Diversity, functional structure and functional redundancy of woodland plant communities: how do mixed tree species plantations compare with monocultures?

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Abstract

Managing forest plantation stands in a way that retains productivity targets, but that also fosters biodiversity and stand resilience are key sustainable forest management goals. Current forestry policy advocates a diversification of forest stands to achieve these goals, favouring mixed age structures and polycultures over single-aged monocultures. Evidence is lacking, however, to support this management recommendation for biodiversity gains and related ecosystem service delivery. We used indices of taxonomic diversity and functional structure to compare ground vegetation communities in mixed and pure stands of Scots pine (*Pinus sylvestris*) and pedunculate oak (*Quercus robur*) in each of three study regions. We categorised the 91 vascular plant species identified into functional effect and response groups. We tested the hypotheses that ground vegetation communities (i) differ significantly in structure and composition between Scots pine and oak monocultures and (ii) show enhanced levels of taxonomic and functional diversity and functional redundancy in mixed stands of Scots pine and oak compared with monocultures. We explored the implications of any differences in the functional structure of ground vegetation communities in the different stand types on two ecosystem services: nutrient availability and levels of resource provisioning for herbivores. Nine functional response groups (RG) and seven functional effect groups (EG) were identified with considerable overlap in the RG and EG species grouping. Three RGs had traits characteristic of forests (spring flowering herbs, tree saplings and shrubs/ climbers), one RG had traits characteristic of open habitats (annual ruderals) and the remaining RGs had more generalist traits (anemochorous perennials, graminoids and short perennials). No significant differences were found among stand types in terms of taxonomic diversity or richness of the different functional trait groups. Ground vegetation communities in the three study regions also had similar levels of functional redundancy across stand types. However, Scots pine and oak monocultures harboured significantly different abundances of species with distinct functional traits. In all three study regions, anemochorous perennials were significantly more abundant in Scots pine monocultures than oak monocultures, while two core forest groups (shrubs/ climbers, spring flowering herbs) were significantly more abundant in oak monocultures. Mixed stands had intermediate abundances of these functional groups. These differences have implications for the comparative availability of food resources and shelter for wildlife, but also the mobilisation and temporal availability of nutrients in the two monocultures. Thus, mixtures of Scots pine and pedunculate oak can temper significant tree species identity influences on ground vegetation functional diversity.

Key-words: Diversification, functional traits, functional redundancy, ground vegetation, *Pinus sylvestris*, *Quercus robur*

1. Introduction

Plantations make up 7%, i.e. 264 million ha, of forest cover worldwide and this area is increasing rapidly with a growing reliance on plantations for wood products, carbon management, the protection of soil and water and the rehabilitation and diversification of impoverished landscapes (FAO 2010; Pawson, Brin, & Brockeroff 2013). In some countries, plantations constitute a significant proportion of the total forest area, resulting in a strong anthropogenic influence on the composition of forest stands. Often the composition, structure and function of plantations are highly simplified; e.g. in Europe, 29% of forests are composed of a single tree species and many of these are plantations comprised of a single age cohort (Forest Europe, UNECE & FAO 2011). This raises concerns over the implications for biodiversity, particularly for the many forest dependent species that are in decline (Shvidenko, Barber & Persson 2005). Also of concern is the resilience of these simplified forests to environmental change (e.g. drought, invasive species, pests and diseases) and their capacity to deliver anticipated ecosystem services (e.g. nutrient cycling, erosion control, shelter and food resources for wildlife) (Thompson *et al*. 2009; Kanninen 2010).

A consistent mitigation measure that is advocated under current forestry policy is the diversification of forest management units to derive greater structural and/or compositional heterogeneity (Puettmann 2011); structural diversity is generally accepted to enhance levels of biodiversity through the provision of a greater diversity of microhabitats (Simpson 1949; Tews *et al*. 2004). A mixed tree species approach is a particularly attractive option as it combines recommendations for increased stand heterogeneity while potentially retaining, or even enhancing levels of productivity where there is complementary resource use by the tree species in a polyculture (Pretzsch & Schütze 2009; Thompson *et al.* 2009; Jucker *et al*. 2014). There is inconsistent supporting evidence, however, of the comparative benefits of mixed stands over monocultures for forest biodiversity and ecosystem functioning (e.g. resistance to disturbance, or element cycling) (Nadrowski, Wirth & Scherer-Lorenzen 2010; Cavard *et al*. 2011; Gamfeldt *et al.* 2012; Scherer-Lorenzen 2014); this is related to the difficulty in disentangling tree diversity effects from confounding factors such as substrate and topographic heterogeneity (Nadrowski, Wirth & Scherer-Lorenzen 2010). Moreover, the respective roles of tree species identity and tree species richness in influencing wider forest species diversity and ecosystem functioning are not fully understood, making it difficult to predict the likely consequences of various proposed tree species combinations on ecosystem service provision and the functional resilience of associated communities. Differences in traits between tree species, such as canopy phenology, have been shown in some studies to have a greater influence on wider forest species diversity than tree species richness (Barbier, Gosselin & Balandier 2008; Scherer-Lorenzen 2014). Tree species identity has also been found to have stronger effects than tree species richness on forest ecosystem functioning and associated ecosystem service provisioning (e.g. resistance to herbivory, decomposition) (Nadrowski, Wirth & Scherer-Lorenzen 2010).

Ground vegetation is a highly influential component of forest ecosystem processes (Gilliam 2007). It has an impact on recruitment patterns of the overstorey, nutrient cycling and disturbance mediation; it also plays an important role in the provisioning of habitat and foraging material (e.g. pollen, nectar, foliage) for many associated species (Royo & Carson 2006; Gilliam 2007). Ground vegetation, in turn, is strongly influenced by the composition and structure of the overstorey, responding to differences in temperatures and the availability of light, water and soil nutrients at the forest floor level (Barbier *et al*. 2008). Thus, a greater understanding of tree compositional influences on ground vegetation species diversity and functional structure should contribute greatly to the improved management of this component of forest biodiversity and associated ecosystem functions and services. Existing evidence for monoculture compared with mixed tree species effects on ground vegetation is largely based on taxonomic indices of diversity (i.e. species richness, diversity, evenness) with no consistent trends found. Taboada *et al.* (2010) and Augusto, Dupouey & Ranger (2003), for example, found limited significant influences of tree species mixtures compared with pure stands on taxonomic indices of ground vegetation diversity, unlike some other authors (e.g. Simmons & Buckley, 1992; Saetre *et al.,* 1997). Furthermore, where stand age was considered as an explanatory variable in some studies, significant positive correlations between tree species richness and ground vegetation species diversity were not consistently found across all growth stages (Auclair & Goff, 1971; Pharo, Beattie & Pressey, 2000).

Regional differences in species pools and the need for research results to be easily transposable across regions argue in favour of adopting a functional diversity approach which relies on describing the functional traits, rather than the taxonomic identity, of species to help explain forest composition and biodiversity-ecosystem function relationships (Hooper *et al*. 2005). The functional structure of communities can be defined by categorising species both according to functional *response* traits, which reflect the way species respond to the abiotic and biotic environments (e.g. resource availability, disturbance), but also according to functional *effect* traits which characterise species effects on dominant ecosystem functional processes and the related delivery of ecosystem services (e.g. nutrient cycling, disturbance mediation, pollination). A functional diversity approach can also be used as an indirect measure of resilience by assessing levels of functional redundancy in the delivery of one or more ecosystem services among associated communities. This can be achieved, for example, by assessing the number of species present in different functional effect trait groups and the number of distinct functional effect trait groups represented in a community (Díaz & Cabido 2001; Laliberté *et al*. 2010).

A functional diversity approach is achievable with ground vegetation considering the significant species-specific physiological and morphological knowledge that has been acquired, documented and linked to functional processes (Pérez-Harguindeguy *et al.* 2013). There is also a good understanding of traits that typify forest-dependent species and those with the highest conservation value (Hermy *et al.* 1999; Hérault, Honnay & Thoen 2005). Functional diversity analyses represent an alternative approach, therefore, to information-poor species richness analyses on the one hand, and analyses based on taxonomic composition for which results are hard to generalise, on the other.

