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Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession

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ABSTRACT

Aim Lichen epiphytes are important for biodiversity conservation and are also widely applied as environmental indicators. However, biogeographical and ecological knowledge underpinning lichen epiphyte conservation, and the use of lichens as indicators, is based primarily on a limited range of ‘macrolichen’ species. Wider trends in epiphyte biodiversity remain largely unexplored. This paper examines the community structure of lichen epiphytes on aspen (*Populus tremula* L.) in Scotland, including species across all functional groups and comprising, therefore, taxonomically difficult ‘microlichens’.

Location Northern Britain (Scotland).

Methods Epiphytes were sampled from 12 sites throughout Scotland and examined at two scales: between and within aspen stands. Species were classified into contrasting functional groups and ordination by detrended correspondence analysis was used to summarize community structure.

Results Within aspen stands (between trees) epiphyte communities showed successional patterns related to tree age. These successional patterns changed predictably for stands aligned along a climatic gradient (between stands).

Main conclusions A dual climatic–successional trend in epiphyte community structure is presented. Large-scale trends in epiphyte diversity are explained as the local response of species with contrasting functional traits to climate and autogenic succession. Turnover of functional groups between stands is positively related to β -diversity, and ecological limits to the frequency of contrasting functional groups are presented. Accordingly, the study and application of lichen species with similar functional traits may inadequately represent patterns of biodiversity. This prompts criticism of the currently accepted conservation strategy, i.e. (1) an emphasis in the conservation literature on ‘macrolichen’ species with similar ecologies and (2) the application of lichen indices over climatically variable geographical areas.

Keywords

Aspen, β -diversity, biodiversity conservation, climatic gradient, community succession, functional ecology, indicator species, *Populus tremula*, Scotland.

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INTRODUCTION

There is an overwhelming bias in plant biogeography and ecology towards ‘vascular’ or ‘higher’ plants. Consequently, paradigms presented in key textbooks (Pears, 1985; Lomolino *et al.*, 2005) represent a consensus of evidence that is limited in its scope to an estimated 14% of the world’s ‘botanical’

biodiversity (e.g. including plant and fungal species, based on estimates of global richness in Hammond, 1995). Given the modern emphasis on biodiversity conservation (Heywood, 1995; Gaston & Spicer, 2004), and the importance of biogeographical research in tackling major conservation issues, it is critical that biogeographical studies include diverse, though often neglected, components of the world’s biota

(cf. Clark & May, 2002; Klironomos, 2002). Lichens are one example of a biological group that is often neglected in mainstream biogeographical and ecological study. Lichens are extremely biologically diverse (Galloway, 1992; Hawksworth, 2001), and functionally important in terrestrial ecosystems (Knops *et al.*, 1991, 1996; Arseneault *et al.*, 1997). While an ecological understanding of lichen diversity (including macro- and microlichens) is essential for effective conservation, spatiotemporal investigations, providing the link between pattern and process in higher plant communities (Watt, 1947; Gratzner *et al.*, 2004), are severely lacking for lichens. This paper presents an empirical study examining spatiotemporal variation in the structure and function of lichen epiphyte communities, therefore expanding the biogeographical knowledge base and providing an ecological framework for the conservation of epiphyte diversity.

Lichen epiphytes are an important theme in forest ecology and conservation biology, being both biologically diverse (Galloway, 1992; Dietrich & Scheidegger, 1997) and functionally important in forest ecosystems (Slack, 1988; Knops *et al.*, 1991, 1996; Pettersson *et al.*, 1995; Gunnarsson *et al.*, 2004). The sensitivity of lichen epiphytes to environmental change (Ferry *et al.*, 1973; Rose, 1988; Lesica *et al.*, 1991; Gu *et al.*, 2001; Pykälä, 2004) has resulted in their wide use as indicators for pollution monitoring (Hawksworth & Rose, 1970) and to identify forest habitats for biodiversity protection (Rose, 1976; Tibell, 1992; Selva, 1994). Despite their conservation importance and application as environmental indices, comparatively little research has addressed the ecological processes controlling lichen epiphyte diversity. An inadequate understanding of the response of lichen species to spatial and temporal dynamics of forest habitats has therefore weakened the effectiveness of biodiversity protection (Coppins, 2003) and prompted scientific criticism of lichen indices (Rolstad *et al.*, 2002). A particular limitation of previous ecological studies has been a tendency to focus on a relatively small selection of 'macrolichens' with similar functional traits (Gustafsson & Eriksson, 1995; Gauslaa *et al.*, 1998; Ulicza & Angelstam, 1999; Campbell & Coxson, 2001; Werth *et al.*, 2005). Contrastingly, 'microlichens' contribute most to epiphyte diversity but are seldom included in ecological studies [c. 77% of the 1830 species included in the British lichen checklist (Coppins, 2002) are crustose microlichens; cf. also Dietrich & Scheidegger, 1997]. While macrolichens may have the advantage of being easily sampled and identified, the study of species with similar traits and their subsequent application in identifying areas for conservation (e.g. foliose lichens with a cyanobacterial algal partner; Kuusinen, 1996; Hedenås & Ericson, 2000; Gu *et al.*, 2001; Campbell & Fredeen, 2004; Gaio-Oliveira *et al.*, 2004), potentially neglects key ecological processes contributing to the maintenance of epiphyte species richness. Recent research has confirmed that species co-existence, and, consequently, diversity measured at a given scale, may be dependent on the different functional traits of individual species (McKane *et al.*, 2002; Cavender-Bares *et al.*, 2004; Thuiller *et al.*, 2004). Ecological studies of lichen epiphytes, relevant to biodiversity

conservation and the interpretation of indices, may therefore benefit from a more inclusive approach incorporating species with a wider range of divergent traits (e.g. reproductive strategy, growth form or algal partner).

