

Testing indicators of biodiversity for plantation forests

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Abstract

In many parts of the world, plantations make up a considerable proportion of the total forest area. In such regions, the identification of high biodiversity value stands and of management practices to enhance biodiversity is essential if the goals of Sustainable Forest Management are to be achieved. Since complete biodiversity assessments are rarely possible, efforts have been increasingly focussed on the use of indicators. Of particular interest are indicators applicable to individual stands that require no specialist taxonomic or technical knowledge to assess. Candidate biodiversity indicators had been identified in a previous study using data from Irish Sitka spruce (*Picea sitchensis*) and ash (*Fraxinus excelsior*) plantations but had yet to be tested on independent data. In the present study, the provisional indicators for vascular plant, bryophyte, spider and bird diversity were tested on data from Irish Scots pine (*Pinus sylvestris*), oak (*Quercus petraea*/*Quercus robur*), Sitka spruce and lodgepole pine (*Pinus contorta*) plantations. Conifer canopy cover was confirmed as an important biodiversity indicator, due to its influence on below-canopy microclimatic and structural conditions. Bryophyte species richness was higher in relatively high canopy cover plantations on poorly drained soils, while bird species richness was higher in more open plantations with high shrub cover. Coarse woody debris was an important substrate for forest-associated bryophytes, with higher species richness at higher volumes of deadwood. Both proximity to old woodland and stand age were confirmed as positive indicators for forest-associated vascular plants. This is related to dispersal limitation in these species, with nearby woodlands acting as important seed sources and colonisation increasing with time. Stand age was also confirmed as a positive indicator for forest-associated spiders and is related to the development of suitable habitat as the plantation matures. All of the confirmed indicators can be assessed without need for specialist knowledge, are ecologically meaningful and applicable to a range of forests managed under a clearfelling system. They can be used to assess the potential value of stands for the taxonomic groups to which they apply, as well as giving insights into management practices to enhance diversity in these groups.

Keywords

- Indicator;
- Biodiversity;
- Forest plantation;
- Canopy cover;
- Sustainable Forest Management

1. Introduction

Forests support a large proportion of the world's biodiversity (Kapos and Iremonger, 1998). In Europe, the area covered by forest stands at 45% and is increasing due to both planting and natural expansion (Forest Europe et al., 2011). While the proportion of the forest area composed of plantations (usually intensively managed forests, established artificially by planting or seeding) is on average 4% for Europe, in some countries they make up a considerably larger proportion, constituting 89% in the Republic of Ireland, 78% in Denmark and 77% in Britain (Forest Europe et al., 2011). In such countries, the identification of plantations which are potentially of high biodiversity value, and of management practices which can enhance biodiversity in plantations are essential if the goals of Sustainable Forest Management are to be met.

Since a complete assessment of biodiversity is rarely possible, other than at very small scales, there has been an increasing interest in using indicators as surrogate measures of biodiversity (Humphrey and Watts, 2004, Marchetti, 2004 and Niemi and McDonald, 2004). The indicator concept is based on the principle that easily measured features that affect or derive from variation in biodiversity can be used as an index of biodiversity (Ferris and Humphrey, 1999 and Landres et al., 1988). Three types of indicators can be identified – compositional (e.g. species), structural (e.g. physiognomy of forest stands and associated habitats) and functional (processes e.g. nutrient cycling) (Ferris and Humphrey, 1999 and Larsson et al., 2001).

A large amount of work has been undertaken in developing indicators at national and international scales, such as the pan-European indicators for Sustainable Forest Management (MCPFE Liaison Unit Vienna, 2003). However, indicators that can be used by forest managers at the stand scale are also important (Ferris and Humphrey, 1999). In order to be of practical use to forest managers, these indicators need to be easy to assess, repeatable, cost-effective and ecologically meaningful (Ferris and Humphrey, 1999). Despite the popularity of the indicator concept, few indicators have been adequately tested or validated (Niemi and McDonald, 2004 and Noss, 1999). Following an extensive study as part of the BIOFOREST project (Iremonger et al., 2007), Smith et al. (2008) developed a set of indicators of biodiversity for plantation forest stands in Ireland, but likely to be applicable over a wider area with similar climates. These stand- and landscape-scale compositional, structural and functional indicators of biodiversity covered five taxonomic groups – bryophytes, vascular plants, spiders, hoverflies and birds – and used data from 44 Sitka spruce (*Picea sitchensis*) and ash (*Fraxinus excelsior*) plantation forests. However, they remained provisional until tested on independent data and their applicability to plantations of other tree species was unknown. The aim of the present study was

to test these indicators in plantations of a range of tree species of various ages in order to assess their broad applicability.

2. Materials and methods

2.1. Site selection

A total of 21 stands of four different plantation forest types were selected across the Republic of Ireland: nine were plantations of Scots pine (*Pinus sylvestris*), a conifer species of disputed native status (Roche et al., 2009); four were plantations of oak (*Quercus petraea*/*Quercus robur*), both native broadleaved species; four plantations were dominated by Sitka spruce (*P. sitchensis*) and a further four were plantations of lodgepole pine (*Pinus contorta*), both non-native conifer species and the most common and second most common forest types in the Republic of Ireland respectively (Forest Service, 2007; Table 1). All were first rotation (newly established) plantations, although some were established on sites of former woodland. Stands were all greater than five hectares in area and included a range of plantation ages, soil types and climatic conditions (Table 1). One lodgepole pine and three Sitka spruce stands were surveyed in 2010, with the remainder of the stands surveyed in 2011.

