Community gradients of macrolichens in the Noatak National Preserve, Alaska, USA

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Abstract: We describe macrolichen community structure and its relation to environment in the Noatak National Preserve, Alaska. We used a two-way stratified random sample to estimate macrolichen abundance from 88 0.38-ha plots within the Preserve. We found 201 unique macrolichens. Two primary gradients in lichen species composition were related to substrate pH and vegetation type, grading from forested communities to high alpine communities. Site characteristics associated with the community gradient are soil moisture and exposure. Both ends of this gradient, including forests and densely shrubby sites at one end and 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. In addition, the alpine communities tend to be more exposed than those protected by trees and shrubs at the opposite end. 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.

Key Words: lichen community, substrate, two-way cluster

Introduction

Macrolichens contribute a large portion of the biomass and diversity to Arctic environments, including both tundra and boreal forested systems. Within the state of Alaska, most lichen studies have focused on taxonomy (Thomson 1984), lichen's role as reindeer forage (e.g., Pegau 1968; Krog 1973; Flock 1989; Holt et al. 2006, 2007b), their contribution to the nitrogen cycle (e.g., Gunther 1989; Weiss et al. 2005) or how lichens respond to disturbance (e.g., Racine 1981; Racine et al. 2004; Ford et al. 1995; 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 almost completely lacking from the Arctic of 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, the detail of species-level determinations for Arctic North America is 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. 2007c).

We chose to study a previously unexplored area in northwestern Alaska, 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, unpublished) and to the southwest in the Bering Land Bridge National Preserve (Holt et al. 2007c). The objective of this study was to describe lichen community structure and its relation to environment in the Noatak National Preserve. We used a stratified random sample to partition our heterogeneous landscape and increase the precision and efficiency of estimates for variables of interest (Husch et al. 1972). 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 ten 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^o and 15.2^oC, respectively. Similarly, mean January and July temperatures in Kotzebue are -19.4^o and 12.4^oC, 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. 200 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 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 polygons, *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*, comprise only a small portion of the Preserve's vegetation, and occur almost strictly in the southwestern corner of the Preserve. The shrubs 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*, and *Rubus chamaemorus*. The dominant mosses are *Pleurozium schreberi* and *Hylocomium splendens*, 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 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. 2007c), similarity or overlap in cover type categories and the goal of minimizing the number of strata (Holt et al. 2007a), 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 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 type 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-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). 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 handle (60°N; 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). UV light distinguished 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 NPS 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 lichen's response to disturbance (e.g., Ahti 1959; Steen 1965; Holt et al. 2007b). 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, C. arbuscula/mitis* (isomorphs lumped in the field), *Cetraria cucullata,* and *Cetraria islandica/laevigata* (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 if 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 the 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 less plots (92 species total) were deleted to clarify patterns in the diagram. 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 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.

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 (β = -0.25) as the linkage method on Sørensen distances. The optimal number of groups of plots was first evaluated with multi-response permutation procedure (MRPP; Mielke 1984), seeking the solution with fewest number of groups but the greatest gain in *A*-statistics (McCune and Grace 2002). Due 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). The most frequently occurring lichens included *Cetraria cucullata*, *Cladonia amaurocreaea*, *Cetraria islandica*, *C. nivalis* and *C. laevigata*. *Bryoria implexa* and *Cetraria commixta*, 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 (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 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*, *C. tilesii*, *Thamnolia subuliformis*, *Asahinea chrysantha* and *Dactylina ramulosa* were positively associated with this axis. Several mosses were also positively associated with axis one, including *Racomitrium lanuginosum*, *Grimmia* spp. and *Andreaea rupestris.* 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* and *Pleurozium schreberi*. The single strongest lichen species negatively correlated with axis one was *C. pinastri* (r = -0.74). Other strong negative associations included *Hypogymnia physodes*, *Cladonia cornuta*, *H. bitteri* and *C. cenotea.*

Axis two represented 29.2% of the lichen community variation. The three lichen species most positively related to axis two were *Cladonia pocillum*, *Cetraria tilesii* and *Solorina bispora*. Although weakly correlated, *Scorpidium scorpioides*, *Thuidium abietinum* and *Distichium capillaceum* 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 amaurocrea*, *Cladina rangiferina* and *C. stygia*. Moreover, *Aulacomnium turgidum* and *Sphagnum* spp. were negatively associated with axis two. Over two-thirds of all lichen species were negatively associated with axis two. Most environmental variable 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 were 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 gold (Fig. 3).

Plot cluster 5 shared the same hummocky tussock tundra lichens (highlighted in gold) 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. *Cetraria delisei*, *Arctoparmelia subcentrifuga* and *Collema fuscovirens,* comprising the smallest subdivision of the calciphilic group, 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 dashed 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 bispora*, which have the broadest fidelity.

The third species cluster, depicted in green (Fig. 3), represents 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*, *C. nivalis* and *C. laevigata*. These pervasive species occurred in fairly high abundance in nearly 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 dashed 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 then the other plots within this plot cluster.

Gold 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 nor 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*, *Thamnolia vermicularis*, *Sphaerophorus globosus* and *Cladonia stricta*). 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*, *Nephroma expallidum*, *Masonhalea richardsonii* and *Stereocaulon paschale*. 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 *C. gracilis*. Lichens within this well-defined group often flourish in the interspaces 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 the epiphytes as well as several *Cladonia* species (including *C. maxima*, *C. cornuta* and *C. cyanipes*). 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*.

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*, *Lobaria scrobiculata* and *Ramalina roesleri*, were faithful to the forested plots within plot cluster 6. *Hypogymnia bitteri*, *Parmelia sulcata* 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 grade from forested communities to moist tundra to 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). Vascular plant cover is low and bare soil is high. 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 permitted (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 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 which 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. 2007c). 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 depicted in ordinations of lichen species composition contrasts communities responding to differing calcareous and acidic substrates. 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 acidiphilous species (e.g., *Cladonia amaurocrea*, *Cladina 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, 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 significant impact on species establishment and survival and broad geographic coverage. More interesting perhaps, are the different factors that contribute to plot versus species sorting. Plots group according to abiotic factors such as moisture and exposure, while species primarily group by biotic related patterns or lack thereof (e.g., hummock patterning and substrate availability determined by the presence and type of vascular plants). Furthermore, differences in sorting may be linked to the relative scale of each type of factor. Environmental factors that sort plots vary across a large scale, while species, especially small cryptogams, also respond to local patterns in habitat, such as the fine-scale patchiness of the surrounding vegetation. Undoubtedly, fine-scale environmental factors and coarse-scale vegetation factors also contribute to the abundance and distribution of lichen communities on the landscape as a whole. In sum, the dominant patterns of species sorting respond to fine-scaled biotic factors, and often several species clusters overlap to define each plot cluster, which reflects general large-scale factors.

