Can mixed species stands enhance arthropod diversity in plantation forests?

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ABSTRACT

Tree species composition is a key driver of forest biodiversity, influencing structural components of the environment from soil and litter to vegetation layers and the canopy, and ecosystem processes, such as nutrient cycling. Single species stands, particularly intensively managed monoculture plantations, are typically more homogenous in habitat structure and the biotic communities supported, than mixed stands. Thus, international forest policy increasingly promotes the establishment of mixed stands as an alternative to enhance biodiversity in plantations. Forests represent around 10% of the land area of Ireland, with most being monocultures of non-native conifers. By contrast, natural forest cover, primarily comprised of deciduous species, is just 1%. In recent years there has been an increase in mixed plantations; however, optimum tree species combinations, which aim to promote biodiversity under sustainable forest management, have yet to be established. Arthropods (ground-dwelling spiders and Carabid beetles, and night-flying macrolepidoptera) were examined in twenty mixed and monoculture plantations in Ireland (Norway spruce–oak mix, Norway spruce–Scots pine mix, Norway spruce monoculture). Both oak and Scots pine were secondary mix components, comprising between 15% and 40% of stems. Spiders and Carabid beetles were sampled using pitfall traps during summer 2008 and moths using light traps during summer and autumn 2008 and spring 2009.

There was no evidence for an influence of oak or Scots pine on the arthropod fauna when they were a secondary component in a mix. Overall, arthropod communities were similar in species richness, assemblage structure and habitat specialists among the forest types. Furthermore, the mixed stands exhibited similar environmental conditions to monocultures in terms of stand structure, vegetation and litter cover. This suggests that there is limited biodiversity value from an additional canopy species comprising 15–40% of the mix, at least for the taxa and tree species studied here. This has implications for forest policy, where recommendations are often based on the proportion of each mix component, at least in terms of the potential biodiversity value of additional canopy species. Further research is required to determine the proportion at which oak or Scots pine begin to influence the arthropod fauna.

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1. Introduction

Tree species composition is a key driver of forest biodiversity, influencing structural components of the environment from soil and litter to vegetation layers and the canopy (Saetre et al., 1997; Berger and Puettmann, 2000; Elmer et al., 2004; Ammer et al., 2006; Laganière et al., 2008), as well as ecosystem processes such as nutrient cycling (Albers et al., 2004). Single species stands, particularly intensively managed monoculture plantations, are typically homogenous in terms of habitat structure and the biotic communities supported (Lust et al., 1998). In contrast, mixed stands have the potential to support a greater array of species either through species-specific associations, which are directly influenced by the additional tree species (Lepŝ et al., 1998), or

through a broader response of the biota to the more natural and varied stand conditions created (Lust et al., 1998). Furthermore, given an optimum composition of species, mixed stands can offer greater resilience to disturbances such as pest outbreaks (Jactel et al., 2005), disease (Pautasso et al., 2005), fire (Wirth, 2005) or extreme weather events (Dhôte, 2005). As a consequence, international forest policy increasingly promotes the establishment of mixed plantation stands an alternative to enhance biodiversity in plantations (Anon, 2006; European Environment Agency, 2008).

The majority of European plantation forests comprise a single species, usually a conifer (MCPFE et al., 2007), however, recent plantings of mixed stands have increased (European Environment Agency, 2008). This policy shift is also reflected at a national level in Ireland, where planting a mixture of tree species to enhance the biodiversity of managed forests is recommended by national guidelines (Forest Service, 2000). In response to this, the planting of mixed stands has increased across Ireland in recent years (Forest

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Service, 2004), with the aim of reducing the proportion of mono-culture stands in the forest estate and increasing species of native provenance. This is particularly important in Ireland where planta-tions represent 90% of the forested area (9% of the land area) and are typically represented by monocultures of non-native conifer species, primarily Sitka spruce (*Picea sitchensis*) (Forest Service, 2007). In contrast, only 1% of Ireland's land area is native woodland (Forest Service, 2007), which is dominated by deciduous species including oak (*Quercus* sp.), ash (*Fraxinus excelsior*) and birch (*Betula* sp.).

Arthropods are a key component of forest biodiversity, fulfilling vital ecosystem functions including pollination, nutrient cycling, regulation of pest populations, and as a food source for other arthropods, birds and mammals (Cardoso et al., 2011). Arthropod diversity is positively associated with increased landscape hetero-geneity, which can be achieved through planting forests with a mix of tree species (Oxbrough et al., 2005; Ziesche and Roth, 2008), which more closely approximate natural forests than monocul-tures. The aim of this study was to examine what influence the addition of a secondary tree species to a stand (either broadleaf or conifer species) has on arthropod community composition. This was achieved by investigating three arthropod groups: ground-dwelling spiders and Carabid beetles, which fulfil predatory func-tional roles in the forest ecosystem; and moths, which are phy-tophagous. Arthropod assemblages in commercial mixed and monoculture plantations were compared, and the following ques-tions were addressed:

1. Do mixed plantations support a more diverse arthropod fauna than monocultures?
2. Can a mixed stand with a native broadleaf species enhance arthropod diversity to a greater extent than a conifer mix?
3. What recommendations can be made for establishing mixed stand forests with the goal of enhancing plantation biodiversity?

