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Plant community ecology of *Pinus sylvestris*, an extirpated species reintroduced to Ireland

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Abstract Plantation forests can make a significant contribution to the conservation of native biodiversity, especially where native forest cover is low. Ireland is used as a case study to explore the contribution to biodiversity made by stands of *Pinus sylvestris* (Scots pine), a reintroduced species. Despite its disputed native status, *P. sylvestris* is being widely planted in semi-natural habitats in Ireland. The associated vegetation communities have not previously been described and their conservation value is unknown. Baseline information is needed to inform conservation and forest management strategies. Botanical surveys were carried out at 20 plots of *P. sylvestris*-dominated woodland and scrub throughout the Republic of Ireland. Vegetation, structural and environmental data were recorded. Data were analysed using non-parametric and multivariate statistical techniques and a synoptic table was prepared. *P. sylvestris* was found to be a non-specialist in terms of its environmental tolerances. β diversity among plots was high while α diversity within plots was low to moderate. The plots surveyed contained 14.2% of the Irish native flora. There was a low level of constancy of species. Four reasonably well defined vegetation communities were identified. Soil pH, altitude and slope had important roles in partitioning these vegetation types and soil pH was positively correlated with species richness. *P. sylvestris* is well established, well integrated and naturalising in Irish semi-natural habitats. Some of the associated vegetation communities corresponded to habitats of international conservation importance. This research demonstrates that stands of *P. sylvestris* represent an important resource for Ireland's native botanical and habitat diversity.

Keywords Biodiversity · Ireland · Native status · *Pinus sylvestris* · Reintroduction · Vegetation community analysis

Abbreviations

BP	Radiocarbon years before present
DBH	Diameter at breast height (1.3 m)
EU	European Union

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N Number of samples
NMS Nonmetric multidimensional scaling
SD Standard deviation

Introduction

There is currently considerable debate regarding the role played by plantation forests in contributing to biodiversity maintenance and enhancement (Brockerhoff et al. 2008; Hartley 2002; Stephens and Wagner 2007). This is particularly significant in some European countries, where the area of plantations exceeds the area of native forests. In Denmark and the UK, for example, plantations constitute 63.0 and 67.6% of forest cover, respectively. In Ireland, a very low proportion (9.7%) of the land area is covered by forest and a very high proportion of this (86.5%) is comprised of plantations (FAO 2007). In situations where native or semi-natural woodland is so scarce, and particularly where sustainable forest management is applied, non-native plantations assume importance as a resource for biodiversity (Brockerhoff et al. 2008). Due to its island status, small size and low coverage of native woodland, Ireland is a model study site for investigating the contribution that non-native, or questionably native, tree species can make to the conservation of native biodiversity. Ireland's native botanical diversity is considerably lower than elsewhere in northwest Europe. This disparity is a product of Ireland's small size, island status, glacial history and its position at the edge of Europe. Excluding Pteridophytes, apomicts, doubtfully native species and other critical taxa, the vascular flora amounts to just 815 species (Webb 1983). Ireland provides an interesting, and previously undescribed, ecological case study of *Pinus sylvestris* at the western limit of its range.

Pinus sylvestris or Scots pine is the most widely distributed pine species in the world (Vidakovic 1991). Its native range covers approximately 2,700 km north to south and 14,000 km east to west across Asia and Europe (Volosyanchuk 2002). *P. sylvestris* is widely but discontinuously distributed within these limits (Steven and Carlisle 1959). This wide geographic range implies great ecological tolerance, as evidenced by the range of climatic conditions, from severe cold in northern Siberia to the Mediterranean climate of southern Spain and from the wet, oceanic climate of western Scotland to the dry continental climate of central Europe and Asia. *P. sylvestris* forms stable vegetation communities on nutrient-deficient soils, indicating a high competitive ability under these conditions (Carlisle and Brown 1968). It may act as a pioneer species, particularly on raised bogs which have suffered drainage or disturbance (Stoll et al. 1994). However, it is light demanding and will not tolerate heavy shade from other trees (Carlisle and Brown 1968). *P. sylvestris* forms vegetation communities of international conservation importance. For example, *P. sylvestris* is the dominant tree species in the Western Carpathian calcicolous *P. sylvestris* forests of Eastern Europe and the Caledonian forests of Scotland, both of which are listed on Annex 1 of the European Union Habitats Directive (EEC 1992). In addition, *P. sylvestris* is one of the most commercially important Eurasian forest trees (Volosyanchuk 2002).

What is particularly intriguing in this case is that indigenous *P. sylvestris* was once widespread in Ireland but is believed to have been extirpated and subsequently reintroduced. Palaeoecological evidence indicates that, following deglaciation, *P. sylvestris* colonized Ireland by 9,500 BP (radiocarbon years before present; Mitchell 2006). It expanded its range and by 7,500 BP, had become an important component of certain marginal habitats, such as raised bogs, river valleys and uplands. Indeed, *P. sylvestris* was the dominant tree pollen type in almost all western and most upland study sites for at least part of the early post-glacial (Bennett 1984; Bradshaw and Browne 1987). These are mainly areas of acidic rock, but there is evidence that *P. sylvestris* also grew on the karst limestone pavement of the Burren (Watts 1984a). A major *P. sylvestris* decline began around 4,000 BP. The decline was asynchronous (Smith and Pilcher 1973) and may have been caused by a combination of different factors in different parts of Ireland. Competition with *Alnus glutinosa*, the expansion of blanket bog, climate change, progressive soil deterioration, pathogens and human activity have all been cited as possible causes of the decline (Bennett 1984). Late outposts of *P. sylvestris* persisted in Sligo, the Killarney valley, the Burren and on raised bogs in the Midlands (Bradshaw and Browne 1987). The most recent unequivocal specimen, a preserved stump from Clonsast Bog in County Offaly, was radiocarbon dated to 1,620 ± 130 BP (McAulay and Watts 1961). *P. sylvestris* is widely believed to have become extinct in Ireland at this point (Cross 1998; Webb et al. 1996; White and Doyle 1982).