This study compared ground vegetation communities in mixed and pure stands of Scots pine (*Pinus sylvestris* L.) and pedunculate oak (*Quercus robur* L.) across three study regions. These species were selected for their contrasting evergreen and deciduous habits and because they are known successful polycultures. The study objectives were to investigate the influences of tree species identity (Scots pine or oak) and plantation complexity (i.e. monocultures or two species mixtures of Scots pine and oak) on the functional structure and levels of taxonomic diversity and functional redundancy of ground vegetation communities. Functional structure was described by categorising ground vegetation species according to two alternative functional classifications, based on species functional response and functional effect traits, respectively. This allowed for inferences to be made about ground vegetation community responses to environmental conditions, but also their potential influences on forest ecosystem functioning in mixed and pure stands of Scots pine and oak. Functional redundancy served as a proxy for the functional resilience of communities to environmental change. The same tree species identity and monoculture/ polyculture comparisons were repeated in three study regions selected for their differing environmental conditions, particularly for differences in environmental variables known to have a strong influence on ground vegetation community composition (e.g. levels of N deposition, rainfall). This was to check for the consistency of any significant stand type effects on ground vegetation communities, but also to test for any significant stand type and region interactions. Hence, this study aims to contribute towards the evidence base, thereby helping to inform and increase the robustness of existing forest management recommendations across regions differing in species pools and environmental conditions. In particular, we tested the hypotheses that ground vegetation communities (i) differ significantly in structure and composition between Scots pine and oak monocultures and (ii) in support of current forest management policy recommendations, show enhanced levels of taxonomic and functional diversity and functional redundancy in mixed stands of Scots pine and oak compared with Scots pine or oak monocultures. Additionally, we explored the implications of any differences in the functional structure of ground vegetation communities in the different stand types for the provisioning of two ecosystem services, namely nutrient availability (based on measured levels of soil nutrients) and levels of resource provisioning for herbivores (based on measured levels of herbivory).

2. Material and methods

2.1 Study area

A total of 42 forest stands were selected for study, located in three regions of temperate maritime climate: Thetford Forest, East Anglia in south-east England (52° 27' N, 0° 51' E, 10-40m a.s.l.), the New Forest, Hampshire, in southern England (50° 47' N, 1° 38' W, 20-90m a.s.l.) and across a wider area in the centre and east of the Republic of Ireland (most northern stand at 53°20' N, 6°44' W; most western stand at 52° 26' N, 8°6' W, 57-234m a.s.l.). The three study regions together span east and west gradients of precipitation and N deposition with lowest levels of precipitation and highest levels of N deposition in Thetford Forest (see Table A.1 in Supplementary material). In both Thetford Forest and the New Forest, five stands were selected and in Ireland four stands were selected from each of three different forest stand types: Scots pine monocultures, pedunculate oak monocultures, and intimate mixtures of Scots pine and pedunculate oak. The average stand size was 6.8ha and the majority of stands were planted between 1930 and 1954 (Table A.2).

In each region initial stand selection was based on a number of criteria: minimum stand area of 1.5ha, planting age of between 1930 and 1940, stands must have an even shape (i.e. long, thin stands were avoided), and a stand should occur in close proximity (within the same forest management block) as selected examples of the other two stand types of interest to allow for a number of clusters of the different stand types to be sampled across the region. A planting age range was selected to confine the study to a single stage of the forest harvest cycle, thus minimising the influence of stand age as a variable. Enough stands were not always found in each region to accommodate these selection criteria, requiring some older or younger stands to be included in some cases. It was also not possible to establish four (or five, in the case of the English stands) distinct clusters of stands comprising each of the different stand types in each region. Figure 1 illustrates the final distribution of stands across each region using available stands matching as closely as possible the specified criteria.

Thetford Forest was planted largely with Scots and Corsican pine (*Pinus nigra* subsp. *laricio*) in the early 20th century on extensive heathland and marginal agricultural land with smaller areas of oak and beech (Randall & Dymond 1996). The New Forest is a renowned area of ancient woodland pasture that is still actively grazed by livestock; there are diverse plantation types intermingled with ancient oak or beech dominated woodland (Grant & Edwards 2008).

Scots pine and pedunculate oak are native species of Ireland and Great Britain, although pollen records indicate that Scots pine disappeared from the landscapes of our study regions for a long periods of time (>1000 years) until it was reintroduced as a plantation species (Randall & Dymond 1996; Grant & Edwards 2008; Roche, Mitchell & Waldren 2009). Scots pine has been planted with oak in intimate mixtures since the 1930s in Britain and Ireland, serving as a nurse crop for oak (Kerr, Nixon & Matthews 1992). This mixture is being revived more widely as a productive polyculture (Morneau, Duprez & Hervé 2008; Del Rio & Sterba 2009; Matos *et al.* 2010).

2.2 Data collection

2.2.1 Ground vegetation surveys

In each of the selected stands, vascular plants were surveyed in three 2 x 2-m quadrats located ≥50m from the stand edge and mid-way between adjacent trees. In the English stands (Thetford Forest and New Forest regions) positioning of ground vegetation quadrats in each of the selected stands was by random selection of three out of eight possible regularly spaced sample positions around a 50m x 50m quadrat centred in the forest stand. This method was used to allow the data to be compared to other UK-wide studies using the same basic protocol (e.g. Ferris *et al*., 2000). In the Irish stands, positioning of the three ground vegetation quadrats was in areas which were considered to be representative of the stand as a whole in terms of ground vegetation and stand structure (i.e. canopy cover, level of thinning), with quadrats always being positioned >50m apart from each other. The percentage cover of each species of vascular plant was estimated in each quadrat between June and August 2011. In the Irish stands, percentage cover was estimated to the nearest 5% except where cover was below 5%; in this case two cover-abundance units were distinguished: 3% (indicating cover of 1–5%) and 0.5% (indicating cover <1%). In the English stands, cover was estimated using the DOMIN cover-abundance scale. The two cover-abundance scales used for assessments in the English and Irish stands were harmonised by transforming each score to a mean percentage cover, or Domin 2.6 score (Currall 1987). The nomenclature of vascular plants follows Stace (2010).

2.2.2 Environmental variables

Assessments were made of levels of grazing/ browsing pressure, canopy openness, soil moisture, litter depth and, from surface mineral layers (0-10cm), pH, total N, organic matter content (OMC) and available P and K. Modified Ellenberg values were applied using the ground vegetation data as additional assessments of light, moisture, fertility and acidity. See Table A.1 for environmental variable sampling methods.

2.3 Data analysis

2.3.1 Taxonomic diversity

Four metrics were used: (i) the total number of species present in each stand (ii) the mean species richness (S) per 2 x 2-m quadrat (iii) the mean Shannon index of diversity (H′) per 2 x 2-m quadrat calculated as $H' = -\Sigma p_i \ln p_i$, where $p_i = C_i / \Sigma C_i$ and C_i is the mean percentage cover of species i, and ΣC_i is the sum of all cover values included in the quadrat; and (iv) Pielou's Equitability index (J′) per 2 x 2-m quadrat calculated as $J' = H' / \log_2 S$, where H′ and S are the values as calculated above.

2.3.2 Functional response and effect trait selection and cluster analysis

19 functional response and 9 functional effect traits were used in the classification of plant functional types (Tables 1 and 2). Response traits represented key stages of the plant's life cycle; i.e. dispersal, establishment and persistence. Effect traits influenced forest ecosystem services such as food availability for wildlife (i.e. foliage, berries, seed, nectar) and nutrient cycling. Response and effect trait information was collected from existing literature (mainly Grime, Hodgson & Hunt 1988) and the LEDA (Kleyer *et al.* 2008) and Ecological Flora (Fitter & Peat 1994) trait databases. The TRY trait database (Kattge *et al*. 2011) and Woodland Grazing Toolbox (Forestry Commission Scotland, 2016) were used to supplement palatability information. A total of 89 vascular plant species were included in the analysis and four species (*Agrostis curtisii*, *Carex macrocarpa*, *Picea abies* and *Pseudotsuga menziesii*) were excluded due to missing information for a high proportion (>50%) of the selected traits.

Response trait groupings (RGs) were determined by first calculating the Gower dissimilarity matrix from species' trait scores, giving equal weight to all traits considered. This method can deal with both missing values and mixed data (Legendre & Legendre 1998). The resulting matrix was clustered using the Ward method, followed by visual inspection of the dendrogram (Laliberté *et al*. 2010; Figure 2). Significant differences between RGs were tested for using Kruskal-Wallis tests with adjusted p-values for multiple comparisons and Chi square tests (Hérault, Honnay & Thoen 2005). The same procedure was carried out to determine effect trait groupings (EGs).

