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The Influence of Grazing and Other Environmental Factors on Lichen Community Structure along an Alpine Tundra Ridge in the Uinta Mountains, Utah, U.S.A.

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Abstract

This study examined the influence of snowmelt, vascular plants, grazing, substrates, and soil characteristics on the distribution of lichen communities along an alpine tundra ridge in the Uinta Mountains of Utah. Percent cover of lichens, rocks, snow, and vascular plants were estimated at 18 study sites along an altitudinal transect. Vascular plant cover and species diversity were greatest at the lower elevation sites, and differences in plant communities were related to differences in rock cover and grazing. Lichens showed a similar trend, with rock cover, grazing, vascular plants, and timing of snowmelt all defining community structure. We hypothesize that domestic sheep have dispersed fragments of two lichen species from western Wyoming to grazed sites along the study transect. Generally, terricolous and epiphytic lichens differed between the lower and upper sites in species composition and growth-form distribution. Distribution of lichen growth forms was positively correlated with increasing rock cover. Late snowmelt areas were also distinguished by a defined group of lichens.

Introduction

There has been very limited research on the distribution and structure of tundra lichen communities. Creveld (1981) organized an extensive list of lichen species into 382 relévés and then arranged the relévés into vegetation types according to the Braun-Blanquet method of vegetation analysis. More recently Türk and Gärtner (2001) published a review paper examining biological soil crust communities in the subalpine and alpine habitats of the European Alps, including some information about lichens. Phytosociological studies of lichen communities in Greenland have also been published (Daniëls, 1982; Hansen, 1978), along with a more recent review paper concerning lichen-rich soil crusts (Hansen, 2001).

Knowledge about alpine lichens in the Western United States is limited and generally floristic in nature. Anderson (1964) published a comprehensive survey of the lichen genus *Lecidea* in Rocky Mountain National Park, Colorado; many of his collections were from true alpine tundra sites. Egan (1969) described the alpine lichen flora of Mount Audubon, Colorado, and later expanded his research to include three additional sites in New Mexico (Egan, 1971). Komárková (1979) published the results of an extensive phytosociological survey of the alpine zones of the Indian Peaks area of the Colorado Rocky Mountains, which included a comprehensive list of the lichen species. Flock (1976, 1978) evaluated the effects of snow cover and soil moisture on the distribution of lichens and bryophytes on Niwot Ridge in central Colorado. The only previous study dealing specifically with alpine lichens in Utah is a floristic survey of eight alpine tundra sites in central and eastern Utah that resulted in a list of 14 macrolichens (Imshaug, 1957).

More recently, research in alpine tundra zones in the Olympic Mountains of Washington has focused on the structural and functional attributes of lichen communities (Glew, 1997; Gold et al., 2001). Glew (1997) researched the effects of specific types of vascular plant communities on lichen community structure and observed that the structure of the epiphytic lichen community was directly related to the structure and composition of the vascular plant community. Glew (1997) also reported that specific types of vascular plant communities (e.g., krummholz and late snow) tended to support less diverse lichen communities, a phenomenon related to, either directly or indirectly, specific abiotic conditions (e.g., soil moisture, limited light, late-lying snow). Gold et al. (2001) examined several functional parameters of different kinds of alpine soil crust communities including a crust dominated by a thick layer of fruticose lichens. Compared to other sites in their study, soils at the lichen dominated site had the highest organic matter content, soil moisture, and concentrations of soil nitrogen and phosphorous. Although these studies have contributed significantly to our understanding of alpine tundra lichen communities in the Western United States, there is still a need for research that characterizes biotic and abiotic influences on the structure of alpine lichen communities.

Many of the alpine tundra areas of the Western United States having been extensively grazed since the mid to late 1800s (Marr, 1964); however, there have only been a limited number of studies investigating the impact of grazing, herding, and bedding of domestic animals on alpine tundra habitats (Johnson, 1962; Lewis, 1970; Paulsen, 1960; Smith and Johnson, 1965; Strasia et al., 1970; Thilenius, 1979). Data from these studies document the effects of domestic grazers on vascular plant vegetation, but lack any specific reference to lichens. In most cases, grazing-related damage to the vascular plant community was minimal except in bedding or watering areas or along driving trails (Thilenius, 1979). One study suggested that light to moderate grazing by sheep may even increase vascular plant cover (Strasia et al., 1970). It was also noted that grazing precipitated changes in the overall composition of the vascular plant community, with certain species increasing in abundance while others decreased slightly (Strasia et al., 1970). Similar reports are available for Arctic tundra areas where both

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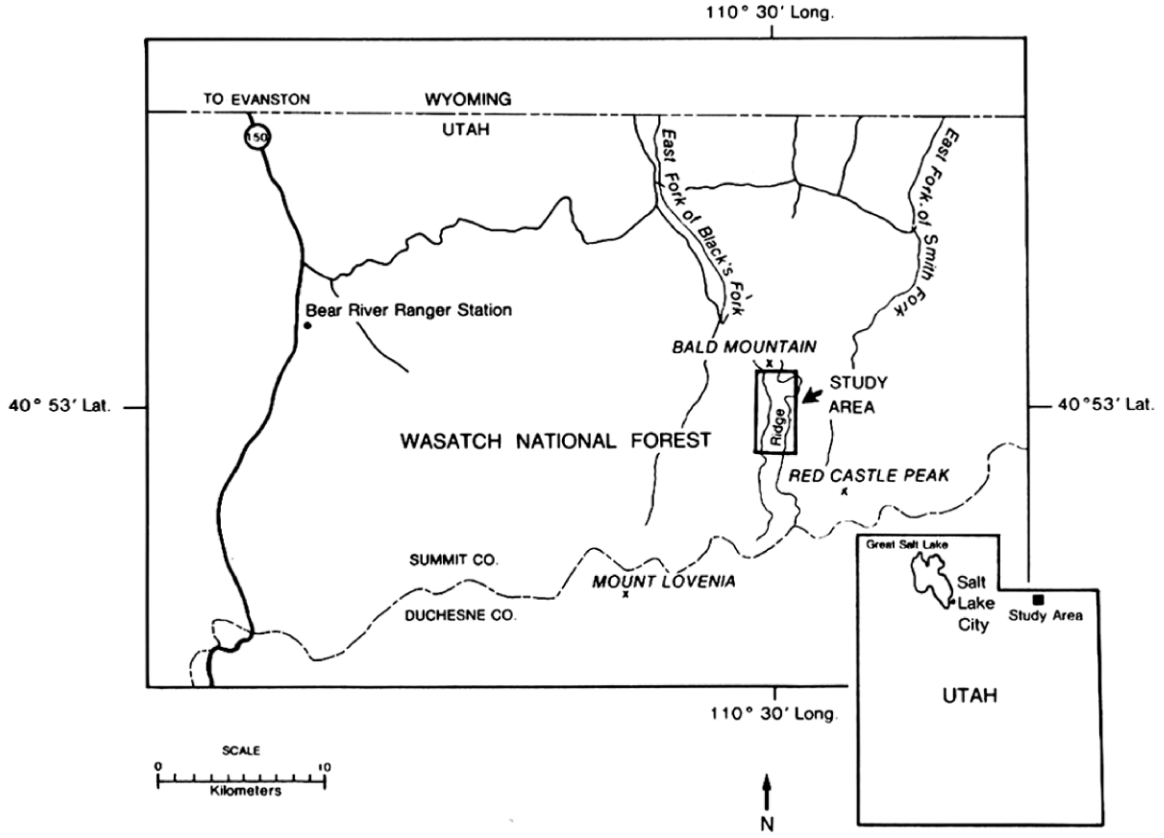

