

Local Variation in Bryophyte and Macro-lichen Cover and Diversity in Montane Forests of Western Canada

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Abstract. The patterns of cover and species diversity (richness and composition) of macro-lichens, bryophytes, and vascular plants are described for a Canadian montane forest in an area where the forest is highly valued both for wood production and for the terrestrial lichen that is a vital part of the diet of the endangered woodland caribou (*Rangifer tarandus caribou* Gmelin). In 180, 6.5 m × 6.5 m plots placed in nine stands within a 375 km² area, we found lichens were abundant, but the ground layer was dominated by feather moss. Mean species richness at the plot level for lichens (23) is about double that of bryophytes (13) and vascular plants (11). Differences in species composition are small with any two plots having in common at least 50% of their vascular plants, 60% of their bryophytes, and 70% of their lichens. Comparisons of 10% of the most open with 10% of the most dense canopy plots revealed that the more open sites have greater lichen cover, higher elevation, older trees, more lichen and vascular plant species, less moderately decayed logs, and lower cover of *Pleurozium schreberi*, the dominant feather moss. Twenty-two species (14%) were found only once; of these five were lichens (9% of the lichen flora), six bryophytes (17% of the bryophyte flora), and 11 vascular plants (17% of the vascular plant flora). None of these is provincially endangered, but all are rare in this particular forest type. Only three of these species occur in the 20% of sites having the most open or dense canopies. Our data indicate that at the local scale, the ground layers of these forests are highly variable and have little local distinctiveness. The lack of strong environmental correlations with species patterns suggests that within the natural forest regime other factors are at least partially responsible for ground layer patterns at the local scale. These may include dispersal and establishment success as well as stochastic disturbance regimes.

Understanding the patterns of cover and species diversity (both richness and composition) of bryophytes and lichens in the forests of boreal Canada is of both fundamental value and management interest. Bryophytes and lichens constitute a large portion of the overall forest understory biomass and overall species richness (MacLean & Wein 1977; McCune & Antos 1981), particularly in coniferous forests. They are seldom included in biological surveys and ecological studies and if they are they tend to be lumped as 'moss or lichen' and diversity is often not examined at the species level. However, this information has become important. Land managers are increasingly required to plan for the maintenance of non-production values, such as biodiversity and our current measure of environmental sustainability is usually some aspect of biodiversity.

In many areas across Canada, the lichens of boreal and montane forests play a crucial role as a winter food source of the endangered woodland

caribou (*Rangifer tarandus caribou* Gmelin—Cumming 1992; Darby & Duquette 1986; Rettie et al. 1997; Stevenson 1986; Thomas et al. 1996). Healthy populations of favored lichens are known to be fundamental to caribou survival, supplying a ready source of digestible carbohydrates that constitute an estimated 66% of caribou winter diet (Cumming 1992; Danell et al. 1994; Rominger et al. 1996; Schaeffer & Pruitt 1991; Stevenson 1986). This study focuses on an area highly valued for both wood production and caribou winter habitat. There is concern that changes in ground lichen cover in these aging forests is partly responsible for decreasing numbers of caribou in the area (Armleder et al. 1996). Our study was established to determine whether the cover of 'caribou lichen' (mainly in the genus *Cladina*) and plant and lichen diversity could be maintained or increased over the long-term, while utilizing the forests for wood production.

Our short-term aim is to describe existing patterns of bryophyte and lichen cover and diversity. Pre-harvest variation in lichen cover and diversity patterns may yield insights into how the ground

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layer might change under post-harvest regimes. This is of interest because it may take considerable time for some species to adjust to the new conditions and long-term monitoring is required to observe effects as lichens are known for their tolerance to a wide range of conditions and climatic extremes (Haie 1967; Pritchard & Bradt 1984).

In order to gain some insight into local variation in ground cover and diversity, and to make some early predictions about post-harvest responses, we describe the natural (pre-treatment) patterns, and contrast sites having the most open and the most dense tree canopies. Specifically, we investigated the following research questions: 1) What is the variation in cover of each caribou lichen species, and the cover and species diversity (richness and composition) of lichens, bryophytes, and vascular plants? 2) Can local species composition and pattern be predicted by environmental regimes? 3) How do the 10% of sites with the most open canopies compare with the 10% of sites with the most dense canopies in terms of a) the cover of each caribou lichen species and the cover and diversity of lichens, bryophytes, and vascular plants, and b) environmental variables?

METHODS

Sample design and field methods.—The forests of the study site are *Pinus contorta* (Lodgepole Pine) dominated and are located in the Upper Foothills and Subalpine Natural Subregions (Beckingham et al. 1996) of the eastern slopes of the Rocky Mountains in Alberta between the towns of Hinton and Grande Cache. These rather open, old growth stands regenerated from wildfire between 61 and 183 years ago, and are characterized by generally rapidly drained, acidic soils and poor nutrient status (Beckingham et al. 1996). Individual trees range from 6.6 to 30.6 cm DBH. *Picea glauca* (White Spruce) frequently forms a sparse secondary canopy below the pine. Feather mosses (mainly *Pleurozium schreberi*) or fruticose (mainly *Cladonia mitis*) lichens tend to dominate the ground layer. The shrub layer is dominated by *Ledum groenlandicum* and/or *Vaccinium vitis-idaea*, with a sparse field layer of *Cornus canadensis*, *Elymus innovatus*, and *Lycopodium* spp. Nine representative stands averaging between 30 and 40 ha each were chosen from a 375 km² area known to be used or thought to be used by caribou for winter foraging. The stands are located along highway 40, north or near the Berland river and headwaters of the Little Smoky River between 53°45' and 53°55'N latitude and 118°18' and 118°30'W longitude at elevations between 1,317 and 1,527 m.

Twenty 6.5 m × 6.5 m plots were randomly established in each of the nine stands. Vegetation and environmental variables were sampled within these 180 plots. The cover of major lifeforms (lichens, bryophytes, shrubs, herbs, graminoids, and fern allies) was measured by placing a measuring tape around the perimeter of the plot (i.e., 6.5 m × 4 = 26 meters), and counting the number of centimeters occupied by each life form. The cover of intact logs, moderately-decayed logs, well-decayed logs, and rocks was measured in the same manner. Intact logs may have been cracked, but were not missing any segments,

whereas well-decayed logs had lost more than half their original form and were soft to the touch. Any logs falling between these two classes were judged as moderately decayed. Rocks were found in only a few plots and were small, and therefore not included in our analyses.

The following variables are quantified for each 6.5 m² plot: stand age (by coring a tree representative of each even-age plot and counting annual rings); canopy density (using a forest densiometer with the mean of the four measurements used expressed as a percent with 0% being no canopy and 100% being completely closed canopy); plot slope; plot aspect; elevation; length of *Hylocomium splendens* penultimate annual increment length [indicating site productivity for bryophytes (Vitt, unpubl. data)]; number of microhabitats within the plot (organic soil, mineral soil, moist depression, rock, upturned tree root, stump, intact logs, moderately-decayed logs, well-decayed logs, or forest floor); and local topography (1 = local ridge, 2 = mid slope, and 3 = local depression). Elevation was quantified using a global positioning system (Trimble® Pathfinder). No general topographic position was recorded because, although local topography was quite variable, all 180 plots occupied a similar position on the landscape, being above the riparian zone on undulating terrain. Soil pH and soil texture were also measured, however, they varied little (soil pH mean = 4.88, S.D. = 0.16, soil texture was either sandy loam or loamy sand; Kalra & Maynard 1991) and were not included in the analyses.