2.3.3 Functional structure and functional redundancy

Species cover abundance in each stand was used to construct a RG abundance matrix, following Hérault, Honnay & Thoen (2005). Having assigned each species to an RG in the clustering step, the summed cover abundance of all species in each RG was calculated for each stand. The RG abundance matrix was standardised for differences in the number of species per stand by calculating the relative abundance: R_{ip} / R_p, where R_i = abundance of each response group, R = total abundance of response groups, p = each stand. RG richness was calculated as the total number of RGs in a stand. Functional redundancy was calculated as the number of species in each RG in each stand.

2.4 Statistical analyses

Generalised linear mixed effects modelling (GLMM) was used to model the effect of the explanatory variables (region, stand type and region x stand type interaction) on the response variables (species richness, J′, H′, RG relative abundance, RG richness and functional redundancy). Region and stand type were fitted as fixed effects and we also tested for a significant region x stand type interaction. Quadrat was nested as a random effect within stand which was also a random effect. Where categorical explanatory variables had a significant effect, post hoc multiple comparisons with Bonferroni corrections were applied. Models of RG and EG richness and functional redundancy used the Poisson distribution as these are integer count data. Models of RG and EG relative abundance used the binomial distribution because these data are proportions. The same procedure was applied in the analyses of the EGs.

The effect of stand location (latitude and longitude) on response variables (i.e. species richness, H′ and J′ diversity indices) was modelled using GLMM in R with no significant effects found. Additionally, residuals from the models were examined for spatial autocorrelation by calculating Moran’s I using the program Spatial Analysis in Macroecology (SAM) (Rangel, Diniz-Filho & Bini, 2010) with no autocorrelation found.

Considering the variation in tree ages and canopy openness between study stands, we tested these as additional potential explanatory variables that could have significant direct influences on ground vegetation communities using GLMM in R. Alongside stand type, we fitted stand age and canopy openness as well as stand type x stand age and stand type x canopy openness interaction terms as predictors in our models using species richness, H' and J' as response variables. As there was no strong correlation between canopy openness and age either across all regions or within regions, all predictors were fitted together in these models.

If differences in ground flora between monoculture types include differences in species identity and composition, we might expect mixed stands to have higher species richness and diversity than would be expected from a simple proportional averaging of the diversities found in the respective monocultures of tree species making up the mixed stands. We explored this idea by testing for differences in 'observed' species richness, H' and J', of mixed stands and that 'expected' from averaging the species richness, H' and J' of oak and Scots pine monocultures. Specifically, we took account of the fact that the proportion of oak was not consistent across mixed stands (ranging from between 10 and 60%), by using a weighted-averaging method, based on the known species richness, H' and J', and tree species composition of our mixed stands in the same region as the mixed stand being compared. Using species richness as an example, the following formula was used to calculate expected species richness in the mixed stands as weighted averages of the pure oak and Scots pine stands:

Species richness per stand = (%oak mix/100) * mean (species richness in all pure oak stands) + (% Scots pine in oak pine mix/ 100) * mean (species richness in all pure Scots pine stands)

Paired Wilcoxon signed rank tests were used to test for differences between the expected and observed values of taxonomic diversity in mixed plots in each region.

Species richness, H' and J' were calculated using the vegan package (Oksanen *et al*. 2013) in R (R Core Team 2014); cluster analysis used the 'cluster' package (Maechler 2014); GLMMs were carried out using the GLIMMIX procedure in SAS 9.3.

2.3.3 Environmental variables

GLMM was used to model the effect of the explanatory variables (stand type, region and region x stand type interaction) on the response variables (environmental variables) using the same procedure as described for taxonomic diversity indices.

3. Results

3.1 Taxonomic diversity

The total number of vascular plant species identified in the survey of forest stands in the New Forest, Thetford Forest and Ireland was 47, 47 and 53, respectively. The three study regions had 16 of these plant species in common; the New Forest and Ireland had the most species in common (28), while Thetford Forest shared 21 species in common with the New Forest and 21 species in common with Ireland (Table A.3). None of the taxonomic diversity metrics considered showed significant differences between stand types, between regions, or as a region x stand type interaction (Table A.4). Our models that additionally fitted canopy openness and stand age showed no significant main effects for any region. We therefore do not present these model outputs. There was no significant correlation between the 'observed' value of species richness, H′ and J′ and the corresponding value 'expected' from weighted averaging. Hence, observed levels of these metrics are not a simple weighted average of what would be observed from pure stands. Paired Wilcoxon signed rank tests showed some significant differences in observed and expected values for some of these metrics, most notably for the New Forest, which showed that mixed stands had significantly higher observed than expected values for all three metrics. This was not consistent across regions, however, with Ireland showing significantly lower observed than expected species richness in mixed stands, and Thetford showing significantly lower observed than expected J′. All other comparisons between observed and expected were not significant ($P>0.05$ in all cases) (Tables A.5 and A.6).

3.2 Response trait clustering

The ground vegetation species clustered into nine RGs with between seven and twelve species in each RG (Figure 2). These RGs included: Tree saplings (RG1), tall zoochorous perennials (RG2), woody shrubs/ climbers (RG3), wind-pollinated, zoochorous graminoids (RG4), short barochorous, creeping/clump-forming herbs and graminoids (RG5), tufted graminoids and upright, clump-forming herbs (RG6), tall anemochorous perennials (RG7), spring-flowering, shade tolerant herbs (RG8) and annuals (RG9) (see Table A.7 for more detailed descriptions of each RG). Highly significant differences (p<0.0001) were identified between the RGs for almost all of the response traits (Table A.8). Exceptions included seed longevity, which only showed a significant difference (p<0.004) between RG1 and RG9 and seed shape which was not significantly different between the different RGs.

3.3 Effect trait clustering

The ground vegetation species clustered into seven EGs with between 8 and 22 species in each EG. EGs comprised: Tree saplings (EG1), medium to tall (i.e. at least 30cm) non-woody ruderals and competitors (EG2), ferns and rushes (EG3), grasses and sedges (EG4), annual herbs (EG5), short to medium height (10-30cm) perennial herbs (EG6) and shrubs/ climbers (EG7) (see Table A.9 for more detailed descriptions of each EG). Highly significant differences (p<0.0001) were identified between the EGs for all of the effect traits (Table A.10).

3.4 Richness, abundance, and redundancy of functional response groups

There was no significant difference in RG richness (i.e. the total number of RGs per stand) between regions ($F_{2,120}$ = 0.50, p = 0.61), stand type ($F_{2,120}$ = 0.07, p = 0.94), or region x stand type ($F_{4,120}$= 2.32, P = 0.06).. There were significant differences, however, in the relative abundances of RGs between stand types and regions, with significant region x stand type interactions (Table 3). Compared with oak monocultures, Scots pine monocultures had significantly lower abundances of woody shrubs/ climbers (RG3) and spring-flowering, shade tolerant herbs (RG8), but significantly higher abundances of tall anemochorous perennials (RG7); these RG differences were consistent across all three regions of study with the exception of no significant difference in abundances of RG3 species between oak and Scots pine monocultures in the New Forest. RG3, RG7 and RG8 species abundances tended to be 'intermediate' in mixed stands, not showing any significant differences in abundance when compared with one or both monocultures. Thetford Forest had a greater abundance, across all stand types, of RGs comprising species of high resource, high disturbance environments (i.e. non-woody perennial competitors and annuals in RG2 and RG9, respectively). Shrubs and climbers (RG3) occurred in significantly greater abundance (all stand types) in Irish stands compared with Thetford Forest and the New Forest.

Comparisons of levels of RG functional redundancy revealed few significant differences between the three stand types and regions (Figure 3). Levels of functional redundancy among tall anemochorous perennial (RG7) species were consistently higher in Scots pine monocultures compared with oak monocultures and 'intermediate' in mixed stands across the three regions, with no significant region x stand type interaction. Across regions, levels of functional redundancy were greatest in Thetford Forest among RGs comprising species of high resource, high disturbance environments (i.e. tall zoochorous perennials and annuals in RG2 and RG9, respectively), while functional redundancy among shrubs/ climbers (RG3) and tufted graminoids (RG6) were significantly greater in the New Forest and/or Ireland compared with Thetford Forest.

