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Commercial spruce plantations support a limited canopy fauna: Evidence from a multi taxa comparison of native and plantation forests

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ABSTRACT

Globally, the total area of plantation forest is increasing as deforestation and fragmentation of native forest continues. In some countries commercial plantations make up more than half of the total forested land. Internationally, there is growing emphasis on forestry policy for plantations to deliver biodiversity and ecosystem services. In Ireland, native forest now comprises just 1% of total land cover while non-native spruce forest makes up 60% of the plantation estate and approximately 6% of the total land cover. The majority of plantation invertebrate biodiversity assessments focus on ground-dwelling species and consequently a good understanding exists for these guilds, especially ground-active spiders and beetles. Using a technique of insecticide fogging, we examine the less well understood component of forest systems, the canopy fauna (Coleoptera, Araneae, Diptera and Hemiptera), in Irish spruce plantations (Sitka and Norway) and compare the assemblage composition, richness and abundance to that of remnant native forest (ash and oak). In addition, we examine the potential for accumulation of forest species in second rotation spruce plantations and identify indicator species for each forest type.

From 30 sampled canopies, we recorded 1155 beetles and 1340 spiders from 144 species and over 142 000 Diptera and Hemiptera from 71 families. For all taxa, canopy assemblages of native forests were significantly different from closed-canopy plantation forests. No indicators for plantation forest were identified; those identified for native forest included species from multiple feeding guilds. Plantations supported approximately half the number of beetle species and half the number of Diptera and Hemiptera families recorded in native forests. Although assemblages in Norway spruce plantations were very different to those of native forest, they had consistently higher richness than Sitka spruce plantations. No differences in richness or abundance were found between first rotation and second rotation Sitka spruce plantations. Compared to other forest types, Sitka spruce plantations contained far greater total abundance of invertebrates, due to vast numbers of aphids and midges. Under current management, Sitka spruce plantations provide limited benefit to the canopy fauna typical of native forests in either first or second rotations. The large aphid populations may provide abundant food for insectivores but may also lead to reduced crop production through defoliation. Progressive forestry management should attempt to diversify the plantation canopy fauna, which may also increase productivity and resilience to pest species.

1. Introduction

Global deforestation continues to fragment and reduce natural forest as afforestation of commercial plantations expands (FAO, 2010). Globally, over 29% of land area is forest, of which 3% is plantation and under current trends this is expected to account for 21% by 2100 (Brockerhoff et al., 2013). At present, some countries have much greater proportions of forested land comprising plantations; for example, Ireland 89%, UK 69%, India 51% and Japan 44% (FAO, 2001; Forest Europe et al., 2011). As the area of plantations increases, so does the importance of management to ensure the needs of regional biodiversity are met. Concerns are often raised about the lack of biodiversity associated with plantation forest (Hartley, 2002; Brockerhoff et al., 2008), and when compared to natural forest, plantations can lack specialist forest species (Helle, 1986; Niemela, 1993; Finch, 2005). In areas where afforestation has occurred on non-forest habitat, as is often the case in Western Europe, plantations may also have negative effects on the biodiversity of open habitats (Butterfield et al., 1995; Brockerhoff et al.,

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2008). However, recent studies have shown that in some situations plantation landscapes can provide conservation benefits for regionally important species (Berndt et al., 2008; Pawson et al., 2008; Pedley et al., 2013). To understand and optimise plantation landscapes, there is a pressing need to examine which aspects of forest biodiversity are supported in plantation habitats.

Forest canopies contain a large proportion of the total diversity of organisms on Earth (Lowman and Wittman, 1996), with a major part of this diversity attributed to invertebrate species. In fact, in the tropics it has been suggested that there are twice as many arboreal forest species than there are ground-dwelling ones (Erwin, 1982). Although the canopy in temperate forests may be less species diverse than in tropical forest, many species utilise temperate forest canopies for at least part of their life cycle (Ulyshen, 2011). Invertebrates are an important component of all forest ecosystems, where they have roles in food-webs and nutrient cycling, and as prey for other invertebrates, small mammals and birds (Askenmo et al., 1977; Wilson et al., 1999; Halaj and Wise, 2001). They are also used to monitor forest change and management (Schowalter, 1995; Ji et al., 2013). Arthropods in particular are strongly influenced by the compositional and structural dynamics of their immediate habitats and the surrounding landscape, and respond quickly to brief, sudden changes in environmental conditions (Robinson, 1981; Marc et al., 1999; Rainio and Niemela, 2003).

The majority of invertebrate research comparing plantation to native forests has been carried out on the non-canopy component, predominately through pitfall trapping of ground invertebrates. Few studies have sampled both the canopy fauna of plantations and native forests in the same landscape. Those studies that have compared canopies of native and plantation forest include short rotation *Eucalyptus* plantations in Australia (Cunningham et al., 2005), tropical hardwood plantations in Thailand (Tangmitcharoen et al., 2006) and coniferous plantations in North America (Schowalter, 1995). What is lacking is an assessment of the canopy invertebrates of non-native plantations in Europe, focusing on what the closed canopy of these commercial forests provide for the regional forest biota of older native forest. It has been shown that the structurally complex canopies of old forests support more species than the relatively simple canopies of young forests (reviewed in Ulyshen, 2011). Similarly, it is likely that commercially mature plantations, which are relatively young compared with remnant old-growth forest, also support less species. However, with increased amounts of plantation forest and continued deforestation of native forest, there is a need to address the degree to which commercial forests support the canopy biodiversity of native forests (Schowalter, 1995). Identifying gaps in biodiversity protection will contribute to evidence-based conservation (Sutherland et al., 2004), helping to meet national and international objectives for conservation (EPA, 2007; EC, 2011).

In this study, we examine the canopy invertebrates (Coleoptera, Araneae, Diptera and Hemiptera) of remnant patches of native forest in Ireland and non-native spruce plantations. Native forests in Ireland, like elsewhere in Western Europe, have undergone severe reduction and fragmentation. Anthropogenic land change has severely impacted Ireland's natural biodiversity; remaining patches of native forest can now only be termed 'semi-natural' having been utilised over centuries for wood fuel and grazing (Peterken, 1996). Only 1% of the surface area of Ireland is comprised of natural forest, and most remaining patches are small (75% are less than 5 ha) and isolated in a landscape of intensive agriculture (Cross, 2012). Commercial conifer plantations form a large part of the total forested land in Ireland; approximately 10% of the surface area of Ireland has been afforested, mainly through the planting of non-native conifers. Forest expansion planned over the next two decades will see the total reach 15% (COFORD Council, 2009).

