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After 33 Years, Trees More Frequent and Shrubs More Abundant in Northeast U.S. Alpine Community

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Abstract

Alpine plant communities are sensitive to global climate change, which has been predicted to cause increases in woody vegetation, possibly at the expense of herbs. We studied a community in western Maine, comparing the frequency and abundance of alpine plants in 2009 with frequency and abundance recorded in 1976. During the 33 years between surveys, the most common tree became more frequent, and as a result, the frequency of trees as a functional group increased. Shrubs did not become more frequent but did become more abundant, driven by the increasing abundance of two *Vaccinium* species. Several species provided evidence of strong affinities for the north or south slope of the mountain, but in most cases such evidence was apparent in a species' frequency or its abundance, not both, indicating that different forces regulate dispersal and vegetative growth of alpine plants, which could have implications for understanding responses to changing environmental conditions. Total species richness of the community increased, with the addition of several lower montane herbs. The changes are consistent with predictions and with observations made in tundra communities elsewhere.

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Introduction

Woody species are predicted to increase in tundra ecosystems as a result of global climate change (Chapin et al., 1996; Epstein et al., 2000), possibly at the expense of herbaceous plants, and some evidence in support of this prediction has been reported. For example, trees have established where they did not previously occur, both in alpine areas (Wardle and Coleman, 1992; Peterson, 1994; Kullman, 2001, 2002), and in arctic tundra (Lescop-Sinclair and Payette, 1995; Danby and Hik, 2007). Increasing shrub abundance also has been reported in alpine (Klanderud and Birks, 2003) and arctic locations (Sturm et al., 2001; Tape et al. 2006; Wilson and Nilsson, 2009). Although many environmental conditions are changing globally (mean annual temperature, annual precipitation, atmospheric CO₂ concentration, nutrient levels, length of the growing season, and more), experimental manipulations suggest that warming, in particular, may benefit woody species. For instance, deciduous shrubs increased their height and cover within two years in response to warming in 11 tundra locations (Walker et al., 2006). Deciduous shrubs benefit from warming because they can respond more quickly than evergreen shrubs to the greater availability of nutrients that result from faster nutrient cycling that follows warming.

Species have not responded consistently to warming in all communities, even within functional groups, however. For example, among shrubs, *Dryas octopetala* and *Cassiope tetragona* had positive growth responses to artificial warming at International Tundra Experiment (ITEX) sites, but *Ledum palustre* and *Vaccinium vitis-idaea* did not, while *V. uliginosum* responded positively in one location but not another (Henry and Molau, 1997). Furthermore, the effect of interactions among changing conditions on alpine plant communities has been explored very little. One experiment in an alpine heath community found little community response to warming alone but dramatic changes in

response to warming and nutrient addition together (Klanderud, 2008). This and other studies (Van Wijk et al., 2004; Jägerbrand et al., 2009) suggest that the response of communities may vary greatly, depending both on the conditions and on the species present (Shaver et al., 2001; Bret-Harte et al., 2004).

Ultimately, the actual responses of alpine communities to changing conditions can be assessed only by comparing communities at different times, before and after conditions have changed. By comparing species lists compiled by 20th century botanists with the lists of species present on the same mountains now, ecologists have shown that species richness has increased in recent decades (Grabherr et al., 1994, 2001; Klanderud and Birks, 2003; Walther et al., 2005; Erschbamer et al., 2009). But species richness is only one way to look at a community, and communities can change dramatically (even without changing species richness) if the abundance of individual species changes.

Few studies evaluate the degree of change in alpine community composition and structure, primarily because the quantitative data from the past that are needed to make these comparisons are unavailable. In addition to documenting the actual changes that have occurred in real communities, such studies are useful because they provide the means to test predictions based on models or experimental manipulations. In this study, we compare the alpine community on a Maine mountain with the community that existed there 33 years earlier.

