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## Investigating the ecology of a threatened ecosystem: Alpine snowbank communities of Mt. Washington, NH

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Investigating the ecology of a threatened ecosystem:  
Alpine snowbank communities of Mt. Washington, NH

by

Kevin Berend

A thesis

Submitted to the Department of Environmental Science and Ecology of The College at Brockport,

State University of New York, in partial fulfillment of the degree of

Master of Science

March 2, 2018

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by

Kevin Berend

2018

Investigating the ecology of a threatened ecosystem:

Alpine snowbank communities of Mt. Washington, NH

by Kevin Berend

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## Abstract

In northeastern North America, alpine snowbank (or snowbed) 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. These communities are highly diverse and may provide many beneficial ecosystem services. Though work has been done to document their location and community composition, little is known about the relationships between plants and abiotic conditions in alpine snowbanks of the Northeast. We studied the relative effects of snowmelt date and temperature on the phenological responses of seven alpine snowbank plants and examined plant traits and community metrics (diversity and richness) across the snowmelt gradient at alpine snowbank sites on Mt. Washington, NH. Peak of observed phenophases was positively correlated with snowmelt date, but lag time (time between snowmelt date and peak phenophase) was negatively correlated with snowmelt date. Higher temperature was an important factor in the quickened phenological response of plants at later-melting sites. There was a clear transition in both community composition and traits across the snowmelt gradient; moving outward from snowbank cores, vascular plant diversity decreased and lichen diversity increased, with no trend evident in bryophytes. This corresponded to a transition in observed traits both within species and at the community-level, with snowbank core habitats having lower leaf dry matter content and greater height, leaf area, and specific leaf area than edge habitats. A similar difference in plant traits was observed among conspecifics between lowland and alpine habitats, though we were unable to conclude whether alpine ecotypes of those species exist. The change in environmental conditions across the snowmelt gradient, mediated by snow persistence, is important in determining plant phenological responses and growing conditions on Mt. Washington in ways as found elsewhere at similar sites worldwide. Due to prevalence of leafy species and reliance on specific environmental conditions, alpine snowbank communities are considered particularly sensitive to environmental change, and may be indicators of climatic trends occurring in northeastern North America.

*Keywords:* Alpine, snowbed, plants, phenology, community, traits, gradient, ecotype, climate, northeast

## General Introduction

The mountains of northeastern North America were formed through a long history of tectonic activity, uplift, glaciation, and erosion, resulting in the dramatic and varied landforms found in the region (Jones and Willey, 2012). Upon the retreat of the Laurentide ice sheet, arctic tundra plant communities were isolated by surrounding spruce-fir and hardwood forests which migrated northward along with climatic warming, and now occupy the lower slopes of the region's peaks (Billings, 1974). Vegetation atop these summits has not changed significantly in the last ~2k years (Spear, 1989). Arctic-alpine plant communities persist to this day in northeastern North America despite extreme conditions including high winds, low temperatures, poor soil, and a short growing season (Korner, 1999). These plants have developed a host of adaptations to deal with these conditions, including dwarf or aerodynamic growth form, overwintering flower or leaf buds, and accessory photosynthetic pigments, and seed dormancy strategies (Bliss, 1962, 1971). Today, the most notable arctic-alpine areas in the region exist in the Adirondack Mountains of New York, White Mountains of New Hampshire, and the Katahdin massif in Maine, but can also be found in high-elevation areas of Vermont, Quebec, Labrador, and Newfoundland (Jones and Willey, 2012).

Snowbank (or snowbed) communities are a rare alpine plant community type found above treeline in areas where snow accumulates and lasts longer into the spring, such as ravine ledges, shallow depressions, and lee of sheer rock faces (Sperduto and Nichols, 2011; Capers and Slack, 2016). These unique habitat conditions provide shelter for a multitude of herbaceous species from lower elevations, resulting in high species diversity (Bliss, 1963) and a potentially high level of ecosystem function. Because of their floristic composition and specific habitat requirements, snowbank communities are considered particularly vulnerable to climatic change (Björk and Molau, 2007; Schöb et al., 2009), and monitoring them may provide clues as to how global warming may affect alpine areas (Löffler et al., 2011). However, little work has been done to closely examine the plant-environment relationships in these communities in northeastern North America.

Recently, scientists and conservationists came together to coordinate alpine research directions in northeastern North America, and “Identifying the location, community composition, duration of snow cover and timing of snow melt in snowbed communities...” was ranked as the highest priority (Capers et al., 2013). The goal of this study was to explore questions pertaining to the ecology of alpine snowbank communities on Mt. Washington, NH in an attempt to better understand these ecosystems and anticipate potential changes in an altered future climate.

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Effects of snow and temperature on the phenology of  
alpine snowbank plants on Mt. Washington, NH

K. Berend, K. Amatangelo, D. Weihrauch, and C. Norment

Abstract

In northeastern North America, alpine snowbank (or snowbed) 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 studied the effects of snowmelt timing and temperature on the vegetative and flowering phenology of seven common snowbank species. We visually observed snowmelt date and plant phenology at Alpine Garden and Lakes of the Clouds sites on Mt. Washington, NH, and collected temperature data using automated dataloggers. We used linear regression models to analyze those relationships. There was no relationship between site area and melt date or elevation and melt date. Snowmelt date was positively correlated with date of peak phenophases, and lag time (time between snowmelt and peak phenophases) was negatively correlated with snowmelt date. Snowmelt timing consistently delayed the onset of plant phenological stages, but later snowmelt had a less pronounced delay. These trends match studies of alpine plant phenology conducted elsewhere, and can likely be attributed to the higher mean daily temperatures experienced by plants at sites that melt later. Plants at those sites accumulate temperature (growing degree days) more quickly and undergo a quickened phenological cycle. Continued monitoring of snowmelt timing and phenology of alpine snowbank plants may yield important clues as to how climate change may affect alpine areas of northeastern North America, especially in terms of diversity, pollination, and abiotic interactions.

*Keywords:* Alpine, snowbed, plants, Mt. Washington, phenology, snowmelt, delay, climate change

## Introduction

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 lee of sheer rock faces, where late-lying snow provides insulation from late-season frosts and a longer-lasting source of water (Bliss, 1963; Capers and Slack, 2016). In these habitats, herbaceous understory species from lower elevations can persist above treeline. As a result, snowbank communities are the most species-rich alpine plant community in northeastern North America (Bliss, 1963), supporting several rare or threatened plant species (Sperduto and Nichols, 2011), browse for mammalian herbivores such as snowshoe hares (Berend, personal observation), and habitat/brood host plants for at least one endemic (and imperiled) butterfly, *Boloria chariclea montinus* (McFarland et al., 2017). However, these communities occur only sparsely. The most extensive sites exist in the Presidential Range of the White Mountains, NH and Mt. Katahdin, ME (Kimball and Weihrauch, 2000), but they can also be found in high-elevation areas of New York State (Carlson et al., 2011), Quebec, and Labrador (Jones and Willey, 2012).

Both snow and temperature are important drivers of ecosystem functions and plant community responses in alpine habitats (Bliss, 1971; Körner, 1999; Schmidt, 2011). Snow is influential in terms of its effects on hydrology, temperature mediation, and growing season length (Holway and Ward, 1965; Beniston, M. et al., 2003; Wipf and Rixen, 2010; Inouye and Wielgolaski, 2013; Petraglia et al., 2014). Alpine plants generally must wait until snowmelt to begin yearly cycles of growth and reproduction. An increase in mean temperatures due to climate change, then, may lead to reduced snowpack levels and/or earlier snowmelt dates in alpine environments (Beniston, 2003), already documented in several studies (Beniston, M. et al., 2003; Dankers and Christensen, 2005; Inouye, 2008). Independent of snow cover, though, temperature itself also plays a large role. For instance, links between accumulated seasonal temperature (or growing degree days, GDD) and the timing of life-history stages (phenology) such as leaf-out and flowering are well established (Körner, 1999; Smith et al., 2012). Commonly, leaf buds or

shoots will not emerge in spring until a threshold GDD is met, so as to avoid late-spring frosts (Inouye, 2000; CaraDonna and Bain, 2016); thus earlier snowmelt does not necessarily lead to advanced phenology (Inouye, 2008; Iler et al., 2013a). In this sense, GDD can act as a timekeeper for plants, determining later-season phenological responses such as flowering that may be less tied to snowmelt timing.

Arctic and alpine areas worldwide are expected to be disproportionately affected by climate change, and are already warming more quickly than the global average (Høye et al., 2007; Rangwala and Miller, 2012; Hoyle et al., 2013; Mountain Research Initiative 2015; Pepin, 2015). Increased spring temperatures and earlier snowmelt due to climate change, therefore, are leading to phenological advancement (or upslope migration) in some alpine plants (Walther et al., 2002; Dunne et al., 2003; Walther et al., 2005a; Lambert et al., 2010; Theobald et al., 2017), potentially disrupting community or pollinator dynamics (Kudo, 2014). Due to the presence of many indicator species that require specific habitat conditions (Björk and Molau, 2007; Grabherr et al., 2010), alpine plant communities are considered particularly sensitive to environmental change (Walker et al., 1993; Löffler et al., 2011). However, the relative importance of snowmelt date and temperature on alpine plant phenology is complex and remains somewhat unclear, and plants may display both linear and non-linear responses to changing climatic conditions (Inouye, 2008; Iler et al., 2013a).

Due to both their rarity and threats from environmental change, alpine snowbank communities are considered “critically imperiled” (S1) by the states of NY, NH, and ME (Gawler and Cutko, 2010; Sperduto and Nichols, 2011; Edinger, G. J. et al., 2014), and there is an immediate research need to better understand these communities (Capers et al., 2013). Capers and Slack (2016) documented community composition in relation to melt date for several snowbank sites on Mt. Washington, but to date no studies have done the same for plant phenology or temperature at snowbank sites in northeastern North America. Given the need for better information on alpine snowbed communities, the objectives of this study were to collect information on snowmelt patterns and factors that may affect it at snowbank sites on Mt.



Washington and examine the relationships and relative effects of snowmelt date and temperature on vegetative and flowering phenology of seven snowbank plant species. We hypothesized that snowbank plant phenology is tied to snowmelt date, but that temperature is also a factor determining plant phenological responses.

## Methods

### **Site description**

Mount 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 New Hampshire (Fig. 1, inset). Treeline is approximately 1504 m, but varies considerably based on exposure and topography (Kimball and Weihrauch, 2000). Mt. 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. The majority 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 Appalachian Mountain Club's (AMC) Lakes of the Clouds hut (LC), 1.8 km southwest of the summit. In summer 2016, we identified 14 snowbank sites across both areas (AG=9, LC=5, Fig. 1) by the presence of indicator species (Sperduto and Nichols, 2011; Capers and Slack, 2016). Sites ranged in area from 10 to 378 m<sup>2</sup>, and in elevation from 1556 to 1744 m (Table S1). All snow depth and phenology observations took place within 1.5 m-radius circular plots placed in the "core" or center of snowbank sites. Where possible, larger sites had more than one plot (total=23, see below), with replicate plots at a given site placed at least 3 m apart.

## Environmental monitoring

Elevation at each site was recorded using a handheld GPS unit (Garmin GPSMAP®64, Garmin Ltd., Olathe, KS), and area was determined using aerial imagery (USDA, 2016) and geospatial analysis software (ArcMap™ 10.2.2, ESRI, Redlands, CA). In July-August 2016, we placed a magnetic survey marker (SurvKap®, Tucson, AZ) flush with the soil surface at the center of each plot and a temperature/light datalogger (OnSet HOBO® Pendant® UA-002-08, Bourne, MA) similarly in one plot at every site, according to GLORIA protocols (Pauli et al., 2015).

In May 2017, plots were relocated beneath the snow using a magnetic survey detector (CST/Berger™, Watseka, IL), and temporarily marked with stakes. We revisited each plot every 3-5 days, and observed snow depth using an avalanche probe (Black Diamond® Equipment, Salt Lake City, UT). Melt date for each plot was recorded as the first date visited in which the entire plot was snow-free (earliest 21 May, latest 25 June). Melt date was averaged for sites with >1 plot.

## Phenology

Beginning with the initial date of exposure, we monitored phenology of seven snowbed species: *Carex bigelowii* Torr. ex Schwein., *Chamaepericlymenum canadense* (L.) Aschers. & Graebn., *Clintonia borealis* (Ait.) Raf., *Coptis trifolia* (L.) Salisb., *Maianthemum canadense* Desf., *Vaccinium cespitosum* Michx., and *V. uliginosum* L. throughout the growing season. *Chamaepericlymenum*, *Clintonia*, *Coptis*, and *Maianthemum* are understory herbs found commonly in hardwood forest habitats of lower elevations in the region, and survive above treeline only in snowbank communities. *Carex bigelowii* is an arctic-alpine sedge common in alpine areas of northeastern North America, while *V. cespitosum* and *V. uliginosum* are arctic-alpine heath shrubs (*V. cespitosum* is a snowbank community indicator) (Bliss, 1963; Sperduto and Nichols, 2011; Capers and Slack, 2016). All nomenclature follows Haines et al. (2011).

Every 4-6 d, we recorded the presence and abundance of vegetative and flowering stages of each species in each plot. Vegetative phases monitored were “Shoots” (leaf bud burst/new growth) and “Leaves” (at least one fully expanded leaf). Flowering phases were “Fl. buds” (flower buds present) and “Flowers” (at least one open flower). Abundance estimates (or phenological scores) of each vegetative and flowering stage were made according to AMC Mountain Watch/National Phenology Network protocol (Denny et al., 2014). For species in which the previous year’s growth, such as dead/dormant leaves (*Carex* and *Coptis*) or woody vegetation (*V. cespitosum* and *V. uliginosum*) existed as a baseline for comparison, phenological score was the percentage of each species in each plot exhibiting a given phenophase. For species in which the previous year’s growth does not persist (*Chamaepericlymenum*, *Clintonia*, and *Mainthemum*), phenological score was based on number of plants observed (by ranked category, 1-6). Percent estimates would have been unreliable for these three species without the previous year’s baseline. Monitoring continued until the end of flowering phenology, on 26 July 2017.

### **Data analysis**

Melt date, phenology scores, and temperature data were averaged by site. We used two-sample t-tests to evaluate differences in both site area and elevation across the two locations (AG/LC) and Pearson’s correlations to evaluate relationships between both melt date and site area and elevation. Site area was log-transformed for normality.

The peak dates of the four phenophases for each species were recorded as the day with highest score. If peak lasted for more than one observation, score was recorded as the average of those days. We then calculated the number of days between melt date and phenophase peaks at each site, called lag time. Peak date was used for analyses, as it has been shown to be a more reliable indicator than date of first appearance (Moussus et al., 2010). All dates were converted to Julian day (1 Jan.=001) for analyses, and *C. bigelowii* Fl. buds data were arcsine-square root transformed for normality.

We calculated GDD for each plot that had a datalogger using the average method (daily max-min/2), with 1 Jan. 2017 chosen as a start date, and 0°C as the threshold temperature. These values were plotted against phenological score for each phenophase and species (Fig. 2). Mean cumulative GDD was calculated for each site at day 201 (the last day of monitoring in which all sites were included), and a two-sample t-test was performed to compare total heat accumulation between locations.

We used linear regression models for each species and phenophase to analyze the effect of melt date, location (AG vs. LC), and their interaction on both date of phenophase peak and lag time. We then performed a second set of linear regression models using temperature data; GDD was the predictor rather than melt date. We analyzed the effect of GDD on peak phenological score, location, and their interaction on date of phenophase peak. We used a Holms-Bonferroni correction for family-wise error rate for each of the three sets of regressions separately. Correlation and regression analyses were performed in Minitab (v. 18, Minitab, Inc., State College, PA).

## Results

Alpine Garden (AG) sites were significantly higher in elevation than Lakes of the Clouds (LC) sites ( $1690.9 \pm 12$  m and  $1592.2 \pm 19$  m, respectively,  $t=4.39$ ,  $p=0.003$ ), but site area was not statistically different ( $98.51 \pm 30.2$  m<sup>2</sup> and  $144.5 \pm 80.0$  m<sup>2</sup>, respectively,  $t= -0.83$ ,  $p=0.434$ ). Pearson correlations showed no relationship between site area and melt date ( $r=0.081$ ,  $p=0.783$ ) or elevation and melt date ( $r=-0.092$ ,  $p=0.754$ ).

### **Melt date & phenology**

In general, LC sites melted out earlier than AG sites ( $153.6 \pm 1.88$  d,  $CV=2.74$  and  $156.7 \pm 4.1$  d,  $CV=7.91$ , respectively), but had a considerably smaller range of melt dates. AG had the earliest-melting site (AG9), but also the latest-melting sites, AG4 and AG7, which saw their first snow-free day almost three weeks after LC.

In the linear regression analyses, melt date significantly affected phenophase peak date in 24 of 28 (85.7%) models (Table 1). Slopes of all regression lines were positive (Fig. 3A), and mean slopes (by phenophase) ranged from 0.438 to 0.629. This indicates that for every day melt date increased by 1, phenophase peaks were delayed by about 0.54 days.

Melt date significantly affected lag time in 25 of 28 (89.3%) models (Table 1). Slopes of all regression lines were negative (Fig. 3B), and mean slopes (by phenophase) ranged from -0.562 to -0.372. This indicates that for every day melt date increases by 1, lag time decreased by about 0.46 days. Sites with later melt date, therefore, had later phenophase peak, but also shorter lag time. Location and Location\*Melt date were significant predictors in phenophase peak or lag time models only rarely. Patterns in new shoot growth were also generally consistent among leafy species in plots regardless of melt date, with *C. bigelowii* emerging first, followed by *Clintonia borealis* and *Maianthemum canadense*, and last *Chamaepericlymenum canadense*.

### **Temperature & phenology**

Temperature data indicated that during the period of snowcover, temperature at the soil surface remained at a constant 0°C (Fig. S1). Occasionally, a late-fall melt event was evident as a temperature spike or drop; afterward, the site was re-covered by snow and returned to 0°C. These seasonal temperature patterns were consistent across all study sites. There was negligible soil GDD accumulation until snowmelt date, after which soil accumulated GDD more quickly than the air (Berend, unpublished data). Cumulative GDD at the end of the growing season was greater at LC (mean 770.2 ±26) than AG sites (mean 676 ±37), and the t-test approached significance ( $t = -2.08$ ,  $df = 9$ ,  $p = 0.068$ ).

In the second set of linear regression models that used GDD as a predictor, GDD was statistically different among phenophase peak dates in only 3 of 28 (10.7%) of models, and only 1 model (*Chamaepericlymenum*, Leaves) had a significant ( $p < 0.05$ ) regression. GDD to peak was consistent among phenophases, despite varying melt dates. There were occasional differences in abundance (e.g.,

*Mainthemum*, Fl. buds & Flowers) or GDD (e.g., *V. uliginosum*, Fl. buds) between Alpine Garden and Lakes of the Clouds sites (Table S5), but in general, bell-shaped curves with distinct maximums were observed for the Shoots and Fl. buds phenophases, and logistic curves for the Leaves and Flowers phases (Figs. 2, S4). These two shapes indicate a smooth transition from both Shoots to Leaves and Fl. buds to Flowers.

## Discussion

The later melt dates and greater variation at Alpine Garden (AG) sites compared to Lakes of the Clouds sites was likely driven by both elevation and topography. AG sites were roughly 100 m higher in elevation and experienced slightly cooler average daily air temperatures (Mount Washington Observatory 2017). Also, they were located on a mostly uniform grade east of the summit, where they received less direct late-afternoon sunlight, and snow cover across them was more unbroken, compared to LC sites (Berend, personal observation). This likely led to local topography at AG sites being a greater factor in melt date, as larger, deeper sites filled with more snow took longer to be exposed than smaller, shallower ones. Also, unbroken snow cover across such areas probably produces a feedback effect, insulating larger areas (or adjacent sites) and delaying snowmelt longer than would be predicted by air temperature alone. Because they did not benefit from this kind of unbroken snow cover beyond the extent of the snowbanks, LC sites melted earlier and more uniformly. The lack of significance by location (AG/LC) in the second set of linear regressions that used GDD as a predictor indicates that regardless of variable melt dates between locations, phenophase peak corresponds strongly to GDD, a trend consistent among species at both locations. Because they melted earlier, LC sites accumulated about 100 more growing degree days (GDD) during the course of the 2017 study period. This raises potential consequences including phenological mismatch of plants and pollinators between locations, should differential melt dates become more exaggerated.

