Plant Ecology & Diversity
Vol. 3, No. 2, June 2010, 203–210

Taylor & Francis
Taylor & Francis Group

SCOTTISH SECTION

Taxon- compared with trait-based analysis of epiphytes, and the role of tree species and tree age in community composition

Jason E.J. Lewis[a] and Christopher J. Ellis[b]*

[a]*Centre for Ecology & Hydrology, Penicuik, Midlothian, UK;* [b]*Royal Botanic Garden Edinburgh, Edinburgh, UK*

(*Received 7 April 2010; final version received 30 June 2010*)

Background: Trait-based assembly rules are a powerful tool in community ecology, used to explore the pattern and process of community structure (richness and composition).
Aims: A preliminary test for the utility of trait-based assembly rules in explaining cryptogamic epiphyte communities (lichens and bryophytes).
Methods: We sampled epiphytes from three different tree species (aspen, birch and pine), and from trees of contrasting age. The community composition of epiphyte species (taxon analysis) and functional groups (trait analysis) was summarised using multivariate ordination (nonmetric multidimensional scaling, NMDS).
Results: Ordination documented a widely observed pattern in which different tree species have taxonomically different epiphyte communities. However, NMDS sample scores were correlated to tree age in the trait-based analysis, but not in the taxon analysis.
Conclusions: Our results point to the existence of a common pattern in community traits during succession (on trees of different age) when measured for epiphyte communities with contrasting taxonomic composition. This pattern is evidenced by consistent trends in lichen growth form and reproductive strategy (sexual vs. asexual).

Keywords: assembly rules; community structure; functional traits; nonmetric multidimensional scaling; succession

Introduction

Understanding and predicting community response to ecological drivers is highly complex for species-rich assemblages. The use of 'assembly rules' is an attempt to make sense of this ecological complexity by combining the dynamic response of co-occurring species into a set of simplified rules (Keddy 1992). Recent developments have supported the use of species' functional traits in conceptualising higher-level assembly rules. Species response to the biotic and abiotic environment has been proposed to be explained by trait characters (Violle et al. 2007), and co-existence mechanisms explaining species co-occurrence have been examined using trait-dispersion (Diaz et al. 1998; Fargione et al. 2003; Stubbs and Wilson 2004; Cornwell et al. 2006; Holdaway and Sparrow 2006).

The use of trait-based assembly rules is potentially important as a unifying concept in community ecology (Wilson 1999; McGill et al. 2006), providing a framework for explaining the complex response of species-rich communities to habitat dynamics. For lichens, consistent variation in easily measured morphological traits has been previously observed with respect to environmental gradients (Kantvilas and Minchin 1989; Ruchty et al. 2001; Rogers 2006). Possibly the most unified trait-based framework has been proposed for epiphytes in the forests of western North America (McCune 1993): the response of contrasting trait groups (e.g. alectorioid lichens, cyanolichens and bryophytes) was used to explain a consistent pattern of community change along similar forest gradients (vertical, successional and moisture). Comparable work in Britain has attempted to explain the community response of epiphytes using trait classification with respect to climatic setting and the age structure of aspen stands (Ellis and Coppins 2006, 2007). However, the use of lichen traits to summarise community change is a developing area of research, and the approach has met with mixed success. In certain studies traits have proved less useful in capturing the community response to ecological processes (Johansson et al. 2007).

In this paper we present a successional framework with which to examine the utility of traits as a generalisation for the lichen community response to habitat dynamics:

(1) We sampled epiphyte communities from different tree species across a spectrum of tree ages. By sampling different tree species we aimed to sample taxonomically contrasting lichen communities.
(2) Using tree age as a framework, we test whether community patterns in terms of trait characteristics are consistent along a gradient in tree age, i.e. between taxonomically contrasting communities, sampled from different tree species.

Previous work has indicated that epiphyte community change during the life-span of a tree may be predictable

*Corresponding author. Email: c.ellis@rbge.org.uk

ISSN 1755-0874 print/ISSN 1755-1668 online

DOI: 10.1080/17550874.2010.505966
http://www.informaworld.com

with respect to epiphyte traits (McCune 1993; Ruchty et al. 2001; Ellis and Coppins 2006), for example transitioning from a community dominated by sexually reproducing crustose lichens on young trees, to one dominated by foliose lichens, bryophytes and asexually reproducing crusts as a tree ages (Ellis and Coppins 2007). We apply this framework using three tree species (aspen, birch and pine) sampled from study sites in north-east Scotland.

