PLANT TRAITS AND COMMUNITY METRICS ACROSS A SNOWMELT GRADIENT AT ALPINE SNOWBANK SITES ON MT. WASHINGTON, NEW HAMPSHIRE

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ABSTRACT. In northeastern North America, alpine snowbank communities are rare plant assemblages that form in sheltered sites above treeline where late-lying snow provides insulation from late-season frosts and a longer-lasting source of water. We measured snowpack and studied community composition and plant traits at the species and community scales across the snowmelt gradient at snowbank sites on Mt. Washington, New Hampshire. We used nonmetric multidimensional scaling ordination and analysis of similarity to examine community composition across the snowmelt gradient and measured plant traits (height, leaf dry matter content, leaf area, and specific leaf area) of four focal species (Carex bigelowii, Chamaepericlymenum canadense, Clintonia borealis, and Maianthemum canadense). We assessed trait variability of the four focal species across the snowmelt gradient and evaluated community-weighted mean trait values and phenotypic plasticity between snowbank core and edge habitats. Analysis of similarity indicated that vascular plant diversity increased \( p < 0.001 \), lichen and bryophyte cover decreased \( p < 0.001; p < 0.025 \), and community-weighted mean leaf area increased \( p < 0.001 \) in the core of snowbank communities where melting dates were later. Analysis of similarity indicated that vascular plant communities varied significantly across the snowmelt gradient. The transition in community composition and trait values across the snowmelt gradient are indicative of changing environmental conditions and ecosystem functions, though more research is needed to determine the extent to which phenotypic plasticity
and ecotypic uniqueness influence trait expression of snowbank species. Genetic analysis may be necessary to evaluate population dynamics among isolated alpine communities, which may be vulnerable to climate change or displacement by exotic or lowland species.

Key words: adaptation, climate change, community-weighted mean, diversity, plasticity, snowbed

In northeastern North America, alpine snowbank (or snowbed) communities are rare plant assemblages that form in sheltered sites above treeline, such as ravine ledges, shallow depressions, and the lee of sheer rock faces, where late-lying snow provides insulation from late-season frosts and a longer-lasting source of water (Berend et al. 2020; Bliss 1963; Capers and Slack 2016). In these habitats, herbaceous understory species from lower-elevation northern hardwood or spruce-fir forest habitats are able to persist above treeline alongside arctic-alpine plants adapted to the harsh conditions (e.g., wind, ice, and ultraviolet radiation) characteristic of alpine areas (Billings and Bliss 1959). Of the many community types that exist in northeastern alpine areas, herbaceous snowbank communities are the most species rich (Bliss 1963), supporting several rare or threatened vascular plant species (e.g., Carex bigelowii Torr. ex Schwein., Geum peckii Pursh, Nabalus bootii DC., Vahlodia atropurpurea (Wahlenb.) Fr. ex Hartm., and Vaccinium cespitosum Michx.) (Sperduto and Nichols 2011). Snowbank sites may provide beneficial ecosystem services and functions to the greater landscape, such as shelter for flowering plants and insect pollinators, berries for birds, and high-quality browse for mammal and invertebrate herbivores (Björk and Molau 2007; McFarland 2003; McFarland et al. 2017; Zwinger and Willard 1996). They also harbor a diverse assortment of bryophytes (and lichens, to a lesser degree), which are important components of these ecosystems in terms of structure and function (Capers and Slack 2016; Dibble et al. 2009). In the Northeast, the most extensive alpine snowbank communities exist in the Presidential Range of the White Mountains, New Hampshire, and Mt. Katahdin, Maine (Kimball and Weihrauch 2000), but they can also be found in high-elevation areas of New York State (Carlson et al. 2011), Québec, and Labrador (Jones and Willey 2012).

In alpine environments, the strongest abiotic driver of species sorting is physical exposure to wind, cold, and ice—mediated predominantly by differential date of snowmelt (Choler 2005). The snowmelt gradient that develops in areas of late-lying snowpack acts as a selective filter, winnowing those species without a combination of adaptations for a specific
microhabitat (Keddy 1992). In regulating exposure of plants, buds, and seeds to physical stressors, the snowmelt gradient across alpine snowbank communities generates concentric rings of plant communities stratified based on snow tolerance and date of snowmelt (Billings and Bliss 1959; Zwinger and Willard 1996).

Environmental stress gradients can drive morphological variability in plants (Milla et al. 2008), and plant phenotypes are highly plastic in response to even steep environmental gradients such as sunlight, temperature, precipitation, soil moisture, nutrients, substrate, and elevation, (e.g., Choler 2005; Cornwell and Ackerly 2009; Fonseca et al. 2000; Guitton et al. 2016; Shimono et al. 2009; Wright et al. 2002). Thus, plant traits—measurable morphological, physiological, or phenological characteristics of an individual plant—may reflect evolutionary responses to environmental conditions and/or particular ecological strategies (Pérez-Harguindeguy et al. 2013; Wright et al. 2004). Traits are directly linked to plant fitness via their effects on growth, reproduction, and survival (Violle et al. 2007), and some commonly measured plant traits, such as leaf dry matter content (LDMC), leaf area, N/P content, specific leaf area (SLA), height, and seed mass are strongly related to establishment, persistence, and dispersal in alpine habitats (Choler 2005).