FIGURE 1. Map of study area in reference to the Wasatch National Forest and Bald Mountain. Inset shows location of study area in reference to the state of Utah.

domestic reindeer and wild caribou are the major grazers (Moser et al., 1979; Olofsson, 2006; Pegau, 1969, 1970; Polezhaev, 1980; Skuncke, 1969). These studies and others (Andreev, 1975; Utkin, 1974) show conclusively that when grazing animals are herded extensively, there are significant changes in both the lichen and vascular plant communities; specifically, the total lichen cover was reduced, some sensitive species were completely eliminated, and there was a proliferation of grass species (Olofsson, 2006; Polezhaev, 1980).

Several studies have examined the effects of trampling by humans, particularly along trails, on tundra landscapes (Bell and Bliss, 1973; Grabherr, 1982; Willard and Marr, 1970, 1971). These studies generally showed that tundra habitats are extremely sensitive to the effects of persistent trampling by human beings. Recovery of tundra landscapes following damage related to human activity was also shown to be extremely slow (Willard and Marr, 1971). Lichens, especially fruticose species, were noted to be particularly sensitive to human-related perturbations. Conversely, crustose and squamulose species on soil and rock substrates were generally less sensitive to human-related impacts (Willard and Marr, 1971).

The overall intent of our research was to obtain both quantitative and qualitative data for biotic and abiotic factors potentially influencing lichen community structure along an altitudinal gradient in the alpine tundra of the Uinta Mountains. We hypothesize that domesticated grazers (sheep) and vascular plant communities measurably influence the composition of alpine lichen communities. We further predict that abiotic factors such as soil chemistry, habitat rockiness, and snowmelt patterns also shape lichen community structure. This initial data set will be particularly crucial in light of the sensitivity of many lichens to various kinds of human-related perturbation compounded by the inherent vulnerability and slow recovery rates indicative of alpine tundra habitats.

Materials and Methods

SITE DESCRIPTION

The Uinta Mountains are located in northeastern Utah and northwestern Colorado. The north-south axis of the range averages between 48 and 65 km wide, whereas the east-west axis is approximately 240 km long. This study was conducted along an alpine tundra ridge that extends south of Bald Mountain and ranges from 3508 to 3938 m a.s.l. (Fig. 1). A transect, 4.5 km in length, consisting of 18 sites, was established along the ridge in 1983 (Fig. 2). The study transect was separated by vegetation type into three sections. The lower meadow sites (1–9) ranged between 3500 and 3600 m a.s.l. Sites 10–18 represented a gradient of increasing elevation from 3630 to 3880 m a.s.l. Sites 1–6, starting at the lower south-facing slope of Bald Mountain, consisted of an open alpine meadow dominated by *Carex rupestris* and *Geum rossii*. Sites 7–9 were located in a broken hummock area with *Carex rupestris*, *Geum rossii*, several *Salix* species, and some *Picea engelmannii*. Sites 10–18 were exposed, windswept, rocky areas with notably lower vascular plant cover. The upper sites were also dominated by *Carex rupestris* and *Geum rossii*, along with *Festuca ovina* and *Selaginella densa* as important subdominants.

FIELD METHODS

Lichen community structure was evaluated along gradients in elevation, vascular plant community composition and structure,

