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Succession and community gradients of arctic macrolichens and their relation to substrate, topography, and rockiness

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Abstract: We describe lichen community structure and its relation to environment in the Bering Land Bridge National Preserve in northwestern Alaska. We used a stratified random sample to estimate macrolichen abundance and several environmental variables from 78 0.38-ha plots within lichen-dominated areas of the Preserve. We found a total of 140 macrolichen taxa. Two primary gradients in lichen species composition were related to habitat rockiness and a substrate-topographic gradient. The strongest gradient, rockiness, correlates with lichen succession. Rocky habitats have less competition from vascular plants and may be more resistant to soil disturbance. The substrate-topography gradient is largely driven by the presence of *Sphagnum* moss contrasting with calcareous parent rock material. To uncover additional underlying patterns in lichen community composition, we deleted rocky and calcareous plots and strictly saxicolous species from the analyses. Although we found similar patterns from the original analysis in this subset, diversity and community composition also varied with differing microtopography. These gradients of lichen community composition can also be divided into three major groups; rocky non-calcareous sites, calcareous areas, and the remaining plots form the alluvial lowland

communities. We used two-way cluster analysis which combines independent clustering of sample units and species into a single diagram. This technique linked individual species and species assemblages with these major trends.

Keywords: Bering Land Bridge National Preserve, Alaska, tundra, lichen, two-way cluster analysis.

Introduction

Nearly half the state of Alaska is blanketed by arctic tundra. This ecosystem extends continuously for hundreds of kilometers, with imperceptible variations to the casual observer. In contrast, forested ecosystems display unmistakable patterns of topographic, climatic, and soil variation. Yet the apparent uniformity of the Alaskan tundra may be merely an artifact of spatial scale. In the absence of their charismatic vascular counterparts, lichens contribute nearly half the vegetative diversity and a large portion of biomass to these arctic environments. Therefore lichen research is integral for our understanding of the variation present in arctic Alaska.

Most lichen studies conducted in Alaska focus on taxonomy or floristics, such as annotated checklists, floras, or range distributions (Thomson 1984). To our knowledge there has been no extensive inventory documenting lichen diversity in the tundra of mainland northwestern Alaska. Talbot et al. (2001), however, described lichen diversity of two isolated Bering Sea islands about 400 km from the Alaska mainland. Most lichen work in the arctic tundra has focused on north-central Alaska (e.g., Moser et al. 1979; Swanson et al. 1985; Auerbach et al. 1997). The continental climate and resulting flora in north-central Alaska can differ significantly in temperature and precipitation from the more oceanic flora found in northwestern Alaska. Moreover, the Beringian element adds species not observed in the arctic tundra further east. Our study centers on the lichen communities of the Bering Land Bridge National Preserve on the Seward Peninsula in northwestern Alaska. The few other lichen studies conducted in this area are reports of taxonomic novelties and reindeer

research with reference to lichens as forage (e.g., Holt et al. 2006, 2007; Pegau 1968; Krog 1973; Flock 1989). Meanwhile, previous ecological studies on the Seward Peninsula primarily focus on vascular plants (Kelso 1989; Epstein et al. 2004; Racine et al. 1987, 2004; Thompson et al. 2004). They identified climate, topography, soil parent material, permafrost, hydrology, and disturbance (including fire and frost action) as the primary factors driving vascular community patterns. Our study investigates many of these factors and their relationship to the lichen communities.

Arctic lichen communities are important not only from a biodiversity perspective, but they also serve several functional roles in the ecosystem. Cyanolichens provide a sizable portion of the fixed nitrogen in these nutrient-poor ecosystems (Gunther 1989; Hobara et al. 2006). Also, several large mammals, including reindeer, caribou, and muskoxen, all rely on lichens for winter and occasional summer forage (Scotter 1964; Ihl and Klein 2001). The eastern half of the Seward Peninsula, including the lower portion of the Bering Land Bridge National Preserve, is often wintering grounds for the Western Arctic Caribou herd, Alaska's largest herd (Dau 2003). The health of lichen resources in the face of grazing pressure is of concern in northwestern Alaska; however, we address this topic in a separate paper (Holt et al. 2007).

The objective of this study was to describe lichen community structure and its relation to environment in the Bering Land Bridge National Preserve. We used a stratified random sample to partition our heterogeneous landscape, to increase the precision and efficiency of estimates

for variables of interest (Husch et al. 1972). We explored how community gradients and diversity related to environment. Furthermore, we compared lichen community composition and environmental factors among the different land cover types used in the stratified sampling.

Materials and Methods

Study Site

The Bering Land Bridge National Preserve is located on the Seward Peninsula in northwestern Alaska ($65^{\circ}14' - 66^{\circ}36'N$, $162^{\circ}44' - 167^{\circ}32'W$; Fig. 1). Temperatures of the Seward Peninsula are tempered by the oceanic influence of the surrounding Bering and Chukchi seas. Weather stations nearest the Preserve are located in Nome, 115 km southwest, and Kotzebue, 65 km northeast. Mean July temperatures in Nome and Kotzebue are 10.6° and $12.4^{\circ}C$, respectively. Mean annual precipitation, falling primarily in late summer, is 44.4 cm in Nome and 28.9 cm in Kotzebue. The bulk of the Preserve comprises moist to wet tussock tundra underlain by continuous permafrost near Kotzebue alternating with discontinuous permafrost near Nome (Van Patten 1990). Rising south from sea level, the Preserve's southern boundary follows the crest of the Bendeleben Mountains to a height of 1040 m elevation. Adding unique geology to an otherwise metamorphic landscape, dolomite rocks outcrop along the east and western boundaries of the Preserve, and historic volcanic activity sprinkles the north and central portions of the Seward Peninsula (Till and Dumoulin 1994). The most notable volcanic features in the Preserve, however, are the basaltic lava flows in the central Seward Peninsula. These flows date from the late Tertiary to the late Quaternary (Hopkins 1963). The two most recent flows, Camille and Lost Jim, are exposed today and vegetation is limited to lichens, bryophytes, and sparse vascular plant cover.

The general vegetation types present in northwestern Alaska are *Eriophorum* tussock

tundra, *Dryas* fell-field, ericaceous-shrub tundra, *Eriophorum-Carex* wet meadow, and solifluction slopes (Viereck et al. 1992). Common shrubs

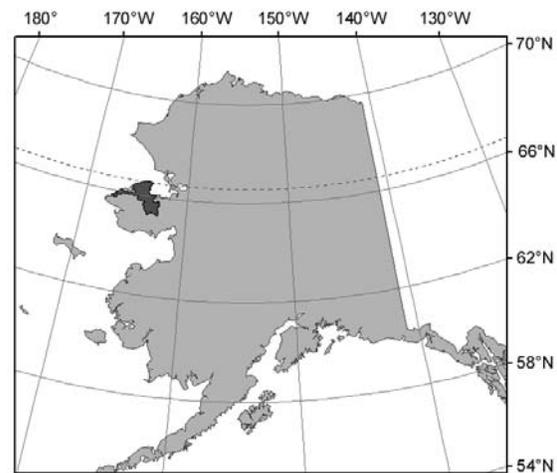


Figure 1. The Bering Land Bridge National Preserve, shaded dark gray, is located in northwestern Alaska. For reference, the approximate location of the Arctic Circle is depicted with a dashed line.

consist of *Salix* spp., *Betula glandulosa*, and *Alnus crispa*. The herb layer contains mixed *Eriophorum* spp. and *Carex* spp., *Vaccinium* spp., *Arctostaphylos* spp., *Empetrum nigrum*, *Cassiope tetragona*, *Ledum palustre* var. *decumbens*, and *Rubus chamaemorus*. The dominant mosses are *Sphagnum* spp. and *Hylocomium splendens*. The lichen flora is dominated by species of *Cladina*, *Cladonia*, *Cetraria*, *Peltigera*, and *Stereocaulon*.

Sampling

We focused our sampling on the central portion of the Bering Land Bridge National Preserve, excluding coastal lowlands in the panhandle and far northern coast. Lichens were the focal point of this study, so we concentrated sampling in lichen-dominated areas. The peripheral northern portions were wetlands depauperate in lichens and thus contributed little towards our objectives. We used a two-way stratified random sample. One of our stratifying variables was GIS land cover data (Markon and Wesser 1997). Land

cover types discriminated low lichen cover from lichen-dominated areas within the central Preserve. Our pilot study indicated that four of the total ten land cover types had a minimum average lichen cover of 10%. These four cover types were the only strata we sampled further. Geographic blocks were the other stratifying variable, used to balance sampling across the area of interest. The central portion of the Preserve was divided into approximately twenty-one roughly equal-area (~ 400 km²) geographic blocks. Within each geographic block, four points from each cover type were randomly selected. In total, data from 78 plots within these two strata were collected in 2003.

