Forest Ecology and Management 321 (2014) 29–41

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.)

N. Barsoum [a,*], L. Fuller [b], F. Ashwood [a], K. Reed [a], A.-S. Bonnet-Lebrun [c], F. Leung [d]

[a] Centre for Ecosystems, Society and Biosecurity, Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, United Kingdom
[b] School of Biological, Earth & Environmental Sciences, University College Cork, The Cooperage, Distillery Fields, North Mall, Cork, Ireland
[c] École normale supérieure, 45 rue d'Ulm, F-75230 Paris, France
[d] University of Exeter, Geography, College of Life and Environmental Sciences, Room C360, Amory Building, Rennes Drive, Streatham Campus, Exeter EX4 4RJ, United Kingdom

ARTICLE INFO

Article history:
Available online 21 October 2013

Keywords:
Biodiversity
Oak (*Quercus robur/petraea*)
Scots pine (*Pinus sylvestris*)
Mixed woods
Spider
Carabid beetle

ABSTRACT

A mixed tree species composition is frequently proposed as a way to increase habitat heterogeneity and support greater biodiversity in commercial forests. However, although international forest policy is increasingly advocating stands of mixed tree species, there is evidence to question the biodiversity benefits conferred by such forests. Using active ground-dwelling spiders and carabid beetles as biodiversity indicator taxa, we investigated the effect of forest stand composition on spider and carabid beetle community structure and composition. We conducted pitfall trapping in the summer of 2011 in 42 plantation forest stands across three different geographical regions in the UK and Ireland. Three common plantation forest stand types were examined: oak monocultures, Scots pine monocultures, and intimate Scots pine and oak mixtures (oak ⩽60% cover). Forest stand type had a weak effect on spider and beetle species richness, with no significant differences in mixed stands compared with monocultures. There were few differences in species composition between the stand types in each region and indicator species analysis found few species specifically affiliated with any of the forest stand types. Land use history is hypothesised to have contributed, at least in part, to the observed important regional differences in spider and beetle assemblages. Our results do not support the perception that intimate mixtures of dominant tree species benefit biodiversity in plantation forest stands. Further research is required to determine the optimum percentages and planting patterns required for mixtures of canopy tree species in order to support forest biodiversity.

1. Introduction

European plantation forests are typically coniferous monocultures, which are generally considered to support limited forest biodiversity due to homogenous habitat provision and in some cases due to a non-native tree species composition (Peterken, 1993; Lust et al., 1998; Dhôte, 2005; Fuller et al., 2008; Forest Europe et al., 2011). By comparison, mixed species stands, comprising two or more prominent canopy layer tree species, are increasingly being considered to achieve a diversity of ecological, forest resilience and productivity goals (Koricheva et al., 2006; Cavard et al., 2011; Pérot and Picard, 2012). For example, oak combined with Scots pine is being revived as a recommended mixture in many regions including central France (Morneau et al., 2008), northern Spain (Del Río and Sterba, 2009) and increasingly in Ireland where it has been specifically promoted in recent years in forestry grant schemes (Guest and Huss, 2012). Traditionally, Scots pine has been considered to act as a temporary nurse crop for oak, serving to protect young oaks from temperature extremes, wind exposure and competition from ground vegetation, whilst at the same time, helping to improve growth form (Brown, 1992; Kerr et al., 1992; Dannatt, 1996). Today, this mixture is gaining interest because of the wide distribution, but also the high ecological and socio-economic value of both tree species (Del Río and Sterba, 2009). Oaks are known in particular, to support high associated species diversity (e.g., 423 phytophagous insect and mite species are associated with oak; in contrast, Scots pine supports 173 associated species;

Abbreviations: DBH, diameter at breast height; CWD, coarse woody debris; m.a.s.l., meters above sea level.

* Corresponding author. Tel.: +44 (0)1420 526 219.
E-mail address: nadia.barsoum@forestry.gis.gov.uk (N. Barsoum).

0378-1127/$ - see front matter © 2013 Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.foreco.2013.08.063

Kennedy and Southwood, 1984). United Kingdom, Irish and wider European forest policy specifically promote the inclusion of broadleaf components for this added ecological value; e.g., the UK Forestry Standard Guidelines call for a minimum of 5% broadleaved trees or shrubs in conifer plantations (Forest Service, 2000; European Environment Agency, 2008; Forestry Commission, 2011).

Biological diversity has been demonstrated to increase with structural diversity, and therefore niche availability (Simpson, 1949; Lack, 1969; Kostylev, 2005). Tews et al. (2004) found in a meta-analysis of habitat heterogeneity and species richness, that the majority of studies reviewed (85%) showed a positive correlation between species richness and vegetation structural variables. The structural complexity of plant communities has, as a result, frequently been directly related to the diversity of other taxa (Bersier and Meyer, 1994; Tanabe et al., 2001; Winter and Möller, 2008). In forest plantations, increasing the number of tree species is thought to potentially increase the diversity of microhabitat types and related food resources. The addition of native tree species is also hypothesised to modify physical conditions (soil and microclimate) and create microhabitats that bear a greater resemblance to native woodland, thereby providing niches for specialist native flora and fauna (Benton, 2003; Tews et al., 2004; Brockerhoff et al., 2008; Fahrig et al., 2010; Oxbrough et al., 2012). However, there are few studies conducted in forest settings that confirm or refute these hypotheses. A small number of recent studies have demonstrated that mixed woods may not always possess higher species diversity than monocultures or support a greater array of forest generalist and specialist species (Cavard et al., 2011; Oxbrough et al., 2012).

In this study, we investigate the effects of stand composition on the abundance and richness of two taxa: ground-dwelling spiders and carabid beetles. Spiders are recognised as potentially useful indicators of forest management impacts as they are influenced by vegetation structure, have a broad geographic range and can be sampled and identified effectively (Uetz 1979, 1991; Oxbrough et al., 2005). Furthermore, spiders are considered to be good bioindicators of changes within forest ecosystems caused by anthropogenic influences (Pearce and Venier, 2006; Malaque et al., 2008) and occupy a key role in forest food webs (Clarke and Grant, 1968; Gunnarsson, 1983; Wise, 2004). Carabid beetles are also often used in studies of forest invertebrate diversity as their taxonomy and ecology are well known and they can be efficiently collected using pitfall traps. In addition, they are potentially suitable bioindicators of invertebrate biodiversity as they are distributed over broad habitat and geographical ranges, are sensitive to environmental change and are comprised of both specialist and generalist species that reflect the diversity of other arthropods (McGeoch, 1998; Cameron and Leather, 2012). Carabid beetles have been extensively studied within broadleaved and coniferous forests, with many studies indicating comparatively low carabid community diversity in coniferous plantations (Niemelä et al., 1992; Jukes et al., 2001; Magura et al., 2002; Fuller et al., 2008).

In our study, we compare ground-dwelling spider and carabid beetle species assemblages, and richness in mixed and monoculture stands in three geographically separate regions. We combine comparable data that have been collected in the three regions using two separate sampling strategies. The following research hypothesis was addressed: plantation forest stands with mixed tree species composition support greater species richness and a different species composition of ground-dwelling spiders and carabid beetles compared with monocultures. Our study also asked the following questions: (1) are any observed effects of forest tree species composition on spider and beetle assemblages consistent across regions? and, (2) do any species have a high affinity with specific forest stand types?

We measured a range of environmental parameters expected to influence spider and carabid species composition in mixed and monoculture stands to investigate whether they differ significantly between forest stand types. We discuss the implications of our findings for forest management practice aimed at enhancing biodiversity in forest plantations.

2. Materials and methods

2.1. Study areas

We selected three forest stand types for study: oak (*Quercus robur* L./*Quercus petraea* (Matt.) Liebl.) monocultures, Scots pine (*Pinus sylvestris* L.) monocultures and intimate Scots pine and oak (*Q. robur*/*petraea*) mixtures. A total of 42 forest stands were selected, located in two forested regions of England (Thetford Forest, East Anglia 0°51′E; 52°27′N and the New Forest, Hampshire 1°38′W; 50°47′N) and across a wider area in central and eastern regions of the Republic of Ireland (Fig. 1). In both Thetford Forest and the New Forest five ⩾1.5 ha homogenous stands within larger woodland blocks were selected from each of the three different forest stand types; in these two forest regions, the selected mixed stands always comprised between 40% and 60% oak. In Ireland, four ⩾5.5 ha stands of each of the three different forest stand types were also selected within larger woodland blocks. The four mixed stands comprised 10% ($n = 2$), 15% ($n = 1$), and 20% ($n = 1$) oak. Forest stands were situated across similar altitudes in the New Forest (20–85 m.a.s.l.) and Thetford Forest (10–40 m.a.s.l.), but across a wider range in Ireland (57–234 m.a.s.l.) (Table 1). All three regions of study have a temperate maritime climate; although the 30 years average for annual precipitation is lowest in the most easterly forest region (391–833 mm in Thetford Forest), intermediate in the New Forest region (455–1232 mm) and highest in the stands located in Ireland (750–1400 mm) (Harris et al., 2012; Walsh, 2012). Edaphic conditions also differ in the three regions, with a patchy mixture of acidic and calcareous brown earths in Thetford Forest (pH in top 40 cm ranging from 3 to 7), heavier surface-water gley and clay soils in the New Forest (pH in top 40 cm ranging from 4 to 5) and brown earth and podzolic soils in Ireland (pH in top 10 cm ranging from 3.5 to 5.5). The majority of the forest stands were planted between the 1930s and 1950s. In the case of Thetford Forest, planting was typically on areas of former heathland in an area that currently comprises plantations of Scots pine, Corsican pine (*Pinus nigra* subsp. *laricio*) and smaller patches of oak and beech plantation (Randall and Dymond, 1996). The New Forest is a renowned area of ancient woodland pasture with diverse plantation types intermingled with ancient woodland dominated by oak or beech. The New Forest is actively used for grazing by cattle, horses and ponies (Grant and Edwards, 2008) (Table 1). *Q. robur*/*petraea* is a native species of Ireland and Great Britain, while the native status of *P. sylvestris* is less certain. Pollen records indicate that Scots pine was once present and well established in all three regions of study, but disappeared from the landscape for long periods of time (>1000 years) (Randall and Dymond, 1996; Grant and Edwards, 2008; Roche et al., 2009).