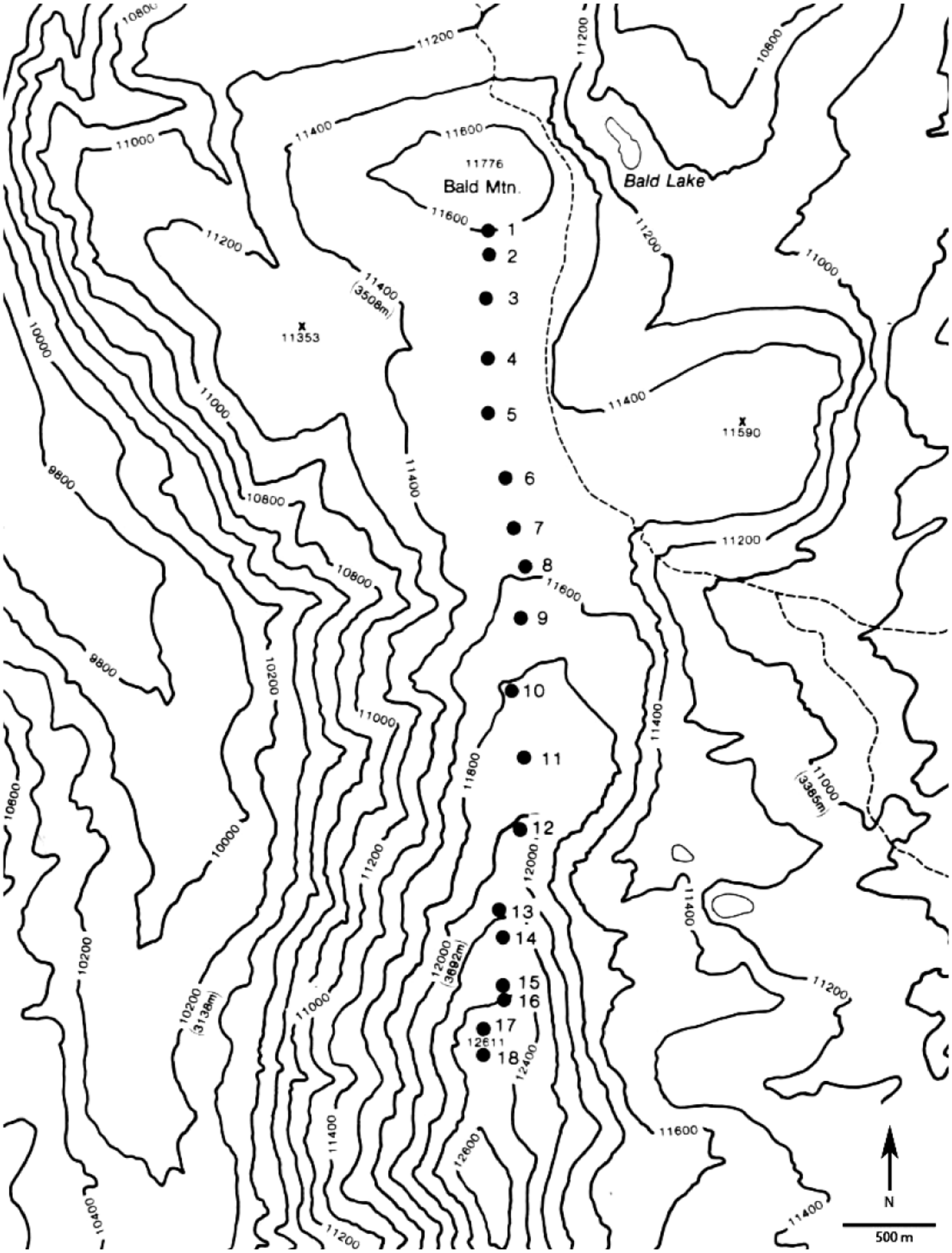

FIGURE 2. Detailed map of the study transect showing meadow sites (1–6), hummock sites (7–9), and rocky ridge sites (10–18). Talus slopes that provide barriers to grazing sheep are located between sites 9 and 10, as well as at sites 14 and 16. Contour interval is 200 m.

rockiness, snowmelt, various soil parameters, and grazing impact. The major vegetation types and physical features of the ridge were identified during the summer of 1982 after thorough examination of aerial photographs followed by detailed on-site investigations. A total of 18 distinctive areas were identified along the length of the ridge.

Following documentation of basic vascular plant community types and physical features along the study transect, permanently marked 10 × 10 m macroplots were established at each site. A random numbers table was used to locate ten 1 m^2 quadrats within each macroplot. A 0.25 m^2 square quadrat was then used to visually estimate percentage cover of lichens, vascular plant species, and rocks (large rocks with any dimension >10 cm in diameter and small rocks with all dimensions <10 cm in diameter) in one randomly identified quadrant of each square meter. Substrate notations were also made for all lichen species. General grazing effects by sheep were qualitatively estimated at each site on the basis of observed herding, grazing, and bedding patterns, a review of historical grazing allotments, and discussions with land managers and local sheep herders. Finally, snowmelt patterns along the study transect were documented using aerial photography. Photographs of the study transect were used to determine whether a site was snow free by the last week of May, June, July, or August of 1983; these data were then used to specifically evaluate lichen species distribution patterns as related to late snowmelt areas.

During the summers of 1980–1983 lichens and vascular plants were collected from each of the 18 transect sites. In addition, two surface (5 cm) soil samples were collected from each transect site for chemical and physical analysis of soil properties.

LABORATORY METHODS

Lichen and vascular plant specimens were processed in the laboratory, and voucher specimens were prepared. Secondary chemistry of lichens was determined using standard chemical spot tests (Huneck and Yoshimura, 1996; Orange et al., 2001). Thin-layer chromatography techniques (Culberson and Kristinsson, 1970; Culberson et al., 1981) were also used as needed to clarify lichen secondary chemistry for select species groups.

For species-level identifications, thin sections of lichen fruiting structures were prepared to determine ascospore size, shape, and color; number of spores per ascus; as well as the dimensions and characteristics of the various hymenial tissues. Voucher specimens of both lichens and vascular plants have been deposited in the Brigham Young University Herbarium.

A Utah Flora (Welsh et al., 2003) was used as the taxonomic authority for all vascular plant species. Lichen taxonomy was based on "A cumulative checklist for the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada" (Esslinger, 1997).

All soil samples were analyzed for macronutrient concentrations and compositional properties using standard soil analysis procedures (Page, 1982). Calcium, magnesium, and potassium were extracted using a 1 N ammonium acetate solution. Phosphorus was extracted using a 0.2 N acetic acid solution, and total nitrogen was determined using standard Kjeldahl methods. Concentrations of nutrient elements were determined using atomic absorption techniques. Organic matter content was determined by wet oxidation using potassium dichromate (Page, 1982). Soil pH was measured using a saturated soil paste and a pH meter. The hydrometer method was used to determine soil particle size distribution and abundance (Page, 1982).

STATISTICAL METHODS

Transect sites were ordinated with respect to soil chemistry variables using the Multivariate Statistical Package (MVSP) statistical software. Centered, standardized Principal Components Analysis (PCA) was run with nine soil parameters for 17 sites (site 16 had no soil). Sites were clustered based on lichen species data. An unweighted pair-group method (UPGMA) was used to agglomeratively and heirarchically build the cluster based on Ruzicka's Similarity Coefficient (Ruzicka, 1958). Sites were additionally ordinated in MSVP with Canonical Correspondence Analysis (CCA), using lichen species data and soil chemistry data as species and environmental data files, respectively. Lichens occurring in at least 3 of the 18 sites were included in this analysis. Rare species were down-weighted. Niche overlap values for lichen species were determined following the method of Colwell and Futuyma (1971) and clustered following an UPGMA algorithm. Important Species Indices (ISI) were calculated for vascular plants and lichens using the methods of Warner and Harper (1972). Student's *t*-test for two independent samples was used to compare average percent lichen cover between the lower, grazed, meadow sites and the upper, ungrazed, rocky sites.

Results

ENVIRONMENTAL VARIATION AT THE SITE

The general pattern of snowmelt along the transect is likely consistent from year to year. In May only a few areas, none within the plots, were snow free. By the end of June, a number of areas in the higher elevation sites were snow free, whereas, the lower meadow sites were still under snow (Fig. 3). We attribute this pattern to the higher sites being windswept, while the lower sites are areas of snowdrift and accumulation. By the end of July, snow cover was patchy, but notably still present at site 9, and adjacent to sites 13 and 17. All sites were snow free by the end of August.