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 southeastern and western US, these protocols focus on epiphytic macrolichens. The lack of trees in the tundra called for modification to these protocols by sampling all terricolous macrolichens and epiphytic macrolichens on shrubs. Our sampling did not include smaller foliose species on rock or trees, such as *Melanelia* and *Allantoparmelia*. However preservation of key elements of the technique facilitates future comparisons.

Sample units were circular fixed-area plots with a 34.7-meter 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). Environmental measurements included topographic variables as well as percent cover of various aspects of the vegetation (Table 1). Aspect and slope were transformed into estimates of potential annual direct incident radiation (McCune and Keon 2002).

Lichen determinations were primarily based on Thomson (1984), Goward et al. (1994), and Goward (1999). We used thin-layer chromatography for identification of some *Bryoria*, *Cladonia*, *Hypogymnia*, and *Stereocaulon*. All *Cladonia* identifications were based on voucher specimens with podetia, and strictly squamulose thalli were not recorded. Specimens from the *Cladonia phyllophora* and *C. cervicornis* groups were identified using Brodo and Ahti (1995). The distinction between *Cladina mitis* and *C. arbuscula* requires spot tests with paraphenylenediamine. In the field, we estimated cover for these isomorphs as a single lumped species and combined their cover values into a single variable (*Cladina mitis/arbuscula*). UV light distinguished the two chemical species of *Thamnolia*, which was also collected from every site at which it occurred. Vouchers were deposited at OSC and the NPS Herbarium in Anchorage, Alaska.

Additional Variables

We indirectly estimated the successional status of each site using two methods; lichen mat thickness and successional scores based on lichen community composition. In other arctic regions, researchers and land managers have used lichen mat thickness, or height, as a surrogate for succession (e.g., Ahti 1959; Steen 1965). This measure assumes that heavy grazing and other ground disturbances manifest as cropped or stunted lichens. Alternatively, tall or long lichens exist in relatively undisturbed areas where they have had more time to grow; thus, tall lichens reflect later successional communities than sites with shorter thalli. In our study, heights of the same seven lichen species were recorded from all sites, though not all seven were necessarily present together at every plot. We combined these measurements into a single variable of lichen height. We could not use simple averages because growth rates differed between species.

Table 1. Characteristics of four cover types in the Bering Land Bridge National Preserve. Mean values in original units and standard errors in parentheses. Different letters indicate statistically different cover types ($\alpha = 0.05$) using transformed variables in ANOVA. Cover types are: L, Dwarf shrub-lichen dominated; M, Mesic-dry herbaceous; P, Open low shrub-dwarf birch/Ericaceous; S, Sparse vegetation. "All" represents the Preserve-wide average across all four cover types, weighted by area of the cover type (weighted SE in parentheses).

	L	M	P	S	ALL
SAMPLE SIZES					
No. plots	20	20	20 ¹	17	78 ²
Area (km ²)	695	2124	2252	605	5676
LICHEN COMMUNITIES					
Alpha diversity	23.9 (1.88) ^a	19.3 (1.11) ^a	22.1 (1.29) ^a	34.1 (1.81) ^b	22.2 (0.08)
Gamma diversity	101	70	90	110	140
Beta diversity	3.2	2.6	3.1	2.2	4.8
Lichen height (cm)	6.69 (0.51)	8.24 (0.38)	7.98 (0.39)	6.48 (0.58)	7.76 (0.005)
Lichen cover (%)	23.1 (3.05) ^a	17.8 (2.22) ^a	16.6 (2.56) ^a	53.2 (4.55) ^b	22.2 (0.45)
DISTURBANCE SCORES					
Successional score ³	2.18 (0.03)	2.15 (0.03)	2.16 (0.01)	2.24 (0.03)	2.17 (0.00002)
SITE CHARACTERISTICS					
Bare duff (%)	3.25 (0.83) ^a	2.60 (2.60) ^{ab}	2.35 (0.32) ^{ab}	1.50 (0.44) ^b	2.51 (0.005)
Bare mineral soil (%)	2.98 (0.83) ^{ab}	0.65 (0.24) ^a	2.08 (1.48) ^a	8.47 (3.52) ^b	2.09 (0.05)
Bryophyte cover (%)	21.2 (3.99) ^a	22.4 (3.01) ^a	7.63 (0.93) ^b	2.41 (0.69) ^c	14.7 (0.29)
<i>Sphagnum</i> cover (%)	26.5 (7.91) ^a	66.6 (8.07) ^b	50.2 (7.68) ^{ab}	0.88 (0.88) ^c	50.9 (2.26)
Elevation (m)	277.8 (25.6) ^a	156.2 (27.2) ^b	161.7 (25.4) ^b	385.5 (43.5) ^a	187.3 (30.72)
Exposed rock (%)	3.85 (1.60) ^a	0.05 (0.05) ^b	1.10 (0.82) ^{ab}	60.0 (4.83) ^c	6.96 (0.59)
Incident Radiation ⁴	-0.69 (0.02)	-0.67 (0.01)	-0.67 (0.02)	-0.75 (0.06)	-0.68 (0.00001)
Slope (deg)	3.61 (0.65) ^{ab}	1.96 (0.46) ^a	3.31 (0.40) ^{ab}	7.32 (2.21) ^b	3.08 (0.02)
Water cover (%)	4.33 (1.17) ^a	2.38 (0.69) ^{ab}	1.68 (0.73) ^{bc}	0.35 (0.35) ^c	1.93 (0.01)
VASCULAR COMMUNITIES					
Forb cover (%)	16.3 (3.38) ^a	8.63 (1.84) ^{ab}	12.4 (3.89) ^{ab}	5.71 (2.44) ^b	11.2 (0.33)
Graminoid cover (%)	33.8 (4.00) ^a	47.4 (3.44) ^{ab}	49.7 (4.38) ^b	3.68 (0.87) ^c	42.3 (0.68)
Subshrub cover (%)	16.2 (2.44) ^{ab}	18.4 (2.95) ^{ab}	25.2 (3.44) ^a	12.8 (2.31) ^b	20.7 (0.30)
Shrub cover (%)	9.10 (1.54) ^{ab}	12.1 (3.20) ^a	16.1 (2.33) ^a	4.09 (1.40) ^b	11.8 (0.19)

¹Original sample size of 21, but all analyses reflect reduced sample of 20 excluding the outlier, 5P.

²Diversity estimates reflect all 78 plots, while all other variables reflect only 77, excluding 5P.

³Successional scores range between one and three.

⁴Calculation based on slope, aspect and latitude, and units are (ln(Rad, MJ/cm²/yr))

We therefore used the following procedure to adjust heights of those species with growth rates strongly differing from the average. First, individual species' heights were regressed against the pooled height of the seven target species that

were available for each plot. Slopes greater than one indicate that a particular species grows faster than average, while slopes less than one indicate slower than average growth rates. Two of the seven species, *Bryocaulon divergens* and

Alectoria nigricans, had slopes much larger than one and consequently were adjusted. Slopes of the other five species were near one and did not require adjustment. Regression coefficients were used to calculate adjusted heights, such that each species would have similar growth rates. To calculate average adjusted lichen height for these two species in a particular plot, the intercept from the regression was subtracted from the observed height value for that plot, and then divided by the slope. The final value for lichen height for a given plot was the average height of all species available at each site, including the five unadjusted species and two adjusted species.

Second, 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 (Holt et al. 2006). Each species was assigned a successional species score of one, two, or three, respectively. Weighted averaging combined our abundance estimates with these species scores to yield successional plot scores for each site. We chose to use this metric to determine the successional status of a site based strictly on its lichen community composition. Although not outlined individually in this paper, specific species and groups of lichens characterize early, mid- and late-successional seral stages and are implicit in this metric.