Due to the low cover values of many bryophyte and macro-lichen species, their intermixed growth, and the architecture of many of the vascular plants, it was difficult to measure individual species cover using the tape around the perimeter of the 6.5 m² plot. However, accurate measurements of the cover and post-harvest cover of caribou lichens are of critical interest to land managers and central to the aims of the overall project. Therefore, we estimated the cover of each species of bryophyte, lichen, and vascular plant using cover classes in five 1.5 m² quadrats in each of the four corners and in the middle of the 6.5 m² plot. This configuration of quadrats allowed for one meter walkways so that there was no trampling of the areas being monitored. Each species was scored using the cover scale: (1 = few stems, 2 = less than 5%, 3 = 5–10%, 4 = 11–25%, 5 = 26–50%, 6 = 51–75%, 7 = 76–100%). Midpoints of classes were used in analyses (1 = 0.5, 2 = 2.5, 3 = 7.5, 4 = 17.5, 5 = 32.5, 6 = 67.5, 7 = 87.5). Therefore, where we refer to groups such as bryophytes or lichens, the precise 6.5 m² plot measurements were used ($n = 180$). Where we refer to individual species, the 1.5 m² quadrat estimates were used ($n = 900$). We determined local species occurrence through examination of all five 1.5 m² quadrats in each plot—thus alpha diversity is the number of species found occurring in a plot based on all species found in the five quadrats.

All terrestrial (including expanded tree bases) mosses, liverworts, and foliose and fruticose lichens were identified to species. Arboreal lichens were not sampled, but were included if they were found on tree bases. Nomenclature follows Moss (1983) for vascular plants, Ireland et al. (1987) for mosses, Stotler and Crandall-Stotler (1977) for liverworts and hornworts, and Esslinger and Egan (1995) for lichens. Crustose lichens are uncommon in the terrestrial habitats sampled and are not included.

Statistical methods.—Pearson product moment correlation was used to determine the relationship between two random variables. Linear regression was used to determine the amount of variation in bryophyte and lichen cover explained by environmental factors (Sokal & Rohlf 1995). Barlett's test of equal variance showed no p values less

TABLE 1. Cover of the major terrestrial caribou lichens and the three most abundant mosses, all of which are feather mosses. Non-zero cover excludes all quadrats in which the species is not found (S.D. = standard deviation).

Species	Number of quadrats (900)	Mean cover (%) (S.D.)	Non-zero cover (%) (S.D.)	Maximum cover (%)
Caribou lichens				
<i>Cladina mitis</i>	809	3.91 (1.2)	4.43 (7.8)	62.5
<i>Cladina rangiferina</i>	612	1.31 (0.9)	1.96 (2.7)	2.5
<i>Cladina stellaris</i>	15	0.01 (0.1)	0.63 (0.5)	2.5
<i>Flavocetraria cucullata</i>	124	0.14 (0.3)	0.52 (0.2)	2.5
<i>Flavocetraria nivalis</i>	496	0.28 (0.5)	0.53 (0.2)	2.5
<i>Cladonia uncialis</i>	173	0.20 (0.5)	1.08 (1.2)	7.5
<i>Stereocaulon tomentosum</i>	387	0.51 (0.7)	1.21 (2.7)	37.5
Feather mosses				
<i>Hylocomium splendens</i>	441	1.04 (0.9)	2.17 (3.9)	37.5
<i>Pleurozium schreberi</i>	871	32.46 (2.1)	34.10 (31.7)	87.5
<i>Ptilium crista-castrensis</i>	575	1.29 (4.5)	2.04 (5.5)	62.5

that 0.05, and analysis of variance was used to determine significant differences between the most open 10% (18 sites) and most dense 10% (18 sites) of canopy covers (Sokal & Rohlf 1995). Clustering and ordination were used to assess differences in species composition between the 180 plots. Abundance data were log transformed prior to analysis to give more weight to the rarer species. Sites were clustered using unweighted pair group metric averaging (UPGMA; $\beta = 0$; using PATN; Belbin 1991a,b) and ordinated using principal components analysis (PCA; using CANOCO 4.0; ter Braak & Smilauer 1998). Changes in species composition were related to their environment by correlating variation along the first and second ordination axes with the environmental variables. Alpha diversity is the number of species found within the 6.5 m plot ($n = 180$); gamma diversity is the total number of species found in the study; beta diversity, or species turnover, is gamma diversity divided by alpha diversity. Local rarity is defined as the species found in only one plot.

RESULTS

Cover.—Overall mean lichen cover per plot was high at 26.4% (S.E. = 1.0%; range 0–69.2%) but mean bryophyte cover was almost twice that at 43.8% (S.E. = 1.6%; range 0–92.5%). In some plots, bryophytes almost completely covered the forest floor and the maximum cover recorded was 92.5%. The feather moss, *Pleurozium schreberi*, was by far the dominant species with mean cover of 32.5% (Table 1). The second and third most abundant bryophytes were the two feather mosses *Ptilium crista-castrensis* and *Hylocomium splendens*.

Shrubs were also abundant on the forest floor having a mean cover of 34.0% (S.E. = 0.8%, range = 9.4–64.8%). Shrub branches tended to be raised above the duff and moss-lichen layer, therefore occupying a different space. Herbs were species-rich, but did not cover a large area with a mean cover of only 3.6% (S.E. = 0.2%, range = 0–14.9%). Graminoids and fern allies were sparse (graminoids mean = 0.3%, S.E. = 0.04%, range = 0–4.0%; fern

allies mean = 0.6%, S.E. = 0.07%, range = 0–6.4%).

The species of lichens preferred by caribou belong to the genera *Cladina*, *Cladonia*, and *Flavocetraria*, and to a lesser degree, *Stereocaulon* (Cichowski 1993). *Cladina mitis*, one of the most favored caribou lichens, was present in 809 of the 900 quadrats (88.4%, Table 1). Despite being widespread, the mean cover of *Cladina mitis* in each quadrat was low at 3.9% (S.E. = 0.2%). The second most abundant lichen, both in terms of number of quadrats occupied and cover within quadrats, was the morphologically similar *Cladina rangiferina* (Table 1). The third *Cladina* (*C. stellaris*) found in the study area was present in only 15 of the 900 quadrats sampled, and even when present it was represented by small patches (Table 1).

The comparatively low cover of each lichen species (less than 4.0%) compared to the total (26.4%) was due to dominance being shared, particularly between *Cladina rangiferina* and *C. mitis*. The combined cover of these two *Cladina* species along with the *Flavocetraria* and *Stereocaulon* species, which are occasionally found in patches of high cover, added up to the high cover of lichens overall. However, each species on its own scores in one of the lower cover classes.

