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Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood

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Abstract

Lichen and bryophyte communities of spruce and pine plantations in different parts of Britain were surveyed and compared to those of semi-natural pine and oak woodlands. In total, 202 lichen species and 111 bryophytes were recorded. Community composition and species-richness were related to measures of climate, stand structure and deadwood (snags, logs and stumps). Plantations had a less species-rich lichen flora than semi-natural stands related to reduced light availability and lack of old trees. Bryophyte species-richness was similar in plantations and semi-natural stands, and was positively correlated with large diameter (>20 cm), well-decayed logs and stumps. Lichens species-richness was higher on decorticate snags (especially in semi-natural Scots pine stands in the Scottish Highlands). Early successional stands were often the richest for lichens, stumps being important for *Calicium* and *Cladonia* species. Three strategies are suggested for enhancing lower plant diversity in planted forests: (1) extending felling rotations; (2) introducing alternative silvicultural systems to clear-felling (e.g. single-tree selection) to foster continuity of woodland conditions and increase deadwood volumes; (3) modifying restocking practices on clear-fells to avoid excessive shading of deadwood. Crown Copyright © 2002 Published by Elsevier Science Ltd. All rights reserved.

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1. Introduction

Epiphytic bryophytes and lichens are important components of biological diversity in natural boreal and temperate forests (Söderström, 1988; Lesica et al., 1991; Esseen et al., 1997). In Britain, ancient semi-natural (native) woodlands provide internationally significant habitats for lichens and bryophytes (Hodgetts, 1996). Key biotopes include lowland pasture woodland (e.g. the New Forest, Suffolk), Atlantic oak-birchwoods (*Quercus–Betula* spp.) in northern and western regions, and native Caledonian pinewoods (*Pinus sylvestris* L.) in the Scottish Highlands (Rose, 1993). The particular value of these woodland types as epiphytic habitat is related to low pollution levels, continuity of woodland conditions over many hundreds of years, the survival of very old trees, and relatively open canopies ensuring adequate light levels for epiphytic growth (Rose, 1992, 1993; Fletcher, 1999).

However, there has been a huge loss and fragmentation of native woodland over the past 2–3000 years as a consequence of clearance for agriculture and conversion to plantations (Spencer and Kirby, 1992; Roberts et al., 1993). Effects on the extent and abundance of epiphytic communities are thought to have been particularly severe, as many species are exacting in their habitat requirements and/or have very low rates of dispersal (Rose, 1993).

Recently, Habitat Action Plans have been developed to encourage the restoration and expansion of the native woodland resource (Anon, 1995), as have a number of Species Action Plans targeted at maintaining and improving habitat for key species (Anon,

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1995). Whilst these action plans will go some way to improving the conservation status of many epiphytic species, the area of new potential habitat will still be quite limited.

Over the last 80–100 years there has been a rapid increase in the amount of planted forest composed mainly of introduced conifer species such as Sitka spruce [(*Picea sitchensis* (Bong). Carr.], Norway spruce (*Picea abies* L.), Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco], larches (*Larix* spp.) and firs (*Abies* spp.). Recent studies have demonstrated the value of these developing ecosystems for a range of species groups (Petty and Avery, 1990; Petty et al., 1995; Humphrey et al., 1999, 2000; Jukes et al., 2001) but there has been little work published on the potential value of conifer plantations for lower plants, or how they might be managed to improve habitat quality.

Deadwood is a key habitat for epixylic bryophytes and lichens in boreal and temperate forests (Harmon et al., 1986; Söderström, 1988; Samuelsson et al., 1994; Esseen et al., 1997; Crites and Dale, 1998), and a significant number of studies, particularly in Fenno-scandian boreal forests have highlighted the value of large diameter, well decayed fallen (logs) and standing deadwood (snags and stumps) for rare and threatened taxa (e.g. Gustafsson and Hallingbäck, 1988; Berg et al., 1994; Kruys et al., 1999). Old, unmanaged stands usually have the highest diversity of deadwood habitats (including a high proportion of large, well-decayed material) and hence have a more diverse lower plant flora (Gustafsson and Hallingbäck, 1988; Kuusinen and Siitonen, 1998; Vellak and Paal, 1999). However, there is also a strong interaction between stand age and light availability, the latter being of particular importance for lichen growth (Rose, 1993). Changes in stand structure through a forest rotation can therefore have an effect on the value of deadwood as a habitat (Crites and Dale, 1998), and this effect will vary depending on forest type (Kuusinen and Siitonen, 1998) and site parameters such as soil and climate (Ferris et al., 2000).

In Britain, there has been very little published information on the specific value of deadwood for lower plants, despite numerous calls for managers to increase deadwood volumes in managed forests (e.g. Ratcliffe, 1993; Hodge and Peterken, 1998; Anon, 2000). The objectives of this study were to:

1. produce an inventory of lichen and bryophyte species associated with a sample of Scots pine, Sitka spruce, Norway spruce and Corsican pine stands planted on a range of different sites across Britain;
2. relate lichen and bryophyte species-richness and composition to climate, stand structure (successional stage and vertical foliage cover) and deadwood;
3. compare plantation communities with those of semi-natural Scots pine and oak woodlands in similar bioclimatic zones and on comparable site types in order to evaluate the potential of conifer plantations as a habitat for native lichens and bryophytes
4. propose management strategies for enhancing habitat quality for lower plants in planted stands.

This study is part of a wider project investigating the biodiversity value of planted forests in Britain (Humphrey et al., 1999).

2. Methods

2.1. Study sites

Assessment sites were selected from within the "lowland", "foothill" and "upland" bioclimatic zones of the Forestry Commission's Ecological Site Classification (ESC—Pyatt and Suàrez, 1997). The zones are defined by annual precipitation totals (lowlands <800 mm; foothills: 800–1500 mm; uplands: >1500 mm). Study sites were established in Sitka spruce plantations and semi-natural oakwoods in the uplands; in Sitka spruce, Scots pine plantations and semi-natural pinewoods in the foothills; and in Corsican pine, Scots pine, Norway spruce plantations and semi-natural oakwoods in the lowlands. Two replicate sites were selected for each species$\times$bioclimatic zone combination (referred to hereafter as "crop type"—see Table 1 for full list of sites). At the majority of sites, a chronosequence of four 1 ha (100×100 m) permanent sample plots was established in forest stands encompassing different growth stages. The four stages were:

1. pre-thicket—age 8–10 years, crop height 2–4 m, incomplete canopy closure;
2. mid-rotation—age 20–30 years, crop height 10–20 m, complete canopy closure, no understorey;
3. economically mature—age 50–80 years, crop height 20–25 m, some understorey development;
4. over-mature [beyond economic maturity and acquiring some of the ecological characteristics of natural old-growth forests sensu Oliver (1981)]—age 60–250 years, crop height >20 m, canopy breaking up, well developed understorey, accumulation of deadwood.

Stage 4 stands were not available in some of the lowland crop types and in the foothills Scots pine chronosequences. In the latter case, over-mature plots were set up in self seeded "old-growth" semi-natural pinewood areas. These represent modified remnants of the original natural boreal forest in Scotland (Worrell, 1996). In the uplands and lowlands, semi-natural oakwood plots were established for comparison with the conifer stands. Only stages 2 and 3 were available in the oakwoods owing to a lack of large areas of newly regenerating oak. The total number of plots sampled was 52. The previous land cover for the plots is given in Table 1.