This paper describes a study to examine trends in the regional diversity of lichen epiphytes on aspen (*Populus tremula* L.) in Scotland. It is important in addressing the response of species across all functional groups (i.e. both macro and microlichens) to climate and successional processes maintaining large-scale patterns of diversity. The study examined epiphyte communities at two scales (i.e. between and within aspen stands), and incorporated often neglected, though highly species-rich, crustose microlichens. The examination of a wider range of epiphyte species with contrasting functional traits provides new insights into the spatiotemporal dynamics maintaining lichen diversity. Implications for biodiversity protection and subsequent limits to the application of lichen indices are suggested. The results are directly relevant to the conservation of aspen epiphytes and contribute to a better understanding of the epiphyte response to habitat dynamics, essential to the long-term maintenance of forest biodiversity.

METHODS

Study sites

Twelve study sites comprised single-clone aspen stands located throughout Scotland, though north of a broad region of airborne SO₂ pollution (NEG-TAP, 2001) (Fig. 1). To reflect

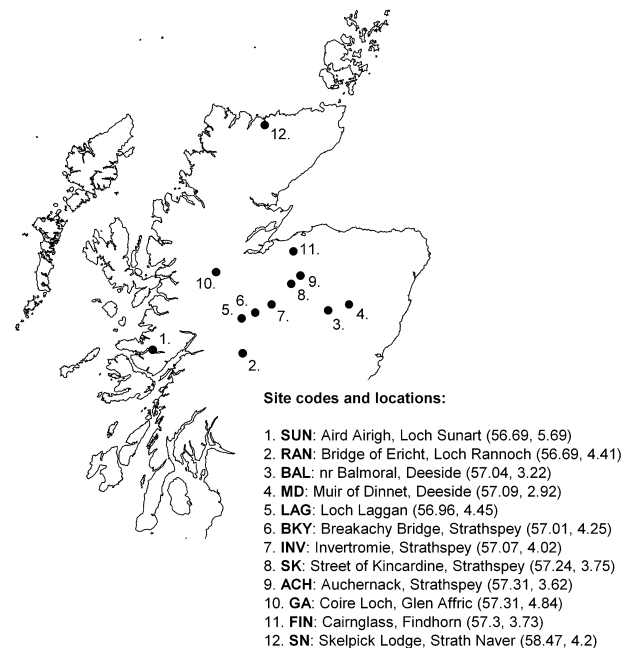


Figure 1 Location of the 12 aspen stand study sites in Scotland. Sites are named, identified by an abbreviated code and positioned (WGS84: lat., long.).

possible biogeographical variation in epiphyte communities, aspen stands were sampled across a steep climatic gradient, i.e. from the most oceanic site at Loch Sunart (SUN, Fig. 1; annual rainfall 2245 mm, minimum mean monthly temperature 4.1 °C) to more continental sites in north-east Scotland (e.g. BAL, Fig. 1; annual rainfall 830 mm, minimum mean monthly temperature -0.5 °C). All stands occur in a historically well-wooded landscape (Roberts *et al.*, 1992), were of the same approximate structure (i.e. slope, aspect and density of trees) and comprised trees of mixed age.

A suite of climate variables was made available for each aspen stand using UK Met Office gridded data sets (Perry & Hollis, 2005): estimated monthly and annual climatic averages for: (1) number of days with rainfall > 1 mm, (2) average, maximum and minimum temperatures (°C) and (3) precipitation (mm). Estimated climate data are the verified averages derived for 5-km grid squares using inverse distance-weighted interpolation of multiple regression residuals, based on point data for the period 1961–2000 at 540 and 4400 monitoring stations across the British Isles (temperature and precipitation, respectively). Individual variables were correlated within though not between parameters (i.e. temperature vs. precipitation) (Table 1).

Field methods

The study aimed to sample trees of different age within each of the 12 aspen stands. Because of their clonal growth by suckering, individual aspen trees within a stand tended to fall into discrete size classes, which corresponded broadly to their age determined by dendrochronology (Ellis, unpubl. data). At seven of the sites, trees could be recognized in three separate age classes, though at five sites trees occurred in two age classes only. Accordingly, at each of the 12 study sites, the community of lichen epiphytes was quantified for either two or three trees of contrasting age. To ensure comparability between sites, sampled trees were subjectively selected to ensure that: (1) each was growing vertically and that the bark surface was not subject to aberration, e.g. by wounding, branching etc., and (2) that the distance between a sampled tree and its neighbours was approximately similar (i.e. mean distance and 1 SE, 455 ± 48 cm), therefore avoiding isolated or crowded (cf. shaded) individuals.

The lichen community of each tree was quantified in a series of 6 × 6 cm quadrats (comprising nine 2 × 2 cm subunits),

positioned at 20 cm intervals along a linear transect that spiralled around the bole. The transect incorporated the shortest distance between ascending nodes marked on opposite sides of the bole at 0, 100 and 200 cm (side *x*) and 50 and 150 cm (side *y*). Lichen species were recorded in the field as presence–absence in each of the nine subunits. A bark sample (c. 2 × 2 cm) was collected from each of the quadrats, incorporating unidentified taxa.

The surface area of the tree bole was estimated for the region between the lowest and highest quadrats (approximating the bole as a series of cylinders), and compared with the sampled quadrat area using simple linear regression (GenStat v. 7.1; VSN International Ltd, Oxford, UK, 2003). A core was collected from each of the sampled trees using a Presler-type increment borer. The tree was bored at a level height of 1 m, the core extracted and placed into an open-ended plastic tube which was labelled and sealed.

