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Biodiversity and Conservation

Identifying practical indicators of biodiversity for stand-level management of plantation forests

George F. Smith, Tom Gittings, Mark Wilson, Laura French,
Anne Oxbrough, Saoirse O'Donoghue., John O'Halloran, Daniel L. Kelly, Fraser
J. G. Mitchell, Tom Kelly, Susan Iremonger, Anne-Marie McKee, Paul Giller

Abstract

Identification of valid indicators of biodiversity is a critical need for sustainable forest management. We developed compositional, structural and functional indicators of biodiversity for five taxonomic groups—bryophytes, vascular plants, spiders, hoverflies and birds—using data from 44 Sitka spruce (*Picea sitchensis*) and ash (*Fraxinus excelsior*) plantation forests in Ireland. The best structural biodiversity indicator was stand stage, defined using a multivariate classification of forest structure variables. However, biodiversity trends over the forest cycle and between tree species differ among the taxonomic groups studied. Canopy cover was the main structural indicator and affected other structural variables such as cover of lower vegetation layers. Other structural indicators included deadwood and distances to forest edge and to broadleaved woodland. Functional indicators included stand age, site environmental characteristics and management practices. Compositional indicators were limited to more easily identifiable plant and bird species. Our results suggest that the biodiversity of any one of the species groups we surveyed cannot act as a surrogate for all of the other species groups. However, certain subgroups, such as forest bryophytes and saproxylic hoverflies, may be able to act as surrogates for each other. The indicators we have identified should be used together to identify stands of potentially high biodiversity or to evaluate the biodiversity effects of silvicultural management practices. They are readily assessed by non-specialists, ecologically meaningful and applicable over a broad area with similar climate

conditions and silvicultural systems. The approach we have used to develop biodiversity indicators, including stand structural types, is widely relevant and can enhance sustainable forest management of plantations.

Keywords: Biodiversity; Forest management; Indicator; Plantation; Species richness; Stand structure; Sustainable forest management

Introduction

Comprehensive biodiversity inventories of natural forests are virtually impossible to undertake because of the time and effort involved (Lawton et al. 1998). Similarly, the resources necessary to complete biodiversity inventories of plantation forests are not usually available, despite the often simplified nature of plantation ecosystems. Therefore, biodiversity assessment and management in plantation forests must rely on the use of biodiversity indicators (Lindenmayer 1999; Noss 1999; Lindenmayer et al. 2000; Larsson 2001). Despite the clear need, however, most indicators that have been published or exist in the 'grey' literature are the product of conventional wisdom and lack scientific validation (Noss 1999; Lindenmayer et al. 2006).

In order for indicators to be practical for sustainable forest management, it is important that they are repeatable, cost-effective, ecologically meaningful and easy to assess, particularly by forest managers or other non-ecologists (Ferris and Humphrey 1999). Indicators can be used by forest managers to assess the effect of site management on biodiversity or to identify sites that potentially are of high biodiversity value, in order to comply with national forest standards (e.g. Forest Service 2000b, c; Forestry Commission 2004) or the requirements of forestry grant schemes (e.g. Forest Service 2000a, 2006). In sites where few indicators are present, management can be reviewed and improved. Forest stands identified as being of potentially high biodiversity can be surveyed and assessed more thoroughly, and management for biodiversity can be prioritised in forest planning and operations. Forest biodiversity indicators can be developed at the regional or landscape scales for use in forest planning, but stand-scale indicators may be the

most practical, as most management operations are carried out at this level (Similata et al. 2006).

At the level of the forest stand, compositional indicators can be particular species or species groups (Noss 1990). The universality and applicability of surrogacy relationships among species groups—where the diversity of one group reflects diversity in another, unrelated group—are the focus of much recent conservation biology research, with mixed results (e.g. Howard et al. 1998; Vessby et al. 2002; Sætersdal et al. 2003; Anand et al. 2005; Oertli et al. 2005; Williams et al. 2006; Similata et al. 2006). Important elements of forest structure that may serve as structural indicators include tree size, vertical foliage distribution, horizontal canopy distribution and density and abundance of deadwood (Noss 1990; Spies 1998). Functional indicators can include processes such as productivity, nutrient cycling rates, disturbance regime and management practices (Noss 1990).

Aspects of stand structure have the potential to be particularly useful biodiversity indicators, especially as structure is the product of site environment and management and directly affects biodiversity and ecosystem function (Spies 1998). Comparison of managed forests and old, natural forests has found that managed forests often lack old-growth features, such as large trees, vertical heterogeneity, diverse tree species assemblages and large-diameter dead wood, that may be important for promoting biodiversity (Halpern and Spies 1995; Hodge and Peterken 1998; Humphrey 2005). Accordingly, many studies of forest biodiversity have paid special attention to stand structure (e.g. Pitkanen 1997; Humphrey et al. 1999, 2002; Ferris et al. 2000). However, quantification of stand structure can be difficult due to its multivariate nature (McElhinny et al. 2005).

In this paper, we develop potential indicators for biodiversity of five groups of plants and animals in plantation forests. These indicators can be used by non-specialists as tools to assess the effectiveness of current management practices in maintaining forest biodiversity and/or to identify stands or forests of potentially high biodiversity value. We pay particular attention to stand structure by developing a forest stand structure classification and assessing how changes in stand structure are reflected by changes in biodiversity.

Methods

Species Groups

This study was part of a larger research programme on biodiversity in commercial forestry plantations in Ireland (O'Halloran et al. 2004; Smith et al. 2005; Iremonger et al. 2007). We were not able to survey all taxonomic groups present in plantation forests, and thus we focused our efforts on five groups: bryophytes, vascular plants, spiders, hoverflies (Diptera: Syrphidae) and birds. These groups vary in mobility and the scales at which forest environment and management are likely to affect their diversity. The ecology and taxonomy of these groups are well-known. Forest understorey vegetation provides food and structural diversity that can be exploited by dependent fauna. Vascular plants in particular are a well-known group in Ireland and have been used as surrogates for total biodiversity in other countries (Ferris and Humphrey 1999; Niemi and McDonald 2004). Bryophytes are an important component of native forest flora, and in oceanic regions attain levels of diversity comparable with higher plants (Kelly 1981, 2005). Spiders represent an intermediate trophic level, and because of their relatively small ranges, they are responsive to changes at the stand and smaller scales (Niemela et al. 1996). Hoverflies are quite mobile and are therefore more sensitive to conditions at larger scales than spiders. They are a diverse group in terms of trophic and habitat requirements and have been used as indicators of disturbance or habitat quality (Sommagio 1999). Birds range over wider areas than members of any of the other taxa, and are therefore affected by environmental variation at the plantation and landscape scales (Pithon et al. 2005). Species assemblages present in the sites surveyed are analysed in more detail in related work (French et al. in press; Oxbrough et al. 2005; Smith et al. 2005; Wilson et al. 2006).

Study design

The study sites were in 44 plantation forests distributed across the Republic of Ireland (Fig. 1). In 12 sites, ash (*Fraxinus excelsior*) stands were sampled, and in 20 sites, Sitka spruce (*Picea sitchensis*) stands were sampled. In the remaining 12 sites, both ash and Sitka spruce stands were present in a non-intimate mix. These two species were chosen as the most commonly planted native broadleaf and the most commonly planted exotic conifer in Ireland. Each forest was in its first rotation and was at least 4 ha in area. The forests ranged in age from 5 yr to 81 yr at

the time of surveying. The majority of the study sites are owned by Coillte Teoranta, the semi-state forestry company, and only a few of the youngest forests were privately owned. Sites were surveyed in 2001 and 2002.