Native *P. sylvestris* woodland persists to the present day in Britain, but is restricted to the Scottish highlands, where it dominates considerable areas (Steven and Carlisle 1959). These Caledonian forests are now recognised as a priority habitat under Annex 1 of the EU Habitats Directive (NATURA 2000 code 91C0; EEC 1992). The species had been reintroduced to Ireland by the eighteenth century AD, probably from Scotland. Pococke (1891) observed a thriving plantation of 20,000 “firres” near Coolnamuck, Carrick-on-Suir, County Tipperary in 1752. A documented reintroduction took place at Killarney, County Kerry around 1800 when *P. sylvestris* of Scottish provenance was planted extensively on the Kenmare and Herbert Estates (Radcliff 1814; Watts 1984b). This sequence of regional extinction and reintroduction of *P. sylvestris* also occurred in England, Wales and Denmark (Bennett 1984; Le Maitre 1998; Mirov 1967).

Since its reintroduction, *P. sylvestris* has been widely planted in Ireland (Cross 1998) and is naturalising in a variety of habitats (Kelly 1981, 1985). Earlier in the twentieth century, extensive plantations of *P. sylvestris* were established but after 1945, more productive exotic species, especially *P. sitchensis*, became favoured for commercial forestry (O’Driscoll 1980). *P. sylvestris* is regarded as ‘semi-native’ within the Irish forestry sector and is Ireland’s only native or semi-native conifer species with forestry potential (Forest Service 2000). Ireland’s Native Woodland scheme provides grant aid to landowners for the planting of native tree species of local genetic provenance (Forest Service 2001). Despite its disputed native status, *P. sylvestris* has been included in this scheme and is being widely planted in semi-natural habitats. Information is therefore urgently required on the plant community ecology of *P. sylvestris* stands and the implications for biodiversity conservation.

Despite its widespread distribution, very few published studies provide vegetation descriptions or classifications applicable to *P. sylvestris* in Ireland. This inadequate description is a product of the species’ disputed native status and declining popularity in commercial forestry. *P. sylvestris* woodlands were excluded from the Irish National Survey of Native Woodland and its associated classification of vegetation communities (Perrin et al. 2006, 2008a, b). White’s (1982) key for the identification of Irish plant communities ascribes all coniferous woodland to the Vaccinio–Piceetea class. However, White and Doyle (1982), in an overview of phytosociological associations in Ireland, argued that there are no native *P. sylvestris* woodlands in Ireland and did not formally record the class. Fossitt’s (2000) broad-scale classification of Irish habitats made some provision for *P. sylvestris* woodland. All coniferous plantations were ascribed to the highly modified/

non-native woodland class and sub-divided, regardless of ground flora, into mixed broadleaved/conifer (WD2), mixed conifer (WD3) and conifer (WD4) categories. In the semi-natural woodland class, the bog woodland (WN7) category was defined on the basis of species composition and referred to woodlands of intact ombrotrophic bogs, bog margins and cutover bog. *Betula pubescens* is the usual dominant but some stands on intact raised bog are dominated by *P. sylvestris* (Heery 1993; O'Connell and Doyle 1990). Bog woodland is a priority habitat under Annex I of the EU Habitats Directive (91D0; EEC 1992) and examples on intact raised bog are very rare in Ireland (Fossitt 2000). Quantitative data on the vegetation communities of *P. sylvestris* stands is required. In this paper we describe naturalised and planted stands of *P. sylvestris* and assess their contribution to Ireland's native biodiversity.

Methods

Study sites

Criteria were drawn up for the selection of suitable survey sites. The criteria stipulated mature woodland or scrub composed of pure *P. sylvestris* or *P. sylvestris* intimately mixed with native tree species, with *P. sylvestris* as a dominant or co-dominant in the canopy. The vegetation had to be reasonably free of non-native and/or invasive species. Planted and naturalised stands and those of unknown provenance were included. Relevant stakeholders were consulted and a desk study was carried out to identify potential survey sites in both the Republic of Ireland and Northern Ireland. After preliminary visits, several sites that failed to meet the selection criteria were rejected. This was due, in part, to invasion by the non-native *Rhododendron ponticum*, which was particularly pernicious in the south-west of the country. Eighteen suitable sites were selected according to the criteria outlined above. We are satisfied that although this survey was not exhaustive, it covered an adequate proportion of the *P. sylvestris* woodlands that would meet the site selection criteria.

Data collection

Field surveys were conducted from May to September 2006 and April to August 2007. Twenty plots were surveyed at 18 sites (Table 1; Fig. 1), as 2 distinct *P. sylvestris*-dominated vegetation types occurred at the Derrycrag and Ballykine sites. A circular 400 m^2 plot was subjectively placed to represent each *P. sylvestris* vegetation type. The circular shape facilitated a study of pollen dispersal, which is not presented here. Five 2×2 m^2 quadrats were placed within the 400 m^2 plot, with one at the centre and at each of the cardinal points. This quadrat size was chosen to capture ground flora diversity, where the dominant structural form varied from herbs to sub-shrubs. In each of these quadrats, floristic data were recorded on the Domin scale (Dahl and Hadac 1941) for woody species and herbs. Nomenclature followed Webb et al. (1996). Structural data were recorded for all trees within the plot with a diameter at breast height (DBH) of 7 cm or greater. DBH was measured using a diameter tape. The height of the tallest tree was estimated using a clinometer and the heights of the remaining trees were then estimated by eye. Each tree was ascribed to a structural class: dominant, co-dominant, intermediate or suppressed. The slope, altitude and Irish grid coordinates of the plot were recorded. In each 4 m^2 quadrat, five 10 cm deep soil samples were taken and bulked in the field. Soil pH was determined in the laboratory using a WTW pH 330 m and combination electrode. Soil organic content

Table 1 Location of the 20 survey plots shown in Fig. 1

Plot number	Plot name	County	Grid references
1	Dale Wood	Kerry	V 88181 80714
2	Clonfinane Bog	Tipperary	M 98815 03715
3	Rockforest	Clare	R 34755 95013
4	Coomhola	Cork	V 98853 59132
5	Glengarriff	Cork	V 90894 56831
6	All Saints Bog	Offaly	N 01203 11216
7	Glenfarne	Leitrim	H 02059 39747
8	The Scalp	Dublin	O 21719 20093
9	Coronation Plantation	Wicklow	O 09708 12792
10	Derrycrag plot 1	Galway	R 73616 99077
11	Derrycrag plot 2	Galway	R 73652 99029
12	Portumna Forest Park	Galway	M 82680 03320
13	Rockvale	Clare	R 38955 98090
14	Torc	Kerry	V 96482 83719
15	Knockastakeen	Tipperary	R 93807 27204
16	Trooperstown	Wicklow	T 15932 96721
17	Derrybawn	Wicklow	T 12365 96360
18	Vale of Clara	Wicklow	T 17212 92127
19	Ballykine plot 1	Mayo	M 10849 57328
20	Ballykine plot 2	Mayo	M 10657 57113

was determined by percentage loss on ignition at 550°C. Approximate soil bulk density was estimated from % organic content (Jeffrey 1970).