Herbarium examination

Bark samples were examined in the herbarium to confirm critical field identification. Identification of specimens was using standard light microscopy at ×6–×40 (Meiji EMZ-TR), ×100, ×400 and under oil at ×1000 (Meiji ML-2300) and standard chemical spot tests with K, C and Pd (Orange *et al.*, 2001). Lugol's iodine was used to stain ascoma tissue where necessary (Orange *et al.*, 2001). The identification of equivocal sterile crusts was confirmed using thin-layer chromatography with solvent systems A and G (Orange *et al.*, 2001). Taxonomic nomenclature follows Coppins (2002).

The age of the trees was estimated using dendrochronology. The tree cores were sanded (180-grain sandpaper) to expose a plane surface. Cores were then stained by immersion first in a solution of 1% phloroglucinol and 95% ethyl alcohol for 1 min and second in 50% aqueous hydrochloric acid for c. 30 s, before rinsing under tap water. Tree rings were counted at ×6–×40 (Meiji EMZ-TR).

Statistical analysis

Species abundance

Frequency of occurrence (% *fo*) of lichen species was calculated for trees sampled in each aspen stand (trees combined) and, within each stand, for individual aspen trees:

Table 1 Correlation matrix for five climate variables examined in the study (product–moment correlation coefficient, *r*)

	Days > 1 mm	Average temp.	Max. temp.	Min. temp.	Precip. (mm)
Days > 1 mm	1				
Average temp.	0.127	1			
Max. temp.	-0.143	0.932***	1		
Min. temp.	0.253	0.977***	0.841***	1	
Precip. (mm)	0.794**	0.487	0.293	0.544	1

P* < 0.005, *P* < 0.001 (with 10 d.f.).

n = 12.

$$\%fo = \left(\frac{100}{tq_i} \right) \times n_i$$

where tq_i is the total number of quadrat subunits examined on tree/in stand j and n_i is the number of subunits from which species i was recorded. Prior to statistical analysis, values of per cent frequency of occurrence were log-transformed, after adding 1 to all data points, to improve normality in the data and equalize the relative importance of rare and common species.

Classification of epiphyte functional groups

Lichen epiphytes were classified into six non-reproductive functional groups, based on the photosynthetic partner and growth form (cf. Hale, 1983): (1) green-algal fruticose, (2) cyanobacterial foliose, (3) tripartite foliose (green-algal and cyanobacterial), (4) green-algal foliose, (5) green-algal crustose and (6) leprose. Given their expected effect on lichen species and communities, bryophytes (mosses and liverworts combined) were also included in the analysis of functional groups. The frequency of contrasting functional groups was compared for individual trees using the product–moment correlation coefficient, r (GenStat v 7.1).

Epiphyte community structure – comparison between stands

A combined ordination of epiphyte communities (sample scores for different aspen stands) and their component species was calculated for the data set by detrended correspondence analysis (DCA), implemented using the program PC-Ord (McCune & Mefford, 1999). Axes were rescaled using 26 segments and rare species were not downweighted. The efficiency of DCA ordination was estimated as the eigenvalue for each axis and the per cent variation explained of the original n -dimensional data set. The first three orthogonal axes were compared with the five climate variables simultaneously, using multiple regression implemented as a general linear model (GenStat v 7.1). Stand scores along a given DCA axis were included as the response variable, with climate data as the explanatory variables. Stepwise selection was used to identify a reduced set of climate variables, optimally explaining the distribution of epiphytes. The analysis successfully identified a single dominant environmental gradient. Trends in the occurrence of lichen epiphyte species, previously classified into the six functional groups, were examined by indirect comparison with DCA axes using vector analysis (McCune & Mefford, 1999; McCune & Grace, 2002).

Epiphyte community structure – comparison within stands

The occurrence of contrasting epiphyte functional groups was plotted for individual trees of different age, from stands aligned along the primary environmental gradient identified by DCA (Fig. 2). Successional change was examined using one-way analysis of variance (GenStat v 7.1) to compare the

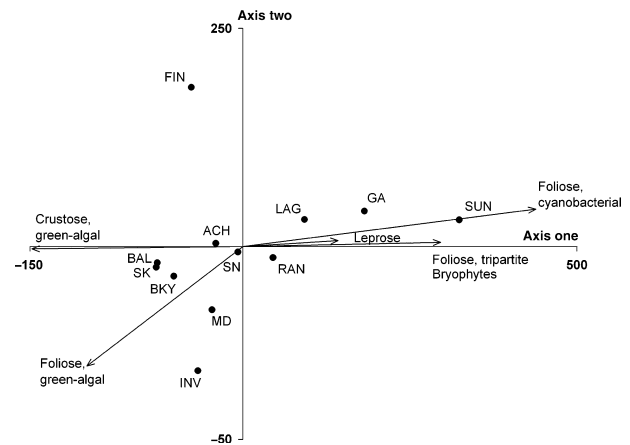


Figure 2 Ordination diagram for the comparison by DCA of epiphyte communities between aspen stands (refer to Fig. 1 for site abbreviations and Table 2 for statistical results). Epiphyte functional groups were compared indirectly to DCA axes and are included as vectors.

occurrence of a functional group between trees of contiguous age within a given stand, though combining comparisons for all stands simultaneously. The least significant difference at a 5% level was used to determine significance between contrasting functional groups.

β-diversity and epiphyte functional groups

Functional turnover among lichen epiphyte communities was compared with β-diversity between aspen stands. β-diversity (i.e. species turnover between stands) was estimated using Sørensen’s coefficient, describing the similarity between stands in the species they support (Magurran, 2003):

$$S_s = \frac{2a}{(2a + b + c)}$$

where a is the total number of species present in both stands i and j , b is the number of species present only in stand i and c is the number of species present only in stand j . A matrix of similarities was calculated to compare all stands. The stand lying to the extreme of the primary environmental gradient (Fig. 2) was chosen as a starting node, and subsequent stands aligned consecutively along a gradient of similarity. The contribution of contrasting functional groups was calculated for each stand as a proportion (Fp):

$$Fp_{ij} = \left(\frac{100}{\sum fo_i} \right) \times \sum fo_j$$

where $\sum fo_i$ is the sum of per cent frequencies for all lichen species in stand i and $\sum fo_j$ is the sum of per cent frequencies for lichen species in functional group j .