Data Adjustments

Comparing average community distances between plots identifies multivariate outliers in species space. One of the total 78 plots, Plot 5P, had an average Sørensen distance of 3.7 standard deviations from the grand mean of all distances. This plot was an outlier because its total lichen cover (2.5%) and richness (13 species) was far lower than the average (26.4% and 24.3 species). In ordinations, the extreme peripheral position of this plot from the remaining plots indicated that the axes gave undue weight to this single point. Plot 5P and *Cladonia cariosa*, which occurred

only in this plot, 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. Transformations were needed within the environmental matrix, comprised 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 primary goal of this study is 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.

Subset analyses were conducted to focus on non-calcareous and non-rocky plots, potentially revealing more subtle patterns. The subset was derived from the original 77 plots within the Preserve (excluding the outlier, 5P). Plots were removed on the basis of greater than 5% rock cover and those occurring on dolomite or limestone. Of the remaining 42 plots, two were identified as outliers. Plot 13P was 2.6 standard deviations from the mean, and 7L was 2.1 standard deviations from the mean. These plots were outliers primarily due to low sample unit totals (24% and 30%, respectively, as compared to the average of 43%). These plots also lacked some nearly ubiquitous taxa present at all other plots (see yellow box in Fig. 5). These plots appeared clearly peripheral to the central cloud of points and were deleted for the subset analysis. We also deleted *Arctoparmelia separata*, *Cetraria hepatizon*, *Pilophorus cereolus*, *Sphaerophorus fragilis*, *Stereocaulon subcoralloides*, and *Umbilicaria carolinana* to eliminate all primarily or strictly saxicolous species. The final subset contained 40 plots and 83 species.

We sought groupings based on lichen community composition using two-way hierarchical agglomerative cluster analyses in PC-ORD 5 (McCune and Mefford 2005). Two-way cluster analysis combines independent clustering of sample units and species into a single diagram. Plots are combined into groups based on compositional dissimilarity, measured with Sørensen distance. Following deletion of the outlier, 5P, we also deleted all species with two or less occurrences to improve interpretability. 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. The optimal number of groups of plots was

assessed with multi-response permutation procedure (MRPP; Mielke 1984), seeking the number of groups where all items in the group are most similar, assessed with an *A*-statistic (McCune and Grace 2002). Large *A*-statistics, close to one, indicate strongly cohesive groups, while lower *A*-statistics, close to zero, suggest weak groupings.

Results

Diversity

We found a total of 140 macrolichen taxa in 78 plots from the Bering Land Bridge National Preserve during summer 2003 (Table 2). Prior to deleting the outlier, the average species richness, not weighted by area, was 24.3 lichen species per plot. 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 compositional heterogeneity among sample units (McCune and Grace 2002). The beta diversity for the entire sampling effort was 4.8, which is rather heterogeneous (Table 1). The most abundant species were *Cetraria cucullata*, *C. laevigata*, *Cladina stygia*, and the composite of *Cladina arbuscula/ mitis*. The most frequently encountered lichens included *Cladonia amaurocraea* in addition to the same four listed above (Table 2).

Community Structure

The two-axis solution recommended by NMS was stronger than expected by chance, based on a randomization test ($p = 0.004$). The best solution yielded a final stress value of 15.2. The final instability was 0.009 and there were 500 iterations in the final solution. Cumulatively, these two axes represented 86.8% of the community variation (Fig. 2).

The first axis accounted for most of the variance, 53.4%. The lichen species with the strongest association with this axis was *Cladonia amaurocraea* ($r = 0.76$). In addition, all *Cladina* species present in the Preserve, except *C. stellaris*

Table 2. Species list of 140 unique taxa, and associated species codes, found in the Bering Land Bridge National Preserve from 78 plots in 2003. "Ave" is the average abundance (cover class scale ranges between 0-6), and "Freq" is the number of plots in which each species was encountered.

Species	Code	Ave	Freq	Species	Code	Ave	Freq
<i>Alectoria nigricans</i>	Alenig	2.1	49	<i>Cladonia gracilis</i> ssp. <i>elongata</i>	Clagre	1.4	27
<i>Alectoria ochroleuca</i>	Aleoch	2.3	41	<i>Cladonia gracilis</i> ssp. <i>turbinata</i>	Clagrt	1.4	12
<i>Arctoparmelia centrifuga</i>	Arccen	2.7	3	<i>Cladonia gracilis</i> spp. <i>vulnerata</i>	Clagrv	1.8	12
<i>Arctoparmelia separata</i>	Arcsep	1.9	14	<i>Cladonia grayi</i>	Clagry	1.3	6
<i>Asahinea chrysantha</i>	Asachr	2.1	32	<i>Cladonia macrophylla</i>	Clamac	1.1	11
<i>Asahinea scholanderi</i>	Asasch	1.5	13	<i>Cladonia macroceras</i>	Clamas	1.5	13
<i>Bryocaulon divergens</i>	Brcdiv	2.2	46	<i>Cladonia maxima</i>	Clamax	2.1	38
<i>Bryoria chalybeiformis</i>	Brycha	1.5	2	<i>Cladonia merochlorophaea</i>	Clamer	1.0	2
<i>Bryoria fuscescens</i>	Bryfus	1.0	1	<i>Cladonia metacorallifera</i>	Clamet	1.0	3
<i>Bryoria nitidula</i>	Brynit	1.6	17	<i>Cladonia nipponica</i>	Clanip	2.0	6
<i>Cetraria andrejevii</i>	Cetand	2.0	3	<i>Cladonia phyllophora</i>	Claphy	1.2	6
<i>Cetraria cucullata</i>	Cetcuc	3.3	73	<i>Cladonia pleurota</i>	Claple	1.3	10
<i>Cetraria delisei</i>	Cetdel	2.5	12	<i>Cladonia pocillum</i>	Clapoc	1.0	7
<i>Cetraria ericetorum</i>	Ceteri	2.3	4	<i>Cladonia pyxidata</i>	Clapyx	1.7	9
<i>Cetraria fastigiata</i>	Cetfas	1.0	1	<i>Cladonia squamosa</i>	Clasqu	1.1	14
<i>Cetraria hepatizon</i>	Cethep	1.4	5	<i>Cladonia stricta</i>	Clastr	1.5	4
<i>Cetraria islandica</i>	Cetisl	2.1	47	<i>Cladonia subfurcata</i>	Clasuf	1.6	36
<i>Cetraria kamezatica</i>	Cetkam	1.8	13	<i>Cladonia sulphurina</i>	Clasul	1.5	48
<i>Cetraria laevigata</i>	Cetlae	3.0	70	<i>Cladonia uncialis</i>	Claunc	2.1	49
<i>Cetraria nigricans</i>	Cetnig	2.5	15	<i>Cladonia species 1</i>	Clai1	2.7	3
<i>Cetraria nivalis</i>	Cetniv	2.2	56	<i>Cladonia species 2</i>	Clai2	2.0	2
<i>Cetraria pinastri</i>	Cetpin	1.2	14	<i>Cladina arbuscula/ mitis</i> ¹	Cldarb/m	3.1	67
<i>Cetraria sepincola</i>	Cetsep	1.5	4	<i>Cladina ciliata</i>	Cldcil	3.2	5
<i>Cetraria tilesii</i>	Cettil	2.1	9	<i>Cladina rangiferina</i>	Cldran	3.4	50
<i>Cladonia acuminata</i>	Claacu	1.0	1	<i>Cladina stellaris</i>	Cldste	2.9	22
<i>Cladonia alaskana</i>	Claala	2.0	1	<i>Cladina stygia</i>	Cldsty	3.7	64
<i>Cladonia albonigra</i>	Claalb	1.0	3	<i>Coelocaulon muricatum</i>	Coemur	1.7	6
<i>Cladonia amaurocraea</i>	Claama	2.6	65	<i>Dactylina arctica</i>	Dacarc	2.3	20
<i>Cladonia bacilliformis</i>	Clabaf	1.1	22	<i>Dactylina beringica</i>	Dacber	1.6	10
<i>Cladonia bellidiflora</i>	Clabel	1.3	35	<i>Dactylina madreporiformis</i>	Dacmad	1.0	2
<i>Cladonia borealis</i>	Clabor	1.2	9	<i>Dactylina ramulosa</i>	Dacram	1.7	12
<i>Cladonia botrytes</i>	Clabot	1.1	10	<i>Evernia perfragilis</i>	Eveper	1.5	4
<i>Cladonia cariosa</i>	Clacai	2.0	1	<i>Hypogymnia castanea</i> Krog ined.	Hypcas	1.5	2
<i>Cladonia cenotea</i>	Clacen	1.2	16	<i>Hypogymnia physodes</i>	Hypphy	1.1	11
<i>Cladonia cervicornis s.l.</i>	Clacer	1.3	11	<i>Hypogymnia subobscura</i>	Hypsub	1.6	8
<i>Cladonia chlorophaea</i>	Clachl	1.0	5	<i>Icmadophila ericetorum</i>	Icmeri	1.2	9
<i>Cladonia coccifera</i>	Clacoc	1.8	30	<i>Lobaria linita</i>	Loblin	1.6	17
<i>Cladonia cornuta</i>	Clacor	1.2	31	<i>Masonhalea richardsonii</i>	Mahric	2.0	8
<i>Cladonia crispata</i>	Clacri	1.1	12	<i>Melanelia stygia</i>	Melsty	1.0	1
<i>Cladonia cyanipes</i>	Clacya	1.1	24	<i>Nephroma arcticum</i>	Neparc	1.9	19
<i>Cladonia decorticata</i>	Cladec	1.0	3	<i>Nephroma expallidum</i>	Nepexp	1.3	12
<i>Cladonia deformis</i>	Cladef	1.3	8	<i>Nephroma parile</i>	Neppar	1.0	1
<i>Cladonia digitata</i>	Cladig	1.0	3	<i>Ochrolechia frigida</i>	Ochfri	1.0	2
<i>Cladonia fimbriata</i>	Clafim	1.1	7	<i>Parmeliopsis ambigua</i>	Papamb	1.0	6
<i>Cladonia furcata</i>	Clafur	1.6	5	<i>Parmeliopsis hyperopta</i>	Paphyp	1.0	1