2.2. Lichen, bryophyte and deadwood assessments

The volume, size and quality of individual pieces of deadwood were measured in all sites except the oak stands (Sites 13, 14, 15 and 16—Table 1). In sites 1–12, the height (h_S) and diameter at breast height (dbh ~1.3 m) of all individual snags ⩾7 cm dbh were recorded within eight, 10×20 m sub-plots per 1 ha plot. There were two of these sub-plots placed diagonally at equidistant intervals between the corners of each 50×50 m quarter of the 1 ha plot. The total area of the eight sub-plots was 1600 m^2. Volumes were calculated for all deadwood types by assuming they were cylindrical. The volume (V_S) of each snag was calculated using the formula:

$$V_s = \pi\ (\mathrm{dbh}/2)2\ h_S$$

Logs and stumps were recorded when they intersected the central line of each of the 10×20 m plots. The combined total length of the line was 180 m. For logs, the diameter at top (d_t) and bottom (d_b) were recorded, together with length (h_F), for stumps, d_t, d_b and height (h_F) were recorded. The volume (V_F) of logs and stumps was calculated using the formula:

$$V_F = \left[\pi(d_t/2)^2\ h_F + \pi(d_b/2)^2\ h_F\right]/2$$

Deadwood quality was described using a visual five-point scale following Hunter (1990): 1—bark intact, small branches present; 2—bark loose or sloughing off, no sapwood degradation; 3—no bark, some sapwood degradation; 4—no bark, considerable sapwood degradation; 5—sapwood and heartwood degradation.

Lichen and bryophyte species were recorded on each individual piece of deadwood measured at sites 1–12. Lichens and bryophytes were also recorded on individual pieces of deadwood within the oak plots (sites 13–16), but size measurements for these pieces of deadwood were not recorded (as mentioned above). Only "true" lichens were recorded, i.e. those which are formed through a symbiotic relationship between an alga and a fungus. Four 10×20 cm quadrats were spaced at even intervals along the length of each piece of deadwood; on the uppermost surface of logs and stumps (i.e. omitting the sides and lower portions), and up to 2 m in height on snags (aspect was selected randomly for snag sampling). The occurrence and abundance (using the DOMIN scale of Dahl and Hadac, 1941) of individual lichen and bryophyte species were recorded within each quadrat. In addition to this assessment of epixylic species, a list was made of bryophytes and lichens occurring on other substrata within each 1 ha (excluding the forest floor). The main substrata assessed were rocks, cliffs (where these occurred) and mature trees (up to 2 m height). No measures of relative abundance were made for these additional species.

2.3. Climatic variables

Climatic information for the 52 assessment plots was obtained from datasets held within the ESC computer-based decision support system (Ray et al., 1998). Two climate variables were used in the analysis: soil moisture deficit (MD) and accumulated temperature (AT). MD is expressed as the maximum accumulated amount by which monthly potential evaporation exceeds precipitation (Bendelow and Hartnup, 1980), and is essentially a measure of dryness. AT expresses the degree of warmth or available heat energy (Bendelow and Hartnup, 1980) and is measured by the number of degree-days above 5°C. The derivation of these variables from meteorological data is described more fully in Humphrey et al. (2000).

2.4. Stand structure assessments

Two 10×10 m quadrats were arranged diagonally across the centre of each 50×50 m quarter of the 1 ha plot, giving eight quadrats in total per plot. Within these quadrats, assessments of dbh, height to the base of the live crown (HTLC), and top height (TOPHT), were made by species, for all living trees ⩾7 cm dbh. In those plots where stocking density was low (e.g. stage 4 stands), the quadrats were extended (proportionately from each corner) to 25×25 m to obtain a sufficient sample of trees. Mean basal area (MBA) was calculated for each 1 ha plot following Hamilton (1975). Vertical stand structure was assessed using a visual cover method within each 50×50 m quarter of the 1-ha assessment plot. Four measurements, each 10 m apart were made along a North-South transect, running through the centre point of each quarter, yielding 16 measures in total for each 1 ha plot. Four vegetation strata were defined: S1 (field) 10 cm–2 m in height; S2 (shrub) 2–5 m; S3 (lower canopy) 5–15 m; and S4 (upper canopy) 15–20 m. Percentage cover of vegetation within each vertical stratum was described to the nearest 5% and expressed as a mean of the 16 stand structure measures. To convert these cover values to a unified measure of stand structure, a Cover Index (C.I.) was calculated following Ferris et al. (2000).

Measurements of photosynthetically active radiation (PAR) were taken under diffuse light conditions at 5-m

Table 1
Location and description of study sites[a]

Site code	Site name	Crop species	Bioclimatic zone	Age (years)	Location	Previous land cover
1	*Glen Affric*					
1.1	Lochan Dubh, Cannich	Scots pine	Foothills	12	57°23′ N 4°48′ W	Heath/grassland
1.2	Knockfin	Scots pine	Foothills	35	57°18′ N 4°51′ W	Heath/grassland
1.3	Plodda Falls	Scots pine	Foothills	96	57°17′ N 4°55′ W	Native pinewood
1.4	Loch Beinn a' Mheadhoinn	Scots pine	Foothills	238[b]	57°16′ N 4°52′ W	Native pinewood
2	*Strathspey*					
2.1	Moor of Alvie	Scots pine	Foothills	8	57°9′ N 3°54′ W	Pine plantation
2.2	An Slugan	Scots pine	Foothills	32	57°12′ N 3°45′ W	Native pinewood
2.3	Glenmore Lodge	Scots pine	Foothills	64	57°10′ N 3°40′ W	Native pinewood
2.4	Airgiod-meall	Scots pine	Foothills	165[b]	57°9′ N 3°43′ W	Native pinewood
3	*Thetford*					
3.1	Lynford	Scots pine	Lowlands	18	52°29′ N 0°42′ E	Heath/grassland
3.2	Horsford Woods	Scots pine	Lowlands	37	52°43′ N 1°15′ E	Heath/grassland
3.3	High Lodge	Scots pine	Lowlands	68	52°26′ N 0°41′ E	Heath/grassland
4	*New Forest/Windsor*					
4.1	Knightwood Inclosure	Scots pine	Lowlands	26	50°51′ N 1°38′ W	Native oakwood
4.2	Denny Lodge	Scots pine	Lowlands	49	50°51′ N 1°32′ W	Native oakwood
4.3	Denny Lodge	Scots pine	Lowlands	66	50°50′ N 1°31′ W	Native oakwood
4.4	The Look Out, Windsor	Scots pine	Lowlands	66	51°23′ N 0°44′ W	Native oakwood
5	*Knapdale*					
5.1	Dunardy	Sitka spruce	Uplands	9	56°4′ N 5°31′ W	Sitka spruce
5.2	Dunardy	Sitka spruce	Uplands	24	56°4′ N 5°31′ W	Sitka spruce
5.3	Gortonronach, Kilmichael	Sitka spruce	Uplands	44	56°5′ N 5°19′ W	Heath/scrub
5.4	Dunardy	Sitka spruce	Uplands	62	56°4′ N 5°30′ W	Heath/scrub
6	*Clunes*					
6.1	South Laggan	Sitka spruce	Uplands	8	57°0′ N 4°52′ W	Sitka spruce
6.2	Clunes	Sitka spruce	Uplands	28	56°58′ N 4°59′ W	Heath/native woodland
6.3	Clunes	Sitka spruce	Uplands	62	56°58′ N 4°59′ W	Heath/native woodland
6.4	South Laggan	Sitka spruce	Uplands	67	57°0′ N 4°53′ W	Heath
7	*Forest of Dean*					
7.1	Ruddle Marsh	Norway spruce	Lowlands	15	51°49′ N 2°34′ W	Native woodland
7.2	Cannop	Norway spruce	Lowlands	31	51°48′ N 2°34′ W	Native woodland
7.3	Ruardean	Norway spruce	Lowlands	56	51°51′ N 2°32′ W	Native woodland
8	*Fineshade*					
8.1	Fineshade	Norway spruce	Lowlands	17	52°34′ N 0°33′ W	Native woodland
8.2	Fineshade	Norway spruce	Lowlands	39	52°34′ N 0°34′ W	Native woodland
8.3	Fermyn Woods	Norway spruce	Lowlands	65	52°27′ N 0°33′ W	Grassland
9	*Kielder*					
9.1	Falstone	Sitka spruce	Foothills	6	55°10′ N 2°27′ W	Sitka spruce
9.2	Falstone	Sitka spruce	Foothills	23	55°9′ N 2°27′ W	Sitka spruce
9.3	Falstone	Sitka spruce	Foothills	57	55°9′ N 2°31′ W	Grassland
9.4	Archie's Rigg	Sitka spruce	Foothills	69	55°8′ N 2°28′ W	Grassland/mire
10	*Glentress*					
10.1	Glentress	Sitka spruce	Foothills	10	55°40′ N 3°9′ W	Sitka spruce
10.2	Glentress	Sitka spruce	Foothills	28	55°39′ N 3°8′ W	Heath/grassland
10.3	Glentress	Sitka spruce	Foothills	55	55°40′ N 3°9′ W	Heath/grassland
10.4	Cardrona	Sitka spruce	Foothills	61	55°37′ N 3°6′ W	Grassland
11	*Thetford*					
11.1	Kings Forest	Corsican pine	Lowlands	8	52°21′ N 0°40′ E	Heath/grassland
11.2	Kings Forest	Corsican pine	Lowlands	33	52°21′ N 0°40′ E	Heath/grassland
11.3	Kings Forest	Corsican pine	Lowlands	59	52°20′ N 0°39′ E	Heath/grassland
11.4	High Lodge	Corsican pine	Lowlands	69	52°26′ N 0°40′ E	Heath/grassland