The higher elevation sites had significantly more large rock cover than the lower sites (Fig. 4). Sites 11–18 were especially rocky and included a talus slope site that had 100% rock cover (site 16). Among the lower meadow sites, site 1, located on the lower, southern slope of Bald Mountain, also had greater rock cover (Fig. 4). Decreasing vascular plant cover was associated with increasing rockiness in the upper portion of the transect (Fig. 4).

Based on physical characteristics, sites were divided into three groups: (1) meadows; (2) hummocks; and (3) rocky. Principal Components Analysis of nine soil variables (percent clay was eliminated as it was constrained by percent sand and silt) showed separation of some exceptional sites (17 and 15), but the remainder of the sites were not clearly separated based on groups or elevation (Fig. 5). Some of the meadow sites had higher silt concentrations (sites 3–6), but neither principal component axis separated these sites from the others.

The vascular plant community in the lower meadow sites was dominated by *Carex rupestris*, *Geum rossii*, *Festuca ovina*, and *Artemisia scopulorum*. The frequency of *Salix cascadensis* generally increased with increasing elevation. Another significant change in the vascular plant community, with increasing elevation, was the occurrence and increasing abundance of the cryptogam, *Selaginella densa* (Fig. 4). This low-growing vascular plant typically serves as an important substrate for a large number of lichen epiphytes. Other dominant vascular plants in the upper sites included *Draba cana*, *Paronychia pulvinata*, and *Lychnis apetala*.

Transect sites 1–5 had been continually grazed and often used as a bedding area for sheep since at least 1916, while sites 6–9 had only been lightly grazed, and sites10–18 had been essentially ungrazed (Zobell, personal communication). Furthermore, there is a talus slope that effectively separates sites 1–9 from sites 10–18. This talus area acts as a natural barrier to sheep movement, and only occasionally do sheep stray from the herd into the upper elevation sites above the talus slope (Redden, personal communication).

LICHEN SPECIES DISTRIBUTION PATTERNS

A total of 65 lichen species in 38 genera were identified from the study transect (Table 1). Dominant species included (in order of decreasing ISI—Important Species Indices) *Lecidea atrobrunnea* (ISI = 1.09), *Aspicilia calcarea* (0.90), *Umbilicaria virginis* (0.89), *Sporastatia testudinea* (0.88), *Lecanora thomsonii* (0.86), *Rhizocarpon geographicum* (0.39), *Lecidea auriculata* (0.35), *Xanthoria elegans* (0.26), and *Allocetraria madriporiformis* (0.26). There was a clear and marked increase in the abundance of lichens at the rockier sites, which were also higher in elevation and ungrazed (Fig. 6). Most of the lichens were crustose in growth form (37 species), with several foliose lichens (17 species). Fruticose (6 species) and squamulose (5 species) growth forms were much less

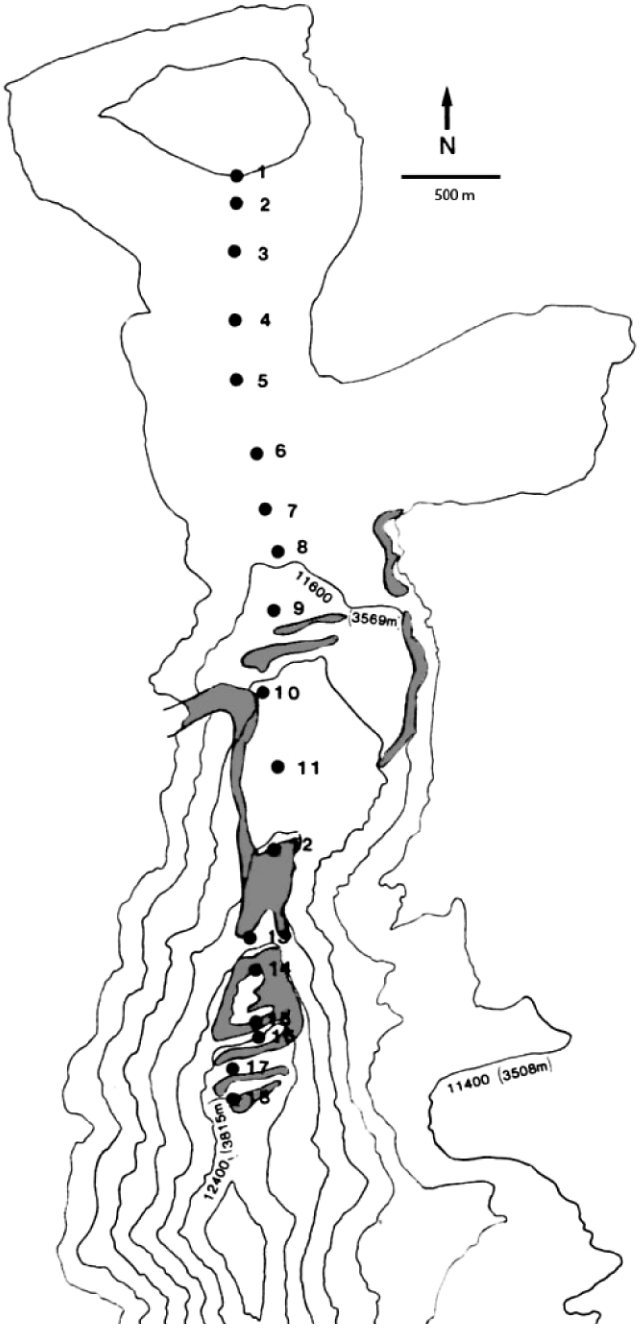

FIGURE 3. Transect map showing snow melt patterns as of the end of June 1983. Shaded areas represent snow-free locations. Contour interval is 200 m.

represented. Crustose lichens also had higher percent cover across all sites than all other growth forms combined, and showed a particularly marked increase in the upper, rocky sites (mean percent cover 14%). Foliose-umbilicate lichen species were restricted to the upper area.