Data analysis

The diversity of vascular plant species was calculated at two scales, α diversity (from five 4 m^2 quadrats within each plot) and β diversity (from 20 400 m^2 plots throughout Ireland), using the following formula:

$$\beta_W = (S_C/S_A) - 1 \quad (1)$$

β_W is Whittaker's index of β diversity, S_C is the species richness in the composite sample and S_A is the average species richness in the sample units (McCune and Grace 2002; Whittaker 1960, 1972). This index was selected as it is one of the simplest and most effective measures of spatial diversity. It is essentially a measure of the extent to which two or more sample units differ (Magurran 2004) and was therefore an appropriate measure of diversity at both scales.

The nested sampling design provided abundance data on the Domin scale from five 4 m^2 quadrats. Ordinal Domin scores are incompatible with many conventional multivariate analysis techniques. The conversion of ordinal scores to mean values of percentage cover classes implied arbitrariness and non-systematic distortion and would produce a considerable increase in the uncertainty of the data (Podani 2006). Preliminary analyses showed that α diversity was low relative to β diversity so, for the purposes of this paper, the patterns of β diversity were deemed to be of greater interest than those of α diversity. Given the relative homogeneity of the quadrats within each plot, it was decided that their

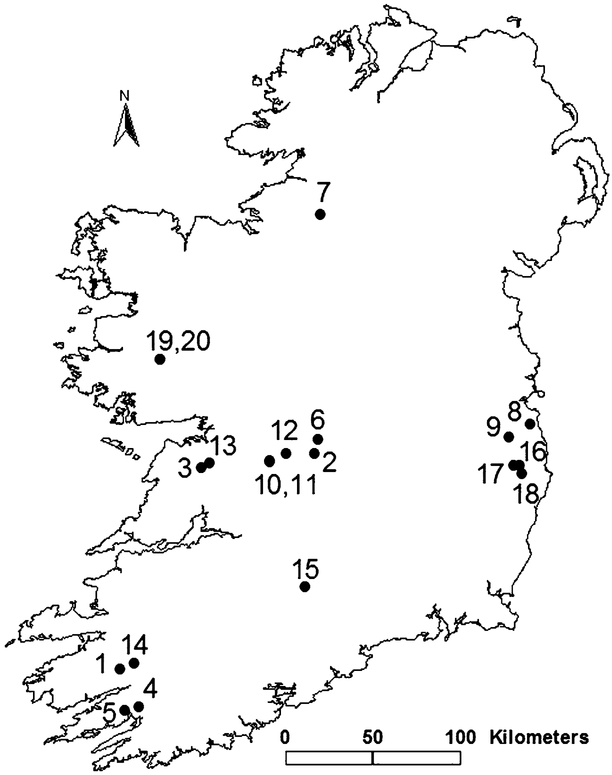

Fig. 1 Distribution of 20 survey plots

floristic data could be combined into robust summary data which would describe the 400 m^2 plot at the stand scale. The Domin values were transformed to estimates of percentage cover using Currall's (1987) 'Domin 2.6' method, which is more accurate than direct averaging. A mean of the resulting values was calculated, providing summary data at the scale of the 400 m^2 plot. The mean values were reconverted to the Domin scale, thereby reducing uncertainty in the data i.e. the false accuracy of percentages that actually represent a range of values. This data format was thought to be the most defensible option given the sampling design used, however, it was incompatible with certain data analysis techniques such as Indicator Species Analysis (Podani 2006).

Data screening, data transformation and multivariate data analyses were carried out using PC-ORD 5 (McCune and Mefford 2005). Data were screened by Outlier Analysis. None of the plots were identified as outliers and all were included in the analysis. *Succisa pratensis* was identified as a marginal outlier (SD = −2.12) but was retained in the dataset, as the species is part of the target population. Rarely occurring species, i.e. those that occurred in only one (5%) of the plots, were deleted to reduce noise in the dataset (McCune and Grace 2002). A hierarchical, agglomerative, polythetic method of Cluster Analysis was used for classification. Sørensen's (Bray–Curtis) distance measure was used with the Flexible Beta linkage method, with parameter β set at −0.25 (Lance and Williams 1967). The dendrogram was scaled by the objective function, which is widely applicable and relatively informative. Nonmetric multidimensional scaling (NMS) was used for ordination and was run from a random starting configuration in slow and thorough auto-pilot mode, with Sørensen selected as the distance measure. The stability criterion was set at 0.00001 and the number of iterations to evaluate stability was set at 15. A Monte Carlo test was carried out with 250 randomized runs. The similarity of plots was assessed by the identification of natural groups on the cluster dendrogram and verified with reference to the structure of NMS ordinations.

Histograms and normal probability plots showed that the environmental data did not fit the normal distribution and were incompatible with parametric statistics (Kent and Coker 1992). The non-parametric Spearman's rank correlation coefficient was calculated for environmental variables, species richness and ordination scores using Data Desk 6.1 (Velleman 1997).

In order to describe the species composition of these groups, floristic data were sorted in a synoptic table following the style of the British National Vegetation Classification (Rodwell 1991). Frequency and abundance values for each species, within each group and overall, are presented. Constant species are those with an overall frequency of IV or V. General associates are those species with an overall frequency of III or less that do not show a marked affiliation to any particular group. Preferential species are distinctly more frequent within one or more of the groups than the others and differential species are those whose affiliation is more exclusive. The most strongly preferential species were used in naming the groups.

Results

Observations in the field have shown that *P. sylvestris* occupies a wide variety of substrates in Ireland including raised bog, limestone pavement and upland blanket bog.

