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Can plantation forests support plant species and communities of semi-natural woodland?

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ABSTRACT

The potential contribution of plantation forests to the conservation of woodland plant diversity needs to be assessed in order for commitments to Sustainable Forest Management (SFM) to be fulfilled. To this end, the plant communities of mature Sitka spruce, Norway spruce, Japanese larch and ash plantations were compared with those of semi-natural oak and ash woodlands at 75 sites across the island of Ireland. A number of different plant communities were recognized in plantations, with only one resembling either of the semi-natural woodland types studied. The exception was a community of ash plantations on base-rich soils, on or adjacent to historic woodland, which was similar to the semi-natural ash woodland community. Despite supporting a plant community similar to semi-natural ash woodlands, the ash plantations supported significantly fewer woodland species. While none of the other plantation communities strongly resembled either the semi-natural oak or ash communities, they had the potential to support high numbers of woodland species. A range of forestry (forest type, canopy cover, grazing), geographic (elevation, historic woodland) and edaphic variables (soil pH, drainage) were found to be important in determining the types of plant communities and numbers of woodland species supported. While geographic and edaphic factors are either impossible or difficult to control, considerable scope exists for enhancing the plant diversity of plantation forests through changes in forest planning and management.

1. Introduction

Forest cover in Europe is increasing due to planting and natural expansion and now covers 45% of the land area (Forest Europe et al., 2011). Forest Europe et al. (2011) report that forest management practices in Europe have changed in ways that promote the conservation and enhancement of biological diversity, which is a key component of Sustainable Forest Management (SFM). While an increase in plantation area is seen as an indicator of decreasing diversity under SFM (MCPFE Liaison Unit Warsaw, 2007), plantation forests may be of great importance to biological diversity in regions where relatively little natural forest remains, as compared to those where semi-natural woodland predominates. In some European countries, plantations constitute a large proportion of the forest area, making up nearly 89% of the forest area in Ireland, 78% in Denmark, 77% in Britain and 42% in Belgium, compared to the European average of 4% (Forest Europe et al., 2011). Forest cover in these four countries is also relatively low (11%, 14%, 12% and 22% respectively) and is largely composed of introduced species, the majority being coniferous (MCPFE Liaison Unit Warsaw, 2007; Forest Europe et al., 2011). This is in sharp contrast with the very limited areas of native coniferous forest in these countries. It is important, therefore, that the potential of these plantations to support woodland species and communities is quantified and that this information is used to inform plantation management practices.

Comparisons of the plant communities of plantations in Britain and Ireland with the phytosociological classifications of semi-natural woodland communities have found that, while many of the plantation communities do not satisfactorily fit any of the semi-natural communities, some similarities do exist (Wallace et al., 1992; Ferris et al., 2000; Wallace, 2003; French, 2005). Direct comparisons of plantations and semi-natural woodlands using large-scale field surveys are rare, the comprehensive study of bryophytes and lichens in Britain by Humphrey et al. (2002a) being a notable exception. They found that plantations can support similar bryophyte communities to semi-natural woodlands. Parallel work on vascular plant communities did not use direct comparison and focused on comparing spruce and pine plantations to phytosociological community classifications, finding that some mature and over-mature sites were similar to semi-natural pine and oak woodlands (Ferris et al., 2000). Kirby (1988) has compared the vascular

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plants of plantations on ancient woodland sites and nearby semi-natural woodland remnants in southern Britain, and found them to support similar communities, although it is suggested these remnants may not be typical of the original woodland area. There have been few field studies directly comparing plantations and semi-natural woodlands in Ireland and, while they have found semi-natural woodlands to be more species-rich than plantations (Magurran, 1988; Fahy and Gormally, 1998; Coroi et al., 2004), their results are informative only at a local scale. French et al. (2008) have described the plant communities of a range of Irish plantation types, including some of the sites used in this study, but there have been no large-scale field surveys directly comparing the plant communities of plantations and semi-natural woodlands in Ireland to date. Information on the key environmental drivers influencing woodland species is also lacking.

In this paper we bring together the results of two large-scale studies of plantations and semi-natural woodlands across the island of Ireland in order to address these information gaps. The objectives are: (i) to compare the plant communities of a range of plantations with two semi-natural woodland types; (ii) to identify the factors important in determining the woodland species richness and plant communities of plantations and (iii) to identify opportunities for the enhancement of plantations in terms of supporting woodland species and semi-natural woodland communities.

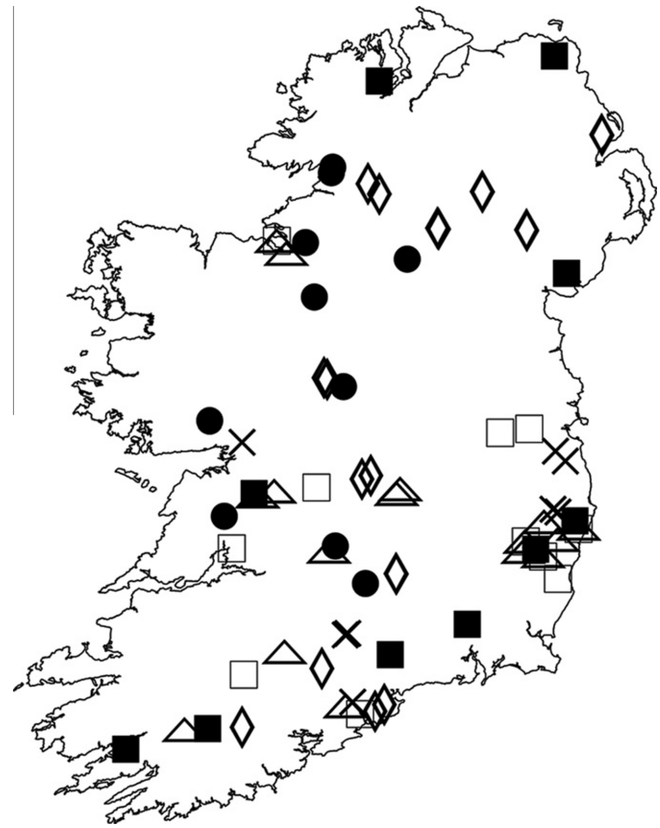

Fig. 1. The location of the seventy-five sites surveyed. Symbols indicate forest type: Sitka spruce plantation – △, Norway spruce plantation – ◇, Japanese larch plantation – X, ash plantation – □, semi natural oak woodland – ■ and semi-natural ash woodland – ●.