Methods

Epiphyte sampling

Three study sites were located in Strathspey, a well-wooded area within the Grampian region of north-east Scotland (Figure 1). The region occupies a relatively continental climatic setting within the oceanic British Isles, with mean monthly temperature range between c. 0.5 and 13 °C, and annual precipitation of 800 mm (Perry and Hollis 2005). Epiphytes were sampled from *Pinus sylvestris* L. (Scots pine) at Strath Nethy (SN), located within the Abernethy Forest, and from *Betula* spp. (birch) at Invertromie (INV). Two species of birch were present at Invertromie (*Betula pendula* Roth. and *Betula pubescens* Ehrh.), though they are not delimited here owing to their apparent hybridisation. Epiphytes were sampled from *Populus tremula* L. (aspen) at both Invertromie and Craigan Breugach (CB), providing the opportunity to consider differences between epiphyte communities for the same tree species, between sites. Nine individuals of *Betula* spp. and *P. tremula* were selected (eight individuals for *P. sylvestris*), aiming to sample trees of contrasting age based on their girth at 1.3 m. All selected trees were growing vertically, were not subject to wounding or disease effects and occurred in stands of similar density (i.e. neither closely grown and shaded, nor occupying an exposed, isolated position).

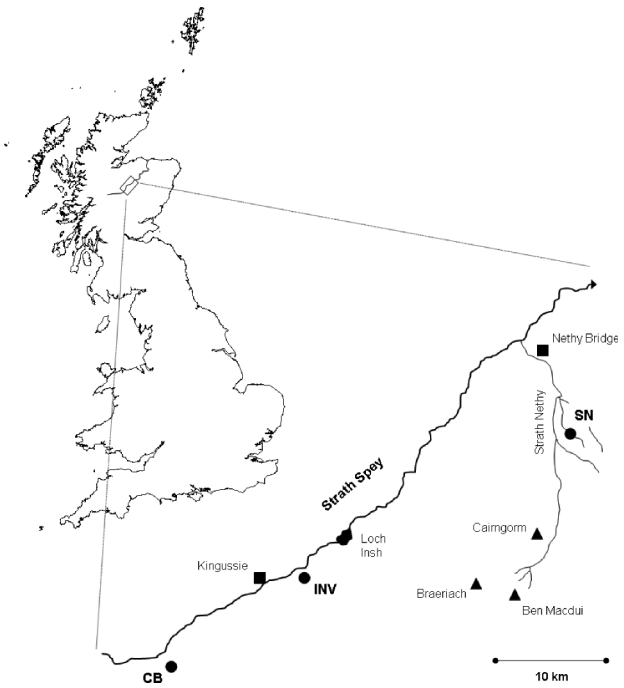

Figure 1. The study region along the River Spey in north-east Scotland: study sites (● – CB, Creagan Breugach [NN 740990], INV, Invertromie [NN 780996], SN, Strath Nethy [NJ 022125]), towns (■) and mountain summits (▲).

Epiphyte communities were sampled from selected trees using quadrats placed onto the bole randomly with respect to aspect and within a stratified height (between 25 cm and 150 cm above the ground). The number of quadrats used to sample an individual tree varied from three to seven depending on tree size. The quadrat size varied for any given tree between 6 cm × 6 cm, 9 cm × 9 cm and 12 cm × 12 cm, in order to retain a linear function between the sampled area and the habitat size, i.e. tree bole area (Pearson's $r = 0.984$, $P < 0.0001$, with 33 df), and to ensure that each quadrat incorporated the full amplitude of ridge-furrow topography (which increased on larger trees). Epiphyte species were quantified as presence–absence in nine sub-units placed within the confines of each quadrat. Following field sampling of epiphytes, selected trees were cored using a Presler-type increment borer at a vertical height of 1 m.

Epiphyte species which were not identified in the field were returned to the herbarium at the Royal Botanic Garden Edinburgh for examination. Equivocal species were identified using standard light microscopy with chemical spot tests (KOH, C and Pd) and thin layer chromatography. Nomenclature follows Smith et al. (2009) for lichens, Smith (2004) for mosses and Paton (1999) for liverworts.

Environmental factors

Tree cores were sanded using fine-grain sandpaper to expose a plane surface. Cores were then stained by immersion first in phloroglucinol for c. 1 minute, and second in 50% HCl for c. 20 s. Cores were rinsed and annual growth rings counted by using light microscopy. When a complete ring-count was not possible the total number of rings (R) was estimated by obtaining a mean value based on number of rings counted (Rc) over a given core length (Ca), and comparing this value to total core length (Cl):

$$R = (Rc / Ca) \times Cl. \quad (1)$$

Three micro-environmental factors were measured for each sampled quadrat: bark rugosity ('roughness'), bark pH and bark water capacity. Bark rugosity was measured along a horizontal transect as the furrow depth and width within each quadrat. Bark rugosity (Bt) was summarised following Ellis and Coppins (2007) as:

$$Bt = \log\left[r / \{(\sqrt{(fl/2)^2 + (fd)^2}) \times 2\} \right], \quad (2)$$

where r and fl are the measured length of bark ridges and furrows, and fd is the average vertical depth of

