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Reproductive strategy and the compositional dynamics of crustose lichen communities on aspen (*Populus tremula* L.) in Scotland

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Abstract: Ecological studies are essential in understanding the response of crustose lichens to habitat dynamics and developing effective conservation strategy. While the combined response of individual crustose species within a community will be tremendously complex, the overall result of individualistic change can be simplified using trait-based analyses. In this paper we examine the response of crustose species with contrasting reproductive traits (predominantly sexual *vs* asexual reproduction) and which occur within a closely defined habitat (as epiphytes on the lower bole of aspen) to environmental drivers measured at two different scales, i.e. between and within aspen stands. Our results point to the important effect of tree age and subsequent shifts in bark quality (pH) on the composition of the crustose community. However, shifts in community composition putatively controlled by bark quality comprise a change from a community dominated by sexual species to a community with mostly asexual crusts. Our results suggest therefore that variation within this crustose community may be driven by the combined effects of allogenic change (tree age and bark quality) and autogenic processes that are related to a species' adaptive life-history traits.

Key words: crustose lichens, pH, reproductive traits, succession

Introduction

Lichen epiphytes are increasingly a key theme in conservation. Lichens are 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). Effective conservation requires a dynamic, process-based understanding of the impact on lichens of major environmental drivers and threats, for example, land-use and habitat structure (Johansson & Ehrlén 2003), pollution levels (Hawksworth & Rose 1970; van Herk *et al.* 2003), and climate change (van Herk *et al.* 2002; Ellis *et al.* 2007). Lichen species will respond to environmental change individualistically, via effects on both resource capture and use, and meta- and population dynamics determined by a species' adaptive traits (Coxson & Coyle 2003; Antoine & McCune 2004; Löbel *et al.* 2006). The response of many individual species comprising a lichen community will therefore scale-up to a complex shift in compositional structure (i.e. considering each species as an individual unit). In this paper, we examine the way in which understanding and predicting the lichen community response to environmental change may be simplified and made tractable through the search for higher-level trait-based rules structuring community composition.

In their recent review of the field, McGill *et al.* (2006) suggested that complexities in community ecology would benefit from an emphasis on species traits. The use of lichen traits (e.g. gross morphology, photobiont type, reproductive strategy) may advantageously define a species' response to the environment, including the net result of diffuse inter-specific interactions (McGill *et al.* 2006). Such trait-based studies might productively focus on systematic change in communities along environmental gradients

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(McGill *et al.* 2006), including the effect of land-use on lichen communities (Stofer *et al.* 2006). Based on McCune's 'similar gradient hypothesis' (McCune 1993), Ellis & Coppins (2006) described a generalized pattern in which the epiphyte communities on aspen in Scotland are structured by trade-offs between groups of functionally similar species, attributed to establishment and growth limits in contrasting environments. Physiological trade-offs between green-algal and cyanobacterial species (Lange *et al.* 1986, 1988), and differences in competitive ability between larger foliose and smaller crustose species (John 1992; John & Dale 1995), were invoked to explain community composition between-sites along a climatic gradient, and within-sites between trees of different age (Ellis & Coppins 2006). This scenario for aspen draws on environmental constraints structuring β-guilds (*sensu* Wilson 1999), i.e. groups of species with similar traits that are aggregated together by environmental filters, and internal community dynamics (Belyea & Lancaster 1999), for example, the successional replacement of *r*-selected by *K*-selected species (MacArthur & Wilson 1967).

The study of aspen epiphytes by Ellis & Coppins was restricted to examination of gross morphology and photobiont-type (green-algal or cyanobacterial), and did not consider the importance of reproductive mode. Previous studies have suggested that reproductive strategy may interact importantly with a species' accompanying traits, to determine distribution and abundance in relation to habitat structure (Dupré & Ehrlén 2002; Driscoll & Weir 2005), and reproductive mode is considered a key trait in standard life-history models (MacArthur & Wilson 1967; Grime 1977, 1979). Accordingly, this paper seeks to integrate the effect of contrasting reproductive modes in the community structure of aspen epiphytes. It focuses on the community composition of frequently neglected though highly diverse crustose microlichens, and considers reproductive mode (sexual or asexual) as an additional ecological trait, examining the different implications for community composition of crustose lichen species with contrasting reproductive strategies.

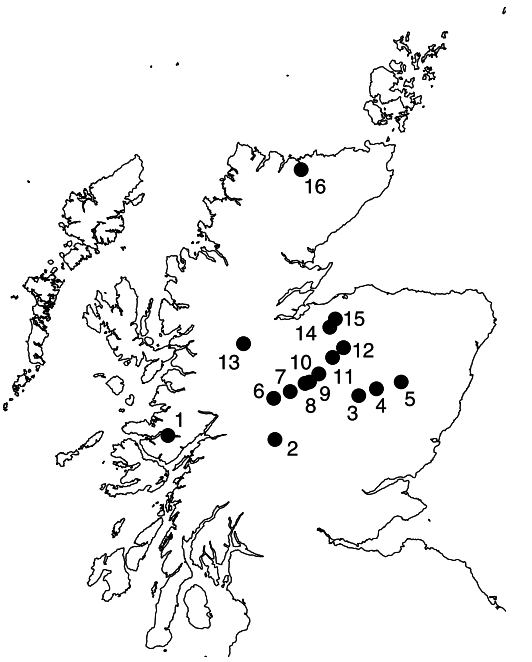

FIG. 1. Location (WGS84) and code of the aspen stand study sites. 1. Aird Airigh, Loch Sunart (56.693/5.686; AA), 2, Bridge of Ericht, Loch Rannoch (56.691/4.417; BrE); 3, Morrone Birkwood (56.997/3.427; Mor); 4, B976, nr Balmoral (57.046/3.22; Bal); 5, Muir of Dinnet, New Kinnord (57.088/2.916; MD); 6, Loch Laggan (56.696/4.446; Lag); 7, Breakachy Bridge (57.008/4.248; Bky); 8, Creag an Breagach (57.067/4.08; Cb); 9, Invertromie (57.076/4.017; Inv); 10, Speybank (57.134/3.916; Sb); 11, Street of Kincardine (57.008/4.248; StK); 12, Auchernack (57.305/3.622; Ach); 13, Corrie Loch, Glen Affric (57.311/4.836; GA); 14, Dulsie Bridge (57.443/3.789; Dul); 15, Cairnglass (57.498/3.734; Cg); 16, Skelpick Lodge (58.472/4.198; SkL).