2. Materials and methods

2.1. Site selection

Seventy-five sites were surveyed across the island of Ireland (Fig. 1) as part of two large-scale studies of plantations and semi-natural woodlands (Smith et al., 2005; O'Halloran et al., 2011) – 55 plantations and 20 semi-natural woodlands. The plantations were of four types: 16 sites were Sitka spruce (*Picea sitchensis*), the most widespread plantation species in Ireland (EPA, 2008), 11 in their first rotation and five in their second (previous research has found both rotations to have similar species richness and plant communities (Moore, 2012) – all other sites were in their first rotation); 20 were Norway spruce (*Picea abies*), a commonly planted conifer in Ireland with a more open canopy than Sitka spruce (Wannebo-Nilsen et al., 2010), with five of these sites planted in a mixture with oak (*Quercus petraea/robur*) and five with Scots pine (*Pinus sylvestris*); eight were Japanese larch (*Larix kaempferi*), another commonly planted conifer in Ireland that is of particular interest because of its deciduous nature; and 11 were ash (*Fraxinus excelsior*), a native tree and the most commonly planted broadleaved species in Ireland (Forest Service, 2007), with two of these sites planted in a mixture with beech (*Fagus sylvatica*), two with sycamore (*Acer pseudoplatanus*) and one with both beech and sweet chestnut (*Castanea sativa*). As this study represents an opportunistic use of sites studied with different aims in mind, oak plantations were not included. All plantations were aged between 30 and 81 years after planting at the time of survey – mainly representing plantations close to, at or just beyond commercial maturity. The semi-natural woodlands were of two types: ten sites were oak–birch–holly woodlands (classified as WN1 by Fossitt (2000) and henceforth oak woodlands), which occur on acid or base poor, reasonably well-drained soils and are usually dominated by *Quercus petraea* (sessile oak); ten sites were oak–ash–hazel woodlands (classified as WN2 by Fossitt (2000)), which occur on more base-rich soils. These two woodland types were selected because they occur on the main soil types on which the plantation types studied are established. Only oak–ash–hazel sites where ash was more dominant than oak were selected (henceforth ash woodlands). Where possible, semi-natural woodland sites selected were historic woodland, i.e. appeared as woodland or scrub on the 1st edition (1837–1842) 6 in. to 1 mile Ordnance Survey maps. However, due to the shortage of suitable sites for study, two of the forests selected did not appear on these maps and are therefore younger; one of these also did not appear on the 3rd edition (1904–1906) maps while the other appeared as scrub. All 75 sites were a minimum of 4 ha in size. The first rotation Sitka spruce, ash and larch plantations were studied in the summers of 2001–2003 and the Norway spruce and second rotation Sitka spruce plantations, and the semi-natural oak and ash woodlands, were studied in the summers of 2007–2008. The summers of 2001 and 2002 were cool at times, with 2002 particularly dull and wet, while 2003 was warm with variable sunshine and rainfall amounts (Met Eireann, 2012). The summers of 2007 and 2008 were both exceptionally wet (Met Eireann, 2012).

2.2. Data collection

Three 10 m × 10 m plots were studied in each site. These were located at least 50 m from the edge of the area of woodland, and at least 50 m apart, in areas that were believed to be representative of the site as a whole. Within each plot, the percentage cover of each terrestrial (including saxicolous and epixylic) species of vascular plant and bryophyte was estimated to the nearest 5%. Below 5% two cover-abundance units were distinguished: 3% (indicating cover of 1–5%) and 0.5% (indicating cover <1%). Lichens, algae and fungi were not recorded. Nomenclature follows Stace (2010) for vascular plants and Smith (2004) for mosses. The percentage cover (as above) of the following functional groups was also recorded: understorey ($\geqslant$2 m tall), shrub (woody species <2 m tall, excluding brambles/briars (*Rubus*/*Rosa* spp.) but including climbing species), bramble/briar, fern, graminoid (grass, rush and sedge), forb (broadleaved herbaceous plants) and bryophyte. Typical woodland species were subsequently identified after French et al. (2008) and using information from Irish and British floras (Watson, 1981; Jermy et al., 1982; Hubbard, 1984; Clapham et al., 1987; Grime et al., 1988; Smith, 1990; Hill et al., 1991, 1992, 1994; Fitter and Peat, 1994; Webb et al., 1996; Paton, 1999; Preston et al., 2002; Smith, 2004).

A range of environmental data was collected in the field and subsequently from laboratory or desktop studies for the 10 m $\times$ 10 m plots (Table 1). Aspect was transformed to a linear scale using the equation $A' = \cos(45 - A) + 1$ (Beers et al., 1966), where A is the aspect in degrees and A' is the transformed aspect. Using this transformation, SW, the driest, sunniest aspect in the northern hemisphere, receives a value of 0 and NE, the shadiest, a value of 2. Proximity to old woodland, defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the third edition 6 in. to 1 mile O.S. maps (1900–1913), and the area of old woodland within 1 km were recorded for all but two sites, where a 3rd edition map was unavailable. It was also noted whether the sites were on or adjacent to historic woodland, defined as areas marked as woodland (deciduous, coniferous or mixed) or scrub on the first edition 6 in. to 1 mile O.S. maps (1831–1843). Five soil samples were collected to a maximum depth of 10 cm from four or five points within the 10 m $\times$ 10 m plot and bulked in the field. Soil pH was determined for a soil:distilled water suspension for the bulked, field moist samples. Samples were air dried prior to analysis for organic matter content (loss on ignition (LOI) – 550 °C $\times$ 5 h), total nitrogen and total phosphorus. Soils collected in 2002 and 2003 were not analyzed for total phosphorus.

2.3. Data analysis

The following biodiversity metrics were calculated for each plot: total species richness (SR), woodland SR, vascular plant SR, bryophyte SR, and Simpson's reciprocal diversity index (1/D). Values for species cover, biodiversity metrics and environmental variables for the three 10 m $\times$ 10 m plots were combined by averaging to remove within-site variation and facilitate between-site comparisons. The canopy species covers were excluded from all analyses, other than the calculation of 1/D, to allow for a better assessment of differences in the below-canopy layers at the sites; calculations of 1/D excluding canopy covers have previously produced ambiguous results (French, 2005). The differences among forest types and plant communities were tested for the various biodiversity metrics and environmental variables. Variables were found to violate the assumptions of normality and/or homogeneity of variance so non-parametric statistics were used throughout. These analyses were conducted using SPSS 16 (SPSS, 2007).