2. Methods

2.1. Study sites

Two types of mixed plantation were selected for study: Norway spruce (*Picea abies* (L.) H. Karst.) with oak (*Quercus robur* L.) and Norway spruce with Scots pine (*Pinus sylvestris* L.), hereafter re-ferred to as oak mix and Scots pine mix respectively. In each of these mix types Norway spruce represented the primary compo-nent (>50% of stems) with oak or Scots pine constituting between 15% and 40% as the secondary species (Table 1). In all stands, the secondary species was dispersed (rather than aggregated) among the primary species. As a consequence of forest policy in Ireland over the last 30–50 years there are relatively few intimately mixed stands which are at a mature stage. However, these two mix types were relatively widely planted and so afforded an adequate level of replication across the island of Ireland (Fig. 1). *Q. robur* is a native species, whereas the status of Scots pine is under dispute; this spe-cies was common across Ireland ∼7500 years ago, but was believed extinct around 1600 years ago, although recent research has sug-gested that it may have survived in a few remnant patches (Roche et al., 2009).

Each mixed stand was matched to a nearby monoculture of Norway spruce (stands within five kilometres of each other), as far as possible, for site history (first rotation or planted on old woodland), soil type, elevation and management history (level of thinning), slope, aspect and drainage (Table 1). Stands ranged in age from 37 to 57 years in age, which represents commercial matu-rity of Norway spruce, and matched sites all planted within 5 years of each other and a wide variety of soil types were represented

(Table 1). Twenty stands were selected in total with five of each mix type matched to a Norway spruce monoculture. However, due to environmental differences between matched sites a paired experimental design was not adopted. For instance, two matched stands were located 50 km apart and several differed in elevation or soil type (Table 1). Instead, all monocultures (whether matched to an oak or Scots pine mix) were considered one forest type in the analyses giving three treatments: oak mix, Scots pine mix and Norway spruce monoculture. All stands were a minimum of four hectares in size (mean size 9.9 ha ± 4.5 SD) and 100 m wide.

2.2. Arthropod sampling

Three ground-dwelling arthropod sampling plots were estab-lished in each stand. These were located in representative areas of the site as a whole in terms of forest structure and vegetation cover. The plots were spaced a minimum of 50 m apart and not within 50 m of the forest edge. Spiders and Carabid beetles were collected using pitfall traps, a method which has been widely used to sample these taxa in forested habitats (Ziesche and Roth, 2008; Oxbrough et al., 2010). Pitfall traps are biased towards catching the more active species present and should not be viewed as an entire sample of the ground-dwelling community. However, the high numbers of individuals caught, coupled with the relative ease of their deployment argue in favour of their use in larger scale studies with multiple sites. At the centre of the plot six pitfall traps were spaced 2 m apart in a linear arrangement. Traps consisted of a plas-tic cup, approximately 7 cm in diameter and 9 cm in depth which had two drainage holes cut horizontally, 1 cm from the top of the cup. Ethylene glycol to a depth of 1 cm was used as a killing and preserving agent. The traps were set in mid May 2008 and pitfall contents were collected approximately every 3 weeks, during a nine week period, giving a total of between 62 and 64 trapping days at each plot. For analyses, data from five pitfall traps in a sam-pling plot were used; with the sixth being kept as a spare in case of accidental trap loss. This use of an extra trap eliminates the need to standardise the data by trap day if only one trap in the plot (as is most frequently the case) is disturbed.

Night flying macrolepidoptera (hereafter referred to as moths) were collected at all stands during the summer of 2008 and at a subset of 12 stands (three of each forest type) during autumn 2008 and spring 2009 (Table 1). Within 10 m of the pitfalls traps, Actinic Heath light traps were deployed. These traps are the most commonly used method for sampling moths as they collect the widest range of species of moth of any trapping technique (Fry and Waring, 2001). Light trapping was carried out in the Summer (June–mid July 2008) to correspond with the peak flight season (Fry and Waring, 2001), and also autumn (late September–mid October) and spring 2009 (late March–April) to sample adult moths which are more active during these periods. Each site was sampled once and adjacent sites were always sampled on the same night. Light traps were located a minimum of 100 m apart and never in direct line of sight, to prevent light interference between the traps. The traps were placed in the centre of a white sheet mea-suring 1.5 m × 1.5 m to increase visibility and also delineating a cut-off point in terms of counting moths around the trap whilst making sure there is no bias towards more conspicuous species. The traps were deployed before dusk on each sampling night and were automatically turned on and off by an attached light sensor at sunset and sunrise. Trapping was only carried out on nights where the temperature was >10 °C at dusk, when wind was not in excess of Beaufort force 4–5 (13–24 mph), and when persistent or heavy rain was not forecast for the night (Merckx et al., 2009). At dawn, netting was placed over each trap and white sheet to ensure moths captured did not escape before species identification.