Materials and Methods

Study sites

Sixteen study sites comprised single clone aspen stands located throughout Scotland (Fig. 1), though north of a broad region of wide-spread air-borne pollution (NEGTAP 2001). To reflect possible biogeographic variation in epiphyte communities, aspen stands were sampled across a steep climatic gradient, i.e. from the most oceanic site at Loch Sunart ('AA', Fig. 1; annual rainfall, 2245 mm; minimum mean monthly temperature, 4·1 °C) to more continental sites

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in north-east Scotland (e.g. 'Bal', Fig. 1; annual rainfall 830 mm; minimum mean monthly temperature, −0·5°C). Climate data were made available for each aspen stand using UK Met Office gridded data-sets (Perry & Hollis 2005): estimated monthly and annual climatic averages for (i) number of days with rainfall >1 mm, (ii) average, maximum and minimum monthly temperatures (°C) and (iii) precipitation (mm). Estimated climate data are the verified averages derived for 5-km grid-squares based on point data for the period 1961–2000 at 540 and 4400 monitoring stations across the British Isles (temperature & precipitation, respectively). A suite of nine climate variables was calculated for 5-km grid-squares comprising sampled aspen stands: (i) no. of days with >1 mm rainfall, (ii) average annual temperature (°C), (iii) mean temperature of the warmest month (°C), (iv) mean temperature of the coldest month (°C), (v) annual temperature range (°C), (vi) total yearly precipitation (mm), (vii) an index of reduced rainfall (total precipitation/average temperature), (viii) an aridity index (total precipitation/[average temperature+10]) and (ix) an index of oceanicity (days >1 mm precipitation/temperature range).

Field methods

The study aimed to sample trees of different age within each of the sixteen 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 (C. J. Ellis, unpublished data). At seven of the sites, trees could be recognized in three separate age classes, though at nine sites trees occurred in two age classes only. Accordingly, at each of the sixteen 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 each was growing vertically and that the bark surface was not subject to aberration, for example, by wounding, branching, etc. The linear distance between the sampled tree and its five nearest neighbours was measured.

The lichen community of each tree was quantified in a series of 6 × 6 cm quadrats (comprising nine 2 × 2 cm sub-units), 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*). The number of quadrats sampled (i.e. sample area) will increase accordingly with the size of the bole (i.e. habitat area). Lichen species were recorded in the field as presence-absence in each of the nine sub-units, and a bark sample (*c.* 2 × 2 cm) was collected from each of the quadrats, incorporating unidentified taxa. Bark topography (B*t*) was estimated for each quadrat using a measure based on Pythagorean theorem (Fig. 2). Within each quadrat a transect was aligned perpendicular to the longitudinal structure of ridges and furrows; the width of ridges (r) and furrows (fl) and the depth of furrows (fd) was therefore measured. A measure of

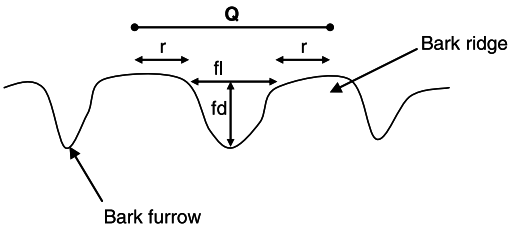

FIG. 2. The calculation of bark topography visualized as a cross-section within the confines of a quadrat (Q). The 'length' of ridge (r) was compared to that of the furrow, by approximating each side of the bark furrow as the hypotenuse of two right-angled triangles with sides fd and fl/2.

ridge versus furrow habitat within each quadrat was devised as the quotient of ridge and furrow 'length'. Approximating the furrows within the bark as a triangle in cross-section, the depth of the furrow (fd) forms one side of two right-angled triangles. This depth is known (fd), while the other side is equal to half of the length of the furrow (fl/2). The 'length' of furrow habitat (fL) can thus be calculated as twice the hypotenuse:

$$fL = [\sqrt{(fl/2)^2 + (fd)^2}] \star 2 \qquad \text{Eq. 1}$$

The log-quotient of ridge versus furrow habitat available in a cross-section of each quadrat was therefore approximated:

$$Bt = LOG[r/fL] \qquad \text{Eq. 2}$$

Surface area of the tree bole was estimated for the region between the lowest and highest quadrats; i.e. approximating the bole as a series of stacked cylinders, based on the girth measured at the height from which each contiguous quadrat was sampled. Bole area was compared to the sampled quadrat area using simple linear regression (Genstat v. 7.1, 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. Specimens were identified 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).

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The bark sample collected from each of the quadrats was examined in the laboratory for pH, electrical conductivity ($\mu S\ cm^{-1}$) and water-holding capacity. Bark samples were examined for pH and conductivity using a modification of the method described by Legrand *et al.* (1996), which is similar to that applied to aspen bark by Kuusinen (1994). The surface of each bark sample was cleaned of extraneous debris; lichens, other fungal material and bryophytes were removed, and the bark sample placed in a drying-oven at 35°C for 24 h. The dried bark sample was broken into small fragments, weighed and placed into a plastic beaker with an equivalent amount of deionized water at the ratio 1 ml:100 mg. The beaker was sealed and left to stand at room temperature (*c.* 21°C) for 24 h. Water in the beaker was agitated after *c.* 6 and 18 h. A temperature-corrected measure of conductivity followed by pH was made for the aqueous solution (Hanna Instruments HI-991300 portable meter with an HI-1288 probe). Soaked bark samples were removed from the beakers, drip-dried in a jet of air and weighed wet. Samples were oven-dried at 80°C for 76 h and reweighed. The water-holding capacity was estimated as percentage H_2O per mg dry weight.

The age of the sampled 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 minute and second in 50% aqueous hydrochloric acid for *c.* 30 seconds, before rinsing under tap-water. Tree rings were counted at × 6–40 (Meiji EMZ-TR).

