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A BASELINE STUDY OF ALPINE SNOWBED AND RILL COMMUNITIES ON MOUNT WASHINGTON, NH

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ABSTRACT. Quantitative data on the abundance and frequency of vascular plants, bryophytes and lichens are lacking for alpine snowbed and rill communities in northeastern North America. Such data are needed to establish whether the communities are changing in response to climate warming, nitrogen deposition or shifts in the timing of precipitation and snowmelt. We surveyed nine sites (five snowbeds and four rills) on Mount Washington (White Mountain National Forest, New Hampshire), recording 54 vascular plant species, 42 bryophytes and 13 lichens. Although vascular plants were most abundant, bryophytes and lichens, which had not been completely surveyed in these communities previously, were important in terms of species richness (as many as eight bryophytes and four lichens in 1 m² quadrats) and were occasionally abundant, particularly bryophytes in rills. We found that snowbeds and rills are separate communities. Some species are shared, but far higher numbers of vascular plants, bryophytes and lichens were found in one community but not the other. The most frequent vascular plants had been reported as common in snowbeds and rills previously. However, several species that are common in these communities elsewhere occurred less often in our sites because of variation occurring both across the region and within the White Mountains. Our research provides baseline information on snowbeds and rill plant communities so that future studies can determine how they respond to changes in environmental conditions.

Key Words: alpine ecology, bryophytes, climate change, community dynamics, lichens, species richness

Snowbed communities are distinct alpine assemblages that occur only where topographic depressions accumulate large amounts of snow during the winter months and where the snowpack does not melt until late spring or early summer. The snowpack and its extended longevity give plants greater insulation and reduced exposure to mechanical stresses but an exceptionally shortened growing season in the harsh alpine zone. Because of these unusual conditions, northeastern snowbeds harbor a number of species that occur nowhere else above

lower elevation forests; thus they contribute unique elements to alpine biodiversity (Björk and Molau 2007). Rills are small in area, developing primarily along streams and on the lips, headwalls and gullies of ravines where late-melting snow runs off; like snowbeds, they contain species occurring nowhere else in the alpine (Sperduto and Kimball 2011).

Alpine communities are sensitive to climate change globally (Field et al. 2014; Lenoir et al. 2008; Pauli et al. 1996; Rodenhouse et al. 2008; Walker et al. 2001; Wilson and Nilsson 2009), and snowbed species are especially vulnerable to changes that could reduce springtime snow cover (Klanderud and Birks 2003; Sætersdal and Birks 1997). Earlier loss of snow cover already is occurring in some alpine areas, affecting plant growth and reproduction, with positive and negative consequences, depending on the species and the conditions (Klanderud and Birks 2003; Wheeler et al. 2015; Wipf et al. 2009). One snowbed community in the Swedish Scandes disappeared entirely within 30 y with the reduction of snow cover (Kullman 2005). Björk and Molau (2007) predicted that snowbed plant communities in Europe, where the duration of wintertime snow cover had declined three to five days per decade, would be invaded by shrubs and boreal species and that bryophytes and graminoids would be most negatively impacted by climate change.

Alpine communities are sensitive not only to warming but also to atmospheric nitrogen deposition and changes in the amount and timing of precipitation. In other parts of the world, changes in these conditions as well as warming have been linked to the movement of trees to higher elevations (Harsch et al. 2009; Kullman 2002), establishment of low elevation species at high elevation sites (Klanderud and Birks 2003, Walther et al 2005) and shifts in alpine community composition (Erschbamer et al. 2009; Gottfried et al. 2012; Jägerbrand et al. 2009; Klanderud 2008; Wilson and Nilsson 2009). Tundra bryophytes have been found to be highly sensitive to the combination of warming and fertilization, although responses vary somewhat among species (Jägerbrand et al. 2011), and bryophytes have recently been used extensively as climate change monitors (Tuba et al. 2011). There is no evidence that snowbeds in the northeastern U.S. are declining because of changes in climate. Nevertheless, because of the small area that snowbeds occupy, the unusual conditions they provide and the threats snowbeds are known to face, researchers with experience in alpine areas of northeastern North America recently indicated that, among all the questions that deserve additional work, research on snowbed communities is needed most urgently (Capers et al. 2013).

Snowbeds have long attracted the attention of botanists. Harshberger (1929) cited a large number of botanists and ecologists, particularly in the Swiss Alps but also in Scandinavia, who studied the flora of “snow patches” (sneetfalchen), starting with Wahlenberg in 1812 and continuing through the 19th century and early in the 20th. Harshberger (1929) was himself the first to publish on snowbed communities of Mount Washington, suggesting, “It could well repay an ecologist to investigate in detail the associations of vegetation with the snow that lingers ... and the relative length of the growing season.” Antevs (1932) was the first to classify Mount Washington alpine communities, describing two “heath meadows” that correspond to snowbed communities. Important later work on snowbeds in the Presidential Range was done by Bliss (1963) and Harries (1965), who also studied alpine soils in the area. More recent classifications of alpine vegetation have been done by Sperduto and Cogbill (1999), Kimball and Weihrauch (2000), Sardinero (2000), Sperduto and Kimball (2011) and Sperduto and Nichols (2012).

Whereas some quantitative data are available from the early, largely descriptive papers, precise location information is not available for the studied snowbeds, so it is not possible to determine how communities have changed at particular locations (but see Sperduto and Nichols 2012). Furthermore, less detailed information has traditionally been recorded on abundance and frequency of bryophytes and lichens (Sperduto and Cogbill 1999; Sperduto and Nichols 2012), and they sometimes were ignored entirely (e.g. Sardinero 2000), although these groups are especially sensitive to changes in vascular plant abundance and to changes in temperature, timing and amount of precipitation and nitrogen deposition (Nash and Wirth 1988; Tuba et al. 2011). Because they often both retain water in summer and share certain species, snowbed (or snowbank, *sensu* Bliss 1963) communities sometimes have been combined with rill (streamside) communities in community classifications, but plants living along alpine streams are exposed to substantially different conditions than those in snowbeds, and these communities may be composed of different species, as explored by this paper.

We conducted surveys of snowbed and rill communities in the Alpine Garden on Mount Washington, New Hampshire, recording the presence and abundance of all vascular plants, bryophytes and lichens. We also recorded the order in which the snowbeds became free of snow because this may affect community composition (Bliss 1963; Billings and Bliss 1959). The snow protects plants during the winter from desiccation, extreme cold, wind-driven ice abrasion and the buildup of

damaging rime ice. Snowmelt also makes snowbed plants less vulnerable to the late-summer drought that often affects other alpine plants. However, most plants cannot begin growing until the snow melts, which does not occur until late June in some areas. The main purpose of our research was to provide quantitative data on vegetation, including bryophytes and lichens, in carefully located alpine snowbed and rill communities so these sites could be surveyed in the future to establish if they have changed as a result of changing environmental conditions.

MATERIALS AND METHODS

Mount Washington, at 1914 m, is the highest peak in the northeastern US. It is part of the Presidential Range, which has the largest expanse of alpine habitat in the eastern US (Bliss 1963; Kimball and Weihrauch 2000). The monthly mean temperature at the summit is below 0°C for every month from October through April, and the mean annual wind speed is 15.3 m s⁻¹, with sustained winter winds routinely reaching 50 m s⁻¹, gusting to more than 70 m s⁻¹ (Grant et al. 2005). The depth to which snow accumulates in snowbeds is determined by wind direction, slope, aspect and the concavity of the topography (Antevs 1932; Billings 1974; Bliss 1963; Kimball and Weihrauch 2000). Because the prevailing winds are from the northwest in the winter on Mount Washington, snow accumulates most deeply on the east and southeast sides of the mountain (Bliss 1963). We surveyed nine snowbed and rill communities in the Alpine Garden (Figure 1), a 100-acre area on the east side of the summit at 1600 to 1650 m that is managed as a Research Natural Area by the US Forest Service (Brackley and Kacprzyński 1989).