(*Continued*)

Table 1 (*continued*)

Site code	Site name	Crop species	Bioclimatic zone	Age (years)	Location	Previous land cover
12	*Clipstone*					
12.1	Clipstone	Corsican pine	Lowlands	9	53°9′ N 1°6′ W	Heath/grassland
12.2	Clipstone	Corsican pine	Lowlands	43	53°9′ N 1°3′ W	Heath/grassland
12.3	Clipstone	Corsican pine	Lowlands	49	53°10′ N 1°5′ W	Heath/grassland
13	*Alice Holt*					
13.2	The Straits	Oak	Lowlands	62	51°9′ N 0°51′ W	Native oakwood
13.3	Goose Green	Oak	Lowlands	177	51°9′ N 0°50′ W	Native oakwood
14	*New Forest*					
14.2	Salisbury Trench	Oak	Lowlands	61	50°55′ N 1°38′ W	Native oakwood
14.3	Fletcher's Thorns	Oak	Lowlands	168	50°50′ N 1°36′ W	Native oakwood
15	*Taynish*					
15.2	Taynish	Oak	Uplands	112[b]	56°0′ N 5°38′ W	Native oakwood
15.3	Taynish	Oak	Uplands	~150[c]	56°0′ N 5°35′ W	Native oakwood
16	*Beasdale/Moidart*					
16.2	Beasdale	Oak	Uplands	112[b]	56°53′ N 5°45′ W	Native oakwood
16.3	Moidart	Oak	Uplands	131[b]	56°47′ N 5°45′ W	Native oakwood

[a] Numbers after the decimal place in the site codes refer to stand stage (1—pre-thicket, 2—mid-rotation, 3—mature, 4—over mature).
[b] Semi-natural stand, mean age. Ages range were: Plot 1.4—183–270; Plot 2.4—100–242; Plot 15.2—60–140; Plot 16.2—19–154; Plot 16.3—55–201.
[c] Semi-natural stand, mean age estimated from historical records.

intervals, along two diagonal transects across each assessment plot. For this purpose, a hand-held sunfleck ceptometer (Decagon Instruments, USA) with an 80-cm probe was used, held at a height of approximately 1.5 m above the ground. A second, calibrated probe was placed outside the assessment plot, in a clearing not obscured by trees. Sets of five readings were taken simultaneously at 30-s intervals with both probes, averaged and then recorded. The data were converted to Leaf Area Index (LAI) values using the canopy radiation model of Goudriaan (1988) for diffuse light conditions. Under these conditions of incident light (PAR_{inc}), only LAI and the light extinction coefficient (K) determine canopy light absorption (PAR_{abs}) i.e. [$PAR_{abs} = PAR_{inc}(1 - e^{(-K \times LAI)})$].

2.5. Analysis

Analyses were undertaken using a combination of SAS (Anon, 1990), Genstat (Anon, 1993) and MVSP V3.1 (Kovach Computing Services, 2000) programmes. Two separate analyses of lichen and bryophyte species counts were carried out. Firstly, the effect of crop type on numbers of lichen and bryophyte species found on all substrata was analysed using a set of generalised linear models with log link functions and poisson error distribution. This was to test for differences between planted and semi-natural stands The species count data were also related to climate, and stand variables (Table 2) using correlation analysis. For the second analysis of species counts, separate linear models were constructed to predict the relative importance of crop type (combining species and bioclimatic zone), stand stage, deadwood type, decay stage, size and volume in determining species-richness of lichens and bryophytes growing directly on deadwood. Data for species recorded on other substrata were excluded, as were the data from the oak stands where no quantitative measures of deadwood were undertaken. Models were simplified by removing any non-significant main effects or interactions. Independent variables, and where appropriate interactions between previously included variables, were added to the model until predictions of species-richness showed no significant improvement. The models can identify factors which co vary, as it is obvious, for example, that certain types of deadwood are commoner in some stand types than others (Table 5). Adjustments were therefore made to take account of variations in deadwood availability between stands.

Relationships between bryophyte and lichen community composition, climate and stand variables were examined using Canonical Correspondence Analysis (CCA), a procedure which allows multivariate and direct gradient analysis of response data with respect to a set of explanatory variables (Ter Braak, 1986). Direct gradient analysis regresses site (plot) scores on environmental scores at each iterative point of the ordination. The resulting axes are therefore constrained to be linear

Table 2
Stand structure and climate variables related to species-richness of lichen and bryophyte communities[a]

Variable	Description	Max.	Min.	Mean	SD
AT	Accumulated temperature (no. day degrees $>5°C$)	2002	771	1405.7	370.5
MD	Soil moisture deficit (mm)	225	24	128.7	63.5
DAMS	Windiness/exposure	18	10	13.4	2.1
S1	Vertical cover field layer (%)	72.6	0	17.3	21.0
S2	Vertical cover shrub layer (%)	40.9	0	4.7	8.2
S3	Vertical cover lower canopy layer (%)	52.5	0	12.9	14.4
S4	Vertical cover upper canopy layer (%)	31.6	0	7.2	9.6
CI	Cover Index	651.6	34	211.8	163.8
TOPHT	Top height (m)	32.9	2.1	15.4	7.5
HTLC	Height to live crown (m)	17.9	0	7.5	5.1
MBA	Mean basal area ($m^2 ha^{-1}$)	60.0	0	27.7	15.7
LAI	Leaf Area Index	10.2	0.5	2.7	1.9
TREESP	No. of tree species per plot	9	1	3.5	2.2
AGE	Crop age (years)	238	6	59.6	49.8

[a] Data are mean values per 1 ha plot; SD, standard deviation

combinations of environmental variables (Ter Braak and Prentice, 1988). The relative contribution of the environmental variables to the ordination axes can be inferred by the signs (+ or −) and the relative magnitude of the canonical coefficients (Ter Braak, 1992). Separate CCAs were carried out for lichens, mosses and liverworts recorded on deadwood (in all plots including oak). Species recorded on other substrata were excluded as no quantitative information on abundance was gathered for these. Plots with very low species counts were excluded from the analyses as these can have a disproportionate effect on the results (Ter Braak, 1992).

3. Results

3.1. *Differences in species-richness of lichen and bryophyte communities between planted and semi-natural stands (all substrata combined)*

Altogether, 202 lichen and 111 bryophyte species were recorded (Table 3). The highest plot count for lichens was 67 (Taynish mature oak—plot 15.3) and the lowest, 0 (Clipstone mid-rotation and mature Corsican pine—plots 12.2 and 12.3). For bryophytes, the corresponding figures were 36 (Taynish and Beasdale mature oak—plots 15.3 and 16.3) and 3 (Glen Affric mature Scots pine—plot 1.3). Over 42% of lichen and 31% of bryophyte species were recorded only once (Table 3) and no single species of either group was recorded in all plots. The most commonly recorded lichen genera were *Cladonia* (25 species); *Parmelia* s. lat. (14 species); *Pertusaria* (nine species) and *Lecanora* (eight species). The most common species were: *Cladonia coniocraea* (40 plots); *Hypogymnia physodes* (37 plots); *Cladonia chlorophaea* s. str. (24 plots); *Cladonia squamosa* (28 plots) and *Lepraria incana* s. lat. (27 plots). The main bryophyte genera were: *Dicranum, Calypogeia, Plagiothecium* and *Polytrichum* (four species in each) and the highest plot count for individual species: *Hypnum cupressiforme* s. str. (48 plots); *Dicranum scoparium* (37 plots); *Eurhynchium praelongum* (31 plots); *Polytrichum formosum* (30 plots); *Plagiothecium undulatum* (29 plots).