Table 1.

A summary of the stand locations and characteristics.

Stand number	Irish grid ref.	Forest type	Age (years) ^a	Soil type ^b	Annual precipitation (mm) ^c
1	S033125	Scots pine	65	Brown earth	1091
2	T144950	Scots pine	65	Podzol	1003
3	T234932	Scots pine	79	Brown podzolic	1262
4	R940330	Oak	72	Brown earth	1066
5	W442862	Sitka spruce	30	Peat	1762
6	N302111	Scots pine	71	Brown earth	979
7	T243955	Scots pine	65	Podzol	937
8	N838334	Oak	73	Brown earth	857
9	N314297	Scots pine	62	Gley	874
10	L799780	Lodgepole pine	28	Peat	1512
11	F870280	Lodgepole pine	28	Peat	1696
12	G568262	Lodgepole pine	31	Peat	1452
13	S361349	Oak	75	Brown podzolic	1132
14	S489634	Oak	151	Brown earth	939
15	T210767	Scots pine	63	Brown podzolic	966
16	R924324	Scots pine	71	Podzol	1176
17	M838042	Scots pine	60	Brown earth	971
18	Q960180	Sitka spruce	37	Peat	1762
19	S201172	Lodgepole pine	30	Podzol	1510
20	S200172	Sitka spruce	33	Brown earth	1099
21	H100898	Sitka spruce	36	Peat	1429

a Number of years after planting at time of study.

b According to the Irish Great Soil Groups (Gardiner and Radford, 1980).

c From Sweeney et al. (2003).

Table options ▼

These plantations are generally managed using a clearfelling/clearcutting and replanting system (Forest Service, 2000), with Sitka spruce and lodgepole pine plantations managed on short rotations of 35–45 years (Anon., 2005c), while the rotation length is generally 70–80 years for Scots pine (Anon., 2005b), and 130–160 years for oak (COFORD, 2002). Thinning is usually carried out at regular intervals, other than on unstable sites; lodgepole pine stands often remain unthinned for this reason (Anon., 2005a). Line and selection thinning is the most commonly used method, where lines of trees, normally following the original planting rows, and suppressed and sub-dominant trees are removed, with groups of dominants and co-dominants broken up to create an even distribution of the final crop of trees (Forest Service, 2000).

2.2. Data collection

Data on the species richness and abundance of vascular plants, bryophytes, spiders and birds were collected, along with several structural and functional

variables, in order to test the indicators developed by Smith et al. (2008) (Table 2). Data on hoverflies were not collected.

Table 2.
The structural, functional and compositional indicators developed by Smith et al. (2008), for which data were collected in the present study.

Structural	Functional	Compositional	
		Plants ^a	Birds ^b
Canopy cover	Age	<i>Rubus fruticosus</i>	Wren (<i>Troglodytes troglodytes</i>) Dunnock (<i>Prunella modularis</i>) Blackbird (<i>Turdus merula</i>) Pheasant (<i>Phasianus colchicus</i>) Robin (<i>Erithacus rubecula</i>) Treecreeper (<i>Certhia familiaris</i>) Stonechat (<i>Saxicola torquata</i>) Greenfinch (<i>Carduelis chloris</i>) Great Tit (<i>Parus major</i>) Blue Tit (<i>Parus caeruleus</i>)
Shrub cover	Elevation	<i>Dryopteris dilatata</i>	
Field layer cover	Available P	<i>Agrostis capillaris</i>	
Ground layer cover		<i>Thuidium tamariscinum</i>	
Conifer litter cover		<i>Hypnum jutlandicum</i>	
Coarse woody debris volume		<i>Dicranum scoparium</i>	
Distance to forest edge		<i>Kindbergia praelonga</i>	
Distance to old woodland		<i>Plagiothecium undulatum</i>	
Area of old woodland within 1km			

^a Presence of the full set of four species in each case.

^b Abundance of these species.

Bryophytes and vascular plants were surveyed in three representative 10 m × 10 m plots, located at least 50 m apart, in each stand. The percentage cover of each species was estimated to the nearest 5%. The structural data collected within each plot were the percentage cover of the canopy (planted trees), shrub layer (woody species <2 m tall, including *Rubus*), field layer (non-woody species) and conifer litter, and the total volume of coarse woody debris (CWD; >10 cm diameter). Five soil samples were collected from the corners and centre of each plot to a depth of 10 cm (excluding litter and fermentation layers) and bulked for analysis. Soils were then air dried and sieved and available P was extracted using Morgan's reagent and quantified by a colorimetric method (Allen et al., 1986).

Active ground-dwelling spiders were sampled using three transects located at least 50 m apart, and adjacent to the vegetation plots where possible, each containing five pitfall traps (Curtis, 1980). Pitfall traps, which were plastic cups, approximately 7 cm in diameter and 9 cm high, filled with 3 cm of ethylene glycol, were in place for a total of 84 days between May and August, and were emptied four times during the trapping period. The cover of vegetation in three layers (ground layer: ≤10 cm, lower vegetation layer: >10–50 cm, upper vegetation layer: >50–200 cm), conifer and broadleaved litter were estimated to the nearest 5% in 1 m x 1 m plots around each pitfall trap and averaged to give transect and stand level values.