Both the CCA analysis and cluster dendrogram of the study sites revealed two main clusters (lower sites, and higher sites plus site 8) and did not support separation of the lichen community into three distinct sub-communities as we saw with the vascular plants, but rather into two different communities separated by the talus slope between sites 9 and 10. The two analyses showed nearly identical topologies, with the same similar sites clustering together in both analyses. We show the CCA biplot (Fig. 7) because it shows the relationship of soil parameters. The relationship of soil parameters is highly similar to that in the soil chemistry PCA (Fig. 5); however, the sites separate more cleanly because of the addition of lichen species data. In the remainder of the analysis we will discuss the distinct communities in the context of the two areas (rocky upper sites, lower meadow sites). Total lichen cover was significantly ($t = 5.52$, $p < 0.0001$) higher in the upper, rocky sites (mean = 19.6%) than in the lower, meadow sites (mean = 6.0%).

The lichen cluster dendrogram, based on niche overlap measurements, revealed several lichen species associations (Fig. 8). We assigned these to categories based on characterizations of the sites given above. In the rocky upper sites there was a sharp contrast between those species that were terricolous and saxicolous. Another group was primarily associated with the meadow sites. Broad-ranging species occurred across the entire transect, while rare species were too rare to determine clear patterns of distribution. A few species appeared to be associated with late snowmelt (e.g., site 9). Many species were markedly more abundant in the rocky upper sites, including *Allocetraria madreporiformis*, *Aspicilia calcarea*, *Dimelaena oreina*, *Lecanora thomsonii*, *Lecidea atrobrunnea*, *Lecidea tessellata*, *Rhizocarpon geographicum*, *Sporastatia testudinea*, *Umbilicaria virginis*, *Xanthoparmelia cumberlandia*, and *Xanthoria elegans*. Not surprisingly, all but one of these taxa (*A. madreporiformis*) was saxicolous, and most were crustose (Table 1).

The grazed sites (1–5) had distinctly different groups of lichen species. Most of the terricolous lichens in this area were crustose or squamulose, with only one fruticose species (*Aspicilia hispida*) and three foliose species (*Cladonia* sp. 3, *Xanthoparmelia chlorochroa*, and *Peltigera rufescens*). The ungrazed/lightly grazed sites (with the exception of the late snowmelt site 9 and talus slope sites 14 and 16) had two fruticose, terricolous species: *Allocetraria madreporiformis* and *Cetraria aculeata*; and three foliose, terricolous species: *Cetraria ericitorum*, *Physconia muscigena*, and *Vulpicida tilesii*. Grazing activity was directly related to the lower elevation occurrence of the two vagrant species (*Aspicilia hispida* and *Xanthoparmelia chlorochora*), both of which were absent from the upper sites.

Epiphytic lichens were also less common at the grazed sites, but this is apparently related to the availability of suitable plant substrates. In particular, *Selaginella densa*, a common vascular plant substrate for epiphytic lichens in alpine tundra habitats, was consistently present in ungrazed or lightly grazed plots (Fig. 4), but absent in the lower sites. Only two epiphytic/humicolous lichens (*Caloplaca tiroliensis*, *Candelariella aurella*) were collected from the lower sites, whereas a total of nine epiphytic/humicolous lichens were collected from the upper sites.

Discussion

Data from this project demonstrated that lichen community distribution and structure are directly influenced by several factors, including domestic sheep grazing, degree of rockiness, nature of the vascular plant community, and snowmelt patterns. Grazing activity had a double impact on lichen community structure at the lower transect sites by ‘‘adding’’ new species while eliminating species sensitive to trampling. In contrast, soil data did not contribute to our understanding of lichen community distribution or structure.

The vagrant (unattached) lichen species *Aspicilia hispida* and *Xanthoparmelia chlorochroa*, found only at the heavily grazed and sheep bedding sites (1–5), are common components of short grass steppe and grazed shrub lands between 1500 and 2300 m in the

TABLE 1

Substrates on which lichens were found growing in this study included soil (S), pebbles and small rocks (P), large rocks (LR), and plants (E). Growth forms included crustose (Cr), fruticose (Fr), foliose (Fo), foliose with umbilicate attachment (Fo-um), and squamulose (Sq). The Important Species Indices (ISI) are calculated as frequency times mean percent cover. Mean percent cover for combined lower sites (1–9) and combined upper sites (10–18) is reported; a dash indicates that a species was not detected along that portion of the transect.

Species	Substrate	Growth form	ISI	Sites 1–9	Sites 10–18
Acarospora smaragdula	P, LR	Cr	0.03	0.18	<0.01
Acarospora sp.	P, LR	Cr	0.01	—	0.04
Allocetraria madreporiformis	S	Fr	0.26	0.19	0.87
Arthronia glebosa	S	Cr	0.01	0.05	—
Aspicilia calcarea	LR, P	Cr	0.90	0.47	1.42
Aspicilia hispida	S	Fr	0.02	0.12	—
Aspicilia sp.	LR, P	Cr	0.19	0.18	0.39
Brodoa oroarctica	LR	Fo	<0.01	—	<0.01
Caloplaca arenaria	P	Cr	0.02	0.09	—
Caloplaca epithallina	E	Cr	<0.01	—	0.04
Caloplaca jungermanniae	E	Cr	<0.01	<0.01	—
Caloplaca tiroliensis	E	Cr	0.02	<0.01	0.07
Calvitimela armeniaca	LR	Cr	0.02	—	0.12
Candelariella aurella	E	Cr	0.02	0.01	0.07
Candelariella rosulans	LR, P	Cr	0.15	0.17	0.17
Catapyrenium cinereum	S	Sq	0.09	0.22	0.06
Cetraria aculeata	S	Fr	0.05	0.09	0.22
Cetraria ericetorum	S	Fr	<0.01	<0.01	—
Cladonia sp. 1	S	Fo	0.11	0.41	0.01
Cladonia sp. 2	S, E	Fo	0.05	0.18	0.21
Cladonia sp. 3	S	Fo	0.11	0.81	—
Dimelaena oreina	LR	Cr	0.19	—	0.97
Evernia divaricata	S	Fr	0.01	—	0.09
Fulgensia bracteata	S	Cr	0.03	0.03	0.06
Lecanora argopholis	LR	Cr	0.01	0.12	—
Lecanora bicincta	LR	Cr	0.01	—	0.12
Lecanora epibryon	E	Cr	<0.01	0.01	<0.01
Lecanora hagenii	E	Cr	<0.01	—	<0.01
Lecanora marginata	LR	Cr	0.01	—	0.06
Lecanora polytropa	LR, P	Cr	0.08	0.20	0.05
Lecanora rupicola	LR	Cr	0.01	—	0.04
Lecanora thomsonii	LR	Cr	0.86	<0.01	2.89
Lecidea atrobrunnea	LR, P	Cr	1.09	0.78	2.44
Lecidea auriculata	LR, P	Cr	0.35	0.24	0.46
Lecidea tessellata	LR, P	Cr	0.18	0.07	0.49
Lecidea sp. 1	S	Cr	<0.01	<0.01	<0.01
Lecidea sp. 2	E	Cr	0.01	0.01	0.11
Lepraria vouauxii	S	Cr	<0.01	0.07	—
Megaspora verrucosa	E	Cr	<0.01	—	0.01
Melanelia tominii	LR	Fo	<0.01	—	0.02
Mycobilimbia berengeriana	S	Cr	<0.01	<0.01	—
Ochrolechia upsaliensis	E	Cr	0.02	0.10	0.06
Peltigera rufescens	S	Fo	0.02	0.13	<0.01
Phaeorrhiza nimbosa	S	Sq	<0.01	—	<0.01
Physcia sp.	LR	Fo	<0.01	<0.01	<0.01
Physconia muscigena	S	Fo	0.07	0.16	0.13
Placidium squamulosum	S	Sq	<0.01	<0.01	—
Protoparmelia badia	LR	Cr	<0.01	0.04	<0.01
Psora decipiens	S	Sq	<0.01	0.02	0.01
Psora luridella	S	Sq	<0.01	0.05	—
Pseudephebe minuscula	LR, P	Fr	0.01	—	0.13
Rhizocarpon disporum	LR, P	Cr	0.12	0.27	0.09
Rhizocarpon geographicum	LR, P	Cr	0.39	0.16	1.02
Rhizoplaca chrysoleuca	LR	Fo-um	<0.01	—	0.03
Rhizoplaca melanophthalma	LR, P	Fo-um	0.08	0.10	0.09
Solorina bispora	S	Fo	<0.01	—	<0.01
Sporastatia polyspora	P	Cr	<0.01	—	<0.01
Sporastatia testudinea	LR, P	Cr	0.88	<0.01	3.17
Staurothele drumondii	LR, P	Cr	0.02	0.07	0.02
Umbilicaria decussata	LR	Fo-um	<0.01	—	0.05