We employed a chronosequence approach where we sampled different sites at different stages of maturity. We selected age classes that would represent the major structural changes that take place over the course of a commercial rotation:

- 5 years: prior to canopy closure (4 pure spruce, 4 pure ash and 4 spruce/ash mix sites)
- 8-15 years: canopy closure phase (4 pure spruce, 4 pure ash and 4 spruce/ash mix sites)
- 20–30 years: mid-rotation, beginning of thinning operations (4 pure spruce sites)
- 35-50 years: approaching commercial maturity of Sitka spruce (8 pure spruce and 4 spruce/ash mix sites)
- 50–81 years: approaching commercial maturity of ash (4 pure ash sites)

To reduce confounding variation among age classes due solely to site environmental factors, study sites were clustered geographically, with each cluster including sites across the range of age 9 species combinations. It was not possible to match pure ash sites, as few such sites existed that met our forest size site selection criterion. Because of logistical difficulties largely caused by an outbreak of foot-and-mouth disease in 2001, and also because of loss of invertebrate traps to disturbance, it was not possible to sample every site for all taxonomic groups. We indicate sample size or degrees of freedom for all statistical tests performed.

Field work

Bryophytes and vascular plants were surveyed in three representative 100 m² plots at least 50 m apart at each site. Percent cover of each species was estimated to the nearest 5%. Forest structure was also assessed in these plots. Top height of the dominant trees and average spacing between trees was measured. Diameter at breast height (dbh, measured at 1.3 m) was measured for all trees in the plot, or for a random subsample of 10 trees in dense stands 15 yrs old or less. The percentage cover of the forest canopy was estimated by eye by two and usually three researchers jointly to reduce variation in estimates. Height, canopy cover, spacing

and mean dbh for each plot were then averaged to produce means for each site. Volume of coarse woody debris (CWD) [> 7 cm diameter was measured in each plot.

Spiders were sampled using pitfall traps (Curtis 1980) arranged in 16 m² plots established at least 50 m apart. Where possible, spider plots were adjacent to vegetation plots. Five pitfall traps were established in each plot, and five plots were established in each monoculture site. In mix sites, five plots were sampled in the spruce component and two in the smaller ash component. Pitfall traps were run for nine weeks and emptied and changed every third week. Cover of litter, bare soil and vegetation in three layers (< 10 cm, 10–50 cm and 50–200 cm) were estimated in each plot using the Braun-Blanquet scale (Mueller-Dombois and Ellenberg 1974).

Hoverflies were sampled using two Malaise traps (Southwood 2000) in each monoculture site and the spruce component of mix sites, and one Malaise trap in the ash component of mix sites. Traps were located in canopy gaps rather than under a closed canopy to increase their effectiveness. Traps were located at least 100 m from each other and were run for a minimum of six weeks. The presence of wet microhabitat features, such as streams and flushes, within 100 m of each trap was recorded. Frequency of standing and fallen CWD in the vicinity of each trap was recorded in four 10 × 100 m transects radiating from the trap towards the four cardinal compass points.

Birds were surveyed using 4–9 point counts (Bibby et al. 1992) per site, depending on the size and structural variation of the site. Points were located at least 100 m from each other, and their location was marked using a GPS. Point counts were conducted for 10 minutes, during which birds more than 50 m away were recorded and the positions of birds within 50 m were estimated. The distance of each sampling point to the nearest forest edge was determined using ArcView GIS. Canopy height (m) and the cover (nearest 5%) of three vegetation layers—canopy, shrub (woody plants 0.5–2 m tall, excluding young planted trees) and field/ground layer (non-woody vascular plants and bryophytes)—were recorded within 30 m of each point.

Soil samples were collected in each 100 m² vegetation plot; subsamples were taken from the four corners and then bulked. The pH of field-moist soils was measured using a pH meter with a glass electrode on a soil:distilled water (1:2) suspension. The soils were then air-dried and sieved prior to further chemical and

physical analyses. Available P was extracted using Morgan's reagent and quantified by a colorimetric method using a spec-trophotometer (Allen et al. 1986). Further environmental data, such as elevation, were collected at the sampling unit or site level, as appropriate. Distance from the site to the nearest old woodland and the area of old woodland within 1 km were determined using 1:10,560 Ordnance Survey maps published from 1900 to 1915. Management information was obtained from the Coillte inventory and forest managers.

For further details on survey methodology, see French et al. (in press) for vegetation, Oxbrough et al. (2005) for spiders, Wilson et al. (2006) for birds and Smith et al. (2005) for all taxonomic groups, environmental and management data and overall study design. Nomenclature follows Smith (2004) for mosses, Stace (1997) for vascular plants and Beaman (1994) for birds.

Data analysis

Structural types

Preliminary analyses of stand structural variables, such as canopy cover and tree size, showed high variability within a given age class. Forest age is only one of many factors that affect stand structure. Other factors include environmental parameters, such as climate and soil fertility, and management factors, such as thinning regime. Although stand age per se can influence biodiversity, particularly through the operation of dispersal and colonisation mechanisms, changes in stand structure in plantation forestry may have a stronger effect on biodiversity through modification of the below-canopy environment. Accordingly, many studies of forest biodiversity focus on stand structure rather than stand age (e.g. Pitkänen 1997; Humphrey et al. 1999, 2002; Ferris et al. 2000).

To improve our investigations of biodiversity and structural changes over the forest cycle, we developed a small number of stand structural types to summarise the structural characteristics of our study sites. Separate analyses of forest structure were conducted for each tree species (ash or Sitka spruce) using data from the vegetation plots. PCA ordination using covariance matrices was conducted on site means of canopy cover, tree height, dbh and spacing. Percent variation explained by individual axes was calculated by dividing the eigenvalue of each axis by the sum of all eigenvalues. Sites were assigned to structural stages using Ward's hierarchical clustering (Legendre and Legendre 1998). All variables were

transformed to a 0–1 scale by ranging (Sneath and Sokal 1973) prior to analysis to place them on equivalent scales. Ordinations were performed using PC-Ord (McCune and Mefford 1997).

Measuring biodiversity

Species richness of each of the taxonomic groups was calculated at the sample unit and site levels. We focus on species richness as our primary measure of biodiversity, as this is the most basic and universal method (Gaston 1996; Magurran 2004). However, total species richness does not indicate whether the species involved are of conservation significance and will also underestimate the conservation value of important but naturally species-poor habitats. To address this issue, we have analysed species richness of various subgroups: species characteristic of forest in Ireland (calculated separately for bryophytes, vascular plants, spiders, hoverflies and birds); hoverflies dependent on deadwood (saproxylic species), wet substrates, ground debris or semi-natural habitats (anthropophobic species: Speight and Castella 2001); and ground-nesting and cavity-nesting birds. Species characteristic of native woodland in Ireland will be referred to as 'forest species', although they may not be typical forest species elsewhere. Plantation forests may have an important role in providing habitat for forest species in regions where semi-natural forests are rare, as is the case in Ireland where less than 1% of the island is occupied by semi-natural forest (Cross 1998).

Species assemblages were identified using non-metric multidimensional scaling ordination (NMS) and flexible-beta clustering (Legendre and Legendre 1998). The results of these analyses will be briefly referred to, but space precludes a complete presentation of the analysis and results. For further details, see French et al. (in press) for vegetation, Oxbrough et al. (2005) for spiders, Wilson et al. (2006) for birds and Smith et al. (2005) for all taxonomic groups. Indicator species of vegetation cluster groups were identified using indicator species analysis (Dufrene and Legendre 1997). The method assesses the constancy and fidelity of species to defined assemblages and produces an indicator value score (IndVal) ranging from 0 to 100 which can be validated using Monte Carlo tests. Ordinations and indicator species analysis were performed using PC-Ord (McCune and Mefford 1997).

Indicators

Changes in species richness over forest structural stages were compared for the five taxonomic groups and the five forest species subgroups. Relationships between potential indicators and species richness were analysed using ANOVA/t-tests for categorical variables and correlation (Pearson's r) for continuous variables. Prior to analysis, variables were inspected for conformity to assumptions of parametric statistics and transformed where necessary. In some cases, transformation was inadequate, and Kruskal–Wallis tests or Spearman's rank correlation as appropriate were used instead (Sokal and Rohlf 1995). Correlations among predictive variables were also investigated. As distance to semi-natural woodland and area of woodland within 1 km were negatively correlated with forest age, partial correlations between species richness and woodland variables were performed to control for the effects of forest age. Differences in species richness between ash and spruce stands were tested using nested ANOVAs, with stand structural stage as the nested factor, to partition variation due to structural stage and not tree species. These analyses were performed using SPSS (2001).