Birds were surveyed using a minimum of three, but up to six, point counts (Bibby et al., 1992) per stand. Point counts were located at least 100 m apart and were conducted for 10 min, during which time the number and species of birds detected within 50 m of the observer were recorded and their positions estimated. Distance software (Thomas et al., 2010) was used to derive species

densities for each bird species at each point and these were averaged to give stand level values. The distance of each point to the nearest forest edge was estimated using ArcMap 9.3. Canopy height and the cover (nearest 5%) of three vegetation layers (canopy, shrub (woody plants 0.5–2 m tall), field/ground (non-woody vascular plants and bryophytes)) were estimated to the nearest 5% within a 30 m radius of each point.

Elevation data were collected at the plot/point level and averaged to give stand level values. The distance from the boundary of the stands to the nearest old woodland (present on the 3rd edition (c. 1900–1915) six-inch-to-one-mile ordnance survey maps) and the area of old woodland within 1 km of the stand centroid were estimated using ArcMap 9.3. The age of the stands was taken as the years after the planting date given in the Coillte (Irish semi-state forestry company) database at the time of survey. Nomenclature throughout follows Stace (2010) for vascular plants, Smith (2004) for mosses and Dudley et al. (2006) for birds (using vernacular common names).

2.3. Data analysis

The species richness of each taxonomic group was calculated at the stand level. To account for differences in sampling effort due to pitfall trap disturbance, the total number of individual spiders recorded in each stand was standardised to the lowest sampling effort (lowest number of trapping days pooled across all 15 traps) and spider species richness estimated from the standardised values using individual-based rarefaction (Gotelli and Colwell, 2001). To account for differences in the numbers of bird point counts, species accumulation curves (Gotelli and Colwell, 2001), with random resampling of the data 100 times, were used to estimate the bird species richness from three point counts for each stand. Analyses were carried out in R version 15.0 (R Development Core Team, 2012) using the *vegan* package (Oksanen et al., 2012). The species richness of various subgroups of species was also calculated: forest-associated species – species characteristic of forest in Ireland; open-associated species – species characteristic of open habitats; generalist species – bird species either not entirely dependent on forest or open habitats, or having associations with both habitats; and ground-nesting birds (cf. Smith et al., 2005).

Relationships between the indicators identified by Smith et al. (2008) and species richness were investigated using ANOVAs or t-tests for categorical variables and correlation analysis (Pearson's) for continuous variables. Where variables did not conform to the assumptions of parametric statistics and transformations were inadequate, Kruskal–Wallis tests or Spearman's rank correlations were used. Correlations among the predictor variables were also investigated. These analyses were carried out in SPSS version 16.0.1 (SPSS, 2007). All correlations with distance to old woodland were partial correlations controlling for forest age and those with elevation were partial correlations controlling for shrub cover. These correlations were carried out in R version 15.0

(R Development Core Team, 2012) using the ppcor package (Kim, 2011). Values reported throughout are means $\pm$ standard error.

3. Results

A number of the indicators identified by Smith et al. (2008) were confirmed, while others were not (Table 3). These are outlined in detail below.

Table 3.

Summary of the relationships between the structural and functional variables and the species richness of the taxonomic groups for all species and for forest-associated, open-associated and generalist species for (A) Sitka spruce and ash from [Smith et al. \(2008\)](#) and (B) Scots pine, oak, Sitka spruce and lodgepole pine from the present study. Open-associated species were not tested for bryophytes or vascular plants, or forest-associated species for birds. Confirmed indicators (i.e. significant relationships in both studies) are highlighted in bold.

		Bryophytes		Vascular plants		Spiders		Birds		
		Forest		Forest		Open		All	Generalist	Open
		All	spp.	All	spp.	All	spp.			
Canopy cover	A	+ ^a	+++ ^b	---	+++ ^b	-				
	B	+ and	0	0 ^a	--- ^c	-	0 ^d	---		
Shrub cover	A								++	
	B							++	++	
Field layer cover	A					+	---			
	B					+	0 ^d	+++		
Ground layer cover	A					-	+			
	B					0 ^d	0			
Conifer litter cover	A						++ ^e			
	B						0			
Coarse Woody Debris (CWD) volume	A	++	+++							
	B	0	+ ^c							
Distance to forest edge	A							---	---	- ^f
	B							0	0	0 ^d
Distance to old woodland	A		0		---					
	B	+	0	--	--					
Area of old woodland within 1 km	A		0		+++					
	B	0	0	0	0					
Age	A		+++		+++		++	- ^g		- ^g
	B	--	0	++	+++	+	+++	+++	+++	0 ^d
Elevation	A							- ^h		
	B							0 ⁱ	0	0 ^d
Available P	A			+ ^j						
	B			0						

Strength of relationships indicated as follows: positive correlations $+p \leq 0.05$, $++p \leq 0.01$, $+++p \leq 0.001$; negative correlations indicated similarly; notable lack of significant relationship indicated by 0.

a Low species richness at high values of this indicator in conifer plantations.

b In broadleaved plantations; high species richness at intermediate levels of this indicator in conifer plantations.

c In conifer plantations.

d Few open-associated species recorded.

e In open spruce forests.

f In older (approx. 23–50+ year old) forests.

g In intermediate (approx. 9–29 year old) forests.

h Ground-nesters ++

i Ground-nesters -

j In mature (approx. 37–47 year old) Sitka spruce plantations.

