

Macrolichen communities in relation to soils and vegetation in the Noatak National Preserve, Alaska

Emily A. Holt, Bruce McCune, and Peter Neitlich

Abstract: Macrolichen community structure and its relation to environment in the Noatak National Preserve, Alaska, is described using a two-way stratified random sample. We found 201 macrolichen taxa. Two primary gradients in lichen species composition were related to substrate pH and vegetation physiognomy, grading from forests to high alpine communities. Site characteristics associated with the first community gradient are soil moisture and exposure. Both ends of this gradient, including protected forests and densely shrubby sites at one end and exposed, high elevation alpine sites at the other end, are relatively dry and well-drained. The mid-region of this gradient consists of mesic, lowland tundra habitats. The second gradient, related to substrate pH, is driven by the presence of *Sphagnum* moss contrasting with calcareous soils and bedrock. Combining these two gradients of lichen community composition, we found six groups of plots using two-way cluster analysis. Further, division of macrolichen species occurring in five or more plots yielded seven species groups, based on a combination of environmental factors and species distribution characteristics. This snapshot of macrolichen communities in Arctic Alaska serves as an important baseline for future comparisons to environments altered by changing climate and land use.

Key words: Arctic, lichen community, substrate, tundra, two-way cluster analysis.

Résumé : Les auteurs décrivent la structure des communautés de macrolichens et leurs relations avec le milieu dans la Noatak National Preserve en Alaska, en utilisant un échantillonnage aléatoire stratifié à deux variables. Ils ont repéré 201 taxons de lichens. On observe deux gradients primaires dans la composition en espèces de lichens en relation avec le pH du substrat et la physiognomie de la végétation, allant de la forêt aux communautés de l'étage alpin supérieur. L'humidité du sol et l'exposition constituent les caractéristiques des sites associés au gradient des premières communautés. À une extrémité du gradient, incluant les aires protégées, on retrouve des forêts et des arbustaies denses, et à l'autre extrémité des sites alpins exposés et situés à haute élévation, sur des sites relativement secs et bien drainés. La région médiane de ce gradient comporte des habitats de toundra mésique en basse altitude. Le second gradient, relié au pH du substrat, est influencé par la présence de sphaignes en contraste avec les sols et la roche-mère calcaires. En combinant ces deux gradients de la communauté lichénique, les auteurs ont identifié six groupes de parcelles en utilisant l'analyse par regroupement à deux variables. De plus, la division des espèces de macrolichens trouvés dans 5 parcelles ou plus identifie 7 groupes d'espèces, en se basant sur une combinaison de facteurs environnementaux et sur les caractéristiques de la distribution des espèces. Cette vue instantanée des communautés des lichens de l'Arctique, en Alaska, constitue une importante ligne de base pour des comparaisons futures avec les milieux affectés par le changement climatique et l'utilisation des terres.

Mots-clés : Arctique, communauté lichénique, substrat, toundra, analyse par regroupement à deux variables.

[Traduit par la Rédaction]

Introduction

Macrolichens contribute a large portion of the biomass and diversity to Arctic environments, including both tundra and boreal forested systems. Changing climate and land uses threaten Arctic ecosystems; thus, research is needed to

document current biodiversity and landscape-level gradients for comparison with the future. Within the state of Alaska, most previous lichen studies have focused on taxonomy (Krog 1968, 1973; Thomson 1984; Flock 1989), the role of lichen as reindeer or caribou forage (e.g., Pegau 1968; Holt et al. 2008a), their contribution to the nitrogen cycle (e.g., Gunther 1989; Weiss et al. 2005), or how lichens respond to disturbance (e.g., Racine 1981; Ford et al. 1995; Racine et al. 2004; Wahren et al. 2005).

Within northwestern Alaska specifically, several large-scale studies have been conducted to classify the major vegetation types, yet lichens are only represented as a single unit (Hanson 1953; Muller et al. 1999). Most species-level lichen work in Alaska has focused on north-central regions of the state or has focused on only a few specific taxa (e.g., Moser et al. 1979; Swanson et al. 1985; Auerbach et al. 1997). Community-level studies of macrolichen ecology are

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almost completely lacking from the Arctic of western North America. Few cases describe macrolichen community ecology, yet are based in more southern subarctic regions (e.g., Lambert and Maycock 1968; See and Bliss 1980). In addition, detailed species-level determinations for Arctic North America are confined to floristic inventories, which do not address the ecology of these communities (e.g., Ahti et al. 1973; Douglas and Vitt 1976; Thomson and Ahti 1994; Talbot et al. 2001). The only comparable study was conducted on the Seward Peninsula of Alaska (Holt et al. 2007).

We chose to study an area in northwestern Alaska previously unexplored for lichens, the Noatak National Preserve. The closest extensive lichen studies to this area were conducted just east in Gates of the Arctic National Park (Neitlich and Hasselbach 1998) and to the southwest in the Bering Land Bridge National Preserve (Holt et al. 2007). These studies identified latitude, vegetation type, habitat rockiness, topography, and substrate as the primary factors driving lichen community patterns. In the present study, our objective was to describe lichen community structure and its relation to environment, specifically including the factors listed above, in the Noatak National Preserve. We used a stratified random sample to partition our heterogeneous landscape, increase the precision and efficiency of estimates for variables of interest (Husch et al. 1972), and to allow for Preserve-wide estimates of lichen community parameters. Furthermore, we identified general groupings of lichen community composition to understand how lichen community patterns relate to the landscape.

Materials and methods

Study site

The Noatak National Preserve, an International Biosphere Reserve, is located on the south slope of the Brooks Range in northwestern Alaska (67°02'–68°39'N, 155°50'–162°55'W; Fig. 1). This Preserve was originally created as a national monument by Presidential proclamation in 1978. Two years later, the area became a Preserve as one of the 10 new areas included in the Alaska National Interest Lands Conservation Act of 1980. These lands were designated a National Preserve to protect the environmental integrity of the lower portion of the Noatak watershed (including the Noatak River and surrounding regions), its wildlife habitat, and its archaeological resources.

Temperatures of the western portions of Noatak National Preserve are tempered by the oceanic influence of the Chukchi Sea, whereas eastern portions of the Preserve have a more interior, continental climate and experience greater temperature extremes. Weather stations nearest the Preserve are located in Ambler, 36 km to the southeast, and Kotzebue, 24 km to the southwest. Mean January and July temperatures in Ambler are –23.2° and 15.2 °C, respectively. Similarly, mean January and July temperatures in Kotzebue are –19.4° and 12.4 °C, respectively. Mean annual precipitation is 55.9 cm in Ambler and 28.9 cm in Kotzebue. Most precipitation falls in late summer, usually August or September. Snowfall is greatest in January. Mean total snowfall in Ambler is 264.4 cm and 148.5 cm in Kotzebue.