(continued)

TABLE 1

(continued)

Species	Substrate	Growth form	ISI	Sites 1–9	Sites 10–18
Umbilicaria virginis	LR	Fo-um	0.89	<0.01	2.90
Vulpicida tilesii	S	Fo	<0.01	0.02	0.01
Xanthoparmelia chlorochroa	S	Fo	<0.01	0.02	—
Xanthoparmelia cumberlandia	S, LR, P	Fo	0.15	0.03	0.57
Xanthoria elegans	LR, P	Fo	0.26	0.02	0.53
Mean percent lichen cover				6.01	19.57

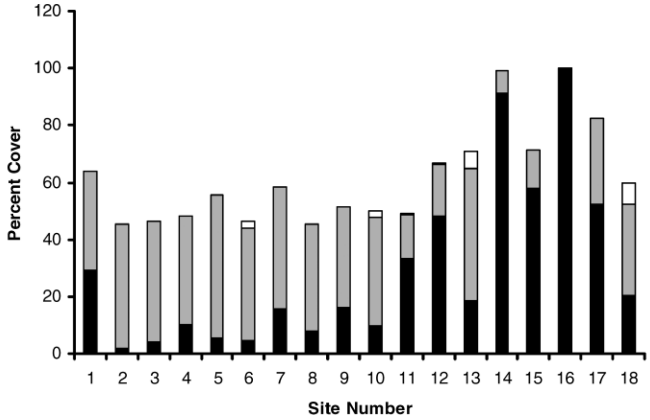

FIGURE 4. Rock cover (black), angiosperm cover (gray), and *Selaginella densa* cover (white) for all 18 sites. Remaining cover was in the categories of bare ground, plant litter, lichens, and mosses. Percent sum cover could exceed 100% in the instances where rocks were overtopped by lichens or angiosperms.

intermountain Western United States (Looman, 1964). Vagrant lichens typically associated with these habitats have been shown to be generally tolerant of grazing impact (MacCracken et al., 1983; Warren and Eldridge, 2001). Examination of the winter grazing sites (western Wyoming) for the Uinta sheep herds showed that both *Xanthoparmelia chlorochroa* and *Aspicilia hispida* were abundant in those locations. We hypothesize that during the grazing history of the Uinta sites unspecialized, small fragments of these two taxa have been transported from the winter range up to the grazed alpine tundra sites on the wool of sheep. In contrast, the more common tundra soil lichens, *Allocetraria madreporiformis*, *Cetraria aculeata*, *Cetraria ericetorum*, *Physconia muscigena*, and *Vulpicida tilesii*, were restricted to the ungrazed and lightly grazed portions of the transect because of their greater sensitivity to grazing (Olofsson, 2006). It has been reported that lichen growth form correlates with susceptibility to grazing impact with fruticose and foliose species generally more susceptible to grazing while crustose and squamulose species, with a much lower vertical profile, are not as impacted (Warren and Eldridge, 2001). The obvious exception to this pattern is the two "introduced"