Generalized linear models, using a Poisson distribution, were used to identify environmental variables related to woodland species richness at the sites. Multi-model inference (Burnham and Anderson, 2002) was used to assess sets of models, with the model sets for testing selected based on the constraint that the number of models tested should not be greater than the sample size. Following data exploration, six variables that did not display problems with collinearity and that were deemed ecologically meaningful were included in the model: forest type, canopy cover, coarse woody debris (CWD) volume, grazing, historic woodland and drainage. Canopy cover was cubed and CWD volume was log-transformed to decrease the influence of outliers. Two interaction terms were included between forest type and canopy cover, and forest type and CWD volume. An 'all combinations' scheme was selected with forest type fixed (it was decided *a priori* to be an important variable), i.e. all possible models containing forest type were tested for the set of variables and interactions in order to quantify the relative importance of all variables compared to each other. Akaike's Information Criterion corrected for small sample sizes (AIC*c*) was used to rank and weight the models and a confidence set of models was selected with a cumulative Akaike weight of $\leqslant$0.95 (i.e. a 95% probability that the best model is being selected). The importance of each variable was estimated by calculating the cumulative Akaike weights of the models containing that variable. Average coefficients and standard errors were also calculated within the confidence set. Analyses were carried out using R version 2.11.0 (R Development Core Team, 2010) and the MuMIn package (Barton, 2009).

Multi-Response Permutation Procedure (MRPP), using species abundance data, was used to test for differences in plant communities between forest types with Sørenson distance measures. The test statistic, T, with its associated p-value, indicates the separation between groups, with more negative values of T representing a stronger separation. However, the p-value is not independent of sample size, so the chance-corrected within-group agreement statistic, A, is calculated; $A = 0$ if the average within-group distance is equal to that expected by chance, $A > 0$ if average within-group distance is less than that expected by chance (McCune and Mefford, 2006). Flexible-beta cluster analysis of the species abundance data, with beta set to 0.25, in conjunction with indicator species analysis (Dufrêne and Legendre, 1997), were used to classify and define ground flora communities. This value of beta limits chaining and is space conserving (Legendre and Legendre, 1998). Analyses were conducted using PC-Ord version 5.6 (McCune and Mefford, 2006).

Canonical Correspondence Analysis (CCA) was used to examine the influence of the environmental variables on the species composition, with Detrended Correspondence Analysis (DCA) used to obtain estimates of gradient lengths (in standard deviation (S.D.) units of species turnover). Species recorded only once were made supplementary to the ordinations and rare species were downweighted. Variables were examined for outliers and canopy cover was cubed and annual precipitation and CWD volume log-transformed to reduce the influence of outliers for these variables. Nominal environmental data were converted to zero/one dummy variables. Total phosphorus and the area of old woodland within 1 km were made supplementary to the ordinations due to missing

Table 1
The environmental data collected for the 10 m $\times$ 10 m plots.

Environmental data
(i) Forestry variables
Forest type
Canopy cover (%)
Total volume of coarse woody debris (CWD > 10 cm diameter) (m^3 100 m^{-2})
Presence/absence of grazing[A]
(ii) Geographic variables
Elevation (m)
Presence/absence of steep slope (>15°)
Aspect (transformed)
Annual precipitation (mm) (data from Sweeney et al., 2003)
Area of old woodland (km^2)[B]
Distance to old woodland (m)
Site on/adjacent to historic woodland or not
(iii) Edaphic variables
Soil pH
LOI (%)
Total N (%)
Total P (g l^{-1})[B]
Drainage (very good, good, moderate, poor)

[A] Judged by presence of dung in quadrat, evidence of grazing, trampling or damage to ground vegetation.
[B] Some missing values for these variables.

values. Automatic forward selection was used to identify the variables best related to the species data. Variables displaying (multi) collinearity, as assessed by examining pairplots (all variables plotted against each other) and variance inflation factors (VIFs) (values greater than 12 suggest multicollinearity), and/or non-significance were removed. Monte Carlo tests, with an unrestricted permutation structure, were used to assess the significance of the environmental variables with 499 permutations for preliminary analyses and 9999 for final solutions. The resulting plot represents the variation in plant community composition explained by the selected environmental variables (Økland, 1996). Ordinations were performed using CANOCO for Windows version 4.51 (ter Braak and Smilauer, 1998).

3. Results

3.1. Species richness and woodland species richness

Semi-natural ash woodlands were significantly more species-rich and diverse than all other forest types and supported significantly more woodland and vascular plant species (Table 2). They also contained significantly more CWD. Both ash plantations and ash semi-natural woodlands occurred on significantly more base-rich soils. Semi-natural oak woodlands were not significantly different in their species richness and diversity from the four plantation types studied and did not support significantly more woodland species than the Norway spruce or ash plantations; these two plantation types had a high proportion of sites on or adjacent to historic woodland.

Multimodel inference selected a set of nineteen models in the 95% confidence set for woodland species richness (Table 3). Historic woodland, forest type and drainage had the highest importance values, with forest type and historic woodland appearing in all nine models; forest type was fixed to appear in all models, but the significant differences in woodland species richness among forest types (Table 2) confirm that this variable is of high importance. Canopy cover had a relatively high importance value also. Grazing, the interaction between forest type and canopy cover and CWD volume had relatively low importance values. The averaged model parameters predict a location on/adjacent to historic woodland to have a positive association with woodland species richness and increased drainage a negative one, although with a slight improvement at the highest drainage level. Canopy cover is predicted to have a negative association with woodland species richness and grazing and CWD volume a slight positive association.

3.2. Plant communities

MRPP analysis indicated a significant difference in species composition on average between the different plantation and native woodland types studied ($T = -23.06$, $A = 0.15$, $p < 0.001$). There were also pairwise significant differences between all groups (Table 4). The most similar plantation forest type to any semi-nat-

Table 2
Values of the diversity variables, of those variables included in the woodland species richness (SR) modeling and of all edaphic variables (mean ± SE) for the different forest types studied. Variables were tested with Kruskall–Wallis H and Mann–Whitney U tests and are significantly different between forest types if indicated by a different superscript lowercase letter.