Table 1
Characteristics of stands.

Site pair	Percentage secondary species in mix	Distance between stands	Stand age (mix/monoculture)	Site history	Elevation (m.a.s.l.)		Soil type	
					Mix	Monoculture	Mix	Monoculture
GARR[*]	15% Oak	6.4 km	48/50 years	Unforested	130	55	Brown Earth/Gley	Gley
GOSF	35% Oak	0.2 km	48/44 years	Unforested	80	70	Brown Earth	Brown Earth
PARK[*]	40% Oak	0.3 km	47/44 years	Unforested	100	97	Brown Earth	Brown Earth
THOM	40% Oak	5.1 km	47/38 years	Old woodland	80	60	Brown podzolic	Peat
WOOD[*]	20% Oak	0.5 km	53/52 years	Unforested	248	250	Peat/Gley	Peat/Gley
CAST	40% Scots pine	8.2 km	53/48 years	Unforested	50	50	Gley	Gley
COOL[*]	40% Scots pine	53.0 km	37/38 years	Unforested	80	130	Brown Earth	Brown Earth/Gley
CRAB[*]	25% Scots pine	0.5 km	37/38 years	Unforested	140	140	Peat	Peat
JENK	15% Scots pine	0.9 km	58/56 years	Unforested	175	160	Gley	Gley
MOTE	35% Scots pine	1.6 km	57/55 years	Old woodland	40	57	Brown podzolic	Brown podzolic

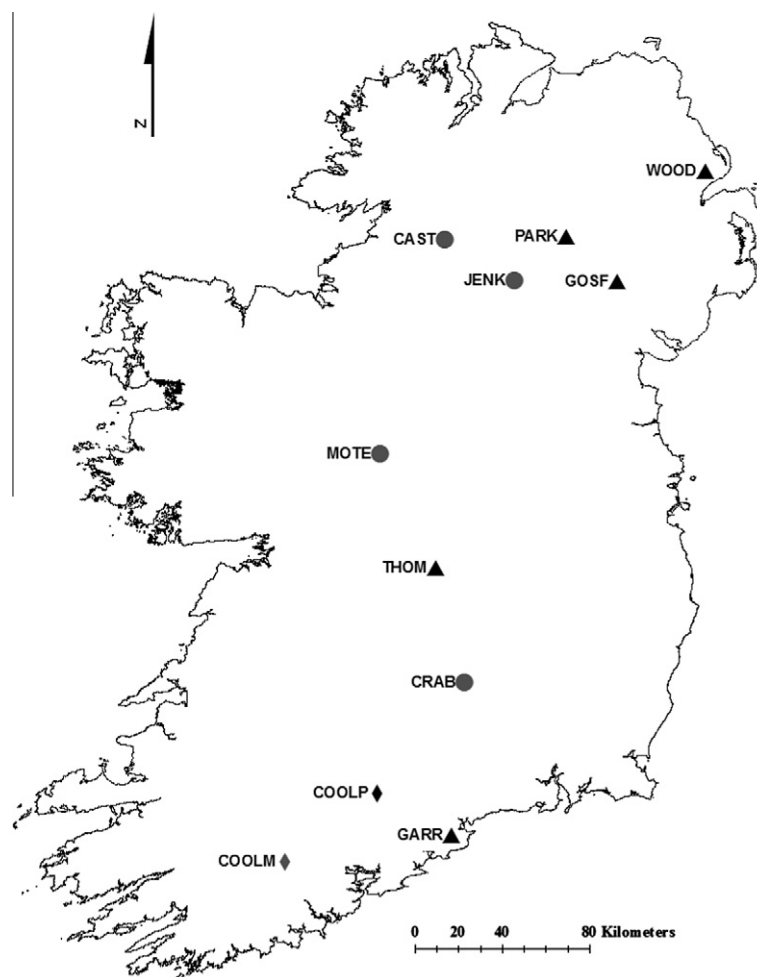[*] Stands used for spring and autumn moth trapping.

Fig. 1. Distribution of matched stands across Ireland: ▲ Norway spruce–oak mix with matching Norway spruce monoculture; ● Norway spruce–Scots pine mix with matching Norway spruce monoculture; ◆ Individual Norway spruce–Scots pine mix; ◆ Individual matching monoculture of Scots pine mix.