2.2. Arthropod sampling

We used pitfall traps to sample active ground-dwelling spider and carabid beetle fauna. Pitfall traps were installed using a soil auger to create a well-defined hole of 7–8 cm diameter with minimum disturbance to the surrounding area. Plastic cups were inserted into these holes to a depth of 9–11 cm. Care was taken to ensure that the rims of each of the pitfall traps were level with the ground and that there were no gaps along the sides of the trap

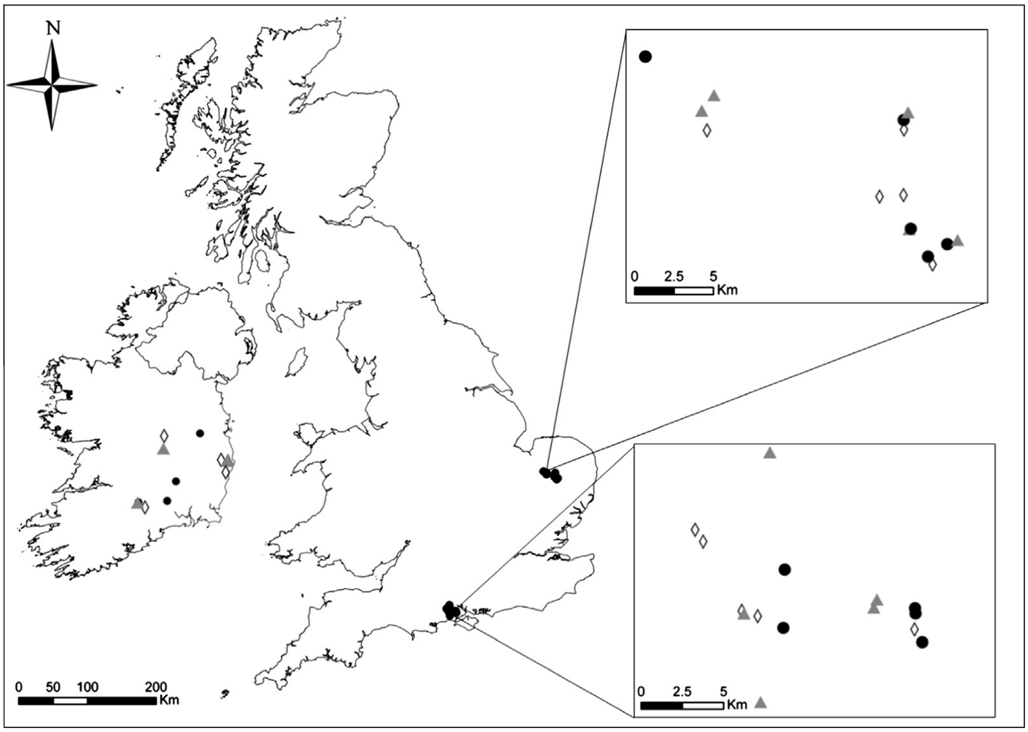

Fig. 1. Locations of the stands in each of the three regions studied. Oak monoculture stands (●), Scots pine monoculture stands (◇), Scots pine and oak mixed stands (▲).

into which invertebrates could fall. About 2–3 cm of 50–70% diluted ethandiol (blue antifreeze) was poured into the cups as a temporary preservative. Drainage holes at the top of plastic cups allowed water to escape and prevent flooding of the traps. Forestry Commission and University College Cork staff collected the contents of each pitfall trap every 2–3 weeks from May to August 2011, totalling 84–90 trapping days. Non-identical pitfall sampling designs were adopted between the UK and Irish sites, as described in further detail below.

2.2.1. Pitfall trapping – English stands

A single pitfall trap was installed within eight 10 m × 10 m sampling plots per forest stand. These eight sampling plots were arranged equidistantly around the perimeter of a 50 m × 50 m quadrat positioned within the centre of each stand. Sampling plots were always at least 25 m from the forest stand edge and 15 m apart from one another. To account for microhabitat heterogeneity, within each of the eight 10 m × 10 m sampling plots a single pitfall trap was installed in one of two microhabitat types; either the open forest floor, or at the base of a tree. At the four open forest floor microhabitat locations, pitfall traps were located in the open spaces between trees, avoiding stumps, piles of deadwood, and areas of dense vegetation or disturbance. The four pitfall traps that were located at tree bases were always positioned on the north-facing side of a Scots pine or oak tree and as close as possible to the base of the tree. In the forest stands comprising mixtures of Scots pine and oak, two of the pitfall traps installed at tree base microhabitats were positioned at the base of oak trees and two were positioned at the base of Scots pine trees. Each trap was covered by a 19 cm × 19 cm square steel lid that was positioned 3 cm above the ground. Lids each had 15 cm-wide entrance holes at all four corners which were kept clear of leaf litter and any other debris.

2.2.2. Pitfall trapping – Irish stands

Three sampling transects were used per forest stand, each consisting of five pitfall traps set 2 m apart in a linear arrangement of 10 m total length. Transects were established a minimum of 50 m apart and a minimum of 50 m from the edge of the forest and any large areas of open space. Sampling of different microhabitat types was not included as a feature of the Irish arthropod sampling procedure. A lid was only placed on traps vulnerable to disturbance from animals.

2.2.3. Species identification

Adult ground-dwelling spiders and carabid beetles were identified to species level due to the difficulties of identifying juveniles. Spiders were identified using Roberts (1993) following the nomenclature of Platnick (2012), and habitat specialists designated based on Nolan (2008) and Harvey et al. (2002). Carabid identification was conducted using the key of Luff (2007); with habitat preference determined using Jukes et al. (2001), Luff (2007) and Thiele (1977).

2.3. Environmental parameters

In all of the forest stands a range of environmental parameters were assessed in 10 m × 10 m sampling plots. In England, environmental parameters were assessed in the eight 10 m × 10 m sampling plots were positioned around each of the eight pitfall traps and in Ireland, three 10 m × 10 m sampling plots were positioned adjacent to each of the three pitfalls plots. The volume of coarse woody debris (CWD) $\geqslant$ 10 cm at it widest point, was assessed in each 10 m × 10 m sampling plot. The CWD considered included: (i) logs and large branches ($\geqslant$45° departure from vertical), (ii) snags (<45° departure from vertical, $\geqslant$1 m tall) and (iii) stumps (<1 m tall). Measurements used to estimate volume for each of the categories of CWD included the length and diameter at the centre for logs and large branches, the height and diameter at breast height (DBH) (1.3 m) for snags, and the height, top diameter and bottom diameter for stumps. The percentage cover of vegetation in three distinct vertical layers was assessed in each 10 m × 10 m sampling plot. These layers included (1) an understory layer: woody vegetation with a height of between 2 m and 5 m, (2) a shrub

Table 1
Summary characteristics of stands in the three study regions (NF = New Forest, TF = Thetford Forest, EIRE = central and eastern Ireland) and three stand types (SP = Scots pine monoculture, SP/OK mix = Scots pine and oak mixtures, OK = oak monoculture). Land cover classes include conifer woodland (C), broadleaf woodland (B), conifer and broadleaf mixed woodland (C/B mix), undefined woodland (W) and non-wooded areas (Bare) that could in some cases be areas of heathland.

Region	Forest stand	Site history		Current stand type	Planting year	Stand area (ha)	Altitude (m.a.s.l.)	Soil type
		Landcover 1870s	Landcover 1905–1910					
NF	Denny Lodge	C	C/B mix	SP	1930	3.94	20	Surface water gley – clay texture
NF	Burley (2512)	C/B mix	C/B mix	SP	1927	6.4	45	Surface water gley – clay texture
NF	Burley (2520a)	Bare	C/B mix	SP	1948	6.61	35	Surface water gley – clay texture
NF	Milkham (2135)	C	C	SP	1953	5.3	90	Surface water gley – clay texture
NF	Milkham (2136)	C	C	SP	1953	3.68	80	Surface water gley – clay texture
NF	Denny Wood	Bare	C/B mix	OK	1900	3.29	20	Surface water gley – clay texture
NF	Denny Lodge	C	C/B mix	OK	1928	2.66	20	Surface water gley – clay texture
NF	Ladycross	C/B mix	C/B mix	OK	1940	4.84	25	Surface water gley – clay texture
NF	Rhinefield	B	B	OK	1951	2.72	35	Brown earth
NF	Holidays Hill	B	C/B mix	OK	1923	1.52	40	Brown earth
NF	Parkhill (4311a)	C	C/B mix	SP/OK mix	1950	12.05	40	Surface water gley – clay texture
NF	Parkhill (4309b)	C	C/B mix	SP/OK mix	1952	5.5	30	Surface water gley – clay texture
NF	Wootton Coppice	C/B mix	C/B mix	SP/OK mix	1930	5.46	35	Surface water gley – clay texture
NF	Burley	C/B mix	C/B mix	SP/OK mix	1929	3.55	35	Surface water gley – clay texture
NF	Bramshaw	B	C/B mix	SP/OK mix	1936	5.29	85	Surface water gley – clay texture
TF	Scotch Plantation	Bare	Bare	SP	1937	7.13	35	Calcareous brown earth
TF	Hockham (3345)	Bare	Bare	SP	1932	5.17	40	Brown earth
TF	West Harling (4751)	C/B mix	C/B mix	SP	1967	3.61	30	Brown earth
TF	Roundham Heath	Bare	Bare	SP	1956	1.61	30	Typical podzol
TF	Big Wood	Bare	Bare	SP	1930	1.73	30	Brown earth
TF	West Harling (4714a)	Bare	Bare	OK	1934	4.87	25	Calcareous Brown earth
TF	Bridgham (3548b)	Bare	Bare	OK	1934	2.41	35	Brown earth
TF	West Harling (4722)	Bare	Bare	OK	1933	2.91	20	Brown earth
TF	Hockham (3335)	Bare	Bare	OK	1932	6.75	40	Brown earth
TF	Didlington	Bare	Bare	OK	1954	4.73	10	Loamy texture
TF	West Harling (4716a)	C/B mix	C/B mix	SP/OK mix	1934	5.15	20	Calcareous brown earth
TF	Bridgham (3548a)	Bare	Bare	SP/OK mix	1934	4.46	30	Brown earth
TF	Hockham (3324a)	Bare	Bare	SP/OK mix	1935	5.21	40	Ground water gley
TF	Mundford (3021a)	C/B mix	C/B mix	SP/OK mix	1941	4.85	25	Brown earth
TF	Mundford (3009b)	C/B mix	C/B mix	SP/OK mix	1932	3.38	15	Brown earth
EIRE	Bansha West	–	W	OK	1939	12	122	Brown earth
EIRE	Demesne (Donadea)	–	Bare	OK	1938	8.6	88	Brown earth
EIRE	Grangemockler	–	W	OK	1936	6.2	155	Brown podzolic
EIRE	Jenkinstown	–	W	OK	1860	7.2	82	Brown earth
EIRE	Ballydrehid	–	Bare	SP	1946	29.1	163	Podzol
EIRE	Ballard	–	Bare	SP	1946	15.1	139	Brown earth
EIRE	Durrow Abbey	–	Bare	SP	1949	12.5	57	Gley
EIRE	Killeagh	–	Bare	SP	1948	19.8	147	Brown podzolic
EIRE	Ballymanus	–	W	SP/OK mix	1932	5.5	234	Brown podzolic
EIRE	Brittas	–	W	SP/OK mix	1940	8.8	131	Brown earth
EIRE	Carrick	–	W	SP/OK mix	1946	9.8	166	Podzol
EIRE	Kilshane	–	W	SP/OK mix	1940	13.3	192	Podzol