Table 2, Continued.

Species	Code	Ave	Freq	Species	Code	Ave	Freq
<i>Parmelia omphalodes</i>	Paromp	1.4	5	<i>Sphaerophorus fragilis</i>	Sphfra	1.6	20
<i>Parmelia sulcata</i>	Parsul	1.7	13	<i>Sphaerophorus globosus</i>	Sphglo	2.2	56
<i>Peltigera aphthosa</i>	Pelaph	1.9	21	<i>Stereocaulon apocalypticum</i>	Steapo	1.3	3
<i>Peltigera canina</i>	Pelcan	1.0	1	<i>Stereocaulon arenarium</i>	Steare	3.0	1
<i>Peltigera horizontalis</i>	Pelhor	2.0	1	<i>Stereocaulon botryosum</i>	Stebot	2.0	1
<i>Peltigera leucophlebia</i>	Pelleu	1.8	19	<i>Stereocaulon glareosum</i>	Stegla	1.0	1
<i>Peltigera malacea</i>	Pelmal	1.0	2	<i>Stereocaulon groenlandicum</i>	Stegro	1.5	2
<i>Peltigera membranacea</i>	Pelmem	1.0	1	<i>Stereocaulon paschale</i>	Stepas	2.2	31
<i>Peltigera neckeri</i>	Pelnec	2.0	1	<i>Stereocaulon subcoralloides</i>	Stesub	1.0	4
<i>Peltigera neopolydactyla</i>	Pelneo	1.0	2	<i>Stereocaulon symphycheilum</i>	Stesym	1.4	7
<i>Peltigera polydactylon</i>	Pelpol	1.0	3	<i>Stereocaulon tomentosum</i>	Stetom	1.3	3
<i>Peltigera praetextata</i>	Pelpra	1.0	1	<i>Stereocaulon vesuvianum</i>	Steves	2.0	2
<i>Peltigera rufescens</i>	Pelruf	1.3	3	<i>Stereocaulon wrightii</i>	Stewri	3.5	2
<i>Peltigera scabrosa</i>	Pelsca	1.5	16	<i>Sticta arctica</i>	Stiarc	1.0	3
<i>Pilophorus cereolus</i>	Pilcer	1.7	3	<i>Thamnia subuliformis</i>	Thasub	2.5	32
<i>Pilophorus robustus</i>	Pilrob	1.0	1	<i>Thamnia vermicularis</i>	Thaver	2.1	47
<i>Pseudephebe minuscula</i>	Psemin	1.0	1	<i>Umbilicaria arctica</i>	Umbarc	4.0	5
<i>Pseudephebe pubescens</i>	Psepub	1.0	2	<i>Umbilicaria caroliniana</i>	Umbcar	2.2	9
<i>Psora decipiens</i>	Psodec	1.0	1	<i>Umbilicaria cylindrica</i>	Umbcyl	1.0	1
<i>Psora nipponica</i>	Psonip	1.0	1	<i>Umbilicaria hyperborea</i> var. <i>hyperborea</i>	Umbhyp	2.1	9
<i>Ramalina almqvistii</i>	Ramalm	1.0	4	<i>Umbilicaria polyphylla</i>	Umbpol	2.0	1
<i>Ramalina intermedia</i>	Ramint	1.0	1	<i>Umbilicaria proboscidea</i>	Umbpro	2.6	17
<i>Siphula ceratites</i>	Sipcer	1.8	6	<i>Umbilicaria rigida</i>	Umbrig	2.5	2
<i>Solorina bispora</i>	Solbis	1.0	2	<i>Umbilicaria scholanderi</i>	Umbsch	3.0	1
<i>Solorina crocea</i>	Solcro	3.0	2	<i>Umbilicaria torrefacta</i>	Umbtor	1.3	3

¹*Cladina arbuscula* and *C. mitis* were combined into a single variable for all analyses due to several ambiguous identifications

and *C. ciliata*, showed a strong positive correlation with this first axis. Also positively associated with axis one was average adjusted lichen height and *Sphagnum* cover. Conversely, ordered by decreasing strength of the relationship, *Cetraria nivalis*, *C. tilesii*, *Thamnia subuliformis*, and *Asahinea chrysantha* were all negatively related to the first axis. Cover of bare soil was also negatively correlated to this axis. Axis one partially represented a bedrock gradient, because plots of calcareous bedrock clustered at the negative end (Fig. 3a). Similarly, topographic position also associated with axis one (Fig. 3b). Upper slope and ridge top sites clustered at the negative end,

while lower slope and lowland sites clustered at the positive end of this gradient.

The second axis represented 33.4% of community variation. The lichens most strongly negatively related to the second axis were *Cetraria laevigata* ($r = -0.48$) and *C. cucullata* ($r = -0.40$). In general, less than a third of all lichen species negatively correlated with this axis, most of which were weak associations. The environmental variable most negatively associated with this axis was graminoid cover. Alternatively, many lichen species had strong positive associations to the second axis. Some of the strongest correlations included *Alectoria*

