unplanted)					x		x		
Racomitrium heterostichum		x							
Radula complanata					x		x		x
Ranunculus acris									x
Ranunculus auricormis									x
Ranunculus flammula					x				

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Ranunculus repens					x		x		x
Rhizomnium punctatum									x
Rhododendron ponticum	x								
Rhynchostegium confertum					x			x	
Rhytidiadelphus loreus	x	x	x	x		x	x	x	x
Rhytidiadelphus squarrosus		x							x
Rhytidiadelphus triquetris		x		x	x		x	x	x
Riccardia chamedryfolia									x
Riccardia multifida									x
Riccardia palmata								x	x
Rorippa species					x				
Rosa species				x	x				x
Rubus caesius									x
Rubus fruticosus agg.	x	x	x	x	x	x	x	x	x
Rubus idaeus	x				x	x	x		x
Rubus spectabilis						x			
Rumex acetosa	x								
Saccogyna viticulosa								x	
Salix aurita	x	x	x						
Salix caprea							x		x
Salix cinerea	x	x	x		x		x	x	x
Salix x multinervis		x							
Salix x pontederiana	x								
Salix x reichardtii									x
Salix species	x			x			x		
Sambucus nigra					x	x	x		x
Sanicula europaea					x		x		x
Scapania gracilis		x							
Scapania nemorea								x	
Scrophularia nodosa					x				x
Senecio aquaticus					x				
Senecio jacobaea	x				x				
Solidago virgaurea								x	x
Sonchus asper					x				

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Sorbus aucuparia	x	x	x		x	x	x	x	x
Sphagnum angustifolium	x	x							
Sphagnum capillifolium	x	x						x	
Sphagnum denticulatum	x	x							
Sphagnum fallax	x	x							
Sphagnum girgensohnii		x							
Sphagnum inundatum	x	x							
Sphagnum palustre	x	x	x					x	
Sphagnum papillosum		x							
Sphagnum subnitens	x				x				
Stachys sylvatica				x					
Stellaria graminea					x				
Stellaria holostea								x	x
Stellaria uliginosa	x			x		x			
Sticta sylvatica									x
Symphoricarpos albus					x				
Taraxacum species					x				x
Taxus baccata					x				
Teucrium scorodonia								x	
Thamnobryum alopecurum					x	x	x		x
Thuidium tamariscinum	x	x	x	x	x	x	x	x	x
Thuja occidentalis							x		
Tortella tortuosa									x
Trichocolea tomentella									x
Tsuga heterophylla									x
Ulex europaeus	x	x			x				
Ulex gallii	x								
Ulmus glabra									x
Ulota crispa s.l.	x				x	x	x	x	x
Urtica dioica					x	x			x
Vaccinium myrtillus	x	x	x	x	x	x		x	
Veronica chamaedrys				x	x		x		x
Veronica montana					x		x		x
Veronica officinalis	x			x		x			x

Species name	Reforestation Sitka spruce				Pure and mixed NS			Native	
	Age class I	Age class II	Age class III	Age class IV	NS	Oak mix	Scots pine mix	Oak	Ash
Veronica serpyllifolia				x			x		
Veronica species						x			
Verrucaria margacea								x	
Viburnum opulus									x
Vicia sepium					x		x		x
Viola riviniana					x	x			
Viola species	x			x	x	x	x		x
Weissia species									x
Zygodon viridissimus									x

Appendix 9: Details of the total number of canopy spider species sampled in each forest type.

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Agyneta conigera	0	0	0	1	0	0	0	3	4
Anyphaena accentuata	1	0	0	0	0	0	0	0	1
Aphileta misera	0	0	0	0	0	0	2	0	2
Araneus diadematus	0	1	0	0	0	0	0	0	1
Bathyphantes gracilis	0	0	0	0	0	0	1	0	1
Clubiona brevipes	3	0	0	0	0	0	0	0	3
Cyclosa conica	1	0	0	0	0	0	0	0	1
Dysdera crocata	1	0	0	0	0	0	0	0	1
Enoplognatha ovata	5	1	1	2	0	0	0	0	9
Entelecara acuminata	0	2	0	0	0	0	0	0	2
Entelecara erythropus	3	0	0	0	0	0	0	0	3
Erigone atra	3	3	0	0	0	0	0	1	7
Erigone dentipalpis	1	0	0	0	0	0	0	0	1
Gnathonarium dentatum	0	0	0	0	0	0	40	3	43
Gongylidium rufipes	0	0	0	0	0	0	1	0	1
Hahnia montana	0	1	0	0	0	0	0	0	1
Hypomma cornutum	0	1	13	0	2	1	1	2	20
Kaestneria dorsalis	4	0	0	0	0	0	0	0	4
Labulla thoracica	0	7	0	0	0	0	0	0	7
Lepthyphantes alacris	0	0	0	0	0	0	0	2	2
Lepthyphantes cristatus	0	0	1	0	0	0	0	0	1
Lepthyphantes obscurus	0	0	2	0	3	5	16	7	33
Lepthyphantes zimmermanni	0	0	1	0	0	0	3	0	4
Linyphia triangularis	0	1	0	0	0	0	0	0	1
Metellina (Meta) mengei	25	7	0	0	0	5	8	6	51
Metellina (Meta) segmentata	1	0	0	0	0	0	0	0	1
Monocephalus castaneipes	1	7	3	6	1	4	4	14	40
Neriene montana	0	1	0	0	1	3	0	3	8
Neriene peltata	19	64	3	10	9	21	8	8	142
Oedothorax agrestis	0	0	0	0	0	1	0	1	2
Oedothorax fuscus	6	2	0	1	0	0	0	0	9

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Paidiscura pallens	44	58	5	13	2	9	15	22	168
Pelecopsis nemoralis	12	21	49	27	15	34	75	150	383
Poeciloneta variegata	0	0	0	0	0	0	2	1	3
Porrhomma convexum	0	0	0	0	0	0	0	2	2
Porrhomma montanum	0	0	0	0	0	0	38	5	43
Porrhomma pallidum	0	0	0	0	0	0	9	7	16
Porrhomma pygmaeum	0	1	0	0	0	0	5	0	6
Rugathodes instabilis	0	0	0	0	0	0	1	0	1
Selimus vittatus	1	0	0	0	0	0	0	0	1
Tetragnatha montana	66	26	0	5	0	0	0	0	97
Theridion varians	0	7	0	1	0	0	0	0	8
Total abundance	197	211	78	66	33	83	229	237	1134
Species richness	18	18	9	9	7	9	17	17	42

Appendix 10: Details of the total number of canopy beetle species sampled in each forest type.

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Acalles (Acalles) misellus	56	2	1	1	0	0	0	0	60
Adalia (Adalia) decempunctata	2	4	0	3	0	0	0	0	9
Anaspis (Anaspis) fasciata	1	2	0	0	0	0	0	0	3
Anaspis (Anaspis) frontalis	0	1	0	0	0	0	0	0	1
Anaspis (Nassipa) rufilabris	1	4	0	1	0	1	2	1	10
Anatis ocellata	0	0	3	0	0	0	0	0	3
Anobium inexspectatum	0	4	0	0	0	0	0	0	4
Anoplus plantaris	0	4	0	0	0	0	0	0	4
Aphidecta obliterate	0	0	2	62	0	1	1	1	67
Athous (Athous) haemorrhoidalis	8	2	0	1	2	0	0	0	13
Athous (Orthathous) campyloides	3	0	4	1	2	6	7	5	28
Bradycellus (Bradycellus) harpalinus	0	0	2	7	0	0	0	0	9
Calodromius spilotus	0	0	0	0	0	1	1	0	2
Calvia (Anisocalvia) quatuordecimguttata	2	0	0	0	0	0	0	0	2
Cantharis (Cantharis) nigricans	1	0	0	0	0	0	0	0	1
Cantharis (Cantharis) rufa	1	0	0	0	0	0	0	0	1
Cartodere (Aridius) nodifer	6	1	0	2	0	0	0	0	9
Cercyon (Cercyon) haemorrhoidalis	0	1	0	0	0	0	0	0	1
Ceutorhynchus assimilis	5	16	0	2	0	0	0	0	23
Cis boleti	1	5	0	0	0	0	0	0	6
Coeliodes rana	2	2	0	0	0	0	0	0	4
Coeliodes transversealbofasciatus	0	1	0	0	0	0	0	0	1
Corticaria serrata	0	1	0	0	0	0	0	0	1
Corticarina similata	0	1	0	0	0	0	0	0	1
Crepidodera fulvicornis	1	0	0	0	0	0	0	0	1
Cryptophagus dentatus	0	0	1	0	0	0	0	0	1
Cyphon ochraceus	1	0	0	0	0	0	1	0	2
Cyphon variabilis	0	0	0	0	2	0	0	0	2