Results

Stand structural types – *Sitka spruce*

The PCA ordination (Fig. 2) shows that the sites form a continuum of changing stand structure over the plantation cycle. Axis 1 explains 73% of the variance in the structural variables and mainly represents increasing height and dbh from left to right (Fig. 2, Table 1). Axis 2 explains 21% of the variation in the data and is most closely associated with increasing canopy cover (Fig. 2, Table 1). Spacing contributes similarly to both axes, with spacing increasing on Axis 1 and decreasing on Axis 2. Several structural variables were highly correlated with each other and with stand age (Table 2). The lowest correlations were generally with canopy cover, which has a hump-shaped relationship with tree height, dbh and age.

Defining five stand stages appeared to provide the best compromise between parsimony and adequate description. Means of structural variables at each stage are shown in Table 3. In the four-cluster solution, there was considerable variation in canopy cover and tree height in amalgamated group III/IV. There was substantial overlap in the age ranges of the oldest three structural stages (Table 3).

Stand structural types – *Ash*

When the four structural variables were analysed for the ash sites, the resulting clusters joined sites that varied widely in tree size and separated others largely on the basis of spacing. Analyses were then performed using only canopy cover, tree height and dbh. This simplified classification was better at forming coherent groupings of larger-tree sites and also clusters of smaller-tree sites.

The PCA ordination of the ash sites does not show as simple a structural pattern as was found for the Sitka spruce sites (Fig. 3). Axis 1 explains 86.9% of the variation in the three structural variables and is positively associated with all structural variables (Table 1). Axis 2 explains 11.4% of the variation in the data; it is positively associated with canopy cover and negatively associated with tree size. As with Sitka spruce stands, the strongest correlations were among tree height, dbh and stand age (Table 4). As these three variables increase, canopy cover increases asymptotically.

In the six-cluster solution and in the ordination diagram (Fig. 3), KILA was separated as an outlier. It was a 45 yr old stand that did not fit well into the stand types with similar canopy cover or tree size (Table 5). The six-cluster solution was

therefore accepted as defining the stand stages, and KILA was excluded from the stand type classification. Mean stand ages in ash Stages I and II and Stages IV and V were quite similar (Table 5).

Indicators

Table 6 summarises the significant relationships between species richness of taxonomic groups and subgroups and structural, compositional and functional variables. See Smith et al. (2005) for further details.

Structural

Species richness varied among structural stages, but there were differences among taxonomic groups in trends across the forest cycle. For example, vascular plant and to a lesser extent spider species richness trends mirrored changes in Sitka spruce canopy cover, whereas bryophyte species richness increased and hoverfly species richness decreased as spruce forests matured (Fig. 4a). Similar patterns were observed in ash forests, most notably an increase in bryophyte species richness, a decrease in hoverfly species richness and a decline in vascular plant species richness corresponding with an increase in canopy cover (Fig. 4b). There were also differences in resolution among different species groups in biodiversity trends among structural stages. The trends of hoverflies and birds were more coarse than that of vascular plants (Fig. 4a; Wilson et al. 2006). Richness of forest species in all taxonomic groups increased with forest maturity in Sitka spruce and ash forests, but again there were differences in scale of response (Fig. 4c, d).

Although birds are shown in Fig. 4 for comparison with other species groups, preliminary analyses found that birds were not as sensitive to changes in forest structure or tree species recorded at the stand scale. Therefore, a separate stand type classification was performed using the structural data from the bird point counts of ash and Sitka spruce forests combined. This resulted in three bird habitat subgroups, Younger, Intermediate and Older (Wilson et al. 2006), corresponding to structural Stages I–II, Stages II–III and Stages III–V, respectively. Indicators for bird diversity were developed in the context of this simplified structural classification.

The importance of canopy cover, particularly in spruce forests, is emphasised by the negative relationship between vascular plant species richness and canopy cover in forests beyond the initial, pre-thicket structural stage (Fig. 5). Canopy cover

in turn influenced the amount of vegetation cover in the lower strata. Canopy cover in more mature (i.e. Stages II–V) Sitka spruce vegetation plots was negatively correlated with cover of other structural layers, such as graminoids (Spearman $\rho = -0.44$, $P = 0.0003$) and forbs (Spearman $\rho = -0.38$, $P = 0.002$) and positively correlated with cover of conifer litter (Spearman $\rho = 0.80$, $P < 0.0001$). Cover in several structural layers was associated with species richness of plant and animal groups or subgroups. In Older ash and spruce forests, the species richness of generalist birds was positively associated with shrub cover ($r = 0.61$, $n = 19$, $P = 0.006$). Similarly, species richness of spider assemblages typical of more open ash and spruce forests was positively correlated with cover of field layer vegetation (<50 cm tall) (young spruce/ash group: $r = 0.45$, $n = 20$, $P = 0.05$; young ash group: $r = 0.40$, $n = 34$, $P = 0.02$; open spruce group: $r = 0.26$, $n = 44$, $P = 0.09$). In contrast, forest spiders in the open spruce assemblage were negatively correlated with field layer cover ($r = -0.48$, $n = 44$, $P < 0.001$) and positively correlated with conifer litter cover ($r = 0.46$, $n = 44$, $P = 0.002$).

Bryophyte species richness was positively associated with volume of CWD in Stage II–V ash and spruce plots ($r = 0.27$, $n = 105$, $P = 0.003$, 1-tailed). When restricted to spruce forests only, the relationship was stronger ($r = 0.42$, $n = 68$, $P = 0.0002$, 1-tailed). Forest bryophytes were also positively associated with CWD volume in Stage II–V ash and spruce plots ($r = 0.35$, $n = 105$, $P = 0.0001$, 1-tailed). The species richness of saproxylic hoverflies was positively correlated with frequency of standing CWD ($r = 0.62$, $n = 20$, $P = 0.002$, 1-tailed) and fallen CWD ($r = 0.57$, $n = 20$, $P = 0.004$, 1-tailed) in spruce forests older than 20 years.

Structural features at the landscape scale were also associated with species richness of some taxonomic groups. In Older ash and spruce forests, distance to the forest edge was negatively correlated with species richness of birds ($r = -0.72$, $n = 19$, $P = 0.001$). Species richness of forest vascular plants in Stage II–V ash and spruce forests was negatively correlated with distance to native woodland ($r = -0.75$, $n = 30$, $P < 0.001$) and positively correlated with area of native woodland within 1 km ($r = 0.75$, $n = 30$, $P < 0.001$) (both are partial correlations controlling for variation due to forest age).

Compositional

Differences in species richness between Sitka spruce and ash stands, when variation due to structure is removed from the analysis, varied by taxonomic group. Vegetation plots in Sitka spruce stands supported a significantly higher number of bryophyte species (9.3 ± 0.6 se) than in ash stands (5.9 ± 0.5 se) ($F_{1,152} = 18.9$, $P < 0.001$). In contrast, ash stands supported significantly more vascular plant species (19.0 ± 0.9 se) than Sitka spruce stands (13.0 ± 1.0 se) ($F_{1,152} = 17.97$, $P < 0.001$). When both plant groups are combined, differences in species richness are not significant ($F_{1,152} = 1.95$, $P = 0.17$). There were also no differences in mean hoverfly species richness between ash (12.5 ± 1.2) and Sitka spruce (11.5 ± 0.7) ($F_{1,55} = 0.05$, $P = 0.82$). Species richness of saproxylic hoverflies, however, was significantly higher in ash compared to Sitka spruce: 2.1 ± 0.3 se in ash and 1.6 ± 0.3 se in Sitka spruce ($F_{1,55} = 11.0$, $P = 0.002$). Spider species richness was higher in Sitka spruce stands (16.4 ± 0.4 se) than in ash (14.4 ± 0.8 se) ($F_{1,170} = 13.2$, $P < 0.001$). There were no significant differences in bird species richness between tree species in any of the three bird habitat subgroups.