furrows. A sample of bark (surface area c. 4 cm^2) was collected from each quadrat and used for analysis of bark pH using a method modified from Legrand et al. (1996), which is similar to that applied to aspen bark by Kuusinen (1994). Cambial remnants were removed from the inner bark, and the bark surface cleaned of debris. Bark samples were dried at 35 °C to constant weight, fractured into splinters and added to deionised water at a ratio of 100 mg : 1 ml. Samples were agitated at 3 h intervals. The pH of the solution in contact with bark samples was measured after 24 h using a Sartorius PP-20 pH meter. Bark samples were drip-dried and weighed in a saturated state. Samples were oven-dried at 80 °C to constant weight (c. 48 h) and water-holding capacity calculated (ml g^{-1}). Product-moment correlation was used to explore relationships between environmental factors, and ranked values (for rugosity, pH and water capacity) were compared for contrasting tree species and study sites using Kruskall–Wallis one-way analysis of variance (Genstat v. 7.1 2003) with a Bonferroni correction used to control the Type I error.

Statistical analysis

Epiphyte communities were summarised for individual tree species using the percent frequency of occurrence (%*fo*). Values of %*fo* were calculated for individual epiphyte taxa, and for epiphyte taxa grouped according to putative ecological (functional) traits. Drawing on previous evidence for the importance of growth form and photobiont partner in the ecological success of lichens, we adopted a combination of these characters as an initial framework of functional traits (Hale 1983): members of the Cladoniaceae, other fruticose lichens, foliose lichens, squamulose lichens, sexual crustose lichens, asexual crustose lichens, and also including bryophytes as an aggregated group. Epiphyte frequency data were arcsine transformed prior to analysis (McCune and Grace 2002). Community variation was summarised separately for taxa and functional trait groups using ordination by nonmetric multidimensional scaling (NMDS; PC-Ord v 4.25, McCune and Mefford 1999). Based on a Sørensen dissimilarity matrix, exploratory analysis used a random starting configuration to perform 40 data runs with a maximum of 400 iterations and an instability criterion equal to 0.00001. Default options were selected for remaining parameters (McCune and Mefford 1999). A Monte Carlo randomisation test (50 randomised runs) was used to evaluate the statistical power of the exploratory analysis (McCune and Mefford 1999; McCune and Grace 2002), and a final solution selected as the minimum number of axes with stress < 15, final stability ≤ 0.00005 and $P = < 0.05$. For the taxon analysis, the %*fo* of individual taxa was compared with NMDS axis scores using product-moment correlation, and statistically significant relationships ($P < 0.05$) included as a joint plot of sample and species scores.

Environmental variables (tree age, and mean values for bark rugosity, pH and water capacity) were compared with NMDS axes scores using multiple least-squares regression, with step-wise selection and the Aikaike information criterion (AIC) used to estimate an optimum solution (Genstat v. 7.1, 2003). NMDS axis scores were compared with standardised values of tree age using product-moment correlation; where there was a significant correlation between NMDS axis scores and tree age, the %*fo* of taxa or functional groups was compared with the respective axis scores using generalised additive models (GAMs), implemented using a two-parameter smoothing spline (Genstat v. 7.1 2003) with a normal error distribution and identity link function.

Results

We sampled a total of 35 trees from three study sites, recording 67 epiphyte species (60 lichens and seven bryophytes) from 111 quadrats. There were significant differences in the measured pH of tree bark when compared among sampled tree species (Figure 2), with pH decreasing in the sequence: *Populus tremula* > *Betula* spp. > *Pinus sylvestris*. The bark pH of *P. tremula* was contrasting between sites however, and was less acidic at Invertromie (INV) than at Creagan Breugach (CB) (Figure 2). Differences in bark pH were significant with Bonferroni correction used to account for multiple tests ($\alpha = 0.017$). Overall differences in bark rugosity were not significant, though inter-species differences were perhaps masked by the presence of relatively smooth bark on some individuals from each species (Figure 2). Considering only the most fissured bark, rugosity values were higher for *P. sylvestris* than *Betula* spp. or *P. tremula*, with the lowest values of rugosity for *P. tremula* at INV. There was no significant difference in bark water capacity compared among tree species (Figure 2); however, statistical variance (var.) in water capacity was notably different between tree species, decreasing in the sequence: *P. tremula* ($v = 0.327$) > *Betula* spp. ($v = 0.0326$) > *Pinus sylvestris* ($v = 0.0159$).

Ordination of quadrat samples by NMDS using taxa as quantified variables (taxon analysis) described an optimum solution with two axes: stress = 14.4, instability = 0.00001, $P < 0.05$. Ordination axis two described c. 34.3% of latent variation in the data, and separated samples from contrasting tree species, while axis one described c. 12.6% of variation and separated *P. tremula* sampled from contrasting sites (INV and CB) and trees of different age from the same site, e.g. samples from *Betula* spp. and *Pinus sylvestris* (Figure 3). Based on multiple linear regression with AIC and the step-wise selection of variables, both axis one and axis two sample scores were best explained in response to a gradient in bark pH, indicating variation in bark chemistry between tree species, and also for different aged trees of the same species (Table 1).