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Dalopius marginatus	10	5	0	0	0	0	0	0	15
Dascillus cervinus	8	0	0	0	0	0	0	0	8
Dasytes aeratus	0	1	0	0	0	0	0	0	1
Deporaus (Deporaus) betulae	0	5	0	0	0	0	0	0	5
Dorytomus (Dorytomus) taeniatus	2	0	0	0	0	0	0	0	2
Dromius (Dromius) meridionalis	0	2	1	0	0	0	0	0	3
Dromius (Dromius) quadrimaculatus	6	14	2	0	0	0	0	0	22
Dryophilus pusillus	0	0	11	2	0	0	0	0	13
Enicmus histrio	0	0	1	0	0	0	0	0	1
Ernobius mollis	0	0	2	0	0	0	0	0	2
Grammoptera ruficornis	3	2	0	0	0	0	0	0	5
Grynobius planus	1	1	0	0	0	0	0	0	2
Halyzia sedecimguttata	16	2	0	0	0	0	0	0	18
Helophorus (Rhopalohelophorus) brevipalpis	3	1	1	5	0	0	0	0	10
Kateretes rufilabris	1	1	0	0	0	0	0	0	2
Kyklioacalles (Palaeoacalles) roboris	1	6	0	0	0	0	0	0	7
Leiopus nebulosus	0	5	0	1	0	0	0	0	6
Liophloeus (Liophloeus) tessulatus	1	1	0	0	0	0	0	0	2
Magdalis (Odontomagdalis) armigera	1	0	0	0	0	0	0	0	1
Malthinus fasciatus	5	0	1	0	0	0	0	0	6
Malthinus flaveolus	2	1	1	0	0	0	0	0	4
Malthodes fuscus	0	0	0	3	0	0	1	0	4
Malthodes guttifer	8	71	1	0	1	0	0	0	81
Malthodes marginatus	3	25	5	1	36	5	5	1	81
Malthodes pumilus	2	0	0	0	0	0	0	0	2
Megasternum concinnum	0	0	1	0	0	0	0	0	1
Micrambe vini	11	18	2	0	1	0	0	1	33
Micrelus ericae	5	1	0	0	0	0	0	0	6
Mniophila muscorum	0	2	0	0	0	0	0	0	2

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Nalassus laevioctostriatus	0	23	0	0	0	0	0	0	23
Ocys harpaloides	15	12	2	3	0	2	1	7	42
Oomorphus concolor	2	2	0	0	0	0	0	0	4
Orchesia (Clinocara) minor	15	0	0	0	0	0	0	0	15
Orchesia (Clinocara) undulate	1	2	0	2	0	0	0	0	5
Orchestes (Orchestes) Quercus	3	5	0	0	0	0	0	0	8
Orchestes (Salius) fagi	36	0	2	26	0	0	0	0	64
Otiorhynchus (Metopiorrhynchus) singularis	2	2	0	0	2	0	1	1	8
Paradromius (Manodromius) linearis	5	0	0	0	0	0	0	0	5
Phyllobius (Dieletus) argentatus	4	20	0	1	7	0	1	0	33
Phyllobius (Pterygorrhynchus) maculicornis	0	1	0	0	1	0	0	0	2
Polydrusus (Eustolus) pterygomalis	12	0	0	4	0	0	0	0	16
Polydrusus (Neoeustolus) cervinus	4	9	0	0	0	0	0	0	13
Polydrusus (Polydrusus) tereticollis	0	46	0	0	0	0	0	0	46
Prasocuris junci	2	0	0	0	0	0	0	0	2
Propylea quatuordecimpunctata	1	0	0	0	0	0	0	0	1
Ptilinus pectinicornis	0	0	1	3	0	0	0	0	4
Rhagium (Hagrium) bifasciatum	0	0	0	0	1	0	0	0	1
Rhagonycha (Rhagonycha) lignosa	0	0	0	1	19	4	0	5	29
Rhamphus (Rhamphus) pulicarius	8	2	1	0	0	0	0	0	11
Salpingus planirostris	9	42	4	9	2	4	0	9	79
Salpingus ruficollis	1	25	4	2	0	0	0	0	32
Sphaeriestes (Sphaeriests) stockmanni	0	1	0	0	0	0	0	0	1
Stenichnus (Cyrtoscydmus) bicolour	2	0	0	0	0	0	0	0	2
Stenichnus (Cyrtoscydmus) poweri	0	1	1	0	0	0	0	0	2
Strophosoma (Strophosoma) capitatum	0	7	0	0	0	0	0	0	7
Strophosoma (Strophosoma) melanogrammum	8	32	45	10	11	5	12	0	123
Tetratoma (Abstrulia) ancora	3	0	0	0	0	0	0	0	3

Species Name	Ash	Oak	Pure Norway spruce	Norway spruce/oak mix	Age class IV afforested Sitka spruce	Age class IV reforested Sitka spruce	Age class III afforested Sitka spruce	Age class III reforested Sitka spruce	Total
Trechus (Trechus) obtusus	0	0	0	0	1	0	0	0	1
Vincenzellus ruficollis	3	0	0	0	0	0	0	0	3
Total abundance	**316**	**447**	**102**	**153**	**88**	**29**	**33**	**31**	**1199**
Species richness	**54**	**52**	**26**	**24**	**14**	**9**	**11**	**9**	**87**

Appendix 11: Assignations to guilds, habitat associations and rarity status of the canopy spiders and beetles identified to species in this study.