Spiders and Carabid beetles (hereafter referred to as beetles) were sorted from the pitfall contents in the laboratory and adults were identified to species using Roberts (1993) and Luff (2007), respectively. Moths were identified in the field using Waring and Townsend (2007). Photographs were taken of ambiguous species for later identification and, where necessary, were killed in a jar using 30% ammonia, stored in a cooling box, and pinned for later identification by an expert. Species from each taxa were assigned to habitat (spiders and beetles) or larval feeding preferences (moths) using the literature (Emmet and Heath, 1991; Roberts, 1993; Forsythe, 2000; Harvey et al., 2002; Luff, 2007; Waring and Townsend, 2007; Bond and Gittings, 2008).

2.3. Environmental variables

The percent cover of vegetation layers was estimated within a 1 m² quadrat surrounding each of the five pitfall traps in each plot using the following classification: ground layer vegetation

(<10 cm); lower vegetation layer (>10 cm–50 cm); upper vegetation layer (>50 cm–200 cm) and understory layer (>200 cm). Litter cover, type and depth was also measured within each quadrat. For analyses, a mean value was calculated across the five quadrats to obtain a representative value per plot. A 20 m × 20 m plot was established adjacent to each pitfall plot where stand structure variables were measured including canopy openness by hemispherical photography at the centre of the 20 × 20, DBH, tree height and the number of stems. In addition, five soil samples (depth 10 cm) were taken from each plot. These were combined in a suspension of distilled water and pH was derived using a glass electrode pH meter. Organic matter content was determined from air dried samples which were then placed in a furnace at 550 °C for 5 h.

2.4. Data analysis

Data were pooled across the three collection periods and for all taxa, and stand data were used as the sample unit in analyses, derived from mean values per pitfall plot/light trap within each stand. Moth species known to be associated with open habitats were omitted from the analyses so capture of these vagrants did not obscure the results.

Partial Redundancy Analysis (RDA) was used to examine the relationship between assemblage structure and forest type for each taxon group. To account for differences in location and environmental variables within forest types a forward selection permutation procedure (Blanchet et al., 2008) was used to identify covariates for the partial RDAs. Ecologically meaningful environmental variables were chosen for the forward selection, i.e. those which are likely to directly influence the taxon group in question, using previous research in Irish plantations and the literature (Emmet and Heath, 1991; Oxbrough et al., 2005; Bond and Gittings, 2008; Oxbrough et al., 2010). This approach has the advantage of reducing the complexity of the model (in comparison with a 'shotgun approach' using all variables) by only including variables with sound ecological basis for inclusion in the model (Anderson, 2008). Collinear variables were also excluded. Initial environmental variables for the forward selection were: cover of ground vegetation (collinear with litter depth r_s = 0.94), lower field layer, leaf litter, needle litter, canopy openness, soil pH, soil organic content and DBH (collinear with tree height r_s = 0.85). For moths, understorey cover and number of planted stems were also included. RDAs were tested for significance using an ANOVA based permutation procedure. Species data were submitted to a Hellinger transformation prior to analyses (Legendre and Gallagher, 2001). Moth data were standardised by total trapping hours and trapping date was used as an additional covariate in the analyses. Variation partitioning was used to examine the relative importance of environmental variables and geographical location for each taxon assemblage using the variables identified by the forward selection procedure. For moths, the above analyses could only be carried out on data collected during the summer period (n = 20), as data were only collected across the three seasons from a subset of sites (n = 12).

Indicator Species Analysis was used to identify species which have a high affinity for the forest types. This method combines relative frequency and relative of abundance of species between groups (forest types). The resulting indicator values were tested for significance using a randomisation test.

A permutation based partial ANOVA (Anderson, 2001) was used to examine differences in species richness, relative abundance of forest-associated species between the forest types; covariables were selected using the forward selection procedure. However, for moths no covariables were used in the ANOVA as the number of stands (n = 12) was too low. Moth richness was estimated using individual based rarefaction (Gotelli and Colwell, 2001) as catches of individuals from light traps may be influenced by length of trap-

ping period (e.g. hours of darkness), which changed within sampling periods. After rarefaction, values were standardised by number of sampling hours across the three sampling periods, and the minimum number of hours among the stands was used to delineate the rarefaction cutoff point for each stand. However, as the rarefaction technique makes certain assumptions on the data i.e. samples taken from similar communities, species abundance distributions, individuals are randomly dispersed (Magurran, 2008), both observed and expected values (after rarefaction) were examined.

One-way ANOVA with Tukey post-hoc test was used to examine differences in environmental variables between forest types. Where data did not conform to the assumptions of normality or homogeneity non-parametric Kruskal Wallis was used and all percentage and proportion data were arcsine transformed prior to these analyses. All analyses were carried out in R version 2.11.1 (R Development Core Team, 2010). The forward selection permutation procedure was carried out in the packfor R package (Dray et al., 2007), RDA, variation partitioning and rarefaction in the vegan package (Oksanen et al., 2010) and Indicator Species Analysis in the labdsv package (Roberts, 2010). All permutation-based analyses used 4999 randomisations.