The Noatak River bisects the Preserve from east to west. The northern boundary of the Preserve follows the crest of

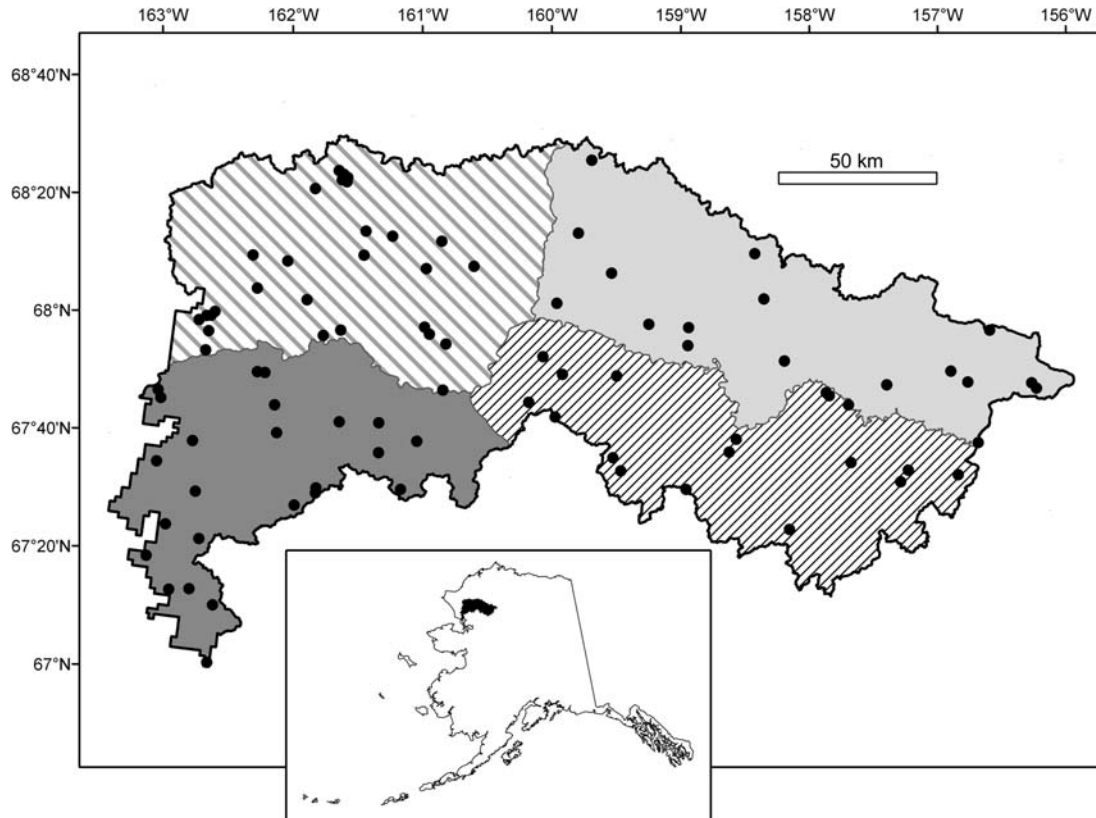
the DeLong Mountains and the southern border snakes through the Baird Mountains. These mountains form the western edge of the Brooks Range. Two hundred million years ago, the Brookian orogeny began as older, oceanic crust underthrust southward beneath younger, oceanic crust in the approximate location of the Noatak National Preserve. These crusts were derived primarily of marine sediments deposited over carbonate rocks (Moore et al. 1994). North of the Preserve, subduction induced metamorphism and rifting (Moore et al. 1994). Lower crustal rocks uplifted causing faulting and folding of these layers, which eroded as clastic debris southward into the Koyukuk basin and north into the Coville basin (Moore et al. 1994). The DeLong Mountains are dominated primarily by limestone, dolomite, sandstone, and shale. On the other hand, graywacke, argillite, quartzite, shale, and chert underlie much of the Baird Mountains. The lowlands adjacent to the River are underlain by a mixture of rock types from both sets of mountains. The elevation in the Preserve ranges from just above sea level (~10 m) near the mouth of the Noatak River to about 1750 m a.s.l. in the Schwatka Mountains along the border with Gates of the Arctic National Park and Preserve.

The general vegetation types present in northwestern Alaska are *Eriophorum* tussock tundra, *Dryas* fell-field, ericaceous shrub tundra, *Eriophorum*–*Carex* wet meadow, solifluction slopes, and boreal forest (Viereck et al. 1992). High-elevation sites in the De Long, Schwatka, and Baird mountains contain sparsely vegetated rocky, alpine communities. These occur along the north, south, and eastern borders of the Preserve. Otherwise, low shrub or tussock tundra dominates much of the Preserve. Forests, dominated by *Picea glauca* (Moench) Voss, comprise only a small portion of the Preserve's vegetation, and occur almost strictly in the southwestern corner of the Preserve. Shrubs consist of *Salix* spp., *Betula glandulosa* Michx., and *Alnus crispa* (Ait.) Pursh. The herb layer contains mixed *Eriophorum* spp. and *Carex* spp., *Vaccinium* spp., *Arctostaphylos* spp., *Empetrum nigrum* L., *Cassiope tetragona* L., *Ledum palustre* L. var. *decumbens* Ait., and *Rubus chamaemorus* L. The dominant mosses are *Pleurozium schreberi* (Brid.) Mitt., and *Hylocomium splendens* (Hedw.) Schimp., with some *Sphagnum* spp. The lichen flora is dominated by species from the genera *Cladina*, *Cladonia*, *Cetraria*, *Peltigera*, and *Stereocaulon*.

Sampling

We used a two-way stratified random sample. One of our stratifying variables was geographic information systems (GIS) land cover data (Markon and Wesser 1998). The original GIS land cover map within the Preserve had 15 different land cover types. Based on previous knowledge of the area (Holt et al. 2007), similarity or overlap in cover-type categories and the goal of minimizing the number of strata (Holt et al. 2008b), we reclassified the cover types into seven new cover types. We then used adaptive sampling with our first year's data to determine the sampling intensity within each of the seven cover types. Cover types with greater lichen species richness and frequency were sampled proportionately more than less diverse cover types. Geographic blocks were the other stratifying variable, used to balance sampling across the area of interest (Fig. 1). The

Fig. 1. Map of the Noatak National Preserve in northwestern Alaska. Points indicate 88 plots sampled in 2004 and 2005. The geographic blocks used in sampling stratification are shown as four differently shaded portions of the Preserve. The north–south division follows the Noatak River. The east–west division between the northern two blocks is the Nimiuktuk River, while the southern east–west border was hand-drawn to create roughly equal area blocks.



Preserve was divided into four geographic blocks whose boundaries coincided with Preserve boundaries and physiographic regions created by the Noatak and Nimiuktuk Rivers. Within each geographic block, several points from each of the seven cover types were randomly located. The number of plots in each geographic block was roughly equal, while each cover type was represented proportionate to its average species richness as mentioned above.

Lichen community composition was evaluated using a variant of long-term lichen monitoring protocol implemented in previous studies (McCune et al. 1997; McCune 2000). Designed for temperate forests and applied to thousands of plots in the continental US, these protocols focus on epiphytic macrolichens. Although the few forested sites we visited could implement these protocols, most sites lacked trees. In such tundra environments, we sampled all terricolous macrolichens and epiphytic macrolichens on shrubs. Preservation of key elements of the technique facilitates future comparisons.

Sample units were circular fixed-area plots with a 34.7 m radius. Each species encountered was assigned an abundance value: 1, rare (<3 thalli); 2, uncommon (4–10 thalli); 3, common (<1% cover); 4, abundant (1%–5% cover); 5, prolific (6%–25% cover); and 6, dominant (>26% cover). All bryophyte taxa present were estimated using the same abundance scale, but these were included in the environmental matrix rather than the community matrix. Environmental measurements included topographic variables, as well as

percent cover of various aspects of the vegetation. Aspect and slope were transformed into estimates of potential annual direct incident radiation, based on the maximum northern latitude the computations can handle (60°N; McCune and Keon 2002).

Lichen determinations were primarily based on Thomson (1984), Goward et al. (1994), and Goward (1999). For the identification of lichen substances in some *Bryoria*, *Cladonia*, *Hypogymnia*, and *Stereocaulon*, we used thin-layer chromatography. All *Cladonia* identifications were based on voucher specimens with podetia, and strictly squamulose thalli were not recorded. Specimens from the *Cladonia phyllophora* Ehrh. ex Hoffm. and *Cladonia cervicornis* Ach. Flot. groups were identified using Brodo and Ahti (1995). UV light was used to distinguish between the two chemical species of *Thamnolia*, which were also collected from every site at which they occurred. Vouchers were deposited at Oregon State University Herbarium (OSC) and the National Park Service Herbarium in Anchorage, Alaska.