Statistical analysis

The community of crustose lichens was quantified using species % frequency of occurrence (% *fo*) calculated at two contrasting scales: (i) tree-scale (% *fo* calculated for species occurring in quadrats sampled from individual trees), and recalculated at (ii) stand-scale (% *fo* calculated for species occurring in quadrats sampled from multiple trees within a stand). Frequency data were arcsine-squareroot transformed prior to analysis (McCune & Grace 2002). Variation in crustose lichen assemblages were summarized at each scale using ordination by nonmetric multidimensional scaling (NMDS; PC-Ord v 4.25, McCune & Mefford 1999), based on a Sørenson dissimilarity matrix. In an exploratory analysis, a random starting configuration was used 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 & Mefford 1999). A Monte Carlo randomization test (50 randomized runs) was used to evaluate the statistical power of the exploratory analysis (McCune & Mefford 1999; McCune & Grace, 2002), and a final solution selected as the minimum number of axes with stress <15 (stress (S) ≈ fit between the rank order of samples in ordination space compared to an original dissimilarity matrix), final stability ≤0·00005 (stability ≈ deviation in S over the preceding n iterations) and P=<0·05.

The % *fo* was calculated at respective scales for macrolichens classified into major functional groups based on gross morphology and photobiont type (*cf.* Hale 1983): fruticose, *Cladoniaceae*, foliose cyanobacterial, foliose tripartite, foliose green-algal and also including bryophytes. Correlations between the % *fo* of macro-lichen groups and NMDS axis scores for crustose lichen assemblages were summarized at each contrasting scale (stand- and tree-scale) using vector analysis (McCune & Grace 2002). Environmental variables were compared at each scale of analysis to the derived NMDS axes, using a general linear model to perform a multiple regression, with stepwise selection to estimate an optimum solution (Genstat v. 7.1, 2003). At the stand-scale, putative explanatory variables included were: the nine climate variables, the mean age of sampled trees and the age range, the average distance from sampled trees to surrounding trees (n=10 or 15, depending on whether two or three trees were sampled, respectively) and the statistical variance in this distance (i.e. standard deviation, s), average measurements for the bark characteristics (bark topography, pH, electrical conductivity and water-holding capacity), and their statistical variances (s). At the tree-scale: climate data were excluded, tree age is estimated for individual sampled trees, and average values and the variances (s) were calculated for the distance from a sampled tree to surrounding trees (n=5) and for the bark measurements of a single tree.

In down-scaling the analysis from between-sites (site-scale) to within-sites (tree-scale), the data were nested at descending scales based on environmentally similar units. Thus, environmental factors selected as explanatory variables at the stand-scale were used to construct a dendrogram, based on a similarity matrix calculated using the coefficient of Euclidean distance, with clustering by Ward's method (McCune & Grace 2002). Sub-groups with similar environmental properties were therefore identified, and tested using one-way analysis of variance with the least square difference (Genstat v. 7.1, 2003). Environmentally similar stands within a single sub-group were then used in the analysis of tree-scale communities.

Successional trends were further examined by plotting values of % *fo* for each of the contrasting functional groups (i.e. % *fo* summed for species within a functional group) against the age of individual trees. However, because the individual history of each stand may have an impact on the local composition of species (Ellis & Coppins, 2007), i.e. by controlling relative abundances in the local pool of species with contrasting traits, general trends in composition were examined after the standardisation of tree age and % *fo* within individual aspen stands:

$$S_t = [(100/av)^{\star} v_i]/100 \qquad \text{Eq. 3}$$

where av is the average value for a stand (i.e. tree age or % *fo*), and v_i is the individual value (age or % *fo*) for a given tree. Standardized values of % *fo* for sexual and asexual crusts and the macrolichen groups were compared to the standardized tree age using simple linear regression (Genstat v. 7.1, 2003).

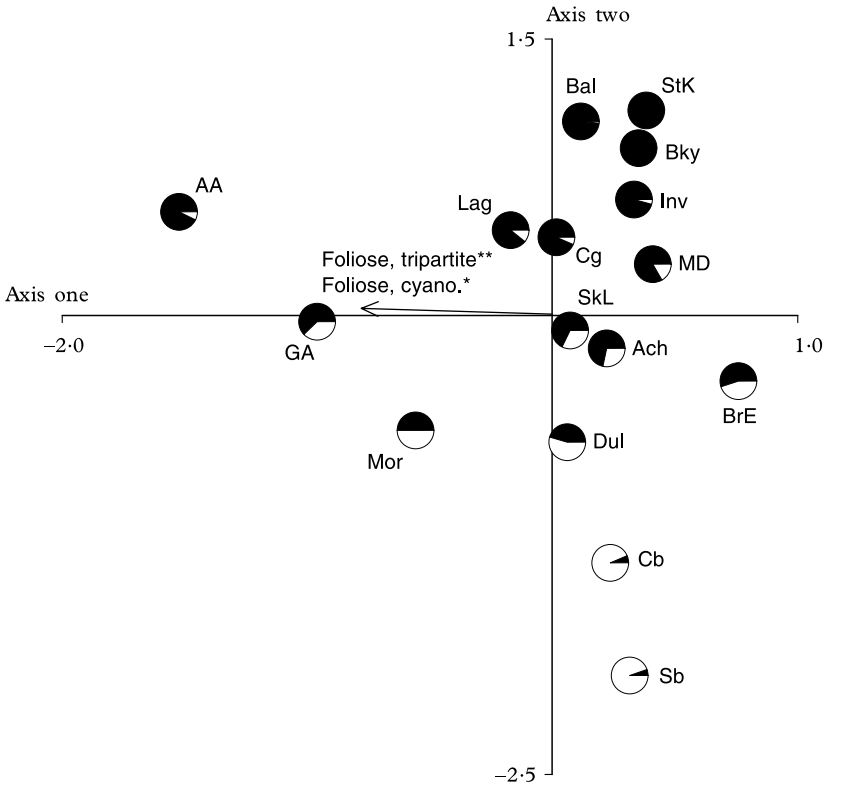

FIG. 3. Ordination of crustose lichen assemblages sampled at a stand-scale, using nonmetric multidimensional scaling to provide an optimal solution; stress=12·422, final instability=0·00001. Pie-charts indicate the relative contribution of facultative sexual and asexual species to each stand (black and white slices, respectively). Vectors show significant relationships (*r*) between the % *fo* of macro-lichen functional groups and stand scores along orthogonal axes: P=<0·02*, <0·01**, with 14 df.