The ordination of quadrat samples using functional traits as quantified variables (trait analysis) described an optimum solution with three axes: stress = 10.09, instability = 0.00001, $P < 0.05$. Ordination axis three described c. 37.3% of latent variation in the data, while axes one and

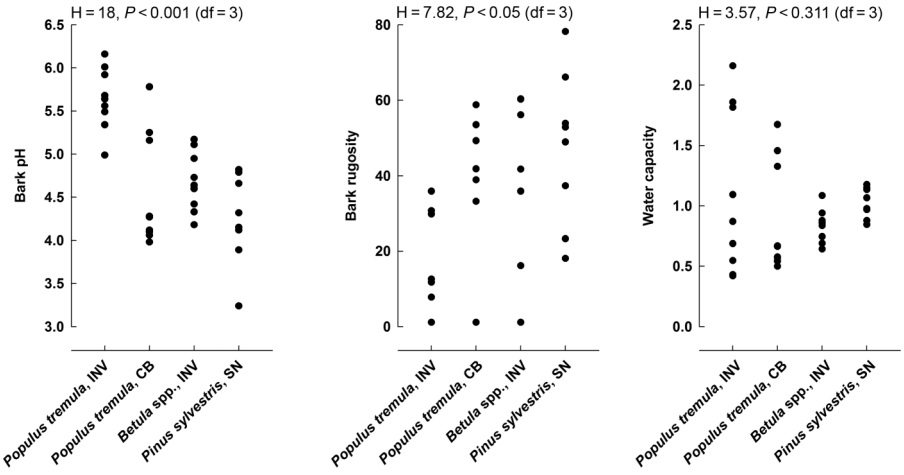

Figure 2. Point-plots showing values for measured bark characteristics compared between tree species.