Trait-based approaches are emerging as a promising way to understand ecological mechanisms underlying species occurrence and establishment (Ali et al. 2017), and the snowmelt gradient in alpine snowbank communities makes them ideal systems to study the interactions of abiotic conditions on plant traits across multiple scales in the alpine environment. Studying trait variation at both the species and community levels can be valuable in understanding species-specific responses and interspecific interactions to environmental conditions, as well as the implications that variation may have for ecosystem functions (Lavorel and Garnier 2002). However, little is known about the trait structure of alpine snowbank communities in northeastern North America or their species-environment interactions involved in community assembly.

Community-weighted mean (CWM) trait values (Garnier et al. 2004) have been used to assess how environmental variables (such as snow cover) structure community composition, selecting for particular advantageous traits at the community, rather than individual or population, level. Shifts in CWM trait values should therefore reflect shifts in community structure or composition (Amatangelo et al. 2014), as well as community-level functional processes. Intraspecific variation in plant traits in response to environmental factors such as water availability (Jung et al. 2010), nutrients, and even herbivory can also be considerable.
and may reflect the resistance of plant community structures to changes in environmental conditions (Kichenin et al. 2013).

Trait plasticity may not be the only driver of individual or community-level trait differences, however. Because of the highly fragmented nature of alpine ecosystems, conspecific populations of alpine plants are often considerably separated by either space (long distance, topographic relief) or time (early/late snowmelt), and there is some evidence from around the world that this separation may lead to genetic divergence among substantially isolated metapopulations of plants (Cortés et al. 2014; Hirao and Kudo 2004; Stöcklin et al. 2009; Yamagishi et al. 2005). Trait differences among conspecifics derived from underlying genetic differences, therefore, could indicate that speciation is ongoing, probably due to constraints on connectivity to neighboring populations and/or local adaptation. Since most arctic-alpine species are ecotypically different from their congeners in the Arctic (Billings 1974; Mooney and Billings 1961), isolation and speciation may result in ecotypic differences between alpine and lowland populations of snowbank species or among populations of alpine species inhabiting adjacent peaks (or even microhabitats on a single peak). Currently, little is known about gene flow and connectivity between alpine snowbank habitats in northeastern North America and identifying alpine-adapted ecotypes of snowbank species could be important in terms of evolutionary or biogeographic history and conservation priorities for species or communities.

Alpine snowbank communities are particularly sensitive to environmental change (Björk and Molau 2007; Galen and Stanton 1995). Owing to both their rarity and reliance on specific environmental conditions, they are listed as “critically imperiled” (S1) by New York, New Hampshire, and Maine (Edinger et al. 2014; Gawler and Cutko 2010; Sperduto and Nichols 2011), and there is an immediate research need to better understand these communities (Capers et al. 2013). Monitoring community change in these habitats, then, may identify broader alpine community change due to climatic shifts. Recently, Sardinero (2000) and Capers and Slack (2016) cataloged community composition at snowbank sites on Mt. Washington, and the latter linked these metrics to snowmelt date. Berend et al. (2020) linked snowmelt timing to plant phenology at snowbank sites. Here, we extend the scope of that work to include systematic observations of snowmelt timing across a gradient at snowbank sites, as well as analysis of individual and community-level plant traits. Better understanding the links between snowmelt, trait plasticity, community
composition, and biogeography of snowbank species may be crucial to understanding their resilience under the threat of climate change.

The objectives of this study were four-fold: 1) evaluate community metrics (diversity and richness) in relation to snowmelt date at snowbank sites on Mt. Washington, New Hampshire; 2) document and describe community-level changes in four plant traits across the snowmelt gradient; 3) assess species-level (phenotypic) differences in traits of four herbaceous snowbank species across the snowmelt gradient; and 4) quantify and compare in situ inter- and intraspecific trait values (and their variability) of snowbank species between alpine and low-elevation sites.

MATERIALS AND METHODS

Mt. Washington (44.270° N, −71.3036° W) is the tallest peak in northeastern North America (1914 m) and lies within the White Mountain National Forest in northern New Hampshire (Figure 1, inset). Treeline is approximately 1500 m above sea level but varies considerably based on exposure and topography (Kimball and Weihrauch 2000). Mount Washington and the Presidential Range make up the largest area of alpine habitat in the eastern United States (1132 ha), but snowbank communities comprise < 1% of this total, at only 3 ha (Bliss 1963; Kimball and Weihrauch 2000).