Correlates of cover.—The strongest predictor of lichen cover was bryophyte cover ($r = -0.67$, $p < 0.001$, Fig. 1). However, cover of bryophytes and lichens is not independent, being measured in the same quadrat. There were also relatively strong, significant correlations between lichen and graminoid cover ($r = 0.29$, $p < 0.001$), and bryophyte and shrub cover ($r = 0.35$, $p < 0.001$). Despite significant correlations, none of the environmental variables explains a large amount of variation in lichen, bryophyte, or vascular plant cover (Table 2). The strongest correlations suggest that where there

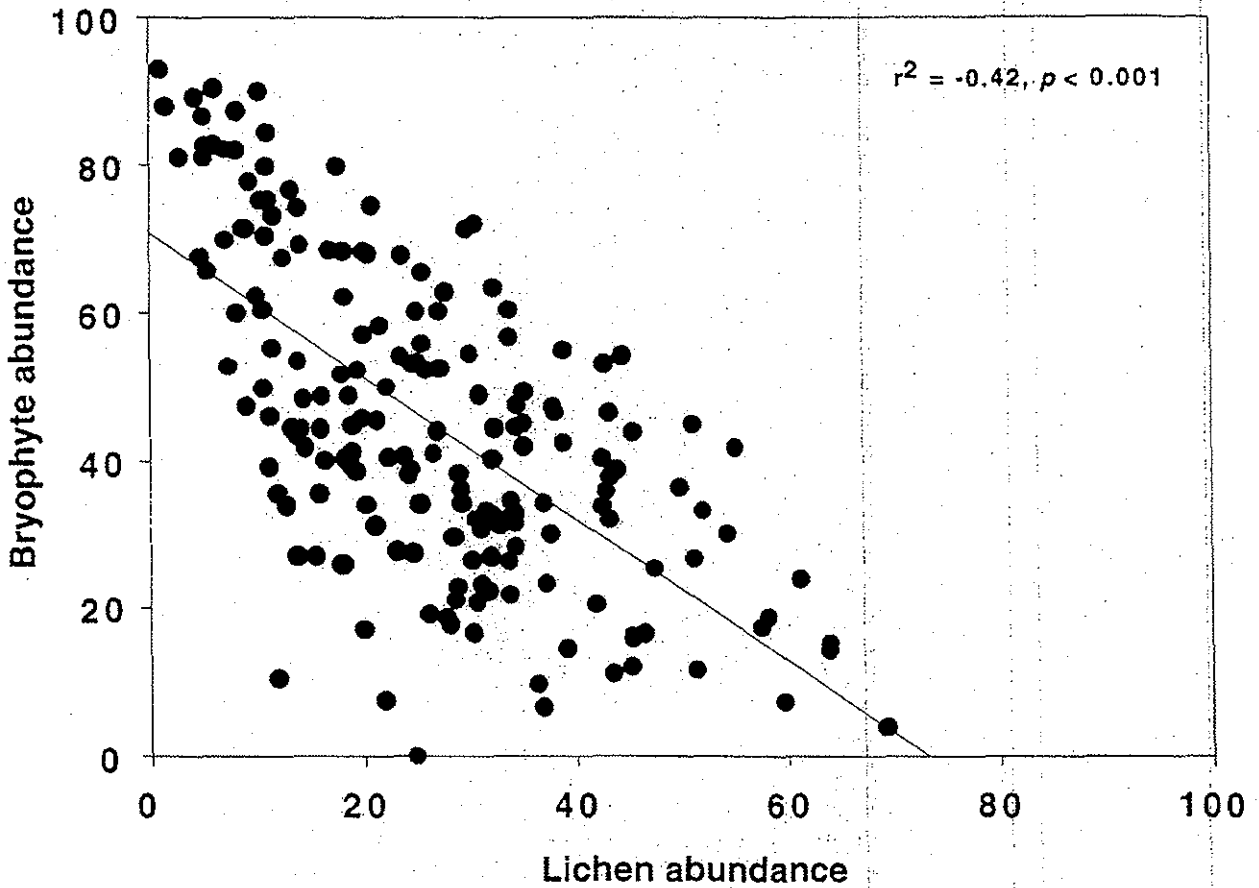


FIGURE 1. Correlation between bryophyte and lichen cover.

are more intact logs, there is greater bryophyte cover and lower lichen cover.

For individual species, no variable explained more than 0.03% of the variation in lichen, bryophyte, or vascular plant cover. Canopy density and graminoid cover both predicted significant variation in the cover of most of the caribou lichens and feather mosses, however, with such low r^2 values, predictive power is weak.

Species diversity.—The total combined number (gamma diversity) of bryophytes and macro-lichens exceeded the number of vascular plants 1.4 to one (Fig. 2). In total, 53 lichens, 37 bryophytes, and 65 vascular plants were found (Table 3). Herbs were

the most species-rich group of vascular plants. The largest group of lichens was *Cladonia* with 21 species, then the foliose lichens (18 spp.), and the remainder was the fruticose lichens (15 spp.). Of the bryophytes, 21 were mosses and 15 were hepatics.

Lichen mean species richness (22.5-alpha diversity) of the 180 plots was double that of the bryophytes (13.4) and vascular plants (10.7). There was little change in species composition between plots for bryophytes and lichens (beta diversity), but relatively high turnover for vascular plants. At 30% species dissimilarity (Bray-Curtis), there were only two groups of lichens and six groups of bryophytes, but 19 groups of vascular plants (data not shown).

TABLE 2. Ability of environmental variables to detect variation in bryophyte, lichen, shrub, herb, and graminoid cover at the 6.5 m² plot level (r^2). Only significant correlations are included (i.e., fern allies, graminoids, elevation, local topography, log (moderate decay), and site productivity excluded). A minus sign indicates a negative correlation.

Variable	Lichen	Bryophyte	Shrub	Herb
Age	—	—	—	0.04*
Aspect	-0.05**	0.06**	—	—
Canopy	-0.11***	0.03*	—	—
Log-intact	-0.25***	0.14***	—	—
Log-decayed	0.06**	-0.06**	—	—
No. microhab.	-0.09***	0.05**	-0.02*	—
Slope	-0.06**	—	—	—