Snow lasting through the winter typically occurs on high-elevation areas of Mount Washington from early November until late April or early May (Harries 1965), but high winds often blow the snow off the summit and exposed ridges, depositing it on snowbeds, other areas of the Alpine Garden and ravines on the eastern side of the mountain. Snowbeds melt out in May and June (Bliss 1966), although snow sometimes remained into July at least historically (Harries 1965). The order in which snowbeds melt out is similar from year to year although the exact date on which the last snow disappears at a particular location varies with conditions, including how much snow falls each winter (Bliss 1966). The date of first snow is now significantly later in the fall and the last snow is earlier in the spring than in 1935, but the

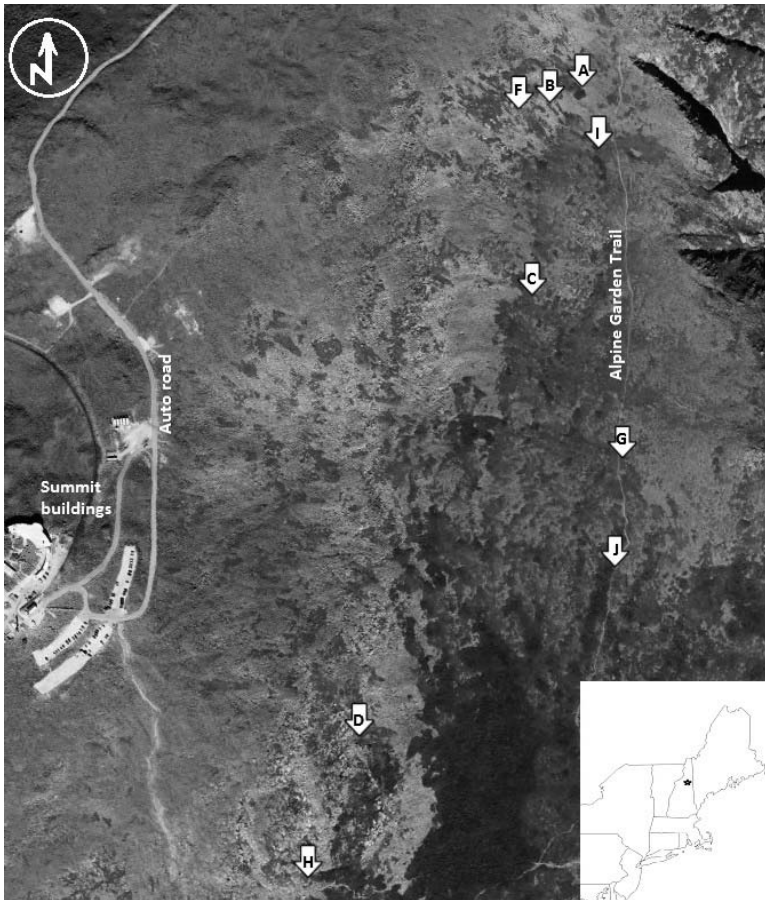


Figure 1. The satellite image shows the summit of Mount Washington, with the weather observatory buildings on the west and the Auto Road approaching the summit from the north. The Alpine Garden is on the eastern half of the image, with the Alpine Garden Trail running through it from north to south. The nine surveyed communities are identified by letter. The most easterly (I, G, J) are in a relatively flat area that is slightly lower than those to their west. These three have permanent water running through them and are rill communities, as is Site C; the other five are snowbed communities, where snow remains later in the spring than elsewhere in the alpine.

period of continuous snow cover, on average, has not changed (Seidel et al. 2009).

Rill communities were identified by the presence of running water in them. Snowbed communities were identified in 2012 by the presence of

indicator species (Slack and Bell 2014). We returned in subsequent years (April, May and June 2013, May and June 2014 and May and June 2015) to confirm that snow remained in the snowbed sites longer than in surrounding areas and to record when the last snow melted in all nine sites. Seven surveys were conducted in late June 2012, one in early September 2012 and one in early June 2013. Three sites were near the Alpine Garden Trail and six were somewhat higher, near or on the east side of the summit cone (Figure 1). In each site, we established at least one transect composed of 1 m² quadrats (a minimum of 10 quadrats in each site), on alternating sides of a 10 m line, following the longest dimension of the snowbed or rill from one end to the other. In each quadrat, we recorded all vascular plants, bryophytes and lichens present and estimated the percent cover of each species. We summed these values across species to calculate total cover of vascular plants, bryophytes and lichens—values that often exceeded 100% cover because the plants often overlap in the quadrats. We also estimated the percent of each quadrat covered by rock and bare ground. Some bryophytes and lichens could not be identified in the field, and small samples of those were collected for identification later. Lichens occurring only on large rocks (felsenmeer) were excluded from the analysis because they were not considered distinctive of snowbed and rill communities. The location of each transect was recorded with a GPS unit (Garmin GPS Map 60, Olathe KS).

We used ordination (Detrended Correspondence Analysis, DCA; Hill and Gauch 1980) executed in PC-ORD (McCune and Mefford 1997) to characterize variation among the sites and to assess the correspondence between the sites and the order in which snow melted in the spring. In preparing data for ordinations, we calculated relative abundance values for each species in each quadrat and then computed mean relative abundance values for each species in the nine sites. These mean values were then entered in the ordination. We also calculated separate frequency values for each species in each site—the proportion of quadrats in each site in which a species occurred—and used those data in separate ordinations. Abundance and frequency are distinct but complementary components of species' distributions, measuring in different ways the importance of individual species in a community (Canham and Thomas 2010). Taxonomy follows Haines (2011) for vascular plants, the Tropicos database (Tropicos.org 2016) for bryophytes and Species Fungorum (speciesfungorum.org 2016) for lichens. We analyzed differences in species richness and abundance in quadrats with t-tests and used correlation between abundance and species richness of different taxonomic groups to look for evidence of

competition, using Systat (Version 7.0, Systat Software, San José, CA) for all statistical analyses. We used EstimateS (Colwell 2013) to calculate the Sørensen similarity index in evaluating differences in species composition among the nine sites. The abundance and frequency data for the nine sites, plus the GPS coordinates of the sites and numerical results of the ordinations have been deposited for long-term storage in an archive maintained by the University of Connecticut; they can be accessed at (<http://hdl.handle.net/11134/20003:1301>).

RESULTS

The order of melt-out in our sites was consistent from year to year, although the exact melt-out date varied somewhat. In 2013, the year we made three visits, three rill sites (G, I, and J) and Site C were free of snow by late May. Snowbeds A, B, D, F and H were still snow-covered in late May, but A, B and H were free of snow by June 8 that year. Some snow remained in F, and snow was more than 1 m deep in D on that date and it did not completely melt until mid- to late-June. Site D, which was high on the east-facing summit cone, was consistently the last place where snow remained on the east side of Mount Washington.

The abundance (Figure 2) and frequency (Figure 3) ordinations both identified a single informative axis, and both separated snowbed communities from rill communities along that axis. However, this axis was apparently unrelated to the date of snow-melt. Site C, which we had tentatively identified as a snowbed, was grouped with rill communities in both ordinations, based on the frequency and abundance of the species occurring there. We found in late spring 2015 that Site C actually lies on the same small stream that flows through rill G, although C is upstream and apparently has flowing water only early in the season, when snow is melting. It is a transitional community, containing several plants found only in snowbeds (*Chamaepericlymenum canadensis*, *Lysimachia borealis* and *Vaccinium cespitosum*) but also several species found only in rills (*Salix uva-ursi*, *Campanula rotundifolia* and *Bistorta vivipara*). Because the ordinations placed Site C with other rill communities, based on its similar community composition, we treated it as a rill in all subsequent analyses. The first axis of the abundance ordination captured 52% of the among-site variation, compared with 77% in the frequency ordination. The ordinations confirmed that the constituents of the rill communities were distinctly different from those in the snowbeds, placing them at opposite ends of Axis 1.