Additional variables

We estimated the successional status of each site using three independent methods; counts of twig annual growth rings, lichen height, and successional scores based on lichen community composition. Just over half our plots contained trees or large shrubs that could be cored or cut down to estimate age based on growth rings. Lichen height has been used elsewhere to measure the response of lichen to disturb-

ance (e.g., Ahti 1959; Steen 1965; Holt et al. 2008a). This measure assumes that grazing and other ground disturbances can result in shorter lichens compared to tall lichens that inhabit undisturbed sites. All except seven plots contained *Cladina rangiferina* L. Nyl., *Cladina arbuscula* Wallr. Rabenh. – *Cladina mitis* (Sandst.) Hustich. (isomorphs lumped in the field), *Cetraria cucullata* (Bellardi) Ach. and *Cetraria islandica* (L.) Ach. – *Cetraria laevigata* Ras. (isomorphs lumped in the field). We measured the length of these four species where available. Strong linear relationships among heights from different species allowed us to average the four measurements into a single variable of average lichen height.

Finally, we created a variable to represent the successional status of each plot. In a previous study, we categorized 46 species into early, mid- or late successional stages using a synthesis of literature reports on succession following grazing and fire (Holt et al. 2006). Each species was assigned a successional species score of one, two, or three to represent these early to late-successional stages, respectively. We used weighted averaging to combine our abundance estimates with these species scores yielding successional plot scores for each site.

Data adjustments

We first determined whether any plots were multivariate outliers by comparing average community distances between plots. Five of the 88 plots: Plots Q3-S4, NE-6d, 04-S1, 04-S8, and NE-2c, had average Sørensen distances of greater than two standard deviations from the grand mean of all distances. These plots were all outliers because their sample unit totals (between 1 and 7) and richness values (between 1 and 5 species) were far lower than average (47.8 and 25.7 species). In ordinations, the extreme peripheral position of all five plots outside the main point cloud indicated axes gave undue weight to these plots. All five plots were, therefore, removed from all analyses.

Modifications to the community matrix were minimal. The coarse, approximately logarithmic, cover class scale alleviated the need for transformation. However, doubleton species, or those documented twice or less in our sampling (69 species total), were deleted from the community matrix to reduce noise and strengthen community relationships. For the two-way cluster analysis, species occurring in four or fewer plots (92 species total) were deleted to clarify patterns in the diagram. Transformations were needed within the environmental matrix, composed primarily of raw cover values. These cover variables were converted to proportions and arcsine square root transformed for all analyses. This transformation improves normality and reduces skewness within variables measured as proportions (Sokal and Rohlf 1995). In addition, slope was log transformed to increase normality.

Analyses

The goal of this study was to understand community structure, and its relationships to environmental gradients. We used multivariate analysis in PC-ORD 5 (McCune and

Mefford 2005). Nonmetric multidimensional scaling (NMS) summarized the multivariate relationships among plots (Kruskal 1964; Mather 1976). NMS avoids assumptions of linearity among community variables (McCune and Grace 2002). In addition, NMS allows use of the Sørensen distance measure that is effective with community data. The “slow and thorough” autopilot mode of PC-ORD sought the best fit (lowest stress and instability from multiple random starting configurations). We used a maximum of 500 iterations in 250 runs of real data. The significance of the best fit was tested as the proportion of randomizations with stress less than or equal to the observed stress, using 250 trials. Randomizations shuffled elements of the community matrix within species. Ordinations were rigidly rotated to load the strongest environmental variable onto a single axis. The final configuration of sample units in species space consists of ordination scores for each plot on each axis. The coefficient of determination is the proportion of variance in Sørensen distance from the original matrix that was represented by Euclidean distance in the ordination. Linear relationships between ordination scores and environmental variables were depicted as joint plots.

We sought groupings of species and plots based on lichen community composition using two-way hierarchical agglomerative cluster analyses in PC-ORD 5 (McCune and Mefford 2005). Two-way cluster analysis independently groups sample units and species, then combines them into a single diagram to allow observation of associations between groups of sample units and species. The data were relativized by species maximum to diminish, but not eliminate, the influence of species totals on species clustering. We used flexible beta ($\beta = -0.25$) as the linkage method on Sørensen distances. The optimal number of groups of plots was first evaluated with multiresponse permutation procedure (MRPP; Mielke 1984), seeking the solution with fewest number of groups but the greatest gain in A-statistics (McCune and Grace 2002). Owing to the absence of a plateau in A-statistics, however, we chose the number of plot and species groups to optimize interpretation.

Results

Diversity

We found a total of 201 unique macrolichen taxa from 88 plots in the Noatak National Preserve, Alaska (Table 1). Previously unpublished and noteworthy collections will be addressed in another paper (unpublished data³). The most frequently occurring lichens included *Cetraria cucullata*, *Cladonia amaurocraea* (Flörke) Schaer., *Cetraria islandica*, *Cetraria nivalis* (L.) Ach. and *C. laevigata*. *Bryoria implexa* (Hoffm.) Brodo and D. Hawk. and *Cetraria commixta* (Nyl.) Th. Fr., however, were the two taxa with the greatest average abundance. The average species richness was 25.7 per plot. Following deletion of outliers and doubleton species, the average species richness was 26.0. Beta diversity, the total number of species from all plots combined divided by the average species richness and all subtracted by one (β_w), is the average compositional difference among plots

³ B. McCune, E. Holt, P. Neitlich, T. Ahti, and R. Rosentrater. Macrolichen diversity in Noatak National Preserve, Alaska. Manuscript in preparation.

Table 1. Macrolichen taxa found in the Noatak National Preserve from 88 plots.

Species	Code	Ave	Freq
<i>Alectoria nigricans</i>	Alenig	1.3	12
<i>Alectoria ochroleuca</i>	Aleoch	1.8	24
<i>Allantoparmelia alpicola</i>	Allalp	1.0	1
<i>Arctoparmelia centrifuga</i>	Arccen	1.3	3
<i>Arctoparmelia separata</i>	Arcsep	2.0	15
<i>Asahinea chrysantha</i>	Asachr	2.2	37
<i>Asahinea scholanderi</i>	Asasch	1.6	5
<i>Bryocaulon divergens</i>	Brcdiv	1.6	29
<i>Brodoa oroarctica</i>	Brooro	2.0	1
<i>Bryoria fuscescens</i>	Bryfus	3.0	3
<i>Bryoria implexa</i>	Bryimp	4.0	1
<i>Bryoria lanestris</i>	Brylan	2.2	6
<i>Bryoria nitidula</i>	Brynit	1.3	7
<i>Bryoria simplicior</i>	Brysim	2.0	2
<i>Bryoria trichodes</i>	Brytra	3.0	1
<i>Cetrelia alaskana</i>	Celala	1.0	1
<i>Cetraria andrejevii</i>	Cetand	2.0	3
<i>Cetraria commixta</i>	Cetcom	4.0	1
<i>Cetraria cucullata</i>	Cetcuc	2.6	71
<i>Cetraria delisei</i>	Cetdel	2.3	15
<i>Cetraria ericetorum</i>	Ceteri	2.3	6
<i>Cetraria fastigiata</i>	Cetfas	2.0	2
<i>Cetraria hepaticon</i>	Cet hep	2.0	4
<i>Cetraria inermis</i>	Cetine	1.1	7
<i>Cetraria islandica</i>	Cetisl	2.3	61
<i>Cetraria kamiczatica</i>	Cetkam	1.3	15
<i>Cetraria laevigata</i>	Cetlae	2.0	58
<i>Cetraria nigricans</i>	Cetnig	1.8	13
<i>Cetraria nivalis</i>	Cetniv	2.0	59
<i>Cetraria orbata</i>	Cetorb	1.0	1
<i>Cetraria pinastri</i>	Cetpin	1.7	40
<i>Cetraria sepincola</i>	Cetsep	1.6	31
<i>Cetraria tilesii</i>	Cettil	2.5	26
<i>Cladina arbuscula</i>	Cldarb	2.6	48
<i>Cladina mitis</i>	Cldmit	2.9	15
<i>Cladina rangiferina</i>	Cldran	2.4	50
<i>Cladina stellaris</i>	Cldste	1.6	8
<i>Cladina stygia</i>	Cldsty	2.4	36
<i>Cladonia acuminata</i>	Claacu	1.2	6
<i>Cladonia alaskana</i>	Claala	1.0	1
<i>Cladonia albonigra</i>	Claalb	1.8	9
<i>Cladonia amaurocraea</i>	Claama	2.7	61
<i>Cladonia bacillaris</i>	Clabac	1.0	1
<i>Cladonia bacilliformis</i>	Clabaf	1.3	8
<i>Cladonia bellidiflora</i>	Clabel	1.0	3
<i>Cladonia borealis</i>	Clabor	1.5	21
<i>Cladonia botrytes</i>	Clabot	1.0	2
<i>Cladonia cariosa</i>	Clacai	1.3	3
<i>Cladonia cenotea</i>	Clacen	1.6	29
<i>Cladonia cervicornis</i>	Clacer	1.0	5
<i>Cladonia chlorophaea</i>	Clachl	1.4	22
<i>Cladonia coccifera</i>	Clacoc	2.1	15
<i>Cladonia coniocraea</i>	Clacon	1.0	2
<i>Cladonia cornuta</i>	Clacor	1.6	36
<i>Cladonia crispata</i>	Clacri	1.5	17
<i>Cladonia cryptochlorophaea</i>	Clacry	1.4	5
<i>Cladonia cyanipes</i>	Clacya	1.8	32