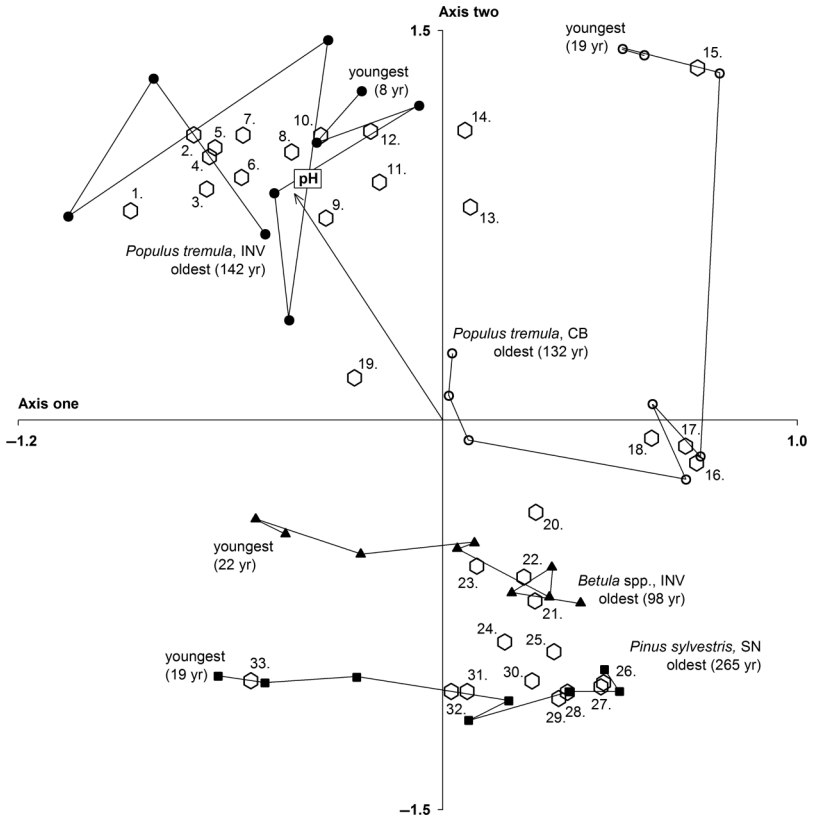

Figure 3. Ordination plot for taxon analysis with axis scores derived using NMDS (cf. Table 1). Symbols show sample scores for contrasting trees and sites (● *P. tremula*, INV; ⬡ *P. tremula*, CB; ▲ *Betula* spp., INV; ■ *P. sylvestris*, SN). Bark variables related to axis scores are plotted as passive vectors (McCune and Grace 2002). Different aged individuals of the same species from the same study site are joined by lines between the youngest to the oldest ramets. Open circles (❍) show equivalent ordination values (calculated by weighted averaging) for those epiphyte species with sample abundance significantly related to ordination scores: 1, *Hypnum cupressiforme*; 2, *Pertusaria pertusa*; 3, *Phaeophyscia orbicularis*; 4, *Xanthoria parietina*; 5, *Orthotrichum stramineum*; 6, *Pertusaria coronata*; 7, *Physcia adscendens*/*tenella*; 8, *Physconia distorta*; 9, *Ramalina farinacea*; 10, *Frullania dilatata*; 11, *Lecania naegelii*; 12, *Lecidella elaeochroma*; 13, *Lecanora chlarotera*; 14, *Lecanora populicola*; 15, *Lecanora carpinea*; 16, *Arthonia patellulata*; 17, *Hypogymnia physodes*; 18, *Cliostomum griffithii*; 19, *Parmelia sulcata*; 20, *Lepraria rigidula*; 21, *Bryoria fuscescens*; 22, *Platismatia glauca*; 23, *Hypogymnia tubulosa*; 24, *Pseudevernia furfuracea*; 25, *Lepraria sylvicola*; 26, *Parmeliopsis ambigua*; 27, *Imshaugia aleurites*; 28; *Hypocenomyce scalaris*; 29, *Parmeliopsis hypopta*; 30, *Ochrolechia microstictioides*; 31, *Lecanora cadubriae*; 32, *Lecidea hypopta*; 33, *Micarea nitchkeana*.

two described c. 22.1% and c. 13.8% of variation in the data matrix, respectively. Based on multiple linear regression with AIC and the step-wise selection of variables, both axis one and axis three sample scores were best explained in response to a gradient in bark rugosity (Table 1), which increased with tree age (Figure 4). Axis two scores were best explained in response to a gradient in estimated bark pH (Table 1).

Table 1. Results for the comparison of measured environmental variables with equivalent sample scores positioned along NMDS ordination axes. A general linear model was used to perform a multiple regression, with stepwise selection and the Aikaike information criterion (AIC) used to estimate an optimum solution. Results are also shown for the correlation of tree age (habitat dynamic) with axis scores for the taxon- and trait-based ordination.

	Multiple least-squares regression					Tree-age correlation	
	Variable	adj-R^2	RSS	*P*	AIC	*r*	*P*
Taxon analysis							
Axis 1 (12.6 %)	pH	0.227	5.66	0.002	0.2521	0.096	n.s.
Axis 2 (34.3 %)	pH	0.538	12.32	< 0.001	0.39	–0.196	n.s.
Trait analysis							
Axis 1 (22.1 %)	Rugosity	0.388	5.454	< 0.001	0.2494	–0.535	< 0.001
Axis 2 (13.8 %)	pH	0.16	7.833	0.01	0.2992	0.158	n.s.
Axis 3 (37.3 %)	Rugosity	0.274	11.42	< 0.001	0.3725	–0.483	< 0.005

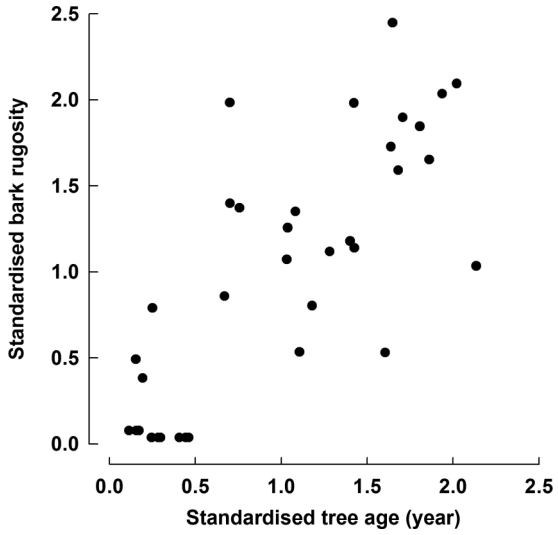

Figure 4. Scatter plot to compare standardised tree age with bark rugosity ($r = 0.773$, $P < 0.001$ with 33 df).

Scores for NMDS axis one and three in the trait-based analysis were significantly correlated with standardised tree age (Table 1). Examined using GAMs, a total of seven trait groups were significantly related to one or both of these axes: the lichen groups fruticose, Cladoniaceae, foliose, squamulose, asexual crustose and leprose tended to increase with decreasing NMDS scores (increasing tree age), while sexual crustose lichens showed the opposite response (Figures 5 and 6).

Discussion

Formative studies in epiphyte ecology described community differences compared between different tree species (Culberson 1955; Hale 1955; Jesberger and Sheard 1972). Accordingly, our study was able to use tree species as a framework from which to sample communities with contrasting species composition. First, epiphyte communities recorded from birch and pine contrasted with those on aspen, and were characterised by the presence of lichen species such as *Ochrolechia microstictioides*, *Platismatia glauca* and *Pseudevernia furfuracea* (Figure 3). This compositional difference might be explained by contrasts in bark pH between aspen, and birch and pine (Figures 2 and 3, Table 1). This interpretation would be consistent with recent evidence highlighting pH as a driver of epiphyte community composition (e.g. Jüriado et al. 2009), and serves to emphasise the unusual substratum characteristics of aspen within the boreal forest setting (Kuusinen 1994). Epiphytes recorded from aspen included a small number of specialist species (e.g. *Arthonia patellulata* and *Lecanora populicola*), which are known only from aspen in the British Isles (Ellis et al. 2007), in addition to a wider range of common species associated with less acidic and possibly more nutrient-rich bark conditions, e.g. *Lecania naegelii*, *Phaeophyscia orbicularis*, *Physconia distorta*, *Ramalina farinacea*, *Xanthoria parietina* and the moss *Orthotrichum stramineum*.