Mountains in the Northeast United States have only 34 km² of alpine habitat (Kimball and Weihrauch, 2000), but the alpine plants of New Hampshire, Maine, New York, and Vermont contribute unique elements to the region's biodiversity. Northeast alpine plants include endemic species, and a number of others reach the southernmost limit of their geographic distributions in these mountains. Alpine communities of the region occur as discrete, mostly small communities, isolated from each other on

more than 50 mountains. All occur at relatively low elevations (<2000 m; most <1500 m). The low altitude of the tree line ecotone in the region has been attributed to deep snow and high winds, especially in the winter (Bliss, 1963). Although the alpine communities of these northern Appalachian mountains traditionally have been classified as temperate alpine, they are more similar to boreal and arctic alpine communities, where dwarf shrub-heaths are common (Nagy and Grabherr, 2009). These communities share few species with those in the western mountains of the United States, and their closest counterparts occur hundreds of kilometers to the north in Greenland, Labrador, and Alaska (Bliss, 1963).

The Northeast's alpine communities have a rich history of botanical exploration that contributed to regional floras and produced species lists from a number of mountains. However, few quantitative studies were undertaken to establish the relative abundance of alpine plants, and no previous study reports on species-level changes in alpine plants communities in the region. We report here on change in the alpine plant community on Avery Peak (Bigelow Mountain) in western Maine between 1976, when an initial survey was done, and 2009, when a second survey was done, using the same methods.

We evaluated changes in frequency and abundance of all vascular plant species above tree line and explored whether changes were limited to particular functional groups (trees, shrubs, forbs, graminoids, lycophytes). Because previous studies have found evidence that change may be occurring more quickly on southern slopes, we also assessed the influence of aspect on the Avery Peak community. We use our results to evaluate three predictions based on previous alpine plant community research, that (1) woody species will increase in response to increased growing season length and warming growing conditions; (2) arctic species near the southern limit of their range are more vulnerable than those with more widespread distributions and, therefore, are more likely to decline (Lesica and McCune, 2004); and (3) total species richness in the alpine community will increase, as has been observed in other alpine communities.

Methods

Bigelow Mountain is the northernmost peak in the Longfellow Range, an irregular series of 13 summits in western Maine. Bigelow is a 16-km-long ridge that is oriented almost exactly east-west. The largest area of alpine and subalpine habitat is at the east end of the ridge, on Avery Peak (45°9'N, 70°16'W), which has a maximum elevation of 1259 m. The bedrock consists of granulite, meta sandstone, calcium-silicate gneiss, and dark gray slates (Doyle, 1967). The alpine habitat on Bigelow has been classified as "dwarf heath-graminoid alpine ridge" (Wilkerson, 2006). Tree species occur to the summit as stunted specimens in the krummholz. In a survey of Maine mountains with alpine communities, May and Davis (1977) described the vascular plant community of Bigelow as relatively depauperate, which they attributed to its dry, windswept terrain.

The alpine summit of Bigelow has been free from major disturbance events for at least several hundred years. Unlike mountains in many part of the world, domestic animals have never been grazed on mountains in the Northeast. Moose occur naturally on the mountain and, no doubt, browse plants in the alpine zone occasionally. The higher elevations on the mountain have occasional outbreaks of spruce budworm, which could affect fir and spruce; the most recent outbreak was in the 1980s (Wilkerson, 2006). Prior to creation of the 14,570-ha Bigelow

Preserve in 1976, land in the region was privately owned, and forests low on the mountain were harvested at least twice early in the 20th century. However, logging activity never reached elevations above 1040 m, and tree line occurs no lower than 1200 m, so this would not have affected the alpine area (Wilkerson, 2006). Forest fires in the region typically are small-scale events triggered by lightning strikes, and there are no records of major burns in the alpine area of Bigelow. A hiking trail runs along the ridgeline over Avery Peak, and there is clear evidence of disturbance by foot traffic. However, this has been limited to a narrow (<1 m wide) strip by construction of scree walls on both sides of the trail along its entire length in the alpine zone.

Alpine communities developed in the Northeast after the retreat of the Wisconsin-age glacial ice sheet. Studies of pollen cores and macrofossils from high-elevation lakes on other mountains in the Northeast indicate that modern alpine plant communities had established by 9000 years before present (BP) (Spear, 1989). Although changing climatic conditions (warming from 9000 to 5000 years BP and cooling temperatures in the past 3000 years) affected lower elevation forests, these changes had little effect on alpine and subalpine communities (Spear, 1989). The community we studied, thus, can be considered a mature (not successional) alpine plant community. While subject to small-scale disturbances, it could reasonably be expected to have a stable age and size structure at the scale of the community.