Table 1 (continued).

Species	Code	Ave	Freq
<i>Cladonia decorticata</i>	Cladec	1.1	8
<i>Cladonia deformis</i>	Cladef	1.0	4
<i>Cladonia digitata</i>	Cladig	1.0	2
<i>Cladonia ecmocyna</i>	Claecm	1.0	1
<i>Cladonia fimbriata</i>	Clafim	1.1	14
<i>Cladonia furcata</i>	Clafur	1.3	7
<i>Cladonia gracilis</i>	Clagra	1.8	48
<i>Cladonia grayi</i>	Clagry	1.2	6
<i>Cladonia kanewskii</i>	Clakan	1.0	3
<i>Cladonia libifera</i>	Clalib	1.0	5
<i>Cladonia macrophylla</i>	Clamac	1.5	11
<i>Cladonia macrophyllodes</i>	Clamao	1.0	1
<i>Cladonia macroceras</i>	Clamas	1.3	16
<i>Cladonia maxima</i>	Clamax	1.7	29
<i>Cladonia metacorallifera</i>	Clamet	1.0	1
<i>Cladonia nipponica</i>	Clanip	1.0	1
<i>Cladonia nitens</i>	Clanit	3.0	1
<i>Cladonia ochrochlora</i>	Claoch	1.0	1
<i>Cladonia phyllophora</i>	Claphy	1.3	10
<i>Cladonia pleurota</i>	Claple	1.2	9
<i>Cladonia pocillum</i>	Clapoc	1.9	30
<i>Cladonia pyxidata</i>	Clapyx	1.6	26
<i>Cladonia scabriuscula</i>	Clasca	1.0	7
<i>Cladonia squamosa</i>	Clasqu	1.1	9
<i>Cladonia stricta</i>	Clastr	1.3	15
<i>Cladonia subfurcata</i>	Clasuf	1.3	12
<i>Cladonia symphylicarpa</i>	Clasyp	1.3	3
<i>Cladonia symphylicarpa</i>	Clasym	1.0	1
<i>Cladonia sulphurina</i>	Clasul	1.4	21
<i>Cladonia trassii</i>	Clatra	1.0	2
<i>Cladonia uncialis</i>	Claunc	2.2	35
<i>Cladonia wainioi</i>	Clawai	1.0	1
<i>Coccocarpia erythroxyli</i>	Cocery	2.0	2
<i>Coelocaulon aculeatum</i>	Coeacu	1.0	1
<i>Coelocaulon muricatum</i>	Coemur	1.4	15
<i>Collema cristatum</i>	Colcri	1.0	1
<i>Collema furfuraceum</i>	Colfur	2.0	1
<i>Collema fuscovirens</i>	Colfus	1.2	6
<i>Collema tenax</i>	Colten	1.0	4
<i>Collema undulatum</i>	Colund	1.0	1
<i>Dactylina arctica</i>	Dacarc	1.9	40
<i>Dactylina beringica</i>	Dacber	2.3	21
<i>Dactylina ramulosa</i>	Dacram	1.7	28
<i>Ephebe hispidula</i>	Ephhis	2.0	1
<i>Evernia divaricata</i>	Evediv	2.3	3
<i>Evernia mesomorpha</i>	Evemes	1.4	7
<i>Evernia perfragilis</i>	Eveper	2.0	2
<i>Hypogymnia bitteri</i>	Hypbit	2.8	11
<i>Hypogymnia physodes</i>	Hypphy	1.5	15
<i>Hypogymnia subobscura</i>	Hypsub	1.9	19
<i>Icmadophila ericetorum</i>	Icmeri	1.5	2
<i>Leciophysma finmarkicum</i>	Lecfin	1.0	1
<i>Leptogium arcticum</i>	Leparc	1.0	1
<i>Leptogium lichenoides</i>	Leplic	1.0	1
<i>Leptogium saturninum</i>	Lepsat	1.6	7
<i>Lobaria kurokawae</i>	Lobkur	1.5	4
<i>Lobaria linita</i>	Loblin	2.3	32

Table 1 (concluded).