Over the three bird habitat subgroups, the strongest positive correlations between bird species richness and the abundance of particular bird species were with abundances of Dunnock (*Prunella modularis*) ($r = 0.55$, $P < 0.001$), Wren (*Troglodytes troglodytes*) ($r = 0.49$, $P < 0.001$) and Blackbird (*Turdus merula*) ($r = 0.47$, $P = 0.001$). Abundances of Goldcrest (*Regulus regulus*) were negatively correlated with bird species richness ($r = -0.30$, $P = 0.048$). When considering Older forests only, ten bird species were significantly correlated with total bird species richness (Table 7a).

Five plant species assemblages were identified in the more mature Sitka spruce stands (Smith et al. 2005), two of which supported significantly higher total plant species richness than the others. Four significant indicator species with indicator values greater than 25 were found for cluster A, representing a more open, vascular-plant rich community, and four for cluster B, a community type particularly rich in bryophyte species (Table 7b). Indicator plant species were not identified for ash forests, as there were no significant differences in total plant species richness among ash plant communities. There was a significant difference in forest species richness between two groups of communities, but this simply contrasted more

mature forests with a characteristic woodland flora (Stages III–V; with younger forests that supported a grassy understorey (Stages II–III).

Functional

There were fewer clear functional indicators of biodiversity than structural and compositional indicators. Species richness of forest vascular plants increased with forest age ($r^2 = 0.53$, $n = 43$, $P < 0.0001$). Forest bryophyte species richness also increased with forest age, but the rate of increase declined in older forests. When forest age was log-transformed, a significant linear relationship was observed ($r^2 = 0.74$, $n = 43$, $P < 0.0001$). Species richness of forest spiders increased with forest age ($r^2 = 0.22$, $n = 31$, $P = 0.008$), but was lower in the oldest ash forests. Species richness of some hoverfly groups was higher in Stage III–V sites where wet microhabitats (e.g. streams or flushes) occurred than in sites without these features (Table 8). In addition, in spruce sites more than 20 years old, saproxylic hoverfly species were more abundant in wet sites (2.5 ± 0.1 se) than in dry sites (1.1 ± 0.4 se) ($t_{19} = 4.0$, $P < 0.001$), reflecting the greater amounts of standing and fallen CWD in wet sites.

Total bird species richness in Older forests was negatively correlated with site elevation ($r = -0.50$, $P = 0.031$, $n = 19$). However, when the nesting habits of bird species were considered, species richness of ground-nesters was positively correlated with elevation ($r = 0.61$, $P = 0.006$, $n = 19$) whereas species richness of cavity-nesters was negatively correlated with elevation ($r = -0.61$, $P = 0.006$, $n = 19$). Available P was positively correlated with vascular plant species richness in Stage V Sitka spruce forests ($r = 0.71$, $P = 0.022$, $n = 18$).

Discussion

We have found that biodiversity of bryophytes, vascular plants, spiders, hoverflies and birds vary in Sitka spruce and ash plantation forests across the forest cycle (Fig. 4). Patterns of variation differ among species groups and subgroups with respect to forest structure and tree species. Several structural, compositional and functional variables cor-related with species richness in one or more groups (Table 6) have the potential to be used as biodiversity indicators in forest management at the stand scale.

Given the species groups we have surveyed, an important question is whether the biodiversity in these groups can act as surrogates for other groups. The variation in responses among the species groups to changes in forest structure and canopy species, and the different sets of indicators identified for them, suggest that no one group can act as a surrogate for biodiversity of all other groups. Other studies have come to similar conclusions (Prendergast et al. 1993; Lawton et al. 1998; Jonsson and Jonsell 1999; Vessby et al. 2002; Oertli et al. 2005; Similä et al. 2006). However, some studies have found that at least some groups of vascular plants can serve as surrogates for other taxa in forest ecosystems (Pharo et al. 1999; Negi and Gadgil 2002; Sætersdal et al. 2003; Kati et al. 2004). In our study, patterns of total species richness in vascular plants, spiders and, to a lesser extent, birds, show similar trends across the forest structural cycle (Fig. 4a, b). Groups with similar ecological requirements are more likely to act as adequate surrogates for each other, such as typical forest species (Fig. 4c, d) or bryophytes that benefit from deadwood habitats and saproxylic hoverflies (Table 6). Similarly, Similä et al. (2006) found that saproxylic beetles and polypore fungi have the potential to act as surrogates for each other in Finnish boreal forests.

For the above reasons, it is necessary to cover a range of different taxonomic groups to make an adequate assessment of the biodiversity of a particular site. Although we have attempted to do this, it is likely that inclusion of additional taxonomic groups in our study might have revealed additional patterns of variation in biodiversity. For example, forests are an important habitat for some species of bats, all of which are of conservation value in Ireland (Hayden and Harrington 2001). As

the features that are important for bats, such as crevices or hollows in trees suitable for roosting, are probably not as important for the taxa we surveyed, patterns of bat diversity would probably be different than those in this study.

The indicators we have identified are summarised in Table 9. Previous authors have identified characteristics that indicators should ideally possess if they are to be effective management tools (Noss 1990; Ferris and Humphrey 1999; Lindenmayer 1999). Preferably, indicators should: (1) show clear links to particular aspects of biodiversity, (2) be sensitive to changes in those features, (3) be applicable over a broad geographical area, (4) be easy and cost-efficient to measure, and (5) be ecologically meaningful. Our study design and data analysis ensure that the indicators we developed meet the first four criteria. The last criterion is addressed in the interpretation of our results below

Structural

The structural indicators we have presented are linked to ecological processes that affect the biodiversity of our surveyed groups. When considering biodiversity over the forest cycle, the clearest indicator for the majority of taxonomic groups is stand structural stage, demonstrating the value of a multivariate structural classification. Other studies have successfully used similar multivariate classifications (e.g. Pitkänen 1997; Leppäniemi et al. 1998), whereas others have used more subjective classifications (e.g. Humphrey et al. 1999; Ferris et al. 2000) or have used age as a surrogate (e.g. Currie and Balmford 1982; Brockerhoff et al. 2003; Eycott et al. 2006). In preliminary analyses of biodiversity patterns, we found that our original age categorisation of stand development did not adequately account for structural variation due to such variables as site fertility and thinning regime (Smith et al. 2005). Trends in biodiversity were usually better predicted by structural type rather than age class. The influence of thinning and stand age on structure and diversity are discussed in more detail below.

There are differences in resolution among different species groups in species richness at different structural stages. For example, species richness of vascular plants exhibited marked differences among stages in Sitka spruce and ash, whereas species richness of birds and hoverflies was less variable (Fig. 4). A fundamental distinction in forest structure to which virtually all taxonomic groups responded was

between the pre-thicket forests of Stage I and structural stages post-canopy closure (Stages II–V). Some species groups, such as vascular plants and spiders, showed a unimodal response to stand structural stage, with high species richness in Stage I, low species richness in intermediate stages and increased richness in later stages. Other groups, such as typical forest plant, invertebrate and bird species, increased through the course of the structural cycle. These patterns have also been identified during succession in natural Douglas-fir (*Pseudotsuga menziesii*) forests (Spies 1998) and over the silvicultural cycle in plantation forests in Britain (Hill 1979; Ferris et al. 2000; Eycott et al. 2006) and New Zealand (Brockerhoff et al. 2003).

Canopy openness was a key biodiversity indicator for vegetation, particularly vascular plants. Several other indicators of biodiversity for plants, spiders and birds were associated with this key factor, such as cover of shrubs, graminoids, conifer litter and all vegetation 11–50 cm tall. Stands with a more open canopy support greater abundance and diversity of understorey vegetation (Hill 1979; Ferris et al. 2000; Eycott et al. 2006), which have the potential to increase diversity of invertebrates (Day et al. 1993; Fahy and Gormally 1998; Humphrey et al. 1999; Oxbrough et al. 2005) and birds (Currie and Balmford 1982; Bibby et al. 1989; Duffy et al. 1997; O’Halloran et al. 1999).