3. Results

A total of 6313 adult spiders were identified belonging to 77 species and 9325 adult beetles involving 37 species and 159 moth species from 2310 individuals were collected. Of these, 24 spider species and 10 beetle species were classified as being associated with forested habitats. For moths, 46 species were associated with trees: 28 species with a larval feeding preference for oak trees, 10 for conifer trees, one of both oak and conifers. Commonly encountered species included *Lepthyphantes zimmermanni* (20% of total adult individuals), *Lepthyphantes tenebricola* (12%) for spiders, *Abax parallelepipedus*, (39%) and *Pterostichus madidus* (14%) for beetles, and Map-winged Swift (*Hepialus fusconebulosa*) and Spruce Carpet (*Thera britannica*) representing 11% and 8% of the individuals respectively for moths.

3.1. Environmental attributes of mixed and monoculture stands

Only one of the environmental variables differed significantly among the forest types (Table 2): leaf litter cover was higher in the oak mixes compared to the other stand types. However, when DBH within mixed stand types is examined, the Norway spruce trees had significantly higher mean DBH than the oak in the mix (mean oak DBH = 16.1 ± 1.1 SE; mean spruce DBH in mix = 35.3 ± 3.0 SE, F = 20.3$_{2,12}$, P <0.001). In contrast, the DBH of Scots pine trees did not differ from Norway spruce trees in that mix type (mean Scots pine DBH = 25.0 ± 1.7 SE; mean spruce = 27.6 ± 3.1 SE, F = 0.2$_{2,12}$, P = 0.83). Furthermore, although the Norway spruce in both mixes did not differ significantly from that in the monocultures (Table 2), spruce in oak mixes had significantly greater DBH than those in Scots pine mixes (means above, U = 55$_{n=10}$, P = 0.002).

3.2. Arthropod assemblages among plantation types

The forward selection procedure identified latitude and ground vegetation cover as covariates for both spiders and beetles, and, latitude, longitude and tree height for moths. The partial redundancy analyses indicated no relationship between assemblage structure and forest type for any of the taxa (spiders $F_{2,17}$ = 0.71, P = 0.85; beetles $F_{2,17}$ = 0.58, P = 0.87; Moths $F_{2,14}$ = 1.01, P = 0.45). Furthermore, variation partitioning suggests that other factors

Table 2
Mean ± SE or median (interquartile range) values of environmental characteristics between forest types: oak mix (Norway spruce with oak); Scots pine mix (Norway spruce with Scots pine); monoculture (monoculture of Norway spruce). Differences tested for significance with one-way parametric ANOVA with Tukey post-hoc tests or non-parametric Kruskal–Wallis.

	Oak mix	Scots pine mix	Monoculture	ANOVA $df_{2,17}$
Stand structure				
Canopy openness (%)	4.4 ± 0.6	7.9 ± 1.2	6.2 ± 1.1	F = 1.74 n.s.
Mean DBH (cm)	28.9 ± 2.1	27.1 ± 2.6	28.1 ± 2.2	F = 0.10 n.s.
Tree height (m)	22.0 ± 1.1	21.6 ± 1.3	21.1 ± 0.90	F = 0.19 n.s.
Number of planted stems	7.3 ± 1.4	8.8 ± 1.7	9.3 ± 1.5	F = 0.36 n.s.
Vegetation cover				
Ground vegetation cover (%)	69.1 ± 5.0	99.0 ± 9.7	68.1 ± 10.2	F = 2.52 n.s.
Lower vegetation cover (%)	12.4 ± 3.9	20.3 ± 8.8	16.9 ± 7.8	F = 0.19 n.s.
Upper vegetation cover (%)	0	0	0	n/a
Understory cover (%)	0.2 (0.3)	3.7 (7.7)	0.1 (0.3)	H = 1.84 n.s.
Litter and soil				
Needle litter cover (%)	26.7 ± 8.4	13.6 ± 7.6	38.8 ± 9.5	F = 1.74 n.s.
Leaf litter cover (%)	10.6 (7.4)	0 (0.5)	0 (0.4)	H = 12.33, P = 0.002
Litter depth (cm)	0.95 ± 0.26	0.40 ± 0.30	1.22 ± 0.36	F = 1.29 n.s.
Soil pH	4.1 ± 0.8	4.4 ± 0.3	4.2 ± 0.8	F = 0.96 n.s.
Soil organic content	17 ± 6	31 ± 13	34 ± 9	F = 0.72 n.s.