layer: Woody vegetation <2 m tall, including brambles and climbing plants and (3) a herb layer: vascular herbs, including graminoids, grasses, rushes, sedges and ferns but excluding climbing plants, bramble and woody species. The percentage cover of litter and bare ground were additionally measured within each of the 2 m $\times$ 2 m quadrats in the English stands. Canopy openness was measured at the four corners of each of the 10 m $\times$ 10 m sampling plots using a canopy scope (Brown et al., 2000). Soil pH was estimated by collecting soil samples to a depth of 10 cm (litter and fermentation layers excluded) from the four corners of each of the 10 m $\times$ 10 m sampling plots. These samples were pooled at the stand level. 5 g of soil was diluted in 20 mL of distilled water and pH was measured using a Metrohm Titrino pH probe with an autosampler.

2.4. Statistical analysis

Data from each region (New Forest, Thetford Forest, and Ireland) were analysed separately. For all analyses, data were pooled across collection periods and forest stands. Data from four missing pitfall traps in Thetford and one in the New Forest were replaced with trap averages.

To test our hypothesis that mixed plantation stands support a greater richness of ground-dwelling spiders and carabids than monocultures, we analysed the effect of stand type on the species richness of all species, habitat generalist species, forest specialist species, and open specialist species with Kruskal–Wallis rank sum tests. We followed significant Kruskal–Wallis tests with post hoc tests of individual factor levels using Wilcoxon pairwise rank sum tests with Bonferroni corrected *p*-values for multiple comparisons.

Species composition was examined using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), to determine if there were any differences in the species composition of ground-dwelling spiders and carabid beetles between each stand type in each region. Species data were Hellinger transformed prior to analysis (Legendre and Gallagher, 2001) and 4999 permutations were used. Latitude can affect species composition (Oxbrough et al., 2012); therefore this was used as a control covariate in the analysis where it was found to have an effect. Where stand type was found to have an effect, post hoc pairwise comparisons were conducted with Bonferroni corrected *p*-values for multiple comparisons.

We carried out indicator species analysis to identify species that have a high affinity for the different stand types. This analysis assesses the relative abundance and relative frequency of a species across groups; in this case, stand type. The analysis assigns each species an indicator value in the form of a percentage to indicate in which group or groups they are most abundantly and frequently found. A Monte Carlo test of statistical significance follows (Dufrene and Legendre, 1997). We ran the analysis using the 'indicspecies' package of R, with 4999 permutations (De Cáceres and Legendre, 2009). Because the number of significant species was low when the probability was set to <.05, and because we were interested in broad trends in species composition, we chose to report species significant at probability <0.1.

We calculated the stand level average for each environmental variable from the plots and carried out the same Kruskal–Wallis testing procedure as described above.

We carried out all analyses in R 2.15.2 (R Core Team, 2012).

3. Results

3.1. Ground-dwelling spiders

3.1.1. Patterns in species abundance and richness

During the sampling period, the total number of individual ground-dwelling spiders trapped in the New Forest, Thetford Forest and Ireland was 2279, 3418 and 2463, respectively (Appendix A.1). In the same order by region, these comprised a total of 81, 86 and 81 spider species. Of these species, in the New Forest, forest specialists constituted less than half (44%) of all spiders captured, while in Thetford Forest there were fewer, at only 27% of all identified spiders. Forest specialist spiders dominated the Irish forest stands, comprising 70% of all spiders captured. Habitat generalist ground-dwelling spiders constituted most of the remaining fraction of spiders in each region, with very few open habitat specialist species occurring in any of the regions (i.e., 4%, 1% and 1% of all spiders in the New Forest, Thetford Forest and Irish stands, respectively).

In the New Forest, Kruskal–Wallis tests showed that there was no significant effect of stand type on the species richness of spiders. In Thetford Forest, however, species richness in Scots pine monocultures was 46% greater than in oak monocultures and 26% greater than in mixed stands. Kruskal–Wallis tests confirmed a positive influence of Scots pine monocultures on species richness of all ground-dwelling spider species compared with mixed stands or oak monocultures (X^2 (2) = 9.05, $p = 0.01$) (Table 2). Habitat generalist spider species richness was similarly affected by stand type (X^2 (2) = 8.86, $p = 0.01$) in Thetford Forest, although the Mann–Whitney post hoc test showed only a marginally significant increase in species richness in Scots pine compared with mixed stands ($p = 0.06$). Stand type also affected forest specialist spiders in Thetford Forest (X^2 (2) = 7.98, $p = 0.02$), with a marginally higher species richness in Scots pine monocultures compared with mixed stands ($p = 0.06$). Kruskal–Wallis tests showed that stand type did not affect species richness in Ireland and this was when considering all species, habitat generalists only, or forest specialists only. However, stand type did affect open habitat specialists (X^2 (2) = 7.97, $p = 0.02$), with richness in Irish Scots pine monoculture stands marginally greater than in mixed or oak monocultures.

3.1.2. Species composition

There was no effect of stand type on the species composition of ground-dwelling spiders in the New Forest ($F_{2,12} = 1.42$, $p = 0.06$) or in Ireland ($F_{2,9} = 1.21$, $p = 0.24$). In Thetford Forest there was a significant effect of stand type on species composition ($F_{2,12} = 2.02$, $p = 0.004$); pairwise comparisons revealed that species composition was significantly different between Scots pine monocultures and oak monocultures ($F_{1,8} = 3.54$, $p = 0.03$), marginally different between Scots pine monocultures and mixed stands ($F_{1,8} = 1.88$, $p = 0.05$), but did not differ between oak monocultures and mixed stands ($F_{1,8} = 0.84$, $p = 1.00$).

Pirata hygrophilus, *Pardosa saltans*, *Tenuiphantes flavipes* and *Tenuiphantes zimmermanni*, and *Ozyptila trux* were the five most frequently caught species in the New Forest. *P. hygrophilus* and *O. trux* are habitat generalists, while the others are forest specialists. These species occurred in all stand types, although only 3 individuals of *O. trux* were caught in New Forest mixed stands. These five species comprised 73% of the New Forest total catch. Thetford Forest shared its three most frequently caught spiders, *P. hygrophilus, P. saltans*, and *T. flavipes* with the New Forest. *Microneta viaria* and *Macrargus rufus*, which are both forest specialists, were the fourth and fifth most trapped species. These five species were trapped in all stand types, and comprised 76% of the catch in Thetford Forest. The five most commonly caught species in the Irish stands were, in order of frequency of occurrence, *Tenuiphantes alacris*, *T. zimmermanni*, *Monocephalus fuscipes*, *Walckenaeria acuminata*, and *Tenuiphantes tenebricola*. With the exception of *W. acuminata,* these are forest specialists. These species occurred across all stand types, and constituted 57% of the total catch in Ireland.

3.1.3. Indicator species analysis

Thetford Forest had the highest number of significant indicator species. Two were affiliated with oak monocultures only, four with Scots pine monocultures only, three with both oak monocultures and mixed stands and one with both Scots pine monocultures and mixed stands (Table 3). The New Forest had the lowest number of significant indicator spider species; one was affiliated only with oak monocultures, another with both oak monocultures and mixed stands, and two with both Scots pine monocultures and mixed stands. In Ireland, three species were significantly associated only with Scots pine monocultures, and one with both oak monocultures and mixed stands. The forest specialist species *Diplocephalus picinus* and *M. viaria* were found to have the same forest stand type

Table 2
Median ± interquartile range of ground-dwelling spider and carabid beetle species richness in oak monoculture, Scots pine monoculture, and Scots pine and oak mixture in each region. Differences between forest types within each region analysed using Kruskal–Wallis tests.