Results

The sampling captured 140 lichen species (Appendix 1), representing *c*. 45% of lichen diversity on aspen in Scotland (B. J. Coppins & C. J. Ellis, unpublished data). Lichens were recorded from 524 quadrats, comprising 40 trees in 16 aspen stands. The area sampled using the spiral transect quadrat method was positively related to the surface area of the lower tree bole (R^2=0·79, P=<0·001 with 38 df) suggesting that the method effectively samples a sub-set of the epiphyte community from trees of different size, integrating the possible effect of habitat area on community structure.

Variation between-stands

Exploratory ordination by NMDS indicated that stand-scale variation in crustose lichen assemblages was best explained using a two-dimensional solution (P=0·0196) (Fig. 3). Accordingly, NMDS axes one and two explained *c*. 0·129 (12·9%) and *c*. 0·733 (73·3%) of stand-scale variation, respectively. There was a significant correlation in the relative contribution to the crustose lichen assemblage of facultatively sexual and asexual species, with the contribution of asexual species negatively related to stand-scores along axis two (r=0·977, P=<0·001 with 14 df). Comparison with co-occurring

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TABLE 1. *Results of analysis by product-moment correlation (r) to compare values for environmental variables selected as optimum explanatory factors at contrasting scales, stand-scale (cf. Fig. 3) and tree-scale (cf. Fig. 5), to the remaining (non-selected) variables. Only significant relationships are shown*

		r	*P*
Stand-scale, axis one:			
total precipitation (mm)	days >1 mm precipitation	0·785	<0·001
	average temp. coldest month	0·528	<0·05
	annual temp. range	−0·616	<0·02
	reduced rainfall index	0·868	<0·001
	aridity index	0·984	<0·001
	oceanicity index	0·818	<0·001
Stand-scale axis two:			
mean tree age (yr)	pH	−0·598	<0·02
	bark topography	−0·522	<0·05
	bark topography, variation (*s*)	−0·607	<0·02
Tree-scale axis one:			
estimated bark pH	conductivity (μS cm^{-1})	0·601	<0·005
	conductivity (μS cm^{-1}), variation (*s*)	0·492	<0·002
	bark water capacity	0·615	<0·005
	bark water capacity, variation (*s*)	0·571	<0·01
	bark topography	0·578	<0·005
	tree age	−0·477	<0·05

macro-lichen groups indicated a significant negative relationship between the frequency of foliose macro-lichens with a cyanobacterial partner (including tripartite species) and stand-scores along axis one (Fig. 3). Multiple regression with stepwise selection identified single variables explaining variation along axes one and two: stand-scores along axis one were best explained by total precipitation (mm), R^2_{adj}=0·484, P=0·002, while scores along axis two were best explained by the average age of individual trees within each stand, R^2_{adj}=0·708, P=<0·001, both with 14 df. However, total precipitation was significantly correlated with all climatic indices, days >1 mm precipitation and average temperature of the coldest month, and significantly negatively correlated with the mean annual temperature range (Table 1). The average age of individual trees within a stand was significantly negatively correlated with bark pH, bark topography and topographic variation (Table 1).

Variation within-stands

Association analysis based on spring precipitation and average tree age identified three groups with similar environmental properties, labelled I, II and III (Fig. 4). Group I comprised sites with a relatively wetter climate (F=<0·001, with 2 df), group II identified two sites with a distinct age structure, comprising older trees (F=<0·001, with 2 df), while group III comprised stands with a mixed age structure and located within a drier climatic setting (Fig. 4). The single largest group (group III) was selected for examination of individual trees. Exploratory analysis by NMDS indicated that variation at the tree-scale was best explained using a two dimensional solution (P=0·0196) (Fig. 5). Accordingly, NMDS axes one and two explained *c*. 0·711 (71·1%) and *c*. 0·141 (14·1%) of stand-scale variation, respectively. Multiple regression with stepwise selection identified a single variable explaining variation along axis one only: scores along axis one were best explained by estimated bark pH, R^2_{adj}=0·546, P=<0·001, with 21 df. The relative contribution of asexual and sexually reproducing crusts was significantly correlated to axis one scores: for example, positively correlated to proportion of asexual crusts (r=0·953, P=<0·001, with 22 df).

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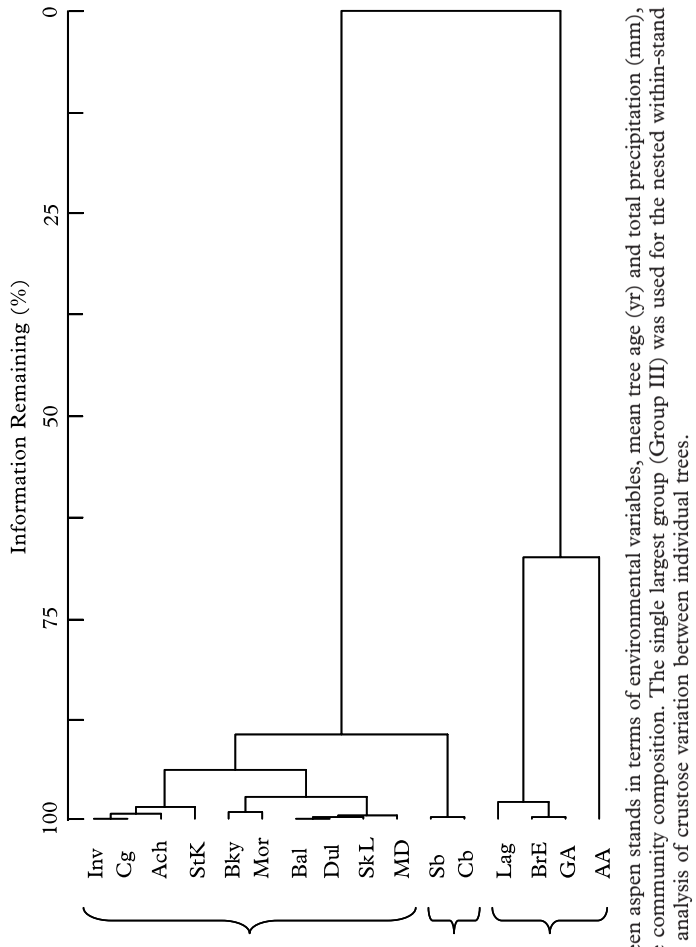

FIG. 4. Dendrogram to show similarity between aspen stands in terms of environmental variables, mean tree age (yr) and total precipitation (mm), (cf. Fig. 3), explaining differences in crustose community composition. The single largest group (Group III) was used for the nested within-stand analysis of crustose variation between individual trees.