Table options ▼

3.1. Structural indicators

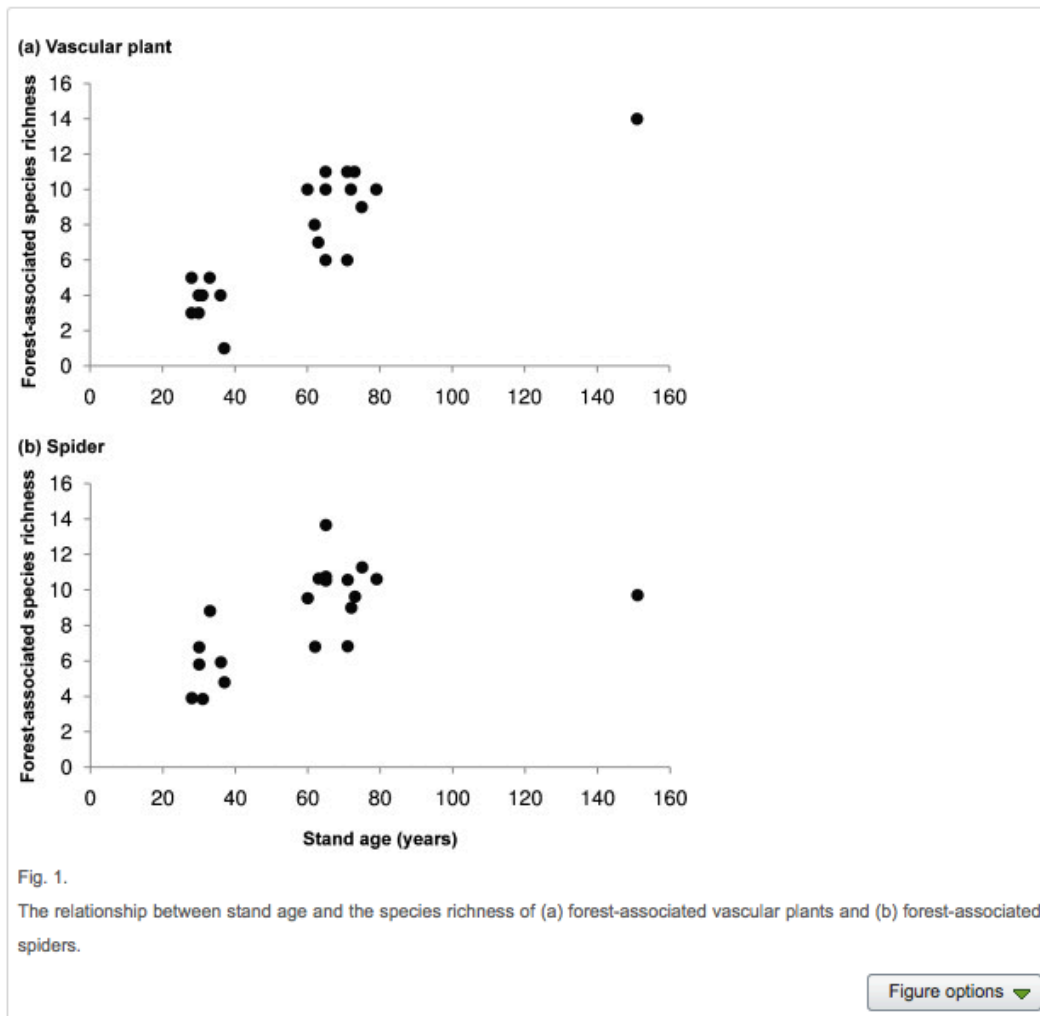
Canopy cover was identified as an important indicator, particularly in conifer plantations. While canopy cover did not have a significant overall correlation with bryophyte species richness, the positive relationship became significant when only conifer plantations were considered (Spearman $\rho = 0.532$, $n = 17$, $p = 0.028$) (Table 3); however, bryophyte species richness dropped off at high levels of conifer canopy cover. Canopy cover was not confirmed as an indicator for forest-associated bryophyte species richness. For vascular plants, the relationship was negative but not significant, although a significant negative relationship was found for forest-associated vascular plants (Spearman $\rho = -0.474$, $n = 21$, $p = 0.03$) (Table 3); this negative relationship became stronger and highly significant when only conifer plantations were considered (Spearman's $\rho = -0.832$, $n = 17$, $p < 0.001$). For spiders, canopy cover was not confirmed as an indicator for open-associated species richness (although few open-associated species were recorded), but was significantly correlated with both total (Spearman $\rho = -0.522$, $n = 21$, $p = 0.015$) and forest-associated spider species richness (Spearman $\rho = -0.512$, $n = 21$, $p = 0.018$). The relationship with forest-associated spider species richness also became stronger when only conifer plantations were considered (Spearman $\rho = -0.638$, $n = 17$, $p = 0.006$).