The linear regression data presented here demonstrate that on Mt. Washington, vegetative and flowering phenology of both herbaceous and woody alpine snowbank plants is closely tied to date of

snowmelt. The later snow melts at a given snowbank site, the later observed phenophases are delayed in the growing season. This is consistent with findings from alpine plant phenology studies elsewhere (e.g., Walker et al., 1995; Price and Waser, 1998; Anderson et al., 2012). This relationship between melt date and phenology can be attributed to the need for plants to accumulate a minimum threshold GDD before initiating new spring growth. This is an advantageous response for plants, as waiting for this thermal indicator minimizes risk of frost damage to new shoots and buds while maximizing productivity and reproductive success.

The later a site melts, though, the time between melt date and all respective phenophase peaks (lag time) decreases. This phenomenon, too has been discovered at other sites throughout the world (Høye et al., 2007; Venn and Morgan, 2007; Kawai and Kudo, 2011), but this is the first confirmation of its occurrence in an alpine system in northeastern North America. The inverse relationship between melt date and lag time can be explained by the lack of significance of the GDD regressions performed in this study, which isolated temperature as an environmental variable aside from snowmelt date. Plants delayed by late snowmelt begin growing under warmer ambient conditions and longer day lengths than those at earlier-melting sites, and accumulate GDD more rapidly. Quicker accumulation leads to an even more condensed growing season and a shorter lag time for all observed phenophases.

In sum, snowmelt is responsible for the initiation of GDD accumulation, while GDD itself (temperature) is responsible for the actual timing of each respective phenophase from that point forward. Earlier-flowering species on Mt. Washington, therefore, may be more responsive to yearly changes in the timing of snowmelt date than later-flowering species, as found elsewhere (Miller-Rushing and Inouye, 2009; Wipf, 2010; Iler et al., 2013b).

Based on our data, the response of snowbank communities to earlier snowmelt should be a linear advancement of phenology, but maybe only to a point. There is evidence from other world alpine areas that phenology cannot advance beyond a certain point, no matter how early snowmelt occurs. Rather, the interacting effects of snowmelt and GDD accumulation (temperature), as well as other factors like unmet

chilling requirements, could lead to non-linear phenological responses (Høye et al., 2007; Inouye, 2008; Iler et al., 2013a). Non-linear trends were not investigated here, but such responses may become more probable under extremely advanced snowmelt. If observed, they are evidence that flowering timing is not keeping pace with changing abiotic conditions.

Solar radiation also plays a large role in influencing photosynthetic responses of plants in terms of its effects on snowmelt and temperature. Bliss (1966) found that soil surface temperatures on Mt. Washington were considerably warmer than ambient air temperature even 10 cm above the soil. By comparing temperature data collected at study plots here with available 2017 air temperature data for Mt. Washington, we confirm that the soil surface (plant growth media) accumulates GDD more quickly than the air (Berend, unpublished data). This effect is likely to be exaggerated the earlier a snowbank site melts, as the loss of the highly-reflective snow layer will mean more solar energy absorbed by the soil as heat and more rapid GDD accumulation.

Both light intensity and photoperiod, too, while not directly evaluated here, may complicate predictions regarding the interactions of snowmelt and temperature on alpine snowbank plant phenology. Photoperiod is a crucial driver of plant phenology, perhaps even more important than snowmelt date in some alpine systems (Venn and Morgan, 2007; Ernakovich et al., 2014). Earlier snowmelt due to climate change or other factors, though, may contribute to non-linear phenological trends because plants may still wait for photoperiod cues to begin seasonal growth. Some species, therefore, may be unable to take advantage of this extra growing time (Keller and Körner, 2003). A longer snow-free, dormant period may have further effects on ecosystem dynamics at snowbank sites such as altered hydrology, productivity, microbial activity (Ernakovich et al., 2014), organic matter content (Shimono et al., 2009), nutrient fluxes (Smith et al., 2012), seed germination success (Bliss, 1962), or insect habitats (Finn and Poff, 2008). Plants may even respond to these cues before melt-out, as research has shown that light is able to penetrate snowpack to a limited depth, stimulating early bud activity and influencing photosynthetic responses (Starr and Oberbauer, 2003). This was also true on Mt. Washington in this study, as light was



able to penetrate up to 30 cm depth and up to 5 days prior to melt-out at snowbank study plots (Berend, unpublished data).

### **Community dynamics**

The dual effects of snowmelt and temperature on alpine plant phenology have several consequences for plant reproductive success and community dynamics. First, earlier snowmelt at a given site may lead to a longer growing season, but also an increased exposure of leaf or flower buds to spring frost (Inouye, 2008). This risk may outweigh the benefits of a longer growing season, decreasing aboveground growth in some species (such as dwarf shrubs; Wipf et al., 2009), while facilitating growth in more tolerant ones (such as graminoids; Jonas et al., 2008). Since the order of melt-out from year to year is consistent among snowbank sites on Mt. Washington (Capers and Slack, 2016), changes in species composition may occur naturally over time (Galen and Stanton, 1995).

Second, differences in growing season length due to variable melt-out can affect reproductive success through impacts on flowering and seed set. Plants at early-melting sites may be pollen-limited, missing key pollinators that depend on warmer ambient temperatures (Kudo and Suzuki, 2002; Kudo, 2014). Plants at late-melting sites, on the other hand, while potentially more successful with pollination, risk early autumn frosts and the completion of seed set (Molau, 1993; Wagner and Reichegger, 1997). Plants that are able to may abandon sexual reproduction at such sites, opting for vegetative propagation instead (Kudo, 1991).

Last, the timing of snowmelt may affect not only the phenology of individual species, but entire communities (Kudo and Suzuki, 1999). Dates of first, peak, and last phenophases rarely shift uniformly (Iler et al., 2013a), and any directional shift in environmental variables can result in substantial reshaping of ecological communities (CaraDonna et al., 2014). Considering a more complete phenological profile in future studies could be informative in this regard. Climatic variation in snowmelt may also lead to altered competitive interactions (Forrest et al., 2010) or changes in nutrient fluxes that may affect interactions

between species (Smith et al., 2012). Biotic and abiotic interactions, though, will vary depending on snowmelt patterns within even highly-localized areas (Kudo and Hirao, 2006), and year-to-year changes may be difficult to discern on such scales. Thus, continued monitoring of snowbank sites will be crucial to assessing community change in alpine areas of northeastern North America.

### **Climate change & conservation**

Climate change will have wide-ranging effects on alpine systems worldwide (Grabherr et al., 2010). Increased average temperatures and a greater percentage of precipitation falling as rain is likely to lead to decreases in both duration and volume (by up to 90%) of snowpack in alpine areas (Beniston, 2003; Beniston et al., 2003). In a recent study, trends in the dates of first and last observed snow depth on Mt. Washington were significant, with first snow occurring 7.0 days/decade later in autumn and last snow occurring 2.8 days/decade earlier in the spring (Seidel et al., 2009). Continued trends in northeastern North America could have dramatic consequences for plants such as the snowbank species studied here that rely on insulating snow cover and protective microhabitats. Earlier loss of snow could lead to changes in temperature regimes and hydrology, leading to the loss or fragmentation of these habitats above treeline (Walther et al., 2005b). We are only beginning to understand the ways these highly-diverse communities contribute to the stability and productivity of the greater alpine ecosystem, and losing them could have wider effects beyond the plants themselves, from endemic insects (McFarland, 2003; McFarland et al., 2017) to birds (D'Oleire-Oltmanns et al., 1995) to mammals (Kausrud et al., 2008). Little is known, though, about how climate change may affect alpine ecosystems in the region.

A reduction in snow cover and a longer growing season could lead to fewer suitable microhabitats for many alpine species, but snowbank communities are likely to be most vulnerable to these changes. Snowbank plants may become more susceptible to spring frost damage and summer desiccation while increasing competitive pressure from external or invasive species (Craine et al., 2012; Komac et al., 2015). Prompt research on such impacts is crucial, as alpine vegetation may respond quickly to altered climates (Cannone et al., 2007).

In fact, recent vegetation change has been observed in alpine plant communities in northeastern North America. Robinson et al. (2010) found significant vegetational change over a 23-year period in the Adirondack Mountains of NY. In that study, vascular plant frequency increased at the expense of bryophytes and lichens—important components of snowbank communities (Capers and Slack, 2016). Capers and Stone (2011) found an increase in tree and shrub abundance over 33 years on Bigelow Mt., ME, and attributed the increase in species richness they found to the encroachment of lower-elevation species into alpine areas. These trends are expected to continue as climatic conditions in the alpine zone become less harsh and shrubs/trees are able to outcompete herbaceous species in transitional communities (Chapin et al., 1996; Callaway et al., 2002). Phenotypic (or phenological) plasticity and evolutionary adaptation may be necessary for plants to track these climatic/abiotic changes (Anderson et al., 2012) but it is unclear whether plants and communities will be able to keep pace.

There are reasons to believe, however, that alpine areas in the region may respond differently to climate change than other areas of the world. Lower treeline, greater precipitation and soil moisture, along with acidic soil conditions, make alpine areas of northeastern North America unusual among other mountainous regions of the world (Cogbill et al., 1997; Jones and Willey, 2012). Seidel et al. (2009) demonstrated that the alpine zone of Mt. Washington is not warming as quickly as lower elevations in the region. Their climate models predict an increase in both cloud cover and precipitation for the region under warming scenarios, and they propose that higher humidity and increased fog/cloud cover may buffer the effects of atmospheric warming. Phenological models using historic climate data have confirmed this trend, finding that despite increases in regional average temperatures, flowering advancement of three species on Mt. Washington was less pronounced in the alpine zone than at lower elevations (Kimball et al., 2014).

These findings indicate that alpine snowbank communities in northeastern North America may not be as threatened as previously thought. Increased precipitation due to climate change may actually lead to increased snowfall and deeper, longer-lasting snowpack at snowbank sites in the region.

Snowbank-obligate species, therefore, may continue to have a suitable habitat under changing climate conditions (Scherrer and Körner, 2011). In fact, longer snow persistence may actually threaten the “true” arctic-alpine species at the margins of snowbanks that depend on spring snowmelt for sufficient yearly growth and reproductive success. Many species that make up the greater alpine tundra community, while locally abundant on alpine peaks, are considered imperiled due to regional rarity and a reliance on specific habitat conditions (listed as S2; NH Nat’l Her. Bur., 2013). *Carex bigelowii*, *Diapensia lapponica*, and even *Potentilla robbinsiana*, for example, are species that may feel increasing stress if faced with extended snow cover duration. Such arctic-alpine species have many adaptations to deal with the cold, wind exposure, and ice they experience year-round (Bliss, 1971), but are generally poor competitors, and may be displaced if alpine conditions become ameliorated under climate change (Scherrer and Körner, 2011).

The most likely scenario, at least in the short term, seems to be a loss of snowbank habitat in some places, with gains (or equilibrium) in others, simply due to the high variability in snowmelt across sites and among years. We recommend that snowbank communities continue to be monitored for changes in phenology and community or ecosystem dynamics into the future, as they are likely to remain sensitive indicators of change (Komac et al., 2015). Integrating snowbank-occurring species into the Appalachian Mountain Club’s Mountain Watch program (McDonough MacKenzie et al., 2017) and continued monitoring of permanent or long-term monitoring plots, such as GLORIA (Grabherr et al., 2000), recently established on Mt. Washington, may be helpful in assessing alpine plant phenological responses and community change as a result of climatic shifts.

## **Conclusions**

Phenological responses to snowmelt of alpine snowbank plants on Mt. Washington studied here match similar studies conducted elsewhere. Vegetative and flowering phenology is highly sensitive to snowmelt date, but there is a substantial interaction effect between snowmelt date and temperature (growing degree days). This is promising for comparisons with other world alpine areas, especially those

with long-term weather records such as on Mt. Washington. Continued monitoring of snowbank melt dates and plant phenology may provide clues as to how those species respond to yearly variations in melt date or temperature, and whether longer-term shifts are evident in response to climate change. A broader profile of phenology (e.g., first, peak, last dates), consideration of non-linear responses, and the incorporation of light data may be necessary to understand these relationships more fully.

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## Tables

**Table 1.** Summary results of linear regression models. Values listed are the number of species (out of seven) with significant ( $p < 0.05$ ) responses (value after Holms-Bonferroni correction in parentheses). A) Responses of phenophase peak date and lag time to factors of melt date, location (Alpine Garden vs. Lakes of the Clouds), and their interaction. B) Phenophase peak date as a response of growing degree days (GDD), location, and their interaction. Phenophase peak is the Julian day when the maximum number of plants displayed a given phase. Lag is the number of days between melt date and phenophase peak (see Methods for description). Complete results in table S2.

A)	Peak				Lag			
	Shoots	Leaves	Fl. buds	Flowers	Shoots	Leaves	Fl. buds	Flowers
Regression	3 (1)	6 (4)	7 (2)	7 (4)	6 (2)	5 (2)	4 (2)	6 (3)
Melt date	4 (2)	6 (6)	7 (7)	7 (7)	6 (3)	6 (3)	6 (3)	7 (4)
Location	0	1 (1)	0	0	1 (0)	1 (1)	1 (0)	0
Melt date*Loc	0	1 (1)	0	0	1 (0)	1 (1)	1 (0)	0

B)	Peak			
	Shoots	Leaves	Fl. buds	Flowers
Regression	0	1 (0)	0	0
GDD	0	1 (0)	1 (0)	1 (0)
Location	0	0	0	0
GDD*Location	0	0	0	0

### Figure captions

**Figure 1.** Overview map of snowbank study sites on Mt. Washington, NH. Alpine Garden (AG) sites were on the slope to the east of the summit, and included sites HR2, HR4, AG1, AG2, AG15, AG16, AG19, AG20, AG21. Lakes of the Clouds (LC) sites were to the south and southwest of the summit and included sites LC2, LC5, MN3, MN4, and TK3. Inset of northeastern United States with Mt. Washington's location in New Hampshire (star).

**Figure 2.** Example plots of cumulative growing degree days (GDD) vs. phenological score (see Methods) for four phenophases of *Clintonia borealis*. Points are average value of scores for all plots visited on a given day; dark circles represent observations from Alpine Garden (AG), and open circles are Lakes of the Clouds plots (LC). See supplementary material (Fig. S4) for plots of remaining six species.

**Figure 3.** Example linear regression results for phenophase Leaves for seven focal snowbank species. a) Melt date vs. peak Leaves, and b) melt date vs. Leaves lag time (number of days between melt and peak). Black lines indicate melt date as a significant ( $p < 0.05$ ) factor; non-significant are gray. Consistent trends in peak and lag time were seen in all four phenophases. See supplementary material (Figs. S2, S3) for complete results.



Figures

Figure 1.

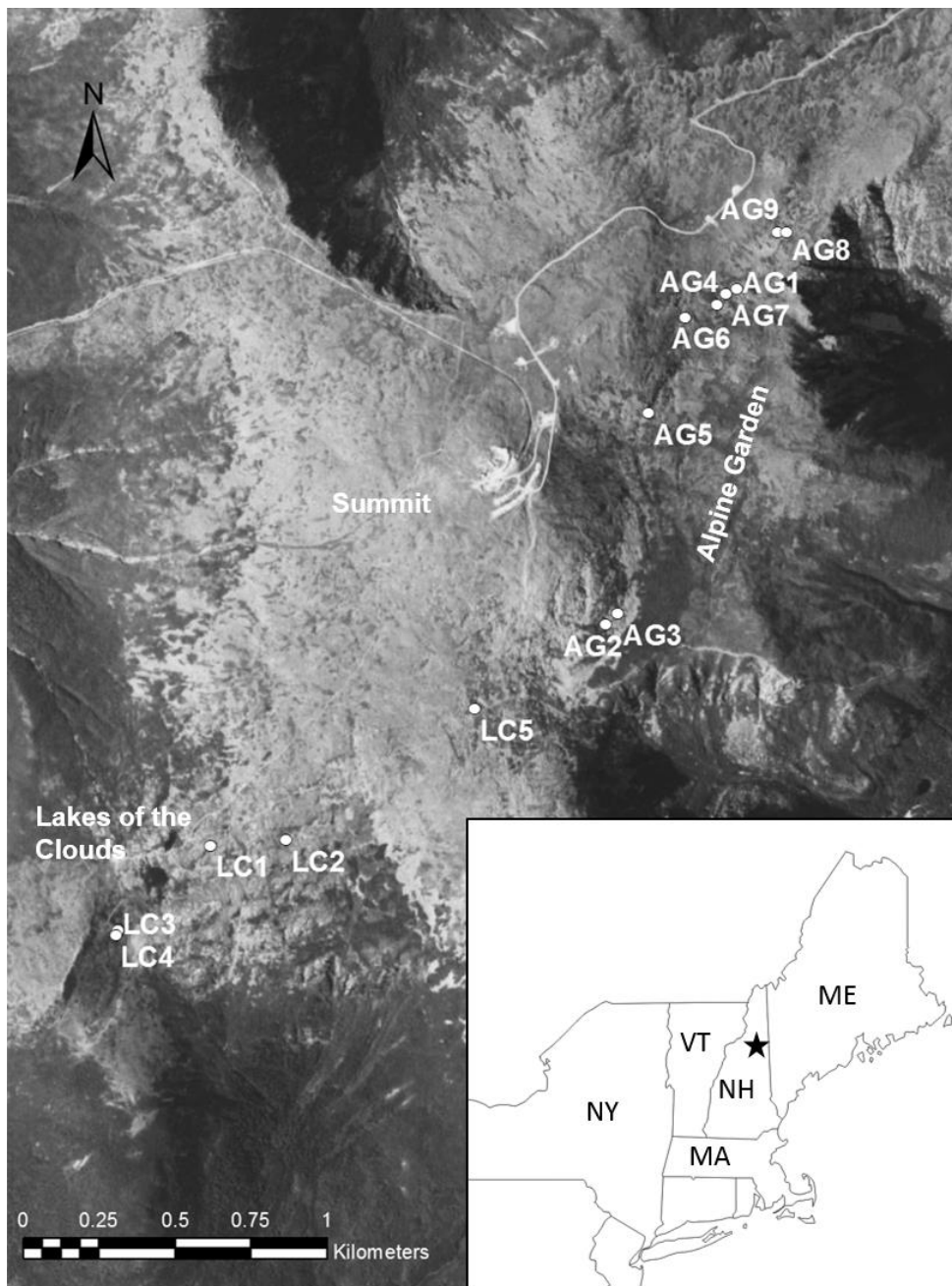


Figure 2.