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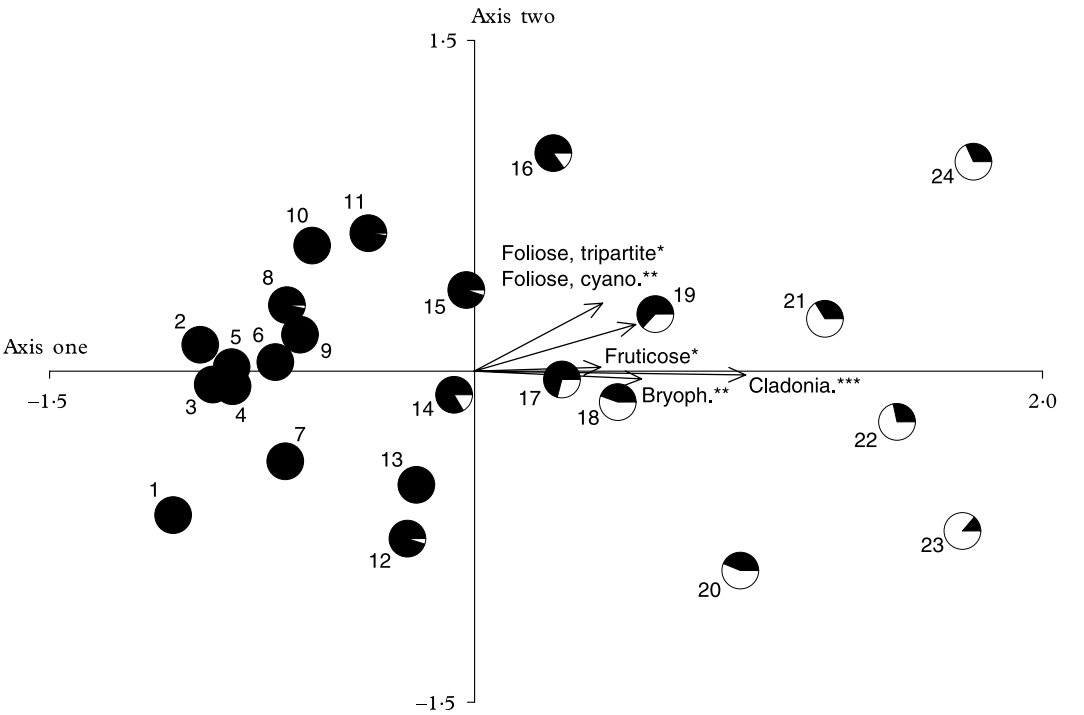

FIG. 5. Ordination of crustose lichen assemblages sampled at a tree-scale, using nonmetric multidimensional scaling to provide an optimal solution; stress=13·8, final instability=<0·00001. Pie-charts indicate the relative contribution of facultative sexual and asexual species to each stand (black and white slices, respectively). Vectors show significant relationships (*r*) between the % *fo* of macro-lichen functional groups and tree scores along axis one: *P*=<0·05*,<0·01**,<0·001***. Numbers identify individual trees from a sub-group of ten sites (with mean pH ± 1 SE), aligned along axis one: 1, Mor-ii=5·13 ± 0·19; 2, Bky-i=5·096 ± 0·09; 3, StK-i=5·03 ± 0·33; 4, Bky-ii=4·99 ± 0·1; 5, StK-ii=4·94 ± 0·23; 6, Bal-i=4·63 ± 0·21; 7, Inv-iii=5·06; 8, MD-ii=4·64 ± 0·15; 9, Inv-ii=4·44 ± 0·13; 10, Cg-ii=4·71 ± 0·17; 11, SkL-i=5·01 ± 0·14; 12, Bal-ii=4·55 ± 0·17; 13, Bky-iii=5·17 ± 0·17; 14, Inv-i=5·25 ± 1·13; 15, Ach-ii=4·57 ± 0·17; 16, Cg-i=4·66 ± 0·23; 17, Ach-iii=4·6 ± 0·3; 18, Ach-i=4·6 ± 0·27; 19, Dul-iii=4·18 ± 0·11; 20, MD-i=4·49 ± 0·27; 21, Dul-ii=4·27 ± 0·14; 22, Mor-i=4·04 ± 0·2; 23, SkL=4·37 ± 0·25; 24, 4·26 ± 0·19.

Estimated pH values were significantly negatively correlated with tree age (Fig. 6), and positively correlated with the remaining three variables pertaining to bark quality (i.e. conductivity, topography and water capacity) and with measured variation in two of these variables (i.e. conductivity and texture): Table 1.

Standardized values of % *fo* for the contrasting functional groups were significantly related to standardized tree age (Fig. 7). Nested at the tree-scale (i.e. excluding high rainfall sites), there were too few occurrences of foliose cyanobacterial and tripartite lichens for their separate analysis, and foliose lichens (predominantly green-algal types) were therefore considered as a single group. *Cladoniaceae* were included in the fruticose functional group. Standardized values of % *fo* for sexual crusts were significantly negatively related to standardized tree age, values for all other lichen groups and bryophytes were positively related to standardized tree age (Fig. 7)

Discussion

Our results provide a clear indication that the broad categorization of lichen reproductive strategies (i.e. sexual versus asexual reproduction) contributes an additional trait with which to understand lichen community