Deadwood volumes increased over the forest cycle, as has been noted in previous studies (Spies et al. 1988; Spies 1998; Humphrey and Peace 2003). Biodiversity of bryophytes (total and forest) and saproxylic invertebrates were positively associated with volume of deadwood. Several other studies have found that deadwood is correlated with diversity of bryophytes and lichens (e.g. Engelmark and Hytteborn 1999; Humphrey et al. 2002), fungi (e.g. Humphrey et al. 2000) and invertebrates (e.g. Berg et al. 1994; Similä et al. 2006).

The plantation-scale structural indicators—distance to forest edge for birds and distance to and area of native woodland near plantations for forest plants—reflect the availability of additional habitats in the immediate landscape to act as supplementary habitat or population sources. Forest edges may provide habitat for bird species that prefer open or shrubby habitats, and the presence of broadleaf scrub at plantation forest edges would improve the habitat value of the

edge for birds (Currie and Balmford 1982; Bibby et al. 1989; Duffy et al. 1997; Iremonger et al. 2006). Native woodlands in close proximity to plantation forests can act as seed sources for forest plants, which are often dispersal-limited (Ehrle and Eriksson 2000; Verheyen et al. 2003; Devlaeminck et al. 2005). The same relationship was not observed for forest bryophytes, most likely because bryophyte spores disperse more easily over longer distances.

Compositional

For an indicator to be easy and cost-effective to measure, it must be capable of ready assessment by non-specialists (Ferris and Humphrey 1999), such as forest inventory staff or individual landowners. Because of the low species diversity of birds in Ireland and the lack of forest specialists (Wilson et al. 2006), the number of indicator bird species is low (Table 7). In fact most of the indicator species are common birds in Ireland and will be familiar to most non-specialists (Coombes et al. 2002). The vascular plant and bryophyte species we have listed are readily identifiable with some practice; they are also common species in Ireland. We have not selected any invertebrate species as compositional bio-diversity indicators, as they require more time-consuming and expensive sampling methods and are not easily identifiable by non-specialists.

Tree species, a potential compositional indicator, produced contrasting results among species groups. Bryophyte and spider species richness were higher in Sitka spruce stands, vascular plant and saproxylic hoverfly species richness were higher in ash stands and no differences in total hoverfly or bird species richness were observed between tree species (Table 6). These results can be explained by the biology of the different taxonomic groups. A greater diversity of vascular plants is facilitated by the lighter ash canopy and also by the more fertile conditions in which the ash stands occurred. Bryophyte species richness is encouraged by the high humidity and lower competition from larger plants in spruce stands. Species richness in spiders is strongly influenced by vegetation structure (Greenstone 1984; Dennis et al. 1998; McNett and Rypstra 2000), and it is likely that the reduction in cover of larger plants in spruce stands facilitated development of ground and lower field layer vegetation that favours ground-dwelling spiders. Our results, however, cannot be extrapolated to other broadleaved or coniferous tree species. For example, the

number of plant-feeding invertebrate species—which form part of the diet of spiders and birds—associated with ash in Britain is relatively low compared to other native broadleaved trees (Key 1995). Therefore, comparisons between Sitka spruce and plantations of other native broadleaved tree species might produce greater contrasts in biodiversity than those we found. Oak (*Quercus* spp.) and birch (*Betula* spp.) would be particularly interesting to study in this context as they support high numbers of plant-feeding invertebrate species (Jones 1959; Atkinson 1992; Key 1995). While some invertebrate species may specialise on other conifer species, differences in forest structure may have a more important potential effect on biodiversity. In particular, pines (*Pinus* spp.) and larches (*Larix* spp.) tend to allow greater light penetration through the canopy and therefore allow greater development of vascular ground flora during the middle part of the forest cycle (Hill 1979; Ferris et al. 2000; French et al. in press).

Functional

Stand age was an adequate positive biodiversity indicator only for forest plants and forest spiders and a negative indicator for birds in intermediate-aged stands, especially species characteristic of open habitats. The increase of forest plant and spider species richness is the result of dispersal and colonisation of a suitable habitat, successional processes seen in natural forests and also in plantation forests. Previous research in Britain (Hill and Jones, 1978; Ferris et al. 2000) and New Zealand (Brockerhoff et al. 2003) has also found that mature plantations of native and exotic species can acquire floras characteristic of native forests. In our study, the flora of mature spruce plantations somewhat resembles that of native acid oak woodland and the flora of mature ash plantations is similar to that in semi-natural ash-hazel woodland (French et al. in press). Dispersal is an important mechanism in the succession of forest vascular plants, as demonstrated by the relationship with proximity to old woodland. For spiders, whose young can disperse long distances by ballooning, a more important factor may be the development of suitable habitat in the form of high cover of conifer litter or bryophytes (Table 9; Oxbrough et al. 2005). For birds, dispersal is likely to be much less important than the development of suitable or unsuitable forest structures with age. Tree size and density were strongly correlated with stand age (Tables 2 and 4), and it is these factors that are probably responsible for the negative relationship between open-

habitat bird species richness and age. In contrast, canopy cover was less well correlated with stand age, and species groups strongly influenced by canopy cover will as a result have weaker relationships with stand age.

One functional process that is partly responsible for the lower correlation between stand age and canopy cover is thinning. Thinning operations decrease canopy cover, at least temporarily, promote larger diameter trees in the longer term and increase deadwood volume. It was not possible to analyse the relationships between thinning and biodiversity explicitly because of the difficulty in obtaining stand-specific information on thinning regime. However, such information as we were able to obtain suggests that Stage II and III Sitka spruce stands were mainly unthinned and that Stage V spruce stands had been subjected to at least three thinning operations. Therefore, thinning can be considered an indicator of biodiversity in Sitka spruce forests (Table 9). In contrast, Brockerhoff et al.(2003) in New Zealand found that more heavily thinned stands supported a greater proportion of exotic species than more dense stands; however, maximum canopy closure in their pine stands was 80%, lower than the average in our Stage III stands. As thinning is a management practice, it is the easiest of our functional indicators to change and may be the most efficient method of influencing stand biodiversity. We recommend that spruce plantations be thinned early and at regular intervals so as to prevent complete canopy closure (Smith et al. 2005).

We identified few other functional indicators, possibly in part as a result of our strategy of clustering sites to reduce environmental variation. The presence of wet microhabitats, such as flushes and temporary ponds or streams, in plantation forests increased hoverfly biodiversity by meeting the habitat requirements for the larval stages of a particular set of species. Wet microhabitats may also increase stand biodiversity of other plant or animal species groups. Wet spruce sites also supported higher amounts of deadwood, due to greater frequency of windthrow, and thereby greater diversity of saproxylic hoverflies (Table 8). Site elevation as an indicator of bird diversity appears to reflect the differences between upland and lowland plantations and surrounding landscapes. Higher available P in Stage V Sitka spruce stands indicates greater richness of vascular plants, perhaps because greater soil fertility permits coexistence of a wider range of species. Eycott et al. (2006) also found that more fertile sites supported higher vascular plant species richness in pine

plantations in lowland England, and Similä et al. (2006) reached the same conclusion in managed boreal forests in Finland. Our sites were of low overall fertility, however, and the true relationship between fertility and vascular plant diversity may be unimodal rather than linear (Grime 1979; Pausas and Austin 2001).

Using indicators

The biodiversity indicators we identify (Table 9) can be used to assess the effect of site management practices on biodiversity and to identify sites that are potentially of high biodiversity value. Used as the former, they are targets to be achieved by management. Presence of few or no indicators in forest stands suggests that management methods should be improved; the indicators also provide information on the changes required. Forest stands identified as being of potentially high biodiversity can be surveyed and assessed more thoroughly, and management for biodiversity can be prioritised in forest planning and operations. Indicators cannot substitute for thorough ecological surveys, particularly when sites of major biodiversity importance may be involved, but they can be employed as a first step in management assessment or in identifying sites of biodiversity value. These indicators cannot identify sites where rare species are present, a failure general to the indicator approach (Niemi and McDonald 2004).