The initial survey of the alpine community was conducted in August 1976 (Stone, 1980). In conducting the survey, a transect was run along the ridgeline, from the continuous krummholz at the west end of the alpine zone, over the summit and down to the krummholz at the eastern end of the zone. Sampling transects were created at 25 m intervals along the main ridgeline transect, running roughly perpendicular to it, downhill to the north and south to the point at which the krummholz became continuous and at least 1 m high. Within each 10 m section on these transects, a random number generator was used to select one location at which the vegetation was sampled. In vegetation samples, a 50 cm square (0.25 m²) frame was placed over the plants; we recorded all species of vascular plants and estimated the percent cover of each. Percent bare rock and percent bare soil also were recorded. The survey was repeated in August 2009, using the same procedures. We used the same random numbers as in 1976 to select locations at which vegetation was sampled, although the samples were certainly not at exactly the same locations as those sampled in 1976 because of changes in the location of the krummholz, measurement errors, and variation in placement of the ridgeline transect and the transects running from the ridgeline downslope. The 2009 survey was designed to provide a fair comparison with that of 1976, eliminating to the degree possible differences in the results that might occur because of microtopographic variation in the site.

In analyzing the data, percent cover of each species was converted to a modified Domin-Krajina scale (Mueller-Dombois and Ellenberg, 1974) ranging from 1 to 8. Because the primary goal of the 1976 survey was to obtain information on alpine plants, species data were not recorded from samples in which the total cover value for all tree species was 75% or greater; these were recorded simply as krummholz. Although we did record species data for such samples in 2009, they were removed from all species-level analyses, so the 1976 and 2009 vegetation samples are comparable. We calculated frequency and determined the median abundance class of all species occurring in samples. Abundance and frequency represent distinct components of species' distributions, capturing complementary elements of occurrence (Canham and Thomas, 2010). They measure in different ways the "importance" of individual species in a community. Plants can

TABLE 1

Species recorded in the alpine zone of Avery Peak in western Maine. The number of samples in which each species occurred is shown for surveys done 33 years apart. Also shown is the relative frequency (the percent of all samples—219 in 1976 and 202 in 2009) for each species. Species are arranged in order of frequency in 2009.

	<i>n</i> , 1976	%	<i>n</i> , 2009	%
<i>Vaccinium uliginosum</i> L.	107	55.7	94	58.4
<i>Vaccinium vitis-idaea</i> L. ssp. <i>minus</i> (Lodd.) Hultén	115	59.9	90	55.9
<i>Rhododendron groenlandicum</i> (Oeder) Kron and Judd	88	45.8	81	50.3
<i>Betula cordifolia</i> Regel	61	31.8	65	40.4
<i>Abies balsamea</i> (L.) P. Mill.	29	15.1	54	33.5 *
<i>Sibbaldiopsis tridentata</i> (Ait.) Rydb.	70	36.5	39	24.2 *
<i>Juncus trifidus</i> L.	54	28.1	31	19.3
<i>Vaccinium angustifolium</i> Ait.	25	13.0	14	8.7
<i>Agrostis mertensii</i> Trin.	6	3.1	8	5.0
<i>Empetrum eamesii</i> Fern. and Wieg. ssp. <i>atropurpureum</i> (Fern. and Wieg.) D. Löve	5	2.6	8	5.0
<i>Mimuartia groenlandica</i> (Retz.) Ostenf.	3	1.6	5	3.1
<i>Carex bigelowii</i> Torr. ex Schwein.	2	1.0	5	3.1
<i>Cornus canadensis</i> L.	14	7.3	2	1.2
<i>Lycopodium clavatum</i> L.	3	1.6	2	1.2
<i>Hierochloa alpina</i> (Sw. ex Willd.) Roemer and J.A. Schultes	11	5.7	1	0.6
<i>Picea mariana</i> (P. Mill.) B.S.P.	3	1.6	1	0.6
<i>Trientalis borealis</i> Raf.	1	0.5	1	0.6
<i>Huperzia appalachiana</i> Beitel and Michel	1	0.5	1	0.6
<i>Clintonia borealis</i> (Ait.) Raf.			1	0.6
<i>Maianthemum canadense</i> Desf.	5	2.6	P	
<i>Nemophanthus mucronatus</i> (L.) Loes.	1	0.5	P	
<i>Sorbus decora</i> (Sarg.) Schneid.	1	0.5	P	
<i>Prenanthes</i> sp.	P			
<i>Coptis trifolia</i> (L.) Salisb.	P		P	
<i>Larix laricina</i> (Du Roi) K. Koch	P		P	
<i>Vahlodea atropurpurea</i> (Wahlenb.) Fries ex Hartman			P	
<i>Oxalis montanum</i> Raf.			P	
<i>Lycopodium obscurum</i> L.			P	