Because prevailing winds are from the northwest, snow accumulates primarily on southeast-facing slopes, especially in topographic depressions. Many of these sites exist in the Alpine Garden Research Natural Area (AG), east of the summit and upslope (west) of the Alpine Garden foot trail. Several other sites exist near the Lakes of the Clouds (LC), 1.8 km southwest of the summit. In June 2016, we identified 15 contiguous snowbank sites across both areas (AG = 9, LC = 6) (Figure 1) by topography and the presence of indicator species (e.g., Deschampsia flexuosa (L.) Trin., Solidago macrophylla Bigelow, Vaccinium cespitosum Michx.; see Capers and Slack 2016; Sperduto and Nichols 2011) and marked the location of each with a handheld global positioning system unit (Garmin GPSMAP®64, Garmin Ltd., Olathe, Kansas; NAD 83 projection). Snowbank sites were the same as those reported in Berend et al. (2020) except for LC6, which was added for this study; see that article for further site descriptions. We also selected six low-elevation sites near the Appalachian Mountain Club’s Pinkham Notch Visitor Center (PNVC) where four focal snowbank species were abundant. These sites were used as low-elevation replicates for comparisons of trait values.
Figure 1. Map of snowbank study sites (white) on Mt. Washington, New Hampshire (summit 1914 m above sea level), and lowland trait collection sites (black, R1–R6) near the Pinkham Notch Visitor Center (PNVC, 619 m above sea level). Alpine sites are labeled based on general location: Alpine Garden (AG) and Lakes of the Clouds (LC). Inset map of Mt. Washington’s location in northern New Hampshire, U.S.A.
In June–July 2016, we established at least one transect at each site extending across the snowmelt/vegetation gradient from the center (or “core”) of the snowbank community to its margins in an adjacent community type. Larger sites could accommodate more than one transect, whereas smaller sites had only one (25 total transects). The core of each transect was determined based on literature descriptions of snowbed communities (Bliss 1963; Capers and Slack 2016; Sperduto and Nichols 2011) and local topography. We sought to follow the snowmelt gradient outward from the snowbeds across a smooth transition in plant communities to its margin (edge). Transects were 6, 9, or 12 m in length, depending on the length of the vegetation gradient and size of a site, and placed horizontally along the elevation contour (except for LC2, which was a flat site in the lee of a ledge; transects there were placed radially). At sites with more than one transect, cores were placed at least 3 m apart, and transects were oriented in alternating directions along the elevation contour (Figure 2), except when local topography or vegetation gradients were unsuitable, such as across rock scree. We placed a magnetic survey marker (SurvKap®, Tucson, Arizona) flush with the soil surface to mark the beginning (core) and end (edge) of each transect so they could be relocated beneath the snow, and along one transect at each site, we placed temperature dataloggers (OnSet HOBO® Pendant® UA-002-08, Bourne, Massachusetts) 10 cm below the soil surface (according to GLORIA protocols; Pauli et al. 2015) every 3 m along the transect, except AG3, LC5 (datalogger constraints), and LC6 (proximity to federally designated wilderness).

From June–July 2016, we collected community composition data every 3 m along each transect (coinciding with snow depth measurement locations) using a 1 m² quadrat. We identified to species and visually estimated percent cover of all vascular plants, bryophytes, and lichens (except saxicolous). Since most species found in these habitats are perennials, year-to-year composition was unlikely to change substantially. We calculated Shannon-Weiner diversity (H’) for each quadrat and used Pearson correlations to investigate the relationship between date of snowmelt and H’ and date of snowmelt and species richness (only core quadrats were used for these analyses).

In May 2017, we returned to study sites while still snow covered, relocated the transects using a magnetic survey locator (CST/Berger™, Watseka, Illinois), and temporarily marked the ends with stakes. We revisited each transect every 3–5 days and recorded snow depth measurements using an avalanche probe (maximum length 320 cm) at the quadrat locations until the entire transect was snow free. The first visit
day when a given quadrat was entirely snow free was recorded as its melt date. Because it lies in federally protected wilderness, no dataloggers or magnetic markers were left at site LC6; neither snow depth nor temperature was monitored there. We calculated the number of days between the melt of core and edge quadrats and the melt rate (see below) across the snowmelt gradient, averaged by site. Sites that were snow free upon first visit (AG3 and AG6) were excluded from analyses, and one additional site (AG4) was excluded from analyses owing to difficulty locating survey markers.

\[
\text{core melt date–edge melt date} \div \text{distance between core and edge}
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In July 2017, we collected specimens of 15 species (Supplemental material, Table S1) for trait analyses from the largest sites: AG4, AG7, AG8, LC1, and LC4. Using cover data from community composition sampling, we calculated the proportional number of vascular species to sample from each site and each transect end (core or edge) based on sample sizes needed for both CWM and focal species analyses and
collected specimens from either the core or edge accordingly. We collected specimens from a 1.5 m radius circle centered on the transect core or edge quadrat and used a random number generator to select individuals. For the CWM analyses, we collected 10 individuals each of the 15 most abundant species across all quadrats, based on rank-abundance curves created from community composition data. Traits of bryophytes and lichens were not measured.

To assess inter- and intraspecific trait variation across the snowmelt gradient at alpine sites, we selected five abundant snowbank species for closer analysis: *Carex bigelowii*, *Chamaepericlymenum canadense* (L.) Aschers. & Graebn., *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., and *Maianthemum canadense* Desf. We randomly collected three specimens of each species in the cores of each transect at the five alpine sites and spread collection across all transect cores for sites with more than one transect. We also collected a total of at least 15 specimens from edge quadrats—distributed proportionally across sites—for comparison.

We aimed to assess trait differences and variability between alpine and low-elevation (or lowland) source populations for four of those species: *Chamaepericlymenum canadense*, *Clintonia borealis*, *Coptis trifolia*, and *Maianthemum canadense*; *Carex bigelowii* was not included because it is not found below treeline. In addition to the collections from alpine site cores distributed across sites (dispersed strategy, three replicates each), we collected an additional 12 (concentrated strategy, total of 15 replicates) from the cores of one large site (AG7) to assess intrasite variability. We duplicated both the dispersed and concentrated collection procedures at six low-elevation sites near PNVC (sites R1–R6), with site R5 serving as the concentrated sampling site (Figure 1).