Our indicators should be considered preliminary until they are verified using independent data (Noss 1990). In addition, the context in which they have been identified, i.e. first rotation Sitka spruce and ash stands managed under a clearfelling system, must be taken into consideration. These indicators should generally be employed at the stand level, rather than at the level of the whole plantation or landscape. They should be used in conjunction: in general, it is misleading to label a stand as having high biodiversity (or not) on the basis of just one or two indicators. We recommend the presence of at least four indicators from two or more groups (compositional, structural and functional) as a general guideline for designating sites or stands as potentially having high biodiversity. We are not aware of any similar recommendations regarding the number of indicators required for a favourable biodiversity assessment.

Conclusions

We have developed a set of provisional, stand-scale indicators of biodiversity for Sitka spruce and ash plantation forests for use in Ireland; they are likely to be applicable over a wider area with similar climates, such as northern Britain. The approach we have used to develop indicators has a wider potential for application. The indicators can be employed by non-specialists as a first step in identifying potentially high biodiversity stands or assessing the biodiversity implications of management interventions. Structural and functional indicators are particularly useful, as their assessment is often relatively simple. Functional indicators can represent management interventions, such as thinning, that can be changed if required; structural indicators provide targets for management to reach. Stand structure strongly affects species richness. A multivariate classification of stand structure into a small number of stages can be used to summarise biodiversity changes over the forest cycle. As species groups vary in their response to changes in stand structure, caution is required when using one group as a surrogate for the biodiversity of another.

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Table 1 Eigenvectors of the first two axes of the Sitka spruce and ash stand structure PCA ordinations showing the relative contributions of canopy cover, tree height, dbh and spacing

	Height	Dbh	Spacing	Canopy cover
<i>Sitka spruce</i>				
Axis 1	0.707	0.590	0.330	0.209
Axis 2	-0.024	-0.057	-0.419	0.906
<i>Ash</i>				
Axis 1	0.593	0.551	-	0.587
Axis 2	-0.368	-0.462	-	0.807

Table 2 Pearson correlations among Sitka spruce forest structural variables and stand age

	Height	Dbh	Spacing	Age
Canopy cover	0.38*	0.33	-0.11	0.33
Height		0.92***	0.69***	0.95***
Dbh			0.74***	0.92***
Spacing				0.61***

Statistically significant correlations are indicated: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. N = 31 sites

Table 3 Mean (and range of site means in brackets) canopy cover (%), tree height (m), dbh (cm) and spacing (m) in Sitka spruce stand structural stages defined by a Ward's hierarchical clustering analysis. Also shown is mean (and range) stand age (yr)

Stand stage	Canopy cover (%)	Height (m)	Dbh (cm)	Spacing (m)	Age (yr)
I	29.6 (11.7–43.3)	2.5 (1.4–3.8)	3.7 (1.6–7.0)	1.6 (1.0–2.0)	4.6 (3–10)
II	80.3 (60.0–93.3)	5.9 (4.3–7.3)	12.4 (10.4–16.5)	1.9 (1.5–2.0)	10.7 (9–13)
III	86.9 (78.3–95.0)	12.7 (9.8–15.7)	19.3 (14.7–24.3)	1.7 (1.4–2.0)	26.3 (14–39)
IV	70.8 (63.3–80.0)	18.8 (16.8–20)	22.4 (21.0–24.8)	2.3 (2.0–2.8)	36.1 (25–43)
V	54.7 (40.0–60.0)	21.1 (18.3–23.0)	39.0 (31.6–44.8)	3.9 (3.0–6.0)	42.6 (37–47)

Table 4 Pearson correlations among ash forest structural variables and stand age

	Height	Dbh	Spacing	Age
Canopy cover	0.76***	0.72***	0.26	0.65***
Height		0.95***	0.54*	0.90***
Dbh			0.64**	0.93***
Spacing				0.63**

Statistically significant correlations are indicated: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. N = 24 sites

Table 5 Mean (and range of site means in brackets) canopy cover (%), tree height (m), dbh (cm) and spacing (m) in ash stand structural stages defined by a Ward's hierarchical cluster analysis. KILA was structurally different than the remainder of the sites and was assigned to its own group in the six-cluster solution

Stand stage	Canopy cover (%)	Height (m)	Dbh (cm)	Spacing (m)	Age (yr)
I	12.2 (5.0–21.7)	3.1 (1.3–5.0)	3.8 (0.9–9.1)	2.1 (1.5–3.5)	6.7 (3–11)
II	57.8 (45.0–80.0)	4.4 (3.0–6.0)	6.3 (4.8–8.9)	1.8 (1.5–2.0)	6.6 (5–10)
III	77.1 (70.0–88.3)	9.0 (6.8–11.5)	10.0 (7.8–13.85)	2.3 (1.8–3.0)	18.3 (8–37)
IV	75.6 (66.7–81.7)	18.8 (16.3–22.0)	17.3 (15.8–19.7)	2.4 (1.5–3.8)	52.7 (44–62)
V	72.2 (70–73.3)	21.6 (18.5–25.0)	29.1 (27.6–30.9)	4.0 (3.0–6.0)	63.3 (47–81)
KILA	43.3	10.5	12.9	2.5	45

Note that mean spacing was not used in the cluster analysis. Also shown is mean (and range) stand age (yr)

Table 6 Summary of relationships between structural, compositional and functional variables and species richness of taxonomic groups and subgroups

	Bryophytes		Vascular plants		Spiders		Hoverflies		Birds			
	All	Forest Spp	All	Forest Spp	All	Open Spp	Forest Spp	All	Saproxylic Spp	All	Generalist	Open Spp
Canopy cover	+	+++ ^b	-	-	-	-	-	-	-	-	-	-
Shrub cover												
Field layer cover												++
Ground layer cover												
Comifer litter cover												
Coarse woody debris		++		+++			++					
Distance to forest edge												
Distance to native woodland		0		-			-					-
Area of native woodland within 1 km		0		+++								
Sitka spruce ^d		+++		0		+++	+++			0		0
Ash ^e		0		+++		+				0		0
Age		+++		+++			++			+++ ^g		+++
Wet microhabitats												
Elevation												
Available P												

Strength of relationships are indicated as follows: + $P < 0.05$, ++ $P < 0.01$ and +++ $P \leq 0.001$. Negative relationships are indicated similarly. Notable lack of relationship is indicated by 0. See text and Smith et al. (2005) for further details

^a But bryophyte species richness low at high values of canopy cover in spruce stands

^b In ash forests; in spruce forests species richness highest at intermediate levels of canopy cover

^c In Old (mainly Stage IV–V) forests

^d Relative to ash forests; only positive relationships shown

^e Relative to Sitka spruce forests; only positive relationships shown

^f In Intermediate (Stage II–III) sites

^g Anthrophobic species and species associated with wet substrates and ground debris. See Table 8

^h Except ground-nesters

ⁱ In Stage V Sitka spruce forests

Table 7 Compositional indicators of biodiversity. (a) Significant correlations of bird species abundance with bird species richness in Older forests (n = 19); (b) Significant indicator values [25 (IndVal) of plant species for species-rich (SR) vegetation communities in Stage II Sitka spruce stands derived by flexible-beta clustering (Legendre and Legendre 1998)

Species	Scientific name	r	P
a)			
Wren	<i>Troglodytes troglodytes</i>	0.78	0.0001
Dunnoek	<i>Prunella modularis</i>	0.63	0.0039
Blackbird	<i>Turdus merula</i>	0.58	0.0087
Pheasant	<i>Phasianus colchicus</i>	0.57	0.0111
Robin	<i>Erithacus rubecula</i>	0.53	0.0204
Treecreeper	<i>Certhia familiaris</i>	0.52	0.0225
Stonechat	<i>Saxicola torquata</i>	0.52	0.0232
Greenfinch	<i>Carduelis chloris</i>	0.51	0.0272
Great Tit	<i>Parus major</i>	0.50	0.0282
Blue Tit	<i>Parus caeruleus</i>	0.47	0.0409
	Species	IndVal	P
b)			
Sitka spruce ^a	<i>Rubus fruticosus</i>	93	0.001
Cluster A	<i>Dryopteris dilatata</i>	73	0.001
SR = 32.7 ± 2.9 n = 15	<i>Agrostis capillaris</i>	72	0.006
	<i>Thuidium tamariscinum</i>	56	0.006
Sitka spruce	<i>Hypnum jutlandicum</i>	65	0.002
Cluster B	<i>Dicranum scoparium</i>	64	0.006
SR = 27.2 ± 2.9 n = 14	<i>Kindbergia praelonga</i>	54	0.017
	<i>Plagiothecium undulatum</i>	25	0.084

^a Mean species richness in the other clusters: C—19.4 ± 1.6 (n = 14), D—14.0 ± 1.3 (n = 15), E—4.7 ± 1.1 (n = 7). See Smith et al. (2005) for further details

Table 8 Species richness (\pm se) per Malaise trap of three hoverfly species groups in wet and dry Stage III-V Sitka spruce stands. Sample size (n) is the number of traps.