Given the extent of land that will be under plantation in the coming years, it is important to understand the biodiversity in afforested and also reforested habitat. As plantations often occur as mosaics of different aged stands, it is likely reforested stands will be colonised by species inhabiting adjacent closed-canopy habitat through metapopulation dynamics (Hanski, 1999). In addition, if permanent closed-canopy habitat is maintained within the local mosaic there is potential for accumulation of forest specialist through successive rotations. To explore the biodiversity potential of plantation forests in Ireland, two types of remnant native forest (ash and oak) were sampled as reference points with which to compare the canopy invertebrates of differing types of non-native plantation forests, first and second rotation Sitka spruce and first rotation Norway spruce. We used a technique of insecticide canopy fogging to sample invertebrates from the five forest types to answer the following questions; (1) Do plantations support canopy invertebrate assemblages similar to native forests and do patterns of species richness, abundance and composition correspond for all taxa? (2) Does the canopy fauna in second rotations plantation change and do these successive rotations support increasing numbers of forest specialists than first rotations?

2. Methods

2.1. Study sites

Thirty closed-canopy forests, comprising five types, were sampled in Ireland (Fig. 1); six ash (*Fraxinus excelsior*) dominated

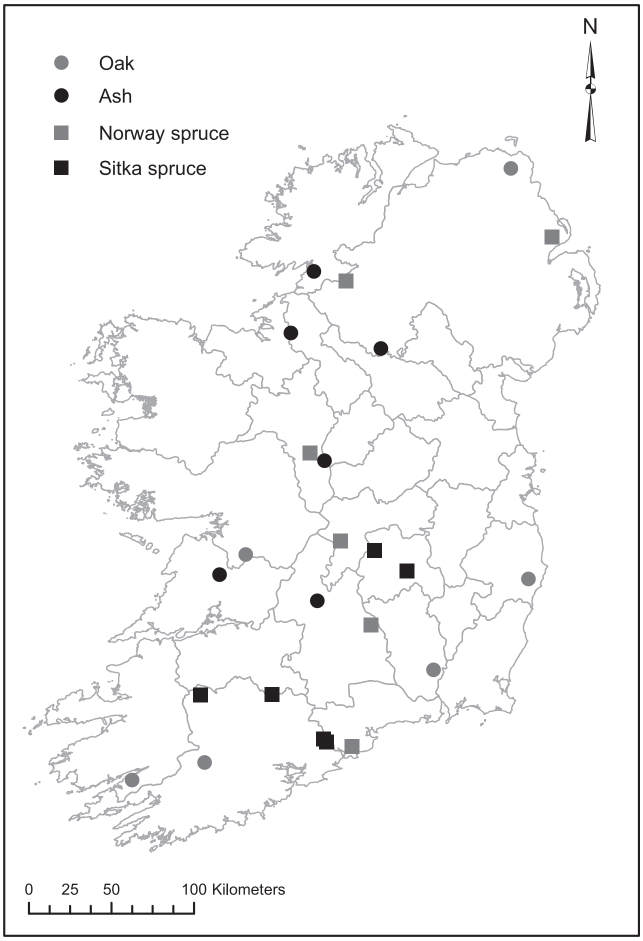

Fig. 1. The distribution of sampled forest sites across Ireland.

semi-natural woodlands (hereafter referred to as ash forest), six oak (*Quercus petraea*) dominated semi-natural woodlands (hereafter referred to as oak forest), six closed canopy (20–50 years old) first rotation Sitka spruce (*Picea sitchensis*) plantations (hereafter referred to as afforested Sitka plantations), six second rotation Sitka spruce plantations (hereafter referred to as reforested Sitka plantations) and six Norway spruce (*Picea abies*) first rotation plantations. Forest sites were matched as closely as possible for soil type, altitude and tree density (mean basal area per m^2). All stands were a minimum of 6 ha in size and 100 m in width.

Ash and oak forests were selected as they are the most common native tree encountered in Irish semi-natural forests, 22% and 18% respectively (Higgins et al., 2004). Native forest types comprised a mix of tree species, i.e. oak-dominated forests comprise oak, birch and holly, while ash-dominated forests comprised ash, oak and hazel. We defined natural forests as broadleaved forests containing tree species that are native, as specified in Kelly (1991), that are not currently intensively managed, and have been continuously present on historical maps dating from the 1830s–1840s (the oldest available for Ireland). In the case of natural forests in Northern Ireland, forests were chosen based on their inclusion in a data base of ancient and long-established woodland (The Woodland Trust, 2007). Both ash and oak forests were therefore at least 150 years old.

Norway and Sitka spruce were chosen for the study as they are two of the dominant species in the forest estate in Ireland, with Sitka comprising approximately 60% and Norway spruce 4% (Forest Service, 2007). Sampled plantations ranged from mid rotation 20–30 year old closed-canopy stands to 60 year old commercially mature stands. Although differences in age between surveyed natural and plantation forest exist it is not possible to sample older stands due to the commercial felling regime of Irish plantations. Therefore, the sampled sites represent a range of closed-canopy forests that is available to the invertebrate community.

2.2. Invertebrate sampling

Sampling was conducted once at each site using a thermal fogging method to capture the invertebrate component of the forest canopy. All sampling was carried out between April and August in 2008 and 2009. In 2008, three ash and three oak forests, and all Norway spruce plantations were sampled. During 2009, a further three ash and oak forests were sampled along with all Sitka spruce plantations. Due to logistical and meteorological reasons it was not possible to sample all sites in a single year.

A petrol-driven fogging machine (SwingFog SN50-PE, SwingTec Ltd., Germany) was used with a natural pyrethroid (Pybuthrin 33). Pyrethroid insecticide was chosen as it is non-persistent in the environment, with no phytotoxic effects and the levels used by this method are not harmful to mammals (Straw et al., 1996). In each stand, a fogging plot was established in an area that represented the site as a whole and that was at least 50 m 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 that corresponded to the forest type being sampled. Sampling of the canopy was not limited to the target tree however, as inevitably the canopy of surrounding trees was interspersed with the target canopy and this was also sampled; this may have included understory species in the native forests.

Prior to fogging, 16 plastic sheets, with a combined area of 24 m^2, were suspended 1 m above the ground; this sized area is known to adequately sample canopy invertebrates (Stork and Hammond, 1997; Guilbert, 1998). Suspended sheets are more suitable than ground sheets, as they reduce the risk of contamination by ‘tourist’ insects from the ground. Sampling sheets were arranged around the central tree on the eight cardinal and ordinal compass bearings, separated by 0.5 m from each other and all trees. Each canopy was fogged until fully covered in insecticide (typically 6–9 min duration). Canopy fogging was only carried out in dry, calm conditions (wind-speeds of less than 8 km h^{-1}) and after a dry, calm night to minimise fog dispersion. Sample sheets remained in place for 3 h after fogging to adequately collect the falling invertebrates (Stork and Hammond, 1997). Catches from the 16 sample sheets from one site were pooled. Samples were collected *in situ* using soft paintbrushes to transfer invertebrates into bottles containing 70% alcohol.