Species Name	Family	Forest Specialist	Tree Association	Guild	Rarity
Spiders					
Agyneta conigera (O.P. Cambridge 1863)	Linyphiidae	No	None	Sheet Web	Local
Anyphaena accentuata (Walckenaer 1802)	Anyphaenidae	Yes	Mixed Forest	Active Hunter	Common
Aphileta misera (O.P. Cambridge 1882)	Linyphiidae	No	None	Sheet Web	Local
Araneus diadematus Clerck 1757	Araneidae	No	None	Orb web	Common
Bathyphantes gracilis (Blackwall 1841)	Linyphiidae	No	None	Sheet Web	Common
Clubiona brevipes (Blackwall 1841)	Clubionidae	Yes	Mixed Forest	Active Hunter	Common
Cyclosa conica (Pallas 1772)	Araneidae	Yes	Mixed Forest	Orb web	Local
Dysdera crocata C.L. Koch 1838	Dysderidae	No	None	Active Hunter	Common
Enoplognatha ovata (Clerck 1757)	Theridiidae	No	None	Scaffold Web Hunter	Common
Entelecara acuminata (Wider 1834)	Linyphiidae	Yes	Mixed Forest	Sheet Web	New Irish Record
Entelecara erythropus (Westring 1851)	Linyphiidae	No	None	Sheet Web	Common
Erigone atra Blackwall 1833	Linyphiidae	No	None	Sheet Web	Common
Erigone dentipalpis (Wider 1834)	Linyphiidae	No	None	Sheet Web	Common
Gnathonarium dentatum (Wider 1834)	Linyphiidae	No	None	Sheet Web	Local
Gongylidium rufipes (Linnaeus 1758)	Linyphiidae	No	None	Sheet Web	Common
Hahnia montana (Blackwall 1841)	Hahniidae	Yes	Mixed Forest	Sheet Web	Common
Hypomma cornutum (Blackwall 1833)	Linyphiidae	Yes	Mixed Forest	Sheet Web	Common
Kaestneria dorsalis (Wider 1834)	Linyphiidae	No	None	Sheet Web	Local
Labulla thoracica (Wider 1834)	Linyphiidae	No	None	Sheet Web	Common
Lepthyphantes alacris (Blackwall 1853)	Linyphiidae	Yes	None	Sheet Web	Common
Lepthyphantes cristatus (Menge 1866)	Linyphiidae	No	None	Sheet Web	Local
Lepthyphantes obscurus (Blackwall 1841)	Linyphiidae	Yes	Mixed Forest	Sheet Web	Common
Lepthyphantes zimmermanni Bertkau 1890	Linyphiidae	Yes	Mixed Forest	Sheet Web	Common
Linyphia triangularis (Clerck 1757)	Linyphiidae	No	None	Sheet Web	Common
Metellina (Meta) mengei (Blackwall 1870)	Theridiidae	No	None	Orb web	Common
Metellina (Meta) segmentata (Clerck 1757)	Theridiidae	No	None	Orb web	Common
Monocephalus castaneipes (Simon 1884)	Linyphiidae	No	None	Sheet Web	Local
Neriene montana (Clerck 1757)	Linyphiidae	Yes	Mixed Forest	Sheet Web	Common
Neriene peltata (Wider 1834)	Linyphiidae	Yes	None	Sheet Web	Common
Oedothorax agrestis (Blackwall 1853)	Linyphiidae	No	None	Sheet Web	Local
Oedothorax fuscus (Blackwall 1834)	Linyphiidae	No	None	Active Hunter	Common
Paidiscura pallens (Blackwall 1834)	Theridiidae	Yes	Mixed Forest	Scaffold Web Hunter	Common

Species Name	Family	Forest Specialist	Tree Association	Guild	Rarity
Pelecopsis nemoralis (Blackwall 1841)	Linyphiidae	Yes	Mixed Forest	Sheet Web	Local
Poeciloneta variegata (Blackwall 1841)	Linyphiidae	No	None	Sheet Web	Local
Porrhomma convexum (Westring 1851)	Linyphiidae	No	None	Sheet Web	Local
Porrhomma montanum Jackson 1913	Linyphiidae	No	None	Sheet Web	Local
Porrhomma pallidum Jackson 1913	Linyphiidae	No	None	Sheet Web	Local
Porrhomma pygmaeum (Blackwall 1834)	Linyphiidae	No	None	Sheet Web	Common
Rugathodes instabilis (O.P. Cambridge 1871)	Theridiidae	No	None	Scaffold Web Hunter	Local
Selimus vittatus (C.L. Koch 1836)	Theridiidae	No	None	Sheet Web	Common
Tetragnatha montana Simon 1874	Tetragnathidae	No	None	Orb web	Common
Theridion varians Hahn 1833	Theridiidae	No	None	Scaffold Web Hunter	Common
Beetles					
Acalles (Acalles) misellus Boheman 1844	Curculionidae	Yes	Broadleaves	Xylophagous	Local
Adalia (Adalia) decempunctata (Linnaeus 1758)	Coccinellidae	Yes	Broadleaves	Active Hunter	Common
Anaspis (Anaspis) fasciata (Forster 1771)	Scraptiidae	Yes	Broadleaves	Phytophagous	Common
Anaspis (Anaspis) frontalis (Linnaeus 1758)	Scraptiidae	Yes	Mixed Forest	Phytophagous	Common
Anaspis (Nassipa) rufilabris (Gyllenhall 1827)	Scraptiidae	Yes	Mixed Forest	Phytophagous	Common
Anatis ocellata (Linnaeus 1758)	Coccinellidae	Yes	Conifers	Active Hunter	Common
Anobium inexspectatum Lohse 1954	Anobiidae	Yes	Broadleaves	Xylophagous	**Notable B**
Anoplus plantaris (Naezen 1794)	Curculionidae	Yes	Broadleaves	Phytophagous	Local
Aphidecta obliterata (Linnaeus 1758)	Coccinellidae	Yes	Conifers	Active Hunter	Common
Athous (Athous) haemorrhoidalis (Fabricius 1801)	Elateridae	No	None	Xylophagous	Common
Athous (Orthathous) campyloides Newman 1833	Elateridae	No	None	Xylophagous	**Notable B**
Bradycellus (Bradycellus) harpalinus (Audinet-Serville 1821)	Carabidae	No	None	Active Hunter	Common
Calodromius spilotus (Illiger 1798)	Carabidae	Yes	Conifers	Active Hunter	Local
Calvia (Anisocalvia) quatuordecimguttata (Linnaeus 1758)	Coccinellidae	Yes	Broadleaves	Active Hunter	Common
Cantharis (Cantharis) nigricans Muller 1766	Cantharidae	Yes	Mixed Forest	Active Hunter	Common
Cantharis (Cantharis) rufa (Linnaeus 1758)	Cantharidae	No	None	Active Hunter	Common
Cartodere (Aridius) nodifer (Westwood 1839)	Latridiidae	No	None	Mycetophagous	Common
Cercyon (Cercyon) haemorrhoidalis (Fabricius 1775)	Hydrophilidae	No	None	Detritiphagous	Common
Ceutorhynchus assimilis (Paykull 1800)	Curculionidae	No	None	Phytophagous	Common
Cis boleti (Scopoli 1763)	Ciidae	Yes	Mixed Forest	Mycetophagous	Common
Coeliodes rana (Fabricius 1787)	Curculionidae	Yes	Broadleaves (*Quercus* spp.)	Phytophagous	Common
Coeliodes transversealbofasciatus (Goeze 1777)	Curculionidae	Yes	Broadleaves (*Quercus* spp.)	Phytophagous	**Notable B**
Corticaria serrata (Paykull 1798)	Latridiidae	No	None	Mycetophagous	Common