	New Forest			Thetford Forest			Ireland		
	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
Spiders									
All species	16 ± 6	21 ± 2	18 ± 18	22 ± 3[a]	32 ± 4A	20 ± 6[a]	25 ± 10	31 ± 3	31 ± 10
Habitat generalists	9 ± 1	13 ± 2	10 ± 9	12 ± 2	19 ± 2[A]	10 ± 5[a]	13 ± 8	17 ± 1	18 ± 9
Forest specialists	7 ± 2	7 ± 2	8 ± 2	10 ± 1	12 ± 2[A]	8 ± 1[a]	11 ± 2	11 ± 3	12 ± 2
Open specialists	1 ± 2	2 ± 0	1 ± 4	1 ± 1	3 ± 2	2 ± 1	1 ± 1[a]	3 ± 1[A]	1 ± 1[a]
Carabids									
All species	8 ± 2	4 ± 2	6 ± 4	16 ± 4[A]	9 ± 4[a]	14 ± 2	8 ± 7	9 ± 4	6 ± 4
Habitat generalists	6 ± 2	3 ± 1	5 ± 4	10 ± 2	7 ± 3	10 ± 3	5 ± 5	5 ± 3	4 ± 3
Forest specialists	1 ± 1	1 ± 0	1 ± 0	2 ± 0[A]	1 ± 1[a]	1 ± 0[a]	1 ± 0	2 ± 2	2 ± 1
Open specialists	0 ± 0	0 ± 0	0 ± 0	2 ± 2	1 ± 1	2 ± 2	3 ± 2	2 ± 2	0 ± 1

[A] is greater than[a].

Table 3
Indicator species analysis of ground-dwelling spiders and carabid beetles, showing the habitat preference of each species. Habitat preference is according to Thiele (1977), Jukes et al. (2001), Harvey et al., (2002), Luff (2007) and Nolan (2008), and includes: G = generalists, F = forest habitat specialists, O = open habitat specialists. Indicator value is presented as a percentage and significance level indicated by .<0.1, *<0.05, **<0.01.

Species	Habitat preference	Oak	Scots pine	Mix
Spiders				
Agyneta subtilis[b]	H	–	100**	–
Centromerus dilutus[b]	H	–	89	–
Clubiona pallidula[b]	H	77	–	–
Diplocephalus latrifrons[b]	F	91	–	–
Diplocephalus picinus[b,c]	F	85[b]* 94[c]*	–	94[b,c]*
Dismodicus bifrons[c]	H	–	95*	–
Gongylidiellum vivum[b]	H	–	77	–
Macrargus rufus[a]	F	81	–	81
Microneta viaria[b,c]	F	95[b]** 98[c]*	–	95[b,c]**
Ozyptila trux[a]	H	92	–	–
Palliduphantes ericaeus[b]	H	–	89*	–
Palliduphantes pallidus[b]	H	–	87	87
Pardosa pullata[c]	O	–	87	–
Pocadicnemis pumila[c]	H	–	93	–
Scotina celans[a]	F		84	84
Tenuiphantes cristatus[b]	H	92*	92*	–
Walckenaeria cucullata[a]	F	–	88*	88*
Carabids				
Leistus fulvibarbis[b]	F	89*	–	–
Nebria brevicollis[b]	H	93*	–	93*

[a] New Forest.
[b] Thetford Forest.
[c] Ireland.

These two stands are near a pheasant rearing station and it is possible that factors associated with the presence of the birds may be boosting the *P. madidus* population. *P. madidus* is a commonly found habitat generalist species in the UK. This particularly high abundance of a single species did not influence our species richness or indicator species analyses.

Forest specialist carabid beetle species comprised a high percentage of all carabids caught in the New Forest stands (55%). By contrast, forest specialist beetle species were notably scarce in Thetford Forest stands, occurring in a proportion of only 0.46% of all carabid beetles caught. This proportion changed little (increasing to 3%) when the disproportionately high numbers of the habitat generalist species *P. madidus* at two Thetford Forest stands (Bridgham 3548*a* + *b*) were removed as a component of the overall regional beetle species composition. Forest specialist carabid beetle species also comprised a high percentage of all carabids caught in the Irish forest stands (49%). Habitat generalist beetle species made up most of the remaining proportion of beetle species identified in all regions. Open habitat specialists were rare in all regions, occurring in proportions of 1%, 0.4% and 3% of all carabid beetles in the New Forest, Thetford Forest and Irish stands, respectively.

The only region in which stand type significantly affected carabid species richness was Thetford Forest. Here total carabid species richness was highest in oak monocultures; that is, 35% higher than in mixtures and 40% higher than in Scots pine monocultures. Kruskal–Wallis tests showed oak monocultures supported significantly higher richness of all species compared with Scots pine monocultures (X^2 (2) = 7.53, $p = 0.02$), although the factor level effect was marginal ($p = 0.06$) (Table 2). Richness of forest specialist carabids in oak monocultures was higher than in Scots pine monocultures or mixtures (X^2 (2) = 7.94, $p = 0.02$), although the factor level effect was again marginal ($p = 0.08$ (oak > Scots pine), $p = 0.06$ (oak > mixed).

affiliations; they occurred frequently in oak and mixed stands but not in Scots pine stands, in both Ireland and Thetford Forest.

3.2. Carabid beetles

3.2.1. Patterns in species abundance and richness

During the sampling period a total of 4059, 16,015 and 3314 adult carabid beetles were identified in the New Forest, Thetford Forest and Ireland, respectively. In the same region order, these comprised a total of 21, 37 and 28 species, respectively (Appendix A.2). Two stands in Thetford Forest (Bridgham 3548*a* + *b*) contributed disproportionately high numbers of one species, *Pterostichus madidus*, a habitat generalist that is commonly found in the UK.

3.2.2. Species composition

There was no effect of stand type on the species composition of carabid beetles in the New Forest ($F_{2,12} = 1.37$, $p = 0.18$), Thetford Forest ($F_{2,12} = 1.78$, $p = 0.08$) or in Ireland ($F_{2,7} = 0.87$, $p = 0.53$). However, the carabid community composition of Thetford Forest showed a strong regional separation from the New Forest and Irish carabid communities which shared many of the most commonly occurring carabid beetle species. The most commonly recovered beetle species in the New Forest was the forest specialist species *Abax parallelepipedus*. Then in the following order, the habitat generalists *P. madidus* > *Pterostichus niger* > *Oxypselaphus obscurus* > *Pterostichus strenuus*. These five most frequently captured species made up 97% of the region's catch total. In Thetford Forest, the most commonly trapped beetles across all stand types, in order of abundance, were *P. madidus* > *Calathus rotundicollis* > *Pterostichus melanarius* > *Carabus problematicus* > *Carabus violaceus*. All of these species are habitat generalists and were caught in all stand types. These species comprised 95% of the catch in Thetford. The five most common carabid beetle species, in order of occurrence across all forest stand types in Ireland, were *A. parallelepipedus*, *P. madidus*, *P. niger*, *P. melanarius*, and *Nebria brevicollis*. The species were caught in all stand types, and comprised 90% of the total catch in the Irish stands.

3.2.3. Indicator species analysis

Thetford Forest was the only region in which indicator species analysis showed any carabid beetle species to have an affinity for one stand type over another (Table 3). The analysis associated one forest specialist (*Leistus fulvibarbis*) with oak monocultures, and one habitat generalist (*N. brevicollis*) with both oak and mixed stands.

3.3. Environmental parameters

There were no significant differences in the measured environmental variables between the three forest types across the regions (Table 4).

4. Discussion

The forest stand types considered in this study (oak monocultures, Scots pine monocultures and Scots pine and oak mixtures) exerted a limited comparative influence on the species composition and richness of both ground-dwelling spiders and carabid beetles and this was true in the three different regions of study. Where significant stand type effects were observed, monoculture stands supported higher richness than mixed stands, but the level of any effect was different in the three forest regions. For example, in Thetford Forest, Scots pine monocultures harboured highest richness of all spider species, habitat generalist species, and forest specialist species, but not open habitat specialists. In contrast, there was significantly higher species richness of spiders with preferences for open habitats in Scots pine monoculture stands compared with the other stand types in Ireland. However, in the New Forest spider species richness was not found to differ significantly between forest stand types. In terms of carabid beetle species richness, oak monoculture stands had significantly higher species richness of forest specialist species compared with Scots pine monocultures and Scots pine and oak mixtures in Thetford Forest, but there was no detectable effect of stand type on carabid beetle richness in either the Irish or New Forest stands. Therefore, our findings do not support the hypothesis that mixed tree species stands support higher species richness of ground-dwelling spiders and carabid beetles. Regional and individual tree species effects were more important influences on spider and carabid beetle assemblages.

The lack of any significant difference in the measured environmental variables (e.g., volume of CWD, composition and structure of ground vegetation, and canopy openness) between the three forest stand types studied, is indicative of a potential high degree of overlap in the ecological resource provisioning of the three stands types. Limited responses by spiders and carabid beetle communities to stand type suggests that this is true for these taxa; i.e., the ecological value of mixed and monoculture stands of Scots pine and oak is highly comparable for these taxa, with the exception of only a small number of spider and carabid species that have stronger affiliations to one or other stand type as revealed by indicator species analysis. High levels of similarity in measured environmental parameters between mixed and monoculture stands were also found by Oxbrough et al. (2012) in Norway spruce (*Picea abies*)-Scots pine mixtures and Norway spruce-oak mixtures compared with Norway spruce monocultures. In that study, the question was raised as to whether the poor mixing ratio of oak with Norway spruce (15–40%) was the reason for the limited differences found between stands for the environmental parameters measured. The mixing ratio of the broadleaf component in our study was comparatively high in all of the English stands (at between 40% and 60% oak in mixed stands), so if distinct environmental conditions were created by a Scots pine and oak mixture, these should have been evident.