Table 3
Lichen and bryophyte data combined for all sites[a]

	Lichens	Mosses	Hepatics	Total
Species count all substrates	202	71	40	313
Species count deadwood	106	51	26	183
RDB species	1	0	0	1
NIEC species	43	N/a	N/a	43
RIEC species	24	N/a	N/a	24
Mean species count/plot	15	11	4	30
Max species count/ plot	67	23	13	103
Min species count/plot	0	2	0	7
Species recorded only once	83	18	15	116
Species recorded in $>50\%$ of plots	6	5	1	12

[a] RDB, Red Data Book species (Church et al., 1996). NIEC, New Index of Ecological Continuity (Rose, 1993); RIEC, Revised Index of Ecological Continuity (Rose, 1976). Mosses and hepatics were combined for subsequent analyses. N/a, not applicable.

Lichen species counts were significantly higher ($P<0.01$) in the native oak and foothills Scots pine stands than in the other crop types (Fig. 1). Species counts were particularly high in the mature upland oak stands (Taynish and Beasdale, Table 1) and in the overmature foothills Scots pine plots (Glen Affric and Strathspey, Table 1). These stands also had a higher proportion of species occurring on substrata other than deadwood. Lichen species-richness was positively correlated with stand age (Table 4), and negatively correlated with the vertical cover index (CI), height to live crown (HTLC) and Leaf Area Index (LAI). High values

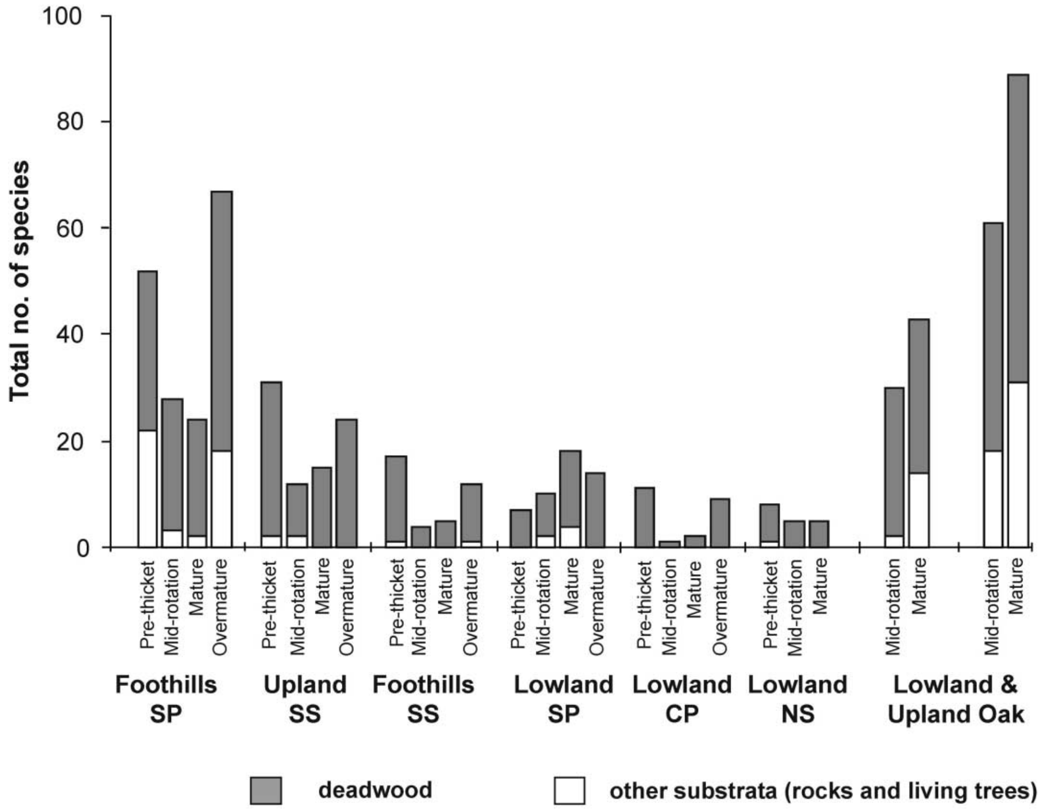

Fig. 1. Total number of lichen species recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak within different climate zones.

for these latter three parameters indicate stands with dense, well-developed, tall canopy layers. There were no significant differences in bryophyte species-richness between planted and semi-natural stands (Fig. 2), nor any effects of stand or climate variables (Table 4).

3.2. Conifer stands only: effects of crop type, stand structure and deadwood on the species-richness of lichens and bryophytes recorded on deadwood

Within the conifer stands, the vast majority of the lower plants recorded were found on deadwood (Figs. 1 and 2). The total number of deadwood pieces sampled was 699, with the highest numbers in the Sitka spruce stands (Table 5). Snag frequency was particularly low in the lowland Corsican pine stands, whilst stump frequency was lowest in the Foothills Scots pine stands (Table 5). Crop type (combining species and bioclimatic zone) was the most significant factor ($P<0.01$) influencing both lichen and bryophytes species counts on deadwood. For lichens the ranking was (Fig. 1): Foothills Scots pine > Upland Sitka spruce > (Foothills Sitka spruce and Lowland Scots pine) > (Lowland Corsican Pine and Lowland Norway spruce) ($P<0.01$). A contrasting pattern was recorded for bryophytes, with the ranking being (Fig. 2): (Upland Sitka spruce, Lowland Norway spruce and Foothills Sitka spruce) > (Lowland Corsican pine and Lowland Scots pine) > Foothills Scots pine ($P<0.01$).

Table 4
Pearson correlations between soil, climate and stand structure variables, lichen and bryophyte species-richness[a]

	Bryophytes (total species count. ha^{-1}	Lichens (total species count ha^{-1}
AT	0.05	−0.24
MD	−0.06	−0.33*
S1	−0.13	−0.08
S4	0.18	−0.31*
CI	0.10	−0.45**
HTLC	−0.14	−0.45**
MBA	0.04	−0.33*
LAI	0.05	−0.39**
TREESP	0.26	0.14
AGE	0.26	0.61**
Bryophytes (total species count ha^{-1})	–	0.47**
Lichens (total species count ha^{-1})	0.47**	–

[a] Species counts are for all substrata. Key to climate and stand variables in Table 2.
* $P<0.05$
** $P<0.01$

Stand stage also had a significant effect on deadwood species-richness, with pre-thicket plots having higher