Species	Code	Ave	Freq
<i>Lobaria pseudopulmonaria</i>	Lobpse	1.3	3
<i>Lobaria pulmonaria</i>	Lobpul	1.0	1
<i>Lobaria scrobiculata</i>	Lobscr	2.1	7
<i>Masonhalea richardsonii</i>	Mahric	2.1	26
<i>Melanelia panniformis</i>	Melpa	1.0	1
<i>Melanelia septentrionalis</i>	Melsep	1.0	3
<i>Melanelia sorediata</i>	Melsor	1.0	2
<i>Melanelia stygia</i>	Melsty	2.6	5
<i>Melanelia trabeculata</i>	Meltra	1.7	3
<i>Multiclavula vernalis</i>	Mulver	1.0	3
<i>Nephroma arcticum</i>	Neparc	1.8	26
<i>Nephroma bellum</i>	Nepbel	1.8	10
<i>Nephroma expallidum</i>	Nepexp	2.5	26
<i>Nephroma helveticum</i>	Nephel	2.0	2
<i>Nephroma parile</i>	Neppar	1.5	6
<i>Ochrolechia frigida</i>	Ochfri	1.3	9
<i>Pannaria conoplea</i>	Pancon	1.5	2
<i>Parmeliopsis ambigua</i>	Papamb	1.5	11
<i>Parmeliopsis hyperopta</i>	Paphyp	1.3	19
<i>Parmelia omphalodes</i>	Paromp	1.9	16
<i>Parmelia saxatilis</i>	Parsax	2.0	1
<i>Parmelia squarrosa</i>	Parsqu	3.0	1
<i>Parmelia sulcata</i>	Parsul	1.9	13
<i>Peltigera aphthosa</i>	Pelaph	2.4	41
<i>Peltigera canina</i>	Pelcan	1.8	12
<i>Peltigera collina</i>	Pelcol	1.0	1
<i>Peltigera didactyla</i>	Peldid	1.3	8
<i>Peltigera extenuata</i>	Pelext	1.6	9
<i>Peltigera horizontalis</i>	Pelhor	1.7	3
<i>Peltigera kristinssonii</i>	Pelkri	1.2	5
<i>Peltigera lepidophora</i>	Pellep	1.0	2
<i>Peltigera leucophlebia</i>	Pelleu	2.1	31
<i>Peltigera malacea</i>	Pelmal	1.6	10
<i>Peltigera membranacea</i>	Pelmem	1.4	5
<i>Peltigera neckeri</i>	Pelnec	1.0	1
<i>Peltigera neopolydactyla</i>	Pelneo	1.4	8
<i>Peltigera polydactylon</i>	Pelpol	1.3	16
<i>Peltigera ponojensis</i>	Pelpon	1.6	5
<i>Peltigera praetextata</i>	Pelpre	1.0	1
<i>Peltigera rufescens</i>	Pelruf	1.8	25
<i>Peltigera scabrosa</i>	Pelsca	2.5	31
<i>Peltigera venosa</i>	Pelven	1.0	2
<i>Phaeophyscia constipata</i>	Phacon	1.0	1
<i>Physconia muscigena</i>	Phemus	1.7	6
<i>Physcia aipolia</i>	Phyaip	1.5	2
<i>Physcia caesia</i>	Phycae	1.0	3
<i>Physcia phaea</i>	Phypha	1.0	1
<i>Pilophorus cereolus</i>	Pilcer	1.3	3
<i>Pilophorus robustus</i>	Pilrob	1.7	3
<i>Pseudephebe pubescens</i>	Psepub	2.0	8
<i>Pseudocyphellaria crocata</i>	Psccro	3.0	1
<i>Ramalina almqvistii</i>	Ramalm	1.5	2
<i>Ramalina pollinaria</i>	Rampol	1.0	1
<i>Ramalina roesleri</i>	Ramroe	1.7	6
<i>Ramalina sinensis</i>	Ramsin	1.3	3
<i>Ramalina thrausta</i>	Ramthr	1.0	2
<i>Solorina bispora</i>	Solbis	1.1	29

Table 1 (concluded).

Species	Code	Ave	Freq
<i>Solorina crocea</i>	Solcro	2.0	9
<i>Solorina spongiosa</i>	Solspo	1.0	2
<i>Sphaerophorus fragilis</i>	Sphfra	2.0	6
<i>Sphaerophorus globosus</i>	Sphglo	1.9	25
<i>Stereocaulon alpinum</i>	Stealp	1.7	13
<i>Stereocaulon apocalypticum</i>	Steapo	2.4	5
<i>Stereocaulon arcticum</i>	Stearc	2.0	1
<i>Stereocaulon arenarium</i>	Stearc	2.0	1
<i>Stereocaulon botryosum</i>	Stebot	2.0	5
<i>Stereocaulon glareosum</i>	Stegla	1.5	2
<i>Stereocaulon groenlandicum</i>	Stegro	2.7	3
<i>Stereocaulon paschale</i>	Stepas	2.1	19
<i>Stereocaulon spathuliferum</i>	Stespa	1.0	1
<i>Stereocaulon subcoralloides</i>	Stesub	1.6	8
<i>Stereocaulon symphycheilum</i>	Stesym	1.6	5
<i>Stereocaulon tomentosum</i>	Stetom	1.7	6
<i>Stereocaulon vesuvianum</i>	Steves	2.0	1
<i>Stereocaulon</i> sp. 1	Stesp1	1.0	1
<i>Sticta arctica</i>	Stiarc	1.3	3
<i>Thamnia subuliformis</i>	Thasub	1.7	41
<i>Thamnia vermicularis</i>	Thaver	1.5	33
<i>Umbilicaria caroliniana</i>	Umbcar	3.0	1
<i>Umbilicaria cylindrica</i>	Umbcyl	1.0	2
<i>Umbilicaria deusta</i>	Umbdeu	2.0	1
<i>Umbilicaria hyperborea</i> var. <i>hyperborea</i>	Umbhyp	1.0	1
<i>Umbilicaria hyperborea</i> var. <i>radicula</i>	Umbhyr	1.2	6
<i>Umbilicaria polyphylla</i>	Umbpol	1.0	1
<i>Umbilicaria proboscidea</i>	Umbpro	2.0	7
<i>Umbilicaria torrefacta</i>	Umbtor	1.6	7
<i>Xanthoria polycarpa</i>	Xanpol	1.0	1

Note: Avg., the average abundance (cover class scale ranges between 0–6); Freq, the number of plots in which each species was encountered.

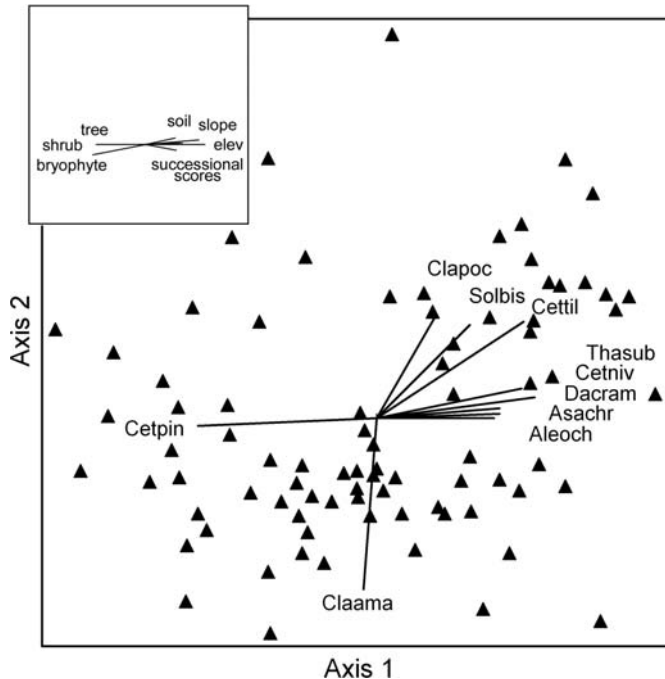
(McCune and Grace 2002). The beta diversity for the entire sampling effort, 6.8, was rather heterogeneous. This compositional change among plots was greatly reduced ($\beta_w = 4.1$) after deleting outliers and doubleton taxa.

Community structure

The two-axis solution recommended by NMS was stronger than that expected by chance, based on a randomization test ($p = 0.004$). The best solution yielded a final stress value of 20.7. The final instability was 0.06 and there were 500 iterations in the final solution. Cumulatively, these two axes represented 77.7% of the community variation (Fig. 2).

The first axis represented most of the variance, 48.5%. The environmental variables with the strongest positive correlations with this axis were elevation ($r = 0.72$), rock cover ($r = 0.72$), slope ($r = 0.57$), and bare soil cover ($r = 0.54$). Ordered by decreasing strength of the relationship, *Cetraria nivalis* (L.) Ach., *Cetraria tilesii* Ach., *Thamnia subuliformis* (Ehrenb.) W.L. Culb., *Asahinea chrysantha* (Tuck.) W.L. Culb. & C.F. Culb. and *Dactylina ramulosa* (Hook. f.) Tuck. were positively associated with this axis. Several mosses were also positively associated with axis one, including *Racomitrium lanuginosum* (Hedw.) Brid., *Grimmia* spp. and *Andreaea ru-*

Fig. 2. NMS ordination of the plots in species space rigidly rotated 272°. Plots are depicted as triangles and lines represent joint plots of the species variables (r^2 cutoff = 0.35). Lichen species codes are in Table 1. Inset in upper left corner is same NMS ordination (r^2 cutoff = 0.25), with joint plots of the environmental and lichen summary variables (bare soil cover, slope, elevation, successional scores, total bryophyte cover, shrub cover, and tree cover).



pestris Hedw. Negative associations with this axis included cover of bryophytes ($r = -0.71$), shrubs ($r = -0.69$), and trees ($r = -0.53$). Some of the strongest bryophytes negatively related to this axis were *Hylocomium splendens*, *Aulacomnium palustre* (Hedw.) Schwaegr., and *Pleurozium schreberi*. The single strongest lichen species negatively correlated with axis one was *Cetraria pinastri* (Scop.) Gray ($r = -0.74$). Other strong negative associations included *Hypogymnia physodes* (L.) Nyl., *Cladonia cornuta* (L.) Hoffm., *Hypogymnia bitteri* (Lynge) Ahti, and *Cladonia cenotea* (Ach.) Schaer.