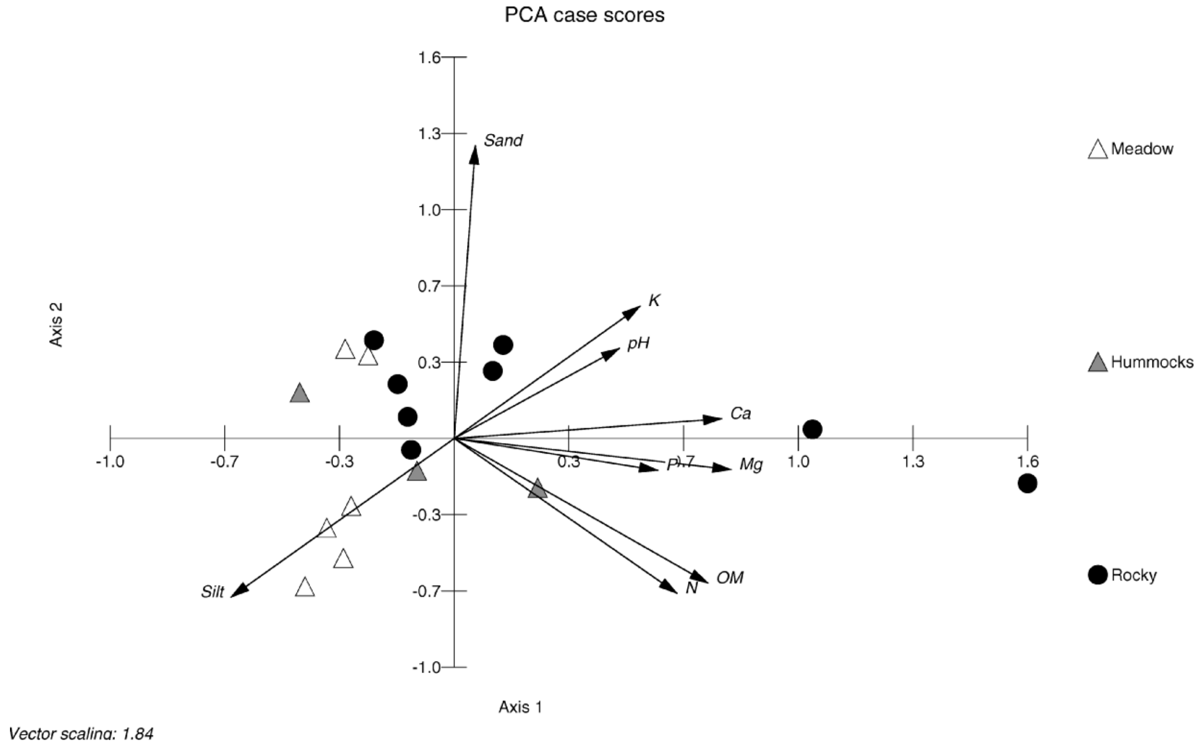

FIGURE 5. Euclidean biplot of centered and standardized Principal Components Analysis (PCA) of soil data. Eigenvalues were 53.2 and 20.0 for the first and second axes, respectively, and thus this figure explains 73.2% of the variability in the data. Meadow sites fall into two groups, the upper group contains sites 1 and 2, the lower group contains sites 3–6. The two outliers in the rocky sites (high positive values on PCA axis 1) are sites 17 and 15 (left to right). Note that the three areas are not separated into discrete groups on either axis.

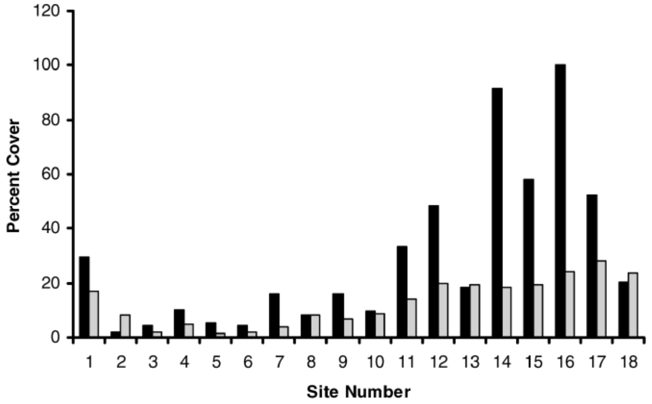

FIGURE 6. Relationship of rock cover (black bars) to lichen cover (gray bars) along the transect.

vagrants—*Xanthoparmelia chlorochroa* (foliose) and *Aspicilia hispida* (fruticose). However, unlike most other fruticose and foliose species, these two taxa are uniquely adapted to domestic grazing activity with sheep effectively fragmenting and dispersing both species (MacCracken et al., 1983). Interestingly, these two species reproduce almost exclusively by unspecialized thallus fragments with sexual reproduction rare to essentially nonexistent. Differences in lichen species and growth form patterns between the lower and upper sites further document the effects of domestic sheep on lichen communities. The potential sensitivity of the vascular plant *Selaginella densa* to grazing impact may also help to explain differences in lichen community structure between the upper and lower transect sites.

Observed differences in the number of epiphytic lichens between the lower and upper sites (2 and 9 species, respectively) appear to be directly related to the distribution of the low-growing vascular cryptogam *Selaginella densa*. This plant, which commonly supports a diverse group of epiphytic lichens, was absent from the lower elevation sites (1–5) but sporadically abundant at sites 6–19 (Fig. 4), thus accounting for the significant difference in the diversity of epiphytic lichens between the lower and upper sites. In alpine habitats, *Selaginella densa* typically occurs with other low-growing vascular plants on rocky ledges with thin soils (Welsh et al., 2003)—conditions uncharacteristic of the lower elevation sites.

Increasing lichen cover was also related to increasing rockiness with decreasing vascular plant cover and increasing elevation along the transect (Fig. 4). This pattern of increasing rockiness, especially larger rocks, was also associated with increasing lichen species diversity. Rocks are common lichen substrates, often supporting a diversity of species and growth forms. Specifically, higher percent cover and diversity of crustose and foliose-umbilicate species at the upper elevation sites were correlated with the increasing availability of rock surface area. The lichen cluster dendrogram, based on niche overlap measurements, further documented this pattern (Fig. 8), with species from the upper rocky sites clustering together (Group I) and the lower elevation meadow species grouping separately (Group II).

The lichen cluster dendrogram also showed a distinct cluster of late snowmelt lichen species (Group IV). Specifically, three species, *Psora decipiens*, *Rhizocarpon disporum*, and *Cladonia* sp., were consistently associated with late snow sites—a species pattern observed by the authors at other late-snow areas in the Western United States. Group III included a group of ubiquitous, broad-ranging species that occurred across the entire study transect. In contrast, Group V contained a group of rare species with very narrow distribution.

The similarity of the lichen community at site 1 (south-facing slope of Bald Mountain) to the upper elevation communities was generally related to the number of larger rocks at that site, which in turn supported a more diverse group of lichen species. Furthermore, higher lichen cover (16.7%) and similar growth-form distributions (more crustose species) also reflected the rockiness at that site in general and the abundance of larger rocks in particular (Fig. 6). However, the relatively smaller number of epiphytic lichens, and a soil community dominated by crustose and squamulose species suggested grazing impact and thus a closer fit with the rest of the lower elevation, grazed sites.