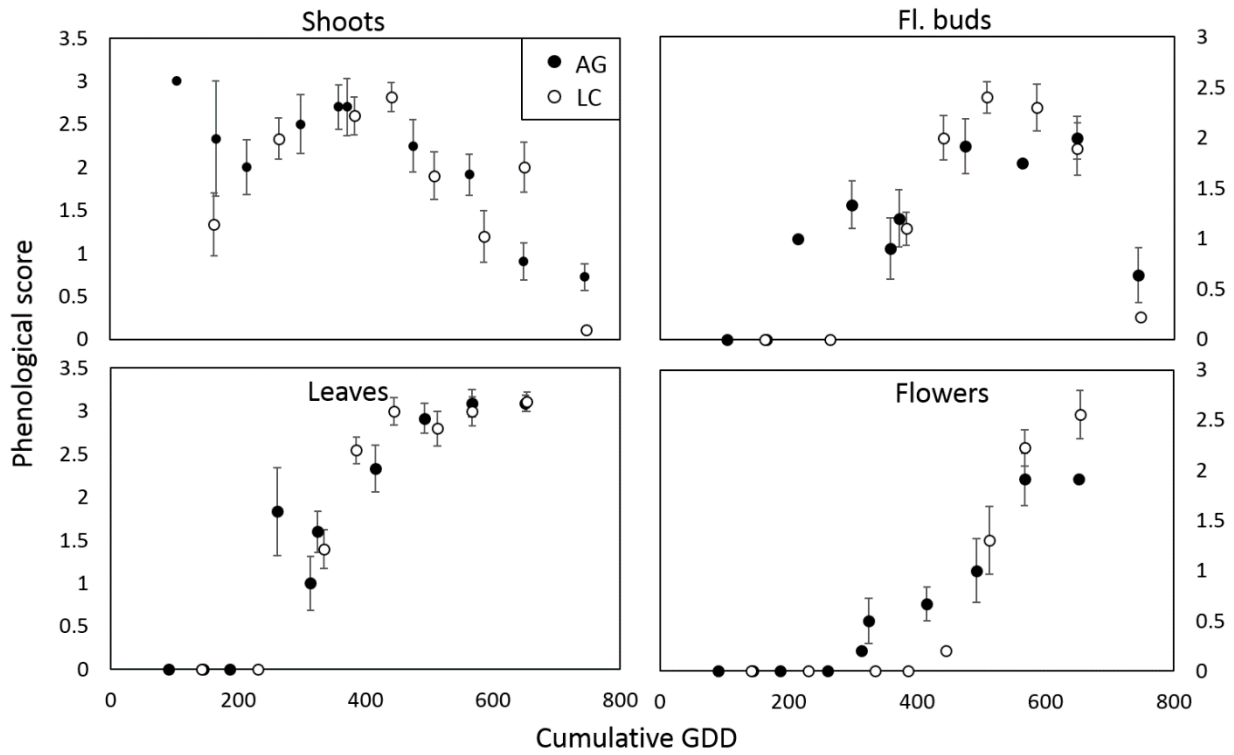
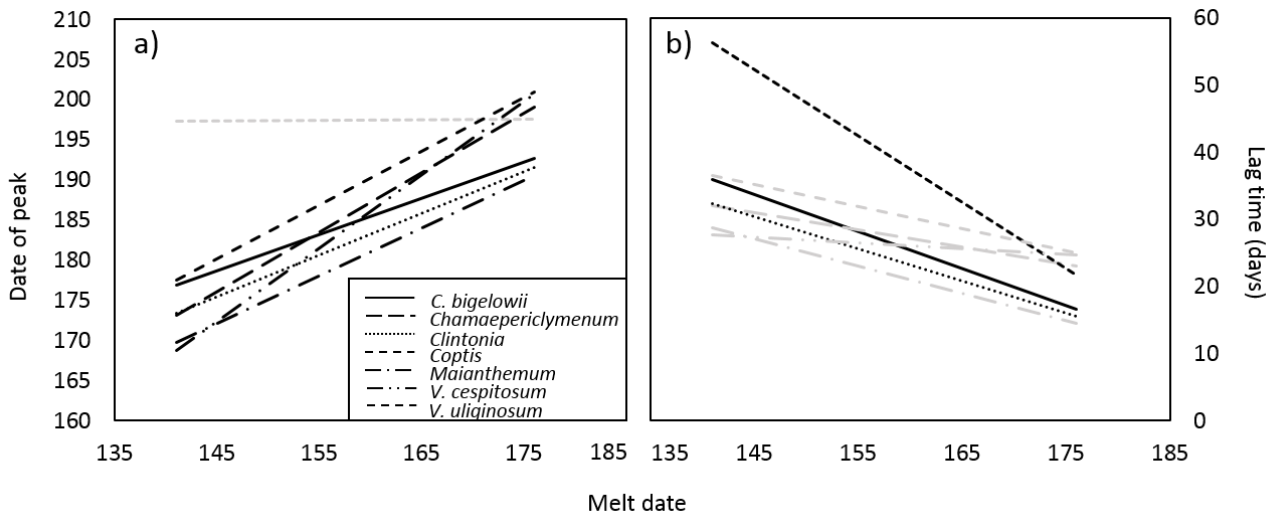


Figure 3.



Supplemental materials

**Table S1.** List of snowbank study sites on Mt. Washington. Melt date is the first observed day visited without snow cover at a plot, listed as Julian day. Two general site groupings were those in the Alpine Garden (AG) and those near the Lakes of the Clouds (LC).

Location	Site	Latitude	Longitude	Area (m <sup>2</sup> )	Elevation (m)	Plot	Melt date
AG	AG1	44.275615	-71.293405	10.4	1686.8	A	158
	AG2	44.265661	-71.298846	254.4	1635.3	A	150
	AG3	44.265989	-71.298358	51.3	1631.3	A	163
	AG4	44.275145	-71.294231	33.4	1701.1	A	172
						B	176
	AG5	44.271929	-71.297072	51.7	1718.8	A	148
	AG6	44.274764	-71.295524	112.7	1744.4	A	141
	AG7	44.275456	-71.293858	236.8	1699.3	A	172
						B	172
C						176	
AG8	44.277279	-71.291324	111.6	1689.2	A	163	
					B	163	
AG9	44.27727	-71.291694	24.3	1712.1	A	141	
LC	LC1	44.258995	-71.314881	299.2	1578.3	A	158
						B	147
	LC2	44.259319	-71.312098	16.8	1606.0	A	155
						B	155
						C	155
	LC3	44.256653	-71.319055	94.1	1556.7	A	155
	LC4	44.256498	-71.319145	378.7	1561.2	A	147
						B	162
						C	166
LC5	44.263171	-71.30429	88.4	1659.1	A	147	

**Table S2.** Full linear regression ANOVA results for four phenophases of peak date to predictors of snowmelt date, location, and their interaction for seven study species.

	Shoots					Leaves					Fl. Buds					Flowers				
	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p
<i>Carex bigelowii</i>	0.530	Regression	171.17	5.89	0.014	0.638	Regression	140.037	8.71	0.005	0.666	Regression	0.216756	8.98	0.005	0.889	Regression	306.682	33.05	0
		Melt date	222.07	7.64	0.02		Melt date	276.191	17.17	0.003		Melt date	0.585663	24.28	0.001		Melt date	880.823	94.92	0
		Location	129.72	4.46	0.061		Location	3.47	0.34	0.374		Location	0.011904	0.49	0.5		Location	4.6	0.5	0.489
		Melt date*Loc.	126.6	4.35	0.063		Melt date*Loc.	6.792	0.42	0.332		Melt date*Loc.	0.012605	0.52	0.488		Melt date*Loc.	4.433	0.48	0.507
<i>Chamaepericlymenum canadense</i>	0.680	Regression	171.28	9.3	0.004	0.809	Regression	273.17	17.94	0	0.827	Regression	202.371	20.12	0	0.803	Regression	154.923	17.29	0
		Melt date	428.67	23.77	0.001		Melt date	707.805	46.48	0		Melt date	590.559	38.72	0		Melt date	410.88	45.85	0
		Location	15.37	0.86	0.377		Location	0.531	0.03	0.856		Location	11.101	1.1	0.321		Location	1.476	0.16	0.694
		Melt date*Loc.	17.08	0.95	0.356		Melt date*Loc.	0.37	0.02	0.88		Melt date*Loc.	11.073	1.1	0.321		Melt date*Loc.	1.742	0.19	0.67
<i>Clinantia borealis</i>	0.154	Regression	83.74	1.73	0.231	0.594	Regression	129.353	6.86	0.011	0.856	Regression	117.004	24.76	0	0.756	Regression	122.943	12.34	0.002
		Melt date	212.88	4.39	0.066		Melt date	371.598	19.71	0.002		Melt date	344.28	72.85	0		Melt date	356.305	35.75	0
		Location	32.44	0.67	0.435		Location	9.667	0.51	0.492		Location	16.642	3.52	0.093		Location	0.623	0.06	0.809
		Melt date*Loc.	33.54	0.69	0.427		Melt date*Loc.	9.757	0.52	0.49		Melt date*Loc.	16.487	3.49	0.095		Melt date*Loc.	0.73	0.07	0.794
<i>Coptis trifolia</i>	0.000	Regression	26.2716	0.76	0.34	0.130	Regression	36.0146	1.65	0.24	0.774	Regression	199.364	11.29	0.007	0.803	Regression	109.553	18.69	0
		Melt date	26.0747	0.76	0.405		Melt date	0.1076	0	0.945		Melt date	392.408	22.23	0.003		Melt date	203.324	34.69	0
		Location	0.0001	0	0.999		Location	3.036	0.14	0.717		Location	3.618	0.2	0.667		Location	4.813	0.82	0.386
		Melt date*Loc.	0.0301	0	0.977		Melt date*Loc.	2.0885	0.1	0.763		Melt date*Loc.	4.291	0.24	0.64		Melt date*Loc.	3.953	0.67	0.431
<i>Mainthemon canadense</i>	0.379	Regression	342.078	3.64	0.052	0.735	Regression	227.289	14.37	0.001	0.632	Regression	200.97	8.44	0.004	0.654	Regression	88.77	7.92	0.009
		Melt date	635.528	6.77	0.026		Melt date	482.765	30.51	0		Melt date	533.38	22.39	0.001		Melt date	241.823	21.57	0.002
		Location	185.262	1.97	0.19		Location	1.065	0.07	0.801		Location	14.36	0.61	0.432		Location	1.964	0.18	0.687
		Melt date*Loc.	196.317	2.09	0.179		Melt date*Loc.	0.609	0.04	0.848		Melt date*Loc.	13.46	0.63	0.439		Melt date*Loc.	2.2	0.2	0.67
<i>Vaccinium cespitosum</i>	0.125	Regression	45	1.62	0.247	0.741	Regression	423.77	13.37	0.001	0.533	Regression	122.195	5.95	0.014	0.645	Regression	88.861	8.88	0.004
		Melt date	51.16	1.84	0.205		Melt date	1148.71	36.06	0		Melt date	347.008	16.89	0.002		Melt date	240.525	24.05	0.001
		Location	104.7	3.76	0.081		Location	17.34	0.54	0.478		Location	0.143	0.01	0.935		Location	25.505	2.55	0.141
		Melt date*Loc.	104.47	3.75	0.081		Melt date*Loc.	17.94	0.56	0.47		Melt date*Loc.	0.177	0.01	0.928		Melt date*Loc.	23.688	2.37	0.155
<i>Vaccinium uliginosum</i>	0.858	Regression	172.826	19.09	0.002	0.876	Regression	174.414	22.27	0.001	0.765	Regression	213.361	9.67	0.016	0.721	Regression	103.795	8.76	0.013
		Melt date	423.106	46.73	0		Melt date	412.309	52.85	0		Melt date	618.379	28.03	0.003		Melt date	295.524	24.93	0.002
		Location	1.896	0.21	0.663		Location	278.121	35.52	0.001		Location	7.712	0.35	0.58		Location	5.197	0.44	0.532
		Melt date*Loc.	3.207	0.35	0.573		Melt date*Loc.	274.778	35.09	0.001		Melt date*Loc.	7.047	0.32	0.596		Melt date*Loc.	4.168	0.35	0.573

**Table S3.** Full linear regression ANOVA results for four phenophases of lag time to predictors of snowmelt date, location, and their interaction for seven study species.

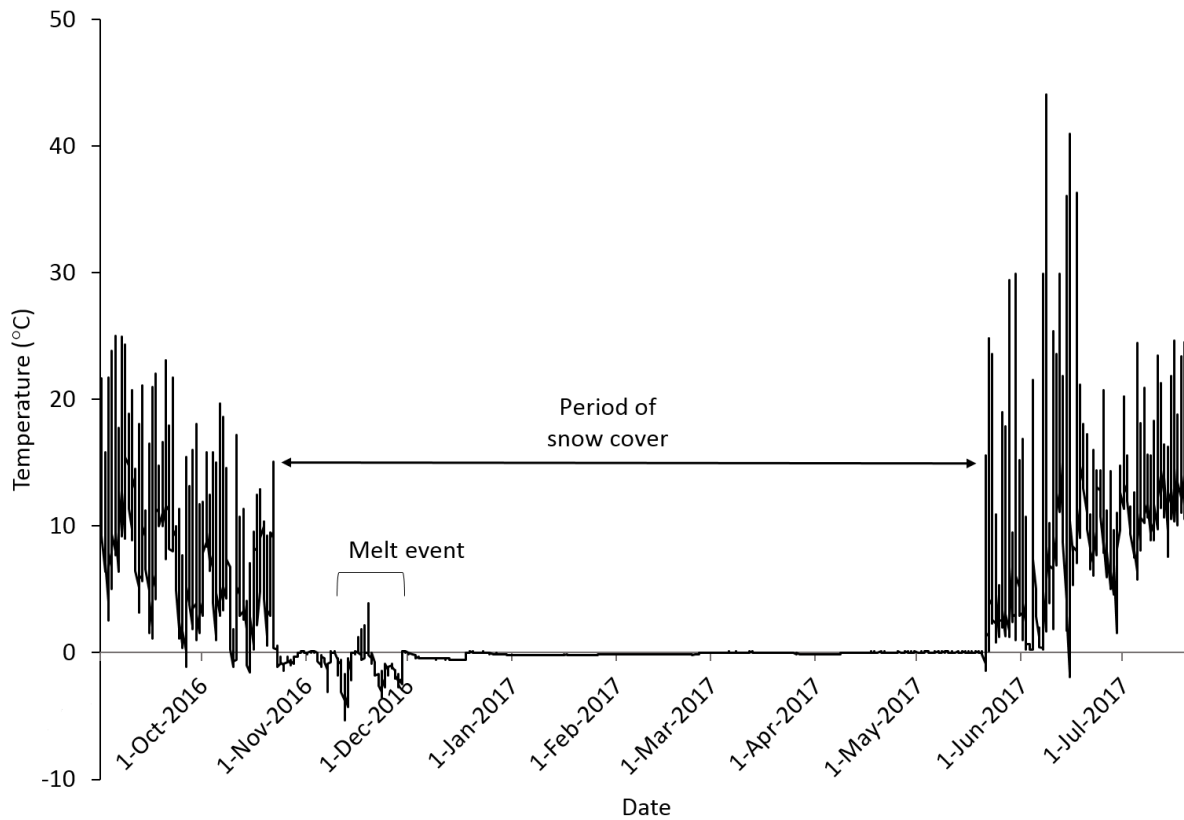
	Shoots					Leaves					Fl. Buds					Flowers				
	R2-edj.	Source	MS	F	p	R2-edj.	Source	MS	F	p	R2-edj.	Source	MS	F	p	R2-edj.	Source	MS	F	p
<i>Corax bigelowii</i>	0.541	Regression	177.65	6.11	0.012	0.696	Regression	163.605	10.17	0.003	0.800	Regression	142.959	17.03	0	0.328	Regression	27.139	2.95	0.091
		Melt date	489.03	16.82	0.002		Melt date	415.691	25.84	0.001		Melt date	293.262	34.94	0		Melt date	38.066	6.31	0.033
		Location	129.72	4.46	0.061		Location	5.47	0.34	0.574		Location	44.468	5.3	0.047		Location	4.342	0.47	0.509
		Melt date*Loc.	126.6	4.35	0.063		Melt date*Loc.	6.792	0.42	0.532		Melt date*Loc.	47.65	5.68	0.041		Melt date*Loc.	4.17	0.45	0.518
<i>Chamaepericlymenum canadense</i>	0.537	Regression	101.69	5.64	0.019	0.215	Regression	31.9477	2.1	0.171	0.548	Regression	58.77	5.84	0.017	0.694	Regression	90.147	10.06	0.003
		Melt date	231.36	12.83	0.006		Melt date	86.6802	5.69	0.041		Melt date	134.871	13.41	0.005		Melt date	244.755	27.31	0.001
		Location	15.37	0.86	0.377		Location	0.5306	0.03	0.856		Location	11.101	1.1	0.321		Location	1.476	0.16	0.694
		Melt date*Loc.	17.08	0.95	0.356		Melt date*Loc.	0.3688	0.02	0.88		Melt date*Loc.	11.075	1.1	0.321		Melt date*Loc.	1.742	0.19	0.67
<i>Clintonia borealis</i>	0.451	Regression	207.99	4.29	0.039	0.584	Regression	124.908	6.62	0.012	0.879	Regression	142.578	30.17	0	0.751	Regression	120.297	12.07	0.002
		Melt date	502.37	10.36	0.011		Melt date	314.375	16.67	0.003		Melt date	340.503	72.05	0		Melt date	328.75	32.99	0
		Location	32.44	0.67	0.435		Location	9.667	0.51	0.492		Location	16.842	3.52	0.093		Location	0.625	0.06	0.809
		Melt date*Loc.	33.34	0.69	0.427		Melt date*Loc.	9.757	0.52	0.49		Melt date*Loc.	16.487	3.49	0.095		Melt date*Loc.	0.73	0.07	0.794
<i>Copris trifolia</i>	0.684	Regression	357.24	10.37	0.002	0.825	Regression	466.85	21.38	0	0.411	Regression	53.213	3.09	0.111	0.872	Regression	178.126	30.39	0
		Melt date	1018.22	29.56	0		Melt date	1346	61.65	0		Melt date	119.034	6.91	0.039		Melt date	517.867	88.36	0
		Location	0	0	0.999		Location	3.04	0.14	0.717		Location	3.474	0.2	0.669		Location	4.813	0.62	0.386
		Melt date*Loc.	0.03	0	0.977		Melt date*Loc.	2.09	0.1	0.763		Melt date*Loc.	4.129	0.24	0.642		Melt date*Loc.	3.953	0.67	0.431
<i>Maianthemum canadense</i>	0.292	Regression	81.904	2.51	0.132	0.514	Regression	88.402	5.99	0.016	0.330	Regression	107.4	3.13	0.074	0.504	Regression	114.57	4.72	0.035
		Melt date	138.863	4.26	0.073		Melt date	226.32	14.3	0.004		Melt date	193.79	5.65	0.039		Melt date	245.71	10.12	0.013
		Location	56.315	1.73	0.225		Location	1.065	0.07	0.801		Location	43.88	1.28	0.285		Location	21.8	0.9	0.371
		Melt date*Loc.	57.17	1.75	0.222		Melt date*Loc.	0.609	0.04	0.848		Melt date*Loc.	47.11	1.37	0.269		Melt date*Loc.	23.57	0.97	0.353
<i>Vaccinium cespitosum</i>	0.755	Regression	398.95	14.34	0.001	0.00	Regression	12.242	0.38	0.767	0.546	Regression	127.655	6.22	0.012	0.840	Regression	237.083	23.7	0
		Melt date	891.79	32.05	0		Melt date	9.755	0.31	0.592		Melt date	338.107	16.46	0.002		Melt date	462.55	46.25	0
		Location	104.7	3.76	0.061		Location	17.339	0.54	0.478		Location	0.143	0.01	0.935		Location	25.505	2.55	0.141
		Melt date*Loc.	104.47	3.75	0.061		Melt date*Loc.	17.937	0.56	0.47		Melt date*Loc.	0.177	0.01	0.928		Melt date*Loc.	23.688	2.37	0.155
<i>Vaccinium uliginosum</i>	0.735	Regression	84.349	9.34	0.011	0.891	Regression	200.695	25.63	0.001	0.176	Regression	34.593	1.57	0.307	0.724	Regression	105.148	8.87	0.013
		Melt date	94.439	10.43	0.018		Melt date	99.643	12.72	0.012		Melt date	29.379	1.33	0.301		Melt date	171.524	14.47	0.009
		Location	1.896	0.21	0.663		Location	278.121	35.52	0.001		Location	7.712	0.35	0.58		Location	3.197	0.44	0.532
		Melt date*Loc.	3.207	0.35	0.573		Melt date*Loc.	274.778	35.09	0.001		Melt date*Loc.	7.047	0.32	0.596		Melt date*Loc.	4.168	0.35	0.575

**Table S4.** Full linear regression ANOVA results for four phenophases of peak date to predictors of growing degree days (GDD), location, and their interaction for seven study species.