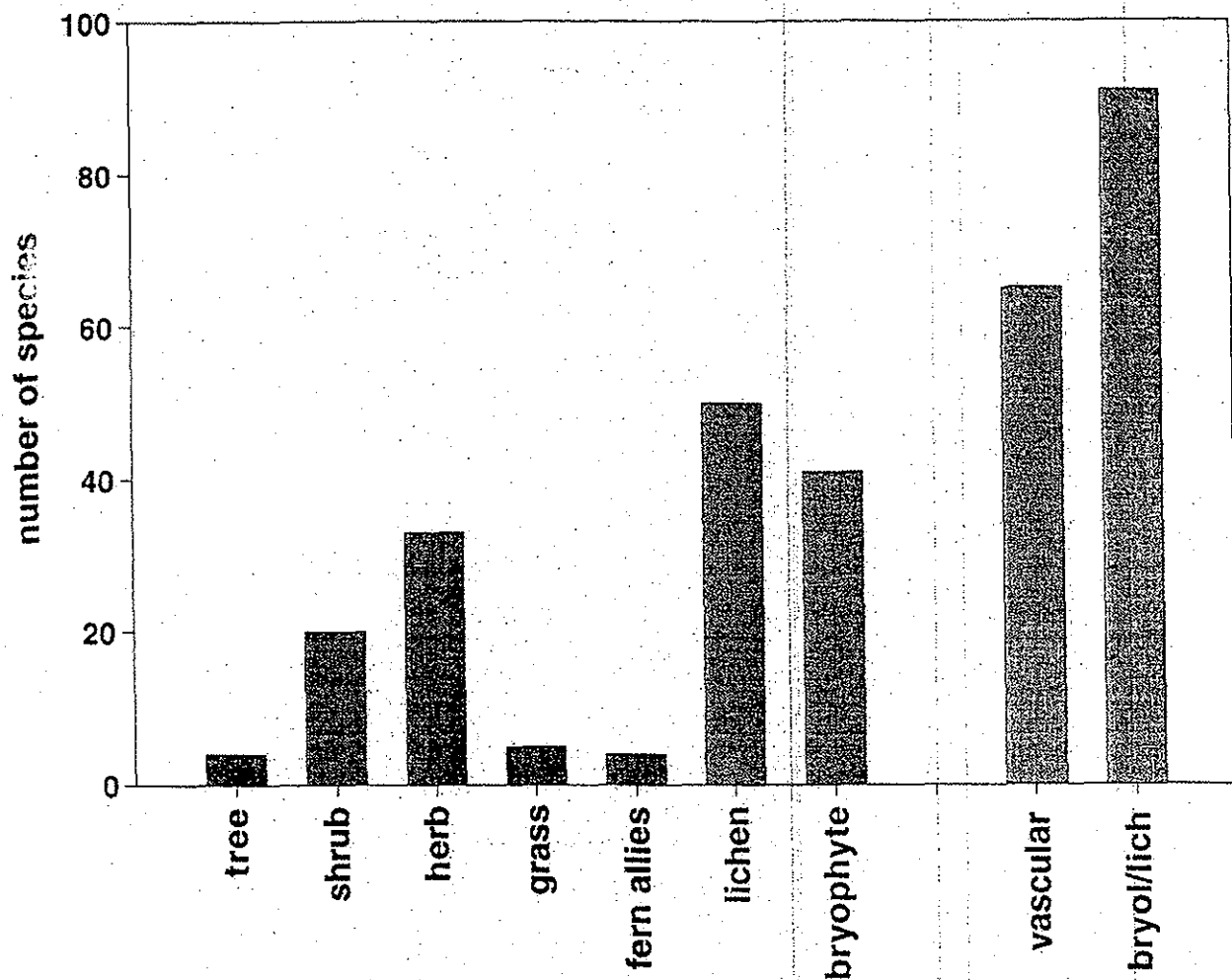


FIGURE 2. Total species richness of bryophytes, lichens, and the five groups of vascular plants. The two right-hand columns are group totals of bryophytes, lichens, and vascular plants.

Eigenvalues, which are the percent variance in the species data explained by an ordination axis, were highest for vascular plants, but overall were low for all three groups (bryophytes: axis 1 = 0.108, axis 2 = 0.096, axis 3 = 0.084, axis 4 = 0.073; lichens: axis 1 = 0.185, axis 2 = 0.071, axis 3 = 0.063, axis 4 = 0.060; vascular plants: axis 1 = 0.157, axis 2 = 0.111, axis 3 = 0.063, axis 4 = 0.053). Therefore, any two plots are likely to have many species in common. Separately, ordinations based on the bryophytes, lichens, or vascular plants yielded a similar central cluster of stands (Fig. 3—shown only for lichens and bryophytes).

Local species rarity.—Twenty-two species (14%) were found only once, and no single plot contained more than one of these. Five of these 22 locally rare species were lichens (9% of the lichen flora), six bryophytes (16% of the bryophyte flora), and 11 vascular plants (17% of the vascular plant flora). None of these is provincially endangered, but all are rare in this particular forest type. Only three of these species occur in the 20% of plots

with extreme canopy cover (4.4 would be expected).

Correlates of species diversity.—No variables, biotic or abiotic, explained significant variation in lichen alpha diversity. Variation in bryophyte alpha diversity was best explained by the cover of moderately decayed logs ($r^2 = 0.07$, $p < 0.001$), followed by the cover of intact logs ($r^2 = 0.03$, $p = 0.018$), and stand age ($r^2 = 0.03$, $p = 0.018$). Neither bryophyte nor lichen cover explained significant variation in bryophyte alpha diversity.

Significant variation in vascular plant alpha diversity was explained by stand age ($r^2 = 0.06$, $p < 0.001$), and cover of well decayed logs ($r^2 = 0.03$, $p = 0.014$). We split vascular plant alpha diversity into shrub and herb species richness, since these are the two dominant components and they may have different patterns of variation. Significant variation in shrub alpha diversity was explained by all three stages of log cover (well decayed: $r^2 = 0.07$, $p < 0.001$; intact: $r^2 = 0.05$, $p = 0.002$; moderately decayed: $r^2 = 0.30$, $p = 0.011$), stand age ($r^2 = 0.06$,

TABLE 3. All species found in the 180 plots. Species with asterisk (*) were found only once.