Mean values calculated per plot within a site. n.s. = non significant at alpha <0.05.
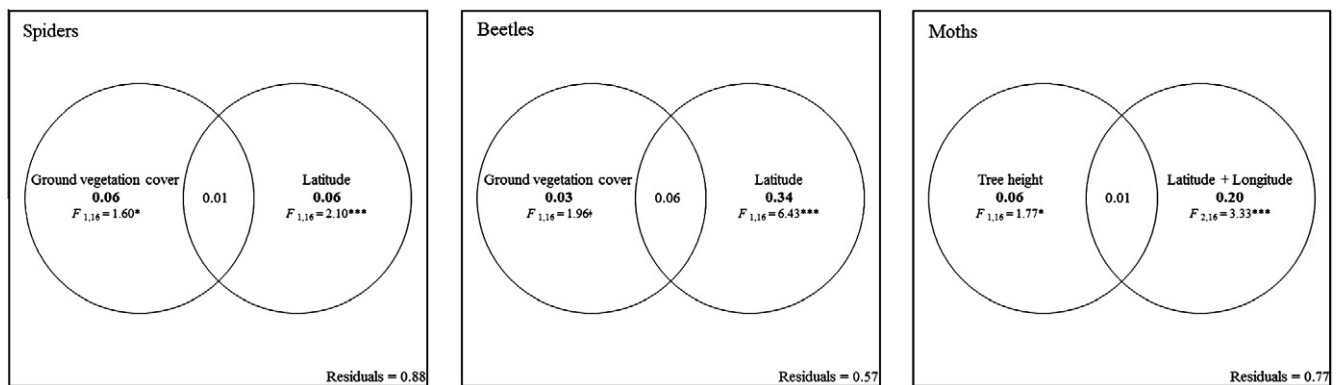

Fig. 2. Variation partitioning of the assemblages for each taxa into two fractions: environment (left) and location (right). Variables selected by a forward selection procedure (see Section 2). Values in bold represent adjusted r squares for the variation partitioned to each fraction tested for significance using RDA ($^{‡}P = \leqslant 0.1$; $^{*}P = \leqslant 0.05$; $^{**}P = \leqslant 0.01$; $^{***}P = \leqslant 0.001$). Residual variation is also given.

Table 3
Mean ± SE species richness and relative abundance of arthropods between forest types: oak mix (Norway spruce with oak); Scots pine mix (Norway spruce with Scots pine); monoculture (monoculture of Norway spruce). Differences tested for significance with a permutation based partial ANOVA. Covariables were identified using a forward selection procedure.

	Oak mix	Scots pine mix	Monoculture	ANOVA	Covariable
Spiders[#]					
Species richness	16.0 ± 1.3	16.5 ± 1.0	15.2 ± 1.0	$F_{2,16}$ = 0.48 n.s.	Latitude
Forest-associated species richness	6.9 ± 0.5	6.8 ± 0.6	6.9 ± 0.4	$F_{2,16}$ = 1.88 n.s.	Latitude
Forest-associated species relative abundance	0.5 ± 0.1	0.4 ± 0.1[b]	0.6 ± 0.1[a]	$F_{2,16}$ = 3.88, P = 0.04	Ground vegetation cover
Beetles[#]					
Species richness	8.6 ± 0.8	7.2 ± 0.6	8.4 ± 0.75	$F_{2,17}$ = 0.38 n.s.	n.s.
Forest-associated species richness	2.3 ± 0.4	2.1 ± 0.5	3.0 ± 0.4	$F_{2,16}$ = 0.91 n.s.	Ground vegetation cover
Forest-associated species relative abundance	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.1	$F_{2,17}$ = 0.44 n.s.	n.s.
Moths[§]					
Species richness	32.0 ± 6.0	38.3 ± 4.3	27.2 ± 4.3	$F_{1,10}$ = 0.14 n.s.	N/A
Expected species richness[†]	30.8 ± 6.4	37.8 ± 4.4	26.4 ± 4.0	$F_{1,10}$ = 0.17 n.s.	N/A
Conifer-associated species richness	4.7 ± 0.3	3.0 ± 1.2	3.7 ± 0.3	$F_{1,10}$ = 7.12, P = 0.04	N/A
Oak-associated species richness	4.3 ± 0.9	8.7 ± 2.3	6.0 ± 1.5	$F_{1,10}$ = 0.79 n.s.	N/A

n.s. = non significant at alpha <0.05.
[a] is significantly greater than[b].
[#] Mean values calculated per plot within a site.
[§] Mean values per site.
[†] after rarefaction on data standardised by trapping hours.

such as location and environmental characteristics of the stands have a significant influence on the arthropod assemblages (Fig. 2) Forest type was not included in the variation partitioning as initial analyses showed that it accounted for <0% of the variance, which is analogous to a random variable (Legendre, 2008).