3.5 Richness, abundance, and redundancy of functional effect groups

No significant difference was found in EG richness (i.e. the total number of EGs per stand) between regions ($F_{2,120}$ = 0.39, P = 0.68), stand types ($F_{2,120}$ = 0.51, P = 0.60) or region x stand type ($F_{4,120}$ = 0.86, P = 0.49). There were significant differences, however, in the relative abundances of EGs (Table 4) between stand types and regions, with significant stand type x region interactions. Scots pine monocultures across all regions had a consistently higher abundance of ferns and rushes (EG3) and significantly lower abundance of shrubs/ climbers (EG7) than oak monocultures, while the abundances of EG3 and EG7 species in mixed stands did not differ significantly from those in the oak and/or the Scots pine monocultures.

Levels of functional redundancy of plant functional EGs were similar among stand types (Figure 4). Only EG3 (ferns and rushes) showed significantly higher levels of functional redundancy in Scots pine compared with oak monocultures, and intermediate levels in mixed stands, in the Irish and Thetford Forest stands. The Irish and New Forest stands otherwise had significantly higher levels of functional redundancy among E7 species (shrubs/climbers) compared with Thetford Forest stands and particularly in mixed stands.

3.6 Environmental variables

Levels of shoot browsing, sward grazing and herbivore ground disturbance were significantly higher in the oak compared with the Scots pine monocultures in the two English regions where herbivore pressure was found to be significantly greater than the Irish sites; levels of herbivory in mixed stands were similar to one or other of the monocultures depending on the region (Table A.1). There was no consistent significant difference in soil moisture between the different stand types, but in all regions levels of soil OMC and available nutrients were significantly higher in Scots pine compared with oak monocultures, with a tendency for intermediate levels of these in the mixed stands. This contrasted with Ellenberg soil fertility levels which were significantly higher in oak compared with Scots pine monocultures in the three study regions. Litter depth was significantly lower in oak stands compared with the other stand types only in Thetford Forest. Soil pH and Ellenberg soil acidity were significantly lower in Scots pine monocultures and intermediate in mixed stands. Ellenberg light levels were always significantly higher in the Scots pine monocultures compared with the other stand types; canopy openness values showed a similar trend, although differences were not found to be significant.

4. Discussion

4.1 Influence of monocultures and tree species mixtures on ground vegetation

4.1.1 Indices of taxonomic diversity

We found no significant differences in ground vegetation species richness, diversity or evenness when comparing species present in mixtures and monocultures of oak and Scots pine in three different geographical regions of study. These first results based only on taxonomic diversity indices do not lend support to forest management recommendations to favour polycultures over monocultures for associated biodiversity gains. Instead these findings concur with the review findings of Barbier, Gosselin & Balandier (2008) and Cavard *et al.* (2011) who reported that significant differences in these diversity indices are observed to occur more often (but not always) between monocultures composed of tree species with contrasting influences on resource availability (e.g. light, water, soil nutrients), suggesting that tree species identity rather than the number of tree species in a stand has the greater influence on ground vegetation structure and composition (e.g. Augusto, Dupouey & Ranger 2003; Mölder, Bernhardt-Römermann & Schmidt, 2008). The lack of any significant difference in taxonomic measures of ground vegetation community diversity between oak and Scots pine monocultures in this study was contrary to our expectations. Considering levels of canopy shading by these two tree species, we had expected more shaded conditions under oak compared with Scots pine based on previous assessments of light conditions in oak and Scots pine stands (Sonohat, Balandier & Ruchaud 2004; Balandier *et al*. 2006); this was not convincingly apparent, however, from our direct measurements of canopy openness which were not significantly different between oak and Scots pine during the summer months (June to August), although Ellenburg light values were significantly higher in Scots pine compared with oak stands in each region of study (Table A.1). This suggests that, despite contrasting traits (e.g. canopy phenology), neither tree species has a more limiting influence on ground vegetation community development than the other. Other successful polycultures comprising tree species of more strongly contrasting shade tolerance traits such as Norway spruce (*Picea abies*) / common alder (*Alnus glutinosa*), Sitka spruce (*P. sitchensis*)/ Scots pine, Norway spruce/ Scots pine are more likely to show strong comparative species identity influences on ground vegetation species diversity, although this remains to be tested. In such cases, the introduction of a deciduous species, oak, into an otherwise heavily shaded environment could have a similar effect to stand thinning which has been shown to promote ground vegetation with traits that deliver functional benefits for wildlife (Neill & Puettmann 2013). The use of taxonomic diversity indices belies, however, some important differences in the functional trait characteristics of ground vegetation in Scots pine and oak monocultures.

4.1.2 Functional structure

Tree identity influences were found to have a significant influence on the functional structure of ground vegetation communities. Across the three study regions, comparisons of the functional structure revealed consistent significant differences in the relative abundances of different functional response and effect trait groupings in the Scots pine and oak monocultures. Scots pine monocultures had significantly lower abundances of woody shrubs/ climbers (RG3; EG7) and spring flowering, shade tolerant herbs (RG8) than oak monocultures, but significantly higher abundances of tall anemochorous perennials (RG7), many of which had traits characteristic of EG3 (ferns and rushes). Among the nine RGs identified in this study, the two most closely associated with oak monocultures (RG3 and RG8) are the only RGs that comprise species with life-history trait combinations that are reflective of their successful adaptation to the closed-canopy forest environment (i.e. shade-tolerant, large seeds associated with a vernal phenology or zoochorous dispersal); spring flowering herbs (RG8) are additionally considered to have the highest conservation value in temperate forests, but pose considerable restoration challenges due to numerous recruitment limitations (e.g. limited seed dispersal, transient seed banks; Hermy *et al.* 1999; Baeten *et al.* 2009). The tall anemochorous perennials (RG7) most closely associated with Scots pine monocultures consisted of relatively competitive species, including fern species such as bracken (*P. aquilinum*). These species have life history traits that ensure rapid and effective recruitment and good regional population persistence (high numbers of diaspores that can form a persistent seed bank; rapid growth of tall shoots). The comparatively low abundances of RG3 and RG8 species in Scots pine monocultures might be explained by the combination of a high number of species with RG7 traits, outcompeting RG3 and RG8 species, but also the evergreen habit of Scots pine which may pose light resource limitations on spring flowering RG8 species.

These results are consistent with findings by Hérault, Honnay & Thoen (2005) and Pitman, Benham & Poole (2014) who also found a significantly greater abundance of anemochorous perennials (traits equivalent to our RG7 species) and a significantly lower abundance of short geophytes (traits comparable to our RG8 species) in conifer plantations compared with broadleaf deciduous forests. Other studies comparing ground vegetation in conifer monocultures with deciduous broadleaf monocultures/semi-natural broadleaf forests have also found that shrub species and forest specialist herbs occur more commonly in broadleaf stands (e.g. *Fraxinus excelsior*, *Quercus robur*/ *petraea*) compared with conifer monocultures, especially heavy shading conifer species (e.g. *Picea sitchensis, Picea abies*; Amezaga & Onaindia 1997; Fahy & Gormally 1998; Coote *et al*. 2012).

We found significant overlap in species groupings according to functional response and effect traits; e.g. RG3 and EG7 were primarily composed of shrubs and climbers. Thus, region and stand influences were frequently the same for corresponding response and effect groups. A significantly lower abundance of shrubs and climbers (EG7) in Scots pine monocultures will reduce the availability of food resources for herbivores, granivores and pollinators as EG7 species are important sources of fleshy and non-fleshy fruit, nectar, pollen and flowers. EG7 species such as *Hedera helix*, *Lonicera pericylymenum*, *Rubus fruticosus*, *Vaccinium myrtillus* (Pollard & Cooke 1994; Tudor *et al.* 2004; Jacobs *et al.* 2009) also have highly palatable foliage and provide valuable shelter for wildlife, including birds and mammals (Snow & Snow 1988). The significantly lower measured levels of herbivore grazing/ browsing in the Scots pine compared with the oak monocultures is indicative of a preference by large herbivores for oak monocultures, likely due to the greater abundance of food resources there in the form of shrubs and herbs. The comparatively high abundances of EG3 species (ferns and rushes) in Scots pine monocultures suggests, conversely, that there is greater potential for the mobilisation of nutrients, oxidation of soils and erosion control. The fern species *P. aquilinum* is known, for example, to increase the soil nutrient status by bringing large amounts of phosphate, nitrogen, and potassium into circulation through litter leaching, stem flow and periodic dieback of foliage (Carlisle, Brown & White 1967; Williams, Kent & Ternan 1987). The significantly higher abundances of ephemeral spring-flowering herbs (e.g. bluebell, *Hyacinthoides non-scripta*; wood-sorrel, *Oxalis acetosella*) in oak monocultures has a similar potential nutrient-retention and release benefit for these stands by rapid uptake of nutrients before the deciduous canopy develops, followed by rapid decomposition of foliage thereafter (Muller 2003). Our soil measurements reflect a significantly greater availability of nutrients in the Scots pine compared with the oak monocultures, although more acidic and potentially drier soils in the winter months under the Scots pine evergreen canopy may pose comparative limitations to nutrient uptake and microbial activity. The latter effect is supported by the significantly greater accumulation of soil organic matter in the Scots pine stands and, in the comparatively low rainfall conditions in Thetford Forest, a significantly deeper litter layer in the Scots pine compared with oak monocultures. A faster turnover of soil organic matter in oak compared with pine stands has been reported elsewhere and may explain the significantly higher Ellenberg fertility scores we obtained in oak monocultures (Matos *et al.* 2010; Pitman, Benham & Poole 2014).