Upon random selection of an individual plant, we measured traits according to Pérez-Harguindeguy et al. (2013): two of the youngest, fully expanded, undamaged leaves (replicates) were clipped at the base of the lamina, blotted dry, and massed on a digital balance (wet weight). Only a single leaf blade was used for *Maianthemum canadense*, *Deschampsia flexuosa*, and *Juncus trifidus* L., while a short stem clipping (~3 cm, with leaves attached) was used for *Empetrum nigrum* L. because individual leaves were too small for processing. In cases when leaf mass was too small to register on the balance (< 0.001 g), as in some *Coptis trifolia* and *Vaccinium* spp., six leaves were used instead, and trait values were averaged as a single replicate. Leaves were scanned, and leaf area was found using ImageJ software (v. 1.51, National Institutes of Health, Bethesda, Maryland). Leaves were dried at 70 °C for 48 h, then
re-massed (dry weight). Leaf dry matter content (LDMC) was calculated as mg dry weight per g wet weight. Specific leaf area (SLA) for each replicate was calculated as leaf area in mm$^2$ per mg dry weight. Replicates were averaged to obtain a single leaf area, LDMC, and SLA value for each individual.

We created three categories of quadrat types for trait analyses: core (first quadrat of transects), transition (intermediate), and edge (last quadrat). All transition quadrats were averaged together within a transect for analyses and for sites with multiple transects, quadrat types were averaged within each other. We calculated species richness and diversity ($H'$) for each taxonomic group (vascular plants, bryophytes, and lichens) at core, transition, and edge quadrats.

We then performed two-sample t-tests to assess differences in richness and $H'$ by site location (AG vs. LC) for each taxonomic group. We used core quadrats for evaluation of vascular plants and bryophytes, but edge quadrats only for tests of lichens, as lichens were rarely found in core or transition quadrats.

Next, we performed a two-way analysis of variation (ANOVA) for each taxonomic group by quadrat type, blocked by site. Lichens had a large number of transects with zero values for diversity, richness, and cover across the gradient, so those cases were excluded for ANOVAs of that group. Bryophyte cover and lichen richness data were square-root transformed, and lichen cover data were log-transformed for normality. We used post-hoc Tukey’s tests for pairwise comparisons to find grouping information of significant ($p < 0.05$) ANOVAs. All ANOVAs were performed in Minitab (v. 18, Minitab, Inc., State College, Pennsylvania).

Using temperature data, we calculated cumulative growing degree days (GDD) for the 2017 study period (day of year 1–201) by the average method (see below); 0 °C was used as the threshold temperature, as in Berend et al. (2020). Snowmelt dates were averaged by quadrat at each site. We averaged abundance of all taxa by quadrat type (core/transition/edge) at each site and square-root transformed all cover data to down-weight highly abundant species (McCune et al. 2002).

\[
\text{daily maximum–daily minimum} \div 2
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We performed a nonmetric multidimensional scaling (nMDS) ordination using vascular plant community composition by quadrat type with a secondary matrix of environmental variables (melt date, GDD, and quadrat type). We did not include quadrats that crossed rock scree areas or the three sites where no dataloggers were present, as nMDS is intolerant of
missing values (McCune et al. 2002); repeating the analyses with those quadrats included did not yield major differences in grouping structure. We then performed a second nMDS ordination using core quadrat data only and all taxa types to look for general floristic similarities across sites. We eliminated rare species (as above) and converted data to presence/absence to reduce stress (McCune et al. 2002). All ordinations were performed in PC-Ord (v. 5.0, MjM Software, Gleneden Beach, Oregon), and Sorenson/Bray-Curtis was used as a distance measure. We used analysis of similarity (ANOSIM) to evaluate differences in community composition for each of the three similarity matrices used in ordinations; the ANOSIMs were performed in PRIMER (v. 6, PRIMER-E Ltd., Auckland, New Zealand).

We calculated mean trait values for the 15 most abundant/frequent vascular plant species collected (Supplemental material, Table S1). We calculated the CWM values for each measured trait (height, LDMC, leaf area, and SLA) as the average trait value for a particular quadrat type at a given site, weighted by the species’ abundance (Garnier et al. 2004), as indicated by cover. Using these data, we performed separate one-way ANOVAs for all four measured traits and post-hoc Tukey’s pairwise comparisons to find groupings of significant ANOVAs. Leaf area data were log-transformed for normality prior to analysis.

To assess trait change across the snowmelt gradient in the four focal snowbank species, we calculated average trait values by site of specimens taken from both core and edge quadrats and calculated the difference between them at each site (core minus edge). We then performed two-sample t-tests for each species to evaluate those differences. Traits were then averaged by site and we performed a two-sample t-test comparing the alpine and lowland values for each trait/species combination. We then performed paired (by species) t-tests of mean trait values between alpine to lowland source populations. We used a Holms-Bonferroni correction for family-wise error rate within each data set.

RESULTS

Core quadrats had consistently greater snow cover than edge quadrats throughout the monitoring period. In general, snowmelt was linear, with edge quadrats melting first and core quadrats melting last (Supplemental material, Figure S1). Mean melt rate was 1.0 ± 0.3 meters per day across the snowmelt gradient. Date of core exposure varied by site size and other (e.g., topographical) factors (see Berend et al. 2020). Difference in dates of snowmelt between core and edge quadrats ranged from 0 to 13 (mean = 7.81 ± 2.3) days and the rate of melt ranged from 0 to 2.25
(mean = 1.01 ± 0.2) m/day. At the largest sites, this meant that edge quadrats were exposed up to two weeks before core quadrats. However, there was no correlation between site size and number of days between edge and core exposure (r = 0.388, p = 0.213).