	Shoots					Leaves					Fl. Buds					Flowers				
	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p	R2-adj.	Source	MS	F	p
<i>Corax bigelowii</i>	0.000	Regression	38.2193	0.59	0.643	0.062	Regression	42.996	1.18	0.407	0.572	Regression	0.10293	4.56	0.068	0.000	Regression	14.253	0.12	0.946
		Melt date	0.0078	0	0.992		Melt date	61.28	1.68	0.232		Melt date	0.24692	10.94	0.021		Melt date	34.34	0.28	0.618
		Location	80.0441	1.24	0.308		Location	2.601	0.07	0.8		Location	0.03188	1.41	0.288		Location	7.01	0.06	0.82
		Melt date*Loc.	53.214	0.82	0.399		Melt date*Loc.	1.212	0.03	0.863		Melt date*Loc.	0.02776	1.23	0.318		Melt date*Loc.	8.489	0.07	0.802
<i>Chamaepericlymenum canadense</i>	0.000	Regression	14.3381	0.16	0.92	0.700	Regression	178.89	7.22	0.029	0.000	Regression	53.51	0.75	0.559	0.000	Regression	19.48	0.3	0.826
		Melt date	0.7334	0.01	0.931		Melt date	522.19	21.08	0.006		Melt date	134.83	1.9	0.217		Melt date	51.02	0.78	0.411
		Location	0.8366	0.01	0.926		Location	45.21	1.82	0.235		Location	20.12	0.28	0.614		Location	6.329	0.1	0.766
		Melt date*Loc.	0.6192	0.01	0.937		Melt date*Loc.	42.99	1.74	0.245		Melt date*Loc.	22.59	0.32	0.593		Melt date*Loc.	7.945	0.12	0.739
<i>Clinantia borealis</i>	0.000	Regression	4.906	0.05	0.983	0.064	Regression	53.49	1.16	0.428	0.000	Regression	14.112	0.24	0.867	0.000	Regression	17.343	0.23	0.872
		Melt date	10.355	0.11	0.759		Melt date	146.11	3.17	0.15		Melt date	41.681	0.7	0.441		Melt date	1.733	0.02	0.885
		Location	5.209	0.05	0.829		Location	65.71	1.43	0.289		Location	5.573	0.09	0.772		Location	19.161	0.25	0.636
		Melt date*Loc.	7.93	0.08	0.79		Melt date*Loc.	75.36	1.63	0.27		Melt date*Loc.	6.046	0.1	0.763		Melt date*Loc.	19.236	0.26	0.635
<i>Coptis trifolia</i>	0.200	Regression	23.02	1.66	0.288	0.316	Regression	43.056	2.23	0.202	0.920	Regression	80.29	1.24	0.406	0.480	Regression	62.02	3.76	0.078
		Melt date	11.75	0.85	0.399		Melt date	0.0282	0	0.971		Melt date	113.88	1.75	0.256		Melt date	142.62	8.66	0.026
		Location	45.95	3.32	0.128		Location	29.0733	1.51	0.274		Location	49.95	0.77	0.43		Location	18.69	1.13	0.328
		Melt date*Loc.	39.37	2.85	0.152		Melt date*Loc.	17.4321	0.9	0.385		Melt date*Loc.	28.06	0.43	0.547		Melt date*Loc.	16.53	1	0.355
<i>Maianthemum canadense</i>	0.470	Regression	351.4	3.36	0.113	0.000	Regression	31.41	0.52	0.684	0.000	Regression	54.886	0.96	0.48	0.000	Regression	9.428	0.12	0.941
		Melt date	33.36	0.32	0.597		Melt date	47.68	0.79	0.409		Melt date	48.246	0.84	0.401		Melt date	11.77	0.15	0.722
		Location	532.9	5.1	0.074		Location	28.53	0.47	0.518		Location	3.364	0.06	0.818		Location	2.879	0.04	0.859
		Melt date*Loc.	398.83	3.81	0.108		Melt date*Loc.	20.95	0.35	0.578		Melt date*Loc.	2.92	0.05	0.83		Melt date*Loc.	2.755	0.04	0.862
<i>Vaccinium cespitosum</i>	0.000	Regression	25.3145	0.65	0.613	0.127	Regression	140.71	1.44	0.321	0.000	Regression	44.663	0.72	0.376	0.000	Regression	0.9612	0.02	0.995
		Melt date	35.367	0.9	0.379		Melt date	380.35	3.88	0.086		Melt date	131.89	2.12	0.195		Melt date	0.7172	0.02	0.903
		Location	0.6911	0.02	0.899		Location	18.57	0.19	0.679		Location	0.742	0.01	0.917		Location	0.4699	0.01	0.922
		Melt date*Loc.	0.0467	0	0.974		Melt date*Loc.	20.25	0.21	0.665		Melt date*Loc.	0.95	0.02	0.906		Melt date*Loc.	0.682	0.02	0.906
<i>Vaccinium uliginosum</i>	0.183	Regression	98.06	1.45	0.384	0.000	Regression	37.536	0.4	0.763	0.000	Regression	112.922	0.64	0.656	0.000	Regression	20.6687	0.24	0.861
		Melt date	219.92	3.25	0.169		Melt date	39.8063	0.43	0.56		Melt date	324.235	1.85	0.307		Melt date	50.8718	0.6	0.484
		Location	235.08	3.47	0.159		Location	0.2506	0	0.962		Location	8.637	0.05	0.845		Location	0.3237	0	0.955
		Melt date*Loc.	271.82	4.01	0.139		Melt date*Loc.	0.5108	0.01	0.946		Melt date*Loc.	13.205	0.08	0.81		Melt date*Loc.	0.0197	0	0.989

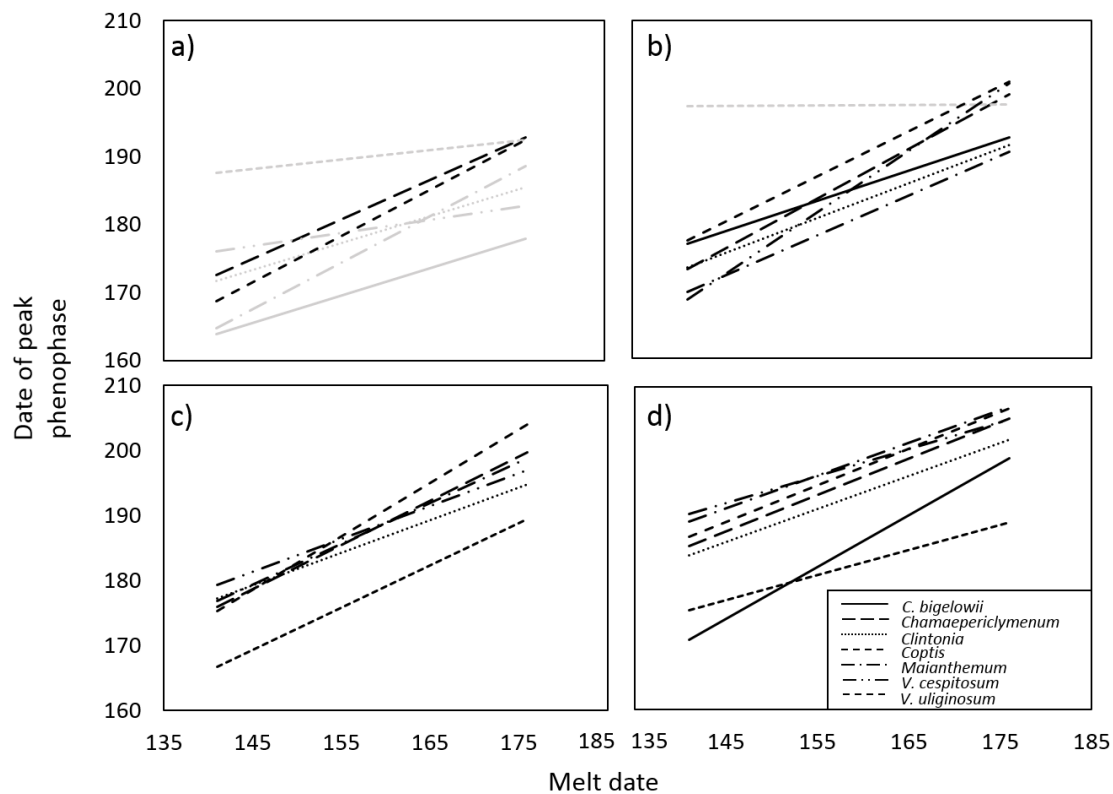
**Table S5.** Mean cumulative growing degree days (GDD) ( $\pm$ SE) to peak phenophase for seven snowbank species at both Alpine Garden (AG) and Lakes of the Clouds (LC) sites. Arranged by increasing GDD for Shoots at AG sites.

Species	Shoots				Leaves				Fl. buds				Flowers			
	AG		LC		AG		LC		AG		LC		AG		LC	
	GDD		GDD		GDD		GDD		GDD		GDD		GDD		GDD	
<i>Carex bigelowii</i>	236.5	(7.1)	287.0	(11.7)	427.7	(6.0)	385.5	(1.8)	413.9	(5.4)	381.1	(1.0)	429.8	(2.6)	463.5	(5.8)
<i>Maianthemum canadense</i>	296.6	(6.5)	215.8	(15.3)	361.7	(5.9)	347.3	(4.1)	466.3	(5.9)	451.8	(10.4)	615.2	(5.0)	555.4	(2.2)
<i>Clintonia borealis</i>	322.0	(13.2)	363.1	(4.9)	389.7	(7.7)	429.3	(3.6)	438.7	(5.1)	482.3	(2.5)	540.8	(2.9)	596.6	(7.5)
<i>Vaccinium uliginosum</i>	345.2	(5.5)	493.8	(12.6)	501.7	(7.3)	536.9	(13.2)	499.7	(11.4)	533.3	(10.1)	595.9	(12.7)	683.8	(7.8)
<i>Vaccinium cespitosum</i>	361.1	(11.0)	375.0	(7.1)	447.1	(9.7)	447.4	(9.5)	498.2	(5.3)	515.1	(2.2)	626.1	(4.4)	689.4	(7.0)
<i>Chamaepericlymenum canadense</i>	383.2	(5.5)	381.9	(0.7)	458.9	(6.4)	444.7	(1.7)	465.7	(4.8)	477.9	(6.3)	552.3	(4.9)	588.7	(3.0)
<i>Coptis trifolia</i>	484.8	(9.9)	505.3	(4.7)	583.9	(11.8)	546.2	(6.8)	327.3	(4.2)	312.9	(5.8)	377.6	(5.4)	373.2	(1.2)

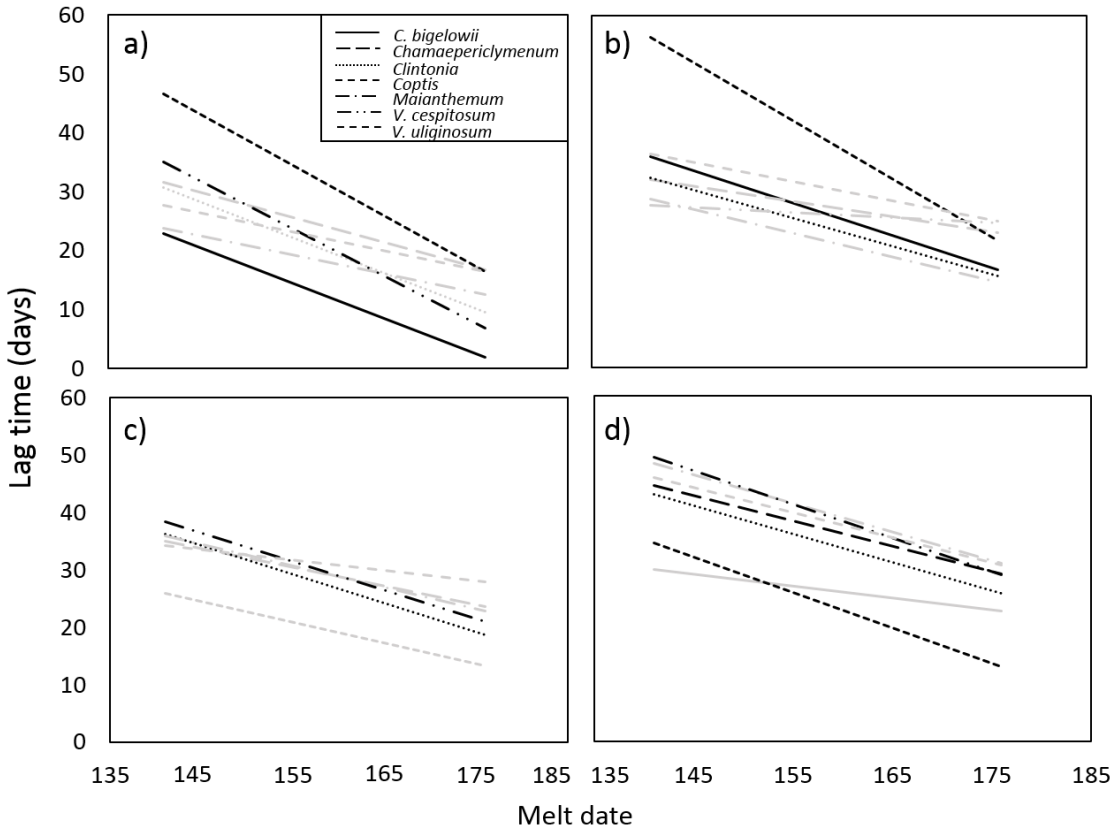


**Figure S1.** Example seasonal temperature data from study site AG6. This site was snow-covered from approximately 23 Oct. 2016 - 21 May 2017, during which time the soil surface remained at 0°C. Note large daily temperature fluctuations before onset of snow cover and after melt-out. A late-fall melt event is indicated by brackets.





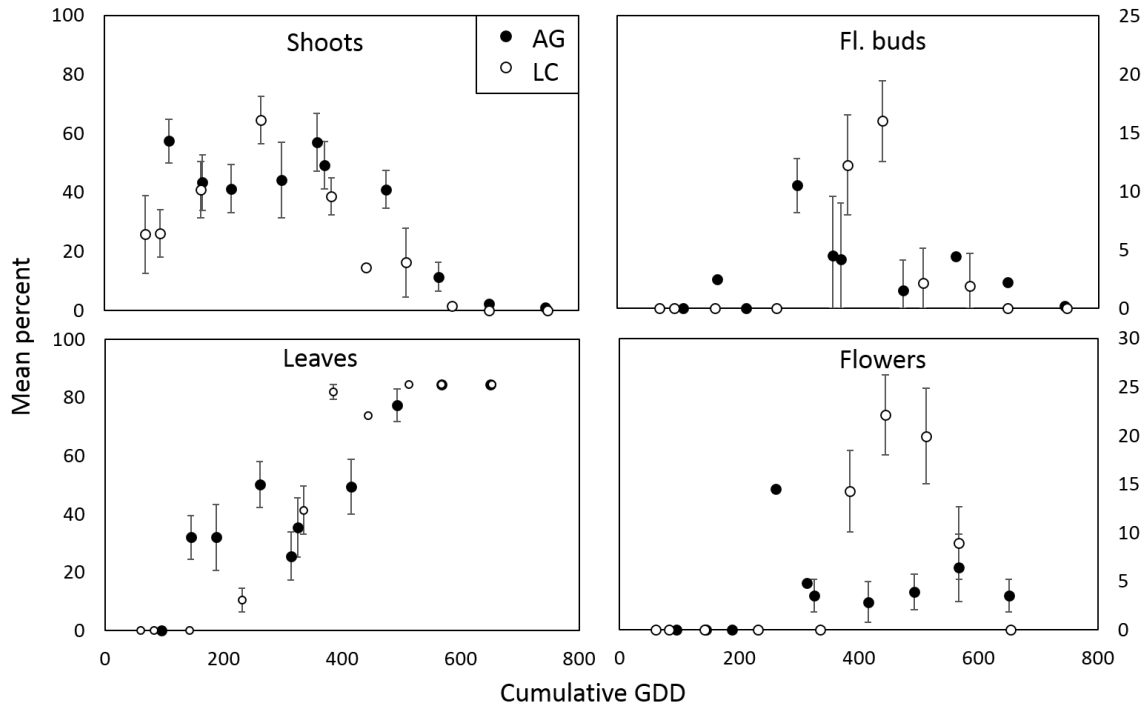
**Figure S2.** Results of linear regression models for response of peak phenophase date to predictor of melt date for seven study species. Phenophases are a) Shoots, b) Leaves (repeated from Fig. 3), c) Fl. buds, and d) Flowers. Black lines indicate melt date as a significant ( $p < 0.05$ ) factor; gray are non-significant. *C. bigelowii* omitted from Fl. buds plot because data were arcsine-square root transformed.



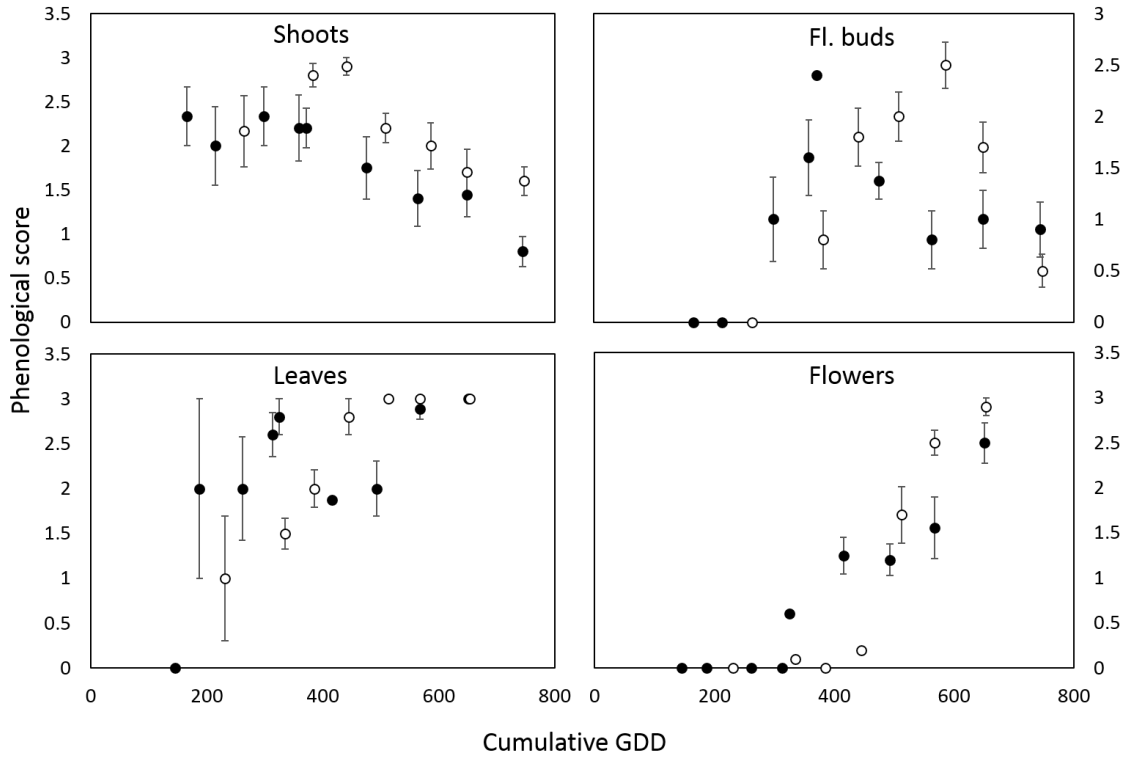
**Figure S3.** Results of linear regression models for response of lag time to predictor of melt date for seven study species. Phenophases are a) Shoots, b) Leaves (repeated from Fig. 3), c) Fl. buds, and d) Flowers. Black lines indicate melt date as a significant ( $p < 0.05$ ) factor; gray are non-significant. *C. bigelowii* omitted from Fl. buds plot because data were arcsine-square root transformed.

**Figure S4.** (A-F) Full phenophase charts for remaining six species. Phenology observations taken as percent of plants exhibiting a given phenophase (*C. bigelowii*, *C. trifolia*, *V. cespitosum*, and *V. uliginosum*) or abundance, as phenological score (*C. canadense* and *M. canadense*) (see Methods). Points represent mean percents or phenological scores from either Alpine Garden (AG, dark circles) or Lakes of the Clouds (LC, open circles) sites for a given day visited plotted against cumulative growing degree days (GDD). Species are A) *Carex bigelowii*, B) *Chamaepericlymenum canadense*, C) *Coptis trifolia*, D) *Maianthemum canadense*, E) *Vaccinium cespitosum*, and F) *V. uliginosum*.