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Table 1. Macrolichen taxa found in the Noatak National Preserve from 88 plots. "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
Alectoria nigricans	Alenig	1.3	12	*Cladonia cervicornis*	Clacer	1.0	5
Alectoria ochroleuca	Aleoch	1.8	24	*Cladonia chlorophaea*	Clachl	1.4	22
Allantoparmelia alpicola	Allalp	1.0	1	*Cladonia coccifera*	Clacoc	2.1	15
Arctoparmelia centrifuga	Arccen	1.3	3	*Cladonia coniocraea*	Clacon	1.0	2
Arctoparmelia separata	Arcsep	2.0	15	*Cladonia cornuta*	Clacor	1.6	36
Asahinea chrysantha	Asachr	2.2	37	*Cladonia crispata*	Clacri	1.5	17
Asahinea scholanderi	Asasch	1.6	5	*Cladonia cryptochlorophaea*	Clacry	1.4	5
Bryocaulon divergens	Brcdiv	1.6	29	*Cladonia cyanipes*	Clacya	1.8	32
Brodoa oroarctica	Brooro	2.0	1	*Cladonia decorticata*	Cladec	1.1	8
Bryoria fuscescens	Bryfus	3.0	3	*Cladonia deformis*	Cladef	1.0	4
Bryoria implexa	Bryimp	4.0	1	*Cladonia digitata*	Cladig	1.0	2
Bryoria lanestris	Brylan	2.2	6	*Cladonia ecmocyna*	Claecm	1.0	1
Bryoria nitidula	Brynit	1.3	7	*Cladonia fimbriata*	Clafim	1.1	14
Bryoria simplicior	Brysim	2.0	2	*Cladonia furcata*	Clafur	1.3	7
Bryoria trichodes	Brytra	3.0	1	*Cladonia gracilis*	Clagra	1.8	48
Cetrelia alaskana	Celala	1.0	1	*Cladonia grayi*	Clagry	1.2	6
Cetraria andrejevii	Cetand	2.0	3	*Cladonia kanewskii*	Clakan	1.0	3
Cetraria commixta	Cetcom	4.0	1	*Cladonia libifera*	Clalib	1.0	5
Cetraria cucullata	Cetcuc	2.6	71	*Cladonia macrophylla*	Clamac	1.5	11
Cetraria delisei	Cetdel	2.3	15	*Cladonia macrophyllodes*	Clamao	1.0	1
Cetraria ericetorum	Ceteri	2.3	6	*Cladonia macroceras*	Clamas	1.3	16
Cetraria fastigiata	Cetfas	2.0	2	*Cladonia maxima*	Clamax	1.7	29
Cetraria hepatizon	Cethep	2.0	4	*Cladonia metacorallifera*	Clamet	1.0	1
Cetraria inermis	Cetine	1.1	7	*Cladonia nipponica*	Clanip	1.0	1
Cetraria islandica	Cetisl	2.3	61	*Cladonia nitens*	Clanit	3.0	1
Cetraria kamczatica	Cetkam	1.3	15	*Cladonia ochrochlora*	Claoch	1.0	1
Cetraria laevigata	Cetlae	2.0	58	*Cladonia phyllophora*	Claphy	1.3	10
Cetraria nigricans	Cetnig	1.8	13	*Cladonia pleurota*	Claple	1.2	9
Cetraria nivalis	Cetniv	2.0	59	*Cladonia pocillum*	Clapoc	1.9	30
Cetraria orbata	Cetorb	1.0	1	*Cladonia pyxidata*	Clapyx	1.6	26
Cetraria pinastri	Cetpin	1.7	40	*Cladonia scabriuscula*	Clasca	1.0	7
Cetraria sepincola	Cetsep	1.6	31	*Cladonia scotteri*	Clasco	1.3	3
Cetraria tilesii	Cettil	2.5	26	*Cladonia squamosa*	Clasqu	1.1	9
Cladonia acuminata	Claacu	1.2	6	*Cladonia stricta*	Clastr	1.3	15
Cladonia alaskana	Claala	1.0	1	*Cladonia subfurcata*	Clasuf	1.3	12
Cladonia albonigra	Claalb	1.8	9	*Cladonia symphycarpia*	Clasym	1.0	1
Cladonia amaurocraea	Claama	2.7	61	*Cladonia sulphurina*	Clasul	1.4	21
Cladonia bacillaris	Clabac	1.0	1	*Cladonia trassii*	Clatra	1.0	2
Cladonia bacilliformis	Clabaf	1.3	8	*Cladonia uncialis*	Claunc	2.2	35
Cladonia bellidiflora	Clabel	1.0	3	*Cladonia wainioi*	Clawai	1.0	1
Cladonia borealis	Clabor	1.5	21	*Cladina arbuscula*	Cldarb	2.6	48
Cladonia botrytes	Clabot	1.0	2	*Cladina mitis*	Cldmit	2.9	15
Cladonia cariosa	Clacai	1.3	3	*Cladina rangiferina*	Cldran	2.4	50
Cladonia cenotea	Clacen	1.6	29	*Cladina stellaris*	Cldste	1.6	8

Table 1, continued.