Turnover of functional groups (Tf) was calculated as a difference in the proportion of functional groups between stands aligned along the similarity gradient:

$$Tf = (Fpx_1i - Fpx_2j) + (Fpy_1i - Fpy_2j) + \dots$$

where Fpx_1i represents the proportion of functional group x_1 in stand i , Fpx_2j is the proportion of functional group x_2 in stand j , Fpy_1i is the proportion of functional group y_1 in stand i and Fpy_2j is the proportion of functional group y_2 in stand j , etc., holding x_1 greater than x_2 and y_1 greater than y_2 , to yield positive values. β -diversity measured between stands along the gradient in similarity (S_s) was compared with the corresponding turnover in functional groups using simple linear regression (GenStat v. 7.1).

RESULTS

Quadrat sampling

One hundred and thirty-eight lichen species (*c.* 40% of lichen species known to occur on aspen in Scotland; Coppins and Ellis, unpubl. data) were recorded from 404 quadrats (3636 subunits) sampled from 31 trees at the 12 sites (Appendix 1). There was a significant positive relationship between the area sampled using the spiral transect quadrat method and the surface area of the lower tree bole: $R^2 = 0.77$, $P < 0.001$ with 29 d.f. The implication is that the method effectively samples a subset of the epiphyte community from trees of different size, integrating the possible effect of spatial area on community richness.

Community structure

Variation in epiphyte communities between aspen stands was well summarized by DCA axis one, pointing to a single major underlying trend at this scale of analysis (Table 2). Accordingly, days per year with > 1 mm of precipitation significantly explained axis one scores (Table 2). Aspen stands are therefore aligned along axis one from those in wetter localities, towards the right of the axis (SUN $>$ GA $>$ LAG $>$ RAN), to a cluster of stands from drier localities positioned to the left of the axis (Fig. 2). Indirect comparison of epiphyte functional groups demonstrates shifts in their occurrence along the climatic gradient (Fig. 2). Foliose cyanobacterial and tripartite lichens and bryophytes increase in frequency in climatically wetter stands. Leprose green-algal lichens also increase along a gradient of increasing wetness, though to a lesser extent. Contrastingly, foliose and crustose green-algal lichens increase in frequency in climatically drier stands. Fruticose lichens had

no relationship with the DCA axes. The ordination was supported by a correlation matrix demonstrating: (1) significant positive correlations between foliose cyanobacterial and tripartite lichens and bryophytes and (2) significant negative correlations between crustose lichens and foliose cyanobacterial and tripartite lichens and bryophytes (Table 3). Considering all lichen functional groups, β -diversity was significantly positively related to turnover in the proportion of functional groups between aspen stands, i.e. negatively related to similarity between stands (Fig. 3).

The occurrence of functional groups on individual trees from stands aligned along DCA axis one (cf. the climatic gradient, Table 2) points to co-varying within-stand trends in community succession (Fig. 4). The occurrence of all functional groups generally increases from younger to older trees within a stand, with the exception of crustose lichens, the occurrence of which decreases significantly between younger and older trees (tested using a one-way analysis of variance and least significant difference at the 5% level; $F < 0.001$ with 73 d.f.).

Considering both between- and within-stand trends (Figs 2 & 4), three distinct spatiotemporal patterns can be recognized:

1. foliose cyanobacterial, foliose tripartite lichens and bryophytes increase in frequency at climatically wetter stands, and, within stands, may increase in frequency on older trees,
2. foliose green-algal lichens become less frequent in stands from wetter localities, though within stands they may be generally more frequent on older than on younger trees,
3. crustose lichens become less frequent in stands from wetter localities, and within stands are generally more frequent on younger than on older trees.

DISCUSSION

The results of this study provide an important addition to previous research on spatiotemporal patterns in plant community structure (Watt, 1947; McCune, 1993; Gratzner *et al.*, 2004). We describe in the following discussion how the observed changes in epiphyte community structure might be explained by the local response of species with contrasting functional traits to climate (spatial variation, between stands) and autogenic succession (temporal processes, within stands). This spatiotemporal explanation of community structure has important implications for the protection of lichen diversity and the application of popular lichen indices.

Table 2 Results for the ordination of aspen epiphyte communities using DCA. Aspen stand scores (response variable) were compared with climate parameters (explanatory variables, Table 1) using general linear models with stepwise selection. Optimum solutions are shown

	Eigenvalue (% variation explained)	Multiple regression with stepwise selection			
		No. of variables	Selected variable(s)	R^2	F probability (P)
Axis 1	0.652 (24.2%)	1	Days $>$ 1 mm	0.833	$<$ 0.001 (10 d.f.)
Axis 2	0.237 (8.8%)	None: excessive residual variance (no statistical relationship)			
Axis 3	0.128 (4.7%)	None: excessive residual variance (no statistical relationship)			

Table 3 Correlation matrix for the frequency of epiphyte functional groups measured between aspen trees (product–moment correlation coefficient, r)

	Fruticose	Foliose, cyanobacterial	Foliose, tripartite	Foliose, green algal	Crustose, green algal	Leprose, green algal	Bryophytes
Fruticose	1						
Foliose, cyanobacterial	-0.194	1					
Foliose, tripartite	-0.213	0.723***	1				
Foliose, green algal	0.333	-0.295	-0.150	1			
Crustose, green algal	-0.039	-0.568***	-0.394*	0.133	1		
Leprose, green algal	-0.119	0.281	-0.046	-0.214	-0.294	1	
Bryophytes	0.075	0.515**	0.351*	-0.280	-0.858***	0.279	1

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$ (with 29 d.f.).