Species diversity

The dataset contained a total of 131 species. According to McCune and Grace's (2002) rule of thumb, β_W values greater than five are considered high and less than one rather low. Thus, the overall β diversity ($\beta_W = 5.57$) was high. The majority of plots exhibited low α diversity (Fig. 2), although Plots 20 (Ballykine plot 2) and 14 (Torc) approached moderate

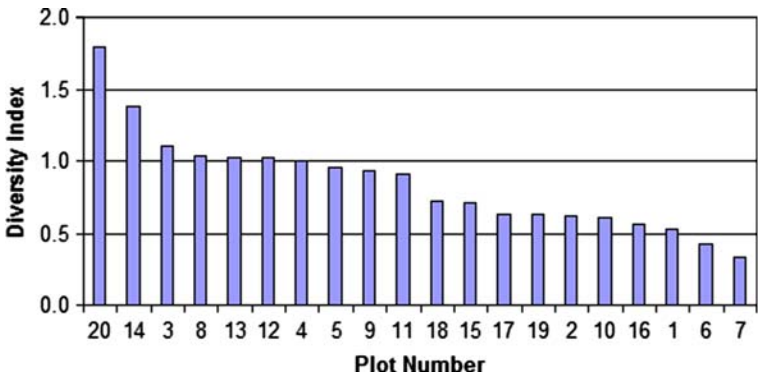

Fig. 2 α diversity within each plot

α diversity. The α diversity of individual plots was low in comparison with the β diversity of the overall dataset.

Five species in the dataset, *Acer pseudoplatanus*, *Fagus sylvatica*, *Larix decidua*, *P. sitchensis* and *R. ponticum*, are considered non-native in Ireland (Webb et al. 1996). The native status of *P. sylvestris* is indeterminate. Following Webb's (1983) rationale, the removal of non-native species, Pteridophytes, apomicts, doubtfully native species and other critical taxa from the dataset yields a total of 116 native species. The *P. sylvestris* plots surveyed represent 14.2% of the Irish native flora.

Classification of putative vegetation communities

During data transformation, the deletion of species occurring in only one plot removed 68 species, or 51.9% of the total. Cluster Analysis produced four natural groups (Fig. 3). NMS found a three-dimensional solution (Fig. 4) with a final stress of 12.7%, which indicated an intermediate solution according to Kruskal's rule of thumb (McCune and Grace 2002). A Monte Carlo test showed that the probability of a similar final stress being obtained by chance was 0.0080.

The natural groups identified by cluster analysis corresponded to reasonably well defined areas on the NMS ordinations. Axis 1, which represented the largest proportion of variance in the data ($r^2 = 0.397$; Fig. 4), exhibited an extremely significant positive correlation with soil pH ($r = 0.708$; Table 2). This axis separated Group 3, so that it was defined by relatively high soil pH values. The remaining groups all exhibited low soil pH values (Fig. 4). Axis 3, which represented the second largest proportion of variance in the data ($r^2 = 0.208$; Fig. 4a), exhibited an extremely significant negative correlation with altitude ($r = -0.713$; Table 2). This axis separated Group 4, so that it was defined by relatively low soil pH and high altitude. Axis 2, which represented the smallest proportion of variance in the data ($r^2 = 0.186$; Fig. 4), exhibited a significant negative correlation with slope ($r = -0.494$; Table 2). This axis separated the remaining groups. Thus, Group 1 was defined by relatively low soil pH and sloping topography and Group 2 by relatively