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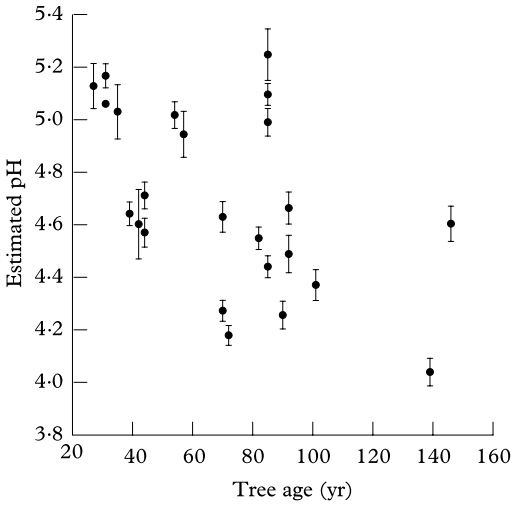

FIG. 6. Comparison of tree age (yr) and average bark pH (± 1 SE): $r = -0{\cdot}472$, $P = <0{\cdot}05$ with 22 df.

structure between and within Scottish aspen stands (Figs 3 & 5). In their original analysis of aspen epiphytes, Ellis & Coppins (2006) suggested that between-stand differences in aspen lichen communities (comprising both macro- and microlichens), were controlled by a steep climatic gradient in wetness across Scotland (with trade-offs between cyanobacterial and green-algal lichens), and that within-stand variation was explained by successional processes, i.e. a lower-bole transition between younger and older trees, from communities dominated by crustose to foliose lichens and bryophytes. Consistent with these patterns, crustose community variation related to total precipitation is indirectly correlated to vectors for tripartite and cyanobacterial foliose lichens (Fig. 3). However, the climatic gradient in wetness is a less important explanatory variable when considered within the crustose growth-form, than considered between lichen growth-forms (i.e. incorporating important differences between foliose cyanobacterial and green-algal lichens; Lange *et al*. 1986, 1988, *cf*. Ellis & Coppins 2006). Stand-scale variation in the composition of crustose lichen communities appears to be more strongly controlled by tree age structure than macroclimate. The diversity and abundance of crusts on the lower aspen bole decreases from younger to older trees (Ellis & Coppins 2006), and is broadly attributable to competition and over-topping by increasingly abundant foliose lichens and bryophytes (Topham 1977; Rogers 1990; John 1992; John & Dale 1995). This is consistent with observed trends in the % *fo* of lichen functional groups on the lower bole of younger to older aspen trees (Fig. 7), though incorporating an apparent difference between sexual and asexual crusts. The introduction of additional traits (i.e. sexual versus asexual reproduction) suggests the increasing presence of bryophytes and macrolichens on older trees (*cf*. vectors for contrasting epiphyte groups in Figs 5 & 7) is related not to a simple decrease in the overall abundance of crusts, but points instead to a transition from a crustose community dominated by sexually reproducing species, to one dominated by asexually reproducing species (Figs 5 & 7). This transition between sexual and asexual crusts is apparent when compared both between- and within- stands: between stands, related to stand age structure (Fig. 3), and within stands (Fig. 5), related to bark pH and co-varying aspects of bark quality that are correlated with tree age (Fig. 6, Table 1).

Our results support previous ecological studies that have aimed to integrate the effect of allogenic and autogenic processes explaining lichen community structure (*cf*. Kantvilis & Minchin 1989; Stone 1989; Hilmo 1994). Within aspen stands, tree age may underlie the response of crustose lichens to pH (Fig. 6), and our results point to the important role of tree age in determining habitat quality for crustose lichens within a site (Figs 5 & 7, Table 1). These within-stand effects apparently scale-up to control between-site variation related to stand age structure (Fig. 3) and are consistent with previous studies to have identified tree age as a factor controlling micro-habitat or site occupancy by lichen species. Tree age may thus comprise the allogenic control of factors such as bark chemistry, texture and moisture (Barkman 1958; Jesberger & Sheard 1973; Kantvilas & Minchin 1989), which change