Species	Code	Ave	Freq	Species	Code	Ave	Freq
Cladina stygia	Cldsty	2.4	36	*Parmeliopsis hyperopta*	Paphyp	1.3	19
Coccocarpia erythroxyli	Cocery	2.0	2	*Parmelia omphalodes*	Paromp	1.9	16
Coelocaulon aculeatum	Coeacu	1.0	1	*Parmelia saxatilis*	Parsax	2.0	1
Coelocaulon muricatum	Coemur	1.4	15	*Parmelia squarrosa*	Parsqu	3.0	1
Collema cristatum	Colcri	1.0	1	*Parmelia sulcata*	Parsul	1.9	13
Collema furfuraceum	Colfur	2.0	1	*Peltigera aphthosa*	Pelaph	2.4	41
Collema fuscovirens	Colfus	1.2	6	*Peltigera canina*	Pelcan	1.8	12
Collema tenax	Colten	1.0	4	*Peltigera collina*	Pelcol	1.0	1
Collema undulatum	Colund	1.0	1	*Peltigera didactyla*	Peldid	1.3	8
Dactylina arctica	Dacarc	1.9	40	*Peltigera extenuata*	Pelext	1.6	9
Dactylina beringica	Dacber	2.3	21	*Peltigera horizontalis*	Pelhor	1.7	3
Dactylina ramulosa	Dacram	1.7	28	*Peltigera kristinssonii*	Pelkri	1.2	5
Ephebe hispidula	Ephhis	2.0	1	*Peltigera lepidophora*	Pellep	1.0	2
Evernia divaricata	Evediv	2.3	3	*Peltigera leucophlebia*	Pelleu	2.1	31
Evernia mesomorpha	Evemes	1.4	7	*Peltigera malacea*	Pelmal	1.6	10
Evernia perfragilis	Eveper	2.0	2	*Peltigera membranacea*	Pelmem	1.4	5
Hypogymnia bitteri	Hypbit	2.8	11	*Peltigera neckeri*	Pelnec	1.0	1
Hypogymnia physodes	Hypphy	1.5	15	*Peltigera neopolydactyla*	Pelneo	1.4	8
Hypogymnia subobscura	Hypsub	1.9	19	*Peltigera polydactylon*	Pelpol	1.3	16
Icmadophila ericetorum	Icmeri	1.5	2	*Peltigera ponojensis*	Pelpon	1.6	5
Leciophysma finmarkicum	Lecfin	1.0	1	*Peltigera praetextata*	Pelpra	1.0	1
Leptogium arcticum	Leparc	1.0	1	*Peltigera rufescens*	Pelruf	1.8	25
Leptogium lichenoides	Leplic	1.0	1	*Peltigera scabrosa*	Pelsca	2.5	31
Leptogium saturninum	Lepsat	1.6	7	*Peltigera venosa*	Pelven	1.0	2
Lobaria kurokawae	Lobkur	1.5	4	*Phaeophyscia constipata*	Phacon	1.0	1
Lobaria linita	Loblin	2.3	32	*Physconia muscigena*	Phcmus	1.7	6
Lobaria pseudopulmonaria	Lobpse	1.3	3	*Physcia aipolia*	Phyaip	1.5	2
Lobaria pulmonaria	Lobpul	1.0	1	*Physcia caesia*	Phycae	1.0	3
Lobaria scrobiculata	Lobscr	2.1	7	*Physcia phaea*	Phypha	1.0	1
Masonhalea richardsonii	Mahric	2.1	26	*Pilophorus cereolus*	Pilcer	1.3	3
Melanelia panniformis	Melpan	1.0	1	*Pilophorus robustus*	Pilrob	1.7	3
Melanelia septentrionalis	Melsep	1.0	3	*Pseudephebe pubescens*	Psepub	2.0	8
Melanelia sorediata	Melsor	1.0	2	*Pseudocyphellaria crocata*	Psccro	3.0	1
Melanelia stygia	Melsty	2.6	5	*Ramalina almquistii*	Ramalm	1.5	2
Melanelia trabeculata	Meltra	1.7	3	*Ramalina pollinaria*	Rampol	1.0	1
Multiclavula vernalis	Mulver	1.0	3	*Ramalina roesleri*	Ramroe	1.7	6
Nephroma arcticum	Neparc	1.8	26	*Ramalina sinensis*	Ramsin	1.3	3
Nephroma bellum	Nepbel	1.8	10	*Ramalina thrausta*	Ramthr	1.0	2
Nephroma expallidum	Nepexp	2.5	26	*Solorina bispora*	Solbis	1.1	29
Nephroma helveticum	Nephel	2.0	2	*Solorina crocea*	Solcro	2.0	9
Nephroma parile	Neppar	1.5	6	*Solorina spongiosa*	Solspo	1.0	2
Ochrolechia frigida	Ochfri	1.3	9	*Sphaerophorus fragilis*	Sphfra	2.0	6
Pannaria conoplea	Pancon	1.5	2	*Sphaerophorus globosus*	Sphglo	1.9	25
Parmeliopsis ambigua	Papamb	1.5	11	*Stereocaulon alpinum*	Stealp	1.7	13

Table 1, continued.

Species	Code	Ave	Freq	Species	Code	Ave	Freq
Stereocaulon apocalypticum	Steapo	2.4	5	*Sticta arctica*	Stiarc	1.3	3
Stereocaulon arcticum	Stearc	2.0	1	*Thamnolia subuliformis*	Thasub	1.7	41
Stereocaulon arenarium	Steare	2.0	1	*Thamnolia vermicularis*	Thaver	1.5	33
Stereocaulon botryosum	Stebot	2.0	5	*Umbilicaria caroliniana*	Umbcar	3.0	1
Stereocaulon glareosum	Stegla	1.5	2	*Umbilicaria cylindrica*	Umbcyl	1.0	2
Stereocaulon groenlandicum	Stegro	2.7	3	*Umbilicaria deusta*	Umbdeu	2.0	1
Stereocaulon paschale	Stepas	2.1	19	*Umbilicaria hyperborea* var. *hyperborea*	Umbhyp	1.0	1
Stereocaulon spathuliferum	Stespa	1.0	1	*Umbilicaria hyperborea* var. *radicicula*	Umbhyr	1.2	6
Stereocaulon subcoralloides	Stesub	1.6	8	*Umbilicaria polyphylla*	Umbpol	1.0	1
Stereocaulon symphycheilum	Stesym	1.6	5	*Umbilicaria proboscidea*	Umbpro	2.0	7
Stereocaulon tomentosum	Stetom	1.7	6	*Umbilicaria torrefacta*	Umbtor	1.6	7
Stereocaulon vesuvianum	Steves	2.0	1	*Xanthoria polycarpa*	Xanpol	1.0	1
Stereocaulon sp. 1	Stesp1	1.0	1				

Table 2. Characteristics of the six plot clusters derived from two-way cluster analysis. Mean values in original units and standard deviations in parentheses.