Ground vegetation communities in Scots pine and oak mixed stands were composed of species from the same functional trait groups as Scots pine and oak monocultures and these occurred in ‘intermediate’ abundances; i.e. no significant difference was found when mixed stands were compared with one or both monocultures. These findings suggest, contrary to our hypotheses, that the diversification of Scots pine or oak monocultures to two-species mixes of Scots pine and oak would not be sufficient to increase the relative abundance of ground vegetation species with favoured traits beyond that which is present in monocultures, particularly in landscapes where both monocultures are present.. Mixed stands can, however, increase the abundance of species with favoured traits (e.g. species of conservation interest such as spring-flowering herbs) compared with Scots pine monoculture stands and reduce the relative abundance of those functional groups which tend to dominate ground vegetation communities under monocultures.

4.1.3 Functional redundancy

Levels of functional redundancy were unaffected by stand type or region for the majority of functional response and effect groups (Figures 3 & 4). Where any significant differences were observed between stand types these were not consistent across regions, with one exception. Consistent significant differences between the different stand types were observed only among tall anemochorous perennials (RG7/EG3); i.e. levels of redundancy were always found to be significantly higher in Scots pine monocultures compared with oak monocultures where the evergreen habit of Scots pine may have favoured shade-tolerant RG7 species. Mixed stand also consistently showed ‘intermediate’ levels of functional redundancy compared with oak and Scots pine monocultures. Inter-regional differences in levels of functional redundancy within functional trait groups included significantly higher levels of redundancy of nitrophilous, tall non-woody competitive perennials (RG2) and annuals (RG9) in Thetford Forest which may be related to the comparatively high total N deposition in this region compared with the New Forest and Irish study regions. There was also significantly lower redundancy of tufted graminoids (e.g. *Carex* species) and upright, clump-forming herbs (RG6) in Thetford Forest which might be explained by the comparatively low levels of rainfall here. The lack of evidence of hypothesised increased levels of functional redundancy among most functional response and effect trait groups in mixed stands compared with monocultures does not support the argument that polycultures should be favoured over monocultures for improved resilience of vascular plant communities, at least not for the majority of ground vegetation functional trait groups in Scots pine-oak mixtures.

5. Conclusions

Our results show that the establishment of polycultures comprised of tree species with contrasting traits (e.g. canopy phenology) can ‘neutralise’ strong tree species identity influences on the composition of ground vegetation. This can allow for the proliferation of ground vegetation species with desirable functional traits that might otherwise be suppressed or excluded in a monoculture of one of the component tree species of a mixed stand; mixtures might similarly reduce the overall abundance of species that would otherwise tend to dominate ground vegetation communities in a monoculture. However, while we were able to detect some significant functional trait differences in ground vegetation communities of oak and Scots pine monocultures, tree species within polycultures that have more strongly contrasting influences on environmental conditions are likely to result in more varied influences on the functional structure of ground vegetation (e.g. Veldman, Mattingly & Brudvig, 2013). From a management viewpoint, our work therefore only weakly supports two-species polycultures of Scots pine and oak as a means of improving functional diversity and associated ecosystem service provision which arises from this increased functional diversity in vascular plant communities. We otherwise found no evidence of higher levels of functional redundancy in Scots pine –oak polycultures compared with monocultures, with the exception of tall anemochorous perennials (RG7/EG3) which showed consistent improved functional resilience in mixed stands compared with oak monocultures across study regions. We also note that there are situations where competitive interactions between tree species in a polyculture negatively impact on productivity (Mason and Connolly, 2013), making such a strategy economically non-viable. In such cases a more realistic strategy to maximise ecosystem service benefits derived by either crop would be the creation of a chessboard pattern of monospecific stand types within the same forest management unit (Mason, 2006; Ampoorter *et al.* 2015). Overall, the effects on taxonomic indices commonly used to assess the effectiveness of management interventions were not significant; thus this study shows that functional diversity assessments are most likely a more sensitive tool.

There are two important caveats to our conclusions that are worth considering. First, our ground vegetation surveys were conducted over a single field season and sampling did not include the spring months before canopy closure. A repeat survey covering also the spring period may improve the number of ground vegetation species detected, particularly the number of spring geophytes. Second, our results pertain to a single stage of the forest harvest cycle which may not be the life stage that typically sustains the highest levels of ground vegetation diversity. Thus, we cannot describe how temporal changes in environmental conditions at different stages of the forest harvest cycle might influence our results. Stand structural changes through a typical forest plantation harvest cycle have previously been reported to have significant influences on ground vegetation community composition (Ferris *et al*., 2000; Aubin *et al*., 2013). Richness, and levels of taxonomic/functional diversity show no consistent pattern; i.e. in some cases they may remain very similar at different stages through a rotation (Aubin *et al.*, 2013), or may decline with highest levels of diversity reported in pre-thicket and over-mature stages and significantly lower levels of diversity in mid-rotation and mature stands (e.g. Eycott *et al.*, 2007 for *Pinus sylvestris* stands in Thetford Forest).

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Appendix A: Supplementary material

Additional Supplementary tables associated with this article are listed below.

Table A.1 Environmental variable means in each region and stand type. GLMMs were applied with region and stand type used as fixed effects. Different lower case letters indicate a significant difference between stand types within a region and different upper case letters indicate a significant difference between regions within stand type

Table A.2 Summary characteristics of stands in the three study regions and three stand types

Table A.3 List of the total number of ground-vegetation species identified in 2 x 2-m survey plots in the three study regions and three forest stand types (SP= Scots pine monocultures, OK = oak monocultures, OK/SP = Oak and Scots pine mixtures)

Table A.4 Mean (standard error) of vascular plant total species richness (TSR), mean species richness (S), mean Shannon diversity Index (H') and mean Pielou Equitability Index (J') in each region x stand type. GLMMs were applied with region and stand type used as fixed effects

Table A.5 Median (interquartile range) observed and expected values for mixed stands in each region. Different letters indicate significant differences in the observed and expected values for each taxonomic diversity metric in each region analysed using paired Wilcoxon signed rank tests ($P<0.05$)

Table A.6 Percentage of oak (OK) and Scots pine (SP) in each mixed stand, the corresponding observed (Obs) and expected (Exp) values of taxonomic diversity metrics in each mixed stand, and the observed minus expected (Obs-Exp) for each taxonomic diversity metric in each mixed stand. SR = species richness, H′ = Shannon Diversity Index, J′ = Pielou's Equitability Index. These values were used to analyse the difference between the observed vs expected values presented in Table A.5

Table A.7 Descriptions of nine plant functional response trait groups and associated additional references

Table A.8 Median of ordinal and continuous response traits and the difference between observed and expected frequencies of each class of nominal response traits (separated by slashes) for each RG. Chi square and Kruskal-Wallis tests were applied with adjusted p-values for multiple comparisons. Different letters indicate significant differences ($p<0.05$-0.001) between RG's

Table A.9 Descriptions of seven plant functional effect trait groups and associated additional references

Table A.10 Median of ordinal effect traits and the difference between observed and expected frequencies of each class of nominal effect traits (separated by slashes) for each EG. Chi square and Kruskal-Wallis tests were applied with adjusted p-values for multiple comparisons. Different letters indicate significant differences ($p<0.05$-0.001) between EGs.