	Plantations				Semi-natural	
n	Sitka spruce 16	Norway spruce 20	Larch 8	Ash 11	Oak 10	Ash 10
Diversity						
Total SR	$23.3^{a} \pm 2.9$	$23.8^{a} \pm 1.9$	$24.8^{a} \pm 0.9$	$25.2^{a} \pm 1.9$	$26.1^{a} \pm 2.3$	$40.9^{b} \pm 3.7$
Woodland SR	$9.8^{ab} \pm 1.2$	$13.3^{c} \pm 1.0$	$7.2^{a} \pm 0.7$	$12.6^{bc} \pm 1.1$	$14.7^{c} \pm 0.7$	$25.5^{d} \pm 1.9$
Vascular SR	$11.9^{a} \pm 2.4$	$14.0^{a} \pm 1.9$	$12.0^{a} \pm 0.7$	$16.1^{a} \pm 1.7$	$13.7^{a} \pm 1.1$	$26.0^{b} \pm 2.7$
Bryophyte SR	$11.4^{ab} \pm 0.9$	$9.8^{ad} \pm 0.5$	$12.8^{bc} \pm 0.7$	$9.2^{a} \pm 0.8$	$12.4^{bcd} \pm 1.3$	$14.9^{c} \pm 1.1$
1/D	$3.4^{a} \pm 0.4$	$3.8^{ab} \pm 0.4$	$4.9^{bc} \pm 0.3$	$5.2^{c} \pm 0.3$	$4.5^{abc} \pm 0.5$	$7.3^{d} \pm 0.6$
Modeled						
Canopy cover (%)	$68.5^{a} \pm 3.3$	$77.6^{a} \pm 1.9$	$76.0^{a} \pm 2.2$	$73.8^{a} \pm 3.7$	$79.8^{a} \pm 2.3$	$69.0^{a} \pm 3.8$
CWD volume (m^3 100 m^{-2})	$0.27^{ab} \pm 0.05$	$0.30^{a} \pm 0.05$	$0.11^{b} \pm 0.02$	$0.24^{b} \pm 0.12$	$0.18^{ab} \pm 0.03$	$0.54^{c} \pm 0.10$
Drainage[A]	$3^{ab} \pm 2$	$2^{bc} \pm 1$	$4^{d} \pm 0$	$4^{ad} \pm 2$	$2^{ce} \pm 1$	$2^{be} \pm 2$
Grazing[B]	12.5	5	75	45.4	20	40
Historic woodland[B]	18.8	50	25	72.7	90	90
Edaphic						
pH[A]	$4.3^{a} \pm 0.4$	$4.2^{a} \pm 0.3$	$4.1^{ab} \pm 0.4$	$5.9^{c} \pm 1.1$	$3.9^{b} \pm 0.3$	$5.8^{c} \pm 1.3$
Total N (%)	$0.62^{a} \pm 0.10$	$0.79^{a} \pm 0.14$	$1.15^{a} \pm 0.21$	$0.54^{a} \pm 0.08$	$0.78^{a} \pm 0.13$	$0.78^{a} \pm 0.14$
Total P ($g\ l^{-1}$)	$0.32^{a} \pm 0.04$	$0.36^{a} \pm 0.03$	No data	$0.46^{a} \pm 0.06$[C]	$0.31^{a} \pm 0.05$	$0.48^{a} \pm 0.06$
LOI (%)	$28.1^{a} \pm 4.6$	$28.9^{a} \pm 5.5$	$45.0^{b} \pm 6.7$	$18.6^{a} \pm 1.6$	$30.9^{ab} \pm 5.9$	$19.8^{a} \pm 3.0$

[A] Median ± interquartile range reported. Drainge: 1 = poor, 2 = moderate, 3 = good, 4 = very good.
[B] Presence/absence variables: percentage of sites in each group with presence of the variables indicated.
[C] Some missing values for this variable, $n = 8$.

Table 3
The Akaike weights for the top nine of the 19 models in the 95% confidence set of models for woodland species richness and the cumulative Akaike weight (wtAIC) for each variable from all 19 models.

Model No.	1	2	3	4	5	6	7	8	9	wtAIC
Historic woodland	X	X	X	X	X	X	X	X	X	1.00
Forest type	X	X	X	X	X	X	X	X	X	1.00[A]
Drainage	X	X		X	X		X	X	X	0.70
Canopy cover		X	X			X	X	X	X	0.54
Grazing				X		X			X	0.26
Forest type x Canopy cover			X			X	X			0.25
CWD volume					X			X		0.16
Akaike weight (ω_i)	0.25	0.16	0.09	0.07	0.06	0.06	0.05	0.04	0.04	

[A] Forest type was fixed to appear in all models.

Table 4
Results of the pairwise MRPP comparison of the different forest types. The *T* statistic indicates separation between groups (more negative indicates greater separation), while *A* is the chance corrected within group agreement (larger values indicate greater separation). All differences are significant at the $p \leqslant 0.01$ level.

		Plantations			Semi-natural	
Plantations		Norway spruce	Larch	Ash	Oak	Ash
Sitka spruce	T	−4.35	−5.26	−9.07	−10.67	−13.76
	A	0.03	0.05	0.08	0.10	0.15
Norway spruce	T		−9.95	−8.35	−12.25	−13.32
	A		0.10	0.07	0.11	0.13
Larch	T			−7.22	−7.57	−10.26
	A			0.10	0.12	0.19
Ash	T				−8.33	−5.89
	A				0.10	0.06
Semi-natural	T					−10.87
Oak	A					0.15

ural woodland was the ash plantations to the semi-natural ash woodlands, while the Sitka spruce and Norway spruce plantations were the most similar forest types overall (Table 4). Values of *A* are low overall, suggesting that the within-group distances are only slightly smaller than the between-group distances, although values less than 0.1 are common in community ecology with values greater than 0.3 considered fairly high (McCune and Mefford, 2006).

Following flexible beta cluster analysis, an eight cluster solution was selected based on differences in plant community composition (Fig. 2). The significant indicator species for each cluster are indicated in Table 5. Despite the significant differences in plant communities between forest types indicated by MRPP, sites did not always cluster according to their forest type and plantations and semi-natural woodlands occurred together in clusters II and IV. Cluster II contains all ten semi-natural ash woodlands, seven ash plantations and one Norway spruce plantation; all of the plantation sites were low elevation sites located on or near old woodland that was also historic woodland. Understorey cover was high, although this was mainly due to high cover in the semi-natural woodlands, but shrub cover was high in both plantations and semi-natural woodlands (Table 6). The indicator species are typical of oak–ash–hazel woodland (Fossitt 2000; Table 5). This is the most species-rich and diverse cluster and a high number of woodland species are supported (Table 6). Cluster IV contains twelve plantations, with representatives from all four plantation types, and two semi-natural oak woodlands. The plant community is dominated by bramble (*Rubus fruticosus* agg.) but the cover of all other functional groups, other than understorey, is still relatively high (Table 6). Vascular species richness is also high and a moderate number of woodland species are supported.