Two-sample t-tests indicated that vascular plant diversity and species richness were greater at LC sites than at the AG sites (t = −3.65, df = 12, p = 0.003 and t = −3.20, df = 10, p = 0.009, respectively). Diversity and richness of bryophytes and lichens were not significantly different between sites. The Pearson correlations between date of snowmelt and H' (r = −0.053, p = 0.813) and date of snowmelt and richness (r = −0.264, p = 0.235) were not significant and did not show any distinct trends. Diversity of vascular plants increased (ANOVA p < 0.001) from the edge to the core of transects, while cover of lichens and bryophytes decreased (ANOVA p < 0.001; p = 0.025) (Table 1; Supplemental material, Figure S2).

In the vascular plant ordination (Figure 3; stress = 16.47), core and edge quadrats were separated in ordination space; transition quadrats occupied a broad swath between those two groups. Later melt date corresponded with core quadrats, while edge quadrats had higher GDD. The ANOSIM of vascular species indicated significant differences in community composition between core and edge (R = 0.536, p = 0.001) and transition and edge (R = 0.245, p = 0.013) quadrats, but not between core and transition quadrats (R = 0.064, p = 0.205). In the ordination of site cores (Supplemental material, Figure S3; stress = 10.50), there was a distinct separation of AG and LC sites in ordination space, but the ANOSIM comparing community composition between AG and LC sites was not significant (R = 0.134, p = 0.115).

Community-weighted mean leaf area and SLA increased (p < 0.001; p = 0.028) with later melt date (Figure 4; Supplemental material, Table S2). Plant height, leaf area, and SLA of the four focal species were generally greater in snowbank cores, while LDMC was lower (Figure 5). In the dispersed sampling strategy, we found that LDMC was generally greater among alpine populations, while leaf area and SLA were greater among lowland populations (Table 2). Results from the concentrated sampling strategy were similar (Supplemental material, Table S3). No overall trends were apparent in plant height between alpine and lowland populations of the focal species. Species from the two habitats tended to respond in the same manner, except for Coptis trifolia. In the dispersed strategy, it had lower LDMC and higher SLA among alpine populations, while height and leaf area gave mixed results based on sampling strategy. A complete list of species identified in quadrats is presented in the Appendix.
Table 1. Mean (± standard error) Shannon-Weiner diversity, species richness, and percent cover of vascular plants, bryophytes, and lichens by quadrat type and site. Quadrat types are core (starting quadrats of transects), transition (intermediate quadrats), and edge (last quadrats of transects). Summary two-way analysis of variance (ANOVA) results also listed for each group of taxa. Source = source of variation (Type = among quadrat types; Site = among sites), MS = mean squares, F = test statistic, p = test significance. See Supplemental Material, Figure S2 for grouping information of significant ANOVAs.

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<th>Core</th>
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<th>Source</th>
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<th>F</th>
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<td></td>
<td>Site</td>
<td>565.400</td>
<td>1.56</td>
<td>0.146</td>
</tr>
<tr>
<td>Bryophytes</td>
<td>5.2 (1.8)</td>
<td>8.1 (1.8)</td>
<td>11.1 (3.1)</td>
<td>Type</td>
<td>5.253</td>
<td>4.18</td>
<td>0.025</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>Site</td>
<td>4.146</td>
<td>3.30</td>
<td>0.003</td>
</tr>
<tr>
<td>Lichens</td>
<td>0.1 (0.0)</td>
<td>2.4 (1.2)</td>
<td>10.1 (3.0)</td>
<td>Type</td>
<td>3.514</td>
<td>12.20</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td>Site</td>
<td>0.687</td>
<td>2.39</td>
<td>0.070</td>
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</tbody>
</table>
DISCUSSION

As no correlation between site size and length of time between edge and core exposure was found, it is likely that high variability in topography, aspect, and other local factors influenced melt-out at individual sites. Also, because no relationship was found between date of snowmelt and diversity or date of snowmelt and species richness, our data suggest those community variables are not highly linked to timing of snowmelt on Mt. Washington. More research is needed to identify and understand the
Figure 4. Change in community-weighted mean trait values (± standard error) across the snowmelt gradient. The three quadrat types were core, transition, and edge. Traits measured were height, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Significance of one-way analyses of variance indicated (*p < 0.05 and †p < 0.10, see Supplemental material, Table S2). Letters indicate grouping based on Tukey’s pairwise comparisons; quadrat types that share a letter are statistically similar (p > 0.05).

other site-specific environmental variables (e.g., light intensity, soil moisture and depth, and humidity, as well the local factors listed above) influencing diversity and richness at snowbank sites.

Analysis of community composition data confirm alpine snowbank sites as rich in vascular plants but scarce in lichens. It is possible that bryophytes, found in the greatest diversity, richness, and cover in transitional quadrats, are outcompeted/shaded by vascular species in snowbank cores and do not populate edge habitats owing to dry conditions and/or physical exposure. Lichens, on the other hand, which are generally found in more open habitats, thrive in the colder, drier, windswept microhabitats at the margins of snowbank communities; lichen diversity, richness, and cover was greatest in those areas (also, see Dibble et al. 2009).