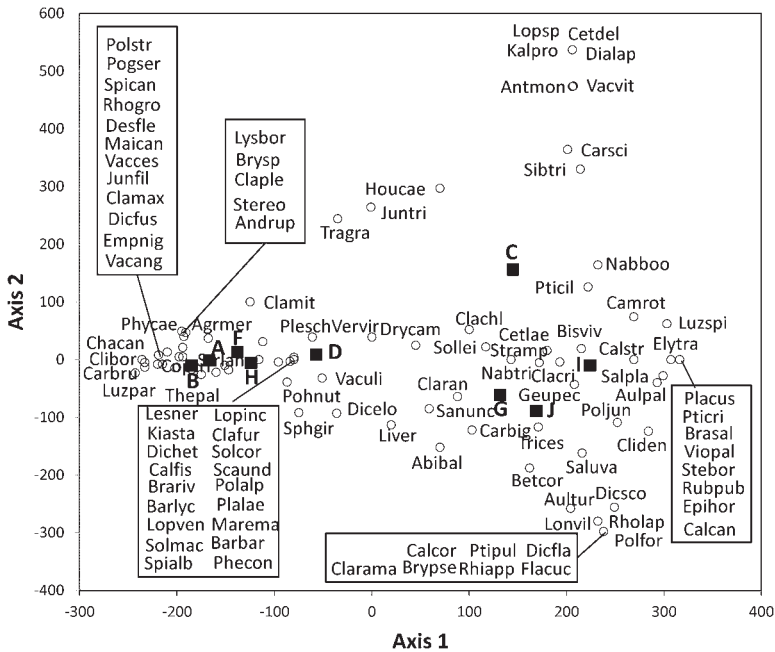


Figure 2. An ordination based on relative abundance data for the 54 vascular plant species, 42 bryophytes and 13 lichens found in nine alpine sites (five snowbeds and four rills—G, J, I and C). The nine sites are shown with solid squares and the centroids for species are shown with open circles. Abbreviations for species combine the first three letters of the genus and the first three of the specific epithet. VASCULAR PLANTS are: Abibal, *Abies balsamea*; Agrmer, *Agrostis mertensii*; Antmon, *Anthoxanthum monticola*; Betcor, *Betula cordifolia*; Bisviv, *Bistorta vivipara*; Calcan, *Calamagrostis canadensis*; Camrot, *Campanula rotundifolia*; Carbig, *Carex bigelowii*; Carbru, *C. brunscens*; Clabor, *Clintonia borealis*; Coptri, *Coptis trifolia*; Chacan, *Chamaepericlymenum canadensis*; Desfle, *Deschampsia flexuosa*; Dialap, *Dianopsis lapponica*; Drycam, *Dryopteris campyloptera*; Elybra, *Elymus brachycaulus*; Empnig, *Empetrum nigrum*; Epihor, *Epilobium hornemanii*; Geupec, *Geum pecki*; Houcae, *Houstonia caerulea*; Junfil, *Juncus filiformis*; Juntri, *J. trifidus*; Lonvil, *Lonicera villosa*; Lysbor, *Lysimachia borealis*; Kalpro, *Kalmia procumbens*; Luzpar, *Luzula parviflora*; Luzspi, *L. spicata*; Maican, *Maianthemum canadense*; Nabboo, *Nabalus boottii*; Nabtri, *N. trifoliatus*; Phecon, *Phegopteris connectilis*; Rholap, *R. lapponicum*; Rubpub, *Rubus pubescens*; Salpla, *Salix planifolia*; Saluva, *S. uva-ursi*; Sibtri, *Sibbaldiopsis tridentata*; Sollei, *Solidago leiocarpa*; Solmac, *S. macrophylla*; Stebor, *Stellaria borealis*; Spican, *Spinulum canadense*; Spialb, *Spiraea alba* var. *latifolia*; Stramp, *Streptopus amplexifolius*; Strlan, *S. lanceolatus*; Thepal, *Thelypteris palustris*; Trices, *Trichophorum cespitosum*; Vacang, *Vaccinium angustifolium*; Vacces, *V. cespitosum*; Vaculi,

In surveys of the nine sites, we found 54 species of vascular plants in 26 families, 42 bryophyte taxa (30 mosses and 12 liverworts) in 20 families and 13 lichens in four families (Table 1). Bryophytes and lichens were generally less frequent than vascular plants. Seventy-eight percent of bryophytes and lichens occurred in only one or two of the nine sites, compared with 41% of vascular plants. Among vascular plants, 16 (30%) occurred in five or more sites, compared with eight bryophytes and lichens (15%). No quadrat had fewer than four vascular plants and one had 15 species. The maximum number of bryophytes and lichens in quadrats was eight (the maximum for bryophytes was eight and for lichens was four); more than 60% of quadrats had no lichens, compared with 15% with no bryophytes. The number of species varied widely among both snowbeds and rills, whether comparing among sites (Table 2) or by quadrat (Table 3), but the difference was statistically different only for lichens, which had more species in rills, on average (Table 3). Total cover of vascular plants was far higher than cover of bryophytes and lichens. Vascular plants covered the entire surface of the ground in 80% of quadrats (mean cover of $132 \pm 3.6\%$) overall, while bryophytes and lichens combined achieved 100% cover in only 1.4% of quadrats (mean cover of $26 \pm 2.4\%$) overall. We found no difference between snowbeds and

←

V. uliginosum; Vacvit, *V. vitis-idaea*; Vervir, *Veratrum viride*; Viopal, *Viola palustris*. BRYOPHYTES are: Andrup, *Andreaea rupestris*; Aulpal, *Aulacomnium palustre*; Aultur, *A. turgidum*; Barbar, *Barbilophozia barbata*; Barlyc, *Barbilophozia lycopodioides*; Brariv, *Brachythecium rivulare*; Brasal, *Brachythecium salebrosum*; Brypse, *Bryum pseudotriquetrum*; Brysp, *Bryum sp.*; Calcor, *Calliargon cordifolium*; Strstr, *C. straminium*; Calfis, *Calypogeia fissa*; Cliden, *Climacium dendroides*; Dichet, *Dicranella heteromalla*; Dicolo, *Dicranum elongatum*; Dicfla, *D. flagillare*; Dicfus, *D. fuscescens*; Dicsco, *D. scoparium*; Kiasta, *Kiaeria starkei*; Lesner, *Leskea nervosa*; Lopinc, *Lophozia incisa*; Lopven, *L. ventricosa*; Lopsp, *Lophozia sp.*; Marema, *Marsupella emarginata*; Placus, *Plagiomnium cuspidatum*; Plalae, *Plagiothecium laetum*; Plesch, *Pleurozium schreberi*; Pogser, *Pogonatum urnigerum*; Pohnut, *Pohlia nutans*; Polalp, *Polytrichastrum alpinum*; Polfor, *Polytrichastrum formosum*; Poljun, *P. juniperinum*; Polstr, *P. strictum*; Pticil, *Ptilidium ciliare*; Ptipul, *P. pulcherrimum*; Pticri, *Ptilium crista-castrensis*; Rhiapp, *Rhizomnium appalachianum*; Sanunc, *Sanionia uncinata*; Scaund, *Scapania undulata*; Solcor, *Solenostoma cordifolium*; Sphgir, *Sphagnum girgensohnii*; Liver, *unidentified liverwort*. LICHENS are: Cetlae, *Cetraria laevigata*; Cetdel, *Cetrariella delisei*; Clarama, *Cladonia amaurocraea*; Clachl, *C. chlorophaea*; Clacri, *C. crispata*; Clafur, *C. furcata*; Clamax, *C. maxima*; Clamit, *C. mitis*; Claple, *C. pleurota*; Claran, *C. rangiferina*; Flacuc, *Flavocetraria cucullata*; Stereo, *Stereocaulon sp.*; Tragra, *Trapeliopsis granulosa*.