All other clusters contain solely conifer plantations or semi-natural woodlands. Cluster I contains larch plantations, which completely lack an understorey, support few woodland species in total and have a grass-dominated plant community (Tables 5 and 6). Cluster III contains Sitka spruce and Norway spruce plantations that have a bryophyte-dominated plant community with only two indicator species, support relatively few vascular plants and have low diversity on average. Cluster V contains the remaining eight

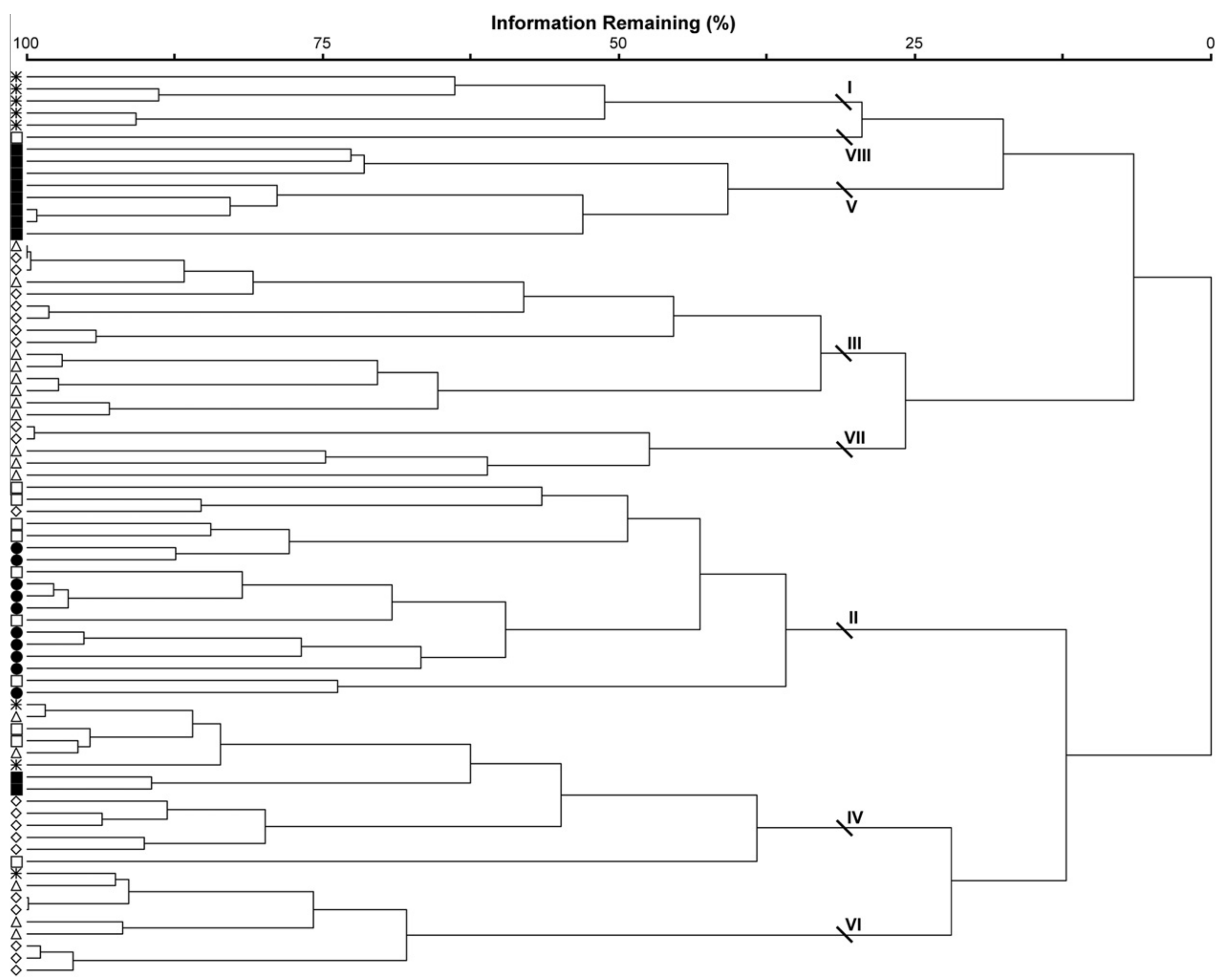

Fig. 2. Dendrogram from the flexible beta cluster analysis of the species abundance data for the Sitka spruce plantation – △, Norway spruce plantation – ◇, Japanese larch plantation – ✳, ash plantation – □, semi-natural oak woodland – ■ and semi-natural ash woodland – ● sites. Symbols I–VIII indicate the eight cluster groups.

Table 5
The significant indicator species for seven of the eight cluster groups. Indicator species could not be derived for the 8th cluster as it contained only one site. The ten species with the highest indicator values for each cluster group are given if the indicator value is ⩾ 25. Indicator values ⩾ 25 are highlighed in bold.

Cluster group *n*	I 5	II 18	III 15	IV 14	V 8	VI 9	VII 5
Rhytidiadelphus squarrosus	**70**	0	1	2	0	4	0
Agrostis capillaris	**69**	0	3	13	0	6	0
Anthoxanthum odoratum	**69**	0	0	3	0	2	0
Galium saxatile	**68**	0	3	1	0	5	0
Campylopus introflexus	**67**	0	0	0	1	1	0
Pseudoscleropodium purum	**67**	0	2	14	1	3	0
Polytrichastrum formosum	**62**	0	5	10	4	11	1
Deschampsia flexuosa	**60**	0	0	0	0	0	0
Dicranum scoparium	**57**	0	11	2	4	1	0
Hypnum jutlandicum	**53**	0	**29**	5	2	7	3
Thamnobryum alopecurum	0	**88**	0	0	0	0	0
Geum urbanum	0	**67**	0	0	0	0	0
Crataegus monogyna	0	**61**	3	9	0	3	0
Hedera helix s.l.	0	**61**	1	6	11	13	1
Corylus avellana	0	**60**	0	0	3	1	0
Acer pseudoplatanus	0	**58**	1	0	1	6	0
Fraxinus excelsior	0	**57**	1	2	0	16	0
Eurhynchium striatum	0	**54**	5	4	1	21	0
Circaea lutetiana	0	**53**	0	0	0	1	0
Arum maculatum	0	**51**	0	0	0	1	0
Kindbergia praelonga	4	6	**31**	**28**	7	21	3
Rubus fruticosus agg.	1	12	1	**70**	7	9	0
Atrichum undulatum	0	10	4	**37**	0	5	0
Dryopteris affinis	0	24	1	**37**	8	9	0
Chamerion angustifolium	0	0	1	**36**	0	9	0
Juncus effusus	0	0	0	**30**	0	6	0
Holcus mollis	0	0	0	**29**	0	0	0
Luzula sylvatica	1	0	0	0	**93**	0	0
Ilex aquifolium	0	7	0	3	**81**	0	0
Sorbus aucuparia	1	2	1	2	**72**	0	0
Quercus petraea	0	0	0	0	**70**	0	0
Vaccinium myrtillus	24	0	1	1	**63**	0	0
Frullania tamarisci	0	4	0	0	**57**	4	0
Betula pubescens	0	3	0	0	**53**	7	0
Dicranum majus	2	0	0	0	**52**	1	0
Blechnum spicant	1	0	4	8	**50**	11	0
Pteridium aquilinum	12	0	0	7	**44**	0	0
Agrostis stolonifera	0	8	0	4	0	**57**	0
Thuidium tamariscinum	4	6	15	14	7	**50**	4
Athyrium filix-femina	0	13	5	10	0	**45**	2
Cardamine flexuosa	0	1	5	22	0	**31**	0
Hypericum pulchrum	2	0	7	4	0	**28**	0
Veronica serpyllifolia	0	0	1	1	0	**25**	0
Cephalozia bicuspidata	0	0	1	0	0	0	**34**