Adult spiders and beetles were identified to species level following relevant taxonomic keys (see Appendix A for details). Beetle and spider species found were assigned to categories based on their known feeding guild, rarity and habitat preferences (Appendix A). As there are currently no comprehensive designated species lists for the Irish invertebrate fauna, UK designations were applied. Species-level identification of all individuals was not possible due to time taken to identify the large numbers of specimens sampled, therefore, in order to assess other dominant invertebrate groups, adults from the orders Diptera and Hemiptera were identified to family or super-family level.

2.3. Analysis

Abundance was measured by the numbers of individuals per canopy plot. Sampling effort and species richness were compared among forest types with sample-based rarefaction using the rarefy function in the vegan package (Oksanen et al., 2010) in the statistical software R (R Development Core Team, 2012).

Indicator species analysis was conducted to determine species affinity to forest types for the spider and beetle assemblages using the function multipatt in the R package indicspeices (De Caceres et al., 2010) to calculate indicator values (Dufrene and Legendre, 1997), and permutation (999) to test the significance of the relationships. To avoid selecting species with weak indicator capacity, we only considered those species where $P \leqslant 0.01$.

For each taxonomic group, assemblage composition across the forest types was examined using non-Metric Multidimensional Scaling (NMDS), performed on a matrix of Bray-Curtis dissimilarities of abundance data (square root transformed and Wisconsin double standardization) using the vegan package (Oksanen et al., 2010) in R. Centroids for each forest type were plotted to visualise assemblage differences. Stress values were examined to assess the accuracy in representation: <0.05 excellent; <0.1 good; <0.2 potentially useful; >0.3 close to arbitrary (Clarke and Warwick, 1994).

To examine the stability of sampled communities between the two sampling years, and therefore verify differences in composition were not merely a factor of inter-annual weather variation, we separately tested the ordination placement of ash and oak sites over the 2 years with *t*-test. NMDS axis one and two scores for ash and oak indicated stable invertebrate compositions between years (*t* tests: $P > 0.05$). Therefore, the large differences between forest types sampled in subsequent years in the ordinations are unlikely to be an artefact of inter-annual variation in weather.

To test the difference in community composition between forest types for each taxa we used the R package mvabund (Wang et al., 2012), which allows hypothesis testing by multivariate implementation of generalised linear models. Unlike dissimilarity-matrix-based methods, mvabund does not confound location with dispersion effects (a change in the mean–variance relationship), which can lead to misleading results and inflation of type 1 and 2 errors (Warton et al., 2012). Using likelihood-ratio-tests (LR) in the summary.manyglm function, we tested for significant differences between native (ash and oak combined) and plantation forests.

Species richness, family richness and abundance were compared among forest types using generalised linear models (GLMs) in R. The appropriate error term (normal, Poisson, negative binomial, quasipoisson) for each analysis was selected by comparing Akaike's Information Criterion (AIC) and examining the ratio of deviance/residual degrees of freedom. Differences among forest type means were examined by Tukey pairwise comparisons using the glht function in the multcomp package (Hothorn et al., 2008); pairwise comparisons are calculated using single-step *p*-value adjustments for multiple comparison tests. GLMs used sampling year as a covariate but was non-significant in all models ($P > 0.05$). Spatial autocorrelation of GLM residuals was examined by Moran's I in the ape package v.3.0-6 (Paradis et al., 2004) in R. In all instances, Moran's I was not significant ($P > 0.05$).

To test for spatial autocorrelation in the community data, NMDS ordinations were first carried out for the combined spider and beetle species data and separately for the combined family level data (Diptera and Hemiptera). Axis scores for the two separate ordinations were tested against latitude and longitude with Mantel tests (Legendre and Legendre, 1998) using the mantel.rtest function in the ade4 package (Dray and Dufour, 2007) in R. For both species level and family level data, spatial autocorrelation was not significant on either axis one or two ($P > 0.05$).

3. Results

We identified 1155 beetles and 1340 spiders from 30 canopy fogged forests to species level. In total, 144 species were recorded, of which 42 (18 spiders and 24 beetles) were unique to plantation forests and 59 (13 spiders and 46 beetles) were unique to native ash and oak forests. Additionally, we identified to family level over 142 000 Diptera and Hemiptera from 71 families. Insecticide fogging effectively sampled the canopy invertebrates in the five forest types (Fig. 2). Significant differences in assemblage composition were identified for all sampled groups, although differences in the spider assemblage were less pronounced than for the other groups (Fig. 3).

3.1. Beetles

Significant differences in beetle assemblage composition were recorded between forest types (Deviance = 312.6, $P < 0.001$); compared to native forests all plantation forest types had significantly different species compositions ($P < 0.001$). NMDS showed strong differences in assemblage composition, with ash and oak forests separated from plantation sites and distinct from each other (Fig. 3a). The three plantation types in the ordination have much larger polygons (standard deviation of centroids) than the two native forest types, indicating greater assemblage variation between replicate sites of the same type.

Both ash and oak forests contained significantly greater species richness of beetles than any of the plantation types, and this pattern was also consistent for forest specialist species (Fig. 4, Appendix C). The native forest samples also contained a greater abundance of beetles than plantations; the beetle abundance in both ash and oak was significantly greater than afforested and reforested plantations (Fig. 5, Appendix C). The abundance of forest specialists was also highest in ash and oak but only oak had significantly greater abundance than afforested and reforested Sitka spruce plantations. Although Norway spruce plantations contained significantly fewer forest specialist species than ash and oak, the abundance of forest specialists was not significantly different from native forests.

Indicator species analysis identified indicators for ash and oak forests only (Table 1). For ash forest, a mixture of herbivores, detritivores and mycetophagous species, but no predatory species, were found to be indicators. The three species with the highest ash indicator values are all associated with broadleaf forest (Appendix A) and included two weevils and one Nationally Notable B (UK designation) species, the false darkling beetle *Orchesia (Clinocara) minor*. Indicators in oak forest included carnivores, herbivores and mycetophagous species. Again the three species with the highest indicator values were associated with broadleaf forests and the fourth was associated with deadwood.

The species richness of different beetle feeding guilds was also significantly different between forest types. Richness of detritivore and mycetophagous species was significantly greater in ash forest than in Sitka spruce and herbivore species richness was significantly greater in ash than any plantation forest (Fig. 6, Appendix D). Species richness of herbivores was also significantly greater in oak forests than in any plantation, whereas mycetophagous species richness was only significantly lower in Sitka spruce forests.