$n = 31$.

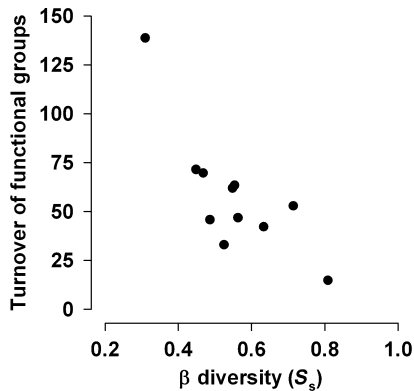


Figure 3 Comparison of β -diversity (i.e. Sørensen's coefficient of species similarity measured between stands, S_s) and the corresponding turnover of functional groups ($R^2 = 0.597$, $P = 0.003$ with 9 d.f.).

A climatic–successional gradient

The study demonstrates a climatic effect on the biogeographical distribution of epiphytes in Scotland. This trend appears to be more importantly related to climatic wetness (i.e. days per year with > 1 mm precipitation) compared with temperature (Table 2). Comparisons between functional groups demonstrate the contrast between species whose frequencies increase in aspen stands from wetter localities compared with species that are restricted to, or are increasingly frequent, in stands from drier localities (Figs 2 & 4). Patterns in the community structure of lichen epiphytes on aspen reflect therefore a general longitudinal gradient in climate across Scotland, from the wet and oceanic Atlantic seaboard to the drier and more continental north-east (Manley, 1962). However, frequencies of epiphyte functional groups are also related to the age structure of trees at a site, suggesting the inter-relationship along a major environmental gradient of both temporal and spatial shifts in community structure (Smith & Huston, 1989; McCune, 1993), i.e. a climatically mediated trend in epiphyte community succession. Accordingly, the epiphyte community of aspen trees from a stand in a drier climatic locality may become progressively more similar with increasing age to those of younger trees at wetter sites. This dual climatic–successional

gradient is manifest as a decrease (on older trees and/or in wetter localities) in the frequencies of green-algal and crustose lichens and a concomitant increase in the frequencies of bryophytes, tripartite and cyanobacterial foliose lichens (Figs 2 & 4). The pattern suggests that predictable limits to the distribution and frequency of epiphyte species may be imposed by constraints to establishment, growth and survival, related to a species' ecological traits (i.e. functional group). These limits may be subject to facilitation or interspecific competition (autogenic processes), along a gradient controlled directly or indirectly by the climatic regime (allogenic processes) and the successional stage (i.e. tree age).

Competitive trade-offs along the climatic gradient

Lichen species whose frequencies increase on aspen in wetter localities are generally associated with cyanobacteria (Figs 2 & 4), either as the primary photobiont (bipartite lichens, i.e. *Degelia atlantica*, *Degelia plumbea* and *Pannaria rubiginosa*) or contained in secondary structures called cephalodia (tripartite lichens, i.e. *Lobaria amplissima* and *Lobaria pulmonaria*). This reflects the wider observation that cyanobacterial species are more abundant in humid forest habitats (Green & Lange, 1991; Ellyson & Sillett, 2003), reaching maximum local frequencies in Europe along the oceanic Atlantic seaboard, e.g. in Brittany and western Scotland (James *et al.*, 1977; Rose, 1988). Conversely, species associated with green-algal symbionts are generally more frequent than cyanobacterial lichens on aspen in drier localities (Figs 2 & 4). In contrast to climatic limits in the local abundance of cyanobacterial epiphytes (James *et al.*, 1977; Green & Lange, 1991; Ellyson & Sillett, 2003), a majority of the green-algal lichen species are widely distributed on diverse substrata and are abundant in various habitats from both continental and oceanic regions of Scotland, and, more widely, in north-west Europe, e.g. *Lecanora chlorotera*, *Lecidella elaeochroma* and *Parmelia sulcata* (cf. Hawksworth & Dalby, 1992; Purvis & James, 1992a,b). The lower frequency of green-algal species on aspen in wetter localities may therefore reflect constraints to the realized niche of otherwise cosmopolitan species, e.g. competitive pressure, imposed in a specific habitat (i.e. the aspen bole). The contrasting climatic responses of