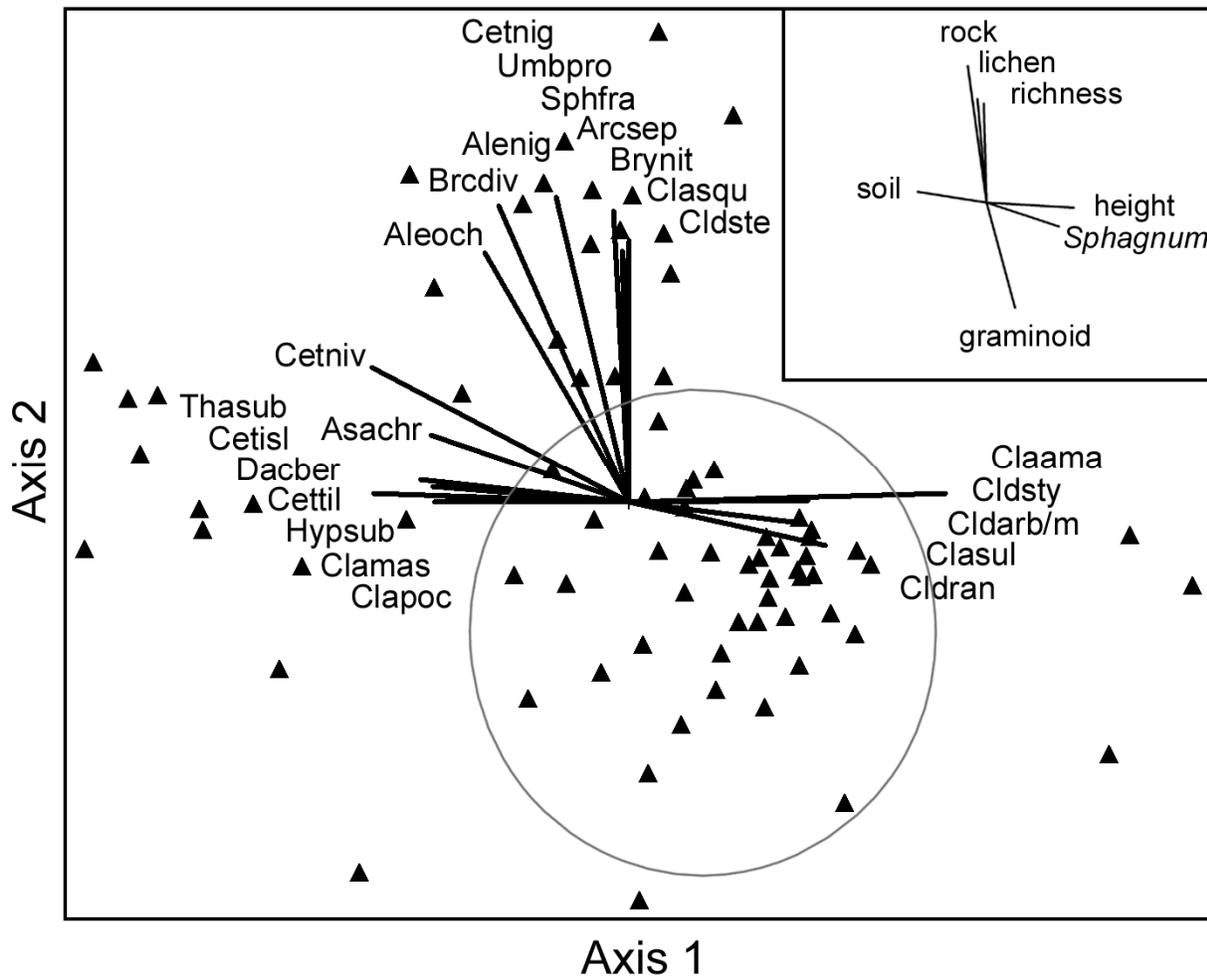


Figure 2. NMS ordination of the plots in species space rigidly rotated 105° and reflected horizontally. Plots are depicted as triangles and lines represent joint plots of the species variables (r^2 cutoff = 0.30). Lichen species codes are in Table 2. Ellipse encloses most of the subset of plots used in further analyses. Inset in upper right corner is same NMS ordination, with joint plot of the environmental and lichen summary variables (bare soil cover, graminoid cover, *Sphagnum* cover, adjusted average lichen height, total lichen cover, lichen species richness, and rock cover).

nigricans, *Bryocaulon divergens*, *Cetraria nigricans*, *Cladina stellaris*, *Umbilicaria proboscidea*, and *A. ochroleuca*. The greatest correlation between community structure and all environmental variables was rock cover, which positively related to the second axis. Moreover, lichen species richness and total lichen cover also had strong positive associations with the second axis.

Lichen Succession

Adjusted average lichen height, a measure of

lichen mat condition, strongly related to community structure ($r = 0.69$ to the first NMS axis). Lichen height also had positive correlations to *Sphagnum* cover ($r = 0.55$) and subshrub cover ($r = 0.37$). Negative correlations with lichen height included bare soil ($r = -0.42$) and elevation ($r = -0.45$). Accordingly, quantitative successional scores were related to lichen community structure ($r = 0.42$ to the second NMS axis). These successional scores were also moderately correlated to several environmental variables. For example, the

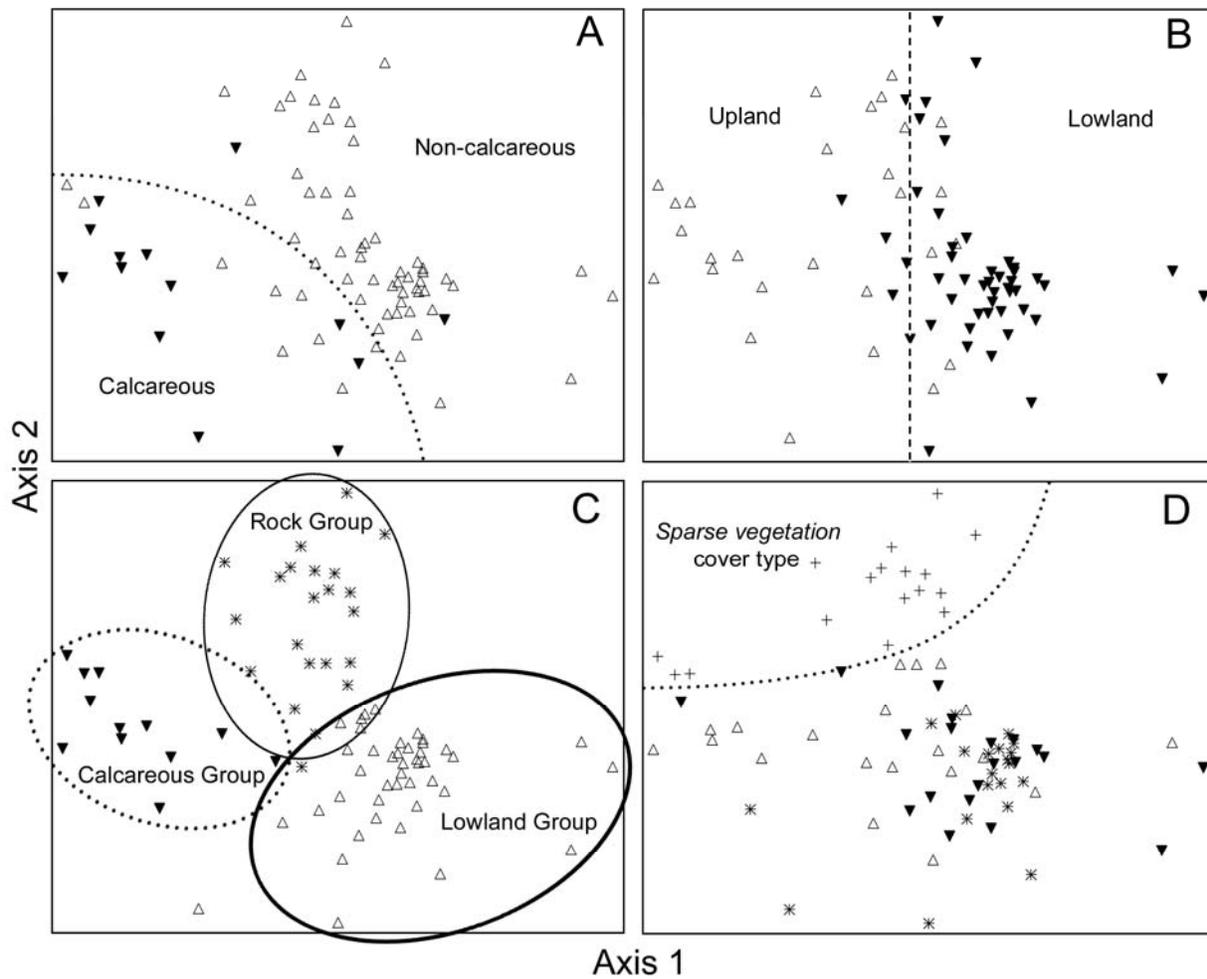


Figure 3. Four overlays of environmental variables onto the main ordination from Fig. 2. Dashed lines and ellipses roughly enclose general groupings of related points to demonstrate overall trends: (A) underlying bedrock type, (B) topographic position, (C) lichen community groups derived from cluster analysis, and (D) cover types used in stratification where: *: *Mesic-dry herbaceous*; ▲: *Open low shrub-dwarf birch/Ericaceous*; ▽: *Dwarf shrub-lichen dominated*; and +: *Sparse vegetation*.

highest correlations occurred between successional scores and overall lichen cover ($r = 0.35$) and rock cover ($r = 0.34$).

Subset Analyses

The two strongest gradients in lichen species composition correlated with high rock cover of non-calcareous rocks and the presence of calcareous rock-derived soils. By deleting the rock dominated plots, strictly saxicolous species, and calcareous plots, we hoped to further explore terricolous lichen community structure on more

acidic substrates. NMS recommended a two-axis solution ($p = 0.004$). The best solution yielded a final stress value of 22.7 and final instability of 0.002. Cumulatively, these axes represented 78.8% of the community variation (Fig. 4).