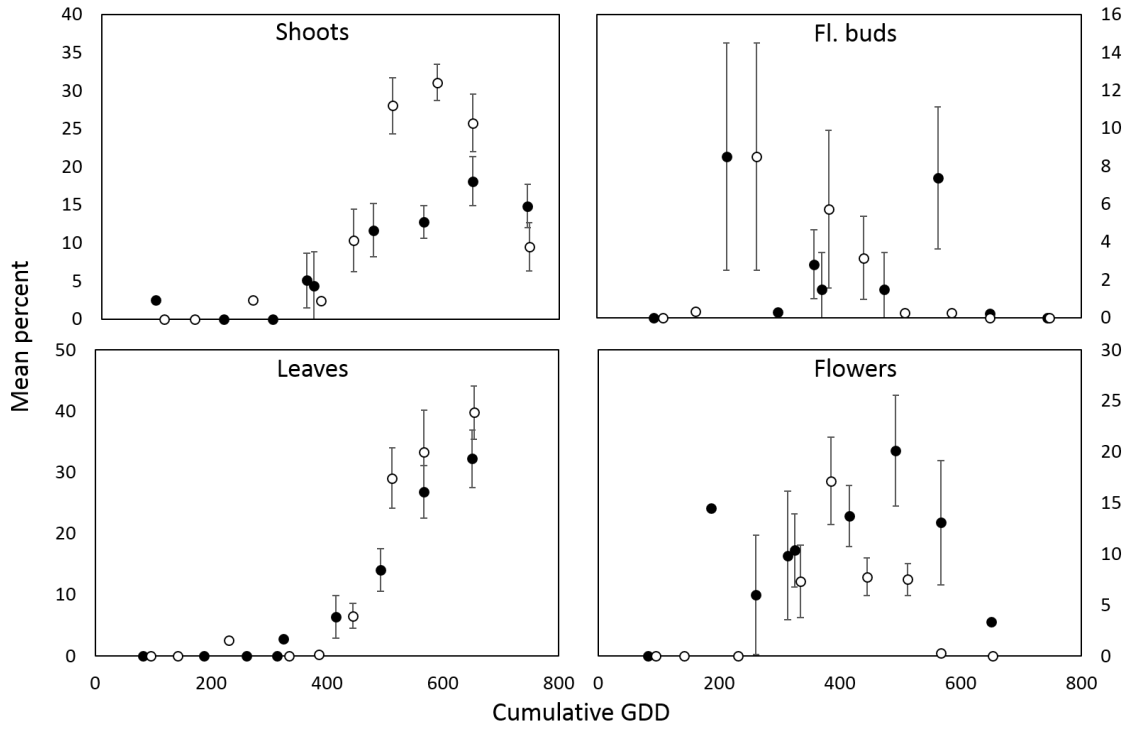
A) *Carex bigelowii*



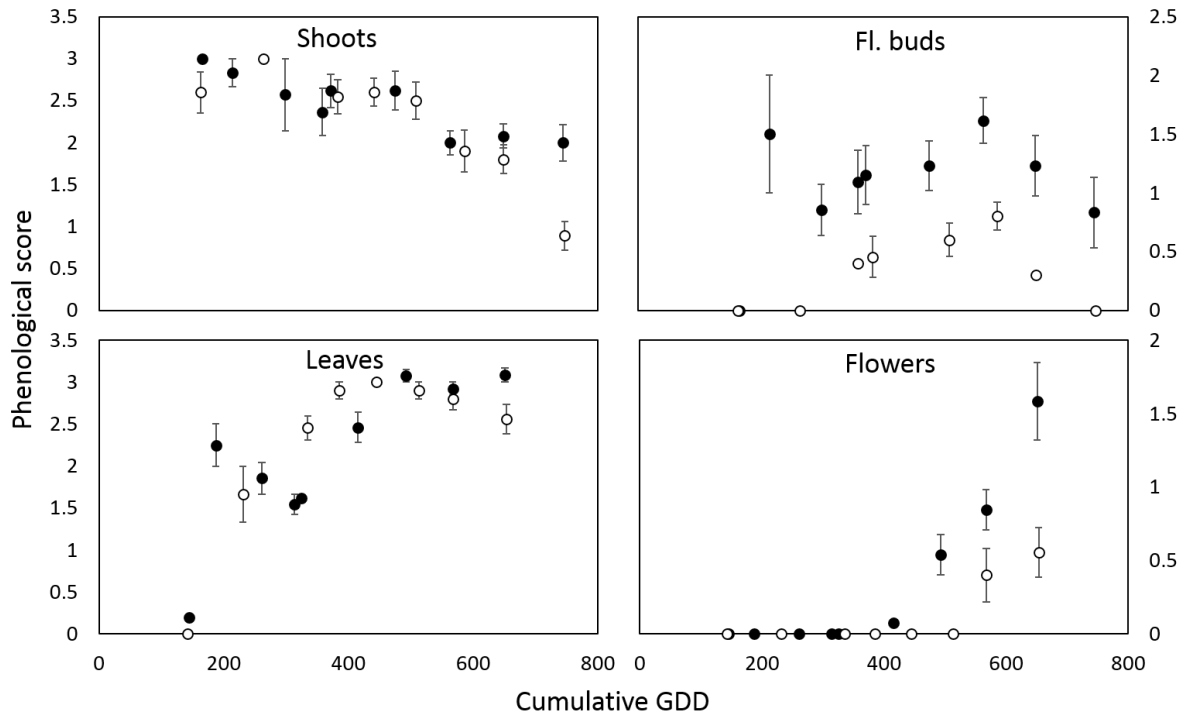
B) *Chamaepericlymenum canadense*



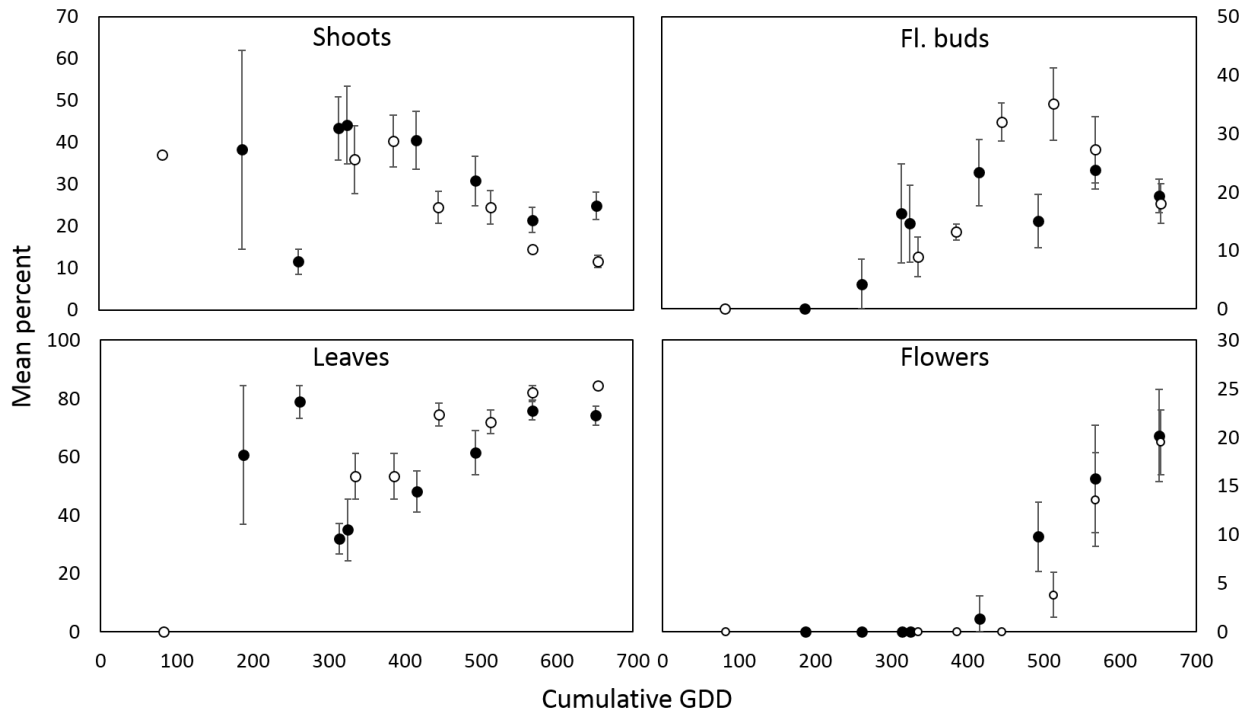
C) *Coptis trifolia*



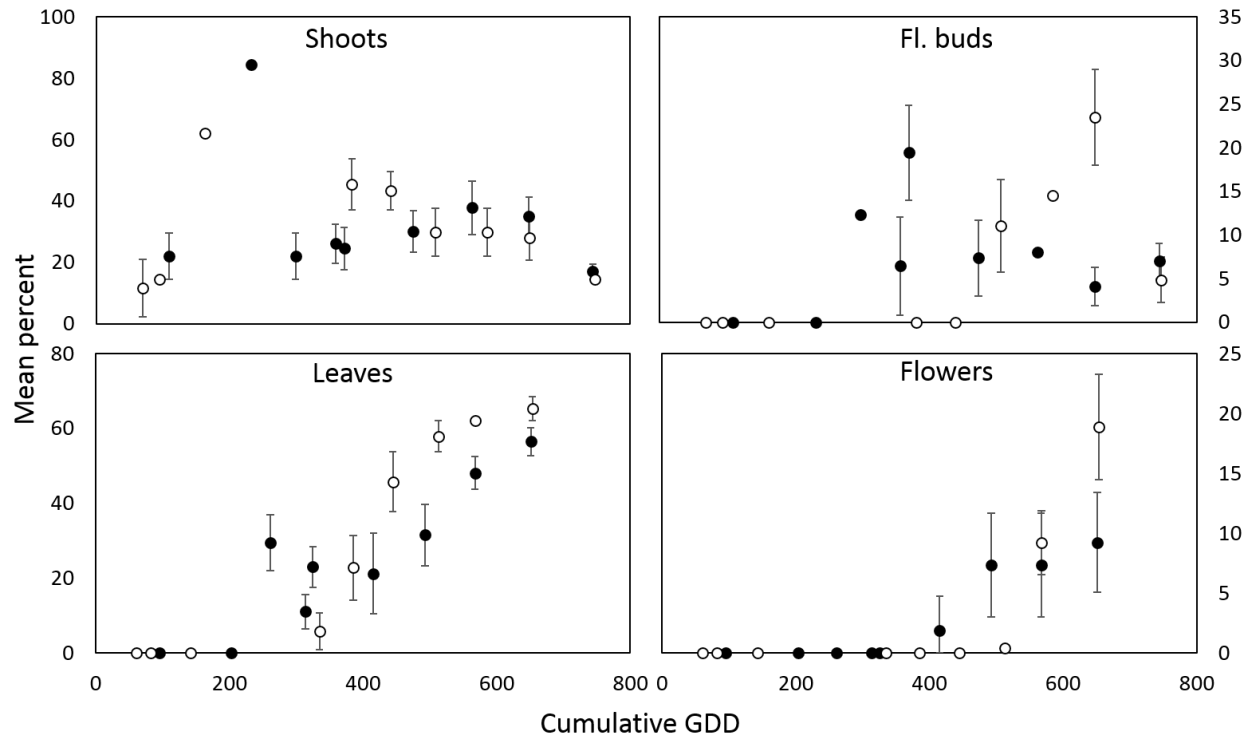
D) *Maianthemum canadense*



E) *Vaccinium cespitosum*



F) *Vaccinium uliginosum*



Plant traits and community metrics across a snowmelt gradient

at alpine snowbank sites on Mt. Washington, NH

K. Berend, K. Amatangelo, D. Weihrauch, C. Norment, and M. Penberthy

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 studied community composition and plant traits across a gradient of snowmelt timing at snowbank sites on Mt. Washington, NH. We used nMDS ordination and ANOSIM to examine community composition across the snowmelt gradient, and measured plant traits (height, leaf dry matter content, leaf area, and specific leaf area) in several comparisons. We calculated community-weighted mean trait values across the snowmelt gradient and phenotypic plasticity of four focal snowbank species (*Carex bigelowii*, *Chamaepericlymenum canadense*, *Clintonia borealis*, and *Maianthemum canadense*) between snowbank core and edge habitats. ANOVAs indicated that vascular plant diversity increased and lichen diversity decreased with later melt date; no trend was evident in bryophytes. ANOSIM indicated that vascular plant and bryophyte/lichen communities were significantly stratified across the snowmelt gradient. In the community-weighted mean trait analyses, height, leaf area, and specific leaf area increased with later snowmelt, and leaf dry matter content decreased; the four focal species showed matching responses in traits across the snowmelt gradient, except for *M. canadense*, which was shorter in snowbed cores, though not significantly. The transition in trait values across the snowmelt gradient is indicative of changing environmental conditions, as well as changing ecosystem functions occurring there. Genetic analysis may be necessary to evaluate population dynamics among isolated alpine communities. Given their sensitivity to environmental conditions, alpine snowbank communities are considered vulnerable to climate change or displacement by exotic or lowland species.

*Keywords:* Alpine, snowbed, plants, northeast, Mt. Washington, traits, gradient, diversity, community-weighted mean, common garden

## Introduction

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 lee of sheer rock faces, where late-lying snow provides insulation from late-season frosts and a longer-lasting source of water (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. (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*, *Geum peckii*, *Nabalus bootii*, *Vahlodia atropurpurea*, and *Vaccinium cespitosum*) (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 (Zwinger and Willard, 1996; McFarland, 2003; Björk and Molau, 2007; McFarland et al., 2017). 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 (Dibble et al., 2009; Capers and Slack, 2016). In the Northeast, the most extensive alpine snowbank communities exist in the Presidential Range of the White Mountains, NH and Mt. Katahdin, ME (Kimball and Weihrauch, 2000), but they also occur in the Adirondack Mountains of NY State (Carlson et al., 2011) and high-elevation areas of Quebec 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, removing all species without a specified 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., Fonseca et al., 2000; Wright et al., 2002; Choler, 2005; Cornwell and Ackerly, 2009; Shimono et al., 2009; Guittar et al., 2016). 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 (Wright et al., 2004; Pérez-Harguindeguy et al., 2013). 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 in the alpine environment. 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 can also be considerable (Albert et al., 2010; Jung et al.,

2010), 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, though. 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 (e.g., early/late snowmelt), and there is some evidence that this separation may lead to genetic divergence among substantially isolated metapopulations of plants (Hirao and Kudo, 2004; Stöcklin et al., 2009; Cortés et al., 2014). 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, (Mooney and Billings, 1961; Billings, 1974), there is the possibility that through isolation and speciation, ecotypic differences may exist 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 habitats in the region, and identifying alpine-adapted ecotypes of snowbank species could be important in terms of taxonomy, biogeographic history, and conservation priorities for species or communities.

Alpine snowbank communities are particularly sensitive to environmental change (Galen and Stanton, 1995; Björk and Molau, 2007). Due to both their rarity and reliance on specific environmental conditions, they are listed as “critically imperiled” (S1) by the states of NY, NH and ME (Gawler and Cutko, 2010; Sperduto and Nichols, 2011; Edinger, G. J. et al., 2014). Monitoring community change in these habitats, then, may identify broader alpine community change due to climatic shifts. Thus, a better understanding of snowbank community composition in relation to snowmelt timing in northeastern North America has been identified as a top priority by researchers in the region (Capers et al., 2013). 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. Here, we extend the scope of this 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.

The objectives of this study were five-fold: 1) evaluate community metrics (diversity and richness) in relation to snowmelt date at snowbank sites on Mt. Washington, NH; 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; 4) quantify and compare *in-situ* inter- and intraspecific trait values (and their variability) of snowbank species between alpine and low-elevation sites; and 5) compare observed traits of one focal snowbank species grown in a common garden to those of conspecifics from the natural environment.

## Methods

### **Site description**

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 (Fig. 1, inset). Treeline is approximately 1500 m, but varies considerably based on exposure and topography (Kimball and Weihrauch, 2000). Mt. 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. The majority 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, but several other sites exist near the Appalachian Mountain Club's (AMC) Lakes of the Clouds hut (LC), 1.8 km southwest of the summit. In June 2016, we identified 15 contiguous snowbank sites across both areas (AG=9, LC=6) (Fig. 1) by topography and the presence of indicator species (Dibble et al.,

2009; Sperduto and Nichols, 2011; Capers and Slack, 2016), and marked the location of each with a handheld GPS unit (Garmin GPSMAP®64, Garmin Ltd., Olathe, KS). We also selected six low-elevation sites near the Appalachian Mountain Club's Pinkham Notch Visitor Center where four focal snowbank species were abundant. These sites were used as low-elevation replicates for comparisons of trait values (see below).

### **Sampling design**

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, while smaller sites had only one (total # transects = 25). The core of each transect was determined based on literature descriptions of snowbed communities (Bliss, 1963; Sperduto and Nichols, 2011; Capers and Slack, 2016) and local topography. We sought to follow the snowmelt gradient outward from the snowbeds across a smooth transition in plant communities to its margin, or “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 flat; 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, except when local topography or vegetation gradients were unsuitable, such as across rock scree. We placed a magnetic survey marker (SurvKap®, Tucson, AZ) 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 in the same manner, we placed a temperature datalogger (OnSet HOBOTM Pendant® UA-002-08, Bourne, MA) every 3 m along one transect at every site (except LC5 and LC6, due to datalogger constraints and proximity to federally-designated wilderness, respectively).

In May 2017, we returned to study sites while still snow-covered, relocated the transects using a magnetic survey locator (CST Magna-Trak® 100), and temporarily marked the ends with stakes. We revisited each transect every 3-5 d and recorded snow depth measurements (max. 320 cm) every 3 m

along them using an avalanche probe (Black Diamond® Equipment, Salt Lake City, UT) until the entire transect was snow-free. The first day visited when a given quadrat was entirely snow-free was recorded as its melt date. Site LC6 was not monitored; because it lies in federally-protected wilderness, no dataloggers or magnetic markers were left there.

## **Vegetation**

From June-July 2016, we collected community composition data every 3 m along each transect (coinciding with snow depth measurements) using a 1 m<sup>2</sup> quadrat. For example, transects 12 m in length had five quadrats, at 0, 3, 6, 9, and 12 m. 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.

## **Trait sampling**

In July 2017, we collected specimens for trait analyses from sites AG4, AG7, AG8, LC1, and LC4. Using cover data from community composition sampling, we calculated the proportional number of species to sample from each site and each end (core or edge) of a transect based on sample sizes needed for both CWM and focal species analyses (below) and collected specimens from either the core or edge accordingly. For example, a species with higher abundance in the core at a given site warranted more samples being collected there. 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 community-weighted mean (CWM) analyses, we collected 10 individuals each of the 15 most abundant/frequent species across all quadrats, based on community composition data: *Carex bigelowii* Torr. ex Schwein., *Chamaepericlymenum canadense* (L.) Aschers. & Graebn., *Clintonia borealis* (Ait.) Raf., *Coptis trifolia* (L.) Salisb., *Deschampsia flexuosa* (L.) Trin., *Empetrum nigrum* L., *Juncus trifidus* L., *Maianthemum canadense* Desf., *Streptopus lanceolatus* (Ait.) Reveal, *Solidago*

*macrophylla* Pursh, *Spiraea alba* Du Roi, *Vaccinium angustifolium* Ait., *V. cespitosum* Michx., *V. uliginosum* L., and *Veratrum viride* Ait. All nomenclature is after Haines et al. (2011).

To assess inter- and intraspecific trait variation across the snowmelt gradient at alpine sites, we selected five abundant snowbank species from the above list for closer analysis: *Carex bigelowii*, *Chamaepericlymenum canadense*, *Clintonia borealis*, *Coptis trifolia*, and *Maianthemum canadense*. We randomly collected (as above) three specimens of each species in the cores of each transect at the five alpine sites. We spread collection across all transect cores for sites with more than one transect (e.g., at sites AG4, AG7, and LC4, each with three transects, we collected one specimen of each species from each transect core). We also collected a total of at least 15 specimens from edge quadrats—distributed proportionally across sites, for comparison.

We also aimed to assess trait differences and variability between alpine and low-elevation (or lowland) source populations for species that were found abundantly in both locations: *Chamaepericlymenum canadense*, *Clintonia borealis*, *Coptis trifolia*, and *Maianthemum canadense*. In addition to the collection from alpine site cores distributed across sites (as above, 3 replicates each), we collected an additional twelve (total of 15 replicates) from the cores of one large site (or “megasite”, AG7) to assess intra-site variability. We duplicated both the dispersed and concentrated collection procedures at six low-elevation sites near PNVC, with site R5 serving as the megasite (Fig. 1).

### **Specimen processing**

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, blotted dry, and weighed on a digital balance (wet weight). Only a single leaf blade was used for *Maianthemum canadense*, *Deschampsia flexuosa*, and *Juncus trifidus*, while a short stem clipping (~3 cm, with leaves attached) was used for *Empetrum nigrum* 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, MD). Leaves were dried at 70°C for 48 h, then re-weighed (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<sup>2</sup> per mg dry weight. Replicates were averaged to obtain a single leaf area, LDMC, and SLA value for each individual.

### **Common garden**

In August 2016, we collected ripe fruits of *Chamaepericlymenum canadense* from eight alpine sites on Mt. Washington and three lowland sites near Pinkham Notch Visitor Center, and allowed them to dry in paper bags. Care was taken to follow available collection guidelines (Guerrant et al., 2014; Hoban and Schlarbaum, 2014). At the College at Brockport, seeds from each collection site were kept separate and prepared according to published germination guidelines (see Cullina, 2000; USDA). Fruits were soaked in a weak water/apple cider vinegar solution for 24 h, pulsed in a dulled blender, and strained to separate seed from pulp. After allowed to air dry completely, seeds were scarified in 90% sulfuric acid for 15 min, and rinsed. Seeds from each collection source were placed in a separate plastic bag (n=11) with a moist mix of peat, vermiculite, and potting soil, and allowed to undergo warm-moist stratification (room temperature) for six weeks. Bags were then moved to 4°C for another 25 weeks for cold stratification. Bags were opened weekly and kneaded gently by hand during both warm and cold stratification periods to mix soil media and allow for gas exchange. At the end of the cold-stratification period, bags were opened slightly, placed flat in a germination chamber at 21°C day/10°C night, and checked daily for signs of germination.