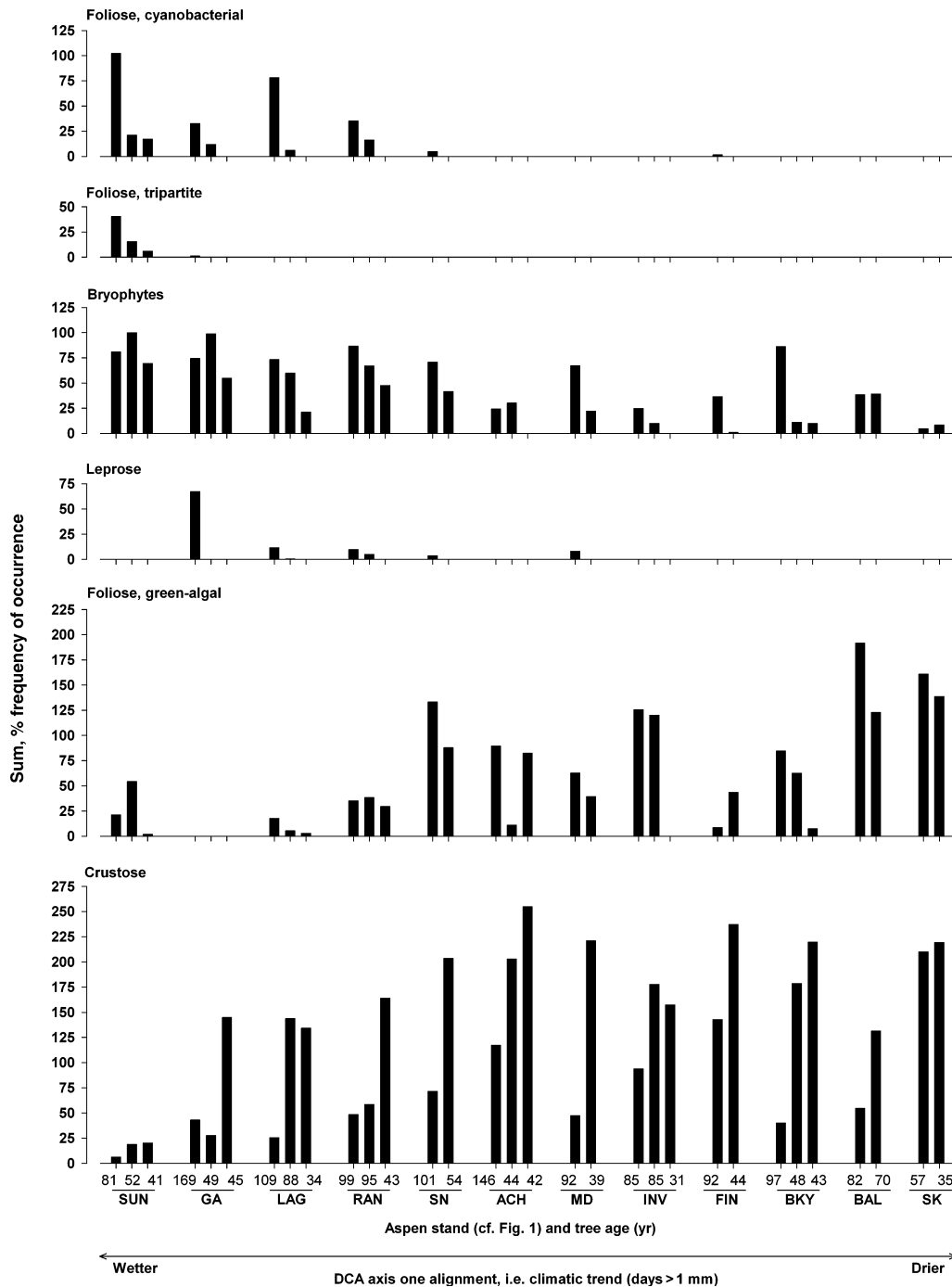


Figure 4 The contribution (per cent frequency) of contrasting functional groups to individual aspen trees of different age in stands aligned along DCA axis one (i.e. along a climatic gradient in wetness, cf. Table 2).

cyanobacterial and green-algal lichen epiphytes can accordingly be attributed to differences in the competitive ability of species groups with divergent functional traits.

Nitrogen limitation may be invoked as a possible factor explaining the competitive displacement of green-algal by cyanobacterial lichens in wetter environments. If lichen thalli undergo frequent cycles of wetting and drying, moisture-dependent poikilohydric growth may become limited by the

availability of key nutrients, i.e. N and P (Crittenden *et al.*, 1994). While growth-rates might be maintained by N₂ fixation in cyanobacterial lichens (Green *et al.*, 1980) the relative fitness of green-algal lichens may be reduced by N-limited-growth. However, differences in epiphyte communities of aspen trees from wetter compared with drier localities point to a trade-off in adaptive strategy (Fig. 4), i.e. lowered competitive fitness of cyanobacterial lichens, relative to green-algal lichens, along a

gradient of increasing climatic dryness. Accordingly, the environment of oceanic western Scotland (e.g. equitable temperatures and high humidity) is likely to provide suitable conditions for N₂ fixation, enabling sufficient thallus hydration over a moderate temperature range (Kershaw & Dzikowski, 1977; MacFarlane & Kershaw, 1977), while effective N₂ fixation may be weakened by environmental conditions associated with increasing climatic continentality, i.e. longer and more intense periods of drying (Kershaw & Dzikowski, 1977) and extended winter temperatures below 5 °C (MacFarlane & Kershaw, 1977). Additionally, photochemical differences between green-algal and cyanobacterial lichens suggest competitive abilities under contrasting climatic regimes:

1. under the drier conditions associated with a more continental climate, photosynthetic compensation and maximum photosynthesis may be achieved by green-algal lichens at a lower thallus water content than by cyanobacterial lichens (Lange *et al.*, 1988);
2. with less frequent rainfall, photosynthetic reactivation may be achieved in green-algal lichens by rehydration from water vapour alone, but may be dependent in cyanobacterial lichens upon the presence of liquid water (Lange *et al.*, 1986, 1993). In contrast, respiration in both cyanobacterial and green-algal lichens may occur upon rehydration by water vapour (Lange *et al.*, 1986, 1993), possibly causing a negative effect on the carbon balance of cyanobacterial lichens if too frequent respiration (thallus rehydration from water vapour) occurs in the absence of photosynthesis (absence of liquid water). Differential rates of thallus suprasaturation and photosynthetic suppression (Lange *et al.*, 1996, 2001) may also be important, though require further experimental comparison between functional groups;
3. given less cloud cover during winter months or in woodlands with an open canopy, the photochemical apparatus of cyanobacteria may be more susceptible than that of green algae to photoinhibition through exposure to prolonged and intense sunlight (Demmig-Adams *et al.*, 1990), with an ecologically significant effect extending to tripartite species (Gauslaa & Solhaug, 1996, 2000).