This research contributes to our understanding of how both biotic and abiotic factors influence lichen community distribution

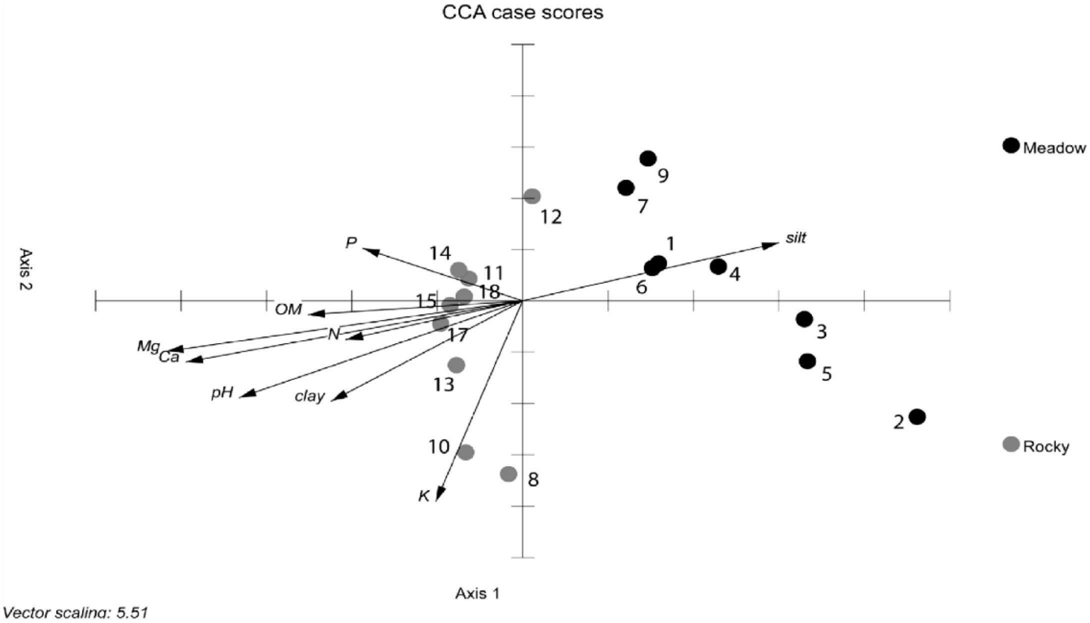

FIGURE 7. Canonical Correspondence Analysis (CCA) of lichen species data. The percentage of variation in the data explained by axis 1 and axis 2 was 26.4% and 12.3%, respectively.

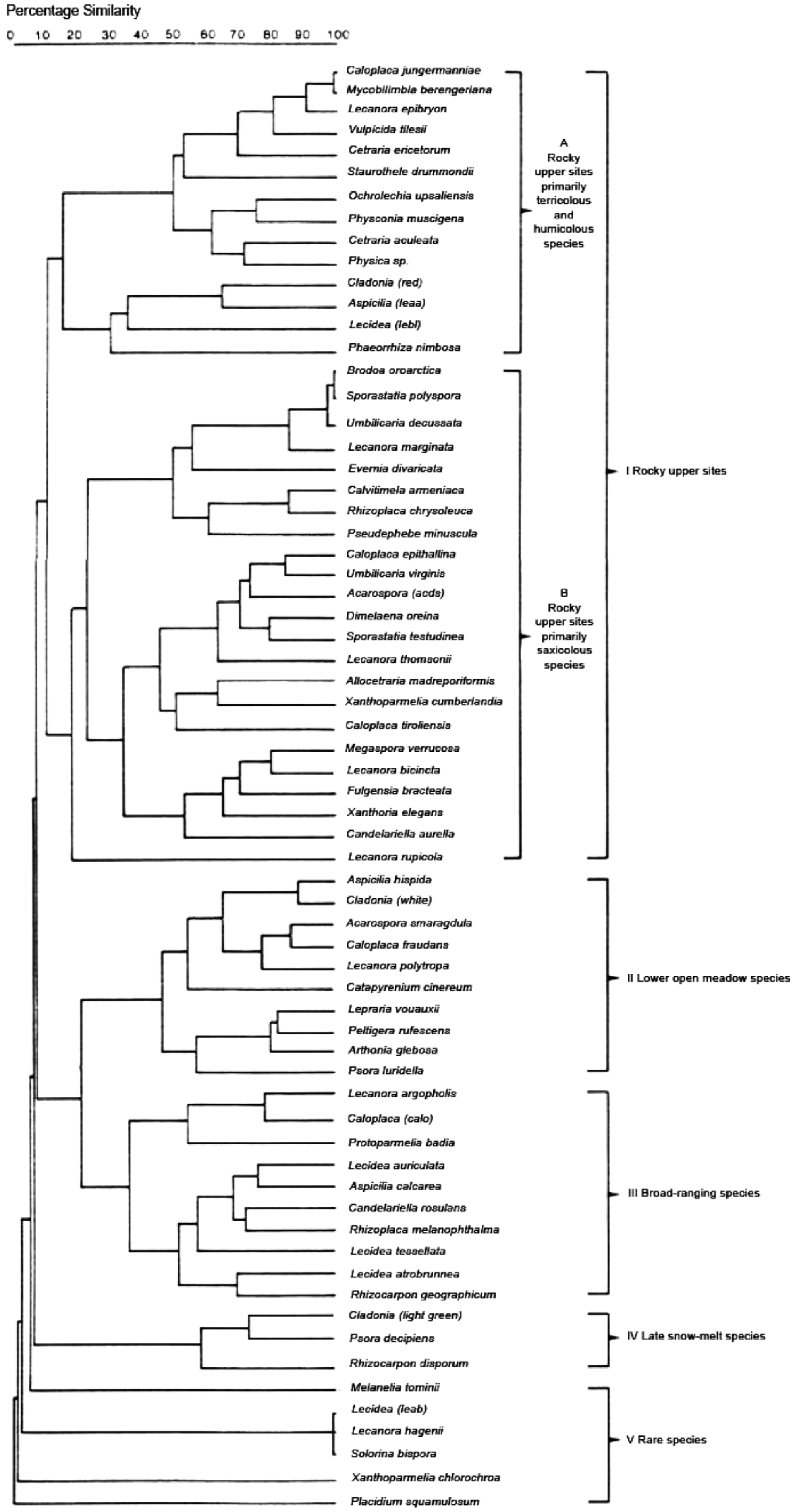

FIGURE 8. Cluster dendrogram of lichen species based on niche overlap values.

and structure in alpine tundra habitats. This information will prove particularly useful as we seek to restore and reclaim fragile, alpine tundra sites that have been historically impacted by human-related activity, such as grazing. Furthermore, these data will provide critical insights into the potential role of alpine tundra lichens as sensitive, early indicators of grazing impact on tundra ecosystems.

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