	Wet sites (n = 17)	Dry sites (n = 8)	t	P
Anthropophobic species	1.9 \pm 0.2	0.9 \pm 0.2	3.15	0.005
Wet substrate species	4.2 \pm 0.2	0.8 \pm 0.2	13.3	<0.001
Ground debris species	3.5 \pm 0.3	1.9 \pm 0.2	4.5	<0.001

Table 9 Summary of stand-scale structural, compositional and functional biodiversity indicators and the taxonomic groups to which they apply.

Indicator	Taxonomic group
Structural	
Structural stage	All ^a
Canopy openness	Vascular plants, spiders, birds
Shrub cover	Birds
Vegetation 11–50 cm tall cover	Spiders
Conifer litter	Forest spiders
CWD	Bryophytes, saproxylic hoverflies
Proximity to forest edge	Birds
Proximity to native woodland	Forest vascular plants
Compositional	
Ash ^b	Vascular plants, saproxylic hoverflies
Sitka spruce ^c	Bryophytes, spiders
Bird species (Table 7a) ^d	Birds
<i>Rubus fruticosus</i>	Vascular plants
<i>Dryopteris dilatata</i>	
<i>Agrostis capillaris</i>	
<i>Thuidium tamariscinum</i> ^d	
<i>Hypnum jutlandicum</i>	Bryophytes
<i>Dicranum scoparium</i>	
<i>Kindbergia praelonga</i>	
<i>Plagiothecium undulatum</i> ^d	
Functional	
Stand age	Forest bryophytes, forest vascular plants, forest spiders
Wet microhabitats	Hoverflies
Lower elevation	Birds
Higher elevation	Ground-nesting birds
Available P	Vascular plants
Thinning frequency	All

^a Relationships between biodiversity and stand structural stage vary by taxonomic group and subgroup, particularly forest species. See text for details

^b Relative to Sitka spruce

^c Relative to ash

^d As these are all common species, they should be used as targets to be achieved by management rather than indicators of high biodiversity stands



Figure 1 Map of sites

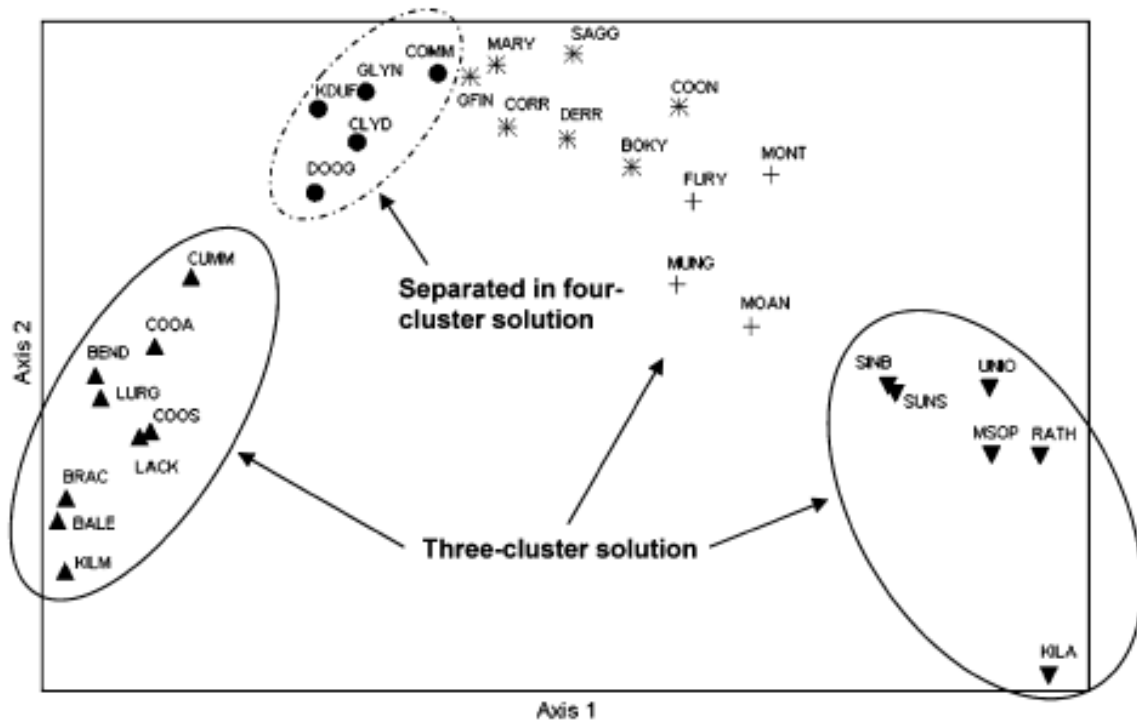


Figure 2 PCA ordination and Ward's cluster analysis of mean canopy cover, tree height, dbh and spacing in 31 Sitka spruce forests. Sites are identified by four-letter codes. At the three-cluster stage, the two groups enclosed by solid rings are separate from the middle group of sites. At the four-cluster stage, the group enclosed by a dashed ring is divided from the middle group. Symbols indicate the stand types based on the five-cluster solution: m = Stage I, d = Stage II, Æ = Stage III, + = Stage IV and . = Stage V. Axis 1 of the ordination explained 73.0% of the variance in the data ($k_1 = 7.087$) and axis 2 explained 21.0% of the variance ($k_2 = 2.044$). Total variance of the dataset was 9.715

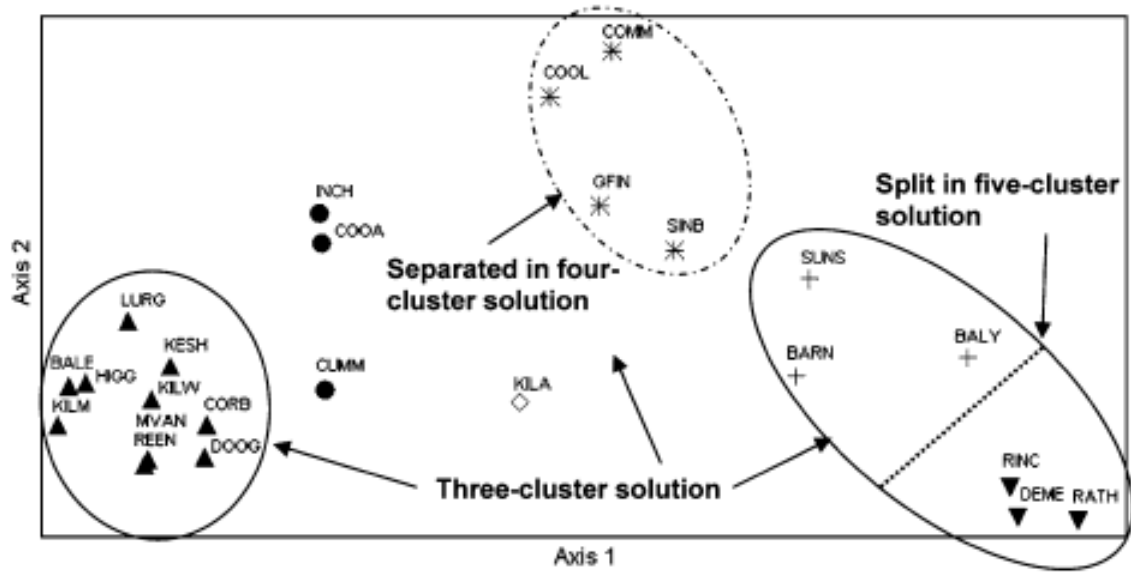


Figure 3 PCA ordination and Ward's cluster analysis of mean canopy cover, tree height and dbh in 24 ash forests. Sites are identified by four-letter codes. At the three-cluster stage, the two groups enclosed by solid rings are separate from the middle group of sites. At the four-cluster stage, the group enclosed by a dashed ring is divided from the middle group. At the five-cluster stage, RINC, DEME and RATH were separate from the others in their group. Symbols indicate the six-cluster solution: m = Stage I, d = Stage II, ▲ = Stage III, + = Stage IV, . = Stage V and e = not assigned. Axis 1 of the ordination explained 86.9% of the variance in the data ($k_1 = 6.028$) and axis 2 explained 11.4% of the variance ($k_2 = 0.793$). Total variance of the dataset was 6.939