The first axis represented the greatest portion of variance in the subset analysis, 54.4%. Many of the same lichen species and environmental variables that associated with axis one in the full dataset also associated with the first subset axis. For example, *Cladonia amaurocraea* and the

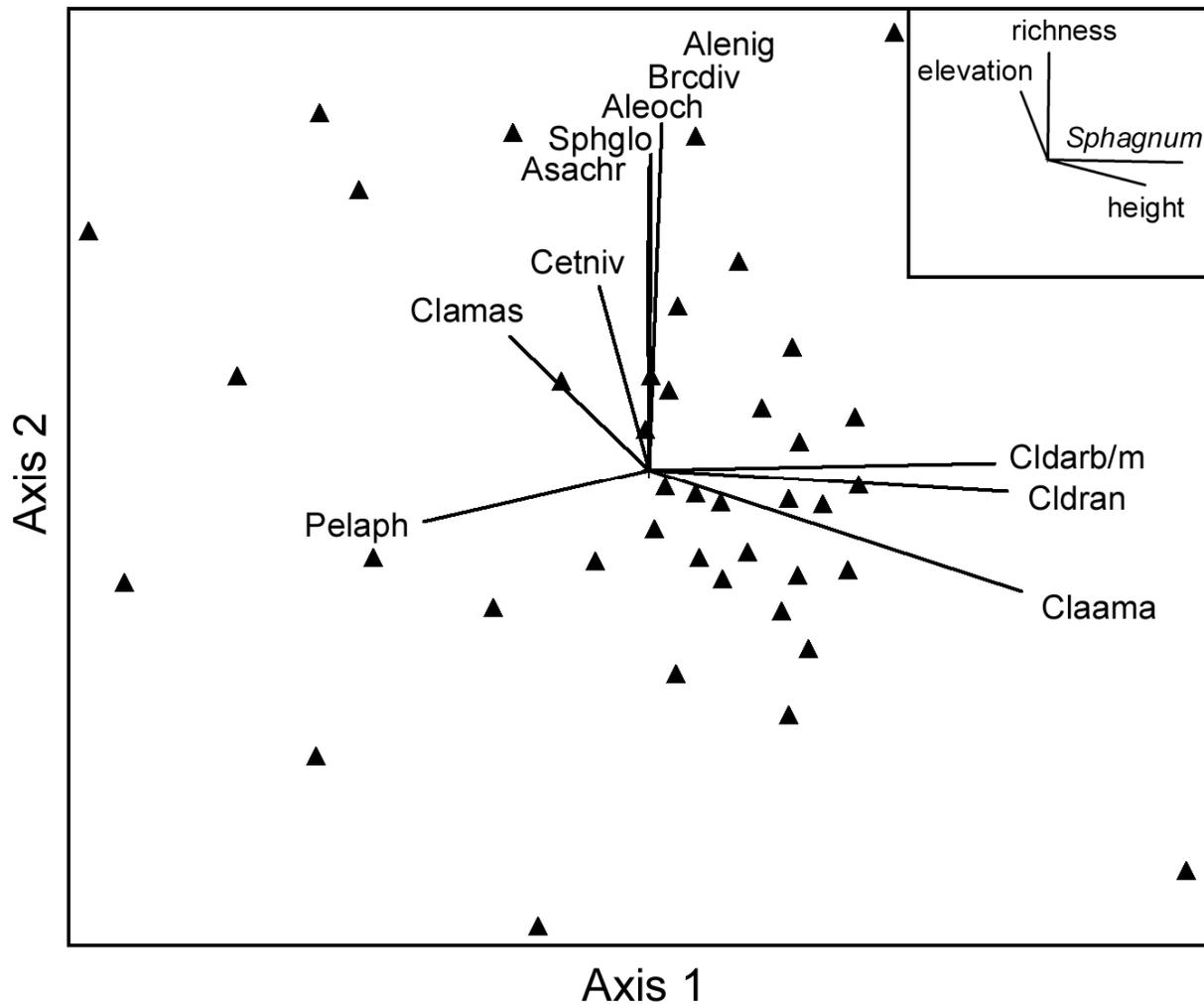


Figure 4. NMS ordination of the 40 subset plots in lichen species space. Plots are depicted as triangles and lines represent joint plots of the species variables (r^2 cutoff = 0.25). Lichen species codes are in Table 2. Inset in upper right corner is same NMS ordination, with joint plot of the environmental and lichen summary variables (*Sphagnum* cover, adjusted average lichen height, lichen species richness, and elevation).

lowland *Cladina* species were positively correlated to this axis. In addition, plots with high *Sphagnum* cover and adjusted average lichen heights had extreme positive axis one scores. Conversely, the plots containing *Peltigera aphthosa*, *Cladonia pyxidata*, *C. macroceras*, *Cetraria cucullata*, and *P. leucophlebia* scored low on subset axis one.

The second subset axis represented 24.5% of variance in the community composition of the 40 plots. Species-rich plots scored high on axis two,

while elevation also positively related to the second subset axis. Species most positively correlated to this axis, in order of decreasing strength, included *Alectoria nigricans*, *Bryocaulon divergens*, *A. ochroleuca*, and *Sphaerophorus globosus*. Several of these species were related to axis two in the main analysis as well. The species most negatively associated with this axis were *Cladonia gracilis* ssp. *turbinata* and *Nephroma arcticum*, although weakly so.

Two-Way Cluster Analysis

We pruned the lichen plot dendrogram to include three clusters, referred to as lichen community groups (Fig. 5). This solution was chosen because only minor increases in the *A*-statistic in MRPP resulted from solutions with greater than three groups. Alternatively, when assessing the appropriate number of species groups, we found *A*-statistics rose with no apparent plateau as the number of groups increased. We divided species, therefore, into seven groups. This number was chosen primarily for interpretability, and groups were defined visually, in part based on their associations with plot groups.

The three lichen community groups are distinguished by their hydrology, rock cover and underlying substrate. The smallest lichen community group includes plots all underlain by calcareous bedrock, henceforth the calcareous group. These twelve plots are indicated by calciphilic lichens. The second lichen community group, the rock group, comprised 22 plots, averaging 47% rock cover. This group is indicated by some saxicolous and dry-associated lichens. The remaining lichen community group was the largest, with 43 plots. We called this the lowland group because its plots contained mesic or wet-associated lichens characteristics of lowlands areas.

The seven species groups differed in substrate affinities, hydrologic preferences and lichen community group associations. The first species group (shown as red box in Fig. 5) contained alectoroid as well as dry-associated lichens, such as *Asahinea chrysantha*, *Thamnolia subuliformis*, and various *Cetraria* and *Dactylina* species. The species from this cluster occurred in nearly every lichen community group, yet varied in abundance. They were fairly common in both the calcareous and rock groups, but in low abundance or absent from the lowland group.

The second species group represented the calciphiles, including *Cetraria tilesii*, *Cladonia pocillum*, *Dactylina beringica*, *Evernia perfragilis*, *Hypogymnia subobscura*, and *Masonhalea richardsonii* (brown box in Fig. 5). The third species cluster contained *Cladina stellaris*, saxicolous lichens, and several dry-habitat species (boxed in green in Fig. 5). This cluster occurred almost exclusively in the rock group yet appeared infrequently, and in low abundance, in the lowland plots. Most of the species from this third cluster are terricolous, yet survive in scattered microhabitats present in rocky plots.

The fourth and largest cluster contained species sporadically present to varying degrees in all lichen community groups (yellow box in Fig. 5). All corticolous species fell into this species cluster. Numerous dry-land *Cladonia* species, several *Peltigera* species, and *Lobaria linita* also belong to this group. The remainder of the cluster was formed by rare saxicolous or rock-associated lichens.

The tightest group of all seven clusters (shown in magenta) contains ubiquitous species, including the two most frequent taxa, *Cetraria cucullata* and *C. laevigata*. These pervasive species occurred in fairly high abundance in nearly every plot, with the exception of plots 3P, 7L and 13P (shaded pink box in Fig. 5). The sixth species group (shown in blue) reflects the common *Cladonia* species (e.g., *C. amaurocraea*, *C. gracilis* ssp. *elongata*) and lowland *Cladina* species (excluding *C. ciliata* and *C. stellaris*). These species were not present in calcareous plots and were generally less abundant than the ubiquitous species in the magenta species group.

The final group (turquoise box in Fig. 5) aggregated species that occur primarily in lowland plots. Although fairly common in these lowland plots, their abundance is even lower than that of the blue species group. The species that comprise this group, *Cladonia cenotea*, *C.*

cyanipes, *C. crispata*, *Nephroma arcticum* and *Peltigera scabrosa*, often occupy very moist sites.