The higher diversity and species richness of vascular plants at LC vs. AG sites found here may be due to differences in elevation and distance to treeline. The higher elevation of AG sites (Berend et al. 2020) makes them more isolated and farther from pockets of lower-elevation species, such as Abies balsamea (L.) Mill. Infiltration by such species may have increased diversity and richness values at LC sites, especially in patchy or
transitional zones (Harrison 1999). This is probably the case for site LC6, in Oakes Gulf—by far the most species-rich site. Along with *A. balsamea*, which was observed in close proximity to other LC transects but only recorded at LC6, it had several species found at no other sites, including *Arnica lanceolata* Nutt., *Campanula rotundifolia* L., *Carex capillaris* L., *Chamerion angustifolium* (L.) Holub, *Epilobium hornemannii* Dietr., and *Lonicera villosa* Muhl., indicating that environmental filtering may not be acting as strongly at that site (or other LC sites, to a lesser degree). The LC snowbank sites, in this respect, may represent more of the ravine or moist alpine herb-heath meadow communities (Sperduto and Nichols 2012), rather than the type of herbaceous snowbank communities found in the Alpine Garden (Sperduto and Cogbill 1999; Sperduto and Kimball 2011).

Variation at the scale of the community and within a species suggest that at both scales, plants with lower SLA were favored in alpine habitats and at the edges of snowbank communities. The transition in trait values from the core outward is evidence of the corresponding transition in underlying environmental conditions, as filtering becomes stronger and

Figure 5. Mean difference (± standard error) in measured plant traits of four focal species between snowbank core and edge quadrats (core minus edge). Positive bars indicate higher trait values in the snowbank cores. Traits are a) plant height, b) leaf dry matter content (LDMC), c) leaf area, d) specific leaf area (SLA). Species are *Carex bigelowii* Torr. ex Schwein. (black), *Chamaepericlymenum canadense* (L.) Aschers. & Graebn. (stippled), *Clintonia borealis* (Aiton) Raf. (gray), and *Maianthemum canadense* Desf. (white). Significance levels of paired t-tests between core and edge are indicated (*p < 0.05, †p < 0.10).
Table 2. Results of t-tests of comparisons of plant trait values between alpine and lowland source populations from the dispersed sampling strategy (results from concentrated sampling were similar; see Supplemental material, Table S3). Traits were height, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Significance of t-tests indicated (*p < 0.05); those that remained significant after Holms-Bonferroni correction are in bold. Both two-sample (each species individually) and paired (all species averaged) t-tests were performed (standard error in parentheses for paired t-tests).

<table>
<thead>
<tr>
<th>Species</th>
<th>Height</th>
<th>LDMC</th>
<th>Leaf area</th>
<th>SLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chamaepericlymenum canadense (L.) Aschers. &amp; Graebn.</td>
<td>-11.7</td>
<td>20.1*</td>
<td>-230*</td>
<td>-14.95*</td>
</tr>
<tr>
<td>Clintonia borealis (Aiton) Raf.</td>
<td>0.5</td>
<td>20.2*</td>
<td>-15</td>
<td>-5.19*</td>
</tr>
<tr>
<td>Coptis trifolia (L.) Salisb.</td>
<td>1.7</td>
<td>-59.3*</td>
<td>16</td>
<td>-287.00</td>
</tr>
<tr>
<td>Maianthemum canadense Desf.</td>
<td>-3.6</td>
<td>35.0</td>
<td>-15</td>
<td>-9.20*</td>
</tr>
</tbody>
</table>

Species with traits suited to harsher conditions are no longer outcompeted and become more prevalent. Because calculated trait values for individual species were weighted means of samples taken from both core and edge quadrats, these analyses are a conservative estimate of the differences in trait values across the snowmelt gradient; the actual difference in CWM trait values between core and edge habitats is likely to be greater than in the results shown here. Intraspecific trait variability may be important in affecting the observed variation in community assembly across the snowmelt gradient in alpine habitats (Jung et al. 2010; Kichenin et al. 2013; Luo et al. 2016; Yan et al. 2012) by promoting facilitation and species coexistence (Schôb et al. 2013) or increasing competition for limited resources. For example, soil moisture and sunlight could contribute to the dominance of species with advantageous phenological and leaf traits, which then shade other species. Similar organization of species and functional types by spatial and temporal scales has been observed in other systems (McCune 1993).

It is unclear whether trait differences between alpine and lowland populations of the same species are due to phenotypic plasticity, genetic divergence/evolutionary adaptation among alpine populations, or some combination of the two. First, plants can be highly plastic in response to
environmental conditions (Bradshaw 1965; Sultan 1995), developing different growth forms and adaptive strategies even among alpine conspecifics (e.g., Riebesell 1981; Scheepens et al. 2010; Shimono and Kudo 2003; Shimono et al. 2009). A range of phenotypic responses may be triggered by the specific growing conditions encountered by individuals at a given site (Choler 2005), but very little is known about the degree of phenotypic plasticity with which snowbank species in northeastern North America respond to those factors, especially in relation to their lowland counterparts. Second, habitat fragmentation and vicariance due to Pleistocene glaciation may have led to local speciation or ecotypic variation among populations. This has been observed in other alpine areas, including the Japanese archipelago (Ikeda et al. 2008) and the sky islands of the Sonoran Desert (Pérez-Alquicira et al. 2010, 2018; Weller et al. 2007), with a geologic history similar to that of northeastern North America (Spear 1989), and there is reason to believe the species-species assemblages studied here have responded in kind (Billings 1974). Finally, alpine areas have been found to function according to island biogeography theory (MacArthur and Wilson 1963, 2016), with separate populations interacting (via propagules, pollination, etc.) through immigration and dispersal across discrete peaks (Pérez-Alquicira et al. 2010, 2018; Riebesell 1982; Schönswetter et al. 2008; Weller et al. 2007). In fact, dispersal of propagules has been shown to be greater among alpine species as compared to lowland species in the Swiss Alps (Tackenburg and Stöcklin 2008). It is possible that snowbank communities in northeastern North America, which contain both of those species types, may function similarly, as suitable habitat is highly localized and separated by terrain or harsh conditions. However, little is known about gene flow dynamics between distinct alpine areas in the region or the degree of isolation among species across a peak or range within its limits, and more research is needed. It is also possible that differential selective pressures between the herbaceous species prevalent at lower elevations but found only in snowbanks at higher elevations and the alpine-only species not found below treeline could contribute to different trait-environment responses than those found in this study among the alpine-only species where they are found outside snowbanks. Common garden experiments may be a useful tool for further investigating the genetic and biogeographical components of ecotypic variation and trait plasticity among alpine plant populations in northeastern North America (Berend et al. 2019).