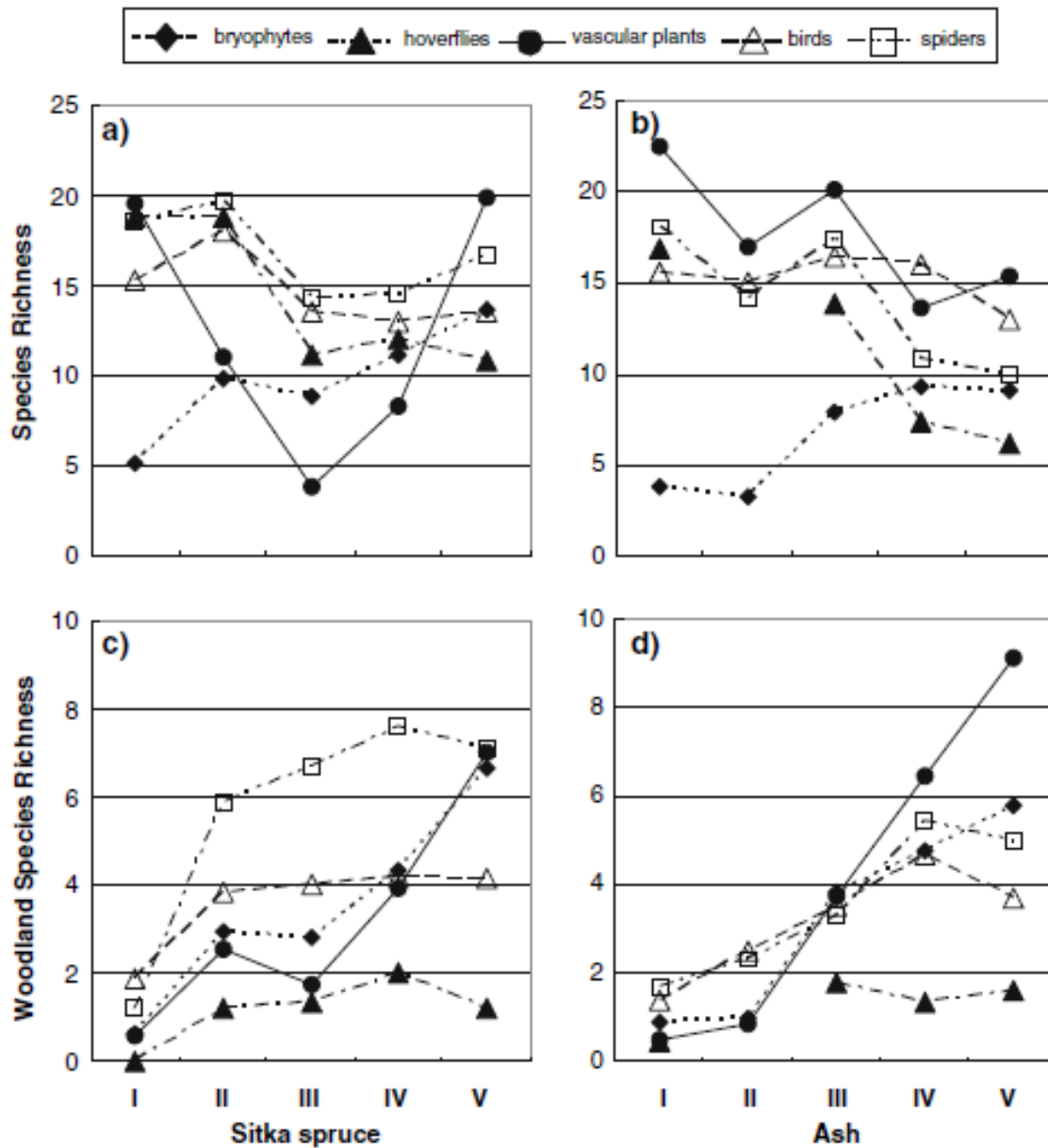


Figure 4 Trends in species richness over the forest cycle for five taxonomic groups: (a) total species richness in Sitka spruce stands, (b) total species richness in ash stands, (c) woodland species richness in Sitka spruce stands and (d) woodland species richness in ash stands. For birds, data from spruce/ash mix sites were combined with data from monoculture sites for both Sitka spruce and ash categories

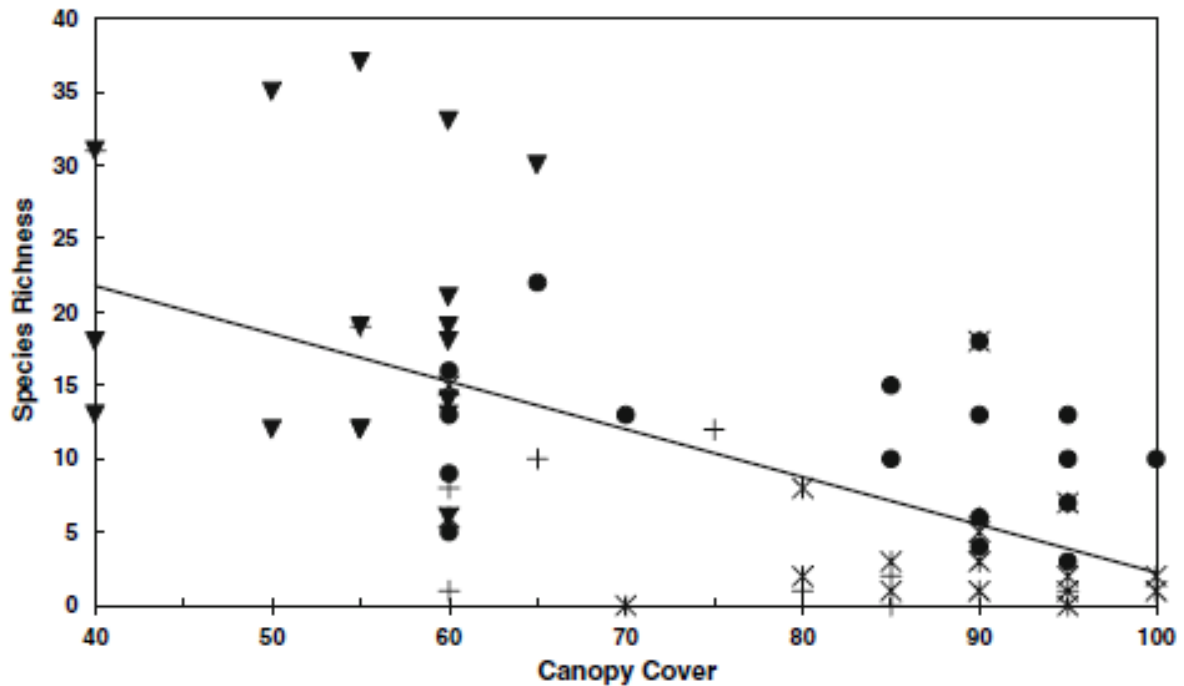


Figure 5 Relationship between vascular plant species richness and canopy cover (%) in 67 100 m² plots in Sitka spruce forests (excluding Stage I). Symbols indicate structural stage: d = Stage II, ∇ = Stage III, + = Stage IV and • = Stage V. Predictions of a linear regression model are shown by a line ($r^2 = 0.392$, $P < 0.0001$)