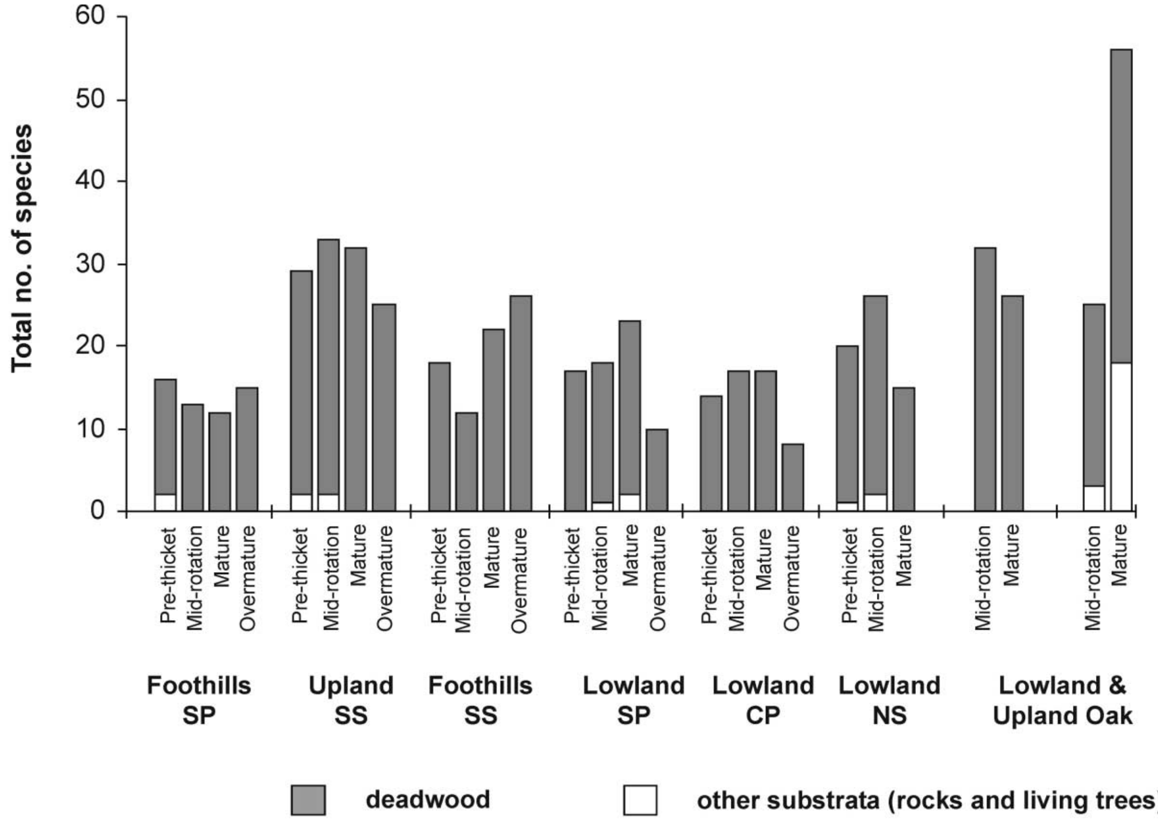

Fig. 2. Total number of bryophyte species (mosses and liverworts) recorded in different stand growth stages of Scots pine, Corsican pine, Sitka spruce, Norway spruce and oak within different climate zones.

lichen counts than over-mature plots followed by mature then mid-rotation plots ($P<0.01$). The difference in bryophyte species-richness between stand stages was less marked. There were significant differences in the value of different types of deadwood for lichens and bryophytes (Fig. 3). Stumps and logs had lower lichen species counts than snags ($P<0.01$), but higher bryophyte counts ($P<0.01$). Bryophyte species-richness was positively related to increasing diameter of logs and to decay class (Fig. 4a), with classes 4 and 5 having significantly higher species numbers than classes 1, 2 and 3 across all deadwood types. There was no significant effect of increasing snag diameter on lichen species-richness, but the relationship with decay class was highly significant (Fig. 4b). Classes 3, 4 and 5 were more species-rich than classes 1 or 2 ($P<0.01$).

Table 5
Total number of deadwood pieces recorded in the different crop types (excluding oak), combining all stand classes

	Stumps	Logs	Snags	Total
Foothills Scots pine	9	23	34	66
Lowland Scots pine	31	49	15	95
Upland Sitka spruce	29	83	89	201
Lowland Norway spruce	28	43	14	85
Foothills Sitka spruce	38	59	76	173
Lowland Corsican pine	22	53	4	79
Total	157	310	232	699

3.3. All stand types: differences in the species-composition of lichen and bryophyte communities recorded on deadwood

Separate CCAs were carried out for lichens and bryophytes. In both cases multi-collinearity was recorded between the vertical cover index (CI) and other variables, so the CI was not included in the analyses.

The first two axes of the lichen CCA (Fig. 5a) accounted for 15.7 and 10.4% of the variability in the data respectively. The eigen values were 0.41 for axis 1 and 0.27 for axis 2. Axis 1 of the ordination separated foothills Scots pine, upland oak and Sitka spruce from lowland Scots pine, oak, Corsican pine, Norway spruce and foothills Sitka spruce and was strongly correlated with accumulated temperature (AT) and moisture deficit (MD) and to a lesser extent with height to live crown (HTLC), Leaf Area Index (LAI) and upper canopy vertical cover (S4). However, there were exceptions to this general trend, with plot 7.2 (Dean mid-rotation Norway spruce) located well to the left on axis 1. The lowland and upland oak plots (characterised by a number of *Parmelia* spp. such as *P. saxatilis*, *P. caperata*, *P. sulcata* and *P. laevigata*) were grouped at the upper end

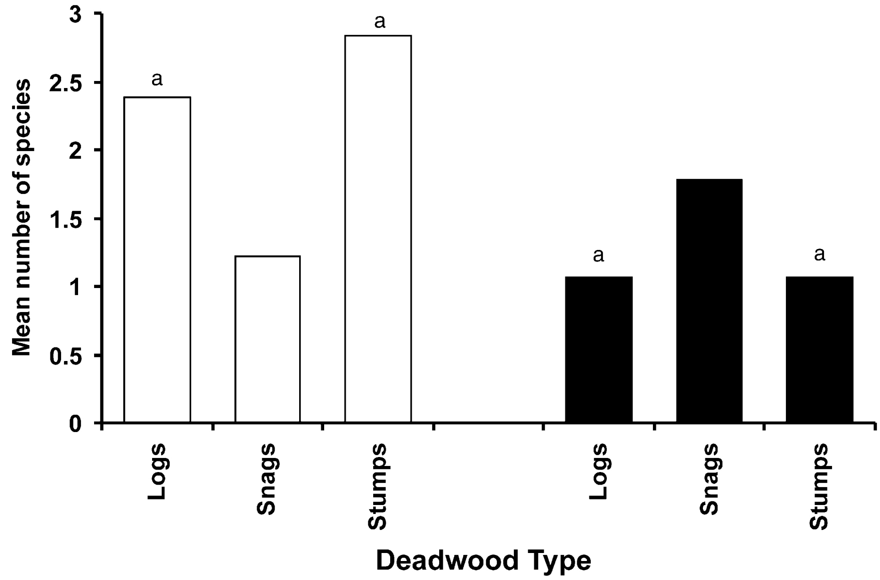

Fig. 3. Mean number of bryophyte (open bars) and lichen (filled bars) species recorded on different types of deadwood (all crop and stand types combined). Bars annotated with different letters are significantly different at the $P<0.05$ level (within each taxonomic group).

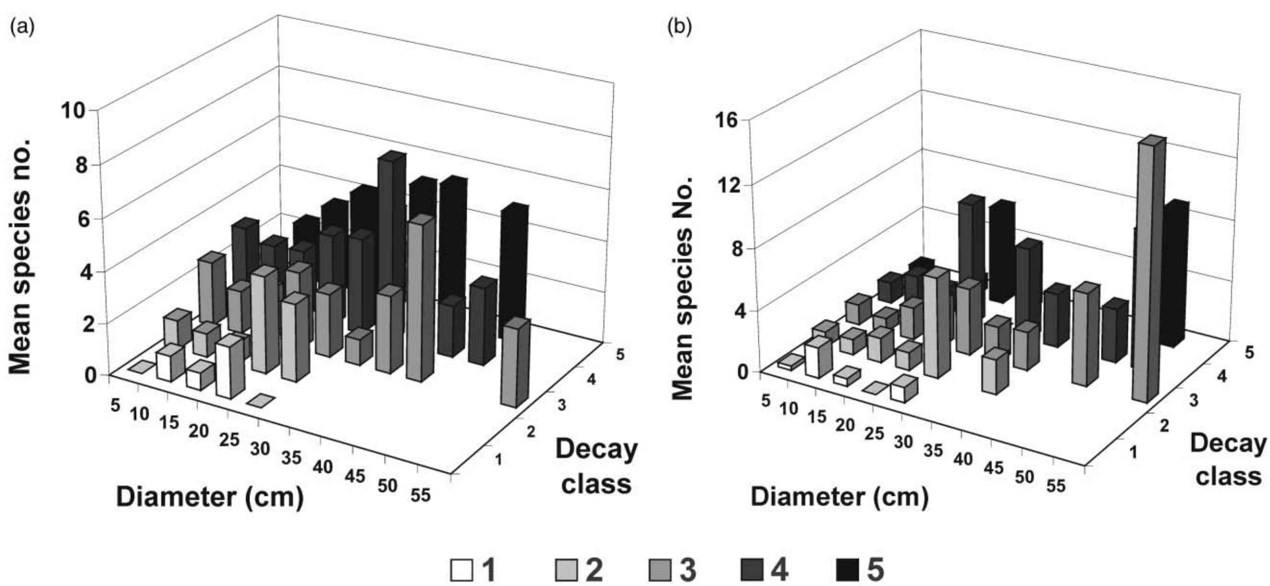

Fig. 4. Mean number of bryophyte species recorded on different sizes and decay stages of logs (a); mean number of lichen species recorded on snags (b). Data combined for all crop and stand types.