Unlike the weak forest stand type effects observed, there were clear regional scale factors that could influence the species abundance, richness and composition of spider and beetle assemblages. Counts of spiders and carabid beetles, for example, were disproportionately high in Thetford Forest stands compared with the New Forest and Irish stands. The proportion of spider and beetle forest specialist species present in Thetford Forest was also much lower than the New Forest and Irish stands, while the proportion of generalist species was comparatively high. Additionally, Thetford Forest was the only region in which any beetle species was associated with a particular stand type; one forest specialist (*L. fulvibarbis*), which has a preference for woodlands with damp litter (Luff, 2007), was associated with oak monocultures, and one habitat generalist (*N. brevicollis*) was associated with both oak and mixed stands. Another species with a preference for damp conditions was entirely absent from our pitfall traps in Thetford Forest, but highly abundant in the New Forest and the Irish sites; this was *A. parallelepipedus* which has been recovered previously in small numbers from Thetford Forest by Jukes et al. (2001), but, similarly to our study, in comparatively high numbers in the New Forest. Jukes et al. (2001) suggest that the limited numbers of *A. parallelepipedus* in Thetford Forest could be related to the much drier conditions here, leading to a likely scarcity of the preferred prey; i.e., slugs and earthworms.

In addition to the likely influence of drier conditions present in Thetford Forest, our findings in the Thetford Forest region may also be related to the relatively 'young' status of this wooded area com-

Table 4
Median ± interquartile range of environmental variables measured in oak monoculture, Scots pine monoculture, and Scots pine and oak mixture in each region.

	New Forest			Thetford Forest			Ireland		
	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
pH	4.4 ± 0.3	4.2 ± 0.3	4.4 ± 0.3	5.3 ± 2.2	3.8 ± 0.1	5.2 ± 1.8	4.6 ± 1.2	4.0 ± 0.2	3.9 ± 0.1
Canopy openness	5.6 ± 2.5	6.3 ± 3.1	2.5 ± 0.8	0.8 ± 0.2	2.0 ± 3.0	4.3 ± 2.0	2.9 ± 1.3	7.0 ± 4.8	2.6 ± 0.8
Volume of coarse woody debris (m^2)	29.3 ± 39.7	7.4 ± 2.8	17.6 ± 20.0	12.7 ± 22.4	31.2 ± 46.1	26.8 ± 44.9	19.3 ± 21.5	10.0 ± 3.2	36.1 ± 10.1
Understory cover (%)	4.4 ± 6.5	5.0 ± 8.8	11.3 ± 11.9	7.5 ± 3.8	3.1 ± 13.8	3.1 ± 3.1	37.5 ± 19.1	3.9 ± 19.3	49.2 ± 33.3
Shrub cover (%)	6.6 ± 6.3	8.8 ± 11.4	11.9 ± 6.9	2.1 ± 6.9	6.9 ± 35.6	5.6 ± 4.4	51.7 ± 17.9	24.7 ± 29.0	21.3 ± 30.5
Herb cover (%)	52.8 ± 22.8	35.3 ± 43.9	81.3 ± 36.9	79.4 ± 28.8	60.6 ± 18.1	72.5 ± 18.8	13.0 ± 10.3	49.2 ± 34.1	56.3 ± 12.2
Litter cover (%)	44.6 ± 9.0	52.8 ± 46.3	29.8 ± 24.0	35.6 ± 11.4	36.3 ± 8.8	31.3 ± 18.9	95.0 ± 2.9	68.5 ± 11.7	92.4 ± 15.2
Bare soil cover (%)	0.4 ± 2.1	0.3 ± 0.6	0.6 ± 1.6	0 ± 0.3	0 ± 0	0.1 ± 0.6	0.1 ± 0.2	0.1 ± 0.2	0.2 ± 0.7

pared to greater periods of woodland continuity in the New Forest and Irish stands. Other influences on the spider and beetle composition in the Thetford Forest stands could be the former predominance of heathland in the region, but also the presence of a high proportion of non-native conifer woodland, including plantations of the Mediterranean tree species Corsican pine (*P. nigra*). These have previously been shown to influence the insect species that occur in the Thetford Forest region, many of which are common in heathland and ruderal habitats in Mediterranean regions but rare elsewhere in Britain (Dolman et al., 2010). Most of Thetford's significant indicator spider species were habitat generalists that were significantly associated with Scots pine monocultures. One such species that appears to be supported by Thetford's Scots pine monocultures, *Agyneta subtilis,* is classed as vulnerable in Britain and is found in coastal and heathland habitats as well as woodland (Harvey et al., 2002). This suggests that the Scots pine monocultures may act as a habitat reserve for some of the sandy heathland species that formerly inhabited the site, just as the deciduous oak woodland also supports a number of specialist deciduous beetle species. These results highlight the clear role of specific stand types for enhancing overall regional species richness and the importance of considering woodland continuity and historical context to help explain current species assemblages.

The spiders *M. viaria* and *D. picinus* were the only two species that emerged as consistent indicators of particular forest stand types in more than one region. These species are known to prefer deciduous woodland (Harvey et al., 2002; Nolan, 2008) and as such were associated with Scots pine and oak mixtures and oak monocultures in Thetford Forest and Ireland. This low number of consistent indicator species across regions suggests that species selected as indicators of a forest type in one region may not be good indicators in other regions, and regional differences again seem to be more important drivers of habitat preferences than tree species composition. This is not unexpected as the distribution and number of spider and carabid species vary significantly across Britain and Ireland (Van Helsdingen, 1996; Harvey et al., 2002; Ferriss et al., 2009). Overall, there were more spiders than carabid beetles associated with a particular stand type. The low number of carabid beetle indicator species significantly affiliated with specific forest stand types (4% of species) is consistent with other research (Oxbrough et al., 2010). The higher percentage of significant spider indicator species showing associations with stand type, suggests that spiders may be more sensitive to the habitat variation attributable to these forest plantation stand types than carabids. In addition, the different levels of stand affiliation in carabids and spiders, along with their different responses to stand type, highlight the importance of choosing varied indicator taxa in biodiversity studies.

While this study, as others (e.g., Barbier et al., 2008; Oxbrough et al., 2012) does not lend support to current discussions around the potential biodiversity benefits of mixed stands over monocultures, other mixtures can be envisaged that may be beneficial. These include intimate mixtures with more main canopy tree species and/or different tree species mixtures to those studied here. Both oak and Scots pine are native to Britain, and as such innately support a high number of phytophagous insect and mite species (Kennedy and Southwood, 1984). In contrast, admixing a native broadleaf to a non-native conifer plantation, where there are likely to be fewer associated native insect species, might substantially increase the abundance and diversity of, for example, insect herbivores and associated predators as other authors have found (e.g., Butterfield and Malvido, 1992; Magura et al., 2002). Admixing a broadleaf to a conifer that casts a dense shade might also increase stand light levels with the consequence of increasing understory vegetation and, thus potentially increasing stand structural diversity (Humphrey et al., 2003). In this study, canopy openness was not significantly different between stand types.

With regards to increasing the number of tree species, Schuldt et al. (2008) have found that intermediate levels of tree species diversity significantly improved the richness and abundance of ground-living spiders compared with single species stands. A similar increase in canopy beetle species richness was observed by Sobek et al. (2009) across a tree diversity gradient. In our study, while spider and carabid beetles assemblages did not respond to Scots pine and oak mixtures, a number of species were strongly affiliated to the tree species present. As in our study, Taboada et al. (2010) found significantly increased carabid beetle species richness in oak-dominated forest stands compared with Scots pine monocultures, although they found a higher proportion of forest specialists in Scots pine plantation stands compared to oak stands. Fuller et al. (2008) corroborate this finding with observations of a significantly higher proportion of forest specialist carabid beetle species in mixed deciduous woodland comprised of oak, birch (*Betula* spp.) and sycamore (*Acer pseudoplatanus*) compared with Scots pine monocultures.

5. Conclusions and recommendations for forest management

It has been suggested that the inclusion of more than one dominant tree species to a forest stand, and particularly a native broadleaf species, could increase habitat heterogeneity and enhance forest biodiversity. However, our study found no significant consistent effect of mixed or monoculture tree species on ground-dwelling spider and carabid beetle diversity. At the levels of mixing considered within this study (10–60% broadleaf component), and considering the two tree species under study, Scots pine and oak, mixed stands showed no influence on spider or beetle diversity compared to monocultures of these species. This supports previous research suggesting that additional broadleaf canopy species confer no clear arthropod biodiversity benefits at levels of up to 60% of the mix (Oxbrough et al., 2012; Barbier et al., 2008), although they may have an influence at greater broadleaf to conifer mixing ratios. European and UK forest management policies currently recommend much lower levels of mixing of broadleaved components in pine forests (such as 5% in the UK) (European Environment Agency, 2008; Forest Service, 2000; Forestry Commission, 2011); further research is needed to establish whether a greater broadleaf component in conifer-broadleaf mixtures will improve their biodiversity value over conifer stands of simpler species composition, but also, which specific species mixtures are most beneficial i.e., which tree species should be combined? How many different tree species should be combined in a mixture before benefits are derived?

There was no clear advantage or disadvantage of oak and Scots pine mixtures for spider and beetle diversity when compared to oak or Scots pine monocultures. Any benefit conferred by one monoculture stand type over the other was dependent on region and study taxa. Thus, for these arthropod species groups and forest stand types, at least, there does not appear to be any clear biodiversity management benefit to promoting a mixed tree species composition, or favouring one tree species for planting over another for biodiversity conservation with the exception possibly of regions with limited broadleaf components in the landscape and especially where the climate is drier; here a broadleaf component is likely to provide more significant benefits as in the case of oak in Thetford Forest which favours a number of specialist spider/carabid species. A combination of these stand types in a landscape matrix is more likely to satisfy any strong species-specific associations with either oak or Scots pine trees.

Table A.1
List of the total number of ground-dwelling spider species caught in pitfall traps from May till August 2011 in the three study regions and three forest stand types (SP = Scots pine monocultures, OK = oak monocultures, OK/SP = Scots pine and oak mixtures. Habitat preference is according to Nolan (2008) and Harvey et al., 2002 and includes: G = generalists, F = forest habitat specialists, O = open habitat specialists. Species highlighted in bold were present at least once across all regions.