Second, there were between-site differences for aspen, which included the greater presence on aspen at CB of *Arthonia patellulata*, *Cliostomum griffithii*, *Hypogymnia physodes* and *Lecanora carpinea*. These differences may be attributable to a multitude of factors which cannot be resolved by the design of this study, either deterministic, e.g. local climatic and micro-climatic differences (Lidén and Hilmo 2005; Werth et al. 2005), site differences in soil quality (Gustafsson and Eriksson 1995; Benner and Vitousek 2007), clonal differences affecting bark chemistry (Bailey et al. 2005), or stochastic differences (Cáceres et al. 2007). Third, epiphyte communities on birch and pine were not identical, e.g. certain epiphytes were more abundant on pine than birch (e.g. *Hypocenomyce scalaris*, *Imshaugia aleurites*, *Lecanora cadubriae*, *Parmeliopsis ambigua* and *P. hyperopta*). Given their similarity in measured characteristics (Figure 2), differences in pine compared with birch epiphyte communities might be explained by invoking contrasts in additional factors, e.g. deciduous compared with evergreen habit (e.g. with implications for shading, stem flow), and temporal stability or physical hardness compared between the spongy and flaky bark of *P. sylvestris* and the more stable bark of mature birch trees.

Given these observed differences in species composition, confirmed between tree species, we were able to examine whether there are consistent patterns in trait composition, i.e. for communities which contrast taxonomically. Using

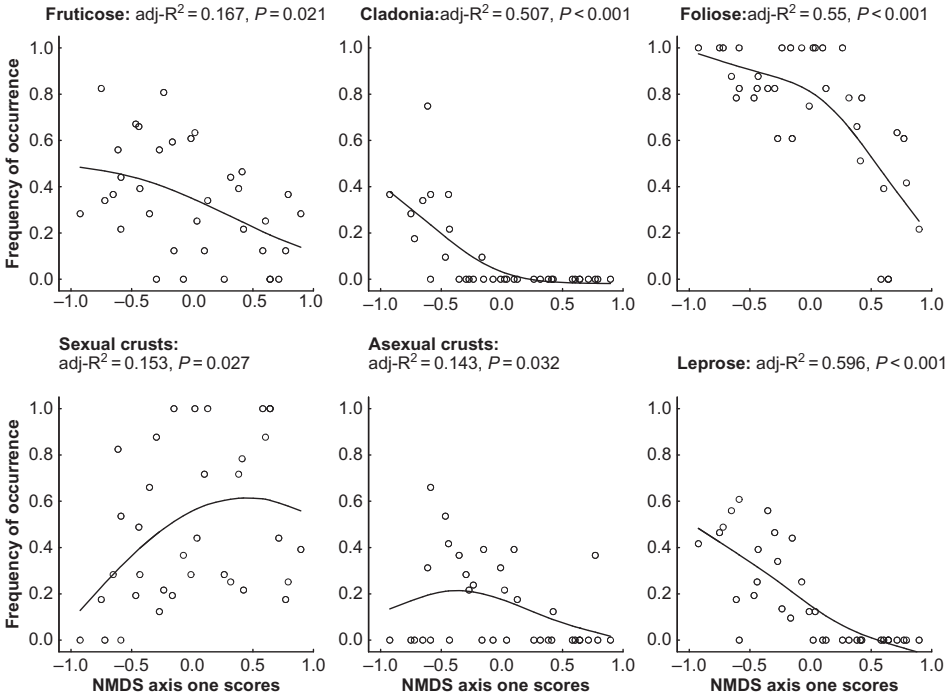

Figure 5. Response curves derived using generalised additive models, to compare frequency of occurrence of epiphyte functional groups with trait-based NMDS axis one scores, which summarises a gradient in tree age (older trees = negative axis values) and bark rugosity (cf. Table 1, Figure 4).