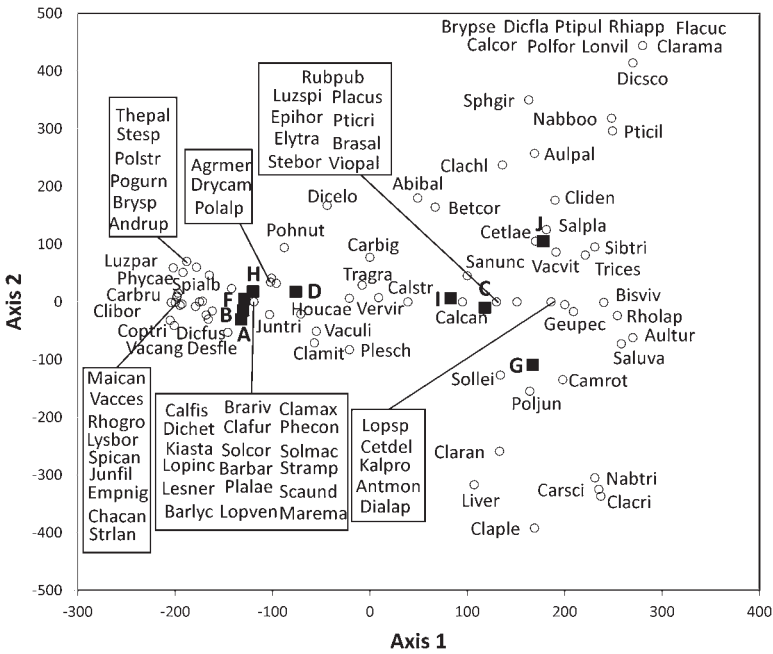


Figure 3. Ordination based on frequency of vascular plant, bryophytes and lichens in five snowbed and four rill communities on Mount Washington. Abbreviations are as in Figure 2.

rills in mean vascular plant abundance, but both bryophytes and lichens were more abundant in rills (Table 4).

The most widespread species in the nine sites were *Carex bigelowii*, which was the only species recorded in all of them, and *Vaccinium uliginosum*, in eight. The most widespread bryophytes were *Dicranum fuscescens*, *Pleurozium schreberi* and *Polytrichastrum alpinum*, and the most widespread lichen was *Cladonia rangiferina*. Each of these four was found in seven sites, including both snowbed and rill communities. Among the most abundant vascular plants were *Vaccinium cespitosum* (mean cover as high as 61% in the quadrats of Snowbed A) and *Agrostis mertensii* (at least 40% cover in four of 20 quadrats in Site F). *Geum peckii* had mean cover of 38% in Rill G. We found many cases in which a particular species was especially abundant only in one quadrat or one transect. *Salix planifolia*, for instance, was recorded in only three sites, but had 70–80% cover in four of the Rill I quadrats, whereas it was completely absent from three others. Widespread species did not occur everywhere and, where they occurred, they often were in low

Table 1. The number of vascular plant species, bryophytes and lichens is shown for each of the nine alpine sites surveyed, as well as the total species richness. The sites are arranged in the order of snowmelt, with those melting earliest on the left and latest on the right. G, I, J, and C are rill communities. The number in parentheses is the number of 1 m² quadrats on each site.

	G (n=10)	I (n=23)	J (n=10)	C (n=20)	A (n=10)	B (n=12)	H (n=10)	F (n=20)	D (n=20)
Vascular plants	16	26	19	27	20	15	22	20	20
Bryophytes	6	11	18	7	3	3	8	7	22
Lichens	4	3	5	7	4	2	2	5	1
Total	26	40	42	41	27	20	32	32	43

Table 2. Species richness (mean \pm SE) of vascular plants, bryophytes and lichens in 1 m² quadrats in snowbeds (n=72) and rills (n=63).

	Snowbeds	Rills	t	p
Vascular plants	8.88 \pm 0.26	8.94 \pm 0.27	-0.16	0.870
Bryophytes	2.28 \pm 0.18	2.57 \pm 0.24	-0.98	0.331
Lichens	0.36 \pm 0.09	0.86 \pm 0.13	-3.21	0.001

abundance. *Carex bigelowii* occurred in all nine sites, but even where it was most frequent (in Snowbed F, where it was recorded in 18 of 20 quadrats) cover never exceeded 10%. *Vaccinium uliginosum* was in eight of our nine sites, but even where it had the highest mean abundance (Rill G, where it covered 90–100% of the surface of the ground in two quadrats), it was absent from two quadrats and had only 5% cover in a third. Other widespread species were nowhere abundant. *Juncus trifidus*, for instance, was recorded in seven of nine sites but in fewer than half of the quadrats in those sites, and it typically had cover of 5% or less. Among bryophytes, the greatest abundance was recorded for *Brachythecium salebrosum*, which occurred in only one site (Rill I), where it achieved cover of 50% or greater in 11 of 23 quadrats; and by *Dicranum fuscescens*, which had cover of 60% or greater in three of 12 Snowbed B quadrats. *Pleurozium schreberi* occurred in seven sites and 23 (17%) of all quadrats, but cover was as much as 10% in only one. *Polytrichastrum alpinum* occurred in seven sites and 49 quadrats (36%), with cover as much as 40–50% in five quadrats but typically it had only 5–10% cover where it occurred. *Cladonia rangiferina* was found in seven sites, including both rills and snowbeds; it had 10% cover in three quadrats though its abundance was typically lower.

The vascular plants with the strongest affinity for the snowbed communities were *Chamaepericlymenum canadense* and *Vaccinium cespitosum*, which appeared in all five snowbeds. Vascular plants with the strongest affinity for the early-melting rill communities were *Campanula rotundifolia*, *Anthoxanthum monticola*, *Nabalus trifoliata*, *Salix uva-ursi* and *Bistorta vivipara*; these occurred in all four of the rills but in none of the snowbeds. The bryophytes with the strongest affinity

Table 3. Abundance (mean percent cover \pm SE) of vascular plants, bryophytes and lichens in 1 m² quadrats in snowbeds (n=72) and rills (n=63).

	Snowbeds	Rills	t	p
Vascular plants	129.5 \pm 5.62	134.4 \pm 4.65	-0.67	0.502
Bryophytes	16.9 \pm 1.18	29.9 \pm 4.39	-2.66	0.009
Lichens	1.6 \pm 0.62	6.0 \pm 1.51	-2.64	0.010

for the snowbeds—those appearing on the negative end of Axis 1 in the ordinations—were *Dicranum fuscescens* and *Andreaea rupestris*, along with the lichens *Cladonia maxima* and *C. pleurota*. Species associated with rills were the bryophytes *Plagiomnium cuspidatum*, *Brachythecium salebrosum* and *Ptilium crista-castrensis*, as well as the lichens *Flavocetraria cucullata* and *Cladonia amaurocraea*. However, because of the generally low frequency of bryophytes and lichens, the affinity for snowbeds or rills in these groups was based in some cases on a single occurrence.

Although cover by vascular plants was high, it did not appear that any species was so abundant as to exclude other species. Although one-third of quadrats had a species with cover of 50% or more, the correlation between those maximum abundance values and species richness in quadrats was positive ($r=0.172$, $p=0.045$), combining all quadrats in our nine sites. Total vascular plant abundance and species richness in quadrats were also positively correlated ($r=0.43$, $p<0.001$). Vascular plant abundance and richness were negatively correlated with the number of bryophytes (but not lichens) in quadrats ($r=-0.22$, $p=0.01$, and $r=-0.15$, $p=0.03$, respectively). However, vascular plant abundance was not correlated with bryophyte/lichen abundance (which was positively correlated with bryophyte richness; $r=0.21$, $p=0.01$), suggesting that vascular plants are not excluding bryophytes but that vascular plant and bryophyte species have different environmental affinities. Mean Sørensen similarity among snowbeds (0.513) and among rills (0.555) was much higher than was similarity between snowbeds and rills (0.315; $F=30.008$, $p<0.001$).