VASCULAR PLANTS	
Trees	<i>Aster sibiricus</i> L.
<i>Abies balsamea</i> (L.) Mill.	* <i>Aster</i> sp.
<i>Picea glauca</i> (Moench) Voss	<i>Calamagrostis canadensis</i> (Michx.) Beauv.
<i>Picea mariana</i> (Mill.) BSP.	<i>Campanula rotundifolia</i> L.
<i>Pinus contorta</i> Loudon	<i>Cornus canadensis</i> L.
Shrubs	* <i>Crepis tectorum</i> L.
<i>Alnus crispa</i> (Ait.) Pursh	<i>Deschampsia caespitosa</i> (L.) Beauv.
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	<i>Elymus innovatus</i> Beal
<i>Betula pumila</i> L.	<i>Epilobium angustifolium</i> L.
<i>Empetrum nigrum</i> L.	<i>Equisetum scirpoides</i> Michx.
<i>Juniperus communis</i> L.	<i>Galium boreale</i> L.
<i>Ledum groenlandicum</i> Oeder	<i>Geum aleppicum</i> Jacq.
<i>Linnaea borealis</i> L.	Graminoid sp.
* <i>Prunus virginiana</i> L.	<i>Hedysarum alpinum</i> L.
<i>Rosa acicularis</i> Lindl.	<i>Hieracium umbellatum</i> L.
<i>Rubus arcticus</i> spp. <i>acaulis</i> (Michx.) Focke	<i>Lycopodium annotinum</i> L.
<i>Rubus pedatus</i> J. E. Smith	<i>Lycopodium clavatum</i> L.
<i>Salix</i> sp.	<i>Lycopodium complanatum</i> L.
<i>Spiraea alba</i> Du Roi	* <i>Maianthemum canadensis</i> Desf.
<i>Spiraea betulifolia</i> Pallas	* <i>Mertensia paniculata</i> (Ait.) G. Don.
<i>Vaccinium caespitosum</i> Michx.	<i>Orthilia secunda</i> (L.) House
<i>Vaccinium membranaceum</i> Dougl.	<i>Oryzopsis pungens</i> (Torr.) A. S. Hitchc.
<i>Vaccinium myrtilloides</i> Michx.	<i>Pedicularis groenlandica</i> Retz.
<i>Vaccinium myrtilus</i> L.	<i>Pedicularis labradorica</i> Wirsing
<i>Vaccinium vitis-idaea</i> L.	<i>Petasites palmatus</i> (Ait.) A. Gray
<i>Viburnum edule</i> (Michx.) Raf.	* <i>Pyrola asarifolia</i> Michx.
Herbs	<i>Pyrola chlorantha</i> Sw.
<i>Achillea millefolium</i> L.	<i>Pyrola virens</i> Schweig.
<i>Aconitum delphinifolium</i> DC.	* <i>Senecio</i> sp.
<i>Antennaria microphylla</i> Rydb.	<i>Smilacina stellata</i> (L.) Desf.
* <i>Antennaria parvifolia</i> Nutt.	<i>Solidago spathulata</i> DC.
* <i>Arnica angustifolia</i> M. Vahl	* <i>Taraxacum officinale</i> Weber
<i>Arnica cordifolia</i> Hook.	<i>Viola adunca</i> J. E. Smith
<i>Arnica latifolia</i> Bong.	<i>Viola</i> sp.
	LICHENS
<i>Alectoria</i> sp.	<i>Cladonia uncialis</i> (L.) F. H. Wigg.
<i>Bryoria</i> sp.	<i>Dactylina arctica</i> (Richardson) Nyl.
<i>Cetraria ericetorum</i> Opiz	* <i>Dermatocarpon miniatum</i> (L.) W. Mann
<i>Cetraria islandica</i> (L.) Ach.	<i>Flavocetraria cucullata</i> (Bellardi) Kärnef. & Thell
<i>Cladina mitis</i> (Sandst.) Hustich	<i>Flavocetraria nivalis</i> (L.) Kärnef. & Thell
<i>Cladina rangiferina</i> (L.) Nyl.	<i>Hypogymnia physodes</i> (L.) Nyl.
<i>Cladina stellaris</i> (Opiz) Brodo	<i>Imadophila ericetorum</i> (L.) Zahlbr.
<i>Cladonia botrytes</i> (K. Hagen) Willd.	<i>Letharia vulpina</i> (L.) Hue
<i>Cladonia cariosa</i> (Ach.) Spreng.	<i>Nephroma arcticum</i> (L.) Torss.
<i>Cladonia carneola</i> (Fr.) Fr.	<i>Nephroma expallidum</i> (Nyl.) Nyl.
<i>Cladonia cenotea</i> (Ach.) Schaer.	<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.
<i>Cladonia cervicornis</i> (Ach.) Flotow	<i>Parmeliopsis hyperopta</i> (Ach.) Arnold
<i>Cladonia chlorophaea</i> (Sommerf.) Spreng.	<i>Peltigera aphthosa</i> (L.) Willd.
<i>Cladonia coccifera</i> (L.) Willd.	* <i>Peltigera leucophlebia</i> (Nyl.) Gyelnik
<i>Cladonia coniocraea</i> (Flörke) Spreng.	<i>Peltigera malacea</i> (Ach.) Funck
<i>Cladonia cornuta</i> (L.) Hoffm.	<i>Peltigera neopolydactyla</i> (Gyelnik) Gyelnik
<i>Cladonia crispata</i> (Ach.) Flotow	* <i>Peltigera retifoveata</i> Vitik.
<i>Cladonia deformis</i> (L.) Hoffm.	* <i>Peltigera rufescens</i> (Weiss) Humb.
<i>Cladonia ecmocyna</i> Leighton	<i>Peltigera scabrosa</i> Th. Fr.
<i>Cladonia fimbriata</i> (L.) Fr.	<i>Platismatia glauca</i> (L.) W. Culb. & C. Culb.
<i>Cladonia furcata</i> (Huds.) Schrad.	<i>Solorina crocea</i> (L.) Ach.
<i>Cladonia gracilis</i> (L.) Willd.	<i>Stereocaulon tomentosum</i> Fr.
<i>Cladonia multiformis</i> G. Merr.	<i>Tuckermannopsis americana</i> (Spreng.) Hale
* <i>Cladonia pleurota</i> (Flörke) Schaer.	<i>Umbilicaria torrefacta</i> (Lightf.) Schrad.
<i>Cladonia pyxidata</i> (L.) Hoffm.	<i>Usnea</i> sp.
<i>Cladonia</i> sp.	<i>Vulpicida pinastri</i> (Scop.) J-E. Matts. & M. J. Lai.
<i>Cladonia sulphurina</i> (Michx.) Fr.	

TABLE 3. Continued.

BRYOPHYTES	
Mosses	
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	<i>Polytrichum piliferum</i> Hedw.
* <i>Buxbaumia</i> sp.	<i>Polytrichum strictum</i> Brid.
* <i>Campylium hispidulum</i> (Brid.) Mitt.	<i>Ptilium cristacastrensis</i> (Hedw.) De Not.
<i>Ceratodon purpureus</i> (Hedw.) Brid.	* <i>Splachnum ampullaceum</i> Hedw.
<i>Dicranum acutifolium</i> (Lindb. & H. Arnell) Weinm.	* <i>Tayloria</i> sp.
<i>Dicranum brevifolium</i> (Lindb.) Lindb.	<i>Tetraplodon minioides</i> (Hedw.) B.S.G.
* <i>Dicranum flagellare</i> Hedw.	Hepatics
<i>Dicranum fuscescens</i> Sm.	<i>Barbilophozia hatcheri</i> (Evans) Loeske
<i>Dicranum muehlenbeckii</i> B.S.G.	<i>Barbilophozia lycopodioides</i> (Wallr.) Loeske
<i>Dicranum polysetum</i> Sw.	* <i>Cephalozia connivens</i> (Dicks.) Lindb.
<i>Dicranum scoparium</i> Hedw.	<i>Cephaloziella rubella</i> (Nees) Warnst.
<i>Dicranum spadiceum</i> Zett.	<i>Cephaloziella</i> sp.
<i>Dicranum undulatum</i> Brid.	<i>Lepidozia reptans</i> (L.) Dum.
<i>Drepanocladus uncinatus</i> (Hedw.) Warnst.	<i>Lophozia longidens</i> (Lindb.) Macoun
<i>Hylocomium splendens</i> (Hedw.) B.S.G.	<i>Lophozia guttulata</i> (Lindb. & H. Arnell) Evans
<i>Pleurozium schreberi</i> (Brid.) Mitt.	<i>Lophozia ventricosa</i> (Dicks.) Dum.
<i>Pohlia nutans</i> (Hedw.) Lindb.	<i>Ptilidium ciliare</i> (L.) Hampe
<i>Polytrichum commune</i> Hedw.	<i>Ptilidium pulcherrimum</i> (G. Web.) Hampe
<i>Polytrichum juniperinum</i> Hedw.	<i>Tritomaria exsectiformis</i> (Breidl.) Loeske

$p < 0.001$), and bryophyte cover ($r^2 = 0.04$, $p = 0.012$). The three variables that correlated significantly with herb alpha diversity were the cover of moderately decayed logs ($r^2 = 0.05$, $p = 0.002$), canopy cover ($r^2 = 0.04$, $p = 0.008$), and bryophyte cover ($r^2 = 0.02$, $p = 0.046$). Because of the high number of plots, these significant correlations are present, but overall they explain very little of the variation in species richness.