Species Name	Family	Forest Specialist	Tree Association	Guild	Rarity
Corticarina similata (Gyllenhall 1827)	Latridiidae	No	None	Mycetophagous	Common
Crepidodera fulvicornis (Fabricius 1792)	Chrysomelidae	Yes	Broadleaves	Phytophagous	Common
Cryptophagus dentatus (Herbst 1793)	Cryptophagidae	Yes	Mixed Forest	Mycetophagous	Common
Cyphon ochraceus Stephens 1830	Scirtidae	No	None	Phytophagous	Common
Cyphon variabilis (Thunberg 1787)	Scirtidae	No	None	Phytophagous	Common
Dalopius marginatus (Linnaeus 1758)	Elateridae	Yes	Broadleaves	Phytophagous	Local
Dascillus cervinus (Linnaeus 1758)	Dascillidae	No	None	Phytophagous	Local
Dasytes aeratus Stephens 1829	Dasytidae	Yes	Broadleaves	Phytophagous	Local
Deporaus (Deporaus) betulae (Linnaeus 1758)	Rhynchitidae	Yes	Broadleaves	Phytophagous	Common
Dorytomus (Dorytomus) taeniatus (Fabricius 1781)	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Dromius (Dromius) meridionalis Dejean 1825	Carabidae	Yes	Broadleaves	Active Hunter	Local
Dromius (Dromius) quadrimaculatus (Linne 1758)	Carabidae	Yes	Mixed Forest	Active Hunter	Common
Dryophilus pusillus (Gyllenhall 1808)	Anobiidae	Yes	Conifers	Xylophagous	Local
Enicmus histrio Joy & Tomlin 1910	Latridiidae	No	None	Mycetophagous	Local
Ernobius mollis (Linnaeus 1758)	Anobiidae	Yes	Conifers	Xylophagous	Common
Grammoptera ruficornis (Fabricius 1781)	Cerambycidae	Yes	Broadleaves	Xylophagous	Common
Grynobius planus (Fabricius 1787)	Anobiidae	Yes	Mixed Forest	Xylophagous	Local
Halyzia sedecimguttata (Linnaeus 1758)	Coccinellidae	Yes	Broadleaves	Mycetophagous	Common
Helophorus (Rhopalohelophorus) brevipalpis Bedel 1881	Hydrophilidae	No	None	Detritiphagous	Common
Kateretes rufilabris (Latreille 1807)	Kateretidae	No	None	Phytophagous	Common
Kyklioacalles (Palaeoacalles) roboris Curtis 1834	Curculionidae	Yes	Broadleaves	Xylophagous	**Notable B**
Leiopus nebulosus (Linnaeus 1758)	Cerambycidae	Yes	Mixed Forest	Xylophagous	Common
Liophloeus (Liophloeus) tessulatus (Muller 1776)	Curculionidae	No	None	Phytophagous	Common
Magdalis (Odontomagdalis) armigera (Geoffroy 1785)	Curculionidae	Yes	Mixed Forest	Phytophagous	Local
Malthinus fasciatus (Olivier 1790)	Cantharidae	Yes	Broadleaves (*Quercus* spp.)	Active Hunter	Local
Malthinus flaveolus (Herbst 1786)	Cantharidae	Yes	Broadleaves	Active Hunter	Common
Malthodes fuscus (Waltl 1838)	Cantharidae	Yes	Broadleaves (*Quercus* spp.)	Active Hunter	Common
Malthodes guttifer Kiesenwetter 1852	Cantharidae	Yes	Mixed Forest	Active Hunter	**Notable B**
Malthodes marginatus (Latreille 1806)	Cantharidae	Yes	Mixed Forest	Active Hunter	Common
Malthodes pumilus (Brebisson 1835)	Cantharidae	No	None	Active Hunter	Rare
Megasternum concinnum (Marsham 1802)	Hydrophilidae	No	None	Detritiphagous	Common
Micrambe vini (Panzer 1797)	Cryptophagidae	No	None	Mycetophagous	Common
Micrelus ericae (Gyllenhall 1813)	Curculionidae	No	None	Phytophagous	Common
Mniophila muscorum (Koch 1803)	Chrysomelidae	Yes	Mixed Forest	Phytophagous	**Notable B**

Species Name	Family	Forest Specialist	Tree Association	Guild	Rarity
Nalassus laevioctostriatus (Goeze 1777)	Tenebrionidae	Yes	Broadleaves	Phytophagous	Common
Ocys harpaloides (Audinet-Serville 1821)	Carabidae	Yes	Mixed Forest	Active Hunter	Common
Oomorphus concolor (Sturm 1807)	Chrysomelidae	Yes	Mixed Forest	Phytophagous	Local
Orchesia (Clinocara) minor Walker 1837	Melandryidae	Yes	Broadleaves	Mycetophagous	**Notable B**
Orchesia (Clinocara) undulata Kraatz 1853	Melandryidae	Yes	Mixed Forest	Mycetophagous	Common
Orchestes (Orchestes) quercus (Linnaeus 1758)	Curculionidae	Yes	Broadleaves (*Quercus* spp.)	Phytophagous	Common
Orchestes (Salius) fagi (Linnaeus 1758)	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Otiorhynchus (Metopiorrhynchus) singularis (Linnaeus 1767)	Curculionidae	Yes	Mixed Forest	Phytophagous	Common
Paradromius (Manodromius) linearis (Olivier 1795)	Carabidae	No	None	Active Hunter	Common
Phyllobius (Dieletus) argentatus (Linnaeus 1758)	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Phyllobius (Pterygorrhynchus) maculicornis Germar 1824	Curculionidae	Yes	Broadleaves	Phytophagous	Local
Polydrusus (Eustolus) pterygomalis Boheman 1840	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Polydrusus (Neoeustolus) cervinus (Linnaeus 1758)	Curculionidae	Yes	Broadleaves	Phytophagous	Local
Polydrusus (Polydrusus) tereticollis (De Geer 1775)	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Prasocuris junci (Brahm 1790)	Chrysomelidae	No	None	Phytophagous	Common
Propylea quatuordecimpunctata (Linnaeus 1758)	Coccinellidae	No	None	Active Hunter	Common
Ptilinus pectinicornis (Linnaeus 1758)	Anobiidae	Yes	Mixed Forest	Xylophagous	Common
Rhagium (Hagrium) bifasciatum (Fabricius 1775)	Cerambycidae	Yes	Mixed Forest	Xylophagous	Common
Rhagonycha (Rhagonycha) lignosa (Muller 1764)	Cantharidae	No	None	Active Hunter	Common
Rhamphus (Rhamphus) pulicarius (Herbst 1795)	Curculionidae	Yes	Broadleaves	Phytophagous	Common
Salpingus planirostris (Fabiricus 1787)	Salpingidae	Yes	Mixed Forest	Active Hunter	Common
Salpingus ruficollis (Linnaeus 1761)	Salpingidae	Yes	Broadleaves	Active Hunter	Common
Sphaeriestes (Sphaeriests) stockmanni (Bistrom 1977)	Salpingidae	Yes	Broadleaves	Active Hunter	Local
Stenichnus (Cyrtoscydmus) bicolor (Denny 1825)	Scydmaenidae	Yes	Mixed Forest	Xylophagous	Local
Stenichnus (Cyrtoscydmus) poweri (Fowler 1884)	Scydmaenidae	No	None	Xylophagous	**Notable B**
Strophosoma (Strophosoma) capitatum (De Geer 1775)	Curculionidae	Yes	Mixed Forest	Phytophagous	Local
Strophosoma (Strophosoma) melanogrammum (Forster 1771)	Curculionidae	Yes	Mixed Forest	Phytophagous	Common
Tetratoma (Abstrulia) ancora Fabricius 1790	Tetratomidae	Yes	Mixed Forest	Mycetophagous	**Notable B**
Trechus (Trechus) obtusus Erichson 1837	Carabidae	No	None	Active Hunter	Common
Vincenzellus ruficollis (Panzer 1794)	Salpingidae	Yes	Broadleaves	Active Hunter	Common

Appendix 12: Diptera (true fly) families sampled in the canopies of afforested and reforested Sitka spruce plantations of age classes III and IV.

Family	Age class IV afforested	Age class IV reforested	Age class III afforested	Age class III reforested	Total
Agromyzidae	4	9	1	3	17
Anisopodidae	28	434	316	124	902
Anthomyiidae	0	0	1	0	1
Asteiidae	0	0	0	2	2
Atheristidae	0	1	0	0	1
Bibionidae	1	1	0	0	2
Brachystomatidae	2	0	0	0	2
Calliphoridae	0	0	7	1	8
Cecidomyiidae	100	209	606	455	1370
Ceratopogonidae	13845	1313	983	1353	17494
Chaoboridae	0	1	0	0	1
Chironomidae	3017	13075	1158	6124	23374
Chloropidae	0	0	1	0	1
Dolichopodidae	2	1	0	6	9
Drosophilidae	2	3	1	0	6
Empididae	119	310	129	159	717
Fannidae	2	3	8	9	22
Heleomyzidae	0	1	3	2	6
Keroplatidae	0	0	3	0	3
Lauxanidae	0	5	15	25	45
Limoniidae	43	91	149	106	389
Lonchaeidae	0	0	1	1	2
Muscidae	0	1	6	2	9
Mycetophilidae	11	46	11	17	85
Phoridae	1	15	15	14	45
Psychodidae	52	304	166	106	628
Scathophagidae	7	2	3	3	15
Scatopsidae	1	0	0	0	1
Sciaridae	77	252	481	559	1369
Sphaeroceridae	0	1	0	0	1
Stratiomyidae	2	0	9	1	12
Syrphidae	5	8	5	0	18
Tipulidae	1	6	4	3	14
Total abundance	**17322**	**16092**	**4082**	**9075**	**46571**
Family richness	**21**	**24**	**25**	**22**	**33**

Appendix 13: Taxa (excluding spiders, beetles and true flies) sampled in afforested and reforested Sitka spruce plantations of age classes III and IV.