3.3. Species richness and habitat associations among plantation types

Overall, the mixed and monoculture stands supported similar numbers of species and relative abundance of species with particular habitat associations (Table 3). However, there was a significantly greater relative abundance of forest associated spider species in the monoculture stands in comparison with the Scots pine mixes. This was primarily driven by higher relative numbers of *Lepthyphantes flavipes*, *L. tenebricola* and *Diplocephalus latifrons*, species which have been frequently sampled in spruce plantations (Oxbrough et al., 2010). In addition, there was a significant difference in the number of conifer associated moth species trapped among the forest types, with the most in the oak mixes.

No significant indicator species were identified for spiders or beetles. For moths, Ingrailed clay (*Diarsia mendica*), Double striped pug (*Gymnoscelis rufifasciata)* and Coxcomb prominent (*Ptilodon capucina*) were associated with the oak mixed stands (Indicator values = 0.87, P = 0.0007; 0.77, P = 0.003 and 0.71, P = 0.05, respectively). The former two species feed on a range of plants and shrubs as larvae whereas the latter feeds on oak as well as a range of other deciduous tree species (Waring and Townsend, 2007). The Pine carpet (*Thera firmata*) was associated with the pine mixed stands (Indicator value = 1.00, P = 0.01); the larvae of this species feeds on Scots pine.

4. Discussion

4.1. Ground-dwelling arthropod diversity in mixed and monoculture plantations

Interestingly, this study found that the forest types support similar arthropod communities whether a mix or a monoculture, and irrespective of mix type. In addition, stand structure, litter and vegetation cover were similar among the three stand types. This indicates that other aspects of environmental variation (e.g. location, stand structure, vegetation, litter, soil), independent of forest type, may be more important than the *a priori* designated forest types studied here.

It was expected that the addition of either oak or Scots pine as a secondary species in a plantation would influence canopy conditions, in particular light penetration, which in turn influence the ground and lower vegetation layers, and also modifying the litter. These factors will influence habitat structure which is particularly important for web spinning spiders, but also the availability of prey for predatory ground-dwelling arthropods and micro-climate conditions (Thiele, 1977; Bultman and Uetz, 1984; Uetz, 1991; Guillemain et al., 1997). Previous research indicates that spiders respond to variation in litter type within mixed conifer and deciduous stands, which is probably related to small-scale differences in the overhead canopy species (Ziesche and Roth, 2008), whereas differences in Carabid beetle reproductive success in mixed and monoculture stands have been linked to variation in micro-climate conditions between forest types (Ziesche and Roth, 2007). Such factors are also important in driving differences in the arthropod fauna of conifer and deciduous monoculture plantations in Ireland (Oxbrough et al., 2005).

Despite the importance of differences in litter type, there was little apparent influence on the assemblage composition of either spiders or beetles. Indeed, in the oak mixes leaf litter cover was significantly higher (Table 2), however no species were particularly associated with this forest type, indicating that at these levels (~10% cover) leaf litter is not an important factor influencing these taxa in this study. However, functional groups which are more closely linked to leaf litter as a food resource may be more affected by variation in cover. For instance, higher soil decomposer biomass and abundance has been found in mixes with greater amounts of deciduous trees (Elmer et al., 2004; Laganière et al., 2008) and collembolan assemblages differ between mixed and monoculture stands (Salamon et al., 2008). Furthermore, the addition of deciduous trees to conifer stands may contribute to an increase in soil pH, which benefits soil-dwelling invertebrates (Ammer et al., 2006) and possibly also some plant species. This may be particularly important in Ireland where successive rotations of non-native conifer species can contribute to lower soil pH (Oxbrough et al., 2010).

Overall, the results indicate that the proportion of secondary component in the mix (15–40%) was not high enough, essentially rendering the mixed stands in this study indistinguishable from each other and also from monocultures, at least from the perspective of the taxon groups examined. Work et al. (2004) have shown that mixes in which the proportion and size of conifer and deciduous trees are approximately equal, support ground-dwelling invertebrate assemblages more similar to monoculture coniferous stands than deciduous ones, suggesting that deciduous proportions need to be higher than 50% to support invertebrate species associated with a deciduous forest. It is likely that the proportion of deciduous trees as well as their distribution within a stand will influence invertebrate assemblages (Laganière et al., 2008; Ziesche and Roth, 2008). Additionally, the oak trees in the mix were much smaller in size than the Norway spruce in those stands, probably caused by their slower growth rate and lack of competitive fitness. This effectively rendered the oak sub-dominant in the canopy which may have further added to their lack of influence.