Bryophyte cover was the only variable significantly correlated with bryophyte species composition along the first PCA axis ($r^2 = 0.15$, $p < 0.0001$). No variables explained significant variation in the second axis for bryophytes. Also, none of the environmental variables explained significant variation in bryophyte species composition. Elevation explained highly significant variation in lichen species composition along both the first PCA axis ($r^2 = 0.29$, $p < 0.0001$) and the second axis ($r^2 = 0.09$, $p < 0.0001$). Elevation was also the only variable to explain significant variation in vascular plant species composition along both the first ($r^2 = 0.07$, $p = 0.0002$) and second ($r^2 = 0.55$, $p < 0.0001$) PCA axes.

Differences between open and dense canopies.—As designed, the difference in canopy density between the 10% most open and 10% most dense plots was highly significant ($r^2 = 0.94$, $p < 0.001$), with the open sites ranging from 45.3–52.3% canopy cover and the dense sites ranging from 72.8–87.0%. The most open 10% of sites had significantly greater lichen cover than the most dense 10% of sites (Table 4) and the trees were older on average. These older sites were also higher in elevation and had less cover of moderately decayed logs.

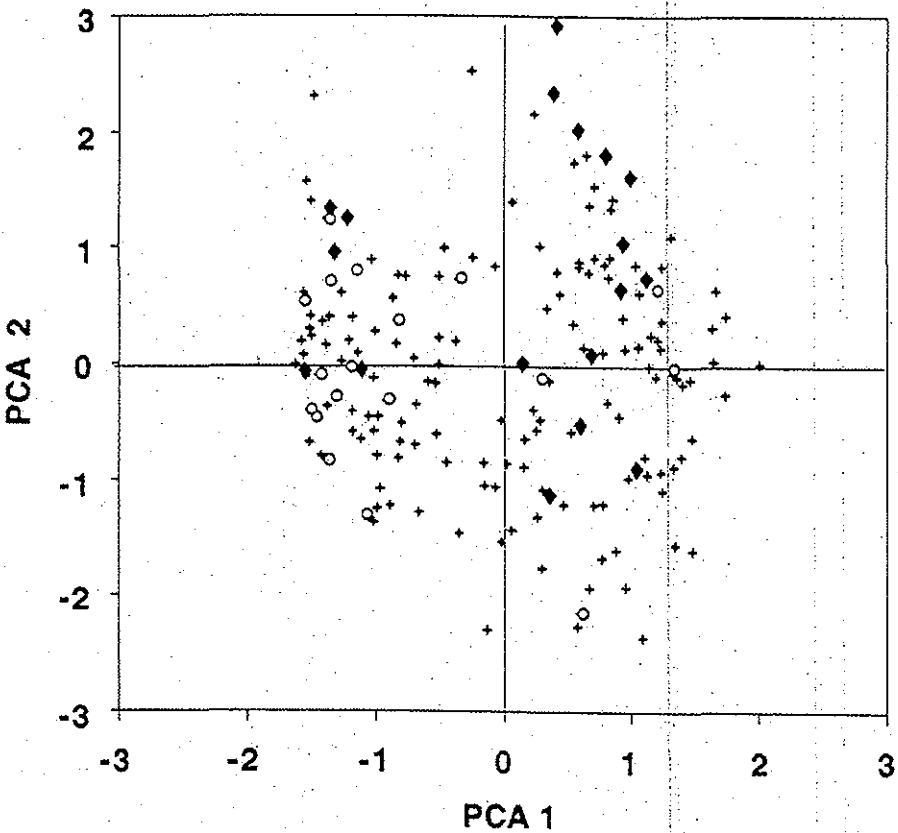
Of the caribou lichens and most abundant bryophytes, the most open 10% of sites had a significantly greater cover of *Flavocetraria nivalis* and *F. cucullata* (Table 4). There was a greater cover of *C. mitis* in the open sites, although the difference was small and not quite statistically significant at the 0.05 level (Table 4). There was little difference in the cover of *Cladina rangiferina* ($r^2 = 0.01$, $p = 0.14$). *Pleurozium schreberi*, the most abundant feather moss, had significantly lower cover in the open plots (Table 4). There were some significant differences in individual bryophyte species, such as *Hylocomium splendens*, but their covers were low and the differences between the averages were small.

Species composition was significantly different between the open and dense sites for all three groups (ANOSIM; lichen $R = 0.27$, $p < 0.000$; bryophyte $R = 0.12$, $p = 0.04$; vascular plant $R = 0.47$, $p < 0.000$). However, the division between the two groups was strongest and clearest for vascular plants (Fig. 4) with groups separating at a higher level of dissimilarity.

Of the 22 locally rare species, only one vascular plant, *Maianthemum canadense*, was found in the 10% of plots with the most dense canopies and only one vascular plant species (*Arnica angustifolia* ssp. *tomentosum*) and one bryophyte species (*Dicranum flagellare*) was found in the 10% most open canopy plots. None of the more common species is restricted to these plots with extreme open and dense canopies.

Mean alpha diversity was significantly higher for vascular plants in the open plots (12.9 vs. 9.1, $n = 36$ —Table 5), but not significantly different for lichens (21.0 vs. 21.2) or bryophytes (13.0 vs. 13.4).

a.



b.