Other taxa	Age class IV afforested	Age class IV reforested	Age class III afforested	Age class III reforested	Total
Acari	122	118	959	2207	3406
Aphidoidea	18662	12288	12017	15813	58780
Aranae (Immature)	23	44	348	221	636
Coleoptera Larvae	88	214	301	42	645
Collembola	1359	17633	37766	49882	106640
Dermaptera	0	0	1	0	1
Diptera larvae	0	3	0	0	3
Hymenoptera	100	284	288	337	1009
Lepidoptera	2	5	43	4	54
Lepidoptera larvae	12	9	13	15	49
Lithobiomorpha	0	0	0	1	1
Neuroptera	0	1	6	2	9
Opiliones	2	1	1	16	20
Opiliones Immature	1	0	0	0	1
Plecoptera	2	38	0	0	40
Protura	0	4	0	2	6
Psocoptera	313	938	672	1023	2946
Pulmonata	5	0	6	3	14
Thysanoptera	1	6	2	1	10
Trichoptera	1	0	7	3	11
Total abundance	**20693**	**31586**	**52430**	**69572**	**174281**
Total taxa	**15**	**15**	**15**	**16**	**20**

Appendix 14: Total abundances and mean relative proportions of Hemipteran families sampled from the canopies of native ash and oak woodland and age class IV Sitka spruce plantations.

Family		Total			Mean Proportion of Total	
Hemiptera	Ash	Oak	Age class IV Sitka spruce	Ash	Oak	Age class IV Sitka spruce
Acanthosomatidae	16	6	0	0.00	0.00	0.00
Anthocoridae	924	720	0	0.20	0.22	0.00
Aphididae	1619	409	30950	0.36	0.13	1.00
Aphrophoridae	2	1	0	0.00	0.00	0.00
Cicadellidae	1086	1480	0	0.24	0.45	0.00
Microphysidae	5	2	39	0.00	0.00	0.00
Miridae	636	539	0	0.14	0.17	0.00
Pentatomidae	16	33	0	0.00	0.01	0.00
Psyllidae	236	53	0	0.05	0.02	0.00
Reduviidae	2	0	0	0.00	0.00	0.00
Tingidae	6	11	0	0.00	0.00	0.00
Total abundance	**4548**	**3254**	**30989**			
Family Richness	**12**	**11**	**2**			

Appendix 15: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in reforested age class I Sitka spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Birds
Vascular plants	*r*	**<u>0.975</u>**	**<u>0.975</u>**	0.359	-0.051	-0.462
	P	**0.005**	**0.005**	0.553	0.935	0.434
	N	**5**	**5**	5	5	5
Non-vascular plants	*r*		**<u>1.000</u>**	0.300	-0.200	-0.600
	P		*	0.624	0.747	0.285
	N		**5**	5	5	5
Lower trunk epiphytes	*r*			0.300	-0.200	-0.600
	P			0.624	0.747	0.285
	N			5	5	5
Ground-dwelling spiders	*r*				<u>0.800</u>	0.500
	P				0.104	0.391
	N				5	5
Ground-dwelling beetles	*r*					**<u>0.900</u>**
	P					**0.037**
	N					**5**

* Where *r* = 1, P-*value* cannot be calculated by definition.

Appendix 16: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in reforested age class IV Sitka spruce plantations. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Birds
Vascular plants	*r*	0.600	0.500	0.100	-0.100	0.200	0.000	<u>0.872</u>
	P	0.285	0.391	0.873	0.873	0.747	1.000	0.054
	N	5	5	5	5	5	3	5
Non-vascular plants	*r*		<u>0.800</u>	0.300	0.300	-0.600	<u>0.866</u>	0.154
	P		0.104	0.624	0.624	0.285	0.333	0.805
	N		5	5	5	5	3	5
Lower trunk epiphytes	*r*			<u>0.800</u>	-0.300	-0.400	<u>0.866</u>	0.051
	P			0.104	0.624	0.505	0.333	0.935
	N			5	5	5	3	5
Canopy epiphytes	*r*				-0.700	-0.100	0.000	-0.205
	P				0.188	0.873	1.000	0.741
	N				5	5	3	5
Ground-dwelling spiders	*r*					-0.500	0.000	-0.154
	P					0.391	1.000	0.805
	N					5	3	5
Ground-dwelling beetles	*r*						-0.866	0.564
	P						0.333	0.322
	N						3	5
Canopy-dwelling inverte-brates	*r*							0.000
	P							1.000
	N							3

Appendix 17: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in reforested age class II Sitka spruce plantations.

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Birds
Vascular plants	*r*	0.200	0.200	-0.700	-0.359	0.100
	P	0.747	0.747	0.188	0.553	0.873
	N	5	5	5	5	5
Non-vascular plants	*r*		-0.200	-0.300	0.667	-0.100
	P		0.747	0.624	0.219	0.873
	N		5	5	5	5
Lower trunk epiphytes	*r*			0.500	0.051	0.500
	P			0.391	0.935	0.391
	N			5	5	5
Ground-dwelling spiders	*r*				0.205	0.000
	P				0.741	1.000
	N				5	5
Ground-dwelling beetles	*r*					0.410
	P					0.493
	N					5

Appendix 18: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in reforested age class III Sitka spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Birds
Vascular plants	*r*	-0.200	0.410	-0.308	0.400	<u>**1.000**</u>	-0.224
	P	0.747	0.493	0.614	0.505	*	0.718
	N	5	5	5	5	**3**	5
Non-vascular plants	*r*		0.564	-0.821	-0.100	**-1.000**	-0.671
	P		0.322	0.089	0.873	*	0.215
	N		5	5	5	**3**	5
Lower trunk epiphytes	*r*			-0.553	0.667	0.000	-0.287
	P			0.334	0.219	1.000	0.640
	N			5	5	3	5
Ground-dwelling spiders	*r*				0.051	<u>**1.000**</u>	<u>**0.918**</u>
	P				0.935	*	**0.028**
	N				5	**3**	**5**
Ground-dwelling beetles	*r*					0.500	0.112
	P					0.667	0.858
	N					3	5
Canopy-dwelling inverte-brates	*r*						<u>**1.000**</u>
	P						*
	N						**3**

* Where *r* = +1 or -1, P-*value* cannot be calculated by definition.