The Northeast is the fastest-warming region in the contiguous United States (Karmalkar and Bradley 2017), and arctic and alpine areas world-
wide are experiencing disproportionate warming compared to lower elevations/latitudes (Pepin et al. 2015; Rangwala and Miller 2012). Warming, along with shifting precipitation patterns, could have dramatic consequences for plants such as the snowbank species studied here that rely on insulating snow cover and protective microhabitats. A reduction in snow cover and a longer growing season could lead to snowbank plants or communities becoming more susceptible to spring frost damage, summer desiccation, or competitive pressure from external or invasive species (Craine et al. 2012; Komac et al. 2015), while increased precipitation due to climate change may actually lead to increased snowfall and deeper, longer-lasting snowpack at snowbank sites in the region. Recent studies of climate scenarios (Seidel et al. 2009; Wason 2016) and alpine plant phenology (Kimball et al. 2014; McDonough MacKenzie et al. 2018) in the region show mixed results and precise predictions remain elusive, but increased average temperatures are extremely likely under all projections. Alpine snowbank communities are particularly sensitive to such environmental changes (Björk and Molau 2007; Galen and Stanton 1995), and significant declines, range shifts, or a complete loss of alpine tundra in some locations are possible (Diaz and Eischeid 2007; Klanderud and Birks 2003; Walther et al. 2005a, 2005b).

Phenotypic (or phenological) plasticity and evolutionary adaptation may be necessary for vascular plants to track rapid climatic/abiotic changes (Anderson et al. 2012; Franks et al. 2014; Matesanz et al. 2010; Nicotra et al. 2010), and warming may drive further trait and/or functional change in arctic-alpine species or communities (Bjorkman et al. 2018). Climate has selective effects on bryophyte communities in alpine regions as well (Austrheim et al. 2005), and trait plasticity in bryophytes can be considerable (Hassel et al. 2005). Temperature increase threatens to decrease productivity and cover of bryophytes in alpine areas (Bjerke et al. 2011), potentially leading to substantial changes in microclimate (Bueno et al. 2016) or other feedback effects (Isard 1986) in snowbank communities. Lichens, too, while not prevalent in snowbanks, can be highly sensitive to water availability (Belnap et al. 2004) and may shift their niche along the snowmelt gradient with changing conditions.

Some changes in community structure have already been documented in alpine communities in the region, including increases in vascular plant frequency over bryophytes and lichens (Robinson et al. 2010) and increases in tree and shrub abundance (Capers and Stone 2011). We have also seen the encroachment of low-elevation or exotic species such as dandelions (Taraxacum officinale F. H. Wigg.) into snowbeds on Mt. Washington, and there is risk that such invasions may displace rare or
threatened species (Capers and Slack 2016; Komac et al. 2015) or lead to a loss of host plants for insect pollinators (Levesque and Burger 1982; McFarland 2003).

In conclusion, both species composition and trait values vary across the snowmelt gradient, indicating that the physical factors characteristic of snowbank habitats, including soil moisture, GDD, temperature, and protection from physical exposure to cold and wind, influence not only what species are present, but also how those species grow and develop. While changing environmental conditions across the gradient allow for different species to proliferate according to their individual tolerances, a gradient of trait values was seen even among conspecifics. Responses to selective pressures among lowland species that are found in snowbanks may be influencing the evolution of those populations, though more research is needed to assess whether ecotypic variation is occurring and the degree of phenotypic plasticity among them. Snowbank communities are likely to remain sensitive indicators of change (Komac et al. 2015; Schöb et al. 2009), and having baseline levels of trait values and variation may be a useful tool for tracking environmental change in alpine snowbanks in our region. *Chamaepericlymenum canadense*, the most plastic in alpine conditions, may be the best species of the four studied here to use as an indicator of environmental conditions. Arctic-alpine bryophytes and lichens should also be monitored in this context. Other long-term monitoring efforts such as GLORIA (recently established on Mt. Washington and Monts Chic-Chocs, Québec, Canada), permanent transects, phenological studies, and common garden experiments should be utilized to track community metrics into the future.

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Supplemental material for this article is provided online at www.researchgate.net/profile/Kevin_Berend/publications.
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APPENDIX

Below is a complete list of all vascular plant, bryophyte, and lichen species identified in quadrats during this study. Nomenclature of vascular plants follows Haines (2011), bryophytes according to the *Flora of North America* (2007, 2014), and lichens after Esslinger (2018). Saxicolous lichens were not identified to species and are not included here.