DISCUSSION

Snowbeds are estimated to occur on less than one percent of the area above timber line, which marks the limit of closed canopy tree growth in the White Mountains' Presidential Range (Kimball and Weihrauch 2000). However our surveys found, as others have, that these communities include species not found elsewhere in the region's alpine habitat. Bliss (1963) estimated that 40% of snowbed species and 35% of rill species occurred above timberline only in these communities. Spurduto and Nichols (2012) documented 90 vascular plants from 28 herbaceous snowbank and rill plots from Mount Washington, including the Alpine Garden, Raymond Cataract, Oakes Gulf, and Tuckerman's Ravine. Thus these communities contribute disproportionately to the overall diversity of alpine areas in northeastern North America. We also found that, although abundance of bryophytes and

lichens is often low in snowbeds, as others have reported (Bliss 1963; Sperduto and Kimball 2011), species diversity can be quite high, making bryophytes and lichens important components of these communities, especially in terms of species richness. Finally, we showed that snowbed communities were distinctly different from rill communities. Although some species were shared, nearly 60% of the vascular plants and fully 70% of bryophytes and lichens occurred in one, but not the other community. Moreover, compared with snowbeds, rill community bryophyte abundance can be relatively high.

Bliss (1963) reported that snowbeds were composed of one group of species that were nearly ubiquitous in alpine habitats of the Northeast (e.g., *Carex bigelowii*, *Vaccinium uliginosum* and *Juncus trifidus*, which were present in nearly of all our sites), plus a second group of species found nowhere else in the alpine, including a number of boreal species typically found at lower elevations (*Lysimachia borealis*, *Veratrum viride* and *Clintonia borealis*, among others). Every species that Bliss listed as common in snowbeds occurred in ours as well. Our snowbed communities also resembled those of Sperduto and Kimball (2011) and Sperduto and Nichols (2012), whose classifications were among the few to list *Empetrum nigrum* as common and often abundant in snowbeds (their alpine heath snowbank community); we found the species in four of our snowbeds (and none of the rills). Many of the bryophytes we found also are widespread in the alpine and are not limited to snowbeds or rills, as is true of the lichen *Cladonia rangiferina*, which was found in seven sites, including both snowbeds and rills. Harries (1965) wrote that *C. rangiferina* did not occur in snowbeds in which the snow remained until late June or July and, indeed, this species was absent from our snowbed where snow remained latest in the growing season. As with the vascular plants, many of the mosses in the snowbeds and rills also are common boreal species, including *Pleurozium schreberi*, *Dicranum scoparium*, *D. fuscescens*, *Sanionia uncinatus*, and the liverwort *Ptilidium ciliare*.

A number of species previously identified as indicator species for snowbeds were present, but not frequent in our sites. *Phyllodoce caerulea* appeared to be limited to snowbeds where snow remained longest, as Bliss (1963) had suggested; it occurred only in our snowbeds that had the latest snow: site F, which had some snow on June 22, 2015 and site D, which still had snow at least 1 m deep on that date. *Harrimanella* (formerly *Cassiope*) *hypnoides* is sometimes listed as a snowbed plant, and it occurred just outside our site where snow melted latest, as well as in snowbeds at higher elevations on the summit cone, where there is long-lying snow, but on stony ground, not in the

snowbeds themselves. Sperduto and Nichols (2012) identified *Harri-manella* as a constituent of a heath snowbank community that occurs where soils are well drained. This suggests that soil type may be as important as elevation in determining which species are present in snowbanks, with herbaceous plants dominant in less well-drained sites where organic soil develops more fully. Sperduto and Nichols (2012) described five snowbed and rill communities, including three that were distinctly different from ours—the alpine heath snowbank, an alpine ravine shrub thicket, and a wooded subalpine bog/heath snowbank—that occur under different conditions. This is a useful reminder that our sites are representative of communities in the Alpine Garden but that snowbeds and rills outside that area may have somewhat different conditions and different constituents. It also helps explain why we did not find some species that were listed previously as common in snowbeds or rills. For instance, *Calamagrostis canadensis* was present in only one of our snowbeds, where it was not abundant, and in one rill community. Harries (1965) identified the species as important in snowbeds with the latest-lying snow and it was, in fact, in our snowbed where the snow melted last (Site D). It also is a nearly constant species in ravine snowbeds on Mount Washington (Sperduto and Nichols 2012), which we did not survey. Sperduto and Kimball (2011) reported that *Salix herbacea* is occasional in snowbeds, and the species does occur in snowbeds on the Great Gulf headwall (Slack and Capers, pers. obs.), but it did not occur in our Alpine Garden snowbeds. Variation in snowbed constituents exists in the larger region as well. Edinger et al. (2014) listed *Ribes glandulosum* as an indicator species for snowbeds in the Adirondacks, and Gawler and Cutko (2010) listed *Kalmia procumbens* as a characteristic species of Maine snowbeds. We found *Kalmia* in one snowbed, *Ribes* in none.

Our rill communities correspond most closely to the “herbaceous snowbank/rill” community of Sperduto and Nichols (2012), specifically to the tea-leaved willow variant and to the “moist alpine herb heath meadow” community. They reported that *Geum peckii* was abundant to dominant in such communities and, indeed, the species occurred in all four of our rills, and it was present in every quadrat in two of them. These communities are distinguished by the presence of *Campanula rotundifolia* and *Bistorta vivipara* (present in all four of our rills), plus *Nabalus boottii* and *Salix planifolia* (present in three). Bliss (1963) also identified a “streamside” community very similar to our rills, with *Geum*, *Salix uva-ursi* and *S. planifolia*, plus *Sibbaldiopsis tridentata* (found in all four of rills), *Trichophorum cespitosum* and *Vaccinium uliginosum* (both of which were present in three). Bliss reported that the

rill communities were small in area but had a lush, diverse plant community, best developed in the Alpine Garden, where we did our surveys. We found *Castilleja septentrionalis* in an extension of one of our rill communities below the Alpine Garden trail. The species is primarily found in the upper ravines. We also found additional bryophytes and lichens there, indicating that the rill communities deserve further study. It is not surprising that the composition of our snowbed and rill communities corresponded most closely to the classifications of Bliss (1963), Sperduto and Kimball (2011), Sperduto and Nichols (2012) and Sardinero (2000), because these classifications were based on research done, at least in part, in the Alpine Garden and elsewhere on Mount Washington.

Bliss (1963) reported that lichen cover averaged 23.9% in rills, compared with 1.7% snowbed communities. We found lichen cover to be low in both snowbeds and rills. Bliss identified *Cetraria islandica* as typical of rills, but this was almost certainly *C. laevigata*, also misidentified earlier as *C. islandica* in the Adirondacks. *Cetraria laevigata* had 70% cover in one rill quadrat and 30% in another, but lichen cover in rill quadrats was more typically less than 5%. Bryophytes, on the other hand, had more species per quadrat and were far more abundant in rills than in snowbeds. The difference in our findings from those of Bliss, in terms of lichen abundance in rills, may result from variation within these communities, as was identified by Sperduto and Nichols (2012). They found three variants of the “herbaceous snowbank/rill community,” including a tea-leaved willow variant that closely corresponds with two of our rill communities and which they reported had high bryophyte abundance (Sperduto and Nichols 2012).

In both snowbank and rill communities, unlike many other alpine communities on Mount Washington, there is almost complete vegetation cover, often with a bryophyte–lichen ground layer that retains moisture until late in the growing season. In this layer, the most important mosses are species in the Polytrichaceae, *Dicranum* species, *Aulacomnium* species and *Sanionia*. Among lichens, *Cladonia* species and *Cetraria laevigata*, especially under *Vaccinium* and other shrubs, occur frequently if not abundantly. Bryophytes and lichen species contribute to species richness on a different spatial scale than do the vascular plants. Bryophyte and lichen richness in quadrats was low in snowbeds (less so for bryophytes in rills), but the total number of species found in each of our nine sites was similar to vascular plant richness, and lichens and bryophytes combined exceeded vascular plant richness in two of the sites. Combining across all sites, we found slightly

more bryophyte and lichen species (55) than vascular plants (54). Bliss (1963) listed only one moss and two lichens in snowbed (“snowbank”) communities and four mosses and eight lichens in rill (“streamside”) communities. Harries (1965) described 15 mosses, 13 lichens and one liverwort in alpine communities, of which six mosses and the liverwort *Ptilidium ciliare* were described as “chionophilous,” or snow-loving; nearly all of these were in our snowbed sites. Bliss wrote (1963) that bryophytes and lichens were less important in snowbeds than elsewhere in the alpine, which we found not to be the case, at least in terms of species richness. Our study suggests that bryophytes, although not abundant, are quite diverse in snowbeds and even more so in rill communities.