After 30 d (on 1 May 2017), seedlings were transplanted into individual 8.9 x 8.9 cm square plastic pots with a mix of peat, vermiculite, perlite, sand, and potting soil, and topped with ~1-2 cm crushed pine straw. Pots were placed in trays of 18 pots each, arranged on benches in the College at Brockport greenhouse, and watered/rotated every 2-3 d. Plants were allowed to grow for the duration of

the summer. During growth, the greenhouse was covered with partial-transmittance shade cloth and temperature was limited to 27°C, as *C. canadense* is intolerant of full sun and high soil temperatures. In August 2017, we processed plants in the lab as described above, collecting trait data (height, LDMC, leaf area, and SLA) for each surviving plant as a separate replicate.

## **Data analysis**

### *Diversity metrics*

We created three categories of quadrat types for 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. Using community composition data, we calculated species richness and Shannon-Weiner diversity ( $H'$ ) for each taxon type (vascular plants, bryophytes, and lichens) at core, transition, and edge quadrats.

We then performed two-sample t-tests to assess differences in diversity ( $H'$ ) and species richness by site location (Alpine Garden vs. Lakes of the Clouds) for each taxon. 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 two-way ANOVAs for each taxon by quadrat type, blocked by site. Lichens had a large number of zero values for diversity, richness, and cover, so those cases were excluded for ANOVAs of that taxa type. 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, PA).

### *Ordinations*

Using temperature data, we calculated cumulative growing degree days (GDD) for the 2017 study period (Julian d 1-201) by the average method (daily max-daily min/2; 0°C was used as the threshold



temperature). 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).

We performed two initial non-metric multidimensional scaling (nMDS) ordinations, one for vascular plants only and another for bryophytes and lichens. We used a secondary matrix with additional variables (melt date, GDD, and quadrat type) for these analyses, and overlaid the vectors for environmental variables as a biplot. For the bryophyte/lichen ordination, we eliminated rare species (frequency <5% of quadrats) to improve stress and, where applicable, combined taxa of uncertain identification to the genus level. We did not include quadrats that crossed rock screes, or the two sites where no dataloggers were present (LC5 and LC6), as nMDS is intolerant to missing values (McCune et al., 2002). Repeating the analyses with these sites included, though, did not yield major differences in grouping structure.

We then performed a third nMDS ordination using core quadrat data only and all taxa types to look for general floristic similarities across sites rather than by quadrat type within sites. For this ordination, 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, OR), and Sorenson/Bray-Curtis was used as a distance measure.

We used analysis of similarity (ANOSIM) to evaluate differences in community composition in three separate tests, one for each similarity matrix used in ordinations: vascular plants by quadrat type (core/transition/edge), mosses and lichens by quadrat type, and all taxa (site cores only) by location (AG and LC). ANOSIMs were performed in PRIMER (v. 6, PRIMER-E Ltd., 2013).

#### *CWM calculations*

We calculated mean trait values for the 15 most abundant/frequent vascular plant species, based on specimens collected in the field. To calculate community-weighted mean (CWM) trait values, we used

the average cover of each taxa by quadrat type at each site, as mentioned above. The CWM values for each measured trait (height, LDMC, leaf area, and SLA) were calculated 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. This yielded a CWM value for each quadrat type at each site. Using these data, we performed separate one-way ANOVAs for all four measured traits (response: trait value, factor: quadrat type), and post-hoc Tukey's pairwise comparisons to find groupings of significant ANOVAs. Leaf area data were log-transformed for normality prior to analysis.

#### *Core/edge trait comparisons*

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-edge). We then performed two-sample t-tests using core and edge trait data for each species to evaluate differences statistically.

#### *Alpine/lowland trait comparisons*

We calculated a phenotypic plasticity index (PPI) as a measure of trait variability for each species by site (Valladares et al., 2000). We then performed two sets of analyses based on the two sampling strategies, dispersed and concentrated. Traits and PPI were averaged by site, and we performed a two-sample t-test using trait values for each trait/species combination, comparing the alpine and lowland values for both the dispersed and concentrated data sets. We then performed two-sample t-tests using PPI data for each species/trait combination in the same manner. This test was not possible for the concentrated data set because of insufficient replication (only one alpine and lowland "megasite" each). We then performed paired t-tests (paired by species) using average trait values and PPI by site for both the dispersed and concentrated data sets, again comparing alpine to lowland source populations. We used a Holms-Bonferroni correction for family-wise error rate within each data set (i.e., separately for dispersed-trait values, dispersed-PPI, dispersed-paired t, concentrated-trait values, and concentrated-paired t).

To assess trait variability between the dispersed and concentrated sampling methods, we performed one-sample t-tests for each species/trait combination comparing the average PPI values for the dispersed sites to its same-habitat megasite (total=32 tests). We used a Holms-Bonferroni correction for family-wise error rate separately for alpine and lowland sets of tests.

### *Common Garden*

We calculated germination success and survivorship of seedlings and plants from each collection site. One alpine and two lowland sites did not produce sufficient numbers of plants for analyses ( $n < 15$ ) and were excluded from further comparisons.

## Results

### **Diversity metrics**

Two-sample t-tests indicated that vascular plant diversity and species richness were greater at Lakes of the Clouds sites than at the Alpine Garden sites ( $t = -3.65$ ,  $df = 12$ ,  $p = 0.003$  and  $t = -3.20$ ,  $df = 10$ ,  $p = 0.009$ , respectively) (Fig. 2). Diversity and richness of bryophytes and lichens were not significantly different between sites.

Analyses of diversity, richness, and cover data by quadrat type (core/transition/edge) indicated a consistent transition of communities across the snowmelt gradient (Fig. 3). Vascular plant diversity, richness, and cover, decreased from the core to the edge of transects, while lichens increased in these three metrics (Table 1). Significant differences in both diversity and cover of bryophytes was found, but general increasing or decreasing trends across the snowmelt gradient were not evident, as diversity, richness, and cover of bryophytes was greatest in transition quadrats.

In both the vascular plant and bryophyte/lichen nMDS ordinations, quadrats were stratified by type, with core and edge quadrats distinctly separated. Core quadrats tended to group more tightly than edge quadrats, indicating greater floristic similarity among them. Transition quadrats occupied a broad swath between these two groups. In the vascular plant ordination (Fig. 4; stress=16.47), later melt date

corresponded with core quadrats, while edge quadrats had higher GDD, and these two vectors pointed in opposite directions, as expected. Closely associated species with Axis 1 were core species: *Deschampsia flexuosa*, *Solidago macrophylla*, *Vaccinium cespitosum*, *Clintonia borealis*, and edge species: *Vaccinium vitis-idaea*, *Sibbaldiopsis tridentata*, *V. angustifolium*, and *Empetrum nigrum*. 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.

The correspondence between quadrat type and melt date/GDD was less clear in the bryophyte/lichen ordination (Fig. S1; stress=15.34), as the vectors, while opposite each other, pointed somewhat perpendicular to the core-transition-edge axis. Closely associated species were one core species (the moss *Sciuro-hypnum reflexum*) and two edge species (the moss *Pleurozium schreberi* and the lichen *Cladonia arbuscula*). The ANOSIM of moss/lichen species indicated a significant difference in community composition between core and edge quadrats ( $R=0.385$ ,  $p=0.001$ ), but not between core and transition or transition and edge. Bryophyte and lichen nomenclature follow Flora of North America (2007) and Hinds et al., (2007), respectively.

In the ordination of site cores (Fig. 5; stress=10.50), there was a clear separation of Alpine Garden (AG) and Lakes of the Clouds (LC) sites. Species with strong associations along the main axis of separation, Axis 2, were LC vascular plants *Streptopus lanceolatus*, *Dryopteris campyloptera*, *Luzula parviflora*, *Nabalus trifoliolata*, *Geum peckii* and AG vascular plants *Juncus trifidus*, *Polytrichum* spp. mosses, and the lichen *Cladonia chlorophaea*. The ANOSIM comparing community composition between AG and LC sites was not significant.

### **Community-weighted mean trait values**

CWM trait values changed considerably across the snowmelt gradient. Height, leaf area, and SLA all decreased from core to edge quadrats, while LDMC increased (Fig. 6). ANOVAs indicated significant

( $p < 0.05$ ) decrease in leaf area and SLA, while the increase in LDMC approached significance ( $p = 0.053$ ; Table 2).

### **Core/edge trait comparisons**

Plant height, leaf area, and SLA generally were greater in snowbank cores, while LDMC was lower (Fig. 7). Several of the t-tests were significant, seeming to confirm trends among the other species that showed similar but non-significant responses. One possible exception to the overall trends was *Maianthemum canadense*, which tended to grow shorter in snowbank cores compared to the edge, though the difference was not statistically significant.

### **Alpine/lowland trait comparisons**

LDMC was greater among alpine populations, while leaf area and SLA were greater among lowland populations. No overall trends were apparent in plant height (Table 3). Species from the two habitats tended to respond the same, except for *Coptis trifolia*. It had lower LDMC and higher SLA among alpine populations, while height and leaf area gave mixed results based on sampling strategy. In general, results were consistent between sampling strategies, whether selecting three individuals of each spread across several sites (dispersed, Table 3) or all individuals from one “megasite” (concentrated, Table S2).

In terms of PPI, *Chamaepericlymenum canadense* was more plastic among alpine populations than the other species studied, which generally showed higher plasticity among lowland populations in most traits, although none of the t-tests were significant (Table 3). No other discernible trends were evident. In the one-sample t-tests that compared PPI of the dispersed sites to the megasite from the same habitat, there was greater trait variability at the megasites for all traits across all four focal species, except *Coptis trifolia* LDMC, lowland (Table S3). PPI was significantly greater ( $p < 0.05$ ) at the megasites in 6/16 (alpine) and 7/16 (lowland) tests after Holmes-Bonferroni correction.

## Common garden

Six alpine and one lowland site produced at least 15 *Chamaepericlymenum canadense* plants in the common garden. Both germination success and survivorship were greater among the lowland (medians=45.1 and 75.6%) vs. alpine sources (medians=23.5 and 46.7%, respectively). Traits were variable, but plants from the lowland tended to grow taller, had lower LDMC, and higher SLA compared with the range of values from alpine sources (Fig. 8, Table S4). Height and leaf area of *C. canadense* plants grown from alpine sources in the common garden were dramatically lower than their naturally-occurring alpine conspecifics (Figure 8, Table S1); to a lesser degree, LDMC was higher and SLA was lower among the greenhouse plants as well.

## Discussion

Analysis of community composition data confirm alpine snowbank sites as rich in vascular plants, but scarce in lichens. In fact, the dominance of tall, leafy, vascular plants is a defining characteristic of these communities (Sperduto and Nichols, 2011). Bryophytes were found throughout the transects, but had the greatest diversity, richness, and cover in transitional quadrats. The intermediate zone between true snowbank and edge habitats seems to be the niche for these non-vascular plants, which are likely outcompeted/shaded by vascular species in snowbank cores and, due to dry conditions and/or physical exposure, do not populate surrounding edge habitats in large amounts. Lichens, on the other hand, are well-adapted to the stresses of the wider alpine zone, and thrive in colder, drier, windswept microhabitats at the margins of snowbank communities. There, lichen diversity, richness, and cover was greatest (also, see Dibble et al., 2009).

The higher diversity and species richness of vascular plants at Lakes of the Clouds (LC) vs. Alpine Garden (AG) sites found here may be due to differences in elevation and distance to treeline. The higher elevation of AG sites (see Ch. 1) makes them more isolated and further from pockets of lower-elevation species, such as *Abies balsamea*. Infiltration by such species may have increased diversity and richness values at LC sites, especially in transitional zones. This is probably the case for site LC6, in

Oakes Gulf—by far the most species-rich site. It had several species found at no other sites, such as *Arnica lanceolata*, *Campanula rotundifolia*, *Carex capillaris*, *Chamerion angustifolium*, *Epilobium hornemannii*, and *Lonicera villosa*. Though LC6 strongly fits the physical description of alpine snowbed sites, some of these plants are not “true,” – or characteristic snowbed species. Being very near treeline, environmental filtering may not be acting as strongly at this site (or other LC sites, to a lesser degree), allowing transitional or marginal species to grow alongside more strictly-defined alpine snowbed species. LC snowbank sites, in this respect, may represent more of the “ravine” or “moist alpine herb-heath meadow” communities, rather than the type of true herbaceous snowbank communities found in the Alpine Garden (Sperduto and Cogbill, 1999; Sperduto and Kimball, 2011).

### **Traits and the snowmelt gradient**

A species’ fundamental niche is governed by its functional traits, which determine the range of habitat conditions in which it can survive (McGill et al., 2006). In snowbank communities, this niche is one of greater soil moisture and temperature, lower wind speeds, and shorter growing season, as compared to more typical alpine communities. The environmental conditions characteristic of snowbed communities are unusual in the alpine landscape, and plants that dominate under those conditions have traits that allow them to take advantage of the more abundant resources and protection from physical damage (Komac et al., 2015). Fast growth rate, tall height, high allocation of biomass to leaves, and strong photosynthetic capacity help snowbed species outcompete the “true” arctic-alpine species adapted to more extreme conditions.

In this study, the decrease in height, leaf area, and SLA, along with the corresponding increase in LDMC across the snowmelt gradient highlights the matching of advantageous traits to localized environmental conditions. Moving outward from the core, the smooth transition in trait values is evidence of the corresponding transition of underlying environmental conditions, as filtering becomes stronger and species with traits suited to harsher conditions are no longer outcompeted, and begin to fill in. But 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 even more exaggerated than results shown here.

However, trait differences also reflect underlying functional differences (Violle et al., 2007). That is, the greater height and leaf area (together, biomass) among plants in snowbank cores indicate greater rates of carbon fixation and water or nutrient uptake, while greater SLA indicates increased photosynthetic capacity and transpiration rates (Poorter and Evans, 1998; Reich et al., 1998a, 1998b). Lower LDMC in snowbank cores corresponds to greater water availability there. Intraspecific trait variability may also be important in affecting community assembly by promoting facilitation and species coexistence (Schöb et al., 2013), especially along stress gradients or where environmental filtering may be strong (Jung et al., 2010; Yan et al., 2012; Kichenin et al., 2013; Luo et al., 2016), such as in alpine habitats.

### **Population dynamics & gene flow**

A major objective of this research was to investigate the potential ecotypic variation (via trait differences) between lowland understory plants and their conspecifics that grow in alpine snowbanks. In general, our results match expectations, in that for conspecific populations, individuals growing in the alpine environment had higher LDMCs and lower SLAs compared to their lowland counterparts due to the increased harshness of growing conditions above treeline. High winds, exposure to UV radiation, risk of frost damage, and a lack of a humidifying overstory all contribute to the growth of smaller, tougher, denser leaves in the alpine environment. It is unclear, however, 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.

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; Shimono and Kudo, 2003; Scheepens et al., 2010). For instance, Shimono et al. (2009) found that *Potentilla matsumurae* (Rosaceae), an alpine forb native to Japan, displays two markedly different growth forms depending on whether it grows in a fellfield (rock scree) or snowbed habitat. These characteristics are retained when grown in a common garden. This species is locally distinct across Japan due to habitat fragmentation during Pleistocene glaciation and subsequent vicariance (Ikeda et al., 2008). The mountains of northeastern North America have undergone a similar history of glaciation and fragmentation, (Spear, 1989), and there is reason to believe its species have responded in kind (Billings, 1974). It is important to note, however, that this study focused solely on snowbeds within the alpine zone of one peak in the White Mountains of New Hampshire. Alpine plant communities, and the species that inhabit them, though, occur throughout northeastern North America. 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, though.

Some preliminary work has been done on this topic. Riebesell (1982) found that the distribution of alpine plants in the Adirondacks of New York roughly follow the model of island biogeography theory, as described by MacArthur and Wilson (1963, 2016). Species richness and immigration indices were correlated with area of alpine habitat and dispersal distance between peaks, respectively, suggesting that gene flow among alpine peaks is ongoing and dynamic. He also stressed the importance of seed dispersers such as birds, which may carry propagules long distances between alpine areas and mitigate isolation due to topographical relief and distance. Some work has been done on gene flow in wind-dispersed species (such as *Carex bigelowii* across arctic and alpine populations; Schönswetter et al., 2008), but further questions remain.

In this context, snowbank communities may be viewed as “islands within islands”. That is, the questions we have about gene flow and isolation regarding adjacent alpine areas in northeastern North America can just as easily be applied to snowbank communities within a single alpine peak or range. For example, is there a limit to how far insect pollinators will travel above treeline, and do snowbank sites

separated by large distances on the same peak (such as AG and LC) risk genetic isolation because of it? Is gene flow occurring between alpine and lowland populations of conspecifics? These questions and more deserve our attention if we are to fully understand the ecology of these ecosystems and devise better conservation plans for alpine areas in the region.

With respect to the trait anomalies of *Coptis trifolia* (lower LDMC, higher leaf area and SLA in alpine habitats), a larger sample size or broader study may be needed to determine if our results were accurate. It differed from other species used in our analysis because it has evergreen leaves that overwinter, becoming dark and leathery (presumably high LDMC/low SLA), in contrast to new-growth leaves that are brighter and more delicate (lower LDMC/higher SLA) (Wright et al., 2005a), and which sprout from the roots of an existing plant. We did not discriminate between these leaf types, collecting either if they were randomly selected. Limiting future studies of trait measurements to new-growth leaves only, for instance, may reduce variability and yield different results.

The traits of *Chamaepericlymenum canadense* plants grown in the common garden also contradicted our expectations. The greenhouse plants—whether alpine or lowland in origin—developed distinctly differently from naturally-occurring plants. They were very short and wiry, and had small, stubby leaves that alternated in pairs all the way up the stem, rather than just the four-leaf whorl at the apex that is characteristic of the species, although many had the whorl as well. We never observed this growth form in natural populations. We anticipated that the ameliorated conditions of the greenhouse would allow for better growth—i.e., greater height, leaf area, SLA, and lower LDMC—among seedlings grown from alpine sources compared to *in-situ* conspecifics. Perhaps there are abiotic cues that these species experience while in the alpine environment that facilitate their growth there. A reciprocal transplant experiment may better take these cues into account. Greater replication is needed among plants grown from lowland sources to compare trends statistically between populations.

While we were unable to demonstrate a difference in trait values among plants grown from seed collected from alpine and low-elevation sources, a larger study focusing solely on this question may be

able to do so. Phenotypic differences in traits between plants grown from different sources, but under uniform conditions, could be evidence of underlying genetic differentiation between populations (Shimono et al., 2009), as well as a potentially strong impetus for preservation efforts or listing under an increased conservation status, as occurs with rare or threatened species or ecotypes. Genetic sequencing may be necessary for such studies, an avenue as yet unexplored in alpine areas of northeastern North America.

### **Climate change & conservation**

Because we were unable to determine if intra-mountain genetic variation/divergence is occurring among snowbank species, more research should be conducted on this topic. As climate change continues to affect growing conditions of alpine plants in northeastern North America, phenotypic plasticity may take on a larger role in adaptation (Matesanz et al., 2010; Nicotra et al., 2010; Franks et al., 2014), and having baseline levels of trait values and variation may be a useful tool for tracking environmental change. *Chamaepericlymenum canadense*, being 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, too, respond to winter warming events, but bryophytes in particular may be negatively affected if above-average temperatures become consistent (Bjerke et al., 2011). A reduction in habitat or loss of these important transitional species could lead to substantial changes in microclimate where they are currently present (Bueno et al., 2016).

Arctic and alpine areas worldwide are experiencing disproportionate warming compared to lower elevations/latitudes (Rangwala and Miller, 2012; Mountain Research Initiative 2015; Pepin et al., 2015), and predictions for mountainous regions include higher average temperatures, decreased snowpack, earlier snowmelt dates, and more precipitation falling as rain (Rawlins et al., 2012). This may lead to significant declines, range shifts, or complete loss of alpine tundra in some locations (Walther et al., 2005a, 2005b; Diaz and Eischeid, 2007). Alpine snowbank communities are particularly sensitive to such

environmental changes (Galen and Stanton, 1995; Björk and Molau, 2007), and declines in alpine snowbank communities have been reported elsewhere (Klanderud and Birks, 2003).

Despite these worldwide trends, the mountains of northeastern North America may follow a different course. Seidel et al. (2009) found that the alpine zone on Mt. Washington is not warming as quickly as the surrounding low-elevation forest matrix, and they point to higher humidity and cloud cover compared to other world regions as factors in thermal buffering. Because regional models predict increased precipitation under climate warming, a lack of significant warming among high-elevations in the region could actually mean more snowfall, not less. Because plant traits are correlated with climate (Wright et al., 2005b), understanding those relationships in alpine areas of northeastern North America may help researchers anticipate species and community range shifts, as well as niche availability under altered climatic conditions (Woodward and Cramer, 1996; Lavorel and Garnier, 2002; Guittar et al., 2016).