	Cluster 1	**Cluster 2**	**Cluster 3**	**Cluster 4**	**Cluster 5**	**Cluster 6**	**All Clusters[a]**
No. 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)	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 (ln(Rad, MJ/cm^2/yr))	-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 (deg)	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)

[a] ”All Clusters” is the value for all 83 plots, excluding the five outliers.

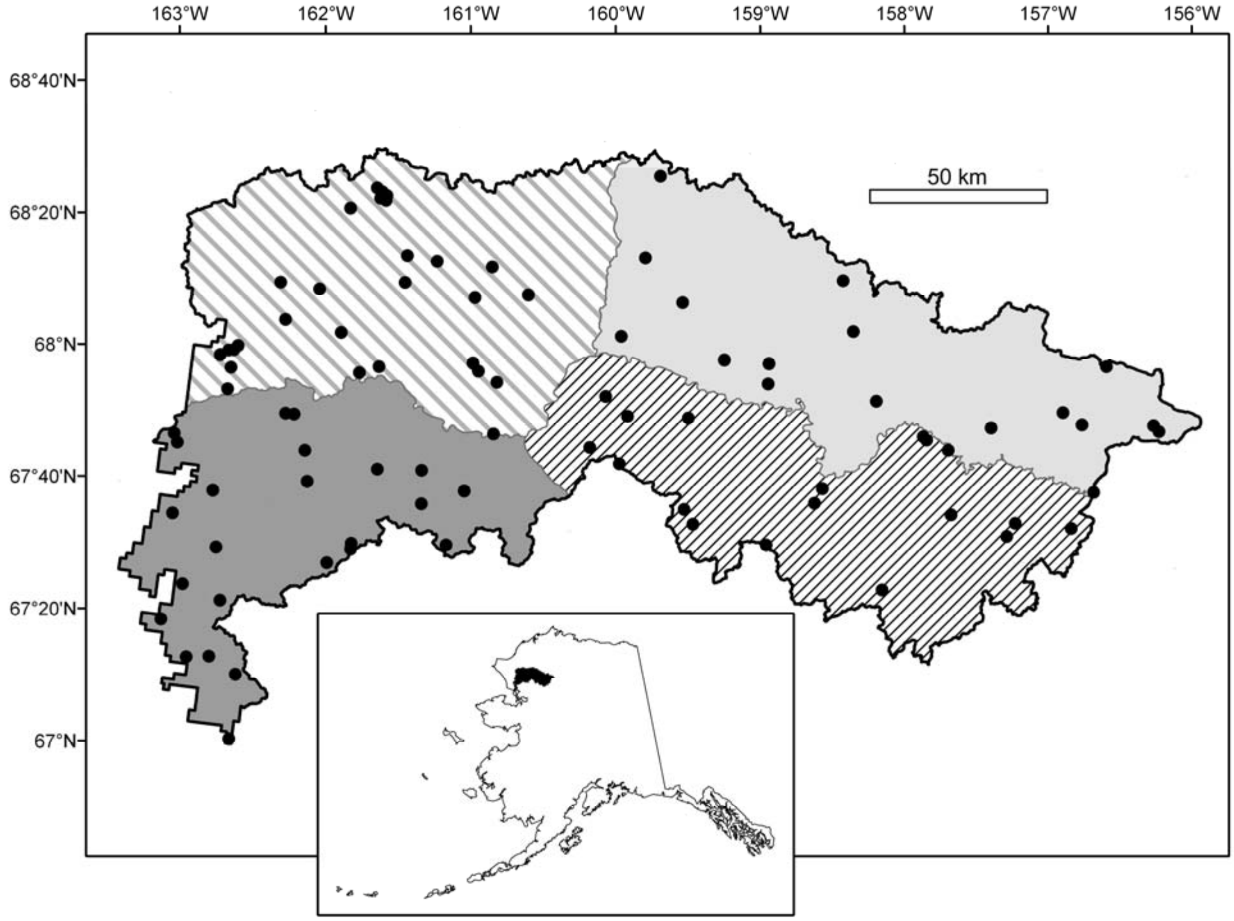


Fig. 1. Map of the Noatak National Preserve in northwestern Alaska. Points indicate 88 plots sampled in 2004 and 2005. The geographic blocks used in sampling stratification are shown as four differently shaded portions of the Preserve. The north-south division follows the Noatak River. The east-west 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.