Although our snowbed and rill communities were separated from each other along the principal axis of the ordination, this appeared to be unrelated to the timing of snowmelt. Nor were the sites arranged along an elevational gradient. Although the snowbed communities are clustered near each other in the ordinations, the latest-melting snowbeds appear to be slightly closer to the rills than are the early-melting snowbeds. Instead of snow-melt date, the gradient separating the sites may be related to moisture. Because they melt last, the late-melting snowbeds may retain moisture until later in the growing season than those that melt out earliest, possibly facilitating a somewhat different cohort of species to occur there. Within the Alpine Garden, it appears to be topography, including slope, depressions and the presence of large rocks and krummholz patches, that enables snowbeds to form (Billings 1974; Bliss 1963; Kimball and Weihrauch 2000). Whatever the conditions necessary for their formation, snowbed and rill communities are sufficiently unusual in the region—even where they occur, most of their species are neither widespread nor abundant—that they should be protected. The GPS unit we used will permit future researchers to locate the snowbeds and rills we surveyed (it is reliably accurate to within 5 m). As a result, species richness as well as the frequency and relative abundance of individual species can be determined for each of our snowbed and rill sites in future years. Quadrat-by-quadrat comparisons would not be possible because of variation in environmental conditions over very short distances, but these would not be necessary to establish general trends in changes in the communities that might then be associated with shifts in particular conditions.

The change in environmental conditions that is most threatening to snowbed and rill communities probably is warming, which could result in earlier snow melt, leaving plants exposed to damaging late-spring

frosts (Klanderud and Birks 2003; Sætersdal and Birks 1997) that could threaten the persistence of boreal species. These occur in the alpine only where protected through the winter by snow. Earlier melt-out also might produce greater late-season desiccation stress than plants now experience, causing changes in community composition and, especially, declines in bryophyte abundance and diversity. Species, including *Phyllodoce caerulea* and *Harrimanella hypnoides*, that occur only where the snow piles up deepest on the steep east slope of the summit cone, also may be vulnerable if the period of snow cover shortens. The rill species that may be most at risk are those that survive only in very moist conditions, such as *Veratrum*, *Epilobium*, *Campanula* and bryophytes in general. Two of the snowbed and rill species are rare already: *Geum peckii* occurs only in the White Mountains and in one Nova Scotia county, and *Nabalus boottii* is locally abundant on Mount Washington but endangered elsewhere in northern New England and the Adirondacks of New York. In addition, the moss *Aulacomnium turgidum*, which occurred in two of our rills, is primarily an Arctic species and is rare in the alpine of the Northeast. Although warming is a concern, its effects could be overcome in alpine areas by the increased wintertime precipitation that climate models predict for the region (Karl et al. 2009; Kunkel et al. 2013).

Warming is occurring already. The Earth's climate has warmed by about 0.6°C in the past 100 years, and most of that warming has come since 1970 (Walther et al. 2002). With greenhouse gas concentrations rising every year, mountainous areas in general are expected to continue warming globally, and those in the northern hemisphere are predicted to warm more than those at tropical or southern latitudes (Nogués-Bravo et al. 2007; Pauchauri and Reisinger 2007). Northern hemisphere snow cover extent has decreased by $7.5 \pm 3.5\%$ during March and April (Lemke et al. 2007) and, throughout higher latitudes, the snow-free period has increased three to six days each decade since 1972, primarily because of earlier melting in the spring (Dye 2002).

Evidence of change in response to changing climatic conditions already has been found among alpine plant communities in Europe and the western US. For instance, early snowmelt has been found to increase the number of alpine herb buds that were killed by late frosts, with implications for the species' fitness (Inouye 2008). Klanderud and Birks (2003) reported that species with narrow habitat requirements, including some snowbed species, had declined in a study on 23 of Norway's mountains since 1930, probably because of warming. In addition to warming, atmospheric nitrogen deposition has increased dramatically in the past 100 years, which has been shown to affect

vascular plant community composition in the historically N-limited alpine environments (Körner 2003; Theodose and Bowman 1997), and has led to declines in bryophytes (Jägerbrand et al. 2011; van der Wal et al. 2003; Walker et al. 2006) and lichens (Cornelissen et al. 2001; Fremstad et al. 2005). Northeastern mountains are also exposed to relatively high levels of ozone and acidic pollutants and these, along with nitrogen, could have especially damaging effects on bryophytes and lichens (Bjerke et al. 2011; Bobbink et al. 2003; Woolgrove and Woodin 1996), which may be declining in the region already (Robinson et al. 2010).

Few of the early alpine studies in northeastern mountains provided quantitative data on species' abundance or frequency, which limits our ability to establish whether these communities have changed (but see Capers and Stone 2011; Robinson et al. 2010). There is evidence that some alpine plants in the northeastern US. may have shifted flowering times less than low-elevation plants in response to warming and, that they may not, to this point, have been exposed to destructively colder temperatures while flowering (Kimball et al. 2014). In fact, it is far from certain that alpine plant communities in the region have been exposed to the warming known to be occurring at lower elevations. Seidel et al. (2009) showed that temperatures on the summit of Mount Washington have not risen as much as those at the base, apparently because the mountain is so high that the summit is exposed to different atmospheric conditions. Even if this is true on the summit of Mount Washington and in the Alpine Garden, it might not be true on other mountains with alpine communities in the White Mountains or even the Presidential Range, or in the high peaks of the Adirondacks where the alpine belt is narrower than on Mount Washington.

Human trampling and arrival of invasive species represent additional threats to vulnerable alpine communities in northeastern North America. Trampling and unofficial trail development have damaged plant communities in the White Mountains, even denuding a few peaks (Sperduto and Cogbill 1999). Trampling was the major factor in the near extirpation of Mount Washington's rarest alpine plant, *Potentilla robbinsiana* (Cogbill 1993). Dandelions (*Taraxacum officinale*) were found in snowbed communities above 1800 m on the upper cone of Mount Washington in 2014 (Bell 2015). Dandelions reached the summit area of Mount Washington at least 50 y ago. Harries (1965) found them in ruderal vegetation at about 1900 m, but they had not invaded any alpine communities at that time. The species had already become abundant in snowbeds and in one *Carex bigelowii* community when found in 2014; a removal program was begun in 2015. The species

has been present in the alpine area on Mount Moosilauke since at least 1993 (C. Cogbill, Harvard Forest, pers. comm.) and a dandelion population has persisted for at least 10 y around a former building site in the alpine area on Mount Marcy in the Adirondacks (J. Goren, Adirondack Mountain Club, pers. comm.). The same dandelion species is known to be invasive in alpine areas of Japan, Chile, the French Alps and Denali National Park (Dunsmore 2008; Matsumoto et al. 2011; Quiroz et al. 2009).

This is the first vegetation analysis of the alpine snowbed and rill communities of Mount Washington that includes all the vascular plants, bryophytes and lichens. We found that bryophytes and lichens, contrary to some previous reports, are an important component of these two communities. This is particularly true of bryophytes, in terms of diversity. We found nearly as many bryophyte species as vascular plants in our snowbed communities and found many more lichens than had been previously reported. Bryophytes, especially mosses, were quite abundant in some quadrats, forming a ground layer in which some of the vascular plants were growing. Diversity of vascular plants was high in both the snowbed and rill communities. Both retained moisture longer into the summer than most other alpine communities, snowbeds because of the long-lying snow and rills because of the proximity of a stream. Many common boreal species that are absent from other alpine communities are able to survive in snowbeds, largely because of the protection from frost and ice damage in the spring. Few of these are regularly present in the rill communities. We found snowbeds and rills to have separate plant communities, though they shared some species.

The main purpose of this vegetation study of these two vulnerable alpine communities was to provide baseline information so future changes in diversity and abundance of species can be established. Snow cover is especially important for snowbed communities, and species of vascular plants and bryophytes have been lost from these sites in Europe as temperatures have increased and the duration of snow cover has declined. Both snowbed and rill communities should be monitored in the future.