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Table 1. List of 19 plant functional response traits compiled from the literature

Plant functional response traits	Description	Trait role*	Missing trait information	Variable type
Seed weight	1. Too small to be measured; 2. <0.2 mg; 3. 0.21-0.50 mg; 4. 0.51-1.00 mg; 5. 1.01-2.00 mg; 6. 2.01-10.00 mg; 7. >10.00 mg	D, E	20%	Ordinal
Seed size	Average in mm (length, breadth)	D, E	41%	Continuous
Seed shape	1. length/breadth ratio <1.5; 2. ratio 1.5-2.5; 3. ratio >2.5=length/breadth	D	22%	Ordinal
Seed production per ramet	1 = 1-10; 2 = 10-100; 3 = 100-1000; 4 = 1000-10000; 5 = >10000	D, E	37%	Ordinal
Seed longevity	Based on Thompson et al. 1998 longevity index. Estimates of seed longevity given when at least five records were present in the Thompson, Bakker & Bekker (1997) database; where there were fewer than five records for a given species, no seed longevity value was proposed.	E	26%	Continuous
Age at first flowering	1 = < 1 year; 2 = 1-5 years; 3 = 5+ years	P	39%	Ordinal
Height	1. <0.1 m; 2. 0.1-0.29 m; 3. 0.30-0.59 m; 4. 0.60-0.99 m; 5. 1.0-3.0 m; 6. >3.0	P	20%	Ordinal
Specific Leaf Area (leaf area mm^2/ leaf mass mg)	1. <15; 2. 15-20; 3. 20-25; 4. 25-30; 5. >30	P	23%	Ordinal
Leaf Dry Matter (% of fresh weight)	1. <15; 2. 15-20; 3. 20-25; 4. 25-30; 5. >30	P	24%	Ordinal
Growth form	1. Basal - leaves confined to a basal rosette, or to a prostrate stem; 2. Semi-basal - Stems erect or ascending, leafy but with the largest leaves towards their base; 3. Leafy - Stems erect or ascending with no basal rosette, leaves of approximately equal size; 4. Small leaves, reduced to spines or scales with the stem as the main photosynthetic organ; 5. Small leafy - as for 'Leafy' except that canopy does not exced 100mm; 6. Large-leaved semi-basal or basal - as for 'basal' or semi-basal' except leaves >10,000mm^2; 7. Small semi-basal - as for 'semi-basal' except that canopy does not exceed 100mm.	P	22%	Nominal
Leaf phenology	1. aestival (duration of canopy spring to autumn); 2. hibernal (mainly autumn to early summer); 3. always evergreen; 4. partially evergreen; 5. vernal (winter to spring)	P	20%	Nominal
Germination requirement	1. immediate; 2. chilling or drying or light or scarification; 3. combinations of the latter	E	25%	Ordinal
Dispersal type	1. barochory ; 2. anemochory; 3. hydrochory; 4. endo- and ectozoochory; 5. myrmecochory	D	22%	Nominal
Clonal propagation	0. yes; 1. no	D, P	20%	Nominal
Life form	1. chamaephyte; 2. geophyte; 3. hemicryptophyte; 4. therophyte; 5. phanerophyte; 6. helophyte	P	20%	Nominal
Life cycle	1. annual; 2. perennial	P	20%	Nominal
Pollination vector	1. autogamy; 2. anemogamy; 3. entomogamy	P	20%	Nominal
Mycorrhiza	0. 74% or less of records report mycorrhiza; 1. 75% or more records report infection with VA mycorrhiza	E, P	25%	Nominal
Flowering period	1. period > 4 months; 2. spring (3-5; March-May); 3. summer (6-7; June-July); 4. autumn (8-9; Aug-Sept)	P	20%	Nominal

* Trait roles are D – Dispersal, E – Establishment, P – Persistence (Weiher *et al*. 1999).

Table 2. List of 9 plant functional effect traits compiled from the literature

Plant functional effect traits	Description	Ecosystem services influenced by ET	Missing ET information	Variable type
Dispersule and germinule form	1. Dispersule and germinule a fruit (or part of a fruit, e.g. nutlet or mericarp) 2. Dispersule and germinule a seed; 3. Dispersule and germinule a spore; 4. Dispersule a fruit, germinule a seed (as in berries and other fleshy fruits); 5. Germinule a seed.	Food Resources	21%	Nominal
Palatability of foliage	1 = Low; 2 = Medium; 3 = High	Food Resources	39%	Ordinal
Insect-pollinated	0 = yes; 1 = no	Food Resources	20%	Nominal
Growth form/ Canopy structure	1. Basal - leaves confined to a basal rosette, or to a prostrate stem 2. Semi-basal - Stems erect or ascending, leafy but with the largest leaves towards their base. 3. Leafy - Stems erect or ascending with no basal rosette, leaves of approximately equal size; 4. Small leaves, reduced to spines or scales with the stem as the main photosynthetic organ; 5. Small leafy - as for 'Leafy' except that canopy does not exced 100mm; 6. Large-leaved semi-basal or basal - as for 'basal' or semi-basal' except leaves >10,000mm^2 7. Small semi-basal - as for 'semi-basal' except that canopy does not exceed 100mm.	Biogeochemical cycles Disturbance mediation	21%	Nominal
Specific Leaf Area (leaf area mm^2/ leaf mass mg)	1. <15; 2. 15-20; 3. 20-25; 4. 25-30; 5. >30	Biogeochemical cycles Disturbance mediation	23%	Ordinal
Leaf Dry Matter (% of fresh weight)	1. <15; 2. 15-20; 3. 20-25; 4. 25-30; 5. >30	Biogeochemical cycles Disturbance mediation	24%	Ordinal
Leaf phenology	1. aestival (duration of canopy spring to autumn); 2. hibernal (mainly autumn to early summer); 3. always evergreen; 4. partially evergreen; 5. vernal (winter to spring)	Biogeochemical cycles Disturbance mediation	20%	Nominal
Mean shoot height (m)	1. <0.1 m; 2. 0.1-0.29 m; 3. 0.30-0.59 m; 4. 0.60-0.99 m; 5. 1.0-3.0 m; 6. >3.0	Biogeochemical cycles Disturbance mediation	20%	Ordinal
Life form	1. chamaephyte; 2. geophyte; 3. hemicryptophyte; 4. therophyte; 5. phanerophyte; 6. helophyte	Biogeochemical cycles Disturbance mediation	21%	Nominal

Table 3. Mean of response group (RG) relative abundance in each region x stand type. Different lower case letters indicate a significant difference between stand types within a region and different uppercase letters indicate a significant difference between regions within stand type (p<0.05-0.001). Numerator degrees of freedom were region = 2, stand type = 2, and region x stand type = 4. Denominator degrees of freedom were region = 120, stand type = 120 and region x stand type = 120. F statistic for the fixed effects of region (R), stand type (S) and region x stand type (RxS) are presented in brackets for each RG. Asterisks = significance of lettering and F statistics (* = p<0.05; ** = p<0.01; *** = p<0.001)

	Ireland			**New Forest**			**Thetford Forest**		
Functional response trait groups*	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
RG1 (R=0.24, S=2.34, RxS=2.90*)	1.13	0.58	0.39 A*	0.28 a*	0.62 ab*	3.23 b B	1.29	0.17	1.01 AB
RG2[†] (S = 0.49)	7.26	0.16	0	0.03	0	0	1.69	9.11	11.88
RG3 (R=56.62, S = 4.69*, RxS = 10.50***)	90.12 a A	48.34 b*** A	19.87 b** A**	0.84 a*** B***	0.94 a*** B***	15.50 b A*	7.18 a* C***	0.74 b B***	1.69 ab B
RG4 (R=0.80, S = 0.02, RxS = 3.99**)	0.05 A*	2.29	0.52	1.17 AB	0.48	2.2	4.60 B	0.43	0.29
RG5 (R=10.77, S = 4.98**, RxS = 2.78*)	0.22 A	1.12 AB	0.08	30.15 a B***	0.73 b*** A	1.75 b**	29 B***	12.17 B*	2.52
RG6 (R=4.85, S = 3.43*, RxS = 3.00*)	0.38 a***	0.78 a***	38.49 b A	1.12 ab	0.11 a*	3.85 b B*	0.57	0.07	0.07 B**
RG7 (R=14.45, S = 14.95***, RxS = 2.52*)	0.88 a* B**	21.07 b A**	10.55 ab	34.77 a** A	95.71 b B	24.38 a***	0.48 a B**	31.54 b** A***	21.11 b*
RG8 (R=10.51, S =5.01**, RxS = 0.74)	0.56 a** A***	0.22 b A***	0.3 ab A***	3.11 a** A*	0.45 b A*	0.22 ab A*	6.18 a** B	1.61 b B	3.54 ab B
RG9[†] (S = 2.12)	0	0.03	0	0	0	0.05	0.78	1.45	0.3

* RG1 - Tree saplings; RG2 – Tall zoochorous perennials; RG3 - Woody shrubs/ climbers; RG4 – Wind-pollinated, zoochorous graminoids; RG5 – Short barochorous, creeping/ clump-forming herbs and graminoids; RG6 – Tufted graminoids and upright, clump-forming herbs; RG7 - Tall anemochorous perennials; RG8 –Spring-flowering, shade tolerant herbs; RG9 – Annuals.