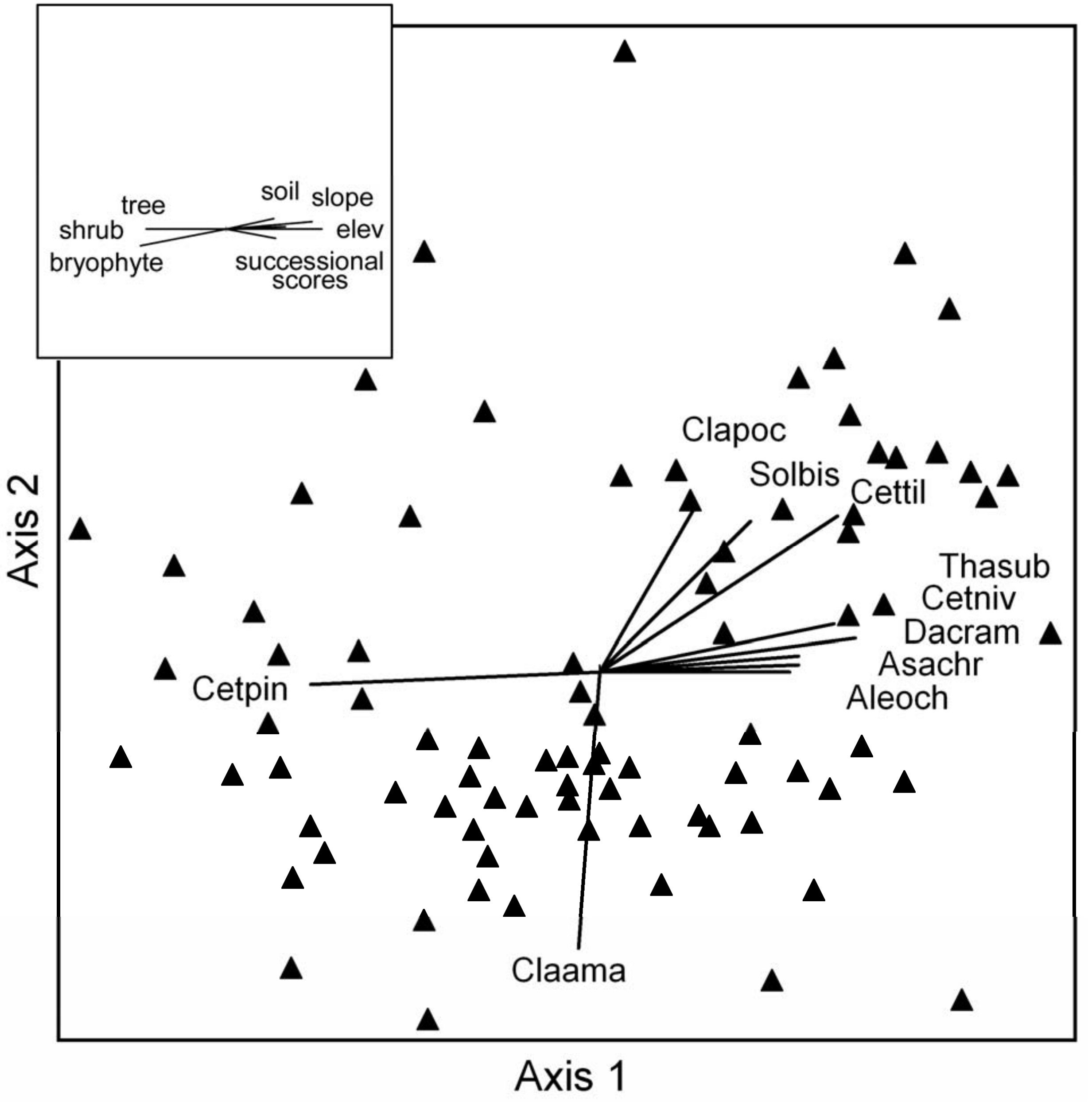
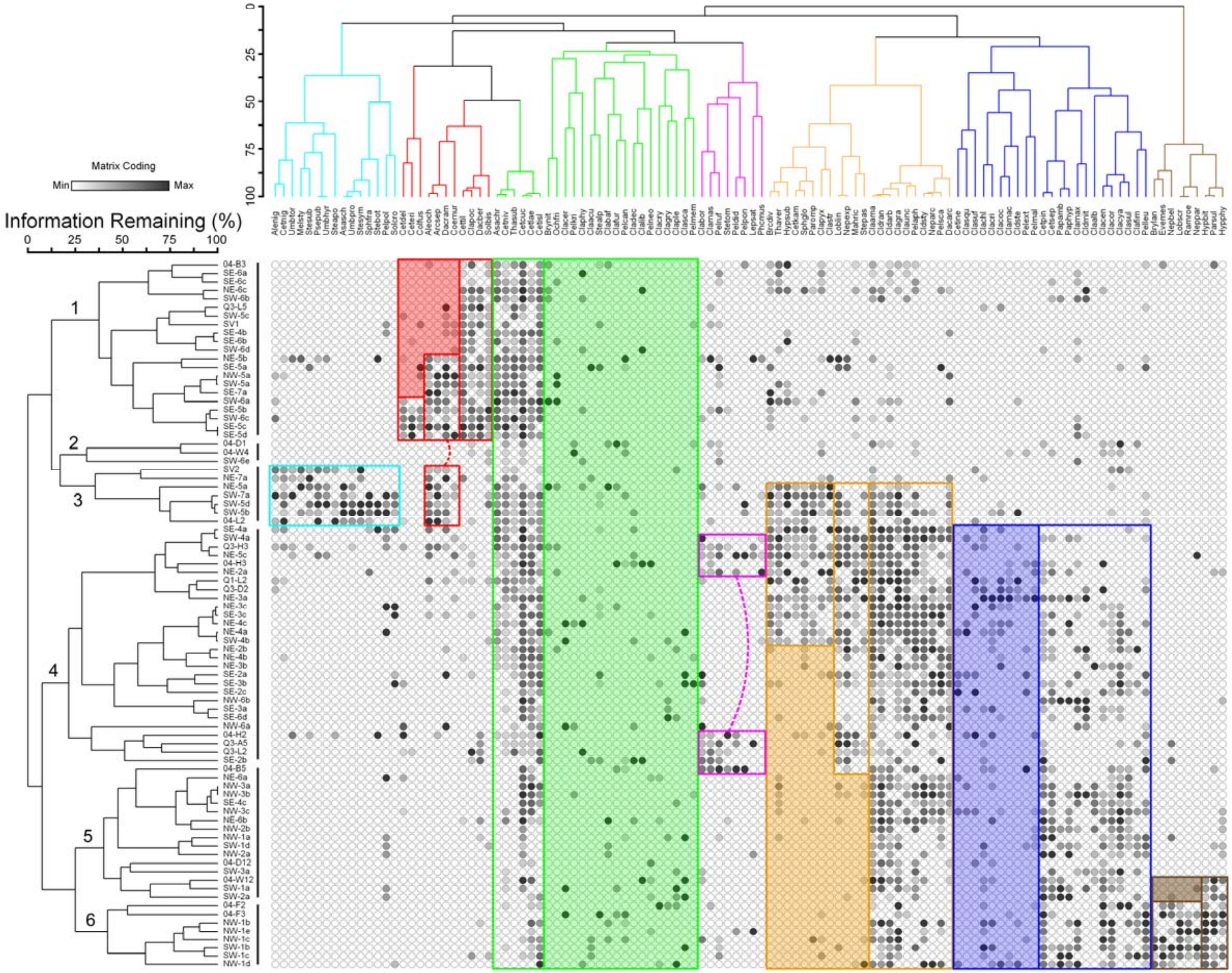


Fig. 2. NMS ordination of the plots in species space rigidly rotated 272°. Plots are depicted as triangles and lines represent joint plots of the species variables (r^2 cutoff = 0.35). Lichen species codes are in Table 1. Inset in upper left corner is same NMS ordination (r^2 cutoff = 0.25), with joint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

Fig. 3 (next page). Two-way cluster analysis dendrogram of 83 plots and 112 macrolichen species (missing species occurring in four or less 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 in Table 1.