of axis 2, with the pre-thicket spruce and pine plots (characterised by *Cladonia* spp. such as *C. macilenta*, *C. portentosa* and *C. polydactyla*) grouped towards the lower end. Axis 2 was strongly correlated with tree age (AGE), the number of tree species in the canopy (TREESP) and upper canopy cover (S4). A negative correlation was recorded with field layer vertical cover (S1).

Axis 1 of the bryophyte CCA (Fig. 5b) accounted for only 10.4% of the variability in the data, and axis 2, 6.8%. (Fig. 5b). The eigen values were 0.29 and 0.19 respectively. Most of the upland and foothills plots were grouped towards the lower end of axis 1 which was negatively correlated with MD, AT and tree species-richness (TREESP). The foothills Scots pine plots were characterised by species such as *Pleurozium schreberi*, *Hylocomium splendens*, and *Rhytidiadelphus loreus*. In contrast, species such as *Brachythecium rutabellum, Eurynchium praelongum* and *Dicranoweisa cirrata* were more abundant in the lowland plots. Axis 2 separated the foothills Sitka spruce plots from the upland Sitka spruce and oak plots and was negatively correlated with measures of vertical canopy cover (S4, S3). Positive correlations were recorded with age and TREESP. The

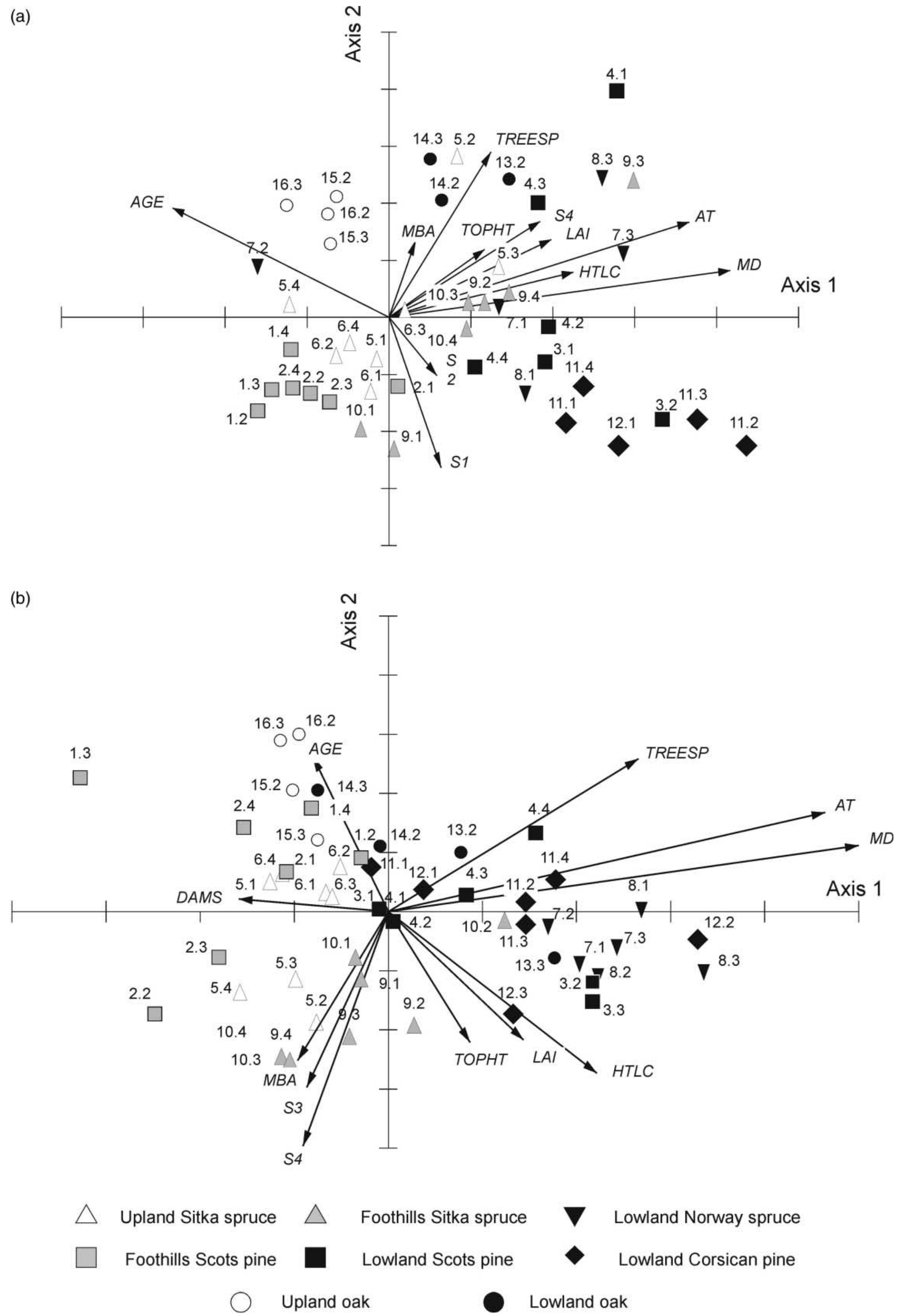

Fig. 5. Canonical correspondence analysis of assessment plots based on: (a) lichen species composition, (b) bryophyte species composition. In both cases axis 1 of the ordination is plotted against axis 2. Plots with very low numbers of epixylic species were omitted. Data labels for plots are coded as per Table 1. Numbers preceding the decimal point refer to sites, numbers after the decimal point refer to stand stage (1—pre-thicket; 2—mid-rotation; 3—mature; 4—over-mature). The stand and climate variables are depicted by arrows, the key to these variables is in Table 2.

upland oak plots had a distinctive bryophyte flora comprising species such as *Isothecium myosuroides*, *Thuidium tamariscinum*, *Bazzania trilobata*. *Plagiothecium undulatm, Plagiomnium undulatum* and *Nowellia curvifolia* dominated the foothills spruce stands, whereas the upland spruce stands contained liverworts such as *Frullania dilatata, F. tamarisci* and *Lejeunea cavifolia* .

3.4. Species of conservation importance

One Red Data list lichen species were recorded: *Bryoria furcellata* (Glen Affric, over-mature Scots pine—plot 1.4). The number of NIEC (New Index of Ecological Continuity—Rose, 1993) lichen species recorded was 43, and the number of RIEC (Revised Index of Ecological Continuity—Rose, 1976) species, 24 (Table 3). These indices give a measure of long-term continuity of woodland conditions at the stand level and of habitat quality for uncommon species (Rose, 1993). However, their relevance is restricted to lowland Britain south of Galloway in southern Scotland (Rose, 1992). The only sites with NIEC or RIEC species falling into this zone were: Alice Holt oak (2 species); New Forest oak (10 species) and New Forest Scots pine (2).