semi-natural oak woodlands that have a plant community typical of oak–birch–holly woodlands (Fossitt, 2000). Understorey cover is relatively high and there is a good cover of all functional groups other than forbs (Table 6). Cluster VI contains Sitka spruce, Norway spruce and a single larch plantation that have a plant community with high cover of *Thuidium tamariscinum* and a reasonable cover of all functional groups with the exception of the understorey. It has high species richness, particularly vascular species richness, and supports a moderate number of woodland species; the majority of the sites in this cluster were planted on or adjacent to old and historic woodland. Cluster VII contains Sitka spruce and Norway spruce plantations that are extremely species-poor and support few woodland species, as well as having extremely low cover of all vegetation functional groups. There is only a single indicator species for this cluster. Cluster VIII contains a single ash plantation from a very poorly drained site that was dominated by grasses.

With a maximum gradient length of 4.207 S.D. units, the preliminary DCA ordination confirmed that CCA was the appropriate model to use on the species data. Automatic forward selection identified seven variables that were included in the final model (Table 7). Sitka spruce and Norway spruce were selected despite their non-significance, as forest type was considered a single variable with six states rather than six separate variables. The total variance in the species data was 5.356 and the estimated total variance explained by the environmental variables selected was 1.958 (36.6%). The eigenvalues for the first three axes were 0.539, 0.417 and 0.287 respectively. The first canonical axis was highly significant according to Monte Carlo tests with 9999 permutations ($F = 7.047$, $p = 0.0001$) as was the sum of all eigenvalues ($F = 3.301$, $p = 0.0001$).

The variation in species composition explained by the environmental variables used in the final CCA ordination is illustrated in the biplot in Fig. 3. Overall, forest type was an important variable in explaining variation in the species data (Table 7). The separation of the semi-natural ash woodlands and ash plantations with the oak–ash–hazel woodland plant community from all other groups (with the exception of the single ash plantation that formed the eighth cluster) is well explained by the selected variables, as indicated along Axis 1. Axis 1 mainly represents a gradient in soil pH, which was the first variable selected (Table 7). The positive association of total phosphorus with this axis also suggests a soil fertility gradient. Elevation and annual precipitation are strongly negatively associated with this axis, while historic woodland and old woodland are both positively associated. The three ash woodlands with the bramble-dominated plant community identified by cluster analysis are those separated from the rest of the ash plantations at the center of Axis 1. The selected variables do not well explain the separation of the two semi-natural oak woodlands with the bramble-dominated community from the other oak woodlands,

Table 6
The values for the diversity variables (SR = species richness) and the covers of the different functional groups for clusters I–VIII (mean ± SE). Variables were tested with Kruskall–Wallis H and Mann–Whitney U tests and are significantly different among clusters I–VII if indicated by a different superscript letter.

Cluster group *n*	I 5	II 18	III 15	IV 14	V 8	VI 9	VII 5	VIII 1
Diversity								
Total SR	$24.9^{ab} \pm 0.9$	$33.3^{a} \pm 2.9$	$20.6^{b} \pm 1.6$	$26.8^{a} \pm 2.1$	$27.2^{ab} \pm 2.5$	$30.8^{a} \pm 3.0$	$11.1^{c} \pm 2.0$	37.7
Woodland SR	$6.7^{a} \pm 0.3$	$20.8^{b} \pm 1.7$	$9.8^{cd} \pm 0.8$	$11.9^{de} \pm 1.1$	$15.1^{f} \pm 0.6$	$15.2^{bef} \pm 1.5$	$6.1^{ac} \pm 1.5$	11.7
Vascular SR	$12.2^{ac} \pm 0.6$	$21.1^{b} \pm 2.1$	$9.8^{c} \pm 1.5$	$16.1^{ab} \pm 2.0$	$14.1^{ac} \pm 1.3$	$19.6^{ab} \pm 2.5$	$2.5^{d} \pm 0.7$	26.0
Bryophyte SR	$12.7^{a} \pm 0.8$	$12.2^{a} \pm 1.0$	$10.8^{a} \pm 0.8$	$10.7^{a} \pm 0.8$	$13.1^{a} \pm 1.4$	$11.1^{a} \pm 1.0$	$8.6^{a} \pm 1.6$	11.7
1/D	$4.9^{a} \pm 0.2$	$6.4^{b} \pm 0.5$	$2.9^{c} \pm 0.2$	$5.0^{a} \pm 0.3$	$4.5^{a} \pm 0.5$	$4.9^{a} \pm 0.3$	$1.3^{d} \pm 0.1$	4.8
Functional groups								
Understorey cover	$0.0^{a} \pm 0.0$	$40.6^{b} \pm 8.0$	$0.5^{ac} \pm 0.3$	$3.1^{c} \pm 1.4$	$38.8^{b} \pm 9.7$	$2.2^{ac} \pm 1.5$	$0.0^{a} \pm 0.0$	0.0
Shrub Cover	$5.3^{ad} \pm 2.9$	$22.7^{b} \pm 4.3$	$0.8^{c} \pm 0.3$	$5.5^{a} \pm 1.8$	$15.4^{b\ d}\ 6.2$	$12.9^{abc} \pm 5.4$	$0.4^{c} \pm 0.1$	0.5
Fern Cover	$2.6^{ab\pm}0.5$	$5.7^{bd} \pm 1.1$	$3.6^{a} \pm 1.8$	$10.6^{c} \pm 2.0$	$11.3^{c} \pm 3.0$	$11.2^{cd} \pm 3.4$	$0.3^{e} \pm 0.1$	0.2
Graminoid Cover	$63.3^{a} \pm 7.7$	$6.9^{bc} \pm 3.3$	$2.8^{b} \pm 1.1$	$10.8^{d} \pm 2.7$	$26.4^{d} \pm 9.9$	$11.6^{cd} \pm 4.2$	$0.0^{e} \pm 0.0$	91.7
Forb Cover	$4.7^{abc} \pm 2.2$	$17.9^{ab} \pm 3.9$	$2.4^{c} \pm 0.7$	$10.7^{a} \pm 4.3$	$1.0^{c} \pm 0.3$	$19.4^{a} \pm 7.9$	$0.1^{d} \pm 0.0$	3.0
Bramble Cover	$0.7^{ab} \pm 0.3$	$7.6^{c} \pm 2.3$	$0.5^{b} \pm 0.2$	$43.8^{d} \pm 4.2$	$4.5^{ac} \pm 2.0$	$6.8^{ac} \pm 2.6$	$0.0^{e} \pm 0.0$	0.2
Bryophyte Cover	$40.0^{ab} \pm 7.7$	$48.3^{a} \pm 4.3$	$45.4^{a} \pm 4.9$	$41.0^{ab} \pm 6.6$	$21.2^{bd} \pm 6.7$	$74.8^{c} \pm 4.1$	$7.7^{d} \pm 2.6$	8.3

Table 7
The environmental variables used in the CCA ordination of the sites. The variance explained (Lambda-A), order selected, F-statistic and significance of each variable are shown.