Spider species	Specialism	Forest region and stand type									Total
		Ireland			New Forest			Thetford Forest			
		SP (*n* = 4)	OK (*n* = 4)	OK/SP mix (*n* = 4)	SP (*n* = 5)	OK (*n* = 5)	OK/SP mix (*n* = 5)	SP (*n* = 5)	OK (*n* = 5)	OK/SP mix (*n* = 5)	
Pirata hygrophilus	G	3	–	1	203	332	204	689	531	736	2699
Pardosa lugubris	F	50	33	17	171	100	305	33	69	113	891
Tenuiphantes alacris	F	380	66	187	–	–	–	6	–	–	639
Tenuiphantes zimmermanni	F	129	89	86	43	16	37	40	12	19	471
Tenuiphantes flavipes	F	21	8	3	32	108	28	69	54	48	371
Monocephalus fuscipes	F	133	37	58	1	2	4	5	2	1	243
Walckenaeria acuminata	G	61	23	67	1	6	9	5	10	18	200
Microneta viaria	F	1	20	–	1	18	7	14	84	53	198
Ozyptila trux	G	11	2	9	11	77	3	19	38	24	194
Robertus lividus	G	6	12	29	10	11	9	17	24	24	142
Diplocephalus latifrons	F	8	51	5	–	6	–	2	52	9	133
Saaristoa abnormis	G	9	10	14	59	9	21	6	1	1	130
Tenuiphantes tenebricola	F	40	24	37	–	–	3	22	2	–	128
Agyneta ramosa	F	25	24	46	2	5	2	8	2	7	121
Diplostyla concolor	G	1	1	3	–	28	6	12	22	33	106
Macrargus rufus	F	–	–	–	1	10	3	12	49	28	103
Agyneta subtilis	G	15	10	31	1	–	–	33	–	–	90
Diplocephalus picinus	F	–	25	25	–	–	–	–	26	3	79
Palliduphantes pallidus	G	3	1	7	20	10	6	13	1	4	65
Gongylidiellum vivum	G	4	4	35	5	2	3	10	–	–	63
Walckenaeria cucullata	F	6	1	12	27	1	9	1	5	–	62
Trochosa terricola	O	6	–	–	16	6	18	3	3	3	55
Dicymbium tibiale	G	11	3	29	2	–	1	2	3	3	54
Walckenaeria atrotibialis	G	11	5	11	–	–	–	7	5	3	42
Pachygnatha listeri	F	7	2	7	4	1	2	12	3	2	40
Bathyphantes nigrinus	G	3	16	11	–	–	–	–	1	–	31
Agroeca brunnea	F	–	–	–	4	6	10	8	–	3	31
Dismodicus bifrons	G	27	1	2	–	–	–	–	–	–	30
Micrargus herbigradus	G	–	1	3	1	1	–	12	3	9	30
Pocadicnemis pumila	G	13	1	1	8	1	5	–	–	–	29
Tenuiphantes tenuis	G	14	5	8	–	–	–	–	–	–	27
Gongylidiellum latebricola	G	–	1	–	18	4	3	–	–	–	26
Linyphia hortensis	F	–	8	12	–	–	1	3	1	1	26
Gonatium rubellum	F	16	2	5	–	–	–	1	–	1	25
Neriene clathrata	G	4	1	3	7	–	3	3	1	1	23
Ceratinella scabrosa	G	14	2	1	–	–	–	3	–	1	21
Zora spinimana	G	1	2	1	4	2	–	5	–	3	18
Centromerus dilutus	G	5	–	1	1	–	2	8	–	–	17
Tenuiphantes cristatus	G	–	–	–	2	–	–	8	6	1	17
Maso sundevalli	G	8	1	5	–	–	–	–	–	2	16
Walckenaeria dysderoides	G	2	1	3	–	–	–	1	4	5	16
Scotina celans	F	–	–	–	7	–	9	–	–	–	16
Pardosa pullata	O	14	–	–	2	–	–	–	–	–	16
Metellina mengei	G	3	2	5	–	–	1	3	–	1	15
Clubiona terrestris	G	–	–	–	1	–	2	2	3	6	14
Harpactea hombergi	G	–	–	–	3	–	4	4	–	3	14
Neriene peltata	G	1	1	3	1	1	2	2	–	3	14
Pachygnatha degeeri	G	–	–	–	–	6	5	1	2	–	14
Walckenaeria vigilax	G	9	–	3	–	1	–	–	–	–	13
Neon reticulatus	G	2	–	2	4	–	2	1	–	1	12
Phrurolithus festivus	O	–	–	–	3	4	4	–	–	1	12
Ceratinella brevis	G	–	1	–	–	1	–	2	6	1	11
Agyneta conigera	G	2	–	2	–	–	–	5	–	1	10
Episinus angulatus	G	–	–	–	3	–	1	6	–	–	10
Ozyptila praticola	F	–	–	–	–	–	–	4	3	3	10
Bathyphantes parvulus	O	–	–	–	–	–	–	3	1	6	10
Zelotes apricorum	O	–	–	–	–	–	10	–	–	–	10
Clubiona comta	G	3	–	3	–	–	1	–	2	–	9
Euophrys frontalis	G	–	–	–	3	–	2	4	–	–	9
Palliduphantes ericaeus	G	–	–	2	1	1	1	4	–	–	9
Walckenaeria cuspidata	G	–	2	–	4	2	1	–	–	–	9
Walckenaeria nudipalpis	G	4	–	–	–	1	–	–	2	2	9
Asthenargus paganus	F	4	1	4	–	–	–	–	–	–	9
Ceratinella brevipes	G	4	1	2	–	–	–	–	–	–	7
Tenuiphantes mengei	G	–	–	–	3	1	–	3	–	–	7
Coelotes terrestris	F	–	–	–	–	–	7	–	–	–	7
Tapinocyba pallens	F	2	1	4	–	–	–	–	–	–	7
Zelotes pedestris	O	–	–	–	–	1	–	3	–	3	7

(*continued on next page*)

Table A.1 (*continued*)

Spider species	Specialism	Forest region and stand type									Total
		Ireland			New Forest			Thetford Forest			
		SP ($n = 4$)	OK ($n = 4$)	OK/SP mix ($n = 4$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	
Robertus neglectus	G	–	–	–	–	–	2	1	3	–	6
Saaristoa firma	G	–	1	5	–	–	–	–	–	–	6
Erigonella hiemalis	F	–	–	–	–	–	–	3	1	2	6
Pocadicnemis juncea	O	5	1	–	–	–	–	–	–	–	6
Pachygnatha clercki	G	–	–	1	–	1	1	–	–	2	5
Rugathodes instabilis	G	–	–	5	–	–	–	–	–	–	5
Xysticus luctator	G	–	–	–	–	–	5	–	–	–	5
Hahnia helveola	F	–	2	–	1	–	–	2	–	–	5
Clubiona lutescens	G	–	–	–	–	–	–	3	1	–	4
Gongylidium rufipes	G	3	–	–	–	–	–	–	1	–	4
Porrhomma campbelli	G	–	–	–	–	3	1	–	–	–	4
Haplodrassus silvestris	F	–	–	–	–	2	2	–	–	–	4
Obscuriphantes obscurus	F	1	1	2	–	–	–	–	–	–	4
Bathyphantes gracilis	G	1	–	1	–	–	–	–	–	1	3
Clubiona pallidula	G	–	–	–	–	–	–	–	3	–	3
Hilaira excisa	G	–	–	–	2	–	1	–	–	–	3
Amourobius fenestralis	F	–	–	–	1	–	–	2	–	–	3
Clubiona corticalis	F	–	–	–	–	–	1	2	–	–	3
Tapinocyba insecta	F	–	–	–	–	–	–	–	2	1	3
Walckenaeria obtusa	F	–	–	–	–	–	1	–	1	1	3
Enoplognatha ovata	O	2	–	–	–	–	–	–	–	1	3
Pirata latitans	O	–	–	–	–	1	1	1	–	–	3
Xysticus cristatus	O	–	–	–	–	2	–	1	–	–	3
Agroeca proxima	G	2	–	–	–	–	–	–	–	–	2
Centromerus sylvaticus	G	–	–	–	–	1	–	–	1	–	2
Cryphoeca silvicola	G	2	–	–	–	–	–	–	–	–	2
Linyphia triangularis	G	–	1	1	–	–	–	–	–	–	2
Maro minutus	G	–	–	–	–	–	–	1	1	–	2
Meioneta saxatilis	G	–	–	–	–	–	–	2	–	–	2
Metellina segmentata	G	2	–	–	–	–	–	–	–	–	2
Metopobactrus prominulus	G	2	–	–	–	–	–	–	–	–	2
Oedothorax fuscus	G	–	1	1	–	–	–	–	–	–	2
Paidiscura pallens	G	1	–	1	–	–	–	–	–	–	2
Porrhomma egeria	G	–	–	–	–	1	1	–	–	–	2
Porrhomma pallidum	G	–	–	–	2	–	–	–	–	–	2
Porrhomma pygmaeum	G	–	–	–	–	–	–	–	–	2	2
Walckenaeria furcillata	G	–	–	–	2	–	–	–	–	–	2
Anyphaena accentuata	F	–	–	–	–	–	–	1	–	1	2
Lepthyphantes minutus	F	–	–	–	–	–	–	1	–	1	2
Minyriolus pusillus	F	–	–	–	2	–	–	–	–	–	2
Erigone dentipalpis	O	–	–	2	–	–	–	–	–	–	2
Micaria pulicaria	O	–	–	–	–	1	1	–	–	–	2
Pardosa nigriceps	O	2	–	–	–	–	–	–	–	–	2
Trochosa robusta	O	–	–	–	–	1	1	–	–	–	2
Trochosa spinipalpis	O	–	–	–	1	–	1	–	–	–	2
Centromerus arcanus	G	–	–	1	–	–	–	–	–	–	1
Clubiona reclusa	G	–	1	–	–	–	–	–	–	–	1
Enoplognatha thoracica	G	–	–	–	–	–	–	–	1	–	1
Ero furcata	G	–	1	–	–	–	–	–	–	–	1
Euryopis flavomaculata	G	–	–	–	1	–	–	–	–	–	1
Gongylidiellum murcidum	G	–	–	–	–	–	–	–	–	1	1
Hahnia montana	G	–	–	–	–	–	–	1	–	–	1
Leptorhoptrum robustum	G	–	1	–	–	–	–	–	–	–	1
Metellina merianae	G	–	1	–	–	–	–	–	–	–	1
Oedothorax gibbosus	G	–	–	1	–	–	–	–	–	–	1
Porrhomma montanum	G	–	–	–	–	1	–	–	–	–	1
Savigyna frontata	G	–	–	–	–	–	–	1	–	–	1
Segestria senoculata	G	–	–	–	–	–	–	–	–	1	1
Tibellus oblongus	G	–	–	–	–	–	–	–	1	–	1
Tiso vagans	G	–	–	–	–	1	–	–	–	–	1
Walckenaeria antica	G	–	–	–	–	1	–	–	–	–	1
Clubiona brevipes	F	–	–	–	–	1	–	–	–	–	1
Moebelia penicillata	F	–	–	–	–	–	–	1	–	–	1
Monocephalus castaneipes	F	–	1	–	–	–	–	–	–	–	1
Neriene montana	F	1	–	–	–	–	–	–	–	–	1
Philodromus dispar	F	–	–	–	–	–	–	1	–	–	1
Dipoena tristis	O	–	–	–	–	–	1	–	–	–	1
Drassodes cupreus	O	–	–	–	1	–	–	–	–	–	1
Erigone atra	O	–	–	1	–	–	–	–	–	–	1
Gonatium rubens	O	–	–	–	–	–	1	–	–	–	1
Ozyptila atomaria	O	–	–	–	–	–	–	1	–	–	1