† Not possible to test Ireland and New Forest for significance because of too many 0's. Effect of stand type was tested in Thetford Forest only – RG2 numDF = 2, denDF =39.77. RG9 num DF = 2, DenDF = 42.

Table 4. Mean of effect group (EG) relative abundance in each region x stand type. Different lower case letters indicate a significant difference between stand types within a region and different uppercase letters indicate a significant difference between regions within stand type (p<0.05-0.001). Numerator degrees of freedom were region = 2, stand type = 2, and region x stand type = 4. Denominator degrees of freedom were region = 120, stand type = 120 and region x stand type = 120. F statistic for the fixed effects of region (R), stand type (S) and region x stand type (RxS) are presented in brackets for each EG. Asterisks = significance of lettering and F statistics (* = p<0.05; ** = p<0.01; *** = p<0.001)

	Ireland			**New Forest**			**Thetford Forest**		
Functional effect trait groups*	Oak	Scots pine	Mix	Oak	Scots pine	Mix	Oak	Scots pine	Mix
EG1 (R=2.55, S =0.98, Rx S = 2.32)	**0.69**	**0.18**	**0.06**	**0.29** **a****	**0.62** **ab**	**2.94**	**0.8**	**0.17**	**1.01**
EG2[†] (S = 0.33)	**0.34**	**0.37**	**0**	**0.05**	**0**	**0.19**	**9.34**	**18.04**	**27.31**
EG3 (R=3.4*, S = 7.02**, Rx S = 2.03)	**0.90** **a**** **A****	**22.19** **b** **A****	**8.47** **ab** **A****	**27.13** **a*** **B**	**35.83** **b** **B**	**15.06** **ab** **B**	**1.21** **a** **AB**	**32.24** **b**** **AB**	**21.37** **b**** **AB**
EG4 (R=11.23***, S = 0.14, Rx S = 8.18***)	**0.82** **a***** **A**	**4.74** **a**** **A****	**44.42** **b** **A****	**53.44** **B*****	**54.03** **B**	**28.51** **A***	**46.69** **a**** **B*****	**10.66** **ab** **A***	**2.85** **b** **B**
EG5[†] (S = 2.24)	**0.15**	**0.05**	**0**	**0**	**0**	**0.47**	**16.76**	**4.32**	**1.89**
EG6 (R=3.19, S = 1.90, Rx S = 1.00)	**1.83** **A***	**0.68** **A**	**0.28** **A**	**3.06** **AB**	**0.54** **AB**	**0.62** **AB**	**2.14** **B**	**2.82** **B**	**2.92** **B**
EG7 (R=59.11***, S = 5.62**, Rx S = 9.90***)	**90.56** **a** **A*****	**49.57** **b***** **A**	**25.56** **b**** **A****	**0.83** **a***** **B****	**0.94** **a***** **B*****	**16.47** **b** **A****	**7.88** **a**** **C*****	**0.55** **b** **B*****	**1.69** **ab** **B**

* EG1 - Tree saplings; EG2 - Medium to tall non-woody ruderals and competitors; EG3 -: Ferns and rushes; EG4 – Grasses and sedges; EG5 – Annual herbs; EG6 – Short to medium height perennial herbs; EG7 - Shrubs/ climbers.

† Not possible to test Ireland and New Forest for significance because of too many 0's. Effect of stand type was tested in Thetford Forest only – EG2 numDF = 2, denDF = 40.53. EG5 numDF = 2, denDF = 42.

Figures

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 (▲).

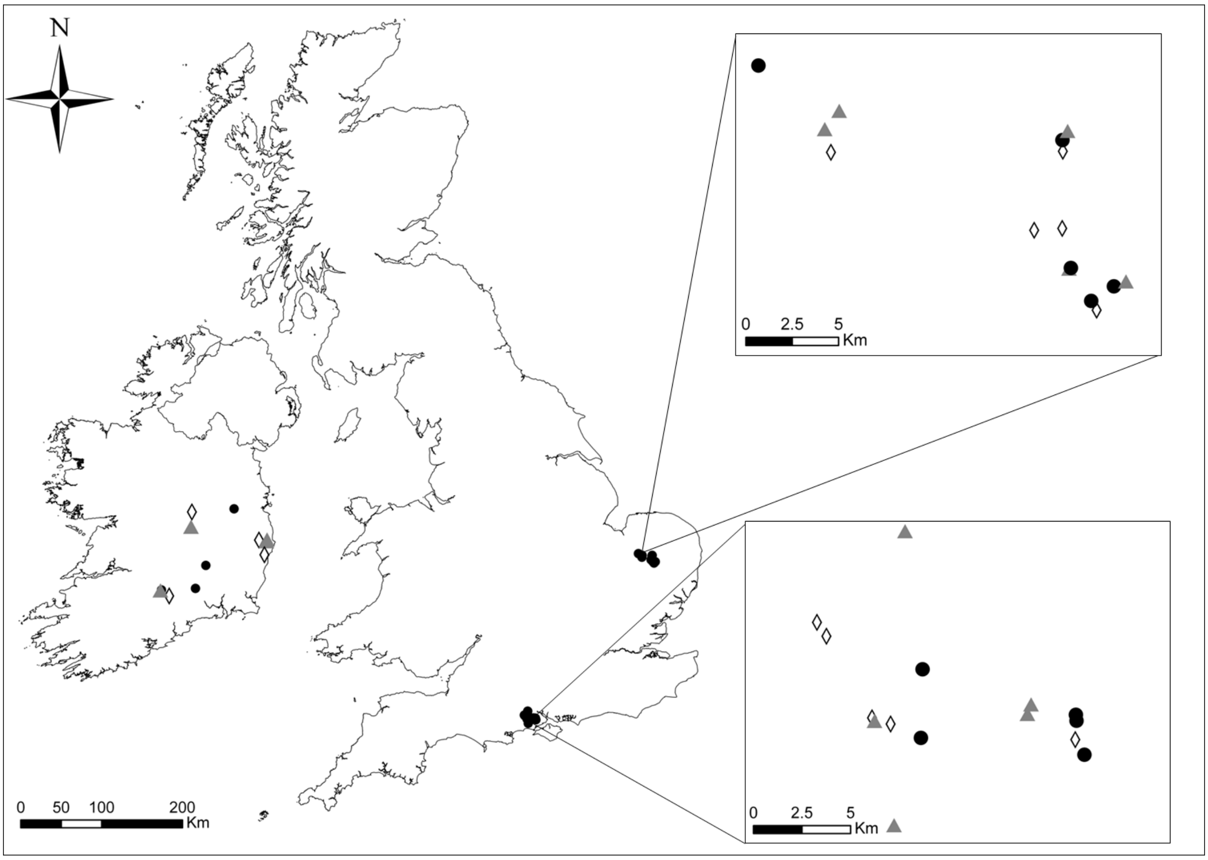

Fig. 2. Dendrogram illustrating clustering of ground vegetation species into nine functional response trait groups.