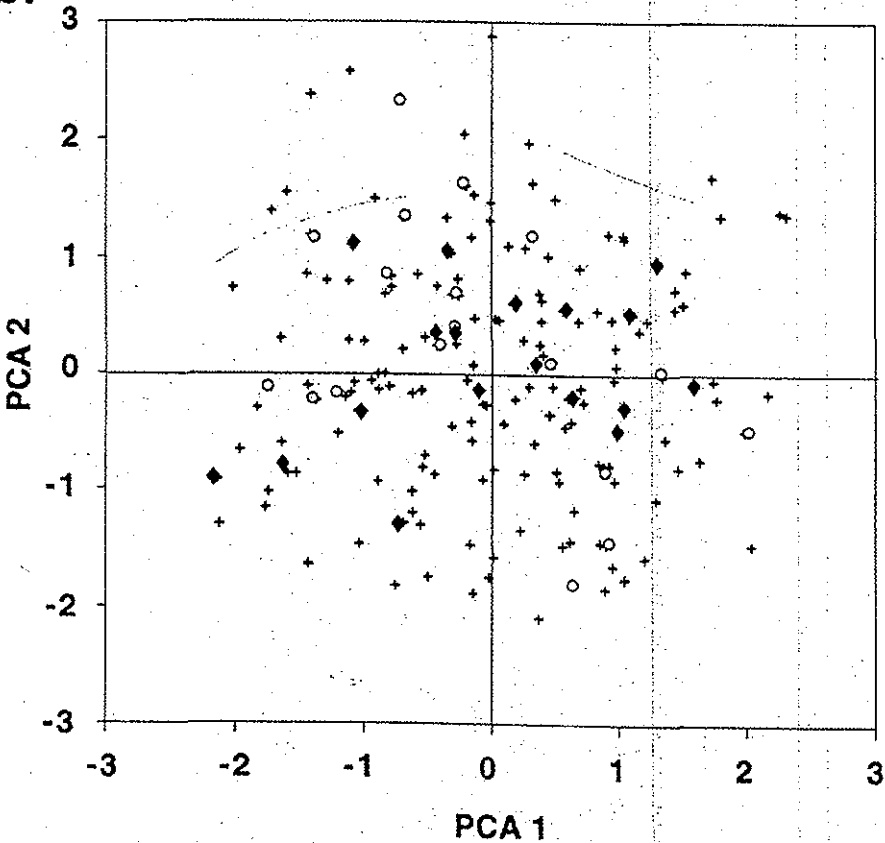


TABLE 4. Differences between the 10% most open canopy sites and the 10% most dense canopy sites. Except for the two dominant *Cladina* species, only variables that were significantly different between the open and dense sites are included. Variables are listed from strongest to the weakest predictor. Cover of individual species (%) was estimated in 900 quadrats (S.D. = standard deviation).

	Mean values for 10% most open (S.D.)	Mean values for 10% most dense (S.D.)	r^2	p
Elevation (m asl)	1,467.0 (42.5)	1,367.0 (24.7)	0.69	<0.001
Age (years)	123.9 (30.0)	95.4 (6.4)	0.30	<0.001
Vascular plant species richness	12.8 (3.6)	9.1 (2.1)	0.30	<0.001
Lichen cover (%)	29.2 (15.2)	16.4 (8.7)	0.23	0.004
Moderately decayed logs (%)	1.1 (1.1)	2.3 (1.3)	0.21	0.005
<i>Flavocetraria nivalis</i> (%)	0.1 (0.2)	0.3 (0.3)	0.11	<0.001
<i>Pleurozium schreberi</i> (%)	25.0 (27.6)	40.9 (33.1)	0.07	<0.001
<i>Flavocetraria cucullata</i> (%)	0.06 (0.1)	0.2 (0.2)	0.05	0.002
<i>Cladina rangiferina</i> (%)	1.3 (2.1)	1.0 (1.6)	0.01	0.170
<i>Cladina mitis</i> (%)	4.4 (8.9)	3.3 (8.5)	0.00	0.360

However, the most striking difference is that even though the alpha diversity for vascular plants is higher in open plots, these plots account for only 68% of the total flora for vascular plants. This compares with open plots accounting for between 85% (lichens) and 78% (bryophytes) of the flora. The 10% most dense plots account for between 40% (vascular plants) and 70–72% (bryophytes and lichens) of the flora. Thus, open canopy plots are overall species-rich when compared to dense canopy plots, but vascular plant richness captures fewer total species than do the other life form groups.

Species-rich vs. species-poor plots.—We compared the 10% of plots having the most and least number of species of the three lifeform groups, and examined whether these species-rich and species-poor plots were affiliated with extreme canopy conditions. Lichen-rich plots contained between 28 and 32 species compared to lichen poor plots with 12 to 17 species. Species-rich bryophyte plots contained 16–21 species whereas species-poor plots had between seven and 10 species. Vascular plant rich plots contained 15–20 species while species-poor plots had between five and seven species. Thus lichen and bryophyte species-rich plots have about twice the number of species, while vascular plant species-rich plots contain about three times as many species. Only 12% of the species-rich plots contained high numbers of both lichens and bryophytes and only 3% contained high numbers of all three plant groups. More importantly, species-rich plots from the extreme canopy covers (the 10% most open or closed) were only species-rich for one

group, not for both bryophytes and lichens or all three groups simultaneously.

Species-rich plots are equally represented under both open and dense canopies, including under the 20% extreme canopy conditions versus the 80% middle conditions. We conclude that the ground layer of plots having natural extreme canopy conditions are not especially unique in terms of numbers and concentrations of species, and combinations of species groups.

DISCUSSION

Terrestrial lichens are an important and diverse component of the ground layer in these montane, pine-dominated forests. However, in the relatively open, old forests of this study, feather mosses often dominate the plots. The only strong correlation with total lichen cover was bryophyte cover (most of which was the feather moss *Pleurozium schreberi*), although these two variables are not independent. Harvesting may produce a drier microclimate that favors lichens in a normally bryophyte-dominated forest, a prediction proposed by Ahti and Oksanen (1990). We know from a study at the northern limit of the boreal forest that in open forests, lichens are able to maintain dominance in the absence of disturbance (Morneau & Payette 1989). Therefore, in theory, selective harvesting may succeed in producing greater abundance of caribou lichen.

There was a weak, significant relationship between lichen cover and canopy density, with canopy densities varying between 43% and 87% clo-

FIGURE 3. Ordination of lichens (a) and bryophytes (b). ♦ = sites that have the 10% most densest canopies. ○ = sites that have the 10% most open canopies. + = the remainder of the sites, equalling to 80% of the total.