Canopy cover also had a strong influence on the below canopy layers, which in turn influenced the species richness of the different taxonomic groups. Canopy cover in the ground vegetation plots was significantly negatively correlated with shrub cover (Spearman $\rho = -0.456$, $n = 21$, $p = 0.038$), and field layer cover (Spearman $\rho = -0.623$, $n = 21$, $p = 0.003$) and positively correlated with conifer litter cover (Spearman $\rho = 0.776$, $n = 17$, $p < 0.001$). The relationship with shrub cover was particularly strong when only conifer plantations were considered (Spearman $\rho = -0.782$, $n = 17$, $p < 0.001$). Shrub cover was confirmed as a positive indicator of generalist bird species richness ($r = 0.615$, $n = 21$, $p = 0.003$) but was also positively correlated with total bird species richness ($r = 0.611$, $n = 21$, $p = 0.003$) (Table 3). For spiders, field layer cover was not confirmed as an indicator of open-associated spider species richness, but there was a significant positive correlation of 10–50 cm (Spearman $\rho = 0.483$, $n = 21$, $p = 0.027$) and 50–200 cm tall vegetation with total spider species richness (Spearman $\rho = 0.592$, $n = 21$, $p = 0.005$) and also a strong positive correlation with forest-associated spider species richness (10–50 cm tall vegetation: Spearman $\rho = 0.658$, $n = 21$, $p = 0.001$; 50–200 cm tall vegetation: Spearman $\rho = 0.740$, $n = 21$, $p = 0.0001$). For conifer litter cover the association with forest-associated spider species richness was strongly negative (Spearman $\rho = -0.801$, $n = 16$, $p < 0.001$), as was the correlation with total spider species richness (Spearman $\rho = -0.704$, $n = 16$, $p = 0.002$). Ground layer cover was not confirmed as an indicator of spider species richness. Total volume of CWD was confirmed as an indicator of forest-associated bryophyte species richness, but not of total bryophyte species richness (Table 3).

The landscape structural indicator, distance to forest edge, was not confirmed as an indicator of bird species richness. Likewise, area of old woodland within 1 km was not confirmed as an indicator of forest-associated vascular plant species richness. However, distance to old woodland was confirmed as a negative indicator of forest-associated vascular plant richness (Spearman rho = -0.578 , $p = 0.003$) and was also significantly negatively correlated with total vascular plant richness (Spearman rho = -0.525 , $p = 0.009$). A significant positive correlation between bryophyte species richness and distance to old woodland was also found (Spearman rho = 0.422 , $p = 0.048$).

3.2. Functional indicators

Age was confirmed as a positive indicator of forest-associated vascular plant (Spearman rho = 0.801 , $n = 21$, $p < 0.001$; Fig. 1a) and spider species richness (Spearman rho = 0.743 , $n = 21$, $p < 0.001$; Fig. 1b). However, no relationship was found for forest-associated bryophyte or open-associated bird species richness, and the relationship with total bird species richness was significantly positive (Spearman rho = 0.682 , $n = 21$, $p = 0.001$) (Table 3). Age was significantly negatively correlated with total bryophyte species richness (Spearman rho = -0.579 , $n = 21$, $p = 0.006$) and positively so with total vascular plant (Spearman rho = 0.622 , $n = 21$, $p = 0.003$), spider (Spearman rho = 0.504 , $n = 21$, $p = 0.02$) and generalist bird species richness (Spearman rho = 0.718 , $n = 21$, $p < 0.001$). No relationship was found between elevation and total bird species richness, but there was a significant negative correlation when only ground-nesters were considered (Spearman rho = -0.451 , $n = 21$, $p = 0.01$). No relationship was found between the available P content of the soil and total vascular plant species richness.



3.3. Compositional indicators

The stands with the presence of the full set of indicators of vascular plant species richness (*Rubus fruticosus*, *Dryopteris dilatata*, *Agrostis capillaris* and *Thuidium tamariscinum*) did not differ significantly either in their species richness (SR) of all plants ($t = -0.98$, $n = 21$, $p = 0.341$; indicator set present: $n = 11$, $SR = 34.2 \pm 3.4$, indicator set absent: $n = 10$, $SR = 30.3 \pm 1.9$) or their SR of vascular plants ($Z = -1.66$, $n = 21$, $p = 0.097$; indicator set present: $n = 11$, $SR = 20.64 \pm 2.9$; indicator set absent: $n = 10$, $SR = 14.4 \pm 1.7$) from those without the full set of indicators. The same was the case for the stands with the presence of the full set of indicators of bryophyte species richness (*Hypnum jutlandicum*, *Dicranum scoparium*, *Kindbergia praelonga* and *Plagiothecium undulatum*), with no significant difference in the species richness (SR) of all plants ($t = 0.59$, $n = 21$, $p = 0.561$; indicator set present: $n = 5$, $SR = 30.2 \pm 2.9$; indicators absent: $n = 16$, $SR = 33.0 \pm 2.5$) or of bryophytes ($t = -1.55$, $n = 21$, $p = 0.138$; indicator set present: $n = 5$, $SR = 17.60 \pm 1.7$; indicator set absent: $n = 16$, $SR = 13.12 \pm 1.5$) from those stands without the full set.

The abundances of none of the ten provisional bird species indicators (Table 2) were correlated with total bird richness, although the correlation for Dunnock was close to significance (Spearman $\rho = 0.421$, $n = 21$, $p = 0.054$). A number of the indicator species (Dunnock, Pheasant, Treecreeper and Greenfinch) occurred in relatively few stands, however, and Stonechat was completely absent.