Matrix Coding
Min
Max
Information Remaining (%)
0
25
50
75
100
Alenig
Cetnig
Umbtor
Melsty
Stesub
Psepub
Umbhyr
Steapo
Asasch
Umbpro
Stesym
Sphfra
Stebot
Pelpol
Solcro
Cetdel
Ceteri
Colfus
Aleoch
Arcsep
Dacram
Coemur
Cettil
Clapoc
Dacber
Solbis
Asachr
Cetniv
Thasub
Cetcuc
Cetlae
Cetisl
Brynit
Ochfri
Clacer
Pelkri
Claphy
Claacu
Stealp
Clabaf
Clafur
Pelcan
Cladec
Clalib
Pelneo
Clacry
Clagry
Claple
Clasca
Pelmem
Clabor
Clamas
Pelruf
Stetom
Peldid
Pelpon
Lepsat
Phcmus
Brcdiv
Thaver
Hypsub
Cetkam
Sphglo
Paromp
Clapyx
Clastr
Loblin
Nepexp
Mahric
Stepas
Claama
Cldran
Cldarb
Clagra
Claunc
Pelaph
Cldsty
Neparc
Pelsca
Dacarc
Cetine
Clasqu
Clasuf
Clachl
Clacri
Clacoc
Clamac
Cldste
Pelext
Pelmal
Cetpin
Cetsep
Papamb
Paphyp
Clamax
Cldmit
Claalb
Clacen
Clacor
Clacya
Clasul
Claflm
Pelleu
Brylan
Evemes
Nepbel
Lobscr
Ramroe
Neppar
Hypbit
Parsul
Hypphy
1
2
3
4
5
6
04-B3
SE-6a
SE-6c
NE-6c
SW-6b
Q3-L5
SW-5c
SV1
SE-4b
SE-6b
SW-6d
NE-5b
SE-5a
NW-5a
SW-5a
SE-7a
SW-6a
SE-5b
SW-6c
SE-5c
SE-5d
04-D1
04-W4
SW-6e
SV2
NE-7a
NE-5a
SW-7a
SW-5d
SW-5b
04-L2
SE-4a
SW-4a
Q3-H3
NE-5c
04-H3
NE-2a
Q1-L2
Q3-D2
NE-3a
NE-3c
SE-3c
NE-4c
NE-4a
SW-4b
NE-2b
NE-4b
NE-3b
SE-2a
SE-3b
SE-2c
NW-6b
SE-3a
SE-6d
NW-6a
04-H2
Q3-A5
Q3-L2
SE-2b
04-B5
NE-6a
NW-3a
NW-3b
SE-4c
NW-3c
NE-6b
NW-2b
NW-1a
SW-1d
NW-2a
04-D12
SW-3a
04-W12
SW-1a
SW-2a
04-F2
04-F3
NW-1b
NW-1e
NW-1c
SW-1b
SW-1c
NW-1d

Appendix 1. Species list of 183 unique bryophyte taxa found in the Noatak National Preserve from 88 plots. "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	Ave	Freq	Species	Ave	Freq
Anastrophyllum minutum	1.2	6	*Climacium dendroides*	1.6	5
Andreaea rupestris	1.7	12	*Conostomum tetragonum*	1.0	1
Anthelia spp.	1.5	2	*Cryptocolea imbricata*	1.0	2
Anthelia juratzkana	2.5	2	*Cephaloziella* spp.	2.3	3
Atrichum spp.	1.0	1	*Dicranum* spp.	2.4	37
Aulacomnium spp.	1.0	3	*Dicranum acutifolium*	1.8	9
Aulacomnium acuminatum	2.6	9	*Dicranum elongatum*	2.2	17
Aulacomnium androgynum	1.0	1	*Dicranum fuscescens*	1.6	5
Aulacomnium palustre	3.1	31	*Dicranum montanum*	2.3	16
Aulacomnium turgidum	2.7	44	*Dicranum scoparium*	2.1	11
Barbilophozia hatcheri	1.0	1	*Dicranum undulatum*	2.0	1
Bartramia ithyphylla	1.0	1	*Dichodontium pellucidum*	1.0	1
Blepharastoma trichophyllum	1.2	12	*Diplophyllum obtusifolium*	1.5	2
Brachythecium spp.	2.0	10	*Distichium* spp.	1.0	1
Brachythecium albicans	1.0	3	*Distichium capillaceum*	1.3	13
Brachythecium erythrorrhizon	1.0	1	*Distichium inclinatum*	1.0	1
Brachythecium turgidum	1.0	2	*Dicranoweisia crispula*	2.3	6
Bryum spp.	1.9	43	*Drepanocladus* spp.	1.7	6
Bryum creberrimum[a]	1.0	1	*Drepanocladus aduncus*	3.0	12
Bryum inclinatum[a]	1.0	1	*Drepanocladus badius*	1.0	1
Bryum intermedium[a]	1.0	1	*Drepanocladus revolvens*	2.8	19
Bryum lisae[a]	1.3	3	*Drepanocladus uncinatus*	2.2	21
Bryum nitidulum[a]	2.0	1	*Encalypta* spp.	1.0	3
Bryum pallescens[a]	1.0	1	*Encalypta ciliata*	2.0	1
Bryum pseudotriquetrum[a]	2.0	4	*Encalypta rhaptocarpa*	1.0	3
Bryum purpurascens[a]	1.0	2	*Fissidens adianthoides*	1.0	1
Bryum stenotrichum[a]	2.0	1	*Funaria hygrometrica*	1.5	2
Calliergon spp.	2.0	1	*Grimmia* spp.	1.5	10
Calliergon giganteum	1.0	1	*Grimmia torquata*	2.0	1
Calliergon sarmentosum	2.5	6	*Gymnomitrion obtusum*	1.0	1
Calliergon stramineum	1.3	3	*Hedwigia ciliata*	1.0	1
Campylium polygamum	2.0	1	*Hygrohypnum alpestre*	2.0	1
Campylium stellatum	1.9	16	*Hylocomium* spp.	1.0	1
Catoscopium nigritum	2.3	3	*Hylocomium pyrenaicum*	1.0	3
Calypogeia integristipula	1.0	1	*Hylocomium splendens*	4.3	63
Calypogeia neesiana	1.0	1	*Hypnum* spp.	2.2	20
Cephalozia spp.	1.0	1	*Hypnum bambergeri*	2.0	2
Cephalozia bicuspidata	1.0	1	*Hypnum cupressiforme*	2.3	12
Ceratodon purpureus	2.1	27	*Hypnum lindbergii*	6.0	1
Chiloscyphus spp.	1.0	1	*Hypnum pratense*	2.7	3
Cinclidium spp.	2.3	3	*Hypnum procerrimum*	2.0	2
Cinclidium arcticum	1.3	3	*Hypnum subimponens*	1.0	1
Cinclidium stygium	4.0	1	*Isopterygium pulchellum*	1.0	2
Cirriphyllum spp.	1.0	2	*Jungermannia* spp.	1.0	3
Cirriphyllum cirrosum	2.0	2	*Kiaeria blyttii*	1.0	2
Cirriphyllum piliferum	1.0	4	*Leptobryum pyriforme*	1.6	11

Appendix 1, continued.