Appendix 19: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in reforested age class I Sitka spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Birds
Vascular plants	*r*	0.763	**0.975**	0.553	0.553	-0.148
	P	0.133	**0.005**	0.334	0.334	0.812
	N	5	**5**	5	5	5
Non-vascular plants	*r*		0.667	**0.947**	**0.921**	-0.296
	P		0.219	**0.014**	**0.026**	0.628
	N		5	**5**	**5**	5
Lower trunk epiphytes	*r*			0.410	0.410	-0.289
	P			0.493	0.493	0.638
	N			5	5	5
Ground-dwelling spiders	*r*				**0.947**	-0.148
	P				**0.014**	0.812
	N				**5**	5
Ground-dwelling beetles	*r*					-0.148
	P					0.812
	N					5

Appendix 20: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in reforested age class III Sitka spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Birds
Vascular plants	*r*	-0.395	0.154	0.359	0.263	<u>0.866</u>	-0.395
	P	0.511	0.805	0.553	0.669	0.333	0.511
	N	5	5	5	5	3	5
Non-vascular plants	*r*		0.205	-0.410	-0.289	-0.866	0.053
	P		0.741	0.493	0.637	0.333	0.933
	N		5	5	5	3	5
Lower trunk epiphytes	*r*			<u>0.800</u>	<u>0.872</u>	0.000	-0.205
	P			0.104	0.054	1.000	0.741
	N			5	5	3	5
Ground-dwelling spiders	*r*				**<u>0.975</u>**	<u>0.866</u>	-0.103
	P				**0.005**	0.333	0.870
	N				**5**	3	5
Ground-dwelling beetles	*r*					0.500	-0.237
	P					0.667	0.701
	N					3	5
Canopy-dwelling inverte-brates	*r*						<u>0.866</u>
	P						0.333
	N						3

Appendix 21: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in reforested age class II Sitka spruce plantations.

		Non-vascular plants	Lower trunk epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Birds
Vascular plants	*r*	0.200	0.300	-0.872	-0.474	0.205
	P	0.747	0.624	0.054	0.420	0.741
	N	5	5	5	5	5
Non-vascular plants	*r*		0.500	-0.616	0.632	-0.205
	P		0.391	0.269	0.252	0.741
	N		5	5	5	5
Lower trunk epiphytes	*r*			-0.410	0.158	-0.051
	P			0.493	0.800	0.935
	N			5	5	5
Ground-dwelling spiders	*r*				0.162	0.105
	P				0.794	0.866
	N				5	5
Ground-dwelling beetles	*r*					0.162
	P					0.794
	N					5

Appendix 22: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in reforested age class IV Sitka spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Birds
Vascular plants	*r*	0.600	0.154	-0.300	-0.600	0.000	0.500	0.447
	P	0.285	0.805	0.624	0.285	1.000	0.667	0.450
	N	5	5	5	5	5	3	5
Non-vascular plants	*r*		-0.667	-0.500	-0.200	-0.200	0.500	-0.447
	P		0.219	0.391	0.747	0.747	0.667	0.450
	N		5	5	5	5	3	5
Lower trunk epiphytes	*r*			0.462	-0.462	0.462	-0.866	**<u>0.918</u>**
	P			0.434	0.434	0.434	0.333	**0.028**
	N			5	5	5	3	**5**
Canopy epiphytes	*r*				0.100	0.100	-0.500	0.224
	P				0.873	0.873	0.667	0.718
	N				5	5	3	5
Ground-dwelling spiders	*r*					-0.800	0.500	-0.447
	P					0.104	0.667	0.450
	N					5	3	5
Ground-dwelling beetles	*r*						**-1.000**	0.224
	P						*	0.718
	N						**3**	5
Canopy-dwelling inverte-brates	*r*							[a]
	P							
	N							3

* Where *r* = -1, P-*value* cannot be calculated by definition.

[a]Cannot be computed, because forest-associated bird species richness is constant.

Appendix 23: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in mixed Norway spruce/Scots pine plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	-0.500	0.800	**0.975**	0.500	-0.500	**1.000**	0.600	**0.975**
	P	0.391	0.104	**0.005**	0.391	0.391	*	0.285	**0.005**
	N	5	5	**5**	5	5	**3**	5	**5**
Non-vascular plants	*r*		-0.700	-0.564	**-1.000**	0.500	-0.500	-0.400	-0.564
	P		0.188	0.322	*	0.391	0.667	0.505	0.322
	N		5	5	**5**	5	3	5	5
Lower trunk epiphytes	*r*			0.718	0.700	-0.400	0.500	**0.900**	0.718
	P			0.172	0.188	0.505	0.667	**0.037**	0.172
	N			5	5	5	3	**5**	5
Canopy epiphytes	*r*				0.564	-0.616	**1.000**	0.462	**1.000**
	P				0.322	0.269	*	0.434	*
	N				5	5	**3**	5	**5**
Ground-dwelling spiders	*r*					-0.500	0.500	0.400	0.564
	P					0.391	0.667	0.505	0.322
	N					5	3	5	5
Ground-dwelling beetles	*r*						-0.500	-0.300	-0.616
	P						0.667	0.624	0.269
	N						3	5	5
Canopy-dwelling inverte-brates	*r*							0.500	**1.000**
	P							0.667	*
	N							3	**3**
Lepido-ptera	*r*								0.462
	P								0.434
	N								5

* Where *r* = +1 or -1, P-*value* cannot be calculated by definition.

Appendix 24: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in pure Norway spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	0.070	0.584	0.073	0.282	-0.272	0.429	0.549	0.488
	P	0.847	0.076	0.852	0.430	0.447	0.397	0.100	0.153
	N	10	10	9	10	10	6	10	10
Non-vascular plants	*r*		**_0.762_**	0.453	-0.196	0.125	0.543	0.359	0.622
	P		**0.010**	0.221	0.588	0.731	0.266	0.309	0.055
	N		**10**	9	10	10	6	10	10
Lower trunk epiphytes	*r*			0.536	0.031	-0.180	_0.771_	0.517	0.526
	P			0.137	0.933	0.619	0.072	0.126	0.118
	N			9	10	10	6	10	10
Canopy epiphytes	*r*				-0.030	-0.590	_0.794_	0.017	0.078
	P				0.939	0.095	0.059	0.965	0.841
	N				9	9	6	9	9
Ground-dwelling spiders	*r*					-0.468	0.143	0.189	0.102
	P					0.173	0.787	0.601	0.778
	N					10	6	10	10
Ground-dwelling beetles	*r*						-0.406	-0.365	-0.025
	P						0.425	0.300	0.946
	N						6	10	10
Canopy-dwelling inverte-brates	*r*							0.029	0.058
	P							0.957	0.913
	N							6	6
Lepido-ptera	*r*								_**0.753**_
	P								**0.012**
	N								**10**

Appendix 25: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in mixed Norway spruce/oak plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling invertebrates	Lepido-ptera	Birds
Vascular plants	*r*	-0.600	0.580	-0.800	0.821	-0.500	**1.000**	-0.300	-0.300
	P	0.285	0.306	0.200	0.089	0.391	*	0.624	0.624
	N	5	5	4	5	5	**3**	5	5
Non-vascular plants	*r*		-0.158	0.400	-0.821	0.700	**-1.000**	0.500	-0.100
	P		0.800	0.600	0.089	0.188	*	0.391	0.873
	N		5	4	5	5	**3**	5	5
Lower trunk epiphytes	*r*			-0.316	0.649	0.158	**1.000**	-0.738	0.105
	P			0.684	0.236	0.800	*	0.155	0.866
	N			4	5	5	**3**	5	5
Canopy epiphytes	*r*				-0.400	**1.000**	-0.500	0.200	0.800
	P				0.600	*	0.667	0.800	0.200
	N				4	**4**	3	4	4
Ground-dwelling spiders	*r*					-0.359	**1.000**	-0.667	0.205
	P					0.553	*	0.219	0.741
	N					5	**3**	5	5
Ground-dwelling beetles	*r*						-0.500	0.100	0.600
	P						0.667	0.873	0.285
	N						3	5	5
Canopy-dwelling inverte-brates	*r*							**-1.000**	0.500
	P							*	0.667
	N							**3**	3
Lepido-ptera	*r*								-0.300
	P								0.624
	N								5

* Where *r* = +1 or -1, P-*value* cannot be calculated by definition.