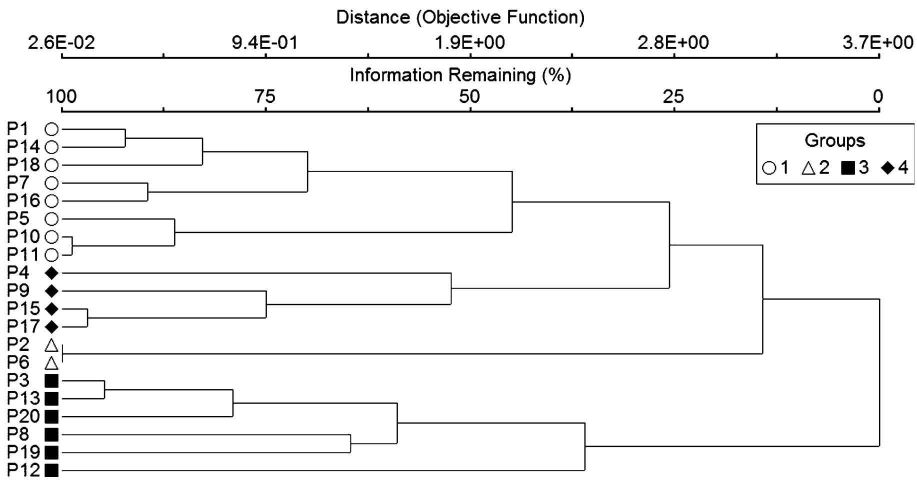

Fig. 3 Cluster Dendrogram labelled with four natural groups

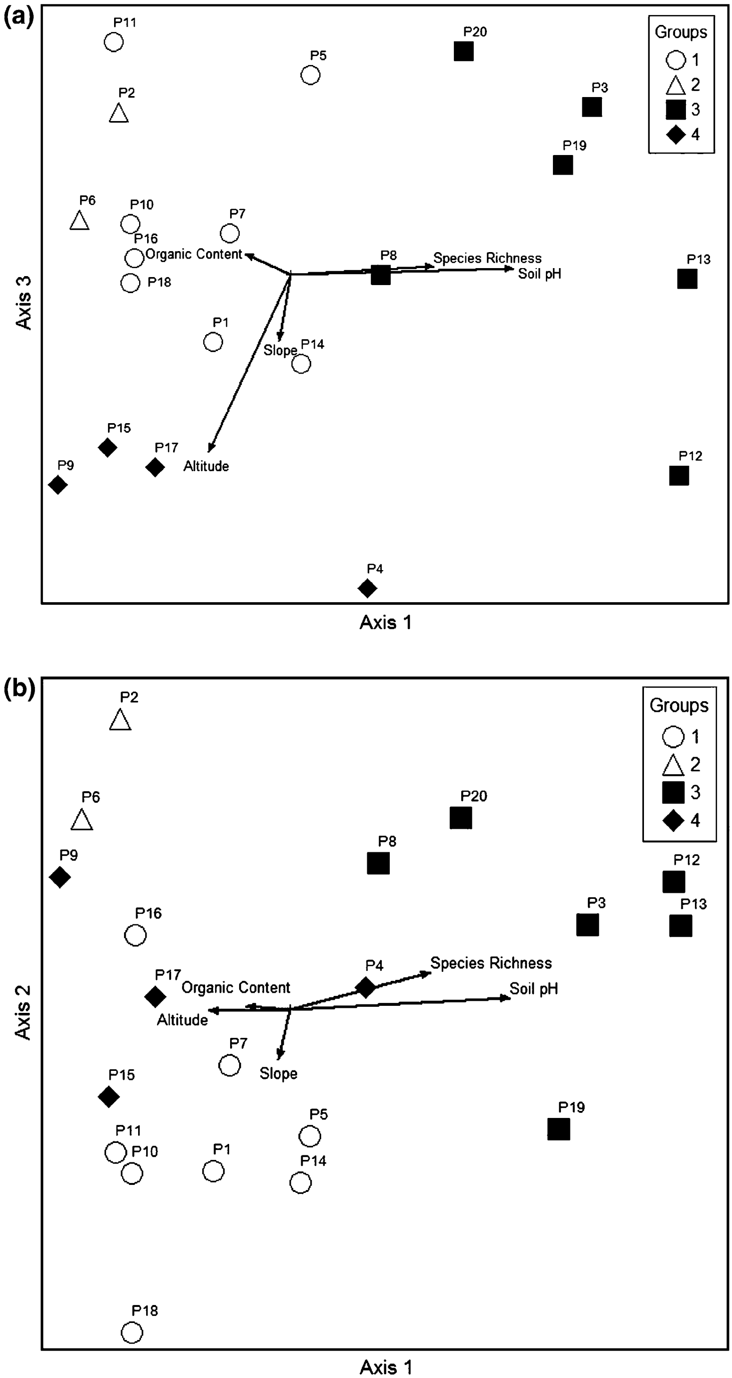

Fig. 4 Nonmetric Multidimensional scaling ordinations of **a** Axes 1 and 3 ($r^2 = 0.605$) and **b** Axes 1 and 2 ($r^2 = 0.585$), showing the four groups derived from cluster analysis and a biplot of environmental variables (r^2 values of axes: 1 = 0.397; 2 = 0.186; 3 = 0.208; total = 0.792)

Table 2 Spearman rank correlations for ordination axes, environmental variables and species richness

	Axis 1	Axis 2	Axis 3	Soil pH	% Organic content	Bulk density	Slope	Altitude
Soil pH	0.708***	0.075	−0.08	–	–	–	–	–
% Organic content	−0.382*	0.087	0.241	−0.630**	–	–	–	–
Bulk density	0.373	−0.072	−0.234	0.627**	−0.999***	–	–	–
Slope	−0.089	−0.494*	−0.501*	0.044	−0.427*	0.429*	–	–
Altitude	−0.552**	−0.181	−0.713***	−0.265	−0.071	0.071	0.620**	–
Species richness	0.855***	0.309	−0.069	0.666***	−0.251	0.249	−0.04	−0.326

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

low soil pH, low altitude and flat topography (Fig. 4b). Species richness exhibits an extremely significant positive correlation with soil pH ($r = 0.666$; Table 2).

Constant species are those with an overall frequency of IV or V (Rodwell 1991). In Irish pinewoods, the constant species are *P. sylvestris*, *Pteridium aquilinum*, *Hedera helix* and *Sorbus aucuparia* (Table 3).

Group 1: Vaccinium myrtillus–Ilex aquifolium

Sites: Dale Wood (1), Glengarriff (5), Glenfarne (7), Derrycrag plot 1 (10), Derrycrag plot 2 (11), Torc (14), Trooperstown (16), Vale of Clara (18), $N = 8$.

This was the most frequent of the putative vegetation types (40% of plots). The preferential species were *I. aquifolium*, *V. myrtillus*, *B. pubescens*, *Quercus petraea* and *Dryopteris dilatata*. The differential taxa included *R. ponticum* and *Quercus* hybrids. This vegetation type consisted of relatively dense high forest stands. The canopy was dominated by *P. sylvestris* with varying abundances of *Quercus*, chiefly *Q. petraea*. The understorey was dominated by *I. aquifolium*, with plentiful *S. aucuparia* and *B. pubescens*. The field layer was dominated by *V. myrtillus* with varying abundances of *P. aquilinum*, *H. helix*, *Blechnum spicant*, *Luzula sylvatica* and *Rubus fruticosus* agg. (Table 3). The mean species richness of this vegetation type was relatively low but was comparable with that of Groups 2 and 4 (Fig. 5). This vegetation type tended to occur on sites with acidic soils and sloping ground at moderate altitudes (Table 3).

Group 2: Calluna vulgaris–Eriophorum vaginatum

Sites: Clonfinane Bog (2), All Saints Bog (6), $N = 2$.

This was the least frequent of the putative vegetation types (10% of plots). The preferential species was *C. vulgaris*. The differential species were *Andromeda polifolia*, *Empetrum nigrum*, *Erica tetralix*, *E. vaginatum* and *Vaccinium oxycoccus*. This vegetation type consisted of relatively dense stands. The canopy was quite low and was dominated by *P. sylvestris* with varying abundances of *B. pubescens*. *B. pubescens* regeneration dominated the understorey. The field layer was dominated by *C. vulgaris* with plentiful *E. vaginatum*. *E. nigrum*, *E. tetralix*, *A. polifolia*, *V. oxycoccus* and *R. fruticosus* agg. were present at low abundances (Table 3). This vegetation type exhibited the lowest mean