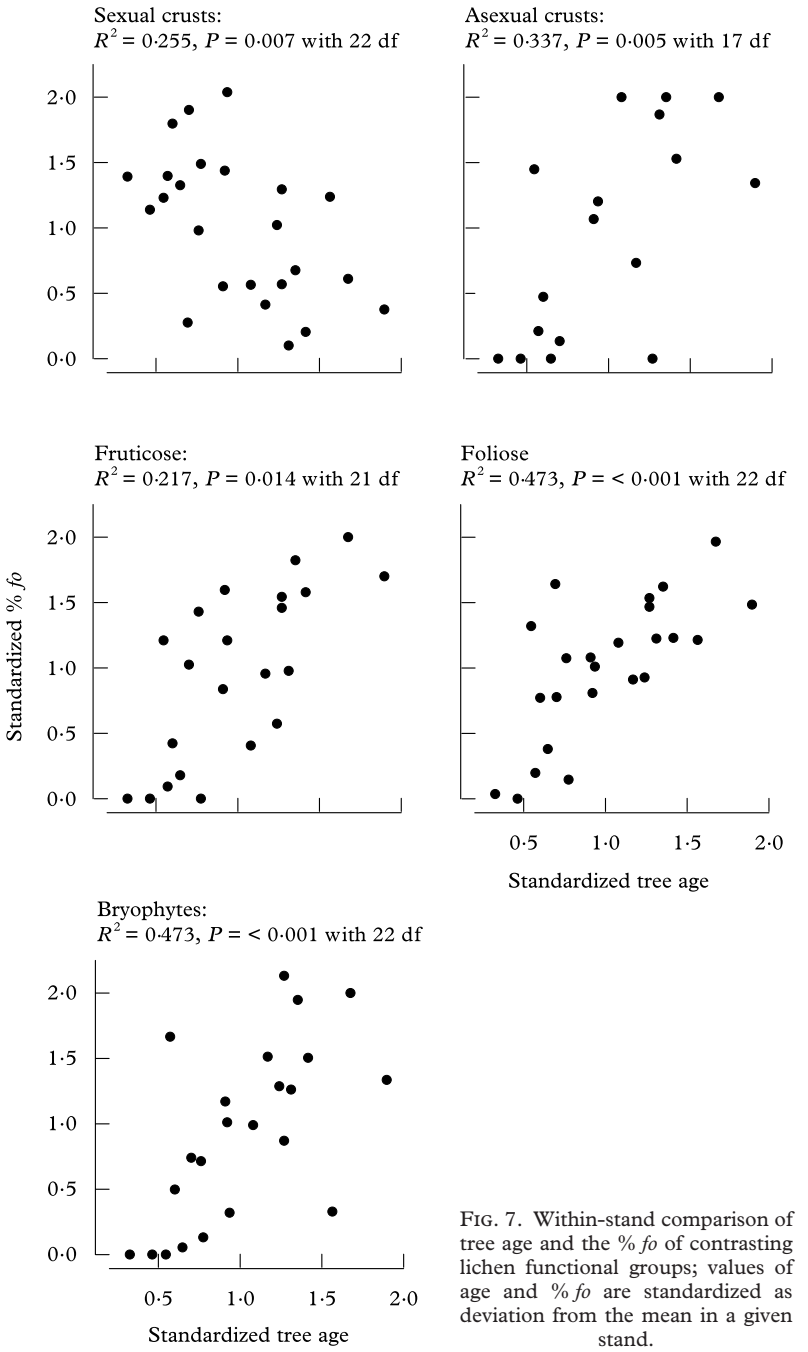

FIG. 7. Within-stand comparison of tree age and the % *fo* of contrasting lichen functional groups; values of age and % *fo* are standardized as deviation from the mean in a given stand.

during the phases of an individual tree's life-span. Estimated bark pH is only partly explained by tree age (R^2=0·22, Fig. 6), and may be further related to phenotypic variation controlled by an amalgam of factors, for example, soil chemistry (Gustafsson &

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Eriksson 1995) and genetic structure and aspen stand clonality (Bailey *et al.* 2005). Compositional variation in lichen crusts putatively explained by the response of lichen species to allogenic change in micro-environment (i.e. bark pH, water capacity and topography: Table 1) is however matched by a shift in the dominance of contrasting reproductive strategies from younger to older aspen trees (Figs 5 & 7). We believe this trait-shift demonstrates the contrasting effects of an adaptive life history trade-off, consistent with autogenic temporal succession in the lichen community. Analogous successional processes have previously been inferred for sexually and asexually reproducing macrolichens (Hedenås & Ericson 2000), and the observed transition between sexual and asexual crusts is broadly consistent with features in the recognition of *r*- and *K*-selected species (MacArthur & Wilson 1967; Begon & Mortimer 1986; Begon *et al.* 1990):

(i) *Propagule size*. The asexual species sampled from aspen have significantly larger diaspores (122 ± 31 μm) compared to the spores of sexually reproducing species ($25{\cdot}5 \pm 3.8$ μm): compared using a Mann-Whitney U-test, U=117·5, $P=<0{\cdot}001$, based on data in Purvis *et al.* (1992), Tønsberg (1992) and Foucard (2001).

(ii) *Investment in survivorship*. The asexual species sampled from aspen generally produce a greater number of lichen substances than sexually reproducing species, with an average of >2 chemicals per species ($2{\cdot}5 \pm 0{\cdot}21$), compared to ≤ 1 chemical per species for sexually reproducing crusts ($0{\cdot}92 \pm 0{\cdot}29$): compared using a Mann-Whitney U-test, U=193, $P=<0{\cdot}001$, based on data in Purvis *et al.* (1992), Tønsberg (1992) and Foucard (2001).

(iii) *Competitive ability and adaptation to stable/unstable micro-habitats*. A greater proportion of asexual crusts are vigorously competitive, with a known ability to grow over and colonize bryophytes and foliose lichens (30% of sampled species) compared to sexual crusts (5·5% of sampled species), while fewer asexual crusts occur in open smooth-bark habitats (10% of sampled species) compared to sexual crusts (44·5% of sampled species): tested using a chi-square test, $\chi^2=12{\cdot}75$, $P=<0{\cdot}01$ with 2 df, based on data in Purvis *et al.* (1992) and field notes (B. J. Coppins, unpublished data).

Features of the asexual crusts sampled from aspen—larger propagule size, greater investment in lichen substances and increased competitive ability—suggest adaptation to a stable habitat in which individual lichens are relatively more crowded and mixed populations are approaching or are at the micro-habitat's carrying capacity (*K*). Differences in propagule size result in local dispersal effects, i.e. diaspores may be locally dispersed within suitable habitats (Hedenås *et al.* 2003), compared to long-range dispersal by spores. The contrasting dispersal strategies point to an adaptation of asexual crusts to establishment within more crowded micro-habitats, consistent with their apparently greater competitive ability, and contrasting with a ruderal strategy of spore-dispersed migration between unoccupied patches (Grime 1977, 1979; Rogers 1990). Similarly, studies have indicated greater investment in chemical or structural defence amongst later-successional *K*-selected organisms (Cates & Orians 1975); the production of certain lichen substances has been linked to herbivore defence (Lawrey 1983; Gauslaa 1985), and tentatively implies a generally greater investment in thallus survivorship by asexual species (Rogers 1990).

The contrasting response in a specific micro-habitat (i.e. the lower bole of aspen) between sexual and asexual crusts matches evidence to suggest that the lichen response to larger-scale drivers (e.g. habitat loss and fragmentation) can be effectively summarized via an equivalent trait-based approach e.g. asexual crusts may be more sensitive to habitat fragmentation and loss compared to sexual crusts (Löbel *et al.* 2006; Ellis & Coppins 2007). Thus, examining the effect of larger scale impacts (i.e. climate change and habitat fragmentation) on traits responsive to micro-habitat and local successional processes may provide a pathway to

investigating community response between scales. The trait based approach may therefore provide a crucial link between the effective local management of habitats and mitigation of regional, larger-scale threats.