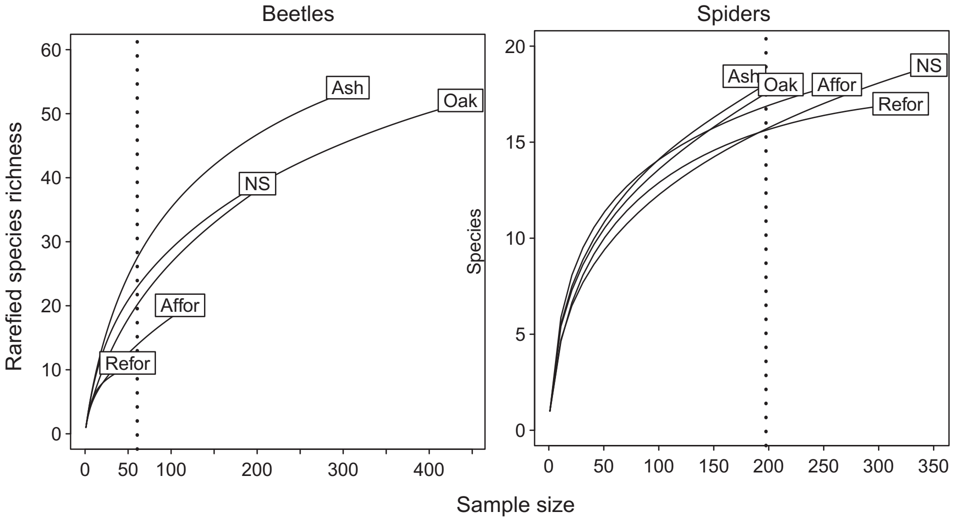

Fig. 2. Sample-based rarefaction curves of the five forest types, sampled with canopy fogging for beetles and spiders. Forest types are Ash = native ash, Oak = native oak, NS = Norway spruce plantations, Affor = first rotation Sitka spruce plantations and Refor = second rotation Sitka spruce plantations. Dotted line indicates the smallest sampled abundance of the five forest groups (beetles, first rotation Sitka spruce $n = 60$; spiders, ash $n = 197$). See Appendix B for expanded rarefaction plots showing confidence intervals.

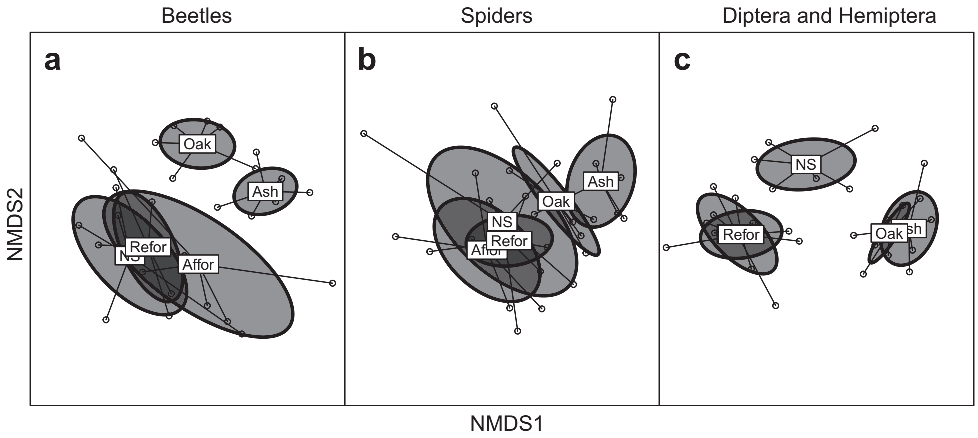

Fig. 3. Non-Metric Multidimensional Scaling (NMDS) ordination comparing assemblage composition of (a) beetles (stress = 0.22), (b) spiders (stress = 0.19) and (c) family level Diptera and Hemiptera (stress = 0.13) assemblages among five forest types. Points are canopy fogged sites with lines connecting to habitat centroids (see Fig. 2 for definition of forest types). Polygons represent standard deviation of forest type centroids.

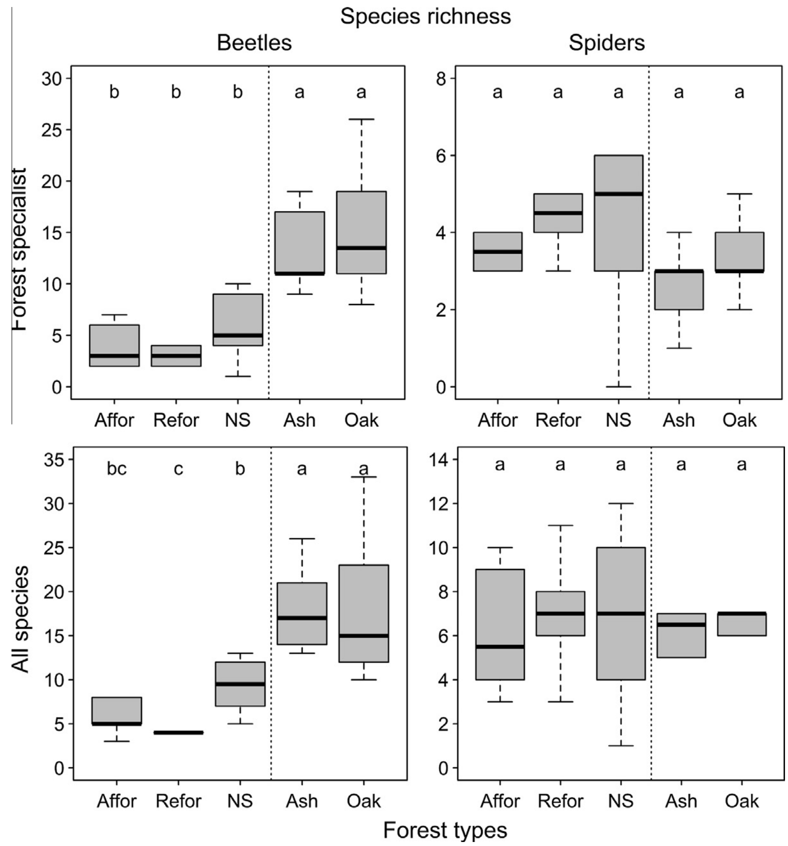

Fig. 4. Species richness of spiders and beetles shown separately for forest species and all sampled species. Results of generalised linear models comparing forest types are presented; means that share a superscript (homogenous sub-sets, a–c, ranked highest to lowest) do not differ significantly (Tukey pairwise comparisons $P < 0.05$). χ^2, F and p-values can be found in Appendix C. Dotted line separates native from plantation forest, see Fig. 2 for definition of forest types.

3.2. Spiders

Although differences were not as strong as those reported for beetles, spider assemblage composition was significantly different between forest types (Deviance = 220.9, $P = 0.003$), and again all plantation forest types were significantly different to native forest assemblages ($P < 0.001$). The NMDS plot shows a similar pattern of site centroids to that shown for beetles, however, the separation between centroid polygons is not as distinct, indicating closer assemblage similarities (Fig. 3b). Ash and oak forests separate from the three plantation types and there is substantial overlap between the plantation forests. The dominant species in all three plantations types was *Pelecopsis nemoralis*, while in ash and oak forests *Theridion pallens* and *Tetragnatha montana* were the dominant species.