Note: P indicates a species was present in the alpine community but was not recorded within samples where abundance was estimated.

* The change in frequency was statistically significant (Fisher's exact test, $P < 0.05$).

increase over time either by becoming more abundant where they were already established or by colonizing new locations. With the most common species—those occurring in more than 10 samples in each survey—we used Fisher's exact tests to test the null hypothesis that species occurred with the same frequency in 2009 as in 1976. We used the non-parametric Mann-Whitney *U* test to evaluate the significance of changes in species' abundance between the two surveys after correcting for multiple intergroup ties (Sokal and Rohlf, 1995). We also analyzed whether the frequency or abundance of these species differed between the north and south sides of the mountain and whether there was evidence of change in that affinity between surveys. We used the same procedure to analyze change in abundance and frequency of functional groups (trees, shrubs, graminoids, forbs, lycopods). Because of concern that the alpine species most threatened by global climate change may be high arctic species at the periphery of their range (Parsons, 1990; Lesica and McCune, 2004), we compared change in the frequency of widespread species with frequency of the five species having the most restricted geographic distributions—those limited to the Arctic and extending south only as far as mountain summits in the Northeast United States and northern Minnesota and Michigan (*Hierochloa alpina*, *Carex bigelowii*, *Empetrum eamesii* ssp. *atropurpurea*, *Vaccinium uliginosum*, and *V. vitis-idaea*).

Finally, we calculated mean species density in samples and compared values from 1976 and 2009, using *t*-tests. In both 1976 and 2009, lists of all species present above tree line were compiled, based on species present in samples and those observed elsewhere in the alpine zone, and we used these to assess whether overall

species richness in the alpine zone had changed. Voucher specimens of species recorded in 1976 were deposited in the herbarium at the University of Vermont (VT), and vouchers from the 2009 survey were deposited in herbaria at the University of Connecticut (CONN) and the University of Maine (MAINE). Taxonomy follows Haines and Vining (1998).

Results

The 1976 survey included 219 samples, of which 27 (12.3%) were eliminated from analyses because cover of tree species was 75% or greater. Of the remaining 192 samples, 16 (8.3%) had no vascular plants in them. The 2009 survey included 202 samples, of which 41 (20.3%) were removed from analyses because tree cover was 75% or greater, an increase in the frequency of tree-dominated samples ($P = 0.043$). Of the 161 remaining samples, 10 (6.2%) had no vascular plants in them, which was not significantly different from 1976.

The identity of the eight most frequent species—those occurring in more than 10 samples both years—did not change during the 33-year period, although the frequency of individual species changed dramatically (Table 1). *Abies balsamea* (a tree) became more frequent, due largely to increases on the north slope, and the herb *Sibbaldiopsis tridentata* declined in frequency. The abundance of three species increased significantly between surveys (Table 2), especially that of the shrub *Vaccinium uliginosum* (Fig. 1).

As a functional group, trees occurred in 42% of all samples in 1976, and this increased to 56% of samples in 2009 (Fig. 2). Forbs

TABLE 2

The median abundance (percent cover) of the eight most frequently occurring species is compared for surveys conducted 33 years apart. The significance of changes in abundance was assessed with the Mann-Whitney *U* test after correcting for multiple intergroup ties. Species are arranged in order of abundance in 2009.