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APPENDIX

Mean abundance (percent cover) in quadrats and frequency values (the number of quadrats as a proportion of all quadrats) are shown for each species in nine surveyed alpine sites: five snowbeds and four rills. The sites are arranged in the order of snowmelt with the earliest on the left and latest on the right.

	Rills				Snowbeds				
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20
VASCULAR PLANTS									
ASTERACEAE									
<i>Nabalus boottii</i> DC.	—	0.26/0.09	0.60/0.60	1.05/0.15	—	—	—	—	—
<i>Nabalus trifoliatius</i> Cass.	2.10/0.90	0.04/0.04	0.10/0.10	0.85/0.25	—	—	—	—	0.25/0.05
<i>Solidago leiocarpa</i> DC.	2.00/0.80	1.52/0.26	0.30/0.30	1.40/0.35	—	0.58/0.25	1.00/0.20	—	0.25/0.05
<i>Solidago macrophylla</i> Pursh	—	11.05/0.65	0.50/0.10	—	2.30/0.60	9.58/0.92	2.00/0.40	12.50/0.95	17.75/0.95
BETULACEAE									
<i>Betula cordifolia</i> Regel	—	—	2.00/0.10	0.25/0.05	0.50/0.10	—	—	—	—
CAMPANULACEAE									
<i>Campanula rotundifolia</i> L.	1.80/0.60	8.57/0.57	0.10/0.10	2.30/0.65	—	—	—	—	—
CAPRIFOLIACEAE									
<i>Lonicera villosa</i> (Michx.) J.A. Schultes	—	—	4.00/0.40	—	—	—	—	—	—
CARYOPHYLLACEAE									
<i>Stellaria borealis</i> Bigelow	—	11.61/0.70	—	—	—	—	—	—	—
CORNACEAE									
<i>Chamaeperichlymenum canadense</i> (L.) Aschers. & Graebn.	—	—	—	0.55/0.15	7.00/1.00	6.67/0.92	1.10/0.70	3.40/0.70	0.95/0.35
CYPERACEAE									

APPENDIX Continued.

	Rills						Snowbeds					
	G n=10	I n=23	J n=10	C n=20	A n=10	D n=20	B n=12	H n=10	F n=20	D n=20		
<i>Carex bigelowii</i> Torr. ex Schwein.	2.60/0.30	0.57/0.22	28.0/1.00	4.50/0.60	0.50/0.10	0.58/0.25	4.20/0.90	3.80/0.90	5.65/0.65			
<i>Carex brunnescens</i> (Pers.) Poit.	-	-	-	-	-	0.08/0.08	0.50/0.10	0.05/0.05	-			
<i>Carex scirpoidea</i> Michx.	6.30/0.90	-	-	23.25/0.50	-	-	-	-	-			
<i>Trichophorum cespitosum</i> (L.) Hartman	6.00/0.50	-	13.6/0.90	4.25/0.25	6.00/0.10	-	-	0.05/0.05	-			
DIAPENSIACEAE												
<i>Diapensia lapponica</i> L.	-	-	-	0.25/0.05	-	-	-	-	-			
DRYOPTERIDACEAE												
<i>Dryopteris campyloptera</i> (Kunze) Clarkson	-	0.05/0.04	-	-	-	-	-	0.75/0.10	-			
ERICACEAE												
<i>Empetrum nigrum</i> L.	-	-	-	-	16.00/0.40	1.67/0.08	5.50/0.40	0.10/0.05	-			
<i>Kalmia procumbens</i> (L.) Gift, Kron & P.F. Stevens ex Galasso et al.	-	-	-	2.50/0.05	-	-	-	-	-			
<i>Phylodoce caerulea</i> (L.) Bab.	-	-	-	-	-	-	-	4.00/0.35	1.00/0.05			
<i>Rhododendron groenlandicum</i> (Oeder) Kron & Judd	-	-	-	-	4.20/0.90	-	4.90/0.80	-	-			
<i>Rhododendron lapponicum</i> (L.) Wahlb.	0.50/0.10	-	3.00/0.10	0.05/0.05	-	-	-	-	-			
<i>Vaccinium angustifolium</i> Ait.	-	-	-	-	-	47.50/1.00	10.00/0.50	-	-			

APPENDIX Continued.

	Rills					Snowbeds				
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
<i>Vaccinium cespitosum</i> Michx.	—	—	—	3.75/0.20	61.00/1.00	16.75/0.92	17.00/0.90	44.50/1.00	9.55/0.50	
<i>Vaccinium uliginosum</i> L.	39.50/0.80	—	9.10/0.40	13.50/0.35	25.60/0.90	32.92/0.92	31.00/0.90	16.55/0.50	0.75/0.10	
<i>Vaccinium vitis-idaea</i> L.	0.10/0.10	—	2.10/0.40	26.05/0.95	—	—	0.10/0.10	—	—	
JUNCACEAE										
<i>Juncus filiformis</i> L.	—	—	—	—	0.50/0.10	—	—	0.25/0.05	—	
<i>Juncus trifidus</i> L.	0.10/0.10	—	—	4.15/0.40	0.30/0.20	0.17/0.17	0.10/0.10	2.95/0.55	0.25/0.05	
<i>Luzula parviflora</i> (Ehrh.) Desv.	—	—	—	—	—	—	0.10/0.10	—	—	
<i>Luzula spicata</i> (L.) DC.	—	6.43/0.43	—	0.90/0.25	—	—	—	—	—	
LILIACEAE										
<i>Clintonia borealis</i> (Ait.) Raf.	—	—	—	—	4.70/0.90	8.42/0.92	13.10/0.60	17.30/0.90	1.40/0.30	
<i>Streptopus amplexifolius</i> (L.) DC.	—	0.22/0.04	—	—	0.10/0.10	—	—	—	—	
<i>Streptopus lanceolatus</i> (Ait.) Reveal	—	—	—	—	0.60/0.20	—	—	—	1.05/0.20	
LYCOPODIACEAE										
<i>Spinulum canadense</i> (Ness.) A. Haines	—	—	—	—	2.40/0.80	—	1.10/0.30	0.05/0.05	—	
MELANTHIACEAE										
<i>Veratrum viride</i> Ait.	—	9.35/0.52	—	3.65/0.55	—	—	1.00/0.20	0.50/0.05	21.50/0.85	
MYRSINACEAE										
<i>Lysimachia borealis</i> (Raf.) U. Manns & A. Anderb.	—	—	—	0.10/0.10	0.20/0.20	0.33/0.33	0.20/0.20	1.05/0.45	—	

APPENDIX Continued.

	Rills						Snowbeds			
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
ONAGRACEAE										
<i>Epilobium hornemannii</i> Reichenb.	-	6.29/0.70	-	-	-	-	-	-	-	
PINACEAE										
<i>Abies balsamea</i> (L.) P. Mill.	-	0.65/0.09	2.60/0.30	-	2.10/0.30	-	-	-	-	
POACEAE										
<i>Agrostis mertensii</i> Trin.	-	3.39/0.39	-	4.35/0.35	-	-	24.00/0.90	23.50/1.00	21.00/0.95	
<i>Anthoxanthum monticola</i> (Bigelow) Y. Schouten & Veldkamp	0.10/0.10	0.04/0.04	0.10/0.10	2.45/0.80	-	-	-	-	-	
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	-	7.78/0.61	-	-	-	-	-	-	0.10/0.10	
<i>Deschampsia flexuosa</i> (L.) Trin.	-	1.74/0.43	-	-	28.5/1.00	33.5/1.00	-	-	-	
<i>Elymus trachycaulus</i> (Link) Gould ex Shimmers	-	1.78/0.09	-	-	-	-	-	-	-	
POLYGONACEAE										
<i>Bistorta vivipara</i> (L.) Delarbre	4.70/0.80	0.43/0.26	5.80/0.90	6.75/0.45	-	-	-	-	-	
RANUNCULACEAE										
<i>Coptis trifoliata</i> (L.) Salisb.	0.10/0.10	0.52/0.17	-	-	1.30/0.90	0.75/0.75	1.80/0.60	0.60/0.60	-	
ROSACEAE										
<i>Geum peckii</i> Pursh	37.50/1.00	4.30/0.26	26.00/1.00	23.50/0.90	-	-	-	-	1.55/0.25	

APPENDIX Continued.