4. Discussion

4.1. Differences in the species-richness of lichen and bryophyte communities between planted and semi-natural stands (all substrata)

Similar distribution patterns were observed in both the lichen and bryophyte species count data. A high percentage of species were recorded only once, and very few species were common to more than half the plots. This "local rarity" phenomenon has been noted in other studies (e.g. Vitt et al., 1995; Collins and Glenn, 1997; Qian et al., 1999; Humphrey et al., 2000), and is partly related to sampling area. It is possible that the 1-ha sampling plot used is too small to capture a representative sample of lower plant diversity in forest stands. Rose (1993) recommends a minimum sampling area of 1 km^2, but again this depends on the objective of the survey. In our case, the objective was to make comparisons between a wide range of different stands types, all of which were less than 1 km^2 in size.

The semi-natural pinewood and oak stands had richer lichen communities compared to the planted stands, with the highest counts recorded in upland oak. The significant correlations recorded between lichen species-richness and measures of stand structure provide some evidence of the possible causative environmental variables. Both the semi-natural oak and pine stand types are characterised by a high abundance of old, large trees, a relatively open canopy structure (low values for S4, HTLC, and LAI—see Table 3), a long-continuity of woodland cover, and historically low levels of sulphurous pollution. All of these factors are known to be very important for maintaining lichen diversity both in British forests (Rose, 1993; Fletcher, 1999) and overseas (e.g. Hazell et al., 1998; Crites and Dale, 1998), but are much less crucial for maintaining bryophyte diversity; hence the lack of difference in species-richness values between planted and semi-natural stands. Both the upland Sitka spruce sites (Clunes and Knapdale) had comparable numbers of bryophyte species to those of the mid-rotation semi-natural oakwood stands.

The significant correlation between stand age and lichen species-richness substantiates the importance of old trees, and related factors, as a habitat for lichens (Hodgetts, 1996). In the oak stands there was a distinctive group of lichen species associated with the bark of the trunks of old trees which was not found in any of the other stands. These were the *Lobaria, Parmelia* and *Pertusaria* spp. The *Lobarion* community is considered to be a "climax" community in western European deciduous forests and although it appears able to maintain itself in the very limited number of sites where it still occurs when left undisturbed, it seems to have little or no ability to colonise new sites, particularly in more fragmented lowland landscapes (Rose, 1993). In north-west Britain, the *Lobarion* community on old trees can often be replaced, as a "climax" community, by the *Parmelion laevigatae* community, especially in high rainfall areas where bark pH is lowered by constant leaching. In Scandinavian boreal forests the *Lobarion* community is restricted to aspen and willow stands (Kuusinen, 1994; Hedenås and Ericson, 2000), with late successional stands being particularly rich (Hazell et al., 1998).

4.2. Conifer stands only: effects of crop type, stand structure and quality and size of deadwood on the species-richness of lichen and bryophyte communities on deadwood

Within the planted stands, there was a strong influence of decreasing moisture deficit on lichen species-richness with northern and western stands (upland Sitka spruce, and foothills Scots pine) being richer than more southerly stands. Southern stands (e.g. Thetford) tend to be drier, have been more affected by pollution in the past (Hitch and Lambley, 1996), and are more remote from sources of diaspores. In contrast to the lichens, bryophyte species-richness was related to crop type, with spruce stands being richer than pine stands regardless of climate zone. These differences in the value of different conifer crop types for lower plants have not previously been investigated in British forests, although there are parallels in Scandinavia where pine is generally considered a more notable habitat for lichens with spruce stands being more important for bryophytes (Esseen et al., 1997).

Low light levels are considered to be highly detrimental to lichen growth (Rose, 1992; Fletcher, 1999) which explains why stand structure had such a significant effect on lichen species-richness; mid-rotation and mature stages having lower species counts than the pre-thicket and over-mature stands. Under denser stand conditions, only the most shade tolerant of lichen species were recorded such as *Hypogymnia physodes* and *Cladonia coniocraea*. However, bryophytes were less affected by shading, and most spruce stands had a reasonable complement of deadwood species in all stand stages.

The results from the deadwood analysis confirm findings from Scandinavian boreal forests (Andersson and Hytteborn, 1991; Esseen et al., 1997; Kruys et al., 1999) that large diameter (>20 cm) decorticate (decay class 3 and above) deadwood provides a more valuable substrata for bryophytes than small diameter, corticate deadwood. The effect of size is in one sense obvious as large pieces of deadwood have a greater potential surface area available for colonisation (Bader et al., 1995). However, larger logs can hold more moisture than small deadwood pieces, they decay more slowly and provide a greater range of microhabitats (Samuelsson et al., 1994). In addition, larger logs are less likely to be overgrown by ground flora, thus providing freedom from competing vascular plant species or dense leaf litter (Crites and Dale, 1998; Kirby et al., 1998).

Intermediate to late decay classes provide additional elements of heterogeneity and hence more niches for different species (Kruys et al., 1999). Decay state is related to time since death, but also the longer a piece of deadwood remains undisturbed in situ, the more likely it is to be colonised (Crites and Dale, 1998), particularly by rare species with low powers of dispersal (Gustaffson and Hallingbäck, 1988; Söderström, 1988). Therefore it may not always be decay state per se which is influencing successful establishment. Although there are differences between forest types, the general consensus is that the diversity of epixylic lichens tends to peak at intermediate decay classes, while mosses and hepatics are more abundant in the final decay stages (Söderström, 1988; Esseen et al., 1997; Kruys et al., 1999). The results from our study tend to support this view; lichen species-richness was higher in decay classes 3–5 than in classes 1–2, whereas bryophyte richness was higher only in stages 4 and 5.

The finding that bryophyte species-richness was higher on logs and stumps, whilst snags were more important for lichens, also support observations from other countries. In Scandinavian mesic, and old growth swamp forests dominated by Norway spruce, logs are not considered to be especially important as lichen habitat (Ohlsson et al., 1997). Bryophytes (particularly hepatics) appear to dominate successional processes on spruce logs in these moist stands, whereas lichens are more common on standing dead trees (Holien, 1996; Kuusinen and Siitonen, 1998). In drier Scots pine-dominated boreal forest, both logs and snags are key habitats for crustose lichens (Esseen et al., 1997). It is possible, therefore, that humidity and soil moisture status (together with size and decay state) are the most important determinants of the relative value of logs for bryophytes and lichens, rather than tree species in itself, although all these factors co vary to some degree.

4.3. Differences in the species-composition of lichen and bryophyte communities on deadwood

The first axis of the lichen CCA is essentially a summation of the differences between northern and southern crop types. Axis 2 was positively correlated with canopy tree age, the number of tree species per stand and upper canopy vertical cover. The lowland and upland oak plots all have high values for these variables which explains why they are grouped at the upper end of the axis. Pre-thicket spruce and pine plots were grouped towards the lower end of axis 2. The negative correlation between this axis and field layer cover is relevant here, because it is known that these stands have a well developed field layer vegetation characterised by tall ericoid vegetation (Ferris et al., 2000). This vegetation supports a range of heathland lichens (e.g. *Cladonia glauca*, *C. gracilis*, and *C. uncialis* subsp. *biuncialis*) which together with the *Cladonia* spp. associated with deadwood in these stands, combine to create a lichen community which is distinctive from that of the other stands.

The foothills pinewood plots (sites 1 and 2) formed a distinctive grouping in the ordination. Lichen growth on living Scots pine trunks is rarely as luxurious as it is on oak, mainly because the pine bark has a low water capacity, a high rate of evapotranspiration (Barkman, 1958) and, under most circumstances, a lower pH than that of oak bark. Scots pine bark is also unstable and flakes off readily (Ahti, 1977; Fletcher, 1999) so the lichen communities are often rather fragmentary and temporary assemblages, and comprise species able to tolerate drier conditions such as *Bryoria*, *Usnea* and *Cladonia* spp. The most important substratum for lichens in native pinewoods is deadwood (Fletcher, 1999). Stumps and snags provide a key habitat for crustose species, and a number of these (e.g. *Calicium viride*, *Chaenotheca brunneola* and *C. trichialis*) were recorded on deadwood in the over-mature pine stands. Both pine and spruce deadwood is recognised as an important habitat for crustose lichens in Scandinavian boreal forest (Ahti, 1977; Esseen et al., 1997), and it is interesting to note that the upland Sitka spruce stands (particularly Clunes—site 6) share some of the species found in the native pinewoods (e.g. *Calicium viride, Cladonia glauca,* and *Cetraria chlorophylla*) and are located in a similar position on the ordination. The Clunes stands were planted on sites previously occupied by native pine and oak–birchwood (Hamilton, 1995) and Humphrey et al. (2000) have recorded a number of rare pinewood specialist fungi within these. It appears, therefore that site history may also be an important determinant of lichen, as well as macro-fungal diversity in planted stands.