	1976	2009	<i>P</i>
	Median cover class	Median cover class	
<i>Vaccinium uliginosum</i>	10–25%	25–33%	<0.01
<i>Rhododendron groenlandicum</i>	10–25%	25–33%	0.26
<i>Vaccinium angustifolium</i>	1–5%	25–33%	0.01
<i>Abies balsamea</i>	10–25%	10–25%	0.14
<i>Betula cordifolia</i>	5–10%	10–25%	0.19
<i>Sibbaldiopsis tridentata</i>	1–5%	1–5%	0.43
<i>Vaccinium vitis-idaea</i>	1–5%	1–5%	0.29
<i>Juncus trifidus</i>	<1%	1–5%	0.03

declined in frequency from 39% to 29%, and graminoids declined from 31% to 22%. The frequency of the five species with the most northerly distributions—those occurring in the High Arctic and extending south only as far as mountain summits in the Northeast United States—declined non-significantly ($P = 0.23$) from 81% to 75%, while the frequency of widespread species was essentially unchanged.

Frequency and abundance data indicated that several species have clear affinities for one side of the mountain or the other (Table 3), although individual species generally expressed these affinities either in frequency data or abundance data but not both. For two species, aspect had a significant effect for the first time in 2009. *Vaccinium uliginosum* was more frequent on the north slope (it had not been in 1976), and *Vaccinium angustifolium* had higher abundance on the south slope than the north slope (aspect did not influence its abundance in 1976). Abundance data showed that three species with higher abundance on the south side of the mountain had a significant increase in abundance on that side, while none of the species with a north-slope affinity increased in this way.

The total number of species recorded in samples was 21 in 1976, and three additional species were recorded elsewhere above tree line (Table 1). In 2009, we recorded 19 species in samples, plus an additional eight species elsewhere in the alpine zone. One forb recorded in the first survey (a *Prenanthes* sp.) was not observed in 2009. The species that recruited to the community since 1976 were two forbs, a grass, and a lycopod (Table 1). The mean number of species in samples did not change in the 33-year period between surveys (3.1 ± 0.16 in 1976 and 3.2 ± 0.18 in 2009, $t_{192,161} = 0.273$, $P = 0.785$). Mean species density in samples did not differ between

north and south slopes either year (3.0 ± 0.19 vs. 3.3 ± 0.32 , respectively, in 1976, $t_{101,91} = -1.48$, $P = 0.14$; 3.1 ± 0.17 vs. 3.2 ± 0.31 , respectively, in 2009, $t_{92,69} = -0.64$, $P = 0.52$), and the changes in mean species density from 1976 to 2009 were not significant.

Discussion

The 2009 survey provided evidence of the increasing importance of woody plants—both trees and shrubs—in the alpine community of Avery Peak. During the 33-year interval since the first survey, the most widespread tree species increased dramatically in frequency. Trees as a functional group also increased, and the proportion of tree-dominated sites (those with >75% cover of trees) rose, reaching one in five samples in 2009. The abundance of three other species, notably including two deciduous shrubs, increased. We also recorded an increase in total species richness of the community with the addition of four lower montane species that had not been recorded previously.

Analysis of the influence of aspect showed that several species have clear affinities for the north or south slope. More importantly, our results suggest that the south and north slopes are becoming increasingly different from each other and that aspect is becoming more important in determining community structure. Three species with south-slope affinities increased significantly in abundance while none with north-slope affinities did, and two species had significant affinities with respect to aspect that had not been present in 1976.

The aspect analysis also shows that the forces driving species occurrence patterns are different from those controlling

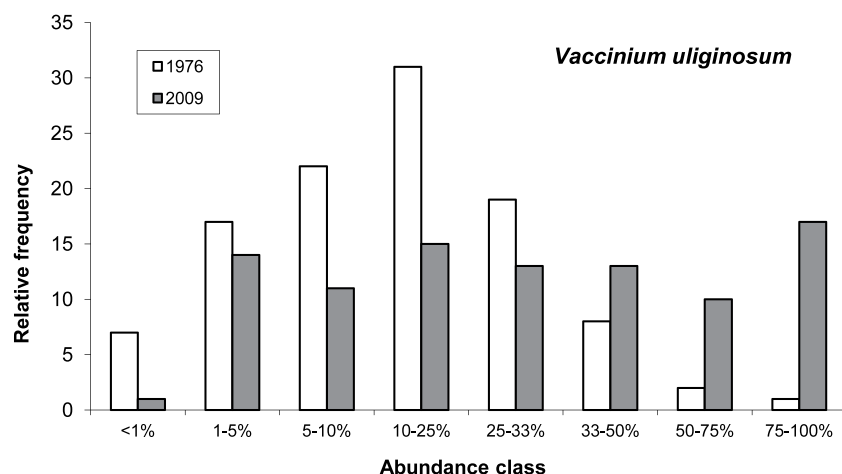


FIGURE 1. The frequency distributions of cover values of *Vaccinium uliginosum* are shown for the 1976 and 2009 surveys. The species had 33% cover or greater in 10% of the samples where it occurred in 1976, but this rose to 43% of such samples in 2009.