No difference in spider species richness or forest specialist species richness was found between the five forest types (Fig. 4). The same was also true for spider abundance and forest specialist abundance (Fig. 5). Large variations in richness and abundance were found within forest replicates, especially for plantation sites

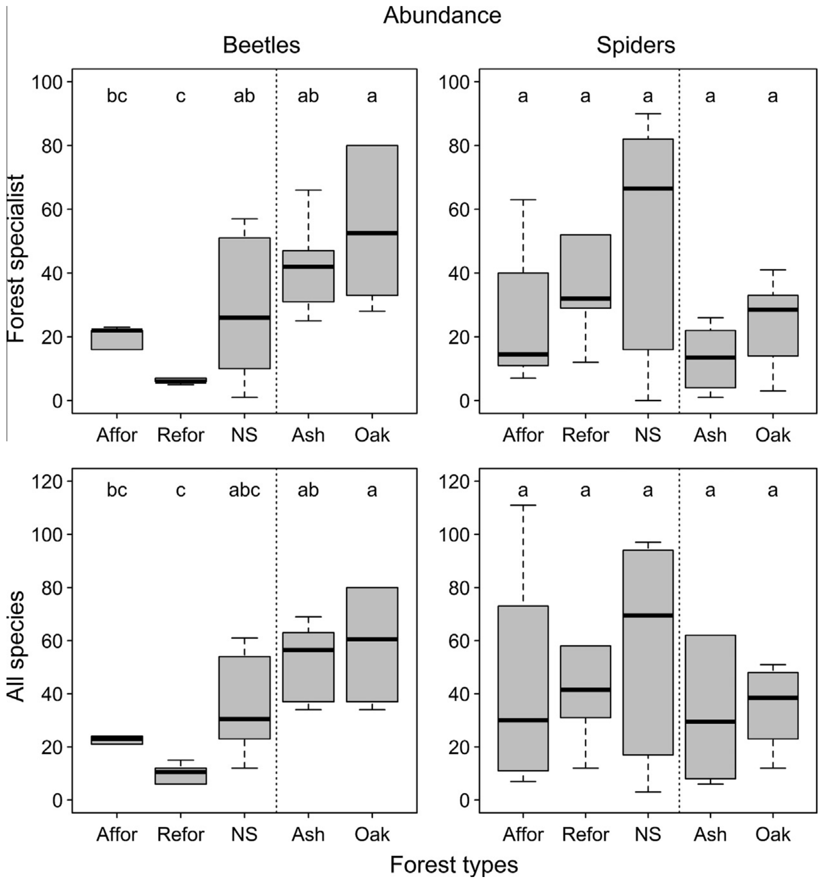

Fig. 5. Abundance of spiders and beetles shown separately for forest species and all sampled species. Results of generalised linear models comparing forest types are presented; means that share a superscript (homogenous sub-sets, a–c, ranked highest to lowest) do not differ significantly (Tukey pairwise comparisons $P < 0.05$). χ^2, F and p-values can be found in Appendix C. Dotted line separates native from plantation, see Fig. 2 for definition of forest types.

Table 1
Beetle and spider indicator species identified from the sampled forests. Asterisk indicates a species with a UK designation.

Forest type	Taxa	Family	Species	Feeding guild	Indicator value	*P*-value
Ash	Coleoptera	Curculionidae	*Acalles (Acalles) misellus*	Herbivorous	0.974	<0.001
	Coleoptera	Melandryidae	*Orchesia (Clinocara) minor*	Mycetophagous	0.913	<0.001
	Coleoptera	Curculionidae	*Polydrusus (Eustolus) pterygomalis*	Herbivorous	0.816	0.002
	Coleoptera	Elateridae	*Athous (Athous) haemorrhoidalis*	Herbivorous	0.803	0.002
	Coleoptera	Coccinellidae	*Halyzia sedecimguttata*	Mycetophagous	0.77	0.008
	Araneae	Tetragnathidae	*Tetragnatha montana*	Orb web	0.769	0.005
Oak	Coleoptera	Salpingidae	*Salpingus ruficollis*	Carnivorous	0.833	<0.001
	Coleoptera	Curculionidae	*Polydrusus (Polydrusus) tereticollis*	Herbivorous	0.816	0.003
	Coleoptera	Tenebrionidae	*Nalassus laevioctostriatus*	Herbivorous	0.816	0.006
	Coleoptera	Ciidae	*Cis boleti*	Mycetophagous	0.745	0.010

where spider abundance was an order of magnitude different in afforested Sitka spruce replicates.

Indicator species analysis identified one spider species, *T. montana*, as an indicator of ash forests. This common orb web spider was the most abundant spider species recorded in ash forest and recorded only once from plantations forests.

No active hunting spiders were record in Sitka spruce plantations in either rotation (Fig. 6). Ash forests had the highest mean species richness of active hunters and orb web spinners. Species richness of sheet web spinners was greatest in plantation forest, but only reforested Sitka spruce plantation had significantly greater richness than ash forests (Fig. 6, Appendix D).

3.3. Diptera and Hemiptera

Assemblage composition of Diptera and Hemiptera (family level data) was also significantly different between the five forest types (Deviance = 718.3, $P < 0.001$), and all plantation forest types had significantly different compositions compared to both native forests combined ($P < 0.001$). Again, the native ash and oak forests were separated from the plantation forests in the ordination (Fig. 3c). However, the family level data also separates Norway spruce plantations with no overlap among any other forest types. Afforested and reforested Sitka spruce assemblages are almost indistinguishable in the ordination, as are the two native forest types.