Category	Variable	Lambda-A	Order selected	F
Forestry	Forest type: Sitka spruce	0.07	11	1.20
Forestry	Forest type: Norway spruce†	–	11[c]	–
Forestry	Forest type: Japanese larch	0.23	3	3.90[**]
Forestry	Forest type: Ash plantation	0.13	5	2.29[**]
Forestry	Forest type: Oak	0.38	2	6.02[**]
Forestry	Forest type: Ash semi-natural	0.19	4	3.17[**]
Forestry	Grazing	0.11	8	1.93[**]
Geographic	Elevation	0.12	6	2.08[**]
Geographic	Steep slope	0.09	9	1.69[*]
Geographic	Annual precipitation	0.08	10	1.53[*]
Geographic	Historic woodland	0.10	7	1.93[**]
Edaphic	Soil pH	0.46	1	6.81[**]

[*] Environmental variable significant at $p \leqslant 0.05$ (Monte Carlo test of significance).
[**] Environmental variable significant at $p \leqslant 0.01$ (Monte Carlo test of significance).
[c] The six forest type variables are a linear combination therefore all information for Norway spruce is represented once all other forest type variables are selected.

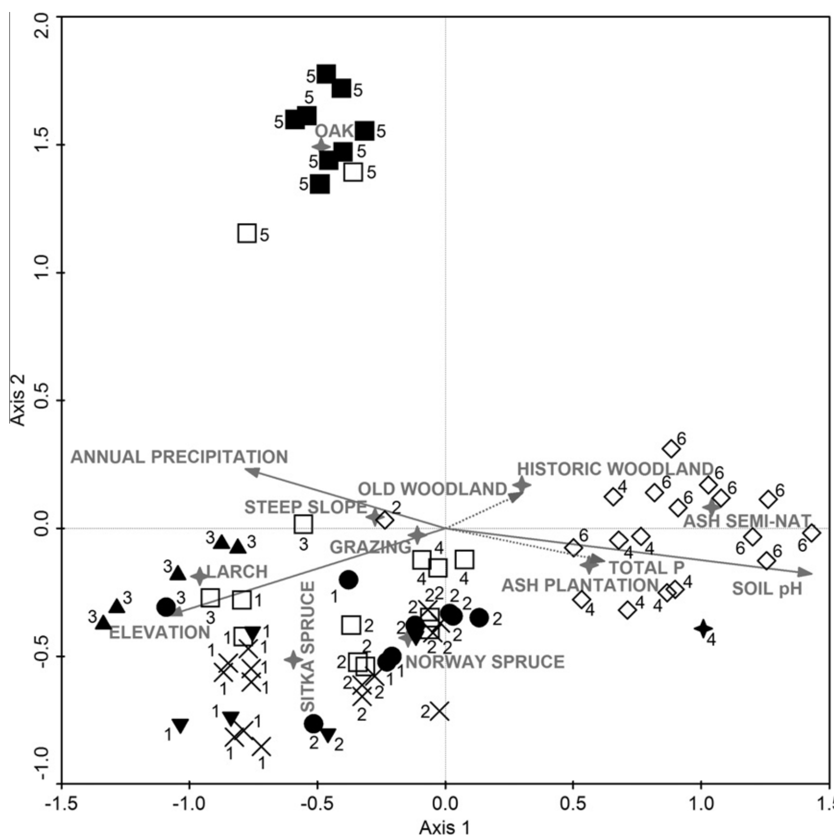

Fig. 3. CCA biplot indicating the variation in plant composition explained by the selected environmental variables (✦ indicates nominal environmental variables; supplementary variables indicated by dotted lines). Symbols indicate cluster group: I – ▲, II – ◇, III–X, IV – □, V – ■, VI – ●, VII – ▼, VIII – ✦; and numbers indicate forest type: Sitka spruce plantation – 1, Norway spruce plantation – 2, Japanese larch plantation – 3, ash plantation – 4, semi-natural oak woodland – 5 and semi-natural ash woodland – 6.

as all are grouped together at the top of axis two, nor the separation of the other plantation plant communities, which are intermixed in the lower left quadrant.

4. Discussion

4.1. Species richness and plant communities

The results of this study have shown that semi-natural oak woodlands are not always more species-rich or diverse than plantations. This is similar to previous findings from Britain (Kirby, 1988; Humphrey et al., 2002a). The fact that the semi-natural ash woodlands stood out from all other forest types in their species richness and diversity appears to stem from their being above-average sites in a Irish context (cf. Perrin et al., 2008). Those plantation types with similar woodland species richness to the semi-natural oak woodlands had a high proportion of sites on or adjacent to historic woodland; this factor was found to be important for woodland species richness. These woodlands may have acted as a source of propagules for these species, which often have very slow dispersal rates (Brunet and von Oheimb, 1998).

Cluster and indicator species analysis have also highlighted the fact that plantations and semi-natural woodlands can support similar species assemblages, but also can differ quite markedly. This echoes the findings of previous studies in both Britain and Ireland (Kirby, 1988; Wallace et al., 1992; Ferris et al., 2000; Wallace, 2003; French, 2005). Only one plantation plant community resembled either of the semi-natural woodland types: the ash plantations in cluster II resembled the semi-natural ash woodlands, although the plantations supported fewer woodland species. This similarity was despite the different sampling years, and therefore also climatological conditions, suggesting that any differences in climate did not have a perceptible influence on plant community composition at the sites. The similarity in community composition between ash plantations and semi-natural ash woodlands was also noted by French et al. (2008) who classified the community of these plantations as 'basophilic forest'. All of the ash plantations in this cluster were planted on low elevation sites on base rich soils, habitats typical of semi-natural ash woodlands in Ireland (Kelly and Kirby, 1982), and on or adjacent to historic woodland (soil pH, elevation and historic woodland were all identified by CCA as being important factors in separating this community from the rest). Those ash plantations planted at high elevations, on poorer soils and not on or adjacent to historic woodland developed the 'bramble-dominated' community described by French et al. (2008) for plantations at all stages of development but that had in common a relatively open canopy.