	Rills						Snowbeds			
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
<i>Rubus pubescens</i> Raf.	—	5.27/0.30	—	—	—	—	—	—	—	
<i>Sibbaldopsis tridentata</i> (Ait.) Rydb.	0.30/0.30	0.28/0.04	2.10/0.80	7.30/1.00	—	—	—	—	—	
<i>Spiraea alba</i> var. <i>latifolia</i> (Ait.) Dippel	—	—	—	—	—	—	0.50/0.10	—	1.55/0.20	
RUBIACEAE										
<i>Houstonia caerulea</i> L.	—	—	—	3.10/0.30	—	—	—	0.25/0.10	1.25/0.45	
RUSCACEAE										
<i>Maitantherum canadense</i> Desf.	—	—	—	—	4.30/0.40	1.92/0.92	2.10/0.40	3.20/1.00	1.40/0.35	
SALICACEAE										
<i>Salix planifolia</i> Pursh	—	34.47/0.61	6.00/0.30	1.50/0.15	—	—	—	—	—	
<i>Salix uva-ursi</i> Pursh	28.50/1.00	3.04/0.09	20.00/0.80	5.50/0.15	—	—	—	—	—	
THELYPTERIDACEAE										
<i>Phegopteris connectilis</i> (Michx.) Watt	—	—	—	—	—	—	—	—	0.05/0.05	
<i>Thelypteris palustris</i> Schott	—	—	—	—	—	—	3.00/0.30	—	0.60/0.15	
VIOLACEAE										
<i>Viola palustris</i> L.	—	1.30/0.39	—	—	—	—	—	—	—	
BRYOPHYTES										
AMBLYSTEGIACEAE										
<i>Calliergon cordifolium</i> (Hedw.) Kindb.	—	—	0.10/0.10	—	—	—	—	—	—	

APPENDIX Continued.

	Rills						Snowbeds			
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
<i>Santonia uncinata</i> (Hedw.) Loeske	5.60/0.30	0.65/0.13	0.90/0.50	0.50/0.05	-	-	-	0.05/0.05	5.25/0.60	
<i>Straminergon stramineum</i> (Dicks. ex Brid.) Hedenäs	-	0.91/0.17	-	-	-	-	-	-	0.10/0.10	
ANASTROPHYLLACEAE										
<i>Barbilophozia barbata</i> (Schreb.) Loeske	-	-	-	-	-	-	-	-	0.05/0.05	
<i>Barbilophozia lycopodioides</i> (Wallr.) Loeske	-	-	-	-	-	-	-	-	0.10/0.10	
ANDREAEACEAE										
<i>Andreaea rupestris</i> Hedw.	-	-	-	-	-	-	-	0.20/0.20	-	
AULACOMNIACEAE										
<i>Aulacomnium palustre</i> (Hedw.) Schwägr.	-	3.41/0.22	0.40/0.40	-	-	-	0.10/0.10	-	-	
<i>Aulacomnium turgidum</i> (Wahlenb.) Schwägr.	11.70/0.80	-	5.40/0.70	-	-	-	-	-	-	
BRACHYTHECIACEAE										
<i>Brachythecium rivulare</i> Schimp.	-	-	-	-	-	-	-	-	0.05/0.05	
<i>Brachythecium salebrosum</i> (Hoffm. ex F. Weber & D. Mohr) Schimp.	-	33.52/0.61	-	-	-	-	-	-	-	
BRYACEAE										

	APPENDIX Continued.											
	Rills						Snowbeds					
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20			
<i>Bryum pseudoitriquetrum</i> (Hedw.) G. Gaertn., B. Mey. & Scherb.	—	—	0.10/0.10	—	—	—	—	—	—	—	—	—
<i>Bryum</i> sp.	—	—	—	—	—	—	—	0.10/0.10	—	—	—	—
<i>Pohlia nutans</i> (Hedw.) Lindb.	—	—	0.20/0.20	—	—	—	0.90/0.50	0.05/0.05	0.60/0.60	—	—	—
CALYPOGEACEAE												
<i>Calyptogeia fissa</i> (L.) Raddi	—	—	—	—	—	—	—	—	—	—	—	0.05/0.05
CLIMACIACEAE												
<i>Climacium dendroides</i> (Hedw.) F. Weber & D. Mohr	—	1.39/0.30	0.60/0.20	—	—	—	—	—	—	—	—	—
DICRANACEAE												
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	—	—	—	—	—	—	—	—	—	—	—	0.05/0.05
<i>Dicranum elongatum</i> Schleich. ex Schwägr.	—	—	0.10/0.10	—	—	—	0.20/0.20	—	—	—	—	0.05/0.05
<i>Dicranum flagellare</i> Hedw.	—	—	0.10/0.10	—	—	—	—	—	—	—	—	—
<i>Dicranum fuscescens</i> Turner	0.50/0.10	—	—	0.15/0.15	15.7/0.90	26.75/0.92	0.80/0.40	5.60/0.65	-0.40/0.20	—	—	—
<i>Dicranum scoparium</i> Hedw.	—	0.22/0.04	1.40/0.60	—	—	—	—	—	—	—	—	—
<i>Kiaeria starkei</i> (F. Weber & D. Mohr) I. Hagen	—	—	—	—	—	—	—	—	—	—	—	0.10/0.10
GYMNOMITRIACEAE												

APPENDIX Continued.

	Rills						Snowbeds			
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
SPHAGNACEAE										
<i>Sphagnum girgensohnii</i>	-	-	4.00/0.30	-	-	-	1.10/0.10	-	-	
Russow										
Unidentified liverwort	0.10/0.10	-	-	-	-	-	-	0.05/0.05	-	
LICHENS										
CLADONIAEAE										
<i>Cladonia amaurocraea</i>	-	-	0.20	-	-	-	-	-	-	
(Flörke) Schaer.										
<i>Cladonia chlorophaea</i> (Flörke ex Sommerf.) Spreng.	-	-	0.10	0.05	-	-	-	0.05	-	
<i>Cladonia crispata</i> (Ach.) Flot.	0.05	-	-	0.05	-	-	-	-	-	
<i>Cladonia furcata</i> (Huds.) Schrad.	-	-	-	-	-	-	-	-	0.05	
<i>Cladonia maxima</i> (Asahina) Ahti	-	-	-	-	0.20	-	-	-	-	
<i>Cladonia mitis</i> Sandst.	0.10	0.04	-	0.30	0.60	0.17	-	-	-	
<i>Cladonia pleurota</i> (Flörke) Schaer.	0.45	-	-	-	-	-	-	0.05	-	
<i>Cladonia rangiferina</i> (L.) Weber ex F.H. Wigg.	0.90	0.04	0.10	0.20	0.20	0.17	-	0.05	-	
PARMELIAEAE										
<i>Cetraria laevigata</i> Rass.	0.20	0.04	0.60	0.55	0.10	?	0.15	-	-	

APPENDIX Continued.

	Rills					Snowbeds				
	G n=10	I n=23	J n=10	C n=20	A n=10	B n=12	H n=10	F n=20	D n=20	
<i>Cetrariella delisei</i> (Bory ex Schaer.) Kärnefelt & A. Thell	-	-	-	0.05	-	-	-	-	-	
<i>Flavocetraria cucullata</i> (Bellardi) Kärnefelt & A. Thell	-	-	0.10	-	-	-	-	-	-	
STEREOCAULACEAE										
<i>Stereocaulon</i> sp.	-	-	-	-	-	-	-	0.10	-	
TRAPELIACEAE										
<i>Trapeliopsis granulosa</i> (Hoffm.) Lumbsch	-	-	-	0.05	-	-	-	0.05	-	