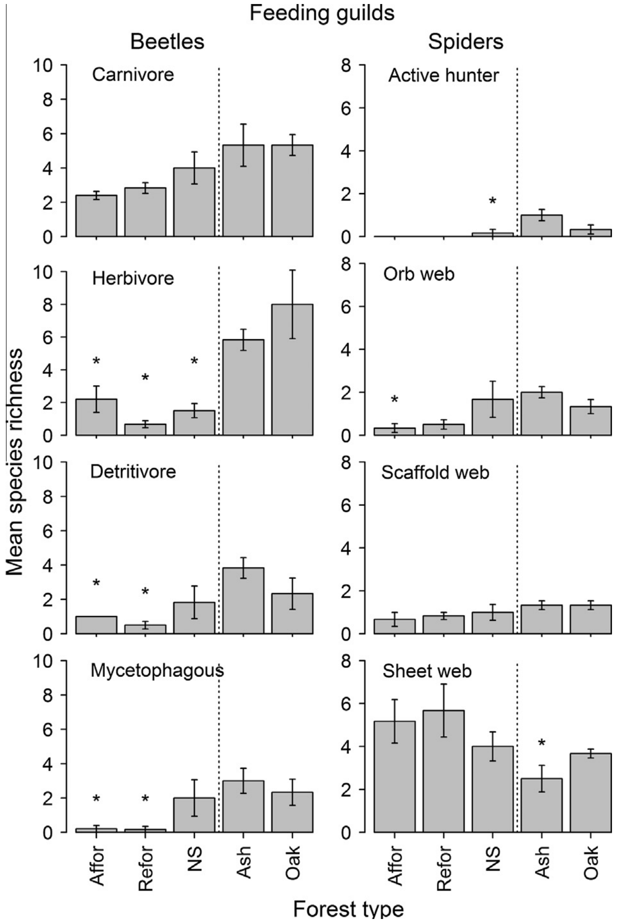

Fig. 6. Means and se for all beetle and spider feeding guilds. Asterisks indicate significant differences from the forest type with the greatest species richness in each plot as derived from generalised linear models (Tukey pairwise comparisons $P < 0.05$). See Appendix D for model statistics and *p*-values. Dotted line separates native from plantation, see Fig. 2 for definition of forest types.

Family level richness and abundance differed significantly between the forest types (Fig. 7). Native ash and oak samples contained significantly more Diptera and Hemiptera families than any of the plantation sampled (Fig. 7a). However, the total abundance of individuals from these groups was significantly higher in plantations, although the samples from these forest types showed much greater variation in abundance (Fig. 7b).

Major differences in assemblages were demonstrated by comparisons of the abundance of individuals from the dominant Diptera and Hemiptera families (Fig. 8). For the Hemiptera, afforested and reforested Sitka spruce were strongly dominated by the aphid family; the average aphid abundance was recorded an order of magnitude higher in Sitka plantations than Norway spruce or native forest types. There were also differences in the dominant Diptera families between forest types. Ceratopogonidae (biting midges) and Chironomidae (non-biting midges) were an order of magnitude higher in afforested Sitka spruce and reforested Sitka spruce respectively, compared to Norway spruce and native forests. The abundances of individuals within families had a more even distribution in the two native and Norway spruce forests compared to the Sitka plantations. Notably missing from the Sitka plantations were many Hemiptera families, such as the leafhoppers (Cicadellidae) and minute pirate bugs (Anthocoridae), which made up a considerable proportion of the native forest assemblage.

4. Discussion

4.1. Canopy fauna of native and plantation forests

The canopy fauna of native forests were significantly different from closed canopy plantation forests for all sampled taxa. Independently, beetle assemblages and family level Diptera and Hemiptera assemblages showed large differences in richness and abundance between forest types. Plantation forests supported approximately half the number of species or families recorded in the native forests. Although assemblages in Norway spruce were very different to those of native forests, assemblages in Norway spruce plantations had consistently higher richness than Sitka spruce plantations across all taxa, which may reflect the non-European native range of Sitka spruce. No differences in richness or abundance were found between first rotation and second rotation Sitka spruce plantations. Sitka spruce plantations of both rotations contained far greater total abundance of invertebrates than any of the other forest types, although this was a result of the vast numbers of aphids (Aphididae) and midges (from the families Ceratopogonidae and Chironomidae). Under current management, plantation forests in Ireland provide limited benefit to the canopy fauna of native forests, and our results show that this is unlikely to change in successive rotations of Sitka spruce, as second rotation plantations did not accumulate additional native canopy biodiversity.

No indicator species for plantation forest were identified from the canopy sampling. From this, combined with the low species

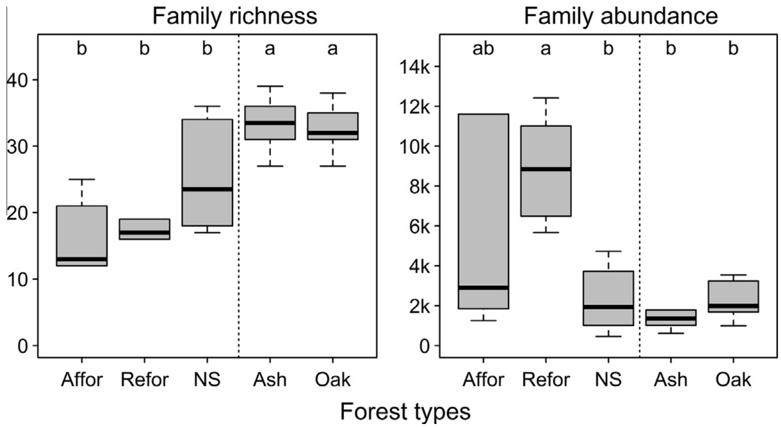

Fig. 7. Family level richness and abundance of Diptera and Hemiptera for the five forest types. Results of generalised linear models comparing forest types are presented; means that share a superscript (homogenous sub-sets, a–c, ranked highest to lowest) do not differ significantly (Tukey pairwise comparisons $P < 0.05$). χ^2, *F* and *p*-values can be found in Appendix E. Dotted line separates native from plantation, see Fig. 2 for definition of forest types.

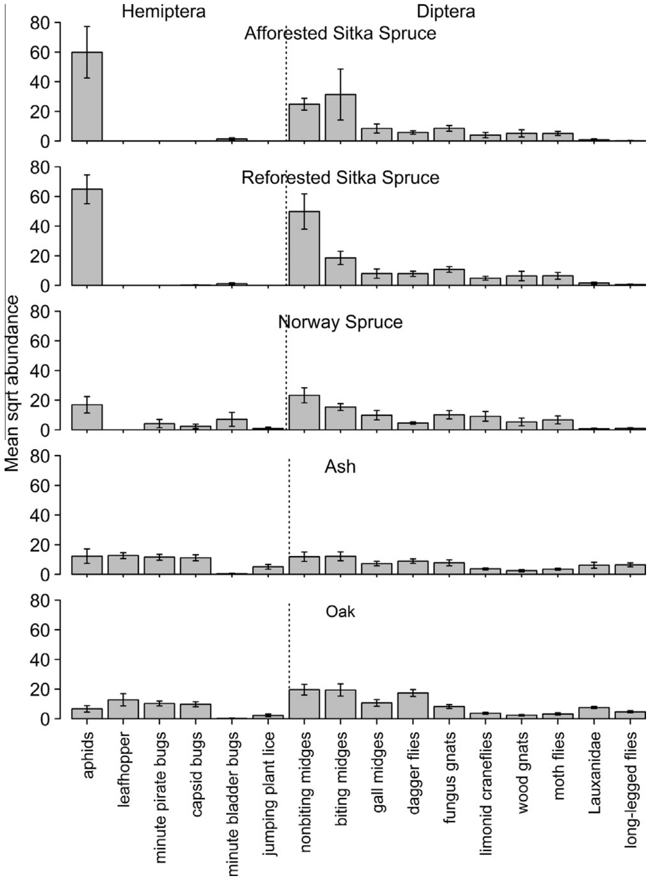

Fig. 8. Mean (square root transformed) and se of the 16 most abundant families from the Diptera and Hemiptera family level data. Each family represent at least 5% of the abundance recorded in any one site.