Table A.1 (*continued*)

Spider species	Specialism	Forest region and stand type									Total
		Ireland			New Forest			Thetford Forest			
		SP ($n = 4$)	OK ($n = 4$)	OK/SP mix ($n = 4$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	
Pardosa amentata	O	–	1	–	–	–	–	–	–	–	1
Pardosa prativaga	O	1	–	–	–	–	–	–	–	–	1
Philodromus fallax	O	–	–	–	–	–	–	1	–	–	1
Pirata uliginosus	O	–	–	–	–	1	–	–	–	–	1
Total number of individuals		1121	515	827	703	799	777	1165	1049	1204	8160
Total number of species		58	54	57	48	48	56	67	46	53	143
Percentage of forest specialists		74%	77%	62%	42%	35%	55%	22%	35%	25%	45%
Percentage of open specialists		3%	0%	0%	3%	2%	5%	1%	0%	1%	2%
Percentage of generalist species		24%	23%	38%	54%	63%	40%	77%	65%	74%	53%

Table A.2
List of the total number of carabid beetle species caught in pitfall traps from May till August 2011 in the three study regions and three forest stand types (SP = Scots pine monocultures, OK = oak monocultures, OK/SP = Scots pine and oak mixtures. Habitat preference is according to Jukes et al. (2001), Luff (2007) and Thiele (1977) and includes: G = generalists, F = forest habitat specialists, O = open habitat specialists. Species highlighted in bold were present at least once across all regions.

Carabid beetle species	Specialism	Forest region and stand type									Total
		Ireland			New Forest			Thetford Forest			
		SP ($n = 4$)	OK ($n = 4$)	OK/SP mix ($n = 4$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	SP ($n = 5$)	OK ($n = 5$)	OK/SP mix ($n = 5$)	
Pterostichus madidus	G	116	207	187	81	1034	421	169	4432	8996	15643
Abax parallelepipedus	F	638	401	557	729	721	791	–	–	–	3837
Pterostichus melanarius	G	136	105	50	–	2	–	5	268	104	670
Pterostichus niger	G	264	13	84	31	17	17	32	74	45	577
Calathus rotundicollis	G	–	9	–	–	1	7	59	259	230	565
Nebria brevicollis	G	49	173	12	–	13	5	13	105	176	546
Carabus problematicus	G	23	–	5	1	15	8	150	69	119	390
Carabus violaceus	G	–	–	–	9	7	11	76	128	102	333
Carabus nemoralis	G	23	16	24	–	–	–	33	31	91	218
Pterostichus strenuus	G	47	14	10	–	32	1	2	2	12	120
Leistus rufomarginatus	F	–	–	–	–	–	–	14	32	12	58
Carabus granulatus	O	18	8	25	–	–	–	–	–	–	51
Oxypselaphus obscurus	G	–	–	–	2	44	1	–	–	3	50
Notiophilus biguttatus	G	–	–	–	4	4	5	1	13	6	33
Harpalus rufipes	O	–	–	–	–	–	–	–	2	30	32
Cychrus caraboides	F	5	–	12	1	–	–	3	3	7	31
Trechus obtusus	O	–	25	–	–	–	–	–	1	–	26
Notiophilus rufipes	G	–	–	–	–	5	1	2	8	4	20
Stomis pumicatus	G	–	–	–	–	–	–	5	1	10	16
Leistus terminatus	G	6	–	8	–	–	–	–	–	–	14
Notiophilus substriatus	O	–	1	1	–	–	–	1	2	8	13
Laemostenus terricola	G	–	–	–	–	–	–	12	–	–	12
Loricera pilicornis	G	3	7	–	–	–	–	1	1	–	12
Badister bullatus	G	–	–	–	–	–	–	3	5	3	11
Trechus secalis	G	–	–	–	–	–	10	–	–	–	10
Harpalus latus	O	3	–	–	1	–	–	3	2	1	10
Pterostichus minor	O	–	–	–	–	10	–	–	–	–	10
Bembidion mannerheimi	G	–	–	–	–	5	3	–	–	–	8
Agonum fuliginosum	O	2	5	1	–	–	–	–	–	–	8
Synchus vivalis	G	–	5	2	–	–	–	–	–	–	7
Clivina fossor	O	–	2	–	–	4	–	–	–	1	7
Platyderus depressus	O	–	–	–	–	–	–	1	3	3	7
Calathus micropterus	G	–	2	–	–	–	–	–	4	–	6
Pterostichus cristatus	G	–	–	–	–	–	–	6	–	–	6
Amara convexior	O	2	–	–	–	–	–	2	1	–	5
Leistus fulvibarbis	F	–	–	–	–	–	–	–	4	–	4
Bembidion guttula	G	–	–	–	–	2	–	–	–	–	2
Badister sodalis	F	2	–	–	–	–	–	–	–	–	2
Platynus assimilis	F	–	–	–	–	2	–	–	–	–	2
Bembidion lampros	G	–	–	–	–	1	–	–	–	–	1
Bradycellus harpalinus	G	–	–	–	–	–	–	–	1	–	1
Leistus spinibarbis	G	–	–	–	–	–	–	–	1	–	1
Notiophilus palustris	G	–	–	–	–	–	–	–	–	1	1
Pterostichus nigrita/rhaeticus	G	–	–	1	–	–	–	–	–	–	1
Trechus quadristriatus	G	–	–	–	–	–	–	–	1	–	1
Amara eurynota	O	–	–	–	–	–	–	–	1	–	1
Amara plebeja	O	1	–	–	–	–	–	–	–	–	1
Amara similata	O	–	–	–	–	–	–	–	1	–	1

(*continued on next page*)

Table A.2 (*continued*)

Carabid beetle species	Specialism	Forest region and stand type									Total
		Ireland			New Forest			Thetford Forest			
		SP (*n* = 4)	OK (*n* = 4)	OK/SP mix (*n* = 4)	SP (*n* = 5)	OK (*n* = 5)	OK/SP mix (*n* = 5)	SP (*n* = 5)	OK (*n* = 5)	OK/SP mix (*n* = 5)	
Chlaenius nigricans	O	–	–	–	–	–	–	–	–	1	1
Curtonotus aulicus	O	1	–	–	–	–	–	–	–	–	1
Elaphrus cupreus	O	–	1	–	–	–	–	–	–	–	1
Harpalus tardus	O	–	–	–	–	–	–	–	1	–	1
Ophonus laticollis	O	–	–	–	–	–	–	–	1	–	1
Pterostichus anthracinus	O	1	–	–	–	–	–	–	–	–	1
Pterostichus vernalis	O	–	1	–	–	–	–	–	–	–	1
Total number of individuals		1340	995	979	859	1919	1281	593	5457	9965	23,388
Total number of species		19	18	15	9	18	13	22	31	23	55
Percentage of forest specialists		48%	40%	58%	85%	38%	62%	3%	1%	0%	17%
Percentage of open specialists		2%	4%	3%	0%	1%	0%	1%	0%	0%	1%
Percentage of generalist species		50%	55%	39%	15%	62%	38%	96%	99%	99%	82%

Acknowledgments

We would like to thank: Jacqui Brunt, Mark Ferryman and Rob Deady for assistance with arthropod sample sorting and assistance with fieldwork, Steve Coventry, Paul Turner, John Lakey, Stephen Whall, Liz Richardson and Mark Oram for organisation of and help with fieldwork, David Williams for help with identification of the more cryptic carabid beetle species, Linda Coote and Mark Wilson for help with Irish site selection and Sandra Irwin, Tom Kelly, John O'Halloran and Daniel Kelly for initial discussions. Thank you also to Linda Coote for providing habitat data from Ireland. Many thanks to the anonymous reviewer for the detailed feedback provided. Funding for this research was provided by the Forestry Commission to Forest Research's Biodiversity Project and matched funding was provided by the European Union (European Regional Development Fund ERDF) within the framework of the European INTERREG IV A 2 Mers Seas Zeeën Cross-border Cooperation Programme 2007–2013 (Project 090316 016-FR MULTIFOR: Management of Multi-Functional Forests). Funding is also gratefully acknowledged from the Planforbio Research Programme which is funded by Ireland's the Department of Agriculture, Food and the Marine under the National Development Plan 2007–2013.