Species	Ave	Freq	Species	Ave	Freq
Lophocolea spp.	1.0	1	*Rhytidiadelphus squarrosus*	1.5	2
Lophocolea bidentata	1.0	1	*Rhytidiadelphus triquetrus*	2.4	7
Lophozia spp.	1.0	13	*Rhizomnium* spp.	3.5	2
Lophozia attenuata	1.0	1	*Rhytidium rugosum*	3.2	42
Marchantia polymorpha	2.0	4	*Riccardia* spp.	2.0	1
Meesia triquetra	2.2	6	*Saelania glaucescens*	1.0	2
Meesia uliginosa	1.5	4	*Scapania* spp.	1.0	2
Mnium spp.	3.0	1	*Scapania hyperborea*	2.0	1
Mnium affine	1.0	1	*Scapania mucronata*	1.0	1
Mnium andrewsianum	1.0	1	*Scapania paludosa*	1.0	1
Mnium cuspidatum	2.3	4	*Scapania uassiretis*	1.0	1
Mnium hymenophylloides	1.7	3	*Scapania undulata*	1.0	2
Mnium punctatum	1.5	2	*Scorpidium scorpidoides*	5.0	1
Myurella spp.	1.0	1	*Scorpidium turgescens*	1.8	5
Oncophorus virens	3.0	1	*Seligeria* spp.	1.0	1
Oncophorus whalenbergii	1.0	1	*Sphagnum* spp.	5.1	34
Orthothecium spp.	1.0	2	*Sphagnum andersonianum*[b]	3.0	2
Orthothecium chryseum	1.0	1	*Sphagnum compactum*[b]	4.0	1
Orthotrichum laevigatum v. macounii	1.0	1	*Sphagnum* (species G)[b]	2.0	1
Orthotrichum speciosum	2.0	1	*Sphagnum girgensonnii*[b]	5.0	1
Paludella squarrosa	2.3	3	*Sphagnum* (species H)[b]	3.0	1
Philonotis spp.	1.0	1	*Sphagnum lindbergii*[b]	3.0	1
Philonotis fontana	2.2	6	*Sphagnum squarrosum*[b]	3.0	1
Plagiochila spp.	1.0	2	*Sphagnum subnitens*[b]	1.0	1
Pleurozium schreberi	3.5	15	*Splachnum luteum*	2.0	1
Plagiomnium spp.	1.0	1	*Splachnum sphaericum*	1.0	4
Plagiopus oederiana	1.0	1	*Syntrichia* spp.	1.0	1
Pohlia spp.	1.0	2	*Tayloria acuminata*	1.0	3
Pohlia cruda	1.0	4	*Tetraphis pellucida*	1.0	1
Pohlia nutans	1.0	2	*Tetraplodon* spp.	1.2	6
Polytrichum spp.	2.3	9	*Tetraplodon mnioides*	1.5	4
Polytrichum formosum	1.0	1	*Tetraplodon pallidus*	1.0	1
Polytrichum juniperinum	3.0	24	*Tetralophozia setiformis*	2.0	8
Polytrichum longisetum	3.0	1	*Thuidium abietinum*	2.2	26
Polytrichum piliferum	2.7	11	*Thuidium delicatulum*	1.8	5
Polytrichum strictum	3.3	24	*Timmia austriaca*	1.0	1
Pseudobryum cinclidioides	4.0	1	*Timmia megapolitana*	3.0	1
Ptidilium ciliare	2.2	32	*Tortella fragilis*	3.0	1
Ptilidium pulcherrimum	3.0	1	*Tortella tortuosa*	2.0	3
Ptilium crista-castrensis	2.6	5	*Tomenthypnum nitens*	3.2	49
Racomitrium spp.	3.0	2	*Tortula* spp.	1.5	4
Racomitrium canescens	1.7	15	*Tortula ruralis*	1.5	2
Racomitrium heterostichum	1.7	7	*Voitia* spp.	1	3
Racomitrium lanuginosum	2.8	25	Leafy liverworts	1.9	12
Radula bolanderi	1.0	1	Thalloid liverwort	1.3	4
Radula obtusiloba	1.0	1			

[a] *Bryum* collections were determined by John Spence.

[b] *Sphagnum* collections were determined or verified by Richard Andrus.