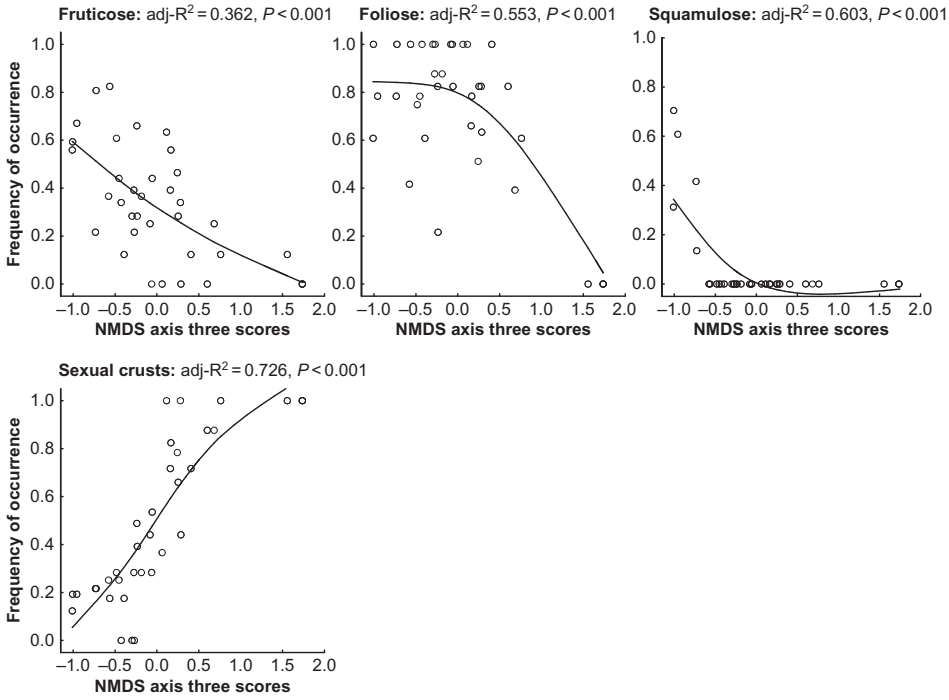

Figure 6. Response curves derived using generalised additive models, to compare frequency of occurrence of epiphyte functional groups with trait-based NMDS axis three scores, which summarises a gradient in tree age (older trees = negative axis values) and bark rugosity (*cf.* Table 1, Figure 4).

tree age as an empirical framework, our analysis provides tentative support for a trait-based approach in understanding epiphyte succession. Our preliminary results indicate that tree age might be a driver of community similarity in terms of traits (lichen growth form and reproductive mode), though not in terms of taxonomic composition (Table 1); that is, epiphyte communities may be controlled by functional traits with respect to tree age (i.e. along a

successional gradient). A gradient in bark rugosity is functionally related to tree age (Figure 4), and was selected in preference to tree age as the best explanatory variable for community composition (Table 1). Older trees of a given species have rougher bark, possibly driving a general pattern in lichen growth form and reproductive mode, from the greater occurrence of sexual crustose lichens on smooth, younger bark, with increased opportunity for the establishment of foliose lichens, *Cladonia* spp., asexual crustose and leprose lichens on older and more fissured bark (Figures 5 and 6). Change in the lichen community may, however, be interpreted as a dual response to environment (i.e. a change in bark quality: rugosity) and/or autogenic successional processes, e.g. the replacement of smaller, sexually reproducing species over time by larger and/or asexually reproducing species (Ellis and Coppins 2007). Similar – though not necessarily identical – successional gradients in epiphyte communities have been reported previously (e.g. Stone 1989; Ruchty et al. 2001). The absence of any similar successional trend for bryophytes may be explained by the coarse aggregation of contrasting growth forms within a single group (e.g. *Frullania dilatata* to *Orthotrichum stramineum*).

In summary, our results tentatively support a trait-based approach in understanding lichen community structure in response to habitat dynamics. However, the quality of evidence for trait-based community assembly is likely to depend on the selection of a delimited model system (ensuring simple comparability across ecological gradients), the ecological relevance of traits measured, and their effective resolution. Studies which have previously claimed evidence for trait-based epiphyte assembly have tended to examine closely defined habitats and have used fairly broad trait definitions along strong gradients (e.g. McCune 1993; Ruchty et al. 2001; Ellis and Coppins 2006, 2007). Trait-based analysis of lichen communities may thus contribute towards a general framework for lichen community ecology within a specified habitat. As a caveat, community patterns derived from trait analysis are broad representations only, and species-specific management must necessarily refer to autecological data. Furthermore, the limits of trait-based analysis with respect to patterns in species richness (as opposed to composition) remain to be fully explored.

Acknowledgements

This study was carried out at the Royal Botanic Garden Edinburgh in contribution to an MSc in Plant Taxonomy and Biodiversity (University of Edinburgh) by JL. We thank Rebecca Yahr for assistance in sampling epiphytes at Strath Nethy, and the Royal Society for the Protection of Birds for access to Invertromie.

Notes on contributors

Jason Lewis is currently a PhD student with the Centre for Ecology and Hydrology. His current work focuses on the lichen epiphyte response to pollution, with the aim of devising robust metrics for detailed pollution monitoring and assessment.

Chris Ellis is an ecologist specialising in lichen epiphytes – his work includes research at the interface of biogeography and community ecology, especially cross-scale interactions between landscape-scale and habitat factors, and the relative importance of traits in understanding community assembly.