richness in Sitka spruce, we conclude that the canopy community in Sitka spruce plantations is a depauperate one, heavily dominated by just a few groups. In contrast, two sets of indicators were identified for ash and oak forests, both including beetle species from several feeding guilds. The dissimilarity between native and plantation canopy beetles implies that many species are either unable to disperse to plantations or are unable to utilise the plantation habitat. This corresponds with what has previously been found for ground-dwelling beetles (Carabidae) in closed canopy conifer plantations, both in Ireland and elsewhere in Europe (Butterfield et al., 1995; Fahy and Gormally, 1998; Finch, 2005; Fuller et al., 2008). Greater beetle richness in Norway spruce compared to Sitka spruce may reflect differences in specific secondary metabolites produced by both these non-native spruce species. Although Norway spruce is not native to Ireland, plant feeding/phloem sucking species, such as many of the herbivorous beetles and Hemiptera, may be better adapted to contend with plant defences of European species than the North American Sitka spruce. Nevertheless, previous research has shown that indigenous herbivorous insects can readily adapt from native conifers to exotic conifers (Bertheau et al., 2009), and that resource relatedness (e.g. bark thickness) was important in determining host colonisation. Likewise, Roques et al. (2006) showed that colonisation of exotic plantation by indigenous insects may be more successful if that exotic species has a native congener. Adaptability from native to exotic host may not transfer as readily from broadleaf species to conifers given, the fundamental differences in resources. Gossner et al. (2009) found that exotics shared more phytophages with natives from the same major plant lineage (angiosperms vs. gymnosperms) than with natives from the other lineages. In regions such as Ireland, where native conifers were absent for thousands of years (Roche et al., 2009), the ability of indigenous fauna to exploit exotic conifer plantation may be limited.

For canopy spiders, ordinations showed less divergence between forest types compared with the other groups sampled. In addition, no differences in spider species richness or abundance were found between forest types. This is somewhat surprising given the large differences found for other groups, especially as spiders are known to be particularly sensitive to environmental conditions and habitat structure (Entling et al., 2007; Muff et al., 2009; Buchholz, 2010), which differ between forest types (Ziesche and Roth, 2008). However, given the large abundance of prey available, especially in the form of aphids, plantation forests may be particularly suited to generalist predators, such as the majority of spider species. The ability of spiders to colonise new habitat via passive aerially disperse (ballooning) may further explain why this taxa is able to exploit plantations. Ballooning dispersal is thought to give spiders a colonisation advantage, enabling them to exploit new or frequently disturbed habitat (Crawford et al., 1995; Nyffeler and Sunderland, 2003). Given the fragmented nature of Ireland's forest estate, the ability to passively disperse on air currents via ballooning may give spiders an advantage when colonising plantation patches compared with those species restricted to ground movements and/or active flight. Orb web hunters, active hunters and scaffold web spinners were found in greater richness in native forests, whereas sheet web hunters (consisting of spiders from the Linyphhiidae family) were found in greatest richness in the Sitka spruce. Linyphiidae are one of the few spider families capable of ballooning as adults, for most families this type of dispersal is restricted to young instars (Bell et al., 2005). These very small bodied spiders are dominant invertebrate predators in crop fields, consuming high numbers of crop pests, especially aphids (Sunderland et al., 1986; Schmidt and Tscharntke, 2005). Furthermore, the majority of Linyphiidae in Britain are not habitat specialists (Pedley et al., 2013) and this is also likely to be true for the Irish population. Therefore, species recorded in the current study may not necessarily be colonising from forested habitats and could be migrating from the adjacent agricultural landscapes, taking advantage of the abundant aphid populations in both habitats.

The dominance of some groups, such as the Linyphiidae and Aphididae, in plantations could prevent establishment or breeding success of other species through interference and resource competition. Although species distribution patterns are often assumed to be ordered by abiotic factors such as temperature, shade and moisture, interspecific competition has also been proposed as an alternative mechanism shaping population dynamics and distributions (Connell, 1983). Spiller (1984) found evidence of exploitative and interference competition with two common orb-weaving spiders. Removal of the smaller species in experimental plots led to an increase in body size and fecundity of the larger species, whereas removal of the larger species increased the abundance and altered web position of smaller species. In crop fields, Linyphiidae are able to dominate, with webs covering half the surface area of a field (Sunderland et al., 1986). In the current study, Linyphiidae comprised 88% and 83% of the total spider abundance in Sitka and Norway spruce respectively, whereas in ash and oak Linyphiidae represented only 25% and 52%. Given the dominance of Linyphiidae in plantations and the potential for dense web coverage, competitive exclusion of other species could contribute to the low species richness in these forests. Although competition has been shown in specific systems, the importance of interspecific competition and the magnitude of the effects in field situations have been disputed (Shorrocks et al., 1984; Gurevitch et al., 1992). To test competition effects, observational and distributional studies, such as the current canopy study, need to be followed by detailed experimental field studies (Niemela, 1993).

Differences in sampling times between forests may have partially confounded our results. Hsieh and Linsenmair (2012) have shown that significantly different canopy spider compositions are obtained from early, mid and late season sampling. Although we attempted to temporally stratify sampling for each forest type, it was not possible to obtain samples from all sites in a single year or across the entire season. However, for the forest type with the most seasonally restricted sampling (ash forests sampled in June and July only) we recorded consistently high species and family richness, indicating that differences between native and plantation forests may have been underestimated. Future canopy invertebrate studies should attempt to control for within-season variation (Hsieh and Linsenmair, 2012).

The potential for plantations to contribute to biodiversity conservation depends heavily on the pre-plantation habitat (Brockerhoff et al., 2008). Plantations may not provide a simple replacement habitat for native forest biodiversity but, compared to intensive or abandoned agricultural land, they offer a less hostile landscape that can support large abundances of less specialist forest species. Large invertebrate populations, such as the aphid populations found in the current study, may have both positive and negative consequences for the forested landscape. For example, dense populations of herbivorous invertebrates can be detrimental to timber production by reducing growth rates through excessive defoliation (Straw et al., 1998; Eyles et al., 2011). Conversely, a large biomass of invertebrates may be beneficial as prey items for insectivores, such as Coal Tit (*Periparus ater*) and Goldcrest (*Regulus regulus*) found in high densities in Irish Sitka spruce plantations (Sweeney et al., 2010b). The interactions of prey abundance and insectivorous birds in plantation canopies is not well understood. In one study, managed spruce plantations have been implicated in the loss of passerine birds in boreal forests in Northern Sweden (Pettersson et al., 1995). Pettersson et al. (1995) found that a decline in epiphytic lichens was related to reduced invertebrate diversity, abundance and number of large invertebrates in managed forests compared to natural forest, suggesting that this reduced the quality of foraging habitats for birds, especially during winter when food is scarce.