4. Discussion

4.1. Confirmed indicators

Several structural indicators and a single functional indicator have been confirmed as indicators of diversity for plantation forest stands for one or more taxonomic group (Table 4). Canopy cover was confirmed as a positive indicator for bryophyte diversity in conifer plantations, most likely due to the lower light intensities in the shade of conifers (Gates et al., 1965) and the ability of bryophytes to survive at relatively low light levels compared to many vascular plants, coupled with their preference for high humidity conditions away from the competition of vascular plants (Bergamini et al., 2001 and Trynoski and Glime, 1982). Though canopy cover was not confirmed as a diversity indicator for the other taxonomic groups, conifer canopy cover had a strong negative association with shrub cover, which was confirmed as a positive indicator of bird diversity. Increased light levels at lower conifer canopy cover allow the vegetation to develop greater below-canopy species and structural diversity (Eycott et al., 2006, Hill, 1979 and Moore, 2012), which in turn is important for supporting diverse bird (MacArthur and MacArthur, 1961 and Sweeney et al., 2010b), and invertebrate assemblages (Humphrey et al., 1999 and Oxbrough et al., 2005). In broadleaved plantations, where significant amounts of light can be transmitted through the leaves (Gates et al., 1965), the levels of grazing by large herbivores may be a more important determinant of shrub cover (Kirby, 2001 and Perrin et al., 2011). While the requirements for bryophytes and the other groups studied may seem to be somewhat conflicting, it is important to note that many of the bryophyte-rich plantations in the present study were on poorly drained peat soils in exposed, high rainfall areas. Such plantations, which have also been found to be rich in epiphytic bryophytes (Coote, 2007), are generally thinned to a limited extent or left unthinned for tree stability reasons (Anon., 2005a and Phillips, 2004). Bryophyte richness was still low at high canopy covers, as previously identified in Sitka spruce plantations (Moore, 2012 and Smith et al., 2008), as light levels fall below the threshold even of shade-adapted species (French et al., 2008 and Hill, 1979).

Table 4.

Summary of the confirmed structural and functional indicators and the taxonomic groups to which they apply.

Indicator	Taxonomic group
Structural	
Canopy cover	Bryophytes ^a
Shrub cover	Birds
CWD	Forest-associated bryophytes ^a
Proximity to old woodland	Forest associated vascular plants
Functional	
Stand age	Forest associated vascular plants and spiders

^a In conifer plantations only.^b Bryophyte species richness low at very high canopy covers.

Table options ▼

CWD volume was confirmed as a positive indicator of forest-associated bryophyte diversity in conifer plantations. Deadwood is an important substrate for bryophytes in conifer plantations (Humphrey et al., 2002a) and the greater the volume present, the greater the chance of a range of decay classes being present, thus the greater the range of species supported (Andersson, 1991). However, the volume of deadwood in Irish forests tends to be low and mainly composed of small diameter pieces (Sweeney et al., 2010a). The stronger association of deadwood with forest-associated bryophytes, as opposed to bryophytes in general, has been noted previously in Sitka spruce plantations and is believed to be due to the greater likelihood of forest-associated species being adapted to exploit deadwood (Moore, 2012). Deadwood is also used by a number of other groups of organisms, including vascular plants, birds, invertebrates and fungi (Harmon et al., 1986) and a large proportion of the species living in forests are dependent on it (Larsson et al., 2001).

Proximity to old woodland was confirmed as a positive indicator of forest-associated vascular plant diversity. These woodlands act as seed sources for these species, which are often dispersal limited (Brunet and von Oheimb, 1998 and Dolman and Fuller, 2003). As in the previous study (Smith et al., 2008), the same relationship was not observed for forest-associated bryophytes, most likely due to the fact that bryophyte spores are more readily dispersed to significant distances from their source (Glime, 2007). The fact that proximity to old woodland was negatively associated with bryophyte species richness in the current study is most likely related to the poorly-drained peat stands, which are located in areas dominated by bog vegetation, and therefore with little native woodland cover (Cross, 2006); as discussed, these stands have high bryophyte species richness. Dispersal limitation may be an issue for other groups such as certain epiphytic lichens (Hauck, 2011 and Sillett et al., 2000) and invertebrates (e.g. oribatid mites (Lindo and Winchester, 2008) and molluscs (Moning and Müller, 2009)), but is less likely to be an issue for spiders, which can disperse

over greater distance by ballooning (Duffey, 1998), or birds (Harrison et al., 1992).

Stand age was confirmed as a positive indicator of forest-associated vascular plant and spider species richness. The dispersal limitation of vascular plants has been discussed above, with the number of species colonising therefore increasing with time (Brunet and von Oheimb, 1998); the same will likely also be the case for other dispersal limited groups. For spiders, which are less dispersal limited, the development of suitable habitat, such as shrub, field, ground or litter layers (Harvey et al., 2002, Oxbrough et al., 2005 and Oxbrough et al., 2012), is probably more important.

4.2. Unconfirmed indicators

For a number of the indicators identified by Smith et al. (2008), no relationship was found in the present study, while for others the relationship was found to be significant but reversed (Table 3). One such indicator in the latter category was canopy cover, along with its negatively associated variable field layer cover, in their relationships with forest-associated vascular plant and spider species richness respectively. In conifer plantations, canopy cover will increase after planting as the trees mature and subsequently decrease with each round of thinning (Hale, 2001, Hale, 2003 and Hill, 1979). In broadleaved plantations there is the same initial increase in canopy cover, but it does not generally reach as high levels, display the same degree of decrease with thinning (Smith et al., 2008) or have as light limiting effects as in conifer plantations (Gates et al., 1965). This may explain the different relationships with canopy cover identified for vascular plants in broadleaved and conifer plantations in the two studies. Forest-associated vascular plant species richness will consistently increase over time (Fig. 1; Smith et al., 2008 and Moore, 2012) while forest-associated spiders will respond to the development of increasingly structurally diverse forest conditions (Oxbrough et al., 2005 and Oxbrough et al., 2010). The lack of young plantations in the present study compared with that of Smith et al. (2008) meant that the more open stands, and hence those with higher field layer cover, all tended to be older, possibly explaining the different relationships identified in the two studies. This most likely also explains the negative correlation of age with bird species richness in intermediate (approx. 9–29 year old) stands in Smith et al. (2008) compared with the positive association for all stands in the present study, as birds are most likely responding to the presence or absence of structural diversity (Sweeney et al., 2010b and Sweeney et al., 2011).