Discussion

Substrate And Topographic Gradient

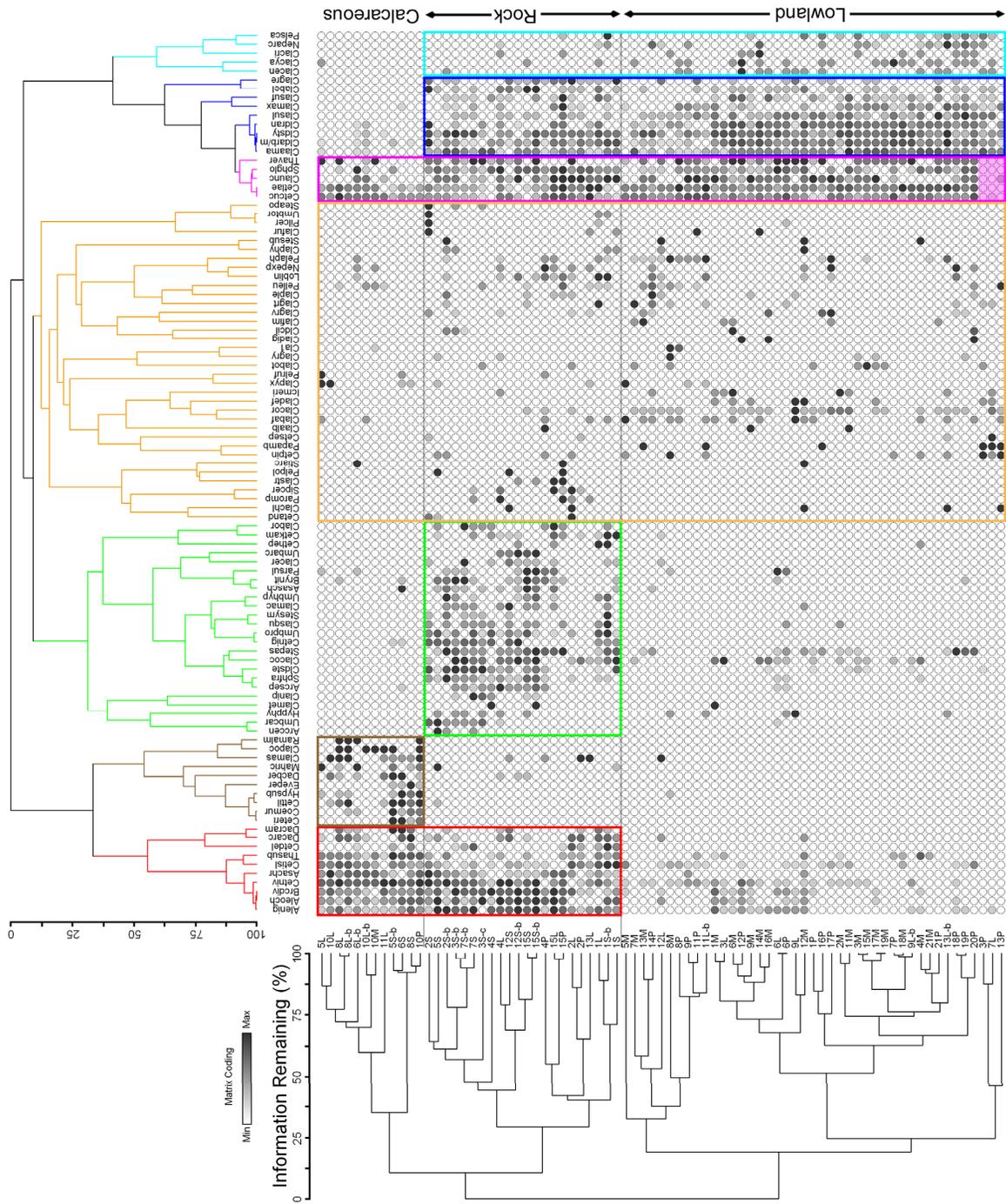
Ordinations based on lichen species composition reveal a gradient that combines substrate and topography along the first axis. This gradient manifests as a trend in vegetation communities ranging from low, moist sites to dry ridge tops. Plots at the moist, tussock end of axis one are dominated by *Sphagnum* and several *Cladina* species. The communities grading toward the dry ridges contained more patches of bare soil and included *Thamnolia subuliformis*, *Asahinea chrysantha*, *Dactylina beringica*, and various species of *Cetraria*.

Substrate characteristics are integral in lichen establishment, growth, and survival (Brodo 1973). Bark pH has been identified as a driver in epiphytic lichen distributions (e.g., Kuusinen 1996; Kermit and Gauslaa 2001). Substrate pH has also been shown to alter juvenile lichen growth in terricolous communities (Robinson et al. 1989). Variations in substrate likely contribute to the patchwork of lichen communities in the Bering Land Bridge National Preserve. The strong gradient in lichen species composition along the first axis corresponds to communities with distinctly different substrate pH. *Sphagnum* species have high cation exchange capacities thereby increasing the acidity of their surrounding environment (Clymo 1964; Andrus 1986). Plots at the positive end of axis

one have high *Sphagnum* cover and low pH. Alternatively, sites on the left end of axis one are relatively dry and alkaline.

The bedrock of the Preserve ranges from volcanic basalts to stratified sedimentary rocks (Till and Dumoulin 1994). The major rock types, as a categorical variable, were strongly patterned on the ordination and differed in lichen community composition (Fig. 3a). Moreover, the calcareous lichen community group, derived from cluster analysis, includes nearly all plots occurring over calcareous parent materials (Fig. 3a, c). Dolomite, or calcium magnesium carbonate, buffers soil pH and contributes to soil magnesium. Lichen communities within the Bering Land Bridge National Preserve respond strongly to substrate differences, which reflect the presence of dolomite and limestone. *Cetraria tilesii*, negatively correlated to axis one, is usually found on calcareous soils and gravels (Thomson 1984). Also, *Cladonia pocillum*, *Dactylina beringica*, *Evernia perfragilis*, *Hypogymnia subobscura*, *Masonhalea richardsonii* and *Ramalina almquistii* group together with *Cetraria tilesii* in the two-way cluster analysis of species to form a calcareous species group (Fig. 5). Other abundant taxa at these plots, *C. nivalis* and *Thamnolia subuliformis*, are not obligate calciphiles yet are often observed in areas underlain by calcareous material. Species sorting by soil type has also been demonstrated among vascular communities in neighboring areas (Kelso 1989; Epstein et al. 2004).

Figure 5 (next page). Two-way cluster analysis dendrogram of 77 plots and 99 macrolichen species (missing doubletons). Each circle represents relative abundance by column (darker is more abundant). The three lichen community groups are indicated to the right, including the calcareous, rock and lowland groups. The seven species groups are indicated with colors. The first cluster, shown in red, contains alectorioid as well as dry-associated lichens. The brown box represents the calciphiles. The third species group, shown in green, contains *Cladina stellaris*, saxicolous lichens, and several dry-habitat *Cladonia* species. The large yellow box highlights several corticolous species growing on shrubs, some mesic lichens and other species found in unusual microhabitats within rocky areas. The magenta box defines nearly ubiquitous lichens present in all plots except plots 3P, 13P and 7L, covered in shaded pink box. The blue box depicts common *Cladonia* species, lowland *Cladonia* species, and the two most common *Cetraria* species. The final species group, including numerous moist-habitat *Cladonia* species, *Peltigera scabrosa*, and *Nephroma arcticum*, is indicated in turquoise.



Calcareous rocks not only alter soil pH, but also relate to topographic position. Dolomite and limestone may remain as high, enduring peaks on the landscape. Calcareous rocks at lower sites, however, may be overlain by alluvial and colluvial deposits and become acidified by accumulation of organic matter. We divided the overall topography of the Preserve into four major categories: ridge, upper slope, lower slope, and lowlands. Again, when this categorical variable or general upland-lowland groupings are overlain onto the ordination of lichen community structure, a clear pattern emerges (Fig. 3b). Similar patterns of high organic matter accumulation and *Sphagnum* encroachment occur in flat lowland areas in boreal regions (Fenton et al. 2005). Likewise, community shifts related to topography and soil parent material have been demonstrated on a large scale throughout the Alaskan Arctic (Epstein et al. 2004). In sum, lichen community structure within the Preserve associates with a gradient of soil pH and topographic position.