In contrast, the Scots pine trees were co-dominant in the canopy and of a similar size to the spruce in the mixes. Scots pine trees generally have a more open canopy than other spruce and pine species and therefore support greater plant and invertebrate diversity (Docherty and Leather, 1997; Nilsson et al., 2008). Additionally, the needle litter structure itself is different from spruce forests (individual needles being much longer), and litter cover tends to be much lower than in stands of other conifer species (Docherty and Leather, 1997; Nilsson et al., 2008). Despite this, the Scots pine mixes in this study did not support a different arthropod fauna from the matching monoculture stands. Again, this may be attributed to the proportion of the Scots pine in the mix being too low to influence the ground-dwelling arthropod fauna. Interestingly, although there were no species with a particular affiliation for a forest type identified using indicator species analysis; relative abundance of forest associated spiders was significantly higher in monoculture stands. The species *L. flavipes*, *L. tenebricola* and *D. latifrons* were primarily driving this difference. These species have been previously identified as indicators of commercially mature Sitka spruce plantations in Ireland (Oxbrough et al., 2010) and have a preference for closed canopy forests or partly shaded habitats (Nolan, 2010). This might suggest a particular association of these species with spruce plantations in Ireland.

4.2. Moth diversity in mixed and monoculture plantations

Availability of larval food plants is an important determinant of moth species occurrence within a habitat, particularly for those which can utilise only one or two plant species (Lepŝ et al., 1998). In forested habitats, moths can be associated with a particular host tree species or the understorey and lower vegetation layers associated with those stand types (Emmet and Heath, 1991).

This is supported by previous research showing that moth species richness is positively related to tree species diversity (Summerville and Crist, 2004). This suggests that, with the adequate presence of host larval plant species, mixed stands would be able to support a moth fauna typical of both forest types. However, in agreement with the findings for ground-dwelling arthropods in this study, there was no indication of a difference in moth species composition between the mixed and monoculture stands. As mentioned in Section 4.1, the oak and Scots pine may not have been present in high enough proportions to facilitate the development of a ground vegetation community typical of oak or Scots pine monoculture plantations, and hence provide the larval food plants with which specialist moth assemblages are associated. In addition, richness of moth species dependent on woody plants is negatively related to decreasing patch size of suitable forest area (Summerville and Crist, 2004), which may suggest that the proportion of suitable host plants (i.e. moths specifically associated with oak or Scots pine trees) was too low in our study sites. Furthermore, conifer-associated moth species were actually sampled in higher numbers in the oak stands, compared to the others (Table 3). This may be related to the greater availability of Norway spruce as a food resource in this habitat, as these trees had significantly greater DBH than spruce in the Scots pine mixes.

Although 28 species of moth were collected in this study whose larvae feed on oak, many of these are not obligate feeders, and can utilise a range of other broadleaf trees and vascular plant species. However, one species which feeds on deciduous trees including oak, Coxcomb prominent (*Ptilodon capucina*), had a preference for the oak mixed stands. Similarly, seven of the ten conifer associated species feed on a range of other conifers, although the remaining three species are known to feed exclusively on Scots pine. Indeed, one of these, the Pine carpet (*Thera fermata*), was identified as an indicator of this forest type. This suggests that the presence of a secondary tree species in a stand may influence the distribution of a few species which are specifically associated with it, though the low cover of these trees (15–40%) may mean that an overall impact on the fauna cannot be detected.

5. Conclusions and recommendations for forest management

Previous research suggests that the inclusion of species of native provenance in mixed plantations, such as oak, or those which create greater habitat heterogeneity, such as Scots pine, will benefit biodiversity. In this study however, there was no clear evidence for an influence of oak or Scots pine on the arthropod fauna when they are a secondary component in a mix. Indeed, the stands supported similar arthropod species whether they comprised one or two tree species and irrespective of mix type. Mixed stands were largely homogenous in structure, vegetation and litter cover, reflecting conditions in Norway spruce monocultures. This suggests that there is limited biodiversity value from an additional canopy species comprising 15–40% of the mix, at least for the taxa and tree species studied here. This has implications for forest policy, particularly in Ireland, where the *Forest Biodiversity Guidelines* (Forest Service, 2000) advocate the planting of native broadleaved species in mixes, but suggest that the primary species should comprise no greater than 80% of the mix (Forest Service, 2000). However, further research is required to determine the proportion at which oak or Scots pine begin to influence the arthropod fauna.

The oak trees were sub-dominant in the canopy, probably due to their slower growth rate and lack of competitive fitness. This indicates that careful consideration should be given to the selection of species combinations to ensure that opportunities for enhancing biodiversity are maximised along with the commercial viability of the trees. Additionally, when deciduous and conifer trees are planted together the configuration of trees within a stand should be considered; for instance, deciduous trees may benefit from being planted in a patch rather than an intimate mix arrangement of single trees. This would encourage lower vegetation growth and differing litter conditions within the patch to the benefit of arthropods, particularly during the closed canopy stages of the conifer forest cycle, prior to thinning. Such heterogeneity is arguably more similar to patches in natural woodlands, and so may also be of benefit for conifer mixes, such as Scots pine. In addition, such measures are likely to facilitate easier harvesting and greater growth of more viable trees.

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