Some research to monitor and track changes in alpine plant communities has already been conducted in the region, though. Robinson et al. (2010) found an increase in vascular plant frequency at the expense of bryophytes and lichens between 1984-2007 in the Adirondack Mountains of New York, and Capers and Stone (2011) found an increase in the prevalence of trees and shrubs over a similar time period on Bigelow Mountain in western Maine. These findings are attributable to a process of “filling”, whereby lowland species expand their range into newly habitable areas (Grabherr et al., 1995; Erschbamer et al., 2009), increasing overall species richness/biodiversity, but potentially compromising the biological integrity of alpine communities. Snowbank communities are particularly vulnerable to this process (Schöb et al., 2009). We have already seen the encroachment of low-elevation or exotic species such as dandelions (*Taraxacum officinale*) into snowbeds on Mt. Washington, and there is risk that such invasions may displace rare or threatened species (Komac et al., 2015; Capers and Slack, 2016) or lead to a loss of host plants for insect pollinators (Levesque and Burger, 1982; McFarland, 2003).

In order to track potential community change in snowbeds and other alpine communities, we recommend continued monitoring efforts, such as GLORIA (recently established on Mt. Washington and Monts Chic-Chocs, Quebec), permanent transects, and phenological studies. Also important should be a focused effort to catalog snowbank community distribution across the region and periodic monitoring of their size and species composition, possibly with permanent plots. Such monitoring may provide clues as to the trajectory northeastern alpine areas will take in response to environmental change in the coming years and give managers and researchers a better understanding of the complex relationships between plants and environmental factors operating in these ecosystems.

### Conclusions

The trait ecology of northeastern alpine snowbank ecosystems obey many rules found elsewhere worldwide, but there remain several unanswered questions. There is more to learn about the relationship of plant species diversity to elevation, distance to treeline, and site area in these communities, and how closely individual or community-level traits are linked to the processes of environmental filtering and community assembly in alpine environments. It is our hope that this work is a further step in our understanding of the ecology of alpine snowbank communities in northeastern North America, especially in regards to anticipating future climatic change. Snowbank communities may be a sensitive indicator of larger-scale environmental change in the region, with implications for the broader landscape; monitoring their health and persistence should remain a priority of alpine researchers.

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Tables

**Table 1.** Mean ( $\pm$ SE) Shannon-Weiner diversity, species richness, and percent cover of vascular plants, bryophytes, and lichens by quadrat type. Quadrat types are: core (starting quadrats of transects), transition (intermediate quadrats), and edge (last quadrats of transects). Summary two-way ANOVA results also listed for each taxa. See Fig. 3 for grouping information of significant ANOVAs.

	<b>Taxa type</b>	<b>Core</b>		<b>Transition</b>		<b>Edge</b>		<b>Source</b>	<b>MS</b>	<b>F</b>	<b>p</b>
<b>Diversity</b>	Vascular	1.78	(0.08)	1.60	(0.07)	1.35	(0.07)	Type	0.716	11.9	0.000
		Site	0.123	2.05	0.046						
	Bryophytes	0.39	(0.08)	0.53	(0.06)	0.30	(0.08)	Type	0.214	3.52	0.042
		Site	0.132	2.17	0.035						
	Lichens	0.04	(0.04)	0.16	(0.04)	0.54	(0.1)	Type	0.107	0.55	0.595
		Site	0.064	0.33	0.969						
<b>Richness</b>	Vascular	11.2	(0.6)	10.6	(0.6)	9.6	(0.6)	Type	10.83	2.76	0.080
		Site	8.866	2.26	0.028						
	Bryophytes	1.8	(0.3)	2.1	(0.2)	1.8	(0.2)	Type	0.523	0.95	0.398
		Site	1.819	3.31	0.003						
	Lichens	0.5	(0.2)	1.3	(0.2)	2.6	(0.4)	Type	0.394	1.84	0.184
		Site	0.229	1.07	0.435						
<b>Cover</b>	Vascular	64.3	(3.9)	59.3	(4.2)	58.9	(7.0)	Type	144.8	0.4	0.674
		Site	565.4	1.56	0.146						
	Bryophytes	5.2	(1.8)	8.1	(1.8)	11.1	(3.1)	Type	5.253	4.18	0.025
		Site	4.146	3.3	0.003						
	Lichens	0.1	(0.0)	2.4	(1.2)	10.1	(3.0)	Type	3.514	12.2	0.001
		Site	0.687	2.39	0.070						



**Table 2.** Full one-way ANOVA results for community-weighted mean trait values by quadrat type.

Quadrat types were core, transition, and edge; leaf area was log-transformed prior to analysis.

	<b>Source</b>	<b>df</b>	<b>adj. SS</b>	<b>MS</b>	<b>F</b>	<b>p</b>
<b>Height</b>	Type	2	401959	200979	2.35	0.108
	Error	42	3590400	85486		
	Total	44	3992359			
<b>LDMC</b>	Type	2	2386700	1193350	3.15	0.053
	Error	42	15899548	378561		
	Total	44	18286248			
<b>log(Leaf area)</b>	Type	2	4.738	2.36922	36.72	0.000
	Error	42	2.71	0.06452		
	Total	44	7.448			
<b>SLA</b>	Type	2	10107	5054	3.92	0.028
	Error	42	54206	1291		
	Total	44	64313			

**Table 3.** Results of t-tests of comparisons of plant trait values and phenotypic plasticity index (PPI) between alpine and lowland source populations from the dispersed sampling strategy (results from concentrated sampling were similar, see Table S2). Traits were height, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Gray boxes indicate higher mean values among alpine source populations, while white boxes indicate higher values among lowland sources. Significance of t-tests before and after Holms-Bonferroni correction (in parentheses) indicated (\* $p < 0.05$ , + $p < 0.10$ ). Both two-sample (each species individually) and paired (all species averaged) t-tests were performed.

Trait value	Species	Leaf			
		Height	LDMC	area	SLA
Trait value	CHCA		* (*)	*	* (*)
	CLBO		*		*
	COTR		*		
	MACA		+		* (*)
PPI	CHCA				
	CLBO				
	COTR			+	
	MACA				
Paired t-tests	Trait value				
	PPI		* (*)		

### Figure captions

**Figure 1.** Map of snowbank study sites (white) on Mt. Washington, NH (summit 1914 m), and lowland trait collection sites (black, R1-R6) near the Pinkham Notch Visitor Center (PNVC, 619 m). Alpine sites are labeled based on general location: Alpine Garden (AG) and Lakes of the Clouds (LC). Boundaries of federally-designated wilderness area, alpine zone, and the Alpine Garden Research Natural Area (RNA) indicated. Inset map of Mt. Washington's location in northern New Hampshire, USA.

**Figure 2.** Boxplots of vascular plant diversity ( $H'$ ) of Alpine Garden ( $n=10$ ) and Lakes of the Clouds ( $n=6$ ) study sites. The two-sample t-test was significant ( $t=-3.65$ ,  $df=12$ ,  $p=0.003$ ), indicating a difference between the two locales. Boxplots of vascular plant species richness not shown, but they displayed a matching trend; the t-test was significant ( $t=-3.20$ ,  $df=10$ ,  $p=0.009$ ).

**Figure 3.** Mean ( $\pm$ SE) Shannon-Weiner diversity ( $H'$ ) of vascular plants, bryophytes, and lichens across the snowmelt gradient. Quadrat types are: core (starting quadrats of transects), transition (intermediate quadrats), and edge (last quadrats of transects). Significance of one-way ANOVAs ( $*p<0.05$ ) and grouping information based on Tukey's pairwise comparisons indicated. Trends in species richness and cover closely follow those shown here; figures for those metrics are not included.

**Figure 4.** nMDS ordination of vascular plant cover by quadrat type (core/transition/edge), with vectors for environmental variables snowmelt date and cumulative growing degree days (CumGDD). Grouping based on ANOSIM indicated in legend.

**Figure 5.** nMDS ordination of core quadrats by study site. Dark circles represent sites in the Alpine Garden (AG), while open circles are those near the Lakes of the Clouds (LC).

**Figure 6.** Change in community-weighted mean trait values ( $\pm$ SE) across the snowmelt gradient. Three quadrat types were core (first), transition (intermediate), and edge (last). Traits measured were: height, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Significance of one-way ANOVAs indicated (\* $p < 0.05$  and † $p < 0.10$ , see Table 2) and letters denote grouping based on Tukey's pairwise comparisons.

**Figure 7.** Mean difference ( $\pm$ SE) in measured plant traits of four focal species between snowbank core and edge quadrats (core – 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). Significance levels of paired t-tests indicated (\* $p < 0.05$ , † $p < 0.10$ ).

**Figure 8.** Mean trait values of *Chamaepericlymenum canadense* plants grown from seed in a common garden at the College at Brockport greenhouse. Traits were height, leaf dry matter content (LDCM), leaf area, and specific leaf area (SLA). Seeds were collected from both alpine (A1-A6, gray) and lowland (L1, black) sources. See Table 6 for complete results.

Figures

Figure 1.

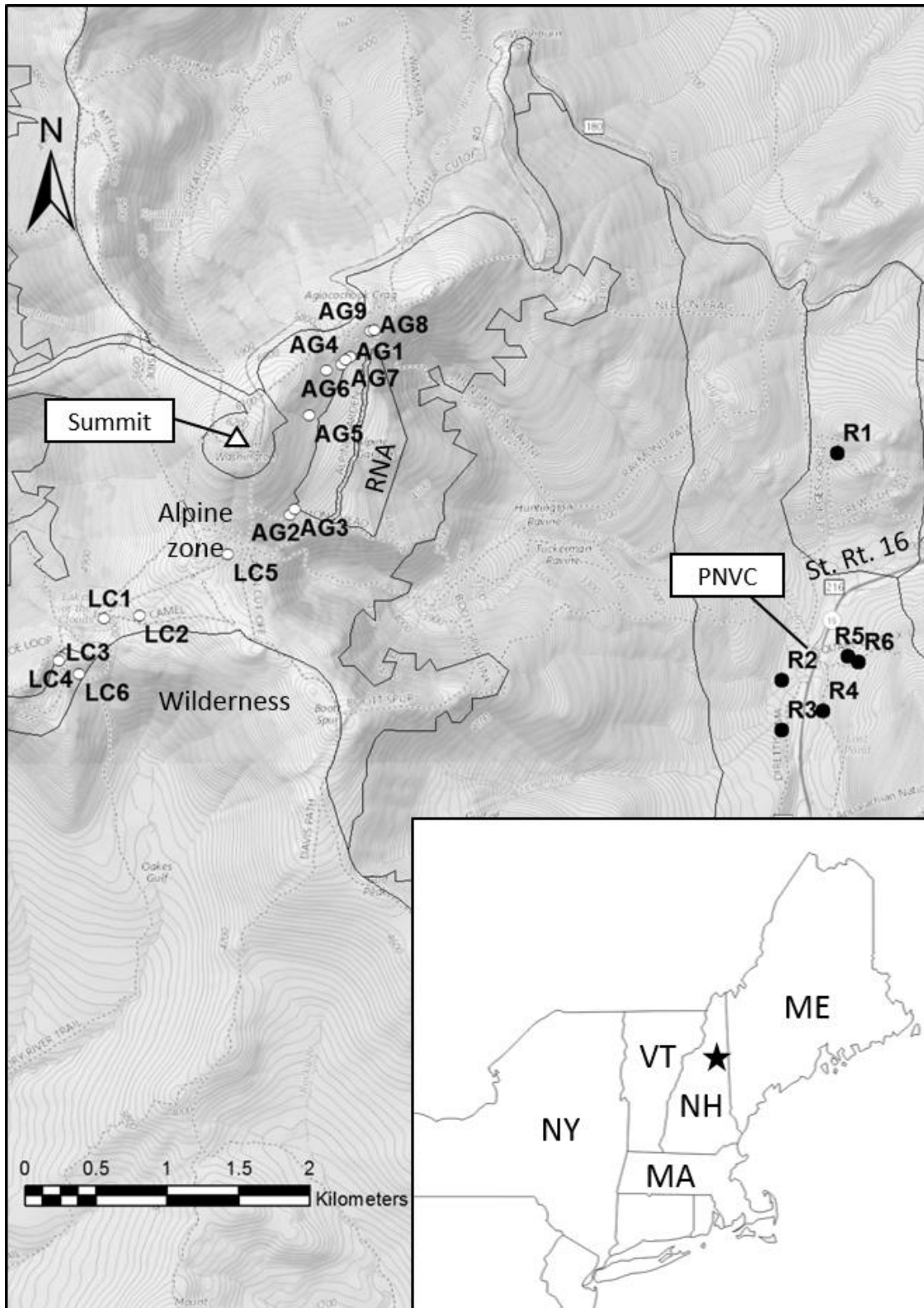


Figure 2.

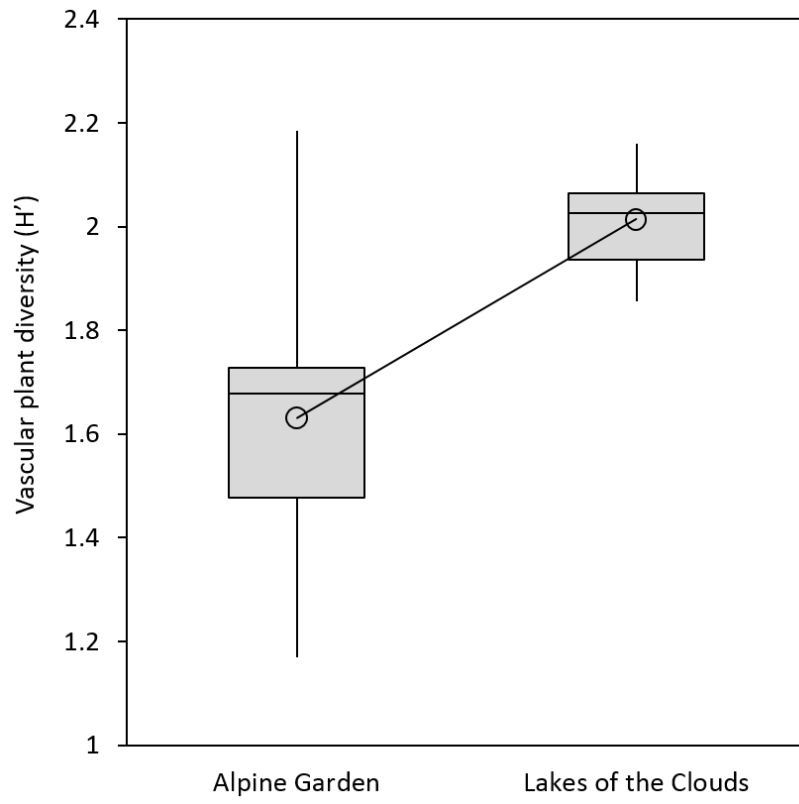


Figure 3.

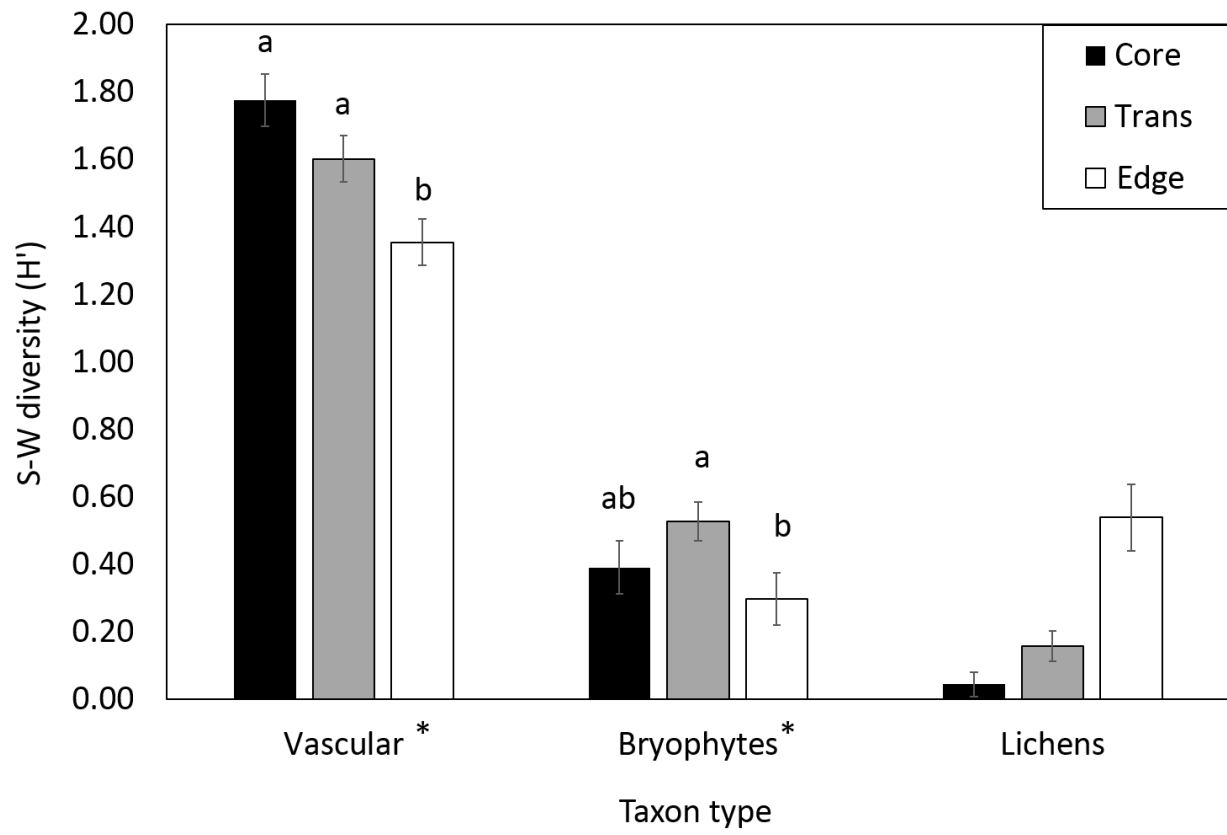


Figure 4.

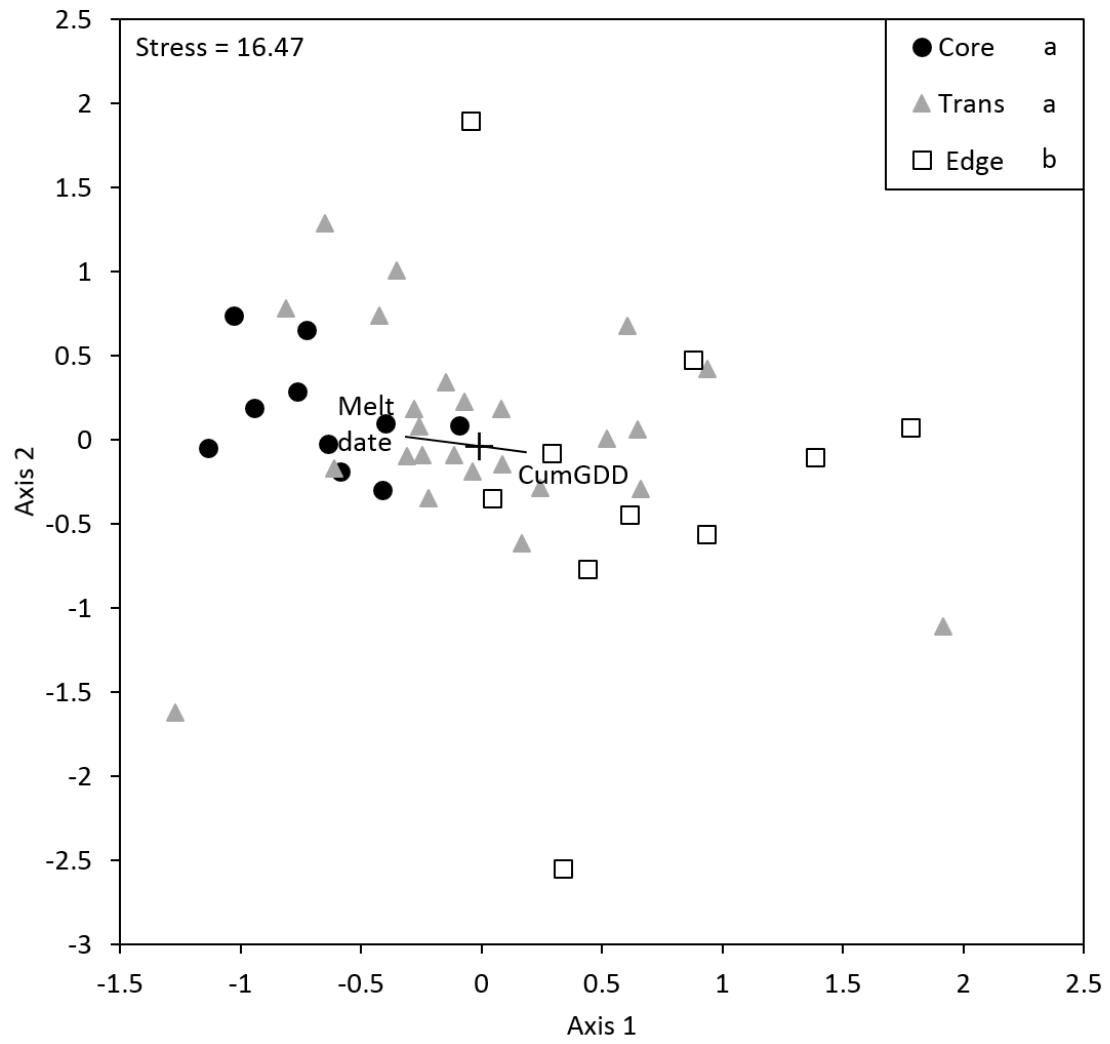




Figure 5.