Rockiness Gradient

The environmental variable with the greatest correlation to lichen community composition is bare rock cover ($r = 0.87$ to axis two). Lava flows are the most prominent landscape features in the Preserve. Rippling basalt clothes more than 400 km² of arctic tundra in the south-central portion of the Preserve. Plots with the highest rock cover are located in the lava beds. Also associated with this axis is high lichen species diversity and high overall lichen cover. Lichen species positively associated with axis two are strictly rock-dwelling (*Umbilicaria proboscidea*) or often saxicolous but also grow directly on gravely soil (e.g., *Alectoria nigricans*, *Cetraria nigricans*, and *Bryocaulon divergens*). In general, plots with high rock cover tend to have the highest species richness ($r = 0.66$). These areas contain elements of both the terricolous lichen flora as well as a plethora of saxicolous species not reflected in our sampling. Overall, plots with high scores on axis two are rocky and speciose.

In all analyses, plots with high rock cover are distinctly different from all other plots. Accordingly, we compared the four cover types which comprised one of our sampling strata: *Dwarf shrub-lichen dominated*, *Mesic-dry herbaceous*, *Open low shrub-dwarf birch/Ericaceous*, and *Sparse vegetation*, and found the strongest differences were between the *Sparse vegetation* cover type and all other cover types (Table 1). Mean values of lichen species richness, overall lichen cover, bryophyte cover, *Sphagnum* cover, exposed rock cover, and graminoid cover for the *Sparse vegetation* cover type are statistically distinct from any of the other cover types (Table 1). Ordination axis two segregates the markedly different *Sparse vegetation* plots, which cluster together in the ordination, peripheral to all other points (Fig. 3d). In general, these plots had less vascular plant cover with which to compete, more rocks providing a variety of substrates, and often thinner soils. These unique environmental characteristics encourage diverse and prolific lichen communities.

Two-way cluster analysis depicts two species groups limited nearly exclusively to rock-dominated plots. The species group containing alectorioid as well as dry-associated lichens (shown in red in Fig. 5), is abundant in rock dominated and limestone-derived plots. Another species cluster (shown in green in Fig. 5) restricted to the rock group contains mostly saxicolous lichens, several dry-habitat *Cladonia* species, and *Cladina stellaris*. Macrolichens from this group often inhabit crevices and other spaces between rocks. These species were seldom encountered in non-rocky plots, yet occasionally found in low abundance in otherwise mesic sites.

Subset Analysis

The two main gradients in the full dataset are presence of calcareous bedrock and rockiness. After removing nearly half the plots, comprising the rocky and calcareous plots and strictly saxicolous species, we found similar patterns

from the original analysis in the subset ordination. The first major trend, along axes one in both analyses, is a gradient of lichen species composition in response to *Sphagnum* cover. Although present in both analyses, the subset analysis highlights the segregation of *Sphagnum*-tolerant lichens, including the *Cladonia mitis/arbuscula* composite, compared to those that are more intolerant, such as *Cetraria cucullata*, *Cladonia pyxidata* and *Peltigera aphthosa*.

The second major trend present in both datasets, along axis two, represents a gradient of increasing lichen species richness associated with increased rockiness. Our removal of the rockiest plots and any strict saxicolous species for the subset analysis did not appear to disrupt this general trend in lichen species richness. Although this gradient of species richness persisted into the subset analysis, the rock signal and its associated lichens disappeared. Instead, a new pattern of species diversity emerges, independent of rockiness. The presence of dry hummocks and open frost boils amid the sea of *Carex/Eriophorum* tussocks spatially diversifies microhabitats, which increases species diversity. Species that commonly occupy open boils or dry hummocks are *Alectoria nigricans*, *Bryocaulon divergens*, *A. ochroleuca*, and *Sphaerophorus globosus*, all of which positively related to axis two in the subset analysis. Furthermore, lichens associated with various microhabitats, ranging from wet to xeric dependent upon the microtopography, are found in the lowland group (see yellow box in Fig. 5). Spatial patterning associated with microtopographic variability has also been reported elsewhere in the arctic (Benscoter et al. 2005). Moreover, these spatially diverse plots tended to be higher in elevation.

Lichen Succession

Disturbance significantly shapes plant communities, especially in the harsh arctic environment (Muller 1952; Churchill and Hanson 1958). In the full dataset, we found successional

scores moderately related to the second ordination axis ($r = 0.42$). However, this axis is probably not a simple successional gradient. Graminoids and disturbance-tolerant lichens (e.g. *Cetraria laevigata*, *C. cucullata*, *Cladonia bacilliformis*, *C. cornuta*) dominated plots scoring low on axis two. However it seems unlikely that given any amount of time that these sites would develop into lush, diverse communities of late-successional species (e.g., *Alectoria ochroleuca*, *Bryocaulon divergens*, *Cetraria nigricans*, *Cladonia stellaris*) like those in the opposing rocky sites. Instead, we hypothesize that axis two contrasts deep soils dominated by graminoids with thin soils that support low graminoid cover. Generally, late-successional lichen species occur in areas with high rock cover. We do not suggest that these rocky sites are free of other types of disturbance, but are simply unfavorable for vascular plant establishment (i.e., exposed rock slabs or rocky tundra) allowing lichens to proliferate. In sum, late-successional species are able to establish and prevail in areas with sparse vascular competitors, whereas lichens tolerant of high vascular plant competition or those able to establish in novel sites exposed by cryoturbation, fire, or grazing, colonize these disturbed patches.

A major factor determining these lichen communities is rockiness. Clearly rock cover will not increase substantially over time in moist tussock tundra sites of the Preserve that are not currently rocky. So despite moderate correlation between successional scores and axis two, this gradient is not temporal but rather spatial. The successional correlation merely reflects sparse vascular vegetation and resistance of rocky sites to disturbance. The distribution of the *Sparse vegetation* cover type across the landscape peppers hotspots of lichen diversity and abundance throughout the Preserve. These rich late-successional lichen communities emerge in sites deficient in vascular plants. In sum, a major pattern in lichen community structure, corresponding to the first ordination axis,

represents a successional gradient in space not time.

We also indirectly measured lichen succession using lichen height as a proxy of lichen age or productivity (Ahti 1959; Steen 1965). Lichen height, however, not only suggests the successional status of a site by quantifying the amount of lichen on the landscape, but also indicates site characteristics. Lichen height associates with a topographic-pH gradient that manifests as tall or short lichens. Such a decreasing trend in lichen height with increasing elevation or topography has also been documented in Newfoundland (Bergerud 1971). In the Bering Land Bridge National Preserve, the ability of *Cladonia rangiferina*, *C. stygia*, and *Cladonia amaurocraea* to grow vertically enables them to survive in moist, lowland areas where they compete with bryophytes and vascular plants. On ridges, lichens struggle with survival in a less competitive environment, so minimal growth or compact horizontal growth benefits lichens by reducing evaporative losses or minimizing wind scour.

Several of the typically tall species cluster together in the two-way cluster analysis (boxed in blue in Fig. 5). This group of species is moderately abundant in both lowland and rocky plots. In rock-dominated sites, these ground-dwelling lichens persist, despite high rock cover, which alludes to the late-successional role of these species. Alternatively, the presence of these species in lowland environments reflects aspects of the growing environment in addition to other disturbances such as grazing. For example, we have no evidence that the northern portion of the Preserve with its taller lichens is less disturbed or grazed, but it seems probable that environmental conditions within these areas, including higher bryophyte and vascular plant cover, support greater vertical lichen growth. We directly address these grazing questions in another paper (Holt et al. 2007). Lichen succession, whether measured by successional scores, diversity or

height, is influenced in tandem by disturbance and environment.

Undeniably, disturbance and environment has shifted over time, naturally or due to human influence, and will continue to in the future. This paper, however, represents merely a snapshot of a dynamic system that is the macrolichen communities in the Bering Land Bridge National Preserve. The species relationships and community structures we have presented serve as a baseline. Comparisons with future assessments may provide evidence depicting how this system responds to changes in climate, disturbance and land use. Substrate, topography and rockiness appear to be the factors most strongly associated with current patterns in lichen community composition and succession. Yet as disturbances increase will rocky sites continue to provide a refuge for diverse and prolific lichen communities? As the environment changes will substrate and topography become more weakly associated with lichen community structure and be replaced by other factors? And finally, will future lichen communities of the Bering Land Bridge be drastically different than they are today?

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