Table 3 Synoptic table of floristic and environmental data

Group Number of plots	1 8	2 2	3 6	4 4	Overall 20
Constant species					
Pinus sylvestris	V (5–8)	V (7)	V (4–7)	V (7–8)	V (4–8)
Pteridium aquilinum	IV (+−7)	III (7)	IV (1–5)	IV (3–7)	IV (+−7)
Hedera helix	IV (+−4)	III (+)	V (+−5)	III (+−1)	IV (+−5)
Sorbus aucuparia	V (+−5)		II (1–2)	V (+−5)	IV (+−5)
General associates					
Blechnum spicant	V (+−4)			V(+−2)	III (+−4)
Rubus fruticosus agg.	III (+−4)	V (+−1)	V (1–4)		III (+−4)
Luzula sylvatica	III (3–7)			III (+−1)	II (+−7)
Agrostis canina	I (1)		III (+)	III (1–3)	II (+−3)
Potentilla erecta	II (+−1)		III (+−1)	III (1–3)	II (+−3)
Polypodium vulgare	II (+−1)		II (+)		II (+−1)
Quercus robur	II (3–4)		II (1–5)		I (1–5)
Fagus sylvatica	I (3)		I (1)		I (1–3)
Group 1—preferential/differential species					
Vaccinium myrtillus	V (1–8)	III (2)		IV (4–6)	III (1–8)
Ilex aquifolium	V (1–8)		III (1–4)	II (+)	III (+−8)
Betula pubescens	V (+−5)	V (5–6)	I (5)	II (+)	III (+−6)
Quercus petraea	IV (+−6)		I (4)		II (+−6)
Quercus hybrids	II (5–6)				I (5–6)
Dryopteris dilatata	II (1–3)		I (4)		I (1–4)
Rhododendron ponticum	II (1–2)				I (1–2)
Group 2—preferential/differential species					
Calluna vulgaris	III (1–5)	V (5–8)	III (4–5)	III (2)	III (1–8)
Eriophorum vaginatum		V (4)			I (4)
Empetrum nigrum		V (3)			I (3)
Erica tetralix		V (1–2)			I (1–2)
Andromeda polifolia		V (1)			I (1)
Vaccinium oxycoccus		V (1)			I (1)
Phragmites australis		III (3)			I (3)
Dryopteris carthusiana		III (1)			I (1)
Eriophorum angustifolium		III (1)			I (1)
Group 3—preferential/differential species					
Corylus avellana	I (2)		V (4–8)		II (2–8)
Fraxinus excelsior			V (1–6)		II (1–6)
Brachypodium sylvaticum			V (+−7)		II (+−7)
Crataegus monogyna			V (+−6)		II (+−6)
Anthoxanthum odoratum	II (+)	III (1)	V (+−4)	II (7)	III (+−7)
Lonicera periclymenum	III (+−4)		V (+−4)		III (+−4)
Viola riviniana/reichenbachiana	I (2)		V (+−2)	II (1)	II (+−2)
Festuca ovina	I (1)		IV (1–5)	II (1)	II (1–5)
Prunus spinosa			IV (1–4)		I (1–4)
Teucrium scorodonia			IV (1–4)		I (1–4)

Table 3 continued

Group Number of plots	1 8	2 2	3 6	4 4	Overall 20
Succisa pratensis			III (1–2)		I (1–2)
Arum maculatum			III (+−3)		I (+−3)
Fragaria vesca			III (+−3)		I (+−3)
Rosa pimpinellifolia			III (+−3)		I (+−3)
Hypericum pulchrum			III (+)		I (+)
Sesleria caerulea			II (4–5)		I (4–5)
Rubus saxatilis			II (4)		I (4)
Geranium sanguineum			II (2–3)		I (2–3)
Thymus praecox			II (1–3)		I (1–3)
Carex flacca			II (1)		I (1)
Geranium robertianum			II (1)		I (1)
Veronica chamaedrys			II (1)		I (1)
Lotus corniculatus			II (+−2)		I (+−2)
Hypochoeris radicata			II (+−1)		I (+−1)
Epipactis helleborine			II (+)		I (+)
Potentilla sterilis			II (+)		I (+)
Taraxacum agg.			II (+)		I (+)
Group 4—preferential/differential species					
Galium saxatile	I (1)			V (+−4)	II (+−4)
Agrostis capillaris	II (1)		II (+−5	IV(3–4)	II (+−5)
Oxalis acetosella	II (2–4)		I (5)	IV (2–4)	II (2–5)
Molinia caerulea	II (1–5)		I (5)	III (4–9)	II (1–9)
Deschampsia flexuosa	I (4)		I (1)	III (4)	I (1–4)
Agrostis stolonifera	I (1)		II (3–4)	III (1–3)	II (1–4)
Dryopteris aemula	I (1)			III (1)	I (1)
Agrostis vinealis				II (4)	I (4)
Holcus lanatus				II (4)	I (4)
Hymenophyllum wilsonii	I (3)			II (3)	I (3)
Arrhenatherum elatius				II (1)	I (1)
Cerastium fontanum				II (1)	I (1)
Cirsium palustre				II (1)	I (1)
Erica cinerea	I (+)		I (3)	II (1)	I (1)
Luzula multiflora				II (1)	I (1)
Lysimachia nemorosa				II (1)	I (1)
Ranunculus repens				II (1)	I (1)
Stellaria holostea				II (1)	I (1)
Trifolium repens			I (1)	II (1)	I (1)
Cardamine sp.				II (+)	I (+)
Dactylis glomerata	I (+)		I (3)	II (+)	I (+−3)
Danthonia decumbens				II (+)	I (+)
Festuca rubra				II (+)	I (+)
Juncus effusus				II (+)	I (+)

Table 3 continued

Group	1	2	3	4	Overall
Number of plots	8	2	6	4	20
Summary data					
Species Richness	15	13	31	17	20
Altitude (m)	100	54.5	45	270	113
Slope (°)	12	0	8	17	11
Soil pH	3.56	3.34	4.46	3.62	3.67
Soil organic content (%)	63.1	96.0	42.2	53.2	58.1
Density (trees/ha)	978	913	600	513	765
Mean canopy height (m)	18	10	12	14	14

Abundance is presented as a bracketed range of Domin values

Species occurring in only one group with a frequency of I have been omitted from the table but are listed below, with their cover scores bracketed. Group 1: *Betula pendula* (4); *Alnus glutinosa* (3); *Hymenophyllum tunbridgense* (1); *Euphorbia hyberna*, *Picea sitchensis*, *Saxifraga spathularis* (+). Group 3: *Filipendula ulmaria* (4); *Carex sylvatica*, *Euonymus europaeus*, *Plantago lanceolata*, *Rhamnus cathartica*, *Rosa canina*, *Stellaria media* (3); *Larix decidua*, *Melampyrum pratensis*, *Polystichum setiferum*, *Viburnum opulus* (2); *Angelica sylvestris*, *Ceratocapnos claviculata*, *Daucus carota*, *Festuca arundinacea*, *Galium verum*, *Koeleria macrantha*, *Ranunculus acris*, *Rubia peregrina*, *Salix* x *multinervis*, *Trifolium pratense*, *Umbilicus rupestris* (1); *Acer pseudoplatanus*, *Antennaria dioica*, *Avenula pubescens*, *Campanula rotundifolia*, *Centaurea nigra*, *Cytisus scoparius*, *Epilobium* sp., *Galium aparine*, *Iris pseudacorus*, *Lapsana communis*, *Lathyrus Montana*, *Lathyrus pratensis*, *Lythrum salicaria*, *Mycelis muralis*, *Phleum pratense*, *Polygala vulgaris*, *Rumex acetosella*, *Salix repens*, *Schoenus nigricans*, *Sedum anglicum*, *Senecio jacobaea*, *Valeriana officinalis*, *Veronica officinalis*, *Vicia cracca* (+)