Axis two represented 29.2% of the lichen community variation. The three lichen species most positively related to axis two were *Cladonia pocillum* (Ach.) O.J. Rich, *Cetraria tilesii*, and *Solorina bisporea* Nyl. Although weakly correlated, *Scorpidium scorpioides* (Hedw.) Limpr., *Thuidium abietinum* (Hedw.) Schimp in B.S.G., and *Distichium capillaceum* (Hedw.) Bruch & Schimp. in B.S.G., were also positively related to axis two. All of these lichen and moss taxa are calciphiles (Hope-Simpson 1941; Steere 1978; Thomson 1984). Lichens strongly associated with the opposing negative portion of this gradient included *Cladonia amaurocraea* (Flörke) Schaer., *Cladonia rangiferina*, and *Cladonia stygia* (Fr.) Ruoss. Moreover, *Aulacomnium turgidum* (Wahlenb.) Schwaegr. and *Sphagnum* spp. were negatively associated with axis two. Over two-thirds of all lichen species were negatively associated with axis two. Most environmental variables were only weakly correlated with this axis. No environmental variables had a correlation to axis two stronger than $|r| = 0.29$.

Two-way cluster analysis

We pruned the plot dendrogram to include six clusters, and we pruned the species dendrogram to include seven primary clusters (Fig. 3). This number of plot and species groupings was chosen primarily for interpretability, and in part based on their associations with species and plot groups, respectively. The six plot groups reflect substrate and associated vascular plant communities. The first plot cluster contains plots underlain by carbonate rocks. These 21 plots are indicated by calciphilic lichens (shown in red in Fig. 3), present nearly exclusively in plots of this cluster. Plot cluster 2, the smallest cluster, contained three nearly empty plots. Lichen species totals and species richness for these three plots were lower than the average of all other plots (Table 2). The third plot cluster contained plots with substantially greater slope and rock cover, yet lower bryophyte and vascular plant cover than the other plots (Table 2). This group was indicated by saxicolous or rock-associated lichens, shown in turquoise (Fig. 3). The fourth and largest plot cluster contains a mix of plots from the Baird Mountains, De Long Mountains, Endicott Mountains, and Noatak Basin. These plots contained many taxa scattered from each lichen species group, but were indicated by species often present in hummocky tussock tundra habitats, shown in yellow (Fig. 3).

Plot cluster 5 shared the same hummocky tussock tundra lichens (highlighted in yellow) and moist-habitat shrub epiphytes (shown in blue in Fig. 3) as the previous plot cluster. The 16 plots within this fifth cluster, however, had higher average shrub and graminoid cover than the 28 plots from plot cluster 4 (Table 2). The sixth plot cluster was the forested plots, which all contained at least 20% tree cover. These few plots were indicated by corticolous lichens that grew primarily on *Picea* (brown box in Fig. 3).

The seven lichen species clusters differed in substrate affinities, hydrologic preferences and frequency (shown as different colors in Fig. 3). The first two species clusters were determined largely by substrate. Rock-associated and saxicolous lichens clustered together in the first primary species cluster, shown in a turquoise box in Fig. 3.

The second primary species cluster, depicted in red (Fig. 3), comprised several calciphiles. This species cluster was further divided into three groups based on plot fidelity. The smallest subdivision of the calciphilic group, comprising *Cetraria delisei* (Bory ex Schaer) Nyl., *Arctoparmelia subcentrifuga* (Oksner) Hale, and *Collema fuscovirens* (With.) J.R. Laundon, had the greatest fidelity, occurring in a narrow range of plots. The next group within this calciphilic cluster had moderate fidelity, occurring in several plots beyond the same narrow range of plots as the first group. These species, however, were not only faithful to roughly half of plot cluster 1, but were also abundant throughout plot cluster 3 (see lower red box connected by broken line, Fig. 3). These lichens, as evidenced by their abundance both in plots underlain by intrusive-derived materials and calcareous bedrock, are only facultatively calciphilic. The final group within the calciphile cluster includes several previously documented lime-loving lichens, *Cetraria tilesii*, *Cladonia pocillum*, *Dactylina beringica*, and *Solorina bisporea*, which have the broadest fidelity.