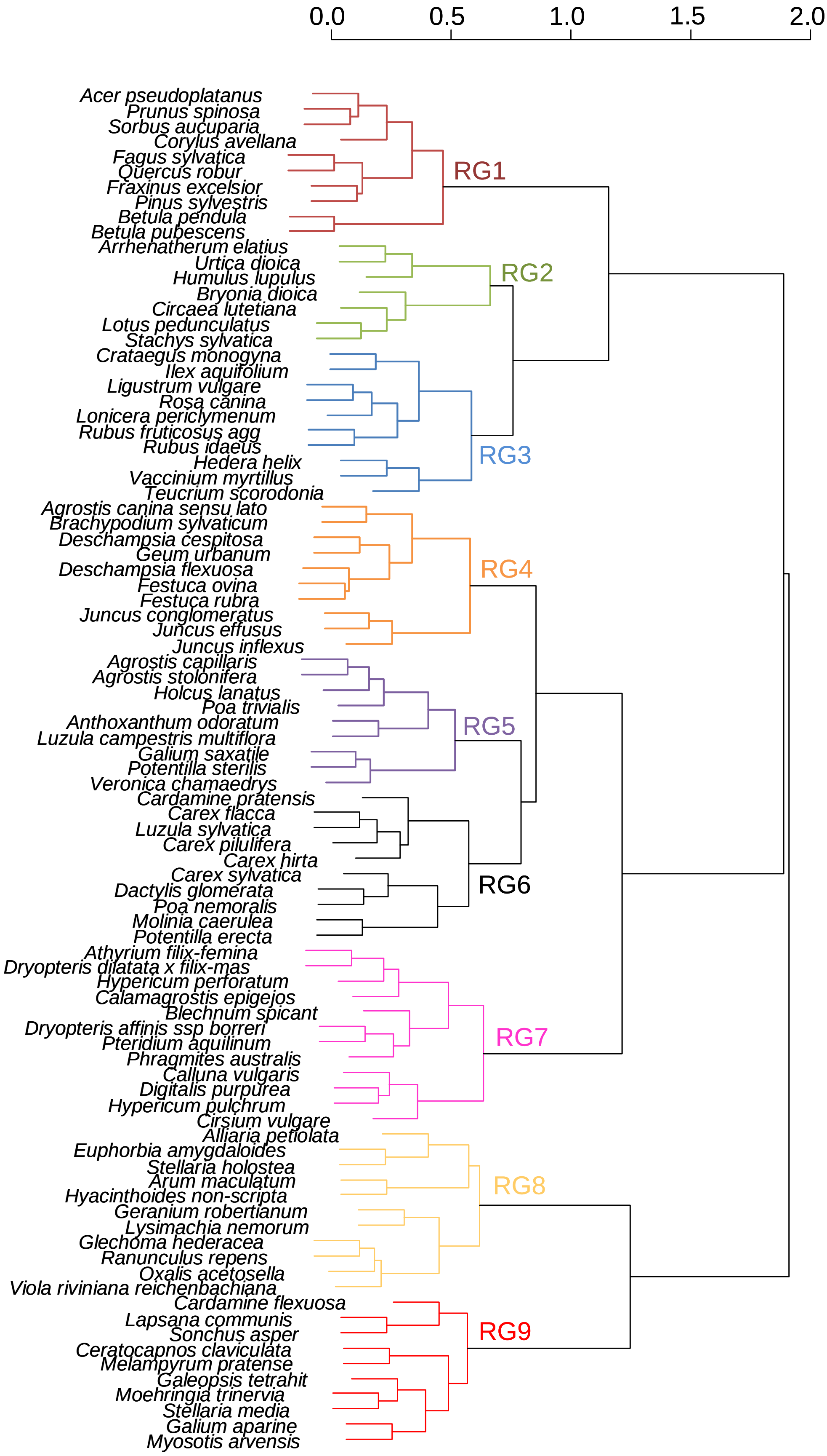

Fig. 3. Functional redundancy of plant functional RGs in each stand type: RG1 - Tree saplings: RG2 – Tall zoochorous perennials; RG3 - Woody shrubs/ climbers; RG4 – Wind-pollinated, zoochorous graminoids; RG5 – Short barochorous, creeping/ clump-forming herbs and graminoids; RG6 – Tufted graminoids and upright, clump-forming herbs; RG7 - Tall anemochorous perennials; RG8 –Spring-flowering, shade tolerant herbs; RG9 – Annuals. y axis shows the mean functional redundancy of each RG. Different lower case letters indicate a significant difference (p<0.05-0.001) between stand types within a region and different upper case letters indicate significant differences between regions within stand type

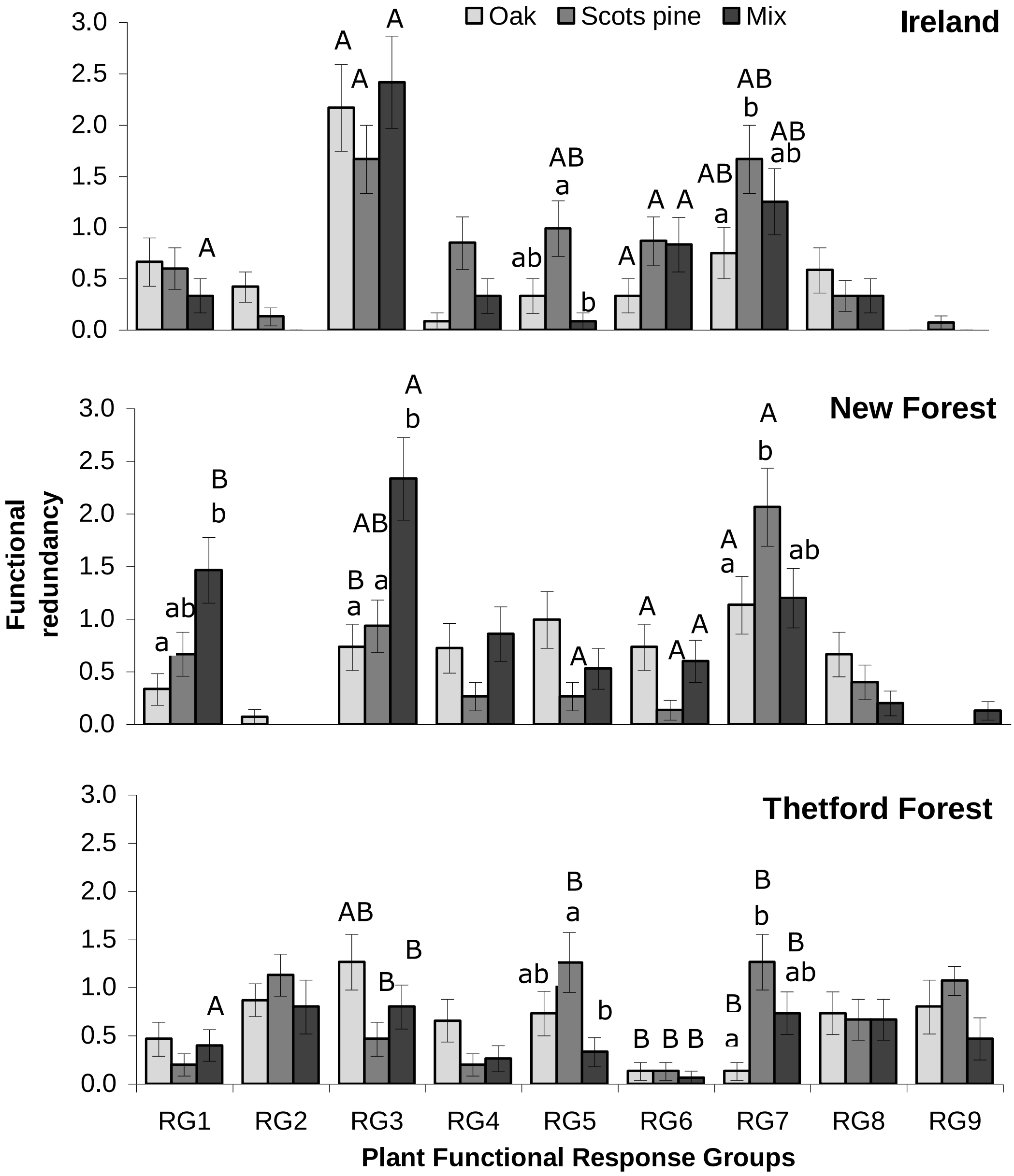

Fig. 4. Functional redundancy of plant functional EGs in each stand type: EG1 - Tree saplings; EG2 - Medium to tall non-woody ruderals and competitors; EG3 -: Ferns and rushes; EG4 – Grasses and sedges; EG5 – Annual herbs; EG6 – Short to medium height perennial herbs; EG7 - Shrubs/ climbers. y axis shows the mean functional redundancy of each EG. Different lower case letters indicate a significant difference (*p*<0.05-0.001) between stand types within a region and different upper case letters indicate significant differences between regions within stand type