Succession and the role of facilitation

Patterns in the occurrence of functional groups within aspen stands point to a predictable successional trend (Fig. 4). Green-algal crustose lichens are most frequent on younger trees, becoming displaced by green-algal foliose lichens and bryophytes on older trees in drier localities, or, increasingly, by bryophytes and cyanobacterial foliose lichens in wetter localities (Fig. 4). Accordingly, crustose lichen species are significantly negatively correlated with cyanobacterial and tripartite foliose lichens and bryophytes (Table 3). Crustose lichens may be generally inferior competitors in comparison with foliose species and bryophytes (Topham, 1977; Rogers, 1990), which may overgrow thin corticolous crusts. Higher frequencies of crustose lichens on younger trees are probably indicative of an open bark community, with lower levels of competition for space and light (John, 1992; John & Dale, 1995). In contrast,

bryophytes and cyanobacterial foliose lichens are positively correlated (Table 3). However, peak frequencies of cyanobacterial foliose lichens occur on older trees than the initial occurrence of bryophytes, while at the wettest sites (SUN and GA) the highest frequencies of cyanobacterial lichens occur after peak bryophyte frequencies (Fig. 4). An inferred successional sequence tentatively supports, therefore, the autogenic role of bryophytes during succession to cyanobacterial-dominated communities, i.e. the replacement of crustose lichens by green-algal lichens and bryophytes, with establishment of cyanobacterial lichens facilitated by the water-relations of bryophyte mats (Veneklaas *et al.*, 1990) including the greater presence of liquid water (Lange *et al.*, 1986, 1993). Analogous scenarios describing autogenic facilitation of cyanobacterial lichens by green-algal lichens and bryophytes have been described during epiphyte succession on *Corylus avellana* and *Quercus* spp. in south-west Norway (Gauslaa, 1985; Ihlen *et al.*, 2001), *Quercus garryana* in western Oregon (Stone, 1989) and in the cool temperate forests of Tasmania (Kantvilas & Minchin, 1989).

The dominance of cyanobacterial lichens in late-successional epiphyte communities may represent a special case in successional ecology. Studies on higher plants suggest that N₂-fixing species tend to be dominant at early successional stages (Walker, 1993), when they contribute increased nutrient availability driving primary succession, i.e. the 'soil-driven' succession hypothesis (Clements, 1916; Connell & Slatyer, 1977). N₂-fixing lichens also occur in early successional habitats, e.g. on rocks and as soil crusts (Topham, 1977; Walker, 1993). However, while non-N₂-fixing higher plants may be at a competitive disadvantage in early successional, low-nutrient soils, green-algal (non-N₂-fixing) lichens are not reliant on the underlying substratum for their nitrogen supply, and may efficiently sequester wet deposited atmospheric nitrogen (Lang *et al.*, 1976; Crittenden, 1989). Thus, while non-N₂-fixing vascular plants may be precluded from primary successional habitats by low soil nitrogen, nutrient competition between N₂-fixing and non-N₂-fixing lichens may be more diffuse. In more continental climatic conditions, the lower photosynthetic efficiency of cyanobacterial compared with green-algal photobionts (see the preceding subsection) may limit cyanobacterial lichen establishment and growth, despite N₂ fixation. Thus, in drier woodland habitats, cyanobacterial lichens are late-successional species, restricted to microhabitats that enable cyanobacterial photosynthesis (i.e. wet moss mats and old tree bark). In oceanic climatic conditions, and moister woodland habitats, combined efficient photosynthesis and N₂ fixation may favour growth and establishment of cyanobacterial lichens, compared with green-algal species, and cyanobacterial lichens may occur earlier in the epiphyte community succession than in comparable, drier habitats.

Implications for biodiversity conservation

Biodiversity protection and maintenance of ecosystem function are closely related concerns in conservation (Hooper

et al., 2005). A positive relationship between β -diversity and turnover in the proportion of contrasting functional groups (Fig. 3) points to the role of morphological and physiological traits (i.e. algal partner and growth form) in controlling epiphyte community structure, and, therefore, in maintaining large-scale patterns of diversity (i.e. between stands along the climatic gradient). We recommend that a large-scale conservation initiative to protect the richness and functional diversity of aspen epiphytes would seek to maintain mixed-age aspen stands at a range of climatically contrasting sites throughout Scotland.

Caveats to the application of lichen indices

The results of this study point to a possible lack in recent applied research of adequately encompassing the species richness of lichen epiphytes. This has resulted in: (1) an emphasis in the conservation literature on macrolichen species with similar ecologies (e.g. as biodiversity indicators) and (2) the application of lichen indices over climatically variable geographical areas.

In many conservation assessments macrolichens are popularly applied as indicators of biodiversity (i.e. foliose, cyanobacterial epiphytes: Kuusinen, 1996; Hedenås & Ericson, 2000; Campbell & Fredeen, 2004). However, our study points to trade-offs between species groups with different functional traits, suggesting that the application of epiphyte species with similar ecologies as biodiversity indicators may leave trends in species richness unaccounted for. Approximately 69% of the 413 British lichen species with an IUCN status above 'least concern' (excluding data-deficient species, Woods & Coppins, 2003) are crustose microlichens. Nevertheless, a contrasting response on aspen of crustose species compared with cyanobacterial or tripartite foliose lichens (Table 3) points to the possible inefficacy of macrolichen indicators in identifying habitats important for crustose species. Similarly, smaller-scale, within-site studies on *C. avellana* in Norway suggested that macrolichens may not be appropriate wholesale indicators of 'habitat quality', as they responded to a different suite of environmental factors compared with microlichens (Ihlen *et al.*, 2001). Indices designed for epiphyte conservation should seek to include a representative range of functional groups (e.g. Coppins & Coppins, 2002) and the link between macrolichen indicators, conservation status and epiphyte species richness requires critical assessment before application.