Frequency classes are denoted by Roman numerals as follows: I, 1–20%; II, 21–40%; III, 41–60%; IV, 61–80%; V, 81–100%

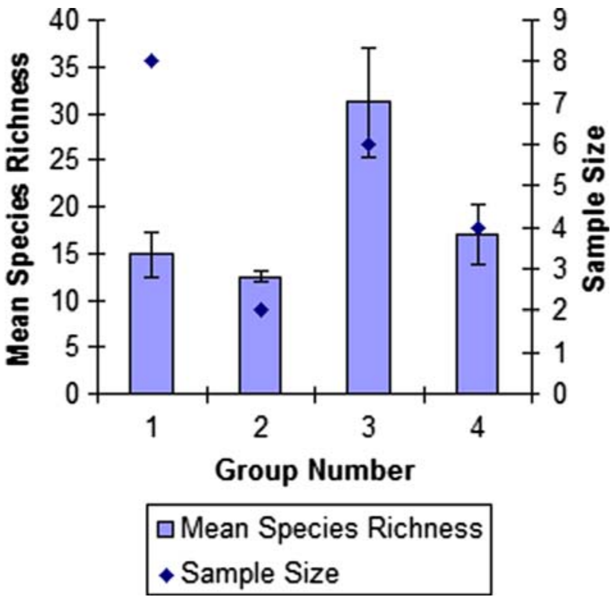

Fig. 5 Mean vascular plant species richness (±standard error) and sample size of natural groups

species richness. However, as the sample size was relatively small and species diversity is likely to increase with the area or number of sites sampled, this assessment of relative diversity may not be statistically sound. In any case, the species richness values for both plots lay within a similar range to those of Groups 1 and 4 (Fig. 5). This vegetation type occurred only on raised bogs in the lowlands. These sites exhibited flat topography and waterlogged, acidic peat soils with a high organic content (Table 3).

Group 3: Corylus avellana–Brachypodium sylvaticum

Sites: Rockforest (3), The Scalp (8), Portumna Forest Park (12), Rockvale (13), Ballykine plot 1 (19), Ballykine plot 2 (20), $N = 6$.

This was the second most frequent of the putative vegetation types (30% of plots). The preferential species were *C. avellana*, *Lonicera periclymenum*, *Anthoxanthum odoratum*, *Viola riviniana/reichenbachiana* and *Festuca ovina*. The differential species included *Crataegus monogyna*, *Fraxinus excelsior*, *B. sylvaticum*, *Prunus spinosa* and *Teucrium scorodonia*. The structure of this putative vegetation type was heterogeneous, as it incorporated both high forest and scrub. Despite this, there was a certain consistency in the species composition of these plots. *P. sylvestris* was structurally dominant, forming a canopy in high forest stands and scattered standards in scrub. *C. avellana* generally dominated the understorey or shrub layer. *F. excelsior*, *C. monogyna* and *P. spinosa* were also present at varying abundances. The field layer was variable but *B. sylvaticum*, *H. helix*, *A. odoratum*, *L. periclymenum*, *V. riviniana/reichenbachiana*, *P. aquilinum*, *F. ovina* and *T. scorodonia* were constant species (Table 3). The mean species richness of this vegetation type was markedly higher than that of the other groups (Fig. 5). The habitats in which this vegetation type occurred were heterogeneous. Rockforest, Rockvale and Ballykine plot 2 occur on limestone pavement. Portumna Forest Park and Ballykine plot 1 occur on limestone-derived soils. The Scalp occurs on relatively acidic soil with granite outcrops. These sites are related by the presence of exposed or outcropping rock and/or relatively high soil pH. With the exception of The Scalp, they generally occur on gentle slopes in the lowlands (Table 3).

Group 4: Galium saxatile–Agrostis capillaris

Sites: Priest's Leap (4), Coronation Plantation (9), Knockastakeen (15), Derrybawn (17), $N = 4$.

This was the third most frequent of the putative vegetation types (20% of plots). The preferential species were *G. saxatile*, *A. capillaris* and *Oxalis acetosella*. The differential species included *Agrostis vinealis*, *Holcus lanatus* and *Hymenophyllum wilsonii*, although these were only occasional even within this group. This vegetation type consisted of a relatively high but open canopy, which was completely dominated by *P. sylvestris*. The understorey was sparse or absent but, where present, it was dominated by *S. aucuparia*. The field layer was variable but was generally dominated by combinations of *P. aquilinum*, *V. myrtillus* and *Molinia caerulea*. *G. saxatile*, *B. spicant*, *A. capillaris* and *O. acetosella* were generally present at lower abundances (Table 3). The mean species richness of this vegetation type was intermediate (Fig. 5). The mean altitude of this vegetation type was markedly higher than that of the other groups. This vegetation type tended to occur on upland sites with acidic soils and sloping topography (Table 3).

Discussion

Spatial diversity

The field surveys demonstrated that *P. sylvestris* occupies a wide variety of substrates in Ireland, displaying the broad edaphic and topographic amplitude described by Carlisle and Brown (1968). It is therefore a non-specialist in terms of its environmental tolerances. In terms of vascular plant species, β diversity among plots was high while α diversity within plots varied from low to moderate. There was a low level of constancy of species within *P. sylvestris* stands in Ireland, which was demonstrated by the large proportion of species lost during the deletion of rare species (51.9%). This reflects variability and diversity in the species composition of *P. sylvestris* stands.