As with the lichens, the first axis of the bryophyte ordination was positively correlated with AT and MD suggesting a north-south trend in changing species composition. The negative correlation between Axis 2, upper canopy cover (S4) and mean basal area (MBA), explains to some extent why over-mature pine plots (1.4, 2.4, 4.4) were grouped at the upper end of the axis with over-mature Sitka spruce plots (5.4, 9.4, 10.4) grouped at the lower end. The pine plots have an open parkland structure, with low canopy cover and basal area, whereas the spruce stands have a higher stem density (Ferris et al., 2000). Because of their open structure and dry microclimate, old-growth pine stands are not noted for their bryophyte flora (Fletcher, 1999) but even so, the Affric, Strathspey and Windsor plots were surprisingly species-poor. Interestingly, the Clunes Sitka spruce plots formed a distinctive grouping with the upland oak plots on axis 2, and shared many characteristic oakwood bryophytes such as the liverworts *Frullania dilatata*, *F. tamarisci*, and *Lejeunea cavifolia*. The occurrence of the pinewood moss *Ptilium crista-castrensis* at Clunes was also notable.

4.4. Species of conservation importance

Bryoria furcellata, the one Red Data list species recorded, is classed as "Vulnerable" in accordance with the revised IUCN categories of risk (World Conservation Union, 1994), and is a Wildlife and Countryside Act 1981, Schedule 8 species (Church et al., 1996). The low frequency of rare species records for lichens and bryophytes contrasts greatly with the findings of Humphrey et al. (2000) who recorded over 30 rare and threatened macro-fungal species within the same set of biodiversity assessment plots used for the lichen and bryophyte survey. The contrasting results are probably due, in part, to under-recording of fungi in the past, in comparison to the long history of intensive recording of lichens and bryophytes (e.g. Ratcliffe, 1968). However, the majority of rare fungi recorded were mycorrhizal and Humphrey et al. (2000) considered that spruce stands with their high rooting density might provide a suitable habitat for these fungi. Also, the key semi-natural woodlands for lichens and bryophytes were under-sampled in this survey, so it is perhaps not surprising that the count of rare species was quite low.

In both Britain and Scandinavia, epiphytic lichens have been used as indicators of forest continuity, and of habitats containing red-listed species (Rose, 1992; Tibell, 1992; Thor, 1998; Jonsson and Jonsell, 1999; Uliczka and Angelstam, 2000). Indices such as the Revised Index of Ecological Continuity (Rose, 1976) and the New Index of Ecological Continuity (Rose, 1993) have been developed to allow an assessment of long-term continuity of woodland conditions conducive to the maintenance and development of diverse lichen communities. As yet no such index had been developed for woodland bryophytes (Rose, 1993), as these appear to be more catholic in their habitat preferences, and are less restricted to ancient, undisturbed habitat (as borne out by this current survey). Although most of the NIEC and RIEC lichen species were recorded in native semi-natural stands (lowland oak), some were also recorded in the planted Scots pine stand in the New Forest. Like the other stands discussed earlier, this stand was established on an ancient woodland site, and it is likely that the species are relicts from the past land cover, although more recent colonisation cannot be discounted. Indices of ecological continuity are being developed for lichens of Scottish native woodlands and western woods, but as yet these are unpublished (P. Quelch, personal communication). Further analysis of the lichen data for the uplands and foothills will be undertaken once these indices are published.

4.5. Conclusions and management recommendation

Clearly, there is more scope for increasing the lower plant diversity of planted forests in the north and west of Britain than the south and east. The effects of pollution and habitat fragmentation have been more severe in the south and woodlands tend to be more isolated ecologically, except in areas such as the Dean or the New Forest. Also the wetter climate in northern Britain is more beneficial to lower plant growth in general, especially bryophytes (Fletcher, 1999). In this study, planted stands had significantly poorer lichen communities than the semi-natural stands, but bryophyte communities were similar in terms of diversity and composition [although falling short of the best examples of ancient oakwood bryofloras (Ratcliffe, 1968)]. Retaining small gaps, streams, and rides and encouraging the growth and survival of broadleaves within plantations will add significantly to the conservation of lower plant diversity. Saxicolous habitats such as rock outcrops, large boulders, old stone walls, etc. can also provide important habitats, and these should be kept free of dense shade (although some shading, preferably by broadleaved trees, will benefit bryophyte communities). Old posts, deer fences, etc. can also harbour a range of lichen species, and these can provide extra habitat in stands where standing deadwood is currently in short supply.

It is unlikely that the main non-native conifer species such as Sitka spruce and Norway spruce will ever develop an epiphytic lichen flora characteristic of native broadleaves such as oak, but there are indications that diversity might increase given time. In Scandinavia, old Norway spruce trees support a diverse range of lichens (Holien, 1996) and it has been suggested that extending the normal felling rotation in boreal stands to 120 years or more would promote the development of late successional epiphytic communities (Kuusinen and Siitonen, 1998). Spruce stands of such an age are rare in British forests, and the value of old spruce as a substratum for lichens remains to be tested. However, even if some stands were retained to 120 years or more before felling, this may not benefit epiphytic lichens in the long-term as many species are considered unable to tolerate drastic changes in light conditions and disappear in response to clearcutting (Berg et al., 1995). Also late successional species are renowned for their poor dispersal abilities (Rose, 1993), and may not be able to recolonise suitable stands when these become available.

A complementary strategy to the above might be to adopt a ''continuous cover'' approach to stand management (sensu Mason et al., 1999) where a diversity of tree age and structure is fostered within, rather than between, stands (Kerr, 1999). A number of silvicultural approaches for maintaining continuity of woodland conditions have been proposed based on the observed effects of natural disturbance (e.g. Fries et al., 1997; see also Quine et al., 1999 for a review). In Scandinavian Norway spruce forests which are not subject to large-scale disturbance by fire, gap-phase dynamics driven by windthrow predominate, and it has been suggested that irregular shelterwood or selection systems (e.g. single tree selection) may be the most appropriate silvicultural option in these stands for maintaining mature woodland conditions, old trees and deadwood (Fries et al., 1997).

The positive correlation between the species-richness of lower plant communities and the size and quality of deadwood fills an important gap in knowledge of the value of deadwood for biodiversity in British forests (Hodge and Peterken, 1998). It is important that continuity of deadwood supply is maintained so that there is no truncation in the delivery of the more valuable later stages of decay (Kruys et al., 1999). In north and west Britain, silvicultural systems such as irregular shelterwood or single-tree selection could have the potential to deliver supplies of large diameter (>20 cm) deadwood within stands, thus enhancing bryophyte diversity (Orange, 1998). However, this approach would not be so appropriate in areas at risk from catastrophic windthrow (Mason et al., 1999).

Much could be done in both pine and spruce plantations to increase their value for lichens of early successional forest stages. Snags, stumps and logs left after clear-felling can provide a key habitat for the Caliciales and Cladonias. Where the forest area is large enough to allow planning at the landscape scale, then a temporally continuous supply of this habitat type will be maintained through normal patch-clear felling, provided that some larger items (>20 cm diameter) are left permanently unshaded during re-stocking to form a reservoir of species for potential colonisation of future stands. This type of management approach is most appropriate where large-scale disturbance regimes are thought to be the dominant influence on forest structure, such as fire in the eastern Scottish highlands, and on exposed topographies where catastrophic windthrow is common (Quine et al., 1999).

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