Our study points to biogeographical variation in species distribution and frequency over relatively small spatial scales (i.e. LAG and BKY are only *c.* 10 km apart). Such rapid variation will weaken the efficacy of established lichen indices over limiting climatic and successional gradients. In contrast, lichen indicators are often applied uniformly over wide geographical areas that are climatically variable (Hawksworth & Rose, 1970; Tibell, 1992; Holien, 1996, 1998). In particular, foliose cyanobacterial lichens are widely accepted as indicators of old-growth woodland (Rose, 1988; Gauslaa, 1995; Kuusinen, 1996; Gu *et al.*, 2001) though their distribution on aspen (i.e.

frequent on young and intermediate-aged trees at wetter localities, Fig. 4) suggests that such species may not become entirely restricted to a microhabitat intimately associated with old-growth habitats (i.e. the boles of very old trees) until limits to their establishment and growth are imposed by competition from other epiphytes under a suboptimal climatic regime. The notion of an environmental threshold beyond which certain species become limited to old-growth habitats supports the careful recognition of discrete biogeographical zones, i.e. a different East of Scotland index of ecological continuity and a contrasting West of Scotland index of ecological continuity (Coppins & Coppins, 2002). Advances in the development of lichen indices should seek to incorporate the complexities of regional and local climate and also the effects of different host trees, e.g. aspen may provide a favourable substratum for the development of cyanobacterial lichens (Gauslaa, 1985, 1995; Kuusinen, 1996), possibly enabling their occurrence to greater frequency at drier sites than on less suitable substrata under an equivalent climate.

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BIOSKETCHES

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Appendix 1 Lichen epiphyte species recorded from aspen during the study, grouped according to their functional-traits. Nomenclature follows Coppins (2002), with specimens labelled 'ad interim' accessioned into the Edinburgh herbarium at RBGE.

Functional group

Fruticose

Bryoria fuscescens
Cladonia chlorophaea
Cladonia coniocraea
Cladonia fimbriata
Cladonia macilenta
Cladonia pyxidata
Ramalina farinacea
Ramalina fastigiata
Ramalina fraxinea
Usnea subfloridana

Foliose, cyanobacterial

Collema fasciculare
Collema occultatum
Collema subflaccidum
Degelia atlantica
Degelia plumbea
Fuscopannaria mediterranea
Leptogium lichenoides
Leptogium saturninum
Lobaria scrobiculata
Nephroma laevigatum
Nephroma parile
Pannaria conoplea
Pannaria rubiginosa
Parmeliella triptophylla
Peltigera collina
Peltigera hymenina
Peltigera praetextata
Protopannaria pezizoides
Sticta limbata
Sticta sylvatica

Foliose, tripartite

Lobaria amplissima
Lobaria pulmonaria
Lobaria virens

Foliose, green algal

Evernia prunastri
Hypogymnia physodes
Hyogymnia tubulosa
Melanelia exasperata
Melanelia fuliginosa subsp. *glabratula*
Melanelia subaurifera
Normandina pulchella
Parmelia saxatilis
Parmelia sulcata
Parmotrema chinense
Parmotrema crinitum
Phaeophyscia orbicularis
Physcia aipolia
Physcia stellaris
Physcia adscendens & *tenella*
Physconia distorta
Platismatia glauca

Appendix 1 *continued*

Functional group

Pseudevernia furfuracea
Xanthoria parietina
Xanthoria polycarpa

Crustose

Anisomeridium biforme
Arthonia didyma
Arthonia muscigena
Arthonia patellulata
Arthonia radiata
Bacidia sp. (ad interim)
Bacidia absistens
Bacidia arcuetina
Bacidia circumspecta
Bacidia igniarii
Bacidia subcircumspecta
Bacidia subincompta
Bacidia vermifera
Biatoridium delitescens
Buellia disciformis
Buellia erubescens
Buellia griseovirens
Calicium viride
Caloplaca ahtii
Caloplaca cerina
Caloplaca cerinella
Caloplaca ferruginea
Caloplaca holocarpa
Caloplaca obscurella
Candelariella superdistans
Catillaria nigroclavata
Catinaria atropurpurea
Chrysothrix candelaris
Cliostomum griffithii
Dimerella pineti
Diplotomma pharcidium
Fuscidea recensa
Japewia subaurifera
Lauderlindsaya acroglypta
Lecania cyrtella
Lecania naegelii
Lecania sambucina
Lecanora cf. '*caladonica*' (ad interim)
Lecanora carpinea
Lecanora chlarotera & *rugosella*
Lecanora expallens
Lecanora persimilis
Lecanora populicola
Lecanora pulicaris
Lecanora sambuci
Lecidella elaeochroma
Leptorhaphis atomaria
Megalaria grossa
Megalaria pulvere
Melaspilea 'sp. D' (ad interim)
Melaspilea sp. (ad interim)
Micarea micrococca
Micarea peliocarpa

Appendix 1 *continued*

Functional group

Mycoblastus fucatus
Ochrolechia androgyna
Ochrolechia microstictoides
Ochrolechia subviridis
Ochrolechia szatalaensis
Ochrolechia tartarea
Opegrapha atra
Opegrapha herbarum
Opegrapha multipuncta
Opegrapha rufescens
Opegrapha soreidifera
Pertusaria albescens
Pertusaria amara
Pertusaria cf. borealis
Pertusaria coronata
Pertusaria hemisphaerica
Pertusaria hymenea
Pertusaria leioplaca
Pertusaria pertusa
Pertusaria pupillaris
Phlyctis argena
Porina aenea
Protoparmelia ochrococca
Scoliciosporum chlorococcum
Scoliciosporum umbrinum
Tephromela atra
Sorediate sp. a (ad interim)
Sorediate sp. b (ad interim)
Leprose
Lepraria elobata
Lepraria jackii
Lepraria lobificans
Lepraria rigidula