Appendix 26: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in pure Norway spruce plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	0.361	0.542	-0.136	0.602	-0.482	0.600	0.395	0.129
	P	0.306	0.105	0.727	0.066	0.159	0.208	0.258	0.723
	N	10	10	9	10	10	6	10	10
Non-vascular plants	*r*		0.394	0.292	0.402	0.022	**<u>0.829</u>**	0.305	0.329
	P		0.260	0.446	0.249	0.953	**0.042**	0.392	0.353
	N		10	9	10	10	**6**	10	10
Lower trunk epiphytes	*r*			0.096	0.429	-0.608	0.696	0.367	0.307
	P			0.807	0.216	0.062	0.125	0.297	0.388
	N			9	10	10	6	10	10
Canopy epiphytes	*r*				-0.264	-0.043	0.441	-0.281	-0.240
	P				0.493	0.913	0.381	0.464	0.533
	N				9	9	6	9	9
Ground-dwelling spiders	*r*					-0.550	**<u>0.829</u>**	0.552	0.147
	P					0.099	**0.042**	0.098	0.686
	N					10	**6**	10	10
Ground-dwelling beetles	*r*						-0.522	-0.343	0.346
	P						0.288	0.333	0.328
	N						6	10	10
Canopy-dwelling inverte-brates	*r*							0.029	0.087
	P							0.957	0.870
	N							6	6
Lepido-ptera	*r*								0.257
	P								0.474
	N								10

Appendix 27: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in mixed Norway spruce/Scots pine plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	0.154	0.600	**_0.975_**	-0.051	-0.410	**_1.000_**	0.600	**_1.000_**
	P	0.805	0.285	**0.005**	0.935	0.493	*	0.285	*
	N	5	5	**5**	5	5	**3**	5	**5**
Non-vascular plants	*r*		-0.616	-0.026	-0.684	-0.132	0.500	-0.616	0.154
	P		0.269	0.966	0.203	0.833	0.667	0.269	0.805
	N		5	5	5	5	3	5	5
Lower trunk epiphytes	*r*			_0.718_	_0.718_	-0.359	0.500	**_1.000_**	0.600
	P			0.172	0.172	0.553	0.667	*	0.285
	N			5	5	5	3	**5**	5
Canopy epiphytes	*r*				0.079	-0.289	_0.866_	_0.718_	**_0.975_**
	P				0.900	0.637	0.333	0.172	**0.005**
	N				5	5	3	5	**5**
Ground-dwelling spiders	*r*					-0.289	-0.500	-0.718	-0.051
	P					0.637	0.667	0.172	0.935
	N					5	3	5	5
Ground-dwelling beetles	*r*						-0.500	-0.359	-0.410
	P						0.667	0.553	0.493
	N						3	5	5
Canopy-dwelling inverte-brates	*r*							0.500	**_1.000_**
	P							0.667	*
	N							3	**3**
Lepido-ptera	*r*								0.600
	P								0.285
	N								5

* Where *r* = 1, P-*value* cannot be calculated by definition.

Appendix 28: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in mixed Norway spruce/oak plantations. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	-0.103	0.224	-0.200	**<u>0.900</u>**	-0.821	-0.500	0.000	-0.205
	P	0.870	0.718	0.800	**0.037**	0.089	0.667	1.000	0.741
	N	5	5	4	**5**	5	3	5	5
Non-vascular plants	*r*		-0.574	-0.211	0.051	0.500	<u>-0.866</u>	**<u>0.975</u>**	0.289
	P		0.312	0.789	0.935	0.391	0.333	**0.005**	0.637
	N		5	4	5	5	3	**5**	5
Lower trunk epiphytes	*r*			0.316	0.447	-0.344	0.500	-0.447	-0.229
	P			0.684	0.450	0.571	0.667	0.450	0.710
	N			4	5	5	3	5	5
Canopy epiphytes	*r*				-0.200	-0.105	-0.500	0.000	<u>0.738</u>
	P				0.800	0.895	0.667	1.000	0.262
	N				4	4	3	4	4
Ground-dwelling spiders	*r*					-0.667	-0.500	0.200	-0.103
	P					0.219	0.667	0.747	0.870
	N					5	3	5	5
Ground-dwelling beetles	*r*						0.500	0.359	-0.079
	P						0.667	0.553	0.900
	N						3	5	5
Canopy-dwelling inverte-brates	*r*							**-1.000**	**-1.000**
	P							*	*
	N							**3**	**3**
Lepido-ptera	*r*								0.410
	P								0.493
	N								5

* Where *r* = -1, P-*value* cannot be calculated by definition.

Appendix 29: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in oak woodlands. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	**0.700**	0.524	0.643	0.182	**0.732**	-0.058	-0.100	-0.330
	P	**0.024**	0.120	0.119	0.614	**0.016**	0.913	0.873	0.351
	N	**10**	10	7	10	**10**	6	5	10
Non-vascular plants	*r*		**0.657**	0.342	0.524	**0.746**	-0.015	0.359	0.082
	P		**0.039**	0.452	0.120	**0.013**	0.978	0.553	0.822
	N		**10**	7	10	**10**	6	5	10
Lower trunk epiphytes	*r*			0.324	0.395	**0.759**	-0.441	**1.000**	0.104
	P			0.478	0.258	**0.011**	0.381	*	0.775
	N			7	10	**10**	6	**5**	10
Canopy epiphytes	*r*				0.286	**0.775**	0.000	0.000	0.185
	P				0.535	**0.041**	1.000	1.000	0.691
	N				7	**7**	4	4	7
Ground-dwelling spiders	*r*					0.413	-0.638	**0.900**	0.521
	P					0.235	0.173	**0.037**	0.123
	N					10	6	**5**	10
Ground-dwelling beetles	*r*						-0.265	0.500	0.082
	P						0.612	0.391	0.822
	N						6	5	10
Canopy-dwelling inverte-brates	*r*							0.500	-0.266
	P							0.667	0.610
	N							3	6
Lepido-ptera	*r*								0.205
	P								0.741
	N								5

* Where *r* = 1, P-*value* cannot be calculated by definition.

Appendix 30: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of species richness between investigated taxonomic groups sampled in ash woodlands. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling inverte-brates	Lepido-ptera	Birds
Vascular plants	*r*	**0.699**	0.164	-0.167	-0.067	0.455	-0.486	<u>**1.000**</u>	-0.177
	P	**0.024**	0.651	0.693	0.854	0.187	0.329	*	0.624
	N	**10**	10	8	10	10	6	**5**	10
Non-vascular plants	*r*		0.535	0.095	-0.327	0.340	-0.143	<u>**0.900**</u>	-0.585
	P		0.111	0.823	0.356	0.336	0.787	**0.037**	0.076
	N		10	8	10	10	6	**5**	10
Lower trunk epiphytes	*r*			0.000	-0.293	0.261	0.600	0.500	**-0.786**
	P			1.000	0.412	0.467	0.208	0.391	**0.007**
	N			8	10	10	6	5	**10**
Canopy epiphytes	*r*				0.157	-0.048	-0.400	**-1.000**	-0.279
	P				0.711	0.911	0.600	*	0.503
	N				8	8	4	**3**	8
Ground-dwelling spiders	*r*					0.226	0.143	-0.600	0.360
	P					0.531	0.787	0.285	0.307
	N					10	6	5	10
Ground-dwelling beetles	*r*						0.314	-0.300	-0.222
	P						0.544	0.624	0.538
	N						6	5	10
Canopy-dwelling inverte-brates	*r*							-0.100	-0.370
	P							0.873	0.470
	N							5	6
Lepido-ptera	*r*								-0.369
	P								0.541
	N								5

* Where *r* = +1 or -1, P-*value* cannot be calculated by definition.