Another relationship found to be reversed in the two studies was that between elevation and ground-nesting birds. In Smith et al.'s (2008) study, the positive relationship with ground-nesting birds was taken to be an indication of differences in habitat availability in the surrounding landscapes between upland and lowland plantations. In the present study the negative relationship could

also be related to landscape scale habitat availability, with lower elevation stands happening to have more suitable habitat in this case. The testing of habitat availability as an indicator would be informative.

One relationship identified by Smith et al. (2008) that was not confirmed in the present study was that between distance to the forest edge and the species richness of birds. It was the vegetation associated with the forest edge, such as scrubby habitats (Pithon et al., 2005), that was believed to be the important factor in that case (Wilson et al., 2006). Some of the stands in the present study may possess more structurally diverse understoreys that provide similar habitats to those at forest edges, thereby reducing the importance of the edge habitats. The relationship between available P in the soil and vascular plant species richness identified by Smith et al. (2008) was also not confirmed. Fertility was low overall, as with the mature spruce stands in the previous study (Smith et al., 2008), but other factors, such as light levels (Hill, 1979), may have had a greater influence on vascular plant species richness in the stands in the present study. Another unconfirmed relationship was that between conifer litter cover and forest-associated spider species richness. The positive relationship identified by Smith et al. (2008) was mainly for young (9–13 year old) stands, which were not included in the present study. Other structurally diverse habitats important to spiders, such as shrub, field and ground layers (Harvey et al., 2002, Oxbrough et al., 2005 and Oxbrough et al., 2012), may also have been available in the stands in the present study, thereby decreasing the importance of conifer litter as a habitat.

The compositional indicators of vascular plant and bryophyte diversity suggested by Smith et al. (2008) did not indicate higher diversity stands in the present study. This may be due to the similarity in species richness of the different communities present at the stands in the present study, as was seen for the ash plantations in the previous study (Smith et al., 2008). The Sitka spruce and lodgepole pine plantations in the present study supported a bryophyte-rich community similar to the community of Smith et al. (2008) from which the set of indicators of bryophyte richness were taken; some Scots pine and oak stands supported a vascular plant-rich community with high cover of *Rubus fruticosus* agg., similar to the community of Smith et al. (2008) from which the set of indicators of vascular plant diversity were taken; and the majority of Scots pine and oak stands supported another vascular plant-rich community similar to that of semi-natural oak-birch-holly woodland (Coote et al., unpublished results) and not reported by Smith et al. (2008). As indicator species analysis takes both the presence and abundance of species into account (McCune and Mefford, 1999), it is also likely that assessing only the presence of indicators developed by this method, as is the case for the indicators of Smith et al. (2008), will not be sufficient to identify high diversity stands.

None of the ten compositional indicators of bird species richness indicated higher diversity at the stands in the present study. As no very young stands were included in the present study, the stands had a narrower range of ecological variation than those in Smith et al.'s (2008) study. Four of the indicator species were relatively uncommon and one species (Stonechat) completely absent in the stands. As Ireland has a low species diversity of birds and lacks forest specialists (Wilson et al., 2006), indicator bird species are comparatively difficult to identify when the younger, more open stands are excluded.

4.3. Implications for forest management

This study has confirmed a set of indicators of stand-scale biodiversity that is much reduced from the set originally proposed by Smith et al. (2008). These indicators appear to be applicable to a range of forest types and ages for stands managed under a clearfelling system; however, it is important to note that they were developed only in first rotation (newly established) plantations. Smith et al. (2008) recommended the presence of at least four of their set of indicators from two or more groups (compositional, structural, and functional) before a stand was considered as having potentially high biodiversity. However, this is likely to be too strict given the lower number of indicators identified in the present study, especially since no compositional indicators were confirmed. Additional research is needed to identify other suitable indicators to add to the set, including the examination of relationships with additional taxonomic groups, before such a recommendation could be given. However, individually, the indicators can be used to assess the diversity of the groups to which they apply and give insights into management practices that could enhance this diversity. As is common to all biodiversity indicators, these indicators are concerned with the number of species present rather than their identity and they cannot distinguish stands where rare species are present (Niemi and McDonald, 2004).