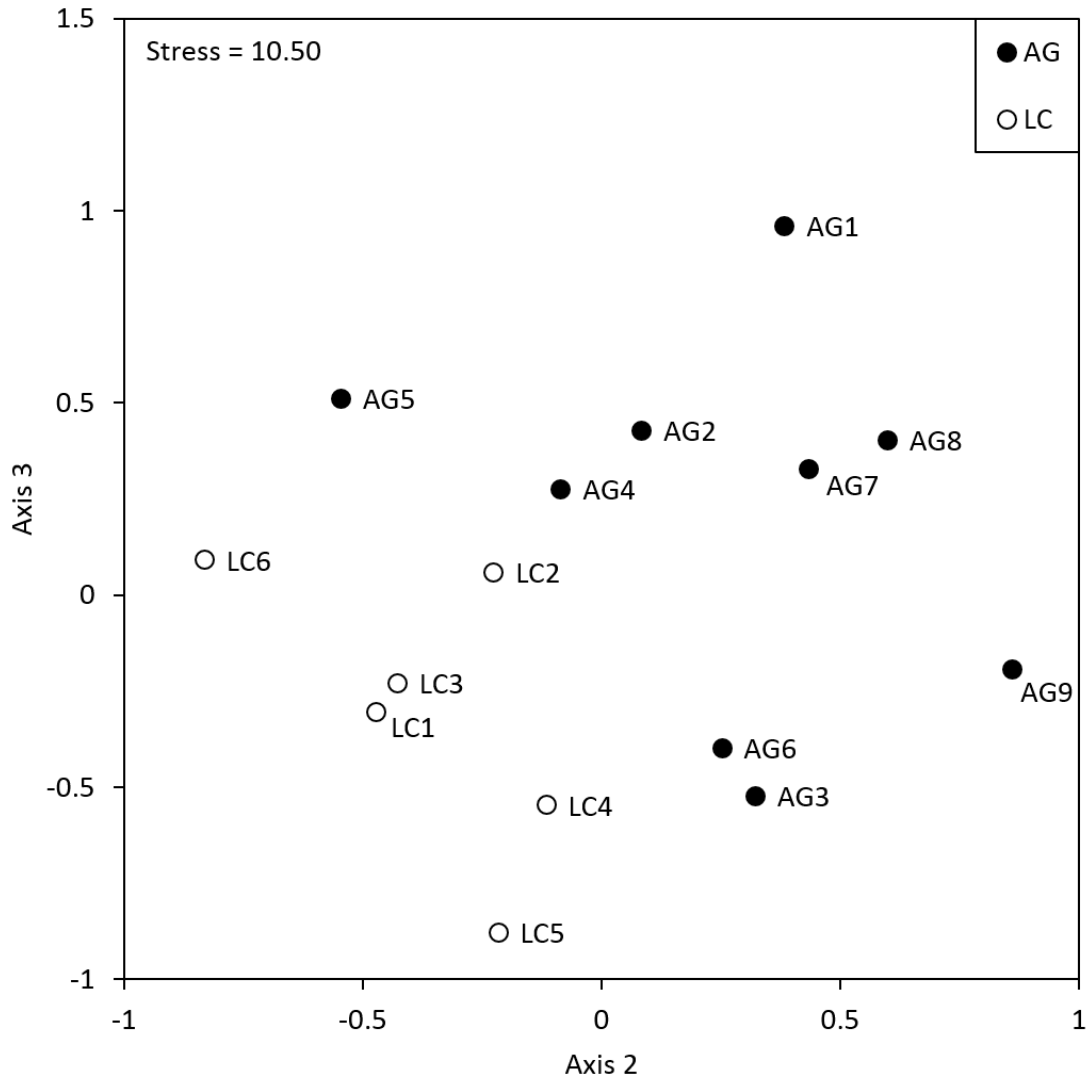


Figure 6.

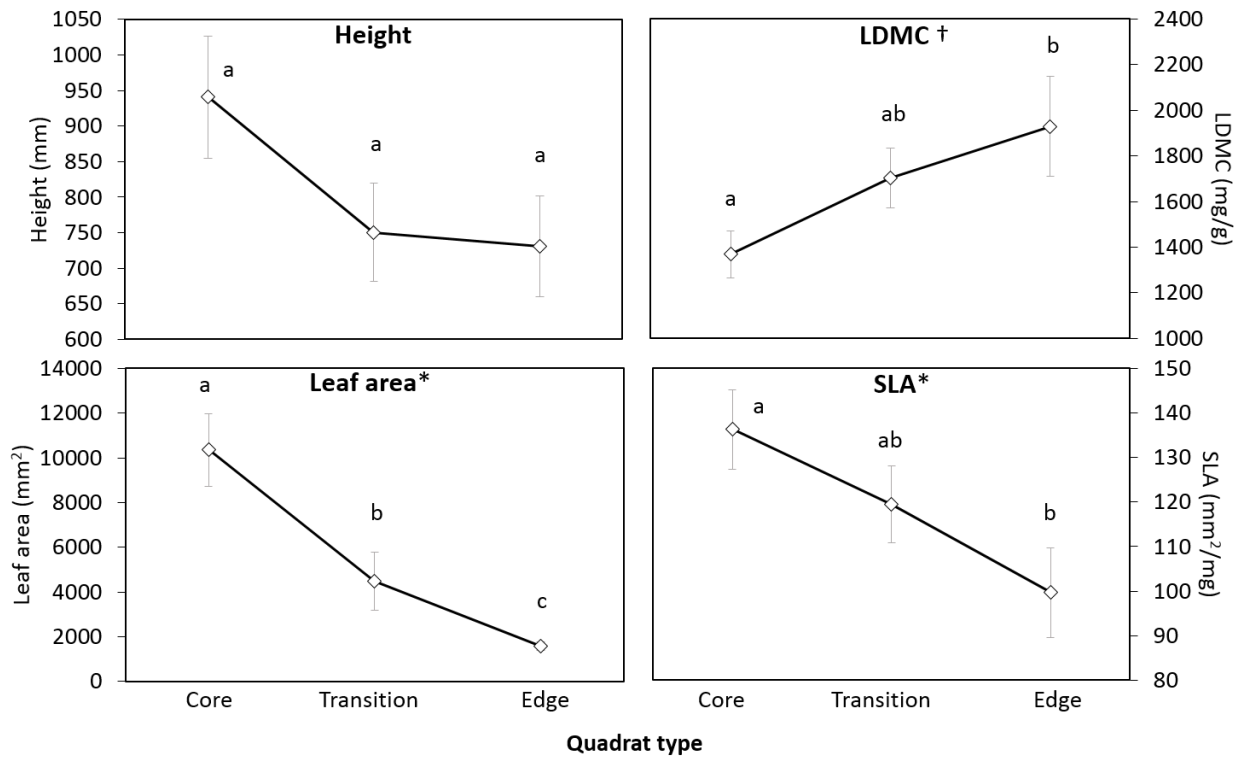


Figure 7.

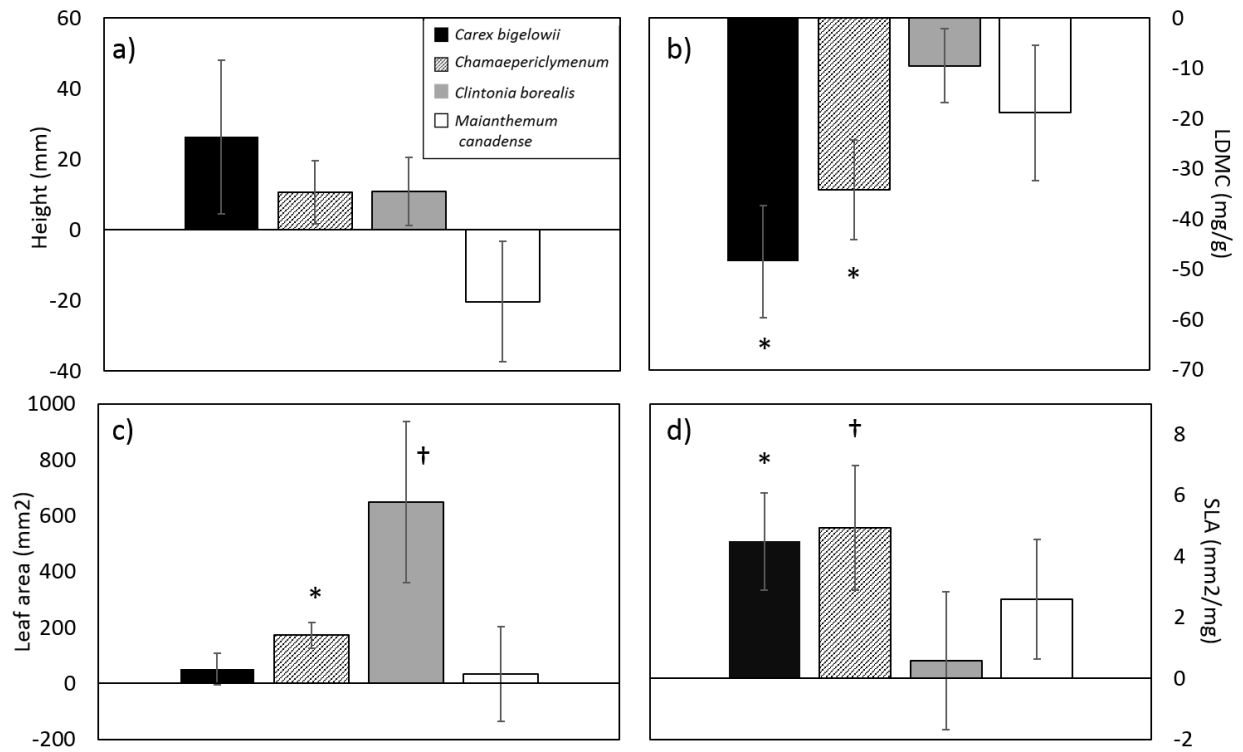
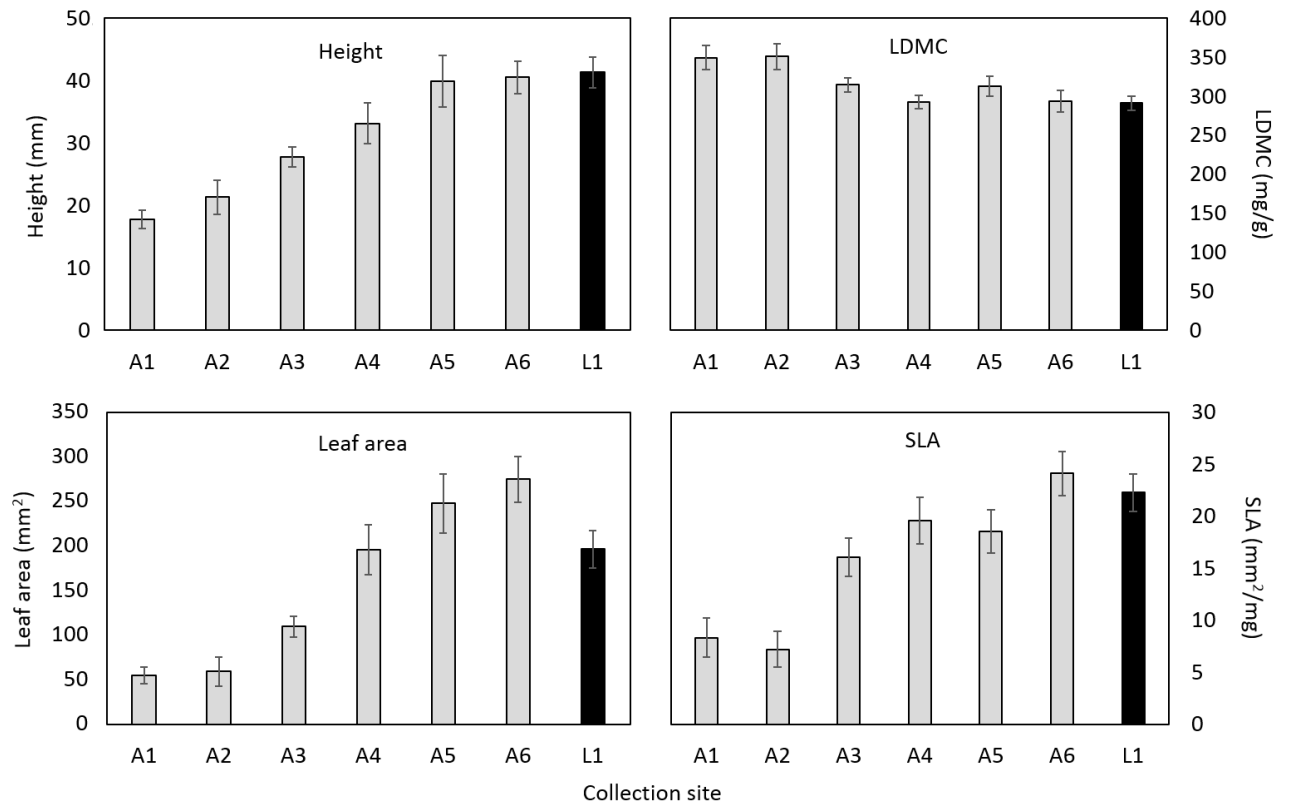


Figure 8.



Supplemental materials

**Table S1.** Mean trait values ( $\pm$ SE) for 15 most abundant/frequent species found across all sampling plots, weighted proportionally by abundance in core and edge quadrats. Note: Mean leaf area was not calculated for *Empetrum nigrum*, as small branch clippings were used for analyses instead of individual leaves (see Methods).

<b>Species</b>	<b>n (Core)</b>	<b>n (Edge)</b>	<b>n (Total)</b>	<b>Height (mm)</b>	<b>LDMC (mg/g)</b>	<b>Leaf area (mm<sup>2</sup>)</b>	<b>SLA (mm<sup>2</sup>/mg)</b>
<i>Carex bigelowii</i>	15	16	31	173.7 (8.4)	308.3 (6.1)	473.1 (23.1)	18.1 (0.7)
<i>Chamaepericlymenum canadense</i>	17	15	32	85.8 (3.7)	245.4 (4.9)	479.5 (35.9)	29.4 (0.9)
<i>Clintonia borealis</i>	17	22	39	125.6 (3.7)	114.9 (3)	3614.3 (165.2)	28.6 (0.7)
<i>Coptis trifolia</i>	13	18	31	44.0 (4.2)	219.1 (10.6)	115.3 (12)	38.1 (3.2)
<i>Deschampsia flexuosa</i>	8	2	10	292.9 (21.5)	253.7 (11.2)	428.3 (36.3)	8.0 (0.7)
<i>Empetrum nigrum</i>	0	10	10	102.7 (17.1)	301.3 (11.6)	N/A -	7.5 (0.7)
<i>Juncus trifidus</i>	4	6	10	177.7 (13.9)	340.7 (11.2)	277.9 (31.1)	10.2 (0.5)
<i>Maianthemum canadense</i>	15	15	30	66.2 (5.5)	226.0 (4.1)	903.2 (68.7)	29.7 (0.7)
<i>Solidago macrophylla</i>	10	0	10	146.4 (17.4)	214.6 (5.5)	1716.0 (234)	32.4 (1.3)
<i>Spiraea alba</i>	4	6	10	131.5 (18.4)	301.5 (20)	127.3 (13.9)	30.3 (3)
<i>Streptopus lanceolatus</i>	10	0	10	301.7 (15.7)	152.9 (3)	1098.7 (67.3)	34.9 (0.6)
<i>Vaccinium angustifolium</i>	1	9	10	88.0 (10.1)	283.3 (13)	50.5 (6.4)	4.4 (0.3)
<i>Vaccinium cespitosum</i>	6	4	10	85.8 (9.1)	287.0 (21.6)	114.0 (16.6)	17.4 (6)
<i>Vaccinium uliginosum</i>	2	8	10	108.1 (10.6)	317.1 (16)	117.3 (18.9)	16.0 (2.4)
<i>Veratrum viride</i>	10	0	10	431.3 (53.7)	182.2 (3.3)	9529.6 (1233.2)	20.1 (1.5)

**Table S2.** Results of t-tests of comparisons of plant trait values and phenotypic plasticity index (PPI) between alpine and lowland source populations from the concentrated sampling strategy. Traits were height, leaf dry matter content (LDMC), leaf area, and specific leaf area (SLA). Gray boxes indicate higher mean values among alpine source populations, while white boxes indicate higher values among lowland sources. Significance of t-tests before and after Holms-Bonferroni correction (in parentheses) indicated (\*p<0.05, +p<0.10). Both two-sample (each species individually) and paired (all species averaged) t-tests were performed. Note no data for PPI two-sample t-test due to sampling/data constraints.

Trait value	Species	Leaf			
		Height	LDMC	area	SLA
	CHCA		* (*)	* (*)	* (*)
	CLBO		* (*)	* (*)	
	COTR	* (*)	* (*)	* (*)	+
	MACA				
PPI	CHCA				
	CLBO	(no data)			
	COTR				
	MACA				
Paired t-tests	Trait value				
	PPI				+

**Table S3.** Results of one-sample t-tests comparing phenotypic plasticity index (PPI) of dispersed sites to the Megasite from the same source elevation (alpine/lowland). Gray boxes indicate higher PPI values at the Megasite, while white box indicates higher value among dispersed sites. Significance of tests after Holms-Bonferroni correction indicated (\*p<0.05).

Source	Species	Height	Leaf		
			LDMC	area	SLA
Alpine	<i>Chamaepericlymenum</i>		*	*	*
	<i>Clintonia borealis</i>				
	<i>Coptis trifolia</i>			*	
	<i>Maianthemum</i>		*		*
Lowland	<i>Chamaepericlymenum</i>	*			*
	<i>Clintonia borealis</i>		*		*
	<i>Coptis trifolia</i>				
	<i>Maianthemum</i>	*	*		*

**Table S4.** Trait values ( $\pm$ SE) of *Chamaepericlymenum canadense* plants grown from seed in a common garden at the College at Brockport greenhouse. Traits were height, leaf dry matter content (LDCM), leaf area, and specific leaf area (SLA). Seeds were collected from 6 alpine sites on Mt. Washington (A1-A6) and 1 lowland source near the Pinkham Notch Visitor Center (L1).

Collection site	Source	Height (mm)	LDMC (mg/g)	Leaf area (mm <sup>2</sup> )	SLA (mm <sup>2</sup> /mg)
A1	Alpine	17.7 (1.5)	349.4 (15.2)	54.6 (9.1)	8.3 (1.9)
A2	Alpine	21.3 (2.8)	350.7 (16.0)	59.3 (16.3)	7.2 (1.7)
A3	Alpine	27.7 (1.6)	314.9 (9.0)	109.4 (11.4)	16.0 (1.8)
A4	Alpine	33.1 (3.2)	292.5 (8.9)	195.5 (28.2)	19.6 (2.3)
A5	Alpine	39.9 (4.1)	312.8 (12.3)	247.5 (32.7)	18.5 (2.1)
A6	Alpine	40.5 (2.7)	293.5 (13.9)	274.7 (25.6)	24.1 (2.1)
L1	Low	41.3 (2.5)	290.9 (9.2)	196.2 (21.2)	22.3 (1.8)

**Figure S1.** nMDS ordination of bryophyte and lichen cover by quadrat type (core/transition/edge), with vectors for environmental variables snowmelt date and cumulative growing degree days (CumGDD).

Grouping based on ANOSIM indicated in legend.