The third species cluster, depicted in green (Fig. 3), repre-

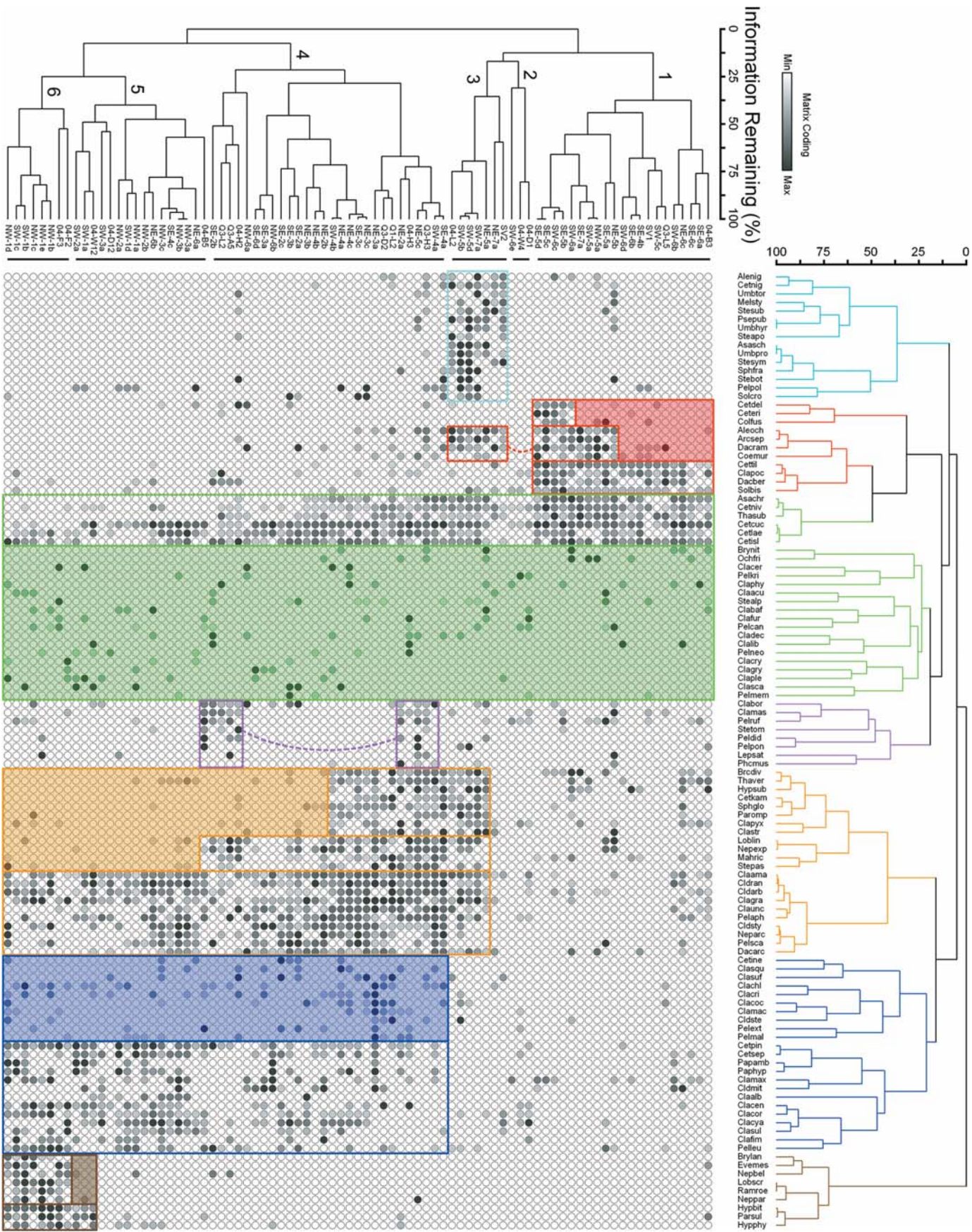


Fig. 3 Two-way cluster analysis dendrogram of 83 plots and 112 macrolichen species (missing species occurring in four or fewer plots). Each circle represents relative abundance by column (darker is more abundant). The six plot clusters are indicated at the branch tips with vertical black lines and at the node with numbers. The seven species clusters are indicated with colors. Lichen species codes are presented in Table 1.

Table 2. Characteristics of the six plot clusters derived from two-way cluster analysis.

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	All Clusters ^a
No. of plots	21	3	7	28	16	8	83
Lichen communities							
Alpha diversity (richness)	20.2 (6.7)	15.0 (7.0)	37.1 (11.1)	32.6 (9.1)	22.8 (5.1)	30.2 (7.2)	27.1 (9.8)
Gamma diversity	95	30	94	144	76	92	201
Beta diversity (β_w)	3.7	1.0	1.5	3.4	2.3	2.0	6.4
Lichen height (cm)	5.35 (7.86)	1.55 (1.58)	9.09 (15.37)	5.26 (2.68)	4.43 (1.35)	4.44 (2.09)	5.23 (6.12)
Lichen cover (%)	7.2 (7.2)	1.0 (1.7)	6.5 (10.6)	10.1 (11.3)	2.5 (2.4)	7.0 (7.9)	7.0 (8.8)
Successional score (1–3)	2.05 (0.17)	1.93 (0.11)	2.17 (0.13)	2.11 (0.15)	2.02 (0.15)	1.70 (0.22)	2.04 (0.20)
Bryophyte communities							
Alpha diversity (richness)	11.3 (4.1)	16.7 (6.5)	10.7 (3.4)	13.6 (3.3)	14.9 (4.0)	13.1 (6.6)	13.1 (4.3)
Gamma diversity	82	34	37	94	82	51	181
Beta diversity (β_w)	6.2	1.0	2.5	5.9	4.5	2.9	12.8
Bryophyte cover (%)	14.4 (16.5)	28.3 (5.8)	3.3 (3.3)	40.6 (25.2)	49.7 (22.2)	61.3 (13.8)	34.1 (26.4)
Vascular plant communities							
Forb cover (%)	16.6 (18.1)	26.3 (31.1)	9.2 (13.3)	15.2 (18.0)	5.5 (10.4)	28.4 (19.1)	14.8 (17.8)
Graminoid cover (%)	18.7 (17.7)	44.0 (41.3)	1.2 (1.1)	36.7 (28.9)	58.4 (16.9)	22.9 (14.4)	32.3 (27.3)
Shrub cover (%)	2.3 (5.0)	27.0 (25.2)	0.4 (1.1)	11.0 (15.3)	20.2 (23.1)	44.5 (17.6)	13.5 (19.5)
Subshrub cover (%)	29.4 (15.1)	27.0 (10.8)	6.3 (10.6)	40.5 (18.5)	43.9 (10.2)	47.1 (13.3)	35.6 (18.3)
Tree cover (%)	0.0	3.3 (5.8)	0.0	0.004 (0.02)	0.2 (0.8)	34.3 (8.0)	3.4 (10.4)
Site characteristics							
Bare duff (%)	11.6 (13.8)	18.7 (27.2)	0.2 (0.4)	20.0 (15.4)	29.1 (16.8)	25.0 (19.6)	18.4 (17.2)
Bare mineral soil (%)	8.9 (8.3)	2.3 (2.5)	7.7 (10.3)	3.1 (3.6)	1.4 (1.4)	1.3 (1.1)	4.4 (6.3)
Elevation (m a.s.l.)	558.1 (238.0)	99.7 (75.2)	841.7 (198.2)	530.3 (178.5)	226.4 (135.7)	140.4 (58.5)	451.8 (269.9)
Exposed rock (%)	36.2 (36.7)	0.3 (0.6)	79.3 (14.7)	5.8 (12.6)	0.0	0.0	17.8 (31.0)
Incident radiation ($\text{MJ}\cdot\text{cm}^{-2}\cdot\text{a}^{-1}$)	−0.70 (0.31)	−0.58 (0.16)	−0.88 (0.40)	−0.61 (0.15)	−0.69 (0.06)	−0.64 (0.05)	−0.68 (0.22)
Slope (°)	12.9 (10.5)	5.0 (8.7)	21.4 (9.5)	6.9 (8.3)	3.1 (2.5)	2.0 (2.8)	8.3 (9.5)
Water cover (%)	1.3 (1.2)	0.9 (0.9)	0.0	0.9 (2.4)	1.1 (1.8)	0.9 (2.5)	0.7 (1.9)

Note: Mean values in original units and standard deviations in parentheses.

^aAll clusters, the value for all 83 plots but excluding the five outliers.

sents ubiquitous taxa. These green boxes encompass all 83 plots, indicating that these species did not favor specific habitat types or substrates. Dividing this cluster into two secondary groups, based on the density of abundances within each box, clearly segregates a group including some of the most frequent taxa, *Cetraria cucullata*, *C. nivalis*, and *C. laevigata*. These pervasive species occurred in fairly high abundance in almost every plot, excepting the nearly empty plots, 04-D1, 04-W4, and SW-6e. The remaining ubiquitous species (shaded green box in Fig. 3) form a less cohesive group as suggested by their long branches in the dendrogram.

Several cyanolichens group together as the fourth species cluster, which are depicted as two pink boxes (Fig. 3) linked by a broken line. Plots containing lichens within this species cluster (SW-4a, Q3-H3, NE-5c, 04-H3, NE-2a, Q3-A5, and Q3-L2) were found nearly exclusively in plot cluster 4. Plots

including taxa in this cyanolichen cluster tended to have greater forb and less graminoid cover than the other plots within this plot cluster.

Yellow boxes highlight the fifth species cluster (Fig. 3). Lichens within this cluster were generally not found in plots from plot cluster 1, plot cluster 2, or in SV2 from plot cluster 3. These taxa, however, when present were fairly abundant in shrubby or wooded habitats. This species cluster was also further subdivided into secondary groups based on plot fidelity. The secondary group with the greatest fidelity included several common dry-habitat lichens often occurring only on dry hummocks (e.g., *Bryocaulon divergens* (Ach.) Kärnefelt, *Thamnolia vermicularis* (Sw.) Ach. ex Schaer., *Sphaerophorus globosus* (Huds.) Vain., and *Cladonia stricta* (Nyl.) Nyl.). These lichens were restricted to plot cluster 3 and a portion of plot cluster 4. Species with moderate fidelity within this species cluster included *Lobaria linita* (Ach.)