Conifer canopy cover was identified as an important variable in the present study and the forest management operation that will have the greatest influence on this is thinning. The most bryophyte-rich plantations will likely remain unthinned, or be thinned to a limited extent for stability reasons (Anon., 2005a and Phillips, 2004) and bryophyte richness was found to be low at very high canopy covers. Therefore, management that favours a closed canopy cannot be recommended, particularly in light of the negative influence of canopy cover on the cover of several below canopy layers in conifer plantations, including shrub cover. Canopy cover has been found to be higher in Sitka spruce plantations at the end of their second rotation (Oxbrough et al., 2010) than for the first rotation plantations studied by Smith et al. (2008), possibly due to the increased productivity resulting from the presence of residues from the first rotation (Gill and McIntosh, 2008) and/or the planting of more productive provenances (Thompson et al., 2005). Therefore it is unlikely, particularly in forest estates going into their second and successive rotations, that structurally diverse below canopy vegetation will develop in spruce plantations without alteration to the thinning regime. The recommendation that spruce plantations be thinned early

and at regular intervals (Smith et al., 2005 and Smith et al., 2008), where stability allows, to prevent complete closure of the canopy must therefore be reiterated. Broadleaves or open canopied conifers, planted alone or in a mixture, will naturally have greater below-canopy light levels (Gates et al., 1965, Hill, 1979 and Moore, 2012), as seen in the oak and Scots pine plantations in the present study. Therefore, such species should be planted, where site conditions allow, as an alternative means of enhancing below-canopy structural diversity, including shrub cover. However, even in the presence of adequate below-canopy light levels, shrub cover can be low if grazing levels are high (Kirby, 2001). Increased light levels may also lead to a greater number of exotic species being supported, as was found in New Zealand (Brockerhoff et al., 2003). In Britain and Ireland, *Rhododendron ponticum* and *Prunus laurocerasus* are common invasive shrub species in forests (Dehnen-Schmutz and Williamson, 2006 and Perrin et al., 2008) that can have harmful effects on woodland biodiversity and ecosystem functioning (Cross, 1982). Therefore, where higher below-canopy light levels are present in areas where grazing animals or invasive shrub species occur, ongoing management will be required.

As well as its influence on canopy cover, thinning also has the added benefit of increasing the volume of deadwood (Brin et al., 2008); its importance as a biodiversity indicator is recognised by its inclusion as one of the pan-European indicators for Sustainable Forest Management (MCPFE Liaison Unit Vienna, 2003). However, the deadwood produced is mainly in stumps and generally of small diameter (Sweeney et al., 2010a). Though small diameter deadwood can play an important role in increasing species diversity (Kruys and Jonsson, 1999), large diameter deadwood is known to be particularly important for bryophytes and saproxylic species (Humphrey et al., 2002a and Humphrey et al., 2005). Overall volumes of large diameter deadwood are low in Irish forests (Sweeney et al., 2010a); a minimum of 20 m³ ha⁻¹ of deadwood greater than 20 cm diameter is recommended as an indicator of saproxylic and epixylic diversity (Humphrey et al., 2005). Therefore, it is recommended that harvesting residues on clearfells, thinnings in stands, patches of windthrow, groups of trees of poorer form or groups of broadleaves are retained to maintain the continuity of habitat for deadwood species throughout the normal forest rotations (Humphrey et al., 2002c). The increase in demand for bioenergy sources has led to an increased interest in whole tree harvesting (Jacobson et al., 2000) and the removal of forest residues (Hoyne and Thomas, 2001), highlighting a potential conflict.

The importance of proximity to old woodland for dispersal-limited woodland species seen in this study has implications for the selection of sites and species for afforestation, as well as the management of existing plantations adjacent to semi-natural woodlands or on sites of former semi-natural woodland. The ability of plantations to support semi-natural woodland species and communities is particularly important in regions where little semi-natural woodland remains. Native species should be favoured for planting, since non-native conifers and densely shading broadleaves could compromise the semi-natural status and

conservation importance of adjacent semi-natural woodland, as well as not supporting semi-natural woodland communities (Coote et al., 2012, Martin, 2011, O'Halloran et al., 2011 and Sweeney et al., 2011). Where conifer plantations are already present, they should be considered for conversion to a native tree species or a native/non-native mix (Humphrey et al., 2002b). These plantations will also require sensitive management to enhance the development of semi-natural plant communities and would be ideal candidates to consider for conversion to continuous cover forestry, where the canopy is maintained without clearfelling (Mason et al., 1999 and Pommerening and Murphy, 2004), and/or non-intervention natural reserves (Humphrey et al., 2002b). With Sitka spruce and lodgepole pine plantations managed on short rotations (Anon., 2005c), plantations of these species will support fewer dispersal-limited forest species, such as forest-associated vascular plants, without extension to their rotation lengths. Commercially over-mature stands, in contrast, have been found to provide important habitat for native woodland species (Humphrey et al., 2003).

5. Conclusions

We have identified a number of biodiversity indicators that are applicable to a range of forest types and ages. They are also likely to be applicable at least to first rotation plantations managed under a clearfelling system over a wider geographic area with similar climate. While some of the indicators identified are indicators of biodiversity in general, others are particular to forest-associated species. Maximising biodiversity in general may be an appropriate goal for commercial plantations, particularly within intensively managed agricultural landscapes (Eycott et al., 2006). However, given the low forest cover and low proportion of semi-natural woodlands in some parts of Europe (Forest Europe et al., 2011), the role of plantations in supporting forest-associated species may be particularly important in these areas.

All of the identified indicators can be assessed without need for specialist taxonomic or technical knowledge and can be used to assess the potential value of stands for the taxonomic groups to which they apply. In order for stands of potentially high overall biodiversity to be identified, further research is required to identify additional biodiversity indicators, particularly those for other taxonomic groups. However, the current indicators can give insights into management practices that can enhance the diversity of the relevant taxonomic groups.

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