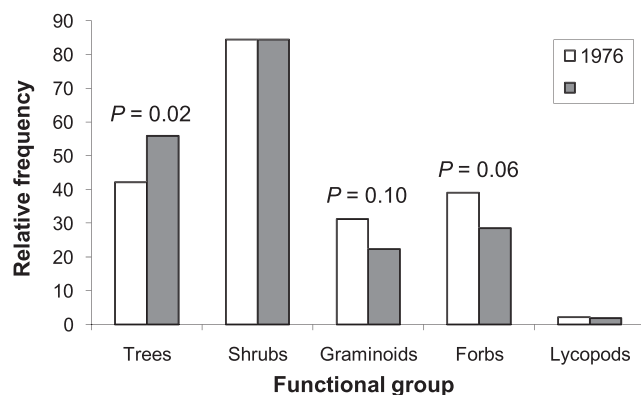


FIGURE 2. The frequency of trees increased in the 33 years between surveys in a Northeast United States alpine plant community. Declines in forbs and graminoids were marginally significant.

abundance. A clear preference for one side of the mountain or the other was reflected in frequency data or in abundance, but not in both. *Sibbaldiopsis tridentata*, for example, was found overwhelmingly on the south side of the mountain in both surveys, but its abundance did not vary from one side to the other. On the other hand, the frequency of *Vaccinium uliginosum* was equally high on the south side of the mountain as on the north, but its abundance in both surveys was significantly higher on the south side. These results suggest that the conditions favorable for the vegetative growth (and vegetative spread) of a species are different from the conditions regulating recruitment such as pollination, maturation of fruit, seed dispersal, and seedling establishment. Changing environmental conditions may affect these forces differently, so additional research would be worthwhile to establish what regulates occurrence and abundance patterns and how they will be affected by warming, nitrogen deposition, and changes in other conditions. On Avery Peak, conditions appear to favor increasing colonization of trees (especially *Abies balsamea*), which increased in frequency, and the vegetative growth of shrubs, which grew larger or spread vegetatively in locations where they had established previously.

The changes recorded are consistent with those reported in tundra communities around the world (Sturm et al., 2001; Klanderud and Birks, 2003; Tape et al. 2006; Cannone et al., 2007; Wilson and Nilsson, 2009) and are also consistent with predictions that shrubs will increase with global warming at the expense of other functional types (Chapin et al., 1996; Epstein et al., 2000), especially in low-alpine settings, where environmental conditions are least severe and where competition plays the greatest role (Calloway et al., 2002; Erschbamer et al., 2009). However, it is impossible to draw conclusions about the cause of the changes in this plant community without precise information on the environmental conditions to which it has been exposed.

All areas of the Northeast are warming (Keim et al., 2003; Trombulak and Wolfson, 2004), and the effects are apparent in less precipitation falling as snow, snow covering the ground fewer days of the winter, and an earlier beginning of the growing season, especially in northern New England. These changes have occurred largely since 1970 (Hayhoe et al., 2007). The mean annual temperature in Farmington, Maine, the nearest weather station with a long-term record (50 km south of Avery), has risen 2.0 °C in the past 115 years, based on a comparison of the mean temperature for the first 10 years for which data are available (1895–1904) with the most recent 10-year period (through 2009; Menne et al., 2010). The mean annual temperature has risen 1.1 °C

just since the 10-year period preceding the 1976 survey. Warming is particularly great during the winter, when the mean temperature is 3.4 °C higher than a century ago. Studies show that warming can lead to increasing dominance of shrubs and trees in tundra communities (Dormann and Woodin, 2002; Walker et al., 2006; Danby and Hik, 2007). Manipulations at 11 tundra sites found that deciduous shrub cover increased with warming (Walker et al., 2006). *Vaccinium uliginosum*, in particular, is thought to benefit from a longer snow-free period (Klanderud and Birks, 2003), which could result from warming.