None of the coniferous plantation plant communities were similar to either semi-natural oak or ash woodlands. Aubin et al. (2008) also found that coniferous plantations in Quebec did not develop compositionally, functionally and structurally similar understories to old native broadleaved woodland, whereas their broadleaved counterparts did. Semi-natural coniferous woodlands with which to compare these coniferous plantation communities are rare in Ireland. The most notable exceptions are yew (*Taxus baccata*) woodland on karst limestone, largely confined to the Killarney area (Kelly, 1981; Perrin et al., 2006) and scattered stands of semi-natural Scots pine (*P. sylvestris*) woodland, all of which are presumed to be derived from introduced stock (Roche et al., 2009). French (2005), however, found significant floristic difference between some of the Sitka spruce and larch stands in this study and phytosociological descriptions of semi-natural Scottish Scots pine woodlands.

The majority of the plantation plant communities identified match those previously described by French et al. (2008). Cluster I matches their 'acidophilic forest: grass-dominated' community, although some sites also have affinities to their 'heath' plant community; cluster III matches their 'acidophilic woodland – bryophyte dominated' community; and cluster VII their 'closed canopy conifer forest: 2nd stage'. The *Thuidium tamariscinum*-dominated plantation community was not recorded by French et al. (2008).

One notable difference between plantation and semi-natural woodland plant communities was the almost complete lack of understorey in plantations. Shrub cover was also low in some of the conifer plantation plant communities. Plantations are often structurally similar to the 'stem exclusion' phase in a natural forest as described by Oliver and Larson (1996) and are often clearfelled before they get beyond this stage (Kerr, 1999), therefore never developing the vertical structure that has been found to be particularly important to birds (MacArthur and MacArthur, 1961).

4.2. Factors influencing woodland species richness and plant communities

For woodland species richness, as well as the importance of historic woodland previously mentioned, drainage was identified as an important factor, having a mainly negative association with this variable. Hardtle et al. (2003) found a positive correlation between species richness and soil moisture in deciduous forests in Germany. They put this down to occurrence of moisture-loving or moisture-tolerant plants, the weakening of the competitiveness of less moisture tolerant species and the release of mineral nutrients by ground water movement. Kelly and Iremonger (1997) found wet alder-ash woodland (*Carici remotae-Fraxinetum*) to be the most species rich of the Irish native woodland types.

For the plant communities identified by cluster analysis, CCA did not identify clear relationships with the environmental variables measured, other than for cluster II. The presence of the bramble-dominated community is likely related to the presence of low or zero grazing at the sites (Kirby and Woodell, 1998), combined with the partial shade under which *Rubus* species are known to thrive (Harmer et al., 2005; French et al., 2008). Conversely, high grazing and high light levels may explain the grass-dominated community in cluster I (Kirby, 2001; French et al., 2008) and low and extremely low light levels the bryophyte-dominated and impoverished communities in clusters III and VII respectively (French et al., 2008). Grazing was identified as an important variable by CCA, although the information collected did not distinguish differences in grazing pressure; both too high and too low levels can be detrimental to plant diversity (Kirby, 2001; Perrin et al., 2011). Canopy cover, on the other hand, was not identified as being important to plant community composition. This may be related to the fact that it is not always directly related to understorey light levels; it quantifies only the dominance of the site by trees and does not take into account lateral light penetration (French, 2005) or the differing light intensities in the shade (diffuse light) of different species (Gates et al., 1965; Jacquemoud and Baret, 1990; McElhinny et al., 2005).

The major influences of forest type in general includes the influence of the canopy species on below canopy light levels, and on the physical and chemical attributes of the litter and soil (Sydes and Grime, 1981; Augusto et al., 2002; Dzwonko and Gawronski, 2002). The additional species planted at some sites (Section 2.1) may have influenced these factors, e.g. adding Scots pine seemed to increase light levels in some Norway spruce plantations (Moore, 2012) while adding beech decreased light levels in ash plantations, while producing persistent leaf litter (French, 2005). Since forest managers will generally plant species on sites where they will grow best, it is difficult to separate the influence of canopy species from edaphic or climatic factors (French et al., 2008). Differences in forest management, e.g. levels and timing of thinning, will also have an influence (French et al., 2008).

4.3. Increasing the value of plantations for woodland species and semi-natural woodland communities

The results presented here suggest that plantations of broadleaves and conifers have the potential to support high numbers of woodland species, and plant communities similar to semi-natural woodland. This echoes the findings of Humphrey et al. (2002b) for Britain and French et al. (2008) for Ireland. Changes in forest planning and management could realize this potential.

The importance of forest type, proximity to historic woodland and edaphic factors identified by this study for the woodland species and plant communities supported by plantations has implications for the selection of sites and species for afforestation, particularly for those sites adjacent to semi-natural woodland or in areas with historic woodland cover. Broadleaved species, preferably native broadleaves suited to the soil type, should be favoured for planting in these areas, since conifers and non-native broadleaves such as beech, as well as not developing a semi-natural plant community, could also compromise the semi-natural status and conservation importance of the adjacent semi-natural woodlands (French et al., 2008). Conifer plantations already present 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 should be considered for conversion to continuous cover forestry and/or non-intervention natural reserves (Humphrey et al., 2002b). In this context, the investigation of the plant communities of oak and other broadleaved plantations adjacent to semi-natural oak woodlands would be informative.

For those forests planted in historically or currently unwooded areas, the number of woodland species supported can still be enhanced through maintaining adequate below-canopy light levels by planting of broadleaves or open canopied conifers, alone or in a mixture (Moore, 2012), or by early and regular thinning of dense-canopied conifers (French et al., 2008). Management of grazing levels is also important; complete absence of grazing is undesirable (Mitchell and Kirby, 1990; Perrin et al., 2006; Perrin et al., 2011) but there is little information on the threshold densities for plantations above which crop damage becomes significant and below which the impact is acceptable (Putman, 1996). Further research is required in this area.

5. Conclusions

The results presented here suggest that there is much scope for the planning and management of plantations so that they support more woodland species, and plant communities closer to those in semi-natural woodlands. These findings are widely applicable to plantation forests in other countries. This research has focussed on the stand level; to fulfil the commitments to SFM, a landscape scale perspective is needed before we can adequately understand the influence of plantations and plantation forest planning and management on plant species and communities (Dettki and Esseen, 1998; Angelstam et al., 2001).

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