4.2. Habitat structure and heterogeneity

Compared to plantations, both native ash and oak forest had greater species richness of beetles, increased diversity of arthropod feeding guilds, increased richness of Diptera and Hemiptera families with more even assemblage structures indicating a more diverse trophic structure. High species richness or diversity is often attributed to greater habitat heterogeneity, which provides a greater variety of niches (Niemela, 2001; Benton et al., 2003; Jimenez-Valverde and Lobo, 2007). Creating more complex understory vegetation and increasing the amount of dead wood and snags (standing dead trees) are key management objectives to increase diversity, and promoting habitats for native forest biodiversity (Hartley, 2002; Lindenmayer and Hobbs, 2004; Sweeney et al., 2010a). In addition to saproxylic species, many others utilise deadwood indirectly or as a secondary resource, e.g. mycetophagous beetles that feed on the saproxylic fungi or detritivores that use deadwood in an advance stage of decay as an additional food source. Increasing management intensity in plantations, such as short rotation lengths, management to reduce windthrow, thinning operations and brash removal, all limit the volume, diversity and decay stages of deadwood, which are commonly cited as reason for reduced biodiversity in managed forests (Simila et al., 2002; Muller et al., 2008). Siitonen (2001) estimated that reduced amounts of deadwood in managed Fennoscandia boreal forests could reduce saproxylic species by >50% in the landscape. Although not tested in this study, reduced abundance and diversity of deadwood may contribute to differences in faunal composition and, in particular, the reduced number of detritivore and mycetophagous beetle species found in these plantation forests.

Obligate invertebrate-host interactions may result in assemblage differences between forests types. In addition, differences in plant structural complexity, foliage density and subsequent microclimate may also result in different assemblage compositions between forest types (Halaj et al., 2000; de Souza and Martins, 2005). Ash and oak forests, comparable in invertebrate composition, were relatively similar in terms of structural complexity; both are broadleaves with relatively large gaps between leaves, in contrast to the more pronounced differences in structure between coniferous and broadleaf trees. The spider species with the greatest association with any forest type was the orb spinner *T. montana,* having a strong association with ash forests. Although *T. montana* is a ubiquitous habitat generalist, this species was not sampled in Sitka spruce plantations and only once in Norway spruce. Being relatively large-bodied (average female body length 8.75 mm) and hunting via a delicately spun web, this species may be unable to utilise the small gaps between conifer needles. In contrast, the dominant spider in all plantation forests was the Linyphiid *P. nemoralis*, with an average female body length of 1.8 mm. This relatively small species may be less confined by the denser foliage of the spruce plantations compared with the generally larger orb web and active hunting species. By manipulating the fractal dimensions of both natural and artificial broadleaf and conifer vegetation, Gunnarsson (1992) demonstrated that the structure of vegetation affected the size distribution of spiders; increased fractal dimension, and hence greater complexity of leaf space, resulted in reduced spider body size within habitats. Contrastingly, Halaj et al. (2000) showed experimentally that foliage complexity in Douglas-fir had a positive correlation with the average spider body size. Although differences in community composition recorded in the current study likely result from a combination of factors, structural complexity and the subsequent differences in microclimate are likely to be important given the very different types of forested surveyed.

4.3. Successive rotations

Understanding the biodiversity effect of reforesting commercial sites is increasingly important given the maturing age of many European plantations. There is potential for management to ensure permanent closed-canopy is maintained locally, which could benefit forest specialist. Findings from the current study indicate that Sitka spruce plantations show very little difference in terms of the invertebrate biodiversity they support through successive rotations, corresponding with what has been found for ground invertebrates (Oxbrough et al., 2010). In the current study, richness and abundance of invertebrates in first and second rotations were not significantly different and there were large overlaps in community composition. Although not significant, our data did suggest that beetle species richness and abundance was lower in reforested sites. Oxbrough et al. (2010) also found fewer forest associated ground spiders and beetles in second rotation plantations but, like the canopy beetles in our study, these differences were small. Corresponding responses of ground and canopy invertebrates in rotations highlights the fact that without targeted management of reforested sites, such as leaving over-mature stands, brash and deadwood and reforesting areas adjacent to mature forest, successive plantation stands may continue to be depauperate of forest specialists. As many species utilising the canopy in temperate forests will also utilise the ground for some part of their development (Ulyshen, 2011), differences in fauna between forest rotations could be related to accumulative litter layer and associated environmental factors. The litter layer has been shown to be a key factor determining dissimilarities in fauna between stand types for ground spiders (Ziesche and Roth, 2008). An historical lack of natural coniferous forest in Ireland could mean the majority of Irish forest fauna may find a thick layer of non-native pine needles unsuitable; if so, this problem will be exacerbated in successive rotations.

5. Conclusions

The majority of research assessing plantation invertebrate assemblages in temperate and boreal regions shows a lack of forest specialists and, when comparing the whole plantation landscape (including clearfell and young restocks), relatively high species richness often results from the inclusion of open-habitat species (Spence et al., 1996; Fahy and Gormally, 1998; Finch, 2005; Oxbrough et al., 2005; Fuller et al., 2008; Mullen et al., 2008). These studies all compare ground invertebrates assemblages to assess closed-canopy forests, ignoring the three-dimensional element of the forest biodiversity. We have shown that canopy fogging clearly delineates the invertebrate communities between forest types and concurs with studies focussing on the better understood ground fauna. Explicitly, this study has demonstrated that plantation forest canopy fauna is not comparable to native Irish forests and contains a species-poor assemblage dominated by aphids and midges. Furthermore, the use of multiple taxa in this study provides a robust description of community composition within plantations, compared to those based on single taxa.

Given the increasing global ratio of plantation over native forest (Brockerhoff et al., 2013), progressive plantation management must aim to incorporate species of regional vulnerability rather than increasing species richer *per se*. Where afforestation occurs onto open habitat, such as heathland, moorland or coastal dunes, incorporating complex mosaics of connected open habitat, avoiding large contiguous event-aged stands and preventing successional processes by providing periodic disturbance to open patches, should be included in management plans (Pedley et al., 2013). Where regional conservation policies look to consider forest biodiversity into commercial forestry, then management should seek to provide those elements that are missing from the plantation landscape, such as over-mature trees, increased volume and diversity of deadwood, and more open canopies that incorporate mixed tree species and increased understory diversity. While these ecological actions often seem in direct opposition to commercial timber extraction, such measures to increase biodiversity in plantations are also likely to benefit timber production through increased pest resilience (Jactel and Brockerhoff, 2007) and forest productivity (Thompson et al., 2009).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.12.010.

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