Rabenh., *Nephroma expallidum* (Nyl.) Nyl., *Masonhalea richardsonii* (Hook.) Kärnefelt, and *Stereocaulon paschale* (L.) Hoffm. These four, large foliose lichens often accumulate in interspaces between dwarf shrubs, and occurred throughout all plots of plot cluster 4. The most widespread subdivision of the hummock-tussock species cluster contains several *Cladina* species (except *C. stellaris* and *C. mitis*), as well as the common lichens *Cladonia amaurocreaea* and *Cladonia gracilis* (L.) Willd. Lichens within this well-defined group often flourish in the interstices between tussocks.

The sixth species cluster contained moist habitat terricolous lichens (primarily *Cladonia* species) and lichens epiphytic on shrubs (shown in blue in Fig. 3). These lichens were concentrated in plot clusters 4, 5, and 6. This cluster was also divided into two secondary groups based on the frequency of abundances within each box. Species occurring more frequently included epiphytes as well as several *Cladonia* species (including *Cladonia maxima* (Asah.) Ahti, *C. cornuta*, and *Cladonia cyanipes* (Sommerf.) Nyl.). Less frequent taxa (shown in the shaded blue box in Fig. 3) were primarily *Cladonia* spp., as well as several species of *Peltigera* and *Cladina stellaris* (Opiz) Brodo.

The seventh species cluster, highlighted in brown in Fig. 3, also grouped epiphytes; however, these lichens were primarily corticolous on *Picea* rather than shrubs or subshrubs. A division of this cluster was also based on plot fidelity. Two-thirds of these species, particularly *Bryoria lanestris* (Ach.) Brodo & D. Hawksw., *Lobaria scrobiculata* (Scop.) P. Gaertn., and *Ramalina roesleri* Hochst., were faithful to the forested plots within plot cluster 6. *Hypogymnia bitteri*, *Parmelia sulcata* Taylor, and *H. physodes*, however, were not restricted to this plot cluster but were also present in several plots from plot cluster 5.

Discussion

Community gradient

The primary gradient in ordinations based on lichen species composition discriminates forested communities, moist tundra, and high alpine communities (Fig. 2). Plots at the forested end of this gradient are high in tree and shrub cover and dominated by shade-tolerant pleurocarpous mosses, characteristic of boreal coniferous forests (Steere 1978). Lichens in these forests tend to be epiphytic on *Picea*, *Alnus*, and *Betula*. Alternatively, the opposing end of this community gradient comprises dry, steep alpine communities (Fig. 2). There is a low level of coverage by vascular plants and large areas of bare soil. Lichens common to these sites are rock-affiliated taxa and widespread calciphiles. Bryophytes include several dry-habitat saxicolous species. The underlying factors that manifest as different vegetative communities reflect variations in site characteristics. The two site characteristics driving these patterns are likely soil moisture and exposure.

Permafrost of varying depths and continuity underlie most of northwestern Alaska (Van Patten 1990). A thick organic layer often overlies permanently frozen soils in foothill or basin regions. Permafrost in the upper profile inhibits drainage, and as a result these sites tend to be saturated with water or ice most of the year. The upland areas, however,

have discontinuous permafrost and are often sloped, so when the active layer thaws annually, thorough soil drainage is facilitated (Van Patten 1990). Soils of level areas, underlain by permafrost, tend to be saturated during the growing season. Growth and establishment of tall woody vegetation in these lowland environments, however, has been associated with well-drained sites (Lloyd et al. 2003). Forests and densely shrubby sites at one end of our gradient occur in flat, low elevation sites where drainage is better than that of lowland tundra habitats.

High elevation alpine communities, alternatively, tend to occur on steep slopes also facilitating adequate drainage. Moreover, some of these sites are talus slopes with little to no soil, retaining little moisture following snowmelt. Low moisture availability at these sites is exemplified by species occupying these habitats, such as *Racomitrium lanuginosum*, which cannot tolerate poor drainage (Tallis 1958; Ellis and Tallis 2003). Accordingly, vascular plants, which require adequate soil moisture, are sparse or absent. Woody vegetation that requires well-drained sites, however, is likely limited by cold conditions and harsh winds (Hobbie and Chapin 1998). This lack of buffering vegetation combined with high elevations increases exposure to wind and solar radiation. Lichens common in these alpine plots (e.g., *Cetraria nivalis*, *C. tilesii*, *Thamnolia subuliformis*, *Asahinea chrysantha*, and *Dactylina ramulosa*) are generally light-colored, which may help reflect excess light. Moreover, these species all contain secondary compounds (e.g., usnic, thamnolic, or vulpinic acid), which absorb harmful UV light and provide extra protection from intense radiation (Rikkinen 1995). In addition, these lichens are low growing to the soil surface, within the ground boundary layer, avoiding harsh, abrading winds.

Substrate pH gradient

The second ordination axis corresponds to a gradient of substrate pH present in the Preserve. Substrate pH can greatly influence vegetation, including both epiphytic and terricolous lichens (e.g., Robinson et al. 1989; Kuusinen 1996; Kermit and Gauslaa 2001; Holt et al. 2007). Limestone and dolomite underlies much of the Preserve. In level areas where water and organic matter accumulate, however, *Sphagnum* predominates. This moss has a high cation exchange capacity, thereby increasing the acidity of its surrounding environment (Clymo 1964; Andrus 1986). These patterns and processes contribute to a patchwork of calcareous and acidic substrates to which the vegetation responds.

A secondary gradient of lichen species composition contrasts calcareous with acid-affiliated communities. Plots at the one end of the gradient are characterized by calciphilic lichens and mosses, such as *Cladonia pocillum*, *Cetraria tilesii*, *Solorina bispora*, *Scorpidium scorpioides*, *Thuidium abietinum*, and *Distichium capillaceum*. Conversely, the opposing end is dominated by acidophilous species (e.g., *Cladonia amaurocreaea*, *Cladonia rangiferina*, *C. stygia*, *Aulacomnium turgidum*, and *Sphagnum* spp.).

Plot and species sorting

Six plot clusters from two-way cluster analysis generally partition the forested and shrubby communities from the rocky, high elevation sites, which also separate along axis one in the ordination (see Figs. 2 and 3). These six groups

are primarily based on bedrock type and dominant vegetation. Patterns in vegetation are largely determined by soil moisture and exposure. The seven species groups from the two-way cluster analysis are based on a combination of environmental factors (e.g., bedrock type, substrate) and species distribution characteristics (e.g., species ubiquity, patchiness or presence of scattered hummocks). Variations within these clusters occurred with respect to fidelity and frequency.

Substrate pH is a principle factor associated with both plot and species clustering, which is not surprising due to its effects on species establishment and survival demonstrated elsewhere (Robinson et al. 1989; Kuusinen 1996; Kermit and Gauslaa 2001; Holt et al. 2007). More interesting perhaps, is the spatial scale that contributes to plot versus species sorting. Although inexorably interdependent owing to the nature of the analysis, plot and species clusters reflect variation of similar factors at different scales. Undoubtedly, biotic and abiotic factors vary across many scales, controlling abundance and distribution of lichen communities on the landscape as a whole. Environmental factors (e.g., elevation, topographic position, regional soil moisture patterns) and the resulting biotic patterns that sort plots, however, vary across large landscape scales. Some species also reflect coarse-scale patterns (e.g., bedrock type), but many species appear to respond to local patterns in habitat, such as the fine-scale patchiness of the surrounding vegetation. Lichens possess a range of environmental tolerances present at many points in space, demonstrated through the varied scales of species sorting. Plots, however, represent an accumulation of species at a single point in space. That 0.38 ha envelope may include variation at many scales, but the community as a whole and its similarity to others is determined by variation at the scale of our plots or larger. In sum, similarity or clustering of lichen communities within the Preserve (i.e., plots) is predominantly determined by regional variation; whereas, shared commonalities among individual lichen species depend on local and regional variation.

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