Appendix 2. Species list of 169 unique vascular plant taxa found in the Noatak National Preserve from 20 plots sampled in 2004[a]. “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	Ave	Freq	Species	Ave	Freq
Aconitium delphinifolium	1.0	1	*Dryas octopetala*	4.4	10
Andromeda polifolia	1.8	5	*Dryopteris fragrans*	1.0	1
Androsace chamaejasme	2.0	2	*Empetrum nigrum*	1.8	10
Anemone spp.	1.0	5	*Epilobium* spp.	1.0	2
Anemone parviflora	1.0	1	*Epilobium angustifolium*	1.0	3
Anemone narcissiflora	1.0	1	*Epilobium latifolium*	4.0	1
Antennaria spp.	1.0	1	*Equisetum arvense*	3.6	8
Antennaria friesiana	1.0	3	*Equisetum scirpoides*	3.8	4
Arctostaphylos spp.	1.8	6	*Eritrichium* spp.	2.7	7
Arctostaphylos rubra	3.4	5	*Erysimum inconspicurum*	1.0	1
Armeria maritima	1.0	1	*Festuca* spp.	1.0	3
Arnica alaskensis	1.0	1	*Galium boreale*	1.0	1
Arnica frigida	1.0	1	*Gentiana glandulosa*	2.0	2
Arnica hallingii	1.0	1	*Gentiana propinqua*	1.0	4
Arnica lessingii	1.7	3	*Geum glaciale*	1.5	2
Artemesia spp.	1.7	3	*Geum rossii*	1.0	3
Artemesia arctica	1.0	2	*Hedysarum mackenzii*	1.0	7
Artemesia glomerata	1.0	1	*Hierochloe* spp.	2.5	2
Artemesia telesii	1.0	1	*Hierchloa alpina*	1.0	1
Aster sibericus	1.0	3	*Juniperus communis*	3.5	2
Astragalus alpinus	1.0	1	*Lagotis glauca*	2.0	2
Betula glandulosa	3.5	13	*Ledum decumbens*	3.2	6
Bupleurum triradiatum	1.0	2	*Ledum procumbens*	2.0	1
Boykinia richardonii	2.3	4	*Loiseularia decumbens*	3.7	3
Campanula spp.	1.0	1	*Louiserularia procumbens*	2.5	2
Campanula lasiocarpa	1.4	5	*Lupinus arcticus*	1.0	1
Cardamine microphylla	1.0	1	*Luzula* spp.	1.0	2
Cardamine purpurea	1.0	1	*Luzula spicata*	1.0	1
Carex spp.	3.2	15	*Lynchis* spp.	1.0	1
Cassiope tetragona	2.6	9	*Lycopodium selago*	1.3	8
Castilleja hyperborea	1.0	1	*Melandrium apetalum*	1.0	1
Cerastium spp.	1.0	4	*Mertensia campanulata*	1.0	1
Cerastium beeringianum	1.0	3	*Mertensia paniculata*	1.0	1
Chrysosplenium tetandrum	1.0	1	*Minuartia* spp.	3.0	1
Claytonia sarmentosa	1.3	3	*Minuartia arctica*	2.0	3
Cnidium cnidiifolium	1.0	1	*Minuartia macrocarpa*	1.0	2
Crepis nana	1.5	2	*Minuartia rubella*	1.0	1
Cystopteris fragilis	1.0	1	*Moneses uniflora*	1.0	2
Cystopteris montana	1.0	1	*Myosotis alpestris*	1.0	1
Delphinium brachycentrum	1.0	1	*Oxytropis* spp.	1.0	3
Diapensia lapponica	1.0	1	*Oxytropis nigrescens*	1.0	1
Dodecatheon spp.	1.0	3	*Papaver* spp.	2.0	2
Dodecatheon frigidum	2.0	2	*Papaver macounii*	1.0	1
Draba alpina	1.0	1	*Papaver nudicaulis*	1.1	7
Draba longipes	1.0	1	*Parnassia* spp.	1.0	1
Dryas integrefolia	3.4	5	*Parnassia palustris*	1.3	4

Appendix 2, continued.

Species	Ave	Freq	Species	Ave	Freq
Parrya nudicaulis	1.0	3	*Salix phelbophylla*	1.3	3
Pedicularis spp.	1.0	6	*Salix pulchura*	4.4	7
Pedicularis capitata	1.5	4	*Salix reticulata*	4.6	9
Pedicularis labradorica	1.0	2	*Salix rotundifolia*	3.3	3
Pedicularis lanata/ kanei	1.5	4	*Saussurea angustifolia*	1.0	7
Pedicularis oederi	1.0	1	*Saxifraga* spp.	1.0	2
Pedicularis verticillata	1.0	1	*Saxifraga bronchialis*	4.0	1
Petasites spp.	1.5	6	*Saxifraga davorica*	1.0	1
Phlox sibirica	1.0	1	*Saxifraga eschscholtzii*	1.0	2
Picea spp.	1.0	2	*Saxifraga flagellaris*	1.0	1
Picea glauca	5.5	2	*Saxifraga fragilis*	1.0	1
Pinguicula vulgaris	1.0	1	*Saxifraga hieracifolia*	1.0	1
Platanthera obtusata	1.0	2	*Saxifraga hirculus*	1.0	4
Poa spp.	1.0	1	*Saxifraga oppositifolia*	1.0	2
Polemonium acutiflorum	1.0	5	*Saxafraga punctata*	1.0	2
Polygonum bistortoides	1.3	7	*Saxifraga tricuspidata*	1.0	2
Polygonum vivparum	1.0	9	*Selaginella selaginoides*	1.0	1
Populus balsamifera	3.0	2	*Senecio*	3.0	1
Potentilla spp.	1.0	1	*Senecio lugens*	1.0	3
Potentilla biflora	1.0	2	*Senecio resedifolius*	1.0	1
Potentilla fruticosa	2.7	9	*Shepherdia canadensis*	1.5	2
Potentilla nivea	1.0	3	*Silene acaulis*	2.1	8
Potentilla palustris	1.0	1	*Solidago* spp.	1.0	1
Pyrola spp.	1.0	1	*Solidago multiradiata*	1.0	4
Pyrola asarifolia	1.0	2	*Spirea beawerdiana*	1.0	1
Pyrola chlorantha	1.0	2	*Stellaria* spp.	1.4	5
Rhododendron spp.	4.0	1	*Taraxacum kamtschaticum*	1.0	1
Rhododendron lapponicum	1.3	3	*Tofieldia* spp.	1.0	1
Rubus acaulis	1.0	1	*Tofieldia pusilla*	1.3	8
Rubus chaemomorus	3.0	3	*Trisetum spicatum*	1.0	3
Rumex spp.	1.0	5	*Vaccinum uligonosum*	3.3	16
Salix spp.	3.6	10	*Vaccinium vitis-ideae*	3.6	9
Salix alaskensis	4.0	4	*Valeriana capitata*	1.7	3
Salix arctica	1.0	2	*Wilhelmsia physodes*	1.0	2
Salix chamissonis	3.0	1	*Woodsia glabella*	1.0	1
Salix fuscescens	2.0	1	*Zygadenus* spp.	1.0	1
Salix glauca	2.0	1	*Zygadenus elegans*	1.0	2
Salix lanata	5.0	3	grass	1.9	14
Salix ovalifolia	2.0	1			

[a] All vascular plant collections were determined by Sarah Nunn.