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Appendix 1. *Lichen species recorded from aspen during the quadrat sampling and their designated functional groups*

Species	Functional group‡
Anisomeridium biforme	Sex. crust, algal
Arthonia didyma	Sex. crust, algal
A. muscigena	Sex. crust, algal
A. patellulata	Sex. crust, algal
A. radiata	Sex. crust, algal
Bacidia absistens	Sex. crust, algal
B. arceutina	Sex. crust, algal
B. circumspecta	Sex. crust, algal
B. igniarii	Sex. crust, algal
B. rubella	Sex. crust, algal
B. subcircumspecta	Sex. crust, algal
B. subincompta	Sex. crust, algal
B. vermifera	Sex. crust, algal
Biatoridium delitescens	Sex. crust, algal
Bryoria fuscescens	Fruticose, algal
Buellia disciforme	Sex. crust, algal
B. erubescens	Sex. crust, algal
B. griseovirens	Asex. crust, algal
Calicium viride	Sex. crust, algal
Caloplaca ahtii	Asex. crust, algal
C. cerina	Sex. crust, algal
C. cerinella	Sex. crust, algal
C. ferruginea	Sex. crust, algal
C. holocarpa	Sex. crust, algal
†*C. obscurella*	Sex. crust, algal
Candelariella superdistans	Sex. crust, algal
Catillaria nigroclavata	Sex. crust, algal
Catinaria atropurpurea	Sex. crust, algal
Chrysothrix candelaris	Asex. crust, algal
Cladonia chlorophaea	*Cladoniaceae*
C. coniocraea	*Cladoniaceae*
C. fimbriata	*Cladoniaceae*
C. macilenta	*Cladoniaceae*
C. pyxidata	*Cladoniaceae*
Cliostomum griffithii	Sex. crust, algal
Collema fasciculare	Foliose, cyano.
C. subflaccidum	Foliose, cyano.
C. occultatum	Foliose, cyano.
Degelia atlantica	Foliose, cyano.
D. plumbea	Foliose, cyano.
Dimerella pineti	Sex. crust, algal
Diplotomma pharcidium	Sex. crust, algal
Evernia prunastri	Fruticose, algal
Fuscidea recensa	Asex. crust, algal
Fuscopannaria mediterranea	Foliose, cyano.
Hypogymnia physodes	Foliose, algal
H. tubulosa	Foliose, algal
Japewia subaurifera	Asex. crust, algal
Lauderlindsaya acroglypta	Sex. crust, algal
Lecania cyrtella	Sex. crust, algal
L. naegelii	Sex. crust, algal
L. sambucina	Sex. crust, algal
Lecanora cf. '*caledonica*'	Sex. crust, algal
L. carpinea	Sex. crust, algal
L. chlarotera	Sex. crust, algal
Lecanora expallens	Asex. crust, algal
L. persimilis	Sex. crust, algal
L. populicola	Sex. crust, algal
L. pulicaris	Sex. crust, algal
L. sambuci	Sex. crust, algal
Lecidella elaeochroma	Sex. crust, algal
Lepraria sp.	Asex. crust, algal
L. elobata	Asex. crust, algal
L. lobificans	Asex. crust, algal
cf. *L. jackii*	Asex. crust, algal
L. rigidula	Asex. crust, algal
Leptogium lichenoides	Foliose, cyano.
L. saturninum	Foliose, cyano.
Leptorhaphis atomaria	Sex. crust, algal
Lobaria amplissima	Foliose, tripartite
L. pulmonaria	Foliose, tripartite
L. scrobiculata	Foliose, cyano.
L. virens	Foliose, algal
Megalaria grossa	Sex. crust, algal
M. pulverea	Asex. crust, algal
Melanelia exasperata	Foliose, algal
M. fuliginosa subsp. *glabratula*	Foliose, algal
M. subaurifera	Foliose, algal
Melaspilea 'sp. D'	Sex. crust, algal
Melaspilea sp.	Sex. crust, algal
Micarea micrococca	Sex. crust, algal
M. peliocarpa	Sex. crust, algal
Mycoblastus fucatus	Asex. crust, algal
Normandina pulchella	Foliose, algal
Nephroma laevigatum	Foliose, cyano.
N. parile	Foliose, cyano.
Ochrolechia androgyna	Asex. crust, algal
O. microstictoides	Asex. crust, algal
O. subviridis	Asex. crust, algal
O. szatalaensis	Sex. crust, algal
O. tartarea	Sex. crust, algal
Opegrapha atra	Sex. crust, algal
O. herbarum	Sex. crust, algal
O. multipuncta	Asex. crust, algal
O. rufescens	Sex. crust, algal
O sorediifera	Asex. crust, algal
Pannaria conoplea	Foliose, cyano.
P. rubiginosa	Foliose, cyano.
Parmelia saxatilis	Foliose, algal
P. sulcata	Foliose, algal
Parmeliella triptophylla	Foliose, cyano.
Parmotrema chinense	Foliose, algal
P. crinitum	Foliose, algal
Peltigera collina	Foliose, cyano.
P. hymenina	Foliose, cyano.
P. praetextata	Foliose, cyano.
Pertusaria albescens	Asex. crust, algal
P. amara	Asex. crust, algal
P. borealis	Asex. crust, algal
P. coronata	Asex. crust, algal

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Appendix 1. *Continued*

Species	Functional group‡
Pertusaria hemisphaerica	Asex. crust, algal
P. hymenea	Sex. crust, algal
P. leioplaca	Sex. crust, algal
P. pertusa	Sex. crust, algal
P. pupillaris	Asex. crust, algal
Phaeophyscia orbicularis	Foliose, algal
Phlyctis argena	Asex. crust, algal
Physcia adscendens	Foliose, algal
P. aipolia	Foliose, algal
P. stellaris	Foliose, algal
P. tenella	Foliose, algal
Physconia distorta	Foliose, algal
Platismatia glauca	Foliose, algal
Porina aenea	Sex. crust, algal
Protopannaria pezizoides	Foliose, cyano.
Protoparmelia ochrococca	Sex. crust, algal
Pseudevernia furfuracea	Foliose, algal
Ramalina farinacea	Fruticose, algal
R. fastigiata	Fruticose, algal
R. fraxinea	Fruticose, algal
Scoliciosporum chlorococcum	Sex. crust, algal
S. umbrinum	Sex. crust, algal
Sticta limbata	Foliose, cyano.
S. sylvatica	Foliose, cyano.
Tephromela atra	Sex. crust, algal
Usnea subfloridana	Fruticose, algal
Xanthoria parietina	Foliose, algal
X. polycarpa	Foliose, algal
*Sorediate crust sp. a	Asex. crust, algal
**Sorediate crust sp. b	Asex. crust, algal

†*C. obscurella* although often lacking ascomata was frequently observed with apothecia in the habitat examined here, and is included as a sexual crust.
*Ellis L.389 (E)
**Ellis L.376-380 (E)
‡Sex. crust=sexual crust; Asex. crust=asexual crust; algal=green algal; cyano.=cyanobacterial.

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