Appendix 31: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in native oak woodlands. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling invertebrates	Lepido-ptera	Birds
Vascular plants	*r*	0.157	0.116	0.393	-0.492	0.201	**<u>0.868</u>**	0.000	-0.041
	P	0.664	0.750	0.383	0.148	0.577	**0.025**	1.000	0.911
	N	10	10	7	10	10	**6**	5	10
Non-vascular plants	*r*		0.327	-0.482	0.309	0.201	0.088	<u>0.738</u>	-0.212
	P		0.356	0.274	0.385	0.578	0.868	0.155	0.556
	N		10	7	10	10	6	5	10
Lower trunk epiphytes	*r*			0.234	-0.143	0.375	0.116	-0.300	0.216
	P			0.613	0.693	0.286	0.827	0.624	0.550
	N			7	10	10	6	5	10
Canopy epiphytes	*r*				0.273	<u>0.748</u>	<u>0.800</u>	-0.400	0.412
	P				0.554	0.053	0.200	0.600	0.359
	N				7	7	4	4	7
Ground-dwelling spiders	*r*					0.108	0.015	0.580	0.006
	P					0.767	0.978	0.306	0.986
	N					10	6	5	10
Ground-dwelling beetles	*r*						0.118	-0.474	0.146
	P						0.824	0.420	0.687
	N						6	5	10
Canopy-dwelling invertebrates	*r*							-0.500	0.015
	P							0.667	0.978
	N							3	6
Lepido-ptera	*r*								-0.158
	P								0.800
	N								5

Appendix 32: Spearman's correlation coefficient (*r*), level of significance (P) and sample size figures (*N*) for pairwise comparisons of forest-associated species richness between investigated taxonomic groups sampled in native ash woodlands. Significant results (P < 0.05) are highlighted in bold. Underlined correlation coefficients (≥ 0.7) indicate taxonomic pairs which might be considered as surrogates relevant for biodiversity surveys (Heino, 2010).

		Non-vascular plants	Lower trunk epiphytes	Canopy epiphytes	Ground-dwelling spiders	Ground-dwelling beetles	Canopy-dwelling invertebrates	Lepido-ptera	Birds
Vascular plants	*r*	0.390	-0.201	0.060	-0.222	0.486	-0.377	<u>0.800</u>	-0.293
	P	0.266	0.577	0.887	0.538	0.154	0.461	0.104	0.411
	N	10	10	8	10	10	6	5	10
Non-vascular plants	*r*		-0.475	-0.175	-0.167	**<u>0.752</u>**	0.176	<u>0.872</u>	-0.468
	P		0.165	0.679	0.644	**0.012**	0.738	0.054	0.172
	N		10	8	10	**10**	6	5	10
Lower trunk epiphytes	*r*			0.299	0.203	-0.361	0.382	-0.600	-0.214
	P			0.471	0.574	0.305	0.454	0.285	0.554
	N			8	10	10	6	5	10
Canopy epiphytes	*r*				0.614	0.062	-0.105	**-1.000**	0.109
	P				0.106	0.885	0.895	*	0.797
	N				8	8	4	**3**	8
Ground-dwelling spiders	*r*					-0.082	0.145	-0.700	0.264
	P					0.822	0.784	0.188	0.461
	N					10	6	5	10
Ground-dwelling beetles	*r*						-0.339	<u>0.821</u>	-0.215
	P						0.511	0.089	0.551
	N						6	5	10
Canopy-dwelling invertebrates	*r*							0.154	-0.376
	P							0.805	0.463
	N							5	6
Lepido-ptera	*r*								-0.211
	P								0.734
	N								5

* Where *r* = -1, P-*value* cannot be calculated by definition.

Appendix 33: PLANFORBIO Extension Day Programme.

PLANFORBIO Extension Day

WEDNESDAY 31 MARCH 2010

Environmental Research Institute (Rm. 1.28),
University College Cork,
Lee Road, Cork.

The aim of this meeting is to share some of the findings of the FORESTBIO and HEN HARRIER research projects as they relate to biodiversity of plantation forests and to provide an opportunity for researchers and practitioners to gain improved understanding of forest biodiversity.

PROGRAMME

09:30   Welcome
            John O'Halloran

09:35   *Approvals and licences – biodiversity implications*
            Speaker: Orla Fahy, Forest Service

10:00   Coillte's work on biodiversity – challenges and opportunities
            Speaker: Pat Neville, Coillte Teoranta

10:25   **Coffee break**

10:45   *PLANFORBIO Research Programme*
            John O'Halloran

10:55   *Forestry and plant diversity*
            Speaker: Linda Coote, Trinity College Dublin

11:15   *Invertebrate biodiversity in various planted forest types*
            Speaker: Rebecca Martin, University College Cork

11:35   *Bird assemblages of native and plantation forests: importance of vegetation structure and management recommendations for bird conservation*
            Speaker: Oisín Sweeney, University College Cork

11.55   *Hen Harriers and forestry in Ireland*
            Speaker: Mark Wilson, University College Cork

12:15   *Round up*
            Chair: John O'Halloran

12.30   **Lunch break**

13.00   Field visit to Garrynagree, Co. Waterford (Norway Spruce/Oak Mix)
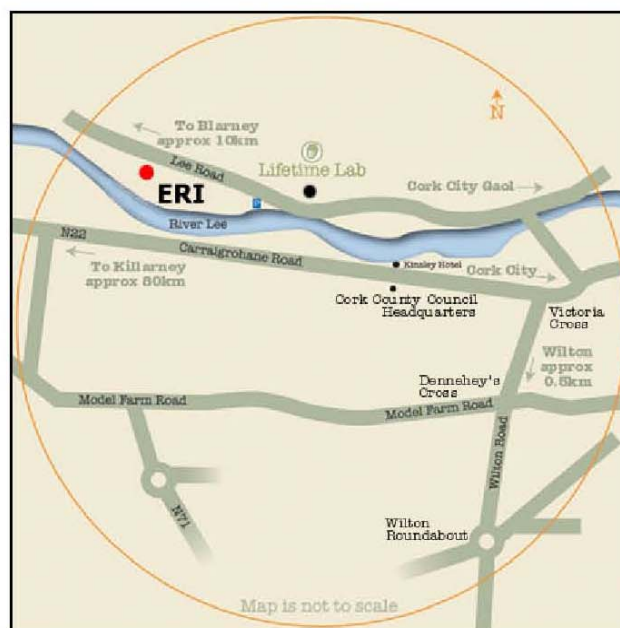   Leaders: Linda Coote & Mark Wilson

VENUE

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Directions by Road

From the City Centre: travel in westerly direction along Western Road past University College Cork and turn right at the traffic lights outside AIB bank. Cross over Thomas Davis Bridge and turn left. ERI is approx. 1 km from the bridge on the left hand side of the road.

From West Cork: travel in easterly direction along Carrigrohane road, pass Kingsley hotel on left and County Hall on right. Continue towards city centre and take left turn at traffic lights outside AIB bank at the beginning of Western Road. Cross over Thomas Davis Bridge and turn left. ERI is approx. 1 km from the bridge on the left hand side of the road.

From South Ring Road – Take Wilton exit at the Sarsfield Road Roundabout, continue to Wilton Roundabout and take 2nd exit. Pass straight through Dennehys Cross and Victoria Cross towards City Centre. Take left turn at traffic lights outside AIB bank at the beginning of Western Road. Cross over Thomas Davis Bridge and turn left. ERI is approx. 1km from the bridge on the left hand side of the road.

Directions by Bus

Take Number 8 bus in Bishopstown direction from Patrick Street (buses travel every 10-15 minutes). Get off at end of Western Road (across from AIB bank), cross road, walk past Sacred Heart Church and over Thomas Davis Bridge. Turn left after crossing bridge and ERI is approx. 1 km along road on left hand side (total walking time from bus stop – approx. 15 minutes).