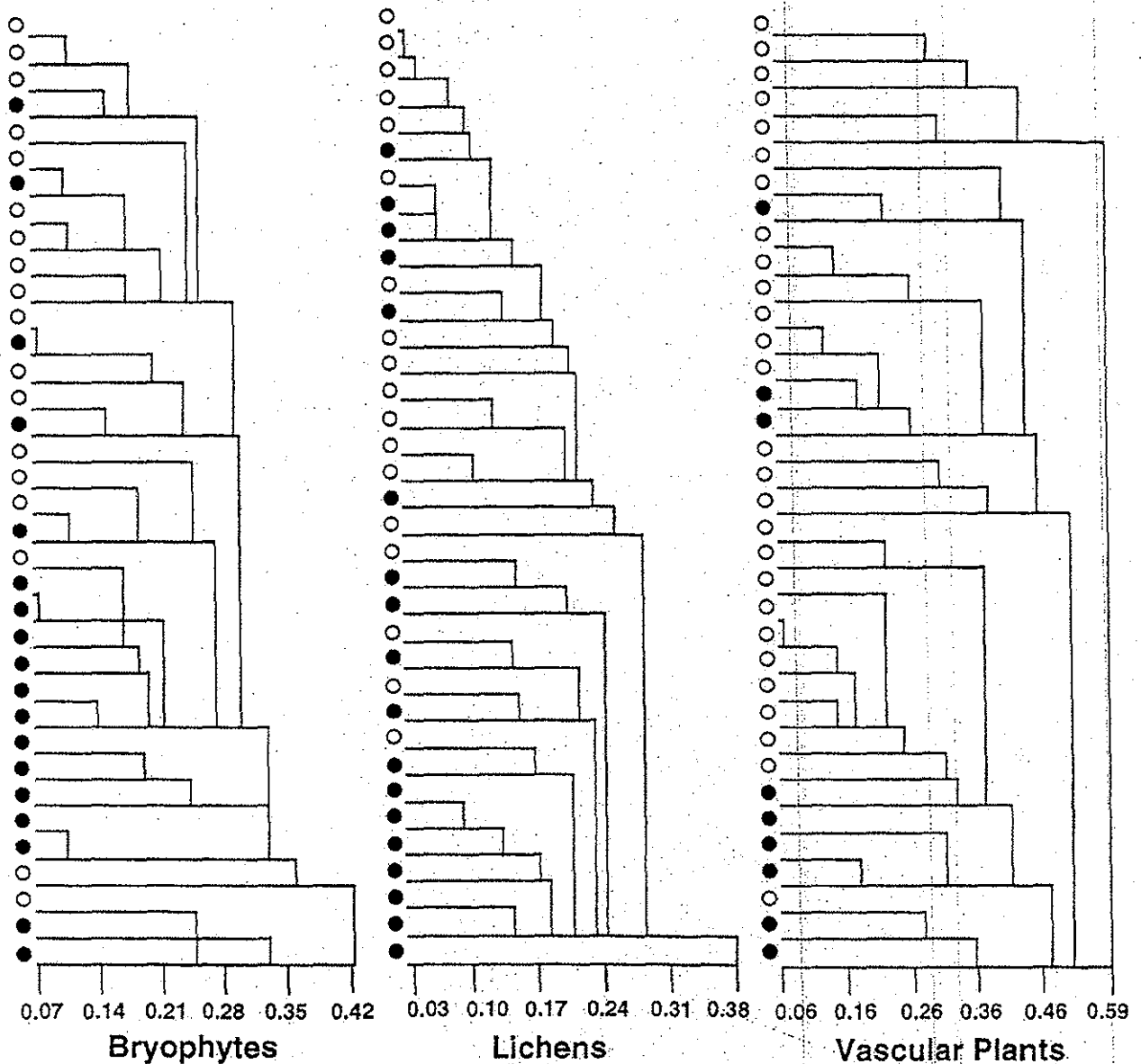


FIGURE 4. Dendrograms of bryophyte, lichen, and vascular plant species composition using Bray-Curtis association measure for 20% extreme canopy conditions. Note the difference in scales on the three dendrograms. Solid circles are plots with dense canopies; open circles are plots with open canopies.

sure. With such a weak correlation it is not possible to predict post-harvest change with any confidence. However, lichen cover response to canopy cover may be non-linear, and a marked increase in lichen cover with canopy openings between 0 (gap or clear cut) and 43% is possible. The key to increasing lichen cover may be to open up the canopy enough to cause substantial mortality of the feather mosses, which presently dominate the ground cover. *Cladonia mitis*, one of the important caribou lichens, is thought to be ecologically suited to disturbed sites and may respond well to the actual disturbance as well as the death of the feather mosses (Ahti 1961).

Not only did canopy cover fail to explain much variation in lichen and bryophyte cover, but none

of the environmental variables performed well. Other studies have also found weak relationships between caribou lichen cover and environmental variables (Webb 1996). This may be because establishment conditions and dispersal success following disturbance, rather than current conditions, are important in determining whether a patch is feather moss, lichen, or vascular plant dominated. A second alternate explanation is that present day cover patterns are only a reflection of past disturbance. In these montane pine-dominated forests, fire is extremely important and heterogeneous. Post fire patterns may be important in controlling present day ground layer dynamics.

In terms of total species richness, this *Pinus contorta*-dominated forest was relatively species-rich

TABLE 5. Alpha, beta, and gamma diversity for vascular plants, bryophytes, and lichens for all sites, plus diversity measurements for the 10% most open, middle 80%, and 10% most closed canopy sites (\pm standard deviation).

Canopy cover	10% most open	Middle 80%	10% most dense	All stands
Alpha diversity				
Vascular	12.9 (3.7)	10.6 (2.8)	9.1 (2.1)	10.7 (3.0)
Bryophyte	13.0 (2.0)	13.5 (2.3)	13.4 (2.6)	13.4 (2.3)
Lichen	21.0 (3.9)	22.9 (3.8)	21.2 (4.3)	22.5 (3.9)
Beta diversity				
Vascular	3.4	6.0	2.9	6.1
Bryophyte	2.2	2.7	1.9	2.8
Lichen	2.1	2.3	1.8	2.4
Gamma diversity				
Vascular	44	63	26	65
Bryophyte	29	36	26	37
Lichen	45	53	38	53
All species				
Alpha diversity	46.9 (7.0)	46.9 (5.9)	43.7 (6.2)	
Beta diversity	2.5	3.2	2.1	
Gamma diversity	118	152	90	

in bryophytes and lichens, with their combined numbers exceeding the number of vascular plants. However, it is not clear whether this pattern is common as existing studies of bryophytes or lichens in North American boreal and montane forests tend to concentrate on the dynamics and habitat preferences of a few important species, rather than total species diversity (e.g., Frego & Carlton 1995; Hedder-son 1992).

These montane forests are characterized by individual plots with high lichen species richness and low vascular plant and bryophyte richness. However, high species turnover of vascular plants compared to low turnover for lichens and bryophytes yields an area in which forest stands are much more variable in their vascular plant flora and more uniform in their ground layers. Significant differences in the biota of the 10% most open plots compared to the 10% most dense plots include greater cover of lichens, and mean alpha species richness and higher species turnover of vascular plants in open plots; however overall differences in the ground layer are minimal. Also, species-rich plots are not over (or under) represented under open canopies.

Under the natural forest regime, these montane pine-forests have a locally variable ground layer, both in terms of abundance and richness. Local environmental parameters do not appear to explain a large amount of this variation, in either abundance or richness of bryophytes and lichens. In contrast, the vascular plant composition and richness is somewhat better explained by environmental parameters, with the vascular plant component of individual plots being more distinct and having greater species turnover between plots.

We interpret these data to indicate that at the local scale lichen and bryophyte species patterns may be greatly affected by factors other than current environmental pattern, especially when substrate differences are limited. Factors that may be partially responsible for local pattern are establishment regimes, dispersal success, and past disturbance variation.

This study in the montane forests of the eastern slopes of the Rocky Mountains documents the species diversity of two much neglected, but conspicuous taxa, bryophytes and lichens. It represents a starting point towards including these important components of biodiversity into management plans. Management of this montane forest through selective cutting in order to enhance certain ground layer species will not necessarily be successful if based on environmental/species patterns alone, as it appears that at the local scale environment has a limited effect on species distribution. A better understanding of past events, including such biological factors as establishment and dispersal, as well as natural disturbance pattern, are needed in order to effectively manage ground layer components.

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