References

Bailey JK, Deckert R, Schweitzer JA, Rehill BJ, Lindroth RL, Gehring C, Whitham TG. 2005. Host plant genetics affect hidden ecological players: links among *Populus*, condensed tannins, and fungal endophyte infection. Canadian Journal of Botany 83:356–361.

Benner JW, Vitousek PM. 2007. Development of a diverse epiphyte community in response to phosphorus fertilization. Ecology Letters 10:628–636.

Cáceres MES, Lücking R, Rambold G. 2007. Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycological Progress 6:117–136.

Cornwell WK, Schwilk DW, Ackerly DD. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471.

Culberson WL. 1955. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. Ecological Monographs 25:215–231.

Diaz S, Cabido M, Casanoves F. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Ellis CJ, Coppins BJ. 2006. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. Journal of Biogeography 33:1643–1656.

Ellis CJ, Coppins BJ. 2007. Reproductive strategy and the compositional dynamics of crustose lichen communities on aspen (*Populus tremula* L.) in Scotland. The Lichenologist 39:377–391.

Ellis CJ, Coppins BJ, Dawson TP. 2007. Predicted response of the lichen epiphyte *Lecanora populicola* to climate change scenarios in a clean-air region of northern Britain. Biological Conservation 135:396–404.

Fargione J, Brown CS, Tilman D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences 100:8916–8920.

Genstat v. 7.1. 2003. Genstat for windows. Oxford: VSN International Ltd.

Gustafsson L, Eriksson I. 1995. Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. Journal of Applied Ecology 32:412–424.

Hale ME. 1955. Phytosociology of corticolous cryptogams in a virgin forest in Wisconsin. Ecology 36:45–63.

Hale ME. 1983. The biology of lichens. London: Edward Arnold.

Holdaway RJ, Sparrow AD. 2006. Assembly rules operating along a primary riverbed-grassland successional sequence. Journal of Ecology 94:1092–1102.

Jesberger JA, Sheard JW. 1972. A quantitative study and multivariate analysis of corticolous lichen communities in the southern boreal forest of Saskatchewan. Canadian Journal of Botany 51:185–201.

Johansson P, Rydin H, Thor G. 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience 14:81–91.

Jüriado I, Liira J, Paal J, Suija A. 2009. Tree and stand level variables influencing diversity of lichens on temperate

broad-leaved trees in boreo-nemoral floodplain forests. Biodiversity and Conservation 18:105–125.
Kantvilas G, Minchin PR. 1989. An analysis of epiphytic lichen communities in Tasmanian cool temperate rainforests. Vegetatio 84:99–112.
Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.
Kuusinen M. 1994. Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle Boreal Finland. Annales Botanica Fennici 31:245–260.
Legrand I, Asta J, Goudard Y. 1996. Variations in bark acidity and conductivity over the trunk length of silver fir and Norway spruce. Trees 11:54–58.
Lidén M, Hilmo O. 2005. Population characteristics of the suboceanic lichen *Platismatia norvegica* in core and fringe habitats: relations to macroclimate, substrate and proximity to streams. The Bryologist 108:506–517.
McCune B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. The Bryologist 96:405–411.
McCune B, Grace JB. 2002. Analysis of ecological communities. Oregon: MjM Software Design.
McCune B, Mefford MJ. 1999. PC-ORD, multivariate analysis of ecological data. Oregon: MjM Software Design.
McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community traits from functional traits. Trends in Ecology and Evolution 21:178–185.
Paton JA. 1999. The liverwort flora of the British Isles. Colchester: Harley Books.
Perry MC, Hollis DM. 2005. The generation of monthly gridded datasets for a range of climatic variables over the UK. International Journal of Climatology 25:1041–1054.
Rogers RW. 2006. Soil surface lichens on a 1500 km climatic gradient in subtropical eastern Australia. The Lichenologist 38:565–576.
Ruchty A, Rosso AL, McCune B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. The Bryologist 104:274–281.
Smith AJE. 2004. The moss flora of Britain and Ireland. Cambridge: Cambridge University Press.
Smith CW, Aptroot A, Coppins BJ, Fletcher A, Gilbert OL, James PW, Wolseley PA, editors. 2009. The lichens of Great Britain and Ireland. London: British Lichen Society.
Stone DF. 1989. Epiphyte succession on *Quercus garryana* branches in the Willamette Valley of western Oregon. The Bryologist 92:81–94.
Stubbs WJ, Wilson JB. 2004. Evidence for limiting similarity in a sand dune community. Journal of Ecology 92:557–567.
Werth S, Tømmervik H, Elvebakk A. 2005. Epiphytic macrolichen communities along regional gradients in northern Norway. Journal of Vegetation Science 16:199–208.
Wilson J. 1999. Guilds, functional types and ecological groups. Oikos 86:507–522.
Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! Oikos 74:159–164.