Classification of putative vegetation communities

There was broad agreement between the cluster analysis and NMS output, as the hierarchy and natural groups corresponded to reasonably well defined areas on the ordinations. This implies that there is a good basis for describing the natural groups as distinct vegetation types. The groups are generally well defined in terms of the environmental conditions in which they occur, their preferential and differential species and they also make good ecological sense. It is acknowledged that the lack of *P* values prevents the identification of statistically significant indicator species. However, the definition of vegetation communities must preserve their ecological integrity above the minutiae of mathematical technique (Rodwell 1991; van der Maarel 2007) and the ecological integrity of these groups appears to be satisfactory.

The putative vegetation types defined in this study correspond to recognisable semi-natural vegetation types. Group 1, the *V. myrtillus*-*I. aquifolium* type appears to represent acid oak woodland with a *P. sylvestris* component. This group is broadly comparable with Fossitt's (2000) oak-birch-holly semi-natural woodland (WN1) category, which is linked to the 'old sessile oak woods with *Ilex* and *Blechnum* in the British Isles' category on Annex 1 of the EU Habitats Directive (91A0) (EEC 1992). All of these plots originated as plantations. The presence of *R. ponticum*, *Picea sitchensis* and *Fagus sylvatica* regeneration within this vegetation type highlights its vulnerability to invasive non-native species. This vegetation type is associated with acidic mor humus soils on sloping ground at moderate altitudes.

Group 2, the *C. vulgaris*-*E. vaginatum* type, clearly represents Fossitt's (2000) semi-natural bog woodland (WN7) category, which is linked to the bog woodland category on Annex 1 of the EU Habitats Directive (91D0) (EEC 1992). This vegetation type is particularly well defined as it contains five perfect differential species and both sites were located on active raised bogs which exhibited very similar environmental conditions—flat topography and acidic, waterlogged peat soils with a high organic content. The vegetation histories of these sites were investigated using paleoecological techniques and both were found to be non-relict, naturalised stands (Heery 1993; O'Connell and Doyle 1990). The small sample size of this group is due to the rarity of this habitat in Ireland (Fossitt 2000).

Group 3, the *C. avellana*-*B. sylvaticum* type, is relatively heterogeneous but appears to represent both naturalised and planted stands with exposed or outcropping rock and/or relatively high soil pH values, which generally occur on gently sloping ground in the lowlands. Most of the differential and preferential species display a preference for soil pH in the range of 5–7 and some such as *T. scorodoniaI* display a preference for rocky habitats

(Grime et al. 1988). Overall, this group corresponds loosely with Fossitt's (2000) semi-natural oak-ash-hazel woodland (WN2) category which, although it is not listed under Annex 1 of the EU Habitats Directive, is limited in extent in Ireland and should be considered as being of conservation importance. However, due to the heterogeneity of the group, there may be some basis for its sub-division. Figure 3 highlights the relative similarity of plots 3, 13 and 20. These plots represent a complex, small-scale vegetation mosaic which is associated with karstic areas of the Burren in western Ireland (Cross 1998) and is of particular conservation interest. They correspond with a transitional habitat—dry calcareous and neutral grassland (GS1) grading into scrub (WS1). They also incorporate elements of limestone pavement (ER2) and dry calcareous heath (HH2; Fossitt 2000). Most of these are listed habitats under Annex 1 of the EU Habitats Directive. Calcareous and neutral grassland corresponds to the priority habitat 'semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (important orchid sites)' (6210). Limestone pavement is also a priority habitat (8240). Dry calcareous heath corresponds to 'European dry heaths' (4030; EEC 1992). The relatively high α diversity of these plots (Fig. 2) contributes to their relatively high species richness (Fig. 5) and heightens their conservation importance.

Group 4, the *G. saxatile-A. capillaris* type, does not correspond clearly to any one habitat type, but its species composition bears some similarity to that of flushes (PF2), exposed siliceous rock (ER1) and particularly to dry-humid acid grassland (GS3), all habitats which do not typically occur under a woodland canopy (Fossitt 2000). Rodwell and Cooper (1995) attributed this tendency to the modest shade cast by *P. sylvestris* stands, which means that there are often few differences in species composition, other than the presence of *P. sylvestris* itself, between the woodland and the habitat that the tree has colonised. Appropriately, this group is characterised by an open structure as it exhibits the lowest density of trees (Table 3). This vegetation type is associated with acid soils in upland situations and these plots all originated as plantations.

Effects of environmental factors on putative vegetation communities

Soil pH accounted for the largest proportion of variance in species composition in *P. sylvestris* stands. Soil pH also exhibited a highly significant positive correlation with species richness (Table 2), a relationship which has been observed throughout temperate regions of Europe (Partel et al. 2004). Altitude and slope also accounted for large proportions of the variance in species composition, but did not exhibit a significant correlation with species richness. This suggests that soil pH, altitude and slope have a role in partitioning distinct vegetation types and that increasing soil pH positively influences the species diversity of *P. sylvestris* stands.

Conclusions

Pinus sylvestris tolerates a wide range of environmental conditions in the Irish context. Varying levels of soil pH, altitude and slope produce markedly different, but reasonably well defined, vegetation communities. Soil pH may potentially act as an indicator of species diversity for *P. sylvestris* woodland in Ireland. In terms of forest management, the quantitative environmental data presented here should inform site selection for new plantings of *P. sylvestris* and species selection at any given site.

Pinus sylvestris is well established, well integrated and naturalising in Irish semi-natural habitats. Its associated vegetation communities are diverse. A low level of species constancy and a high level of β diversity reflect this diversity and variability. These communities contain a high proportion of native species. Furthermore, the comparison of these communities with those described in Fossitt (2000) has shown that, excepting the presence of a questionably native species in the canopy, these habitats exhibit a semi-natural character. Given Ireland's impoverished native flora and low coverage of native woodland, these communities form a significant resource for native biodiversity. In addition, some of the communities described here correspond to habitats of international conservation importance. Woodlands of intact raised bog, in particular, are acknowledged as being very rare in Ireland (Fossitt 2000). Whether or not *P. sylvestris* is native, the communities associated with it in Ireland are of value in conserving Ireland's native botanical and habitat diversity. The baseline vegetation data presented here should inform conservation policy relating to *P. sylvestris* in Ireland, and are broadly relevant in assessing the conservation value of reintroduced species elsewhere.

Future work will include the development of management prescriptions and a formal comparison of these Irish sites with native pinewoods in Scotland, thereby placing Irish pinewoods in the broader context of the flora of north-west Europe.

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