**MOSSES (BRYOPHYTA)**

*Andreaea rupestris* Hedw.

*Cratoneuron filicinum* (Hedw.) Spruce—Common and widespread in snowbeds.

*Dicranum elongatum* Schleich. ex Schwägr.

*Dicranum fuscescens* Turner/*D. fulvum* Hook.—These species combined for analysis owing to difficulty of identification.

*Dicranum polysetum* Sw.

*Dicranum scoparium* Hedw.—Common and widespread in snowbeds.

*Hylocomium splendens* (Hedw.) Schimp.

*Paraleucobryum longifolium* (Ehrh. ex Hedw.) Loeske

*Plagiothecium* spp.—Species identification unavailable.

*Pleurozium schreberi* (Willd. ex Brid.) Mitt.—Common and widespread in snowbeds.

*Pohlia nutans* (Hedw.) Lindb.—Uncertain species identification. Found at site AG7 only.

*Polytrichastrum alpinum* (Hedw.) G. L. Sm.

*Polytrichum commune* Hedw.

*Polytrichum juniperum* Hedw.

*Polytrichum pallidisetum* Funck

*Polytrichum piliferum* Hedw.

*Polytrichum strictum* Menzies ex Brid.

*Ptilium crista-castrensis* (Hedw.) De Not.

*Sciuro-hypnum reflexum* (Starke) Ignatov & Huttunen

*Sphagnum* spp.

**VASCULAR PLANTS (TRACHEOPHYTA)**

*Abies balsamea* (L.) Mill.—Found in quadrats at only one site (LC6), but present near the margins of snowbank sites throughout.

*Amelanchier bartramiana* (Tausch) M. Roem.—Found at site LC1 only.

*Arnica lanceolata* Nutt.—Found in one quadrat at site LC6.

*Betula glandulosa* Michx.

*Betula minor* (Tuck.) Fernald
Calamagrostis canadensis (Michx.) P. Beauv.
Calamagrostis pickeringii A. Gray
Campanula rotundifolia L.—Found at site LC6 only.
Carex bigelowii Torr. ex Schwein.
Carex brunescens Boeckeler
Carex capillaris L.—Found at site LC6 only.
Chamaepericlymenum canadense (L.) Aschers. & Graebn.
Chamerion angustifolium (L.) Holub—Found at site LC6 only.
Clintonia borealis (Aiton) Raf.
Coptis trifolia (L.) Salisb.
Deschampsia flexuosa (L.) Trin.
Deschampsia flexuosa (L.) Trin.
Diphasiastrum sitchense (Rupr.) Holub—Found at site AG4 only.
Dryopteris campyloptera Clarkson
Empetrum nigrum L.
Epilobium hornemanii Dietr.—Found at site LC6 only.
Geum peckii Pursh
Houstonia caerulea L.
Juncus filiformis Walter—Found at site LC6 only.
Juncus trifidus L.
Kalmia polifolia Wangenh.
Kalmia procumbens (L.) Gift, Kron, & P. F. Stevens ex Galasso, Banfi & F. Conti
Lonicera villosa Muhl.—Found at site LC6 only.
Luzula parviflora Desv.
Lysimachia borealis (Raf.) U. Manns & Anderb.
Maianthemum canadense Desf.
Nabalus boottii DC.
Nabalus trifoliolatus Cass.
Phlegopteris connectilis (Michx.) Watt
Phyllocladus caerulea (L.) Bab.
Rhododendron groenlandicum (Oeder) Kron & Judd
Rhododendron lapponicum (L.) Wahlenb.
Rubus pubescens Raf.—Found at site LC6 only.
Sibbaldiopsis tridentata (Aiton) Rydb.
Solidago macrophylla Bigelow
Spinulum annotinum (L.) A. Haines
Spinulum canadense (Nessel) A. Haines
Spiraea alba Du Roi var. latifolia (Aiton) F. Seym.
Streptopus amplexifolius (L.) DC.
Streptopus lanceolatus (Aiton) Reveal
Symphyotrichum puniceum (L.) Á. Löve & D. Löve—Uncertain identification. Found at site LC6 only.
Trichophorum cespitosum (L.) Schur
Vaccinium angustifolium Aiton—Common and widespread.
Vaccinium cespitosum Michx.—Common and widespread.
Vaccinium uliginosum L.—Common and widespread.
Vaccinium vitis-idaea W. D. J. Koch
Veratrum viride Aiton

LICHENS

Cetraria delisei (Bory ex Schaer.) Nyl.
Cetraria laevigata Rass.—Common and widespread.
Cladonia arbuscula (Wallr.) Flot.
Cladonia arbuscula subsp. mitis (Sandst.) Ruoss
Cladonia arbuscula subsp. squarrosa (Wallr.) Ruoss
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.
Cladonia crispata (Ach.) Flot.
Cladonia rangiferina (L.) F. H. Wigg.
Cladonia stellaris (Opiz) Pouzar & Vězda—Found at site LC6 only.
Cladonia stygia (Fr.) Ruoss
Cladonia uncialis (L.) F. H. Wigg.
Flavocetraria cucullata (Bellardi) Kärnfelt & A. Thell—Found at site LC1 only.
Flavocetraria nivalis (L.) Kärnfelt & A. Thell—Found at site LC2 only.
Stereocaulon alpinum Laurer ex Funck—Uncommon, found at AG and LC sites.
Trapeliopsis granulosa (Hoffm.) Lumbsch