Appendix A.

See Tables A.1 and A.2.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Aust. Ecol. 26, 32–46.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. Forest Ecol. Manage. 254 (1), 1–15.

Benton, T.G., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188.

Bersier, L.F., Meyer, D.R., 1994. Bird assemblages in mosaic forests – the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecol. 15, 561–576.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951.

Brown, A.H.F., 1992. Functioning of mixed-species stands at Gisburn, N.W. England. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific Publications, London, pp. 99–113.

Brown, N., Jennings, S.Wheeler., Nabe-Nielsen, J., 2000. An improved method for the rapid assessment of forest understorey light environments. J. Appl. Ecol. 37, 1044–1053.

Butterfield, J., Malvido, J.B., 1992. Effect of mixed-species tree planting on the distribution of soil invertebrates. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-species Stands of Trees, Spec. Publ. No. 11. British Ecological Society, Blackwell, Oxford, pp. 255–265.

Cameron, K.H., Leather, S.R., 2012. How good are carabid beetles (Coleoptera, Carabidae) as indicators of invertebrate abundance and order richness? Biodivers. Conserv. 21, 763–779.

Cavard, X., Macdonald, S.E., Bergeron, Y., Chen, H.Y.H., 2011. Importance of mixed woods for biodiversity conservation: evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environ. Rev. 19, 142–161.

Clarke, R.D., Grant, P.R., 1968. An experimental study of the role of spiders as predators in a forest litter community. Part 1. Ecology 49, 1152–1154.

Dannatt, N., 1996. Thetford forest: its history and development. In: Ratcliffe, P., Claridge, J. (Eds.), Thetford Forest Park: The Ecology of a Pine Forest. Forestry Commission Technical Paper 13, Forestry Commission, Edinburgh.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574.

Del Río, M., Sterba, H., 2009. Comparing volume growth in pure and mixed stands of *Pinus sylvestris* and *Quercus pyrenaica*. Ann. For. Sci. 66, 502–512.

Dhôte, J., 2005. Implication of forest diversity in resistance to strong winds. In: Scherer-Lorenzen, M., Körner, C. (Eds.), Forest Diversity and Function: Temperate and Boreal Systems. Springer-Verlag, Berlin.

Dolman, P.M., Panter, C., Mossman, H.L., 2010. Securing Biodiversity in Breckland: Guidance for Conservation and Research. First Report of the Breckland Biodiversity Audit. University of East Anglia, Norwich.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

European Environment Agency, 2008. European Forests – Ecosystem Conditions and Sustainable Use. In: EEA Report, Copenhagen.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, Siriwardena, G.M., Martin, J.-L., 2010. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 1–14.

Ferriss, S.E., Smith, K.G., Inskipp, T.P. (Eds.), 2009. Irish Biodiversity: A Taxonomic Inventory of Fauna. Irish Wildlife Manuals, No. 38. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

Forest Europe, UNECE, FAO, 2011. State of Europe's Forests 2011. United Nations Economic Commission for Europe.

Forest Service, 2000. Forest Biodiversity Guidelines. Forest Service, Department of the Marine and Natural Resources, Dublin.

Forestry Commission, 2011. The UK Forestry Standard: The UK Government's Approach to Sustainable Forestry. The Forestry Commission, Edinburgh, UK.

Fuller, R.J., Oliver, T.H., Leather, S.R., 2008. Forest management effects on Carabid beetle communities in coniferous and broadleaved forests: implications for conservation. Insect Conserv. Divers. 1, 242–252.

Grant, M.J., Edwards, M.E., 2008. Conserving idealized landscapes: past history, public perception and future management in the New Forest (UK). Veg. Hist. Archaeobot. 17, 551–562.

Guest, C., Huss, J., 2012. Nursing of oak in Ireland. COFORD Connects. <http://www.coford.ie/media/coford/content/publications/projectreports/cofordconnects/SM21-LR.PDF>, (last accessed 09.03.13).

Gunnarsson, B., 1983. Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. Oikos 40, 226–233.

Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H., 2012. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 dataset. Submitted to International Journal of Climatology. Retrieved from: <http://www.badc.nerc.ac.uk/view/badc.nerc.ac.uk__ATOM__dataent_1256223773328276>, (last accessed 01.13).

Harvey, P.R., Nellist, D.R., Telfer, M.G., 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Natural Environment Research Council, Biological Records Centre, Cambridge, UK.

Humphrey, J., Ferris, R., Quine, C., 2003. Biodiversity in Britain's Planted Forests. Forestry Commission, Edinburgh, pp. 51–62.

Jukes, M.R., Peace, A.J., Ferris, R., 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. Forest Ecol. Manage. 148, 271–286.

Kennedy, C.E.J., Southwood, T.R.E., 1984. The number of species of insects associated with british trees – a re-analysis. J. Anim. Ecol. 53, 455–478.
Kerr, G., Nixon, C.J., Matthews, R.W., 1992. Silviculture and yield of mixed-species stands: the UK experience. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Scientific Publications.
Koricheva, J., Vehvilainen, H., Riihimaki, J., Ruohomaki, K., Kaitaniemi, P., Ranta, H., 2006. Diversification of tree stands as a means to manage pests and diseases in boreal forests: myth or reality? Can. J. For. Res. 36, 324–336.
Kostylev, V.E., 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. Ecol. Complex. 2, 272–282.
Lack, D., 1969. The numbers of bird species on islands. Bird Study 16, 193–209.
Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.
Luff, M., 2007. RES Handbook, Part 2: The Carabidae (Ground Beetles) of Britain and Ireland, vol. 4. Field Studies Council, Shropshire, UK.
Lust, N., Muys, B., Nachtergale, L., 1998. Increase of biodiversity in homogeneous Scots pine stands by an ecologically diversified management. Biodivers. Conserv. 7, 249–260.
Magura, T., Tóthmérész, B., Elek, Z., 2002. Impacts of non-native spruce reforestation on ground beetles. Eur. J. Soil Biol. 38, 291–295.
Malaque, M.A., Maeto, K., Ishii, H.T., 2008. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Appl. Entomol. Zool. 44 (1), 1–11.
McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biol. Rev. 73, 181–190.
Morneau, F., Duprez, C., Hervé, J.C., 2008. Les forêts mélangées en France métropolotaine. Caractérisation à partir des résultats de l'Inventaire Forestier National. Rev. Forest. FR. LX, 107–120.
Niemelä, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P., 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. J. Biogeogr. 19, 173–181.
Nolan, M., 2008. Database of Irish Spiders (Araneae), in Irish Wildlife Manuals. National Parks and Wildlife Service. Department of Environment, Heritage and Local Government, Dublin, Ireland.
Oxbrough, A., Gittings, T., O'Halloran, J., Giller, P.S., Smith, G.F., 2005. Structural indicators of spider communities across the forest plantation cycle. Forest Ecol. Manage. 212, 171–183.
Oxbrough, A., Irwin, S., Kelly, T.C., O'Halloran, J., 2010. Ground-dwelling invertebrates in reforested conifer plantations. Forest Ecol. Manage. 259, 2111–2121.
Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? Forest Ecol. Manage. 270, 11–18.
Pearce, J.L., Venier, L.A., 2006. The use of beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: a review. Ecol. Indic. 6, 780–793.
Pérot, T., Picard, N., 2012. Mixture enhances productivity in a two-species forest: evidence from a modelling approach. Ecol. Res. 27, 83–94.
Peterken, G.F., 1993. Woodland Conservation and Management, second ed. Chapman & Hall, London.
Platnick, N.I., 2012. The world spider catalog, version 13.0. American Museum of Natural History, online at: <http://www.research.amnh.org/iz/spiders/catalog>, (last accessed 09.03.13).
R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
Randall, R., Dymond, D., 1996. Why thetford forest? The human and natural history of Breckland before the early 20th century. In: Ratcliffe, P., Claridge, J. (Eds.), Thetford Forest Park: The Ecology of a Pine Forest. Forestry Commission Technical Paper 13, Forestry Commission, Edinburgh.
Roberts, M.J., 1993. The Spiders of Great Britain and Ireland. Harley Books, Colchester, UK.
Roche, J., Mitchell, F., Waldren, S., 2009. Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland. Biodivers. Conserv. 18, 2185–2203.
Schuldt, A., Fahrenholz, N., Brauns, M., Migge-Kleian, S., Platner, C., Schaefer, M., 2008. Communities of ground-living spiders in deciduous: does tree species diversity matter? Biodivers. Conserv. 17, 1267–1284.
Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.
Sobek, S., Steffan-Dewenter, I., Scherber, C., Tscharntke, T., 2009. Spatiotemporal changes of beetle communities across a tree diversity gradient. Divers. Distributions 15, 660–670.
Taboada, A., Tárrega, R., Calvo, L., Marcos, E., Marcos, J.A., Salgado, J.M., 2010. Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. Eur. J. For. Res. 129, 31–45.
Tanabe, S.I., Masanori, J.T., Vinokurova, A.V., 2001. Tree shape, forest structure and diversity of drosophilid community: comparison between boreal and temperate birch forests. Ecol. Res. 16, 369–385.
Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.
Thiele, H., 1977. Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour. Springer-Verlag, Berlin.
Uetz, G., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40, 29–42.
Uetz, G., 1991. Habitat structure and spider foraging. In: Bell, S., McCoy, E., Mushinsky, H. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman & Hall, London.
Van Helsdingen, P.J., 1996. The county distribution of Irish spiders, incorporating a revised catalogue of the species. Ir. Nat. J. 25, 1–92.
Walsh, S., 2012. A Summary of Climate Averages for Ireland 1981–2000. Climatological Note No. 14, Met Éireann, Glasnevin Hill, Dublin 9.
Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecol. Manage. 255, 1251–1261.
Wise, D.H., 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48, 181–188.