Tundra plants also are sensitive to nutrient addition (Chapin et al., 1996; Walker et al., 2001; Britton and Fisher, 2008), and nutrient addition can lead to shifts of community dominance from graminoids to shrubs (Shaver et al., 2001), so we cannot rule out the possibility that atmospheric nitrogen deposition or an interaction between warming and nitrogen deposition has contributed to the changes on Avery Peak. Experimental manipulations in Colorado found that nitrogen addition affected alpine community composition in as little as three years and that the nitrogen levels required to effect some change were no greater than the 6 kg ha⁻¹ yr⁻¹ being deposited at the time of the research (Bowman et al., 2006). Nitrogen deposition in the Northeast reached levels in the 1970s that were 5 to 10 times higher than before industrialization (Galloway et al., 1984), and mean annual wet deposition of nitrogen at the Carrabasset Valley station 9 km south of Avery Peak for the period 2002–2008 was 7.1 kg ha⁻¹ (NADP, 2010).

Other conditions also have changed in tundra ecosystems in the past century, including atmospheric CO₂ levels, and these could interact with nitrogen or warming, just as nutrient additions and warming interact with each other (Chapin et al., 1995). It also is likely that, to some degree, species will respond individually, some to warming and some to nutrient additions (Lesica and McCune, 2004; Britton et al., 2009). Only experimental manipulations at a site can establish beyond question what is causing the observed changes in frequency and abundance.

Warming is presumed to be responsible for the establishment in alpine zones of species previously occurring only at lower elevations (Grabherr et al., 1994, 2001; Klanderud and Birks, 2003; Walther et al., 2005; Erschbamer et al., 2009). Increasing richness appears to be most pronounced low in the alpine zone, which would be consistent with our findings. Three of the four species we recorded that had not been observed in the alpine zone previously are common herbs that occur lower on mountains of the region, and we recorded them in most cases low in the alpine zone, under shrubs and stunted trees. The increase in species richness will be temporary if alpine species ultimately disappear because of competition or the loss of suitable habitat (Grabherr et al., 1994; Walther et al., 2002; Klanderud and Totland, 2005). Species losses resulting from competition have not typically been found with rising richness in high alpine areas, possibly because newly arriving species occupy different microhabitats, (Walther et al., 2005), but competition has apparently displaced species in low to mid-elevation alpine communities (Klanderud and Birks, 2003; Britton et al., 2009; Erschbamer et al., 2009; Wilson and Nilsson, 2009).

We found no evidence that species with high-arctic distributions had declined more than other species. In fact, the five high-arctic species on Avery Peak occurred in 75% of the 2009 samples, and only *Hierochloa alpina* appears threatened because of its low frequency. Three of the other species actually increased in frequency or abundance, including the mostly widely distributed plant in the community, *Vaccinium uliginosum*. Our results are in marked contrast to those of Lesica and McCune (2004), who

TABLE 3

The affinity of the most frequent species for the north and south slopes of Avery Peak's alpine zone is compared for the two survey periods. The frequency values shown are the percentage of samples in which each species occurred and the significance of the difference (Fisher's exact test) between north and south sides of the mountain, plus the significance of any change in the species' affinities from 1976 to 2009. Abundance values are the median cover classes for each survey period and the results of Mann-Whitney *U* tests of differences between north and south slopes, plus the significance of change in abundance on each slope from 1976 to 2009. Species are arranged with those appearing disproportionately on the north slope at the top and those with an affinity for the south slope on the bottom.

	Relative frequency						Abundance					
	1976			2009			Change			1976		
	N	S	P	N	S	P	P	P		N	S	P
<i>Rhododendron groenlandicum</i>	78	10	<0.01	71	10	<0.01	0.67	0.04		10-33	5-10	0.06
<i>Betula cordifolia</i>	50	11	<0.01	50	15	0.04	0.17	0.22		5-10	5-10	0.07
<i>Abies balsamea</i>	22	7	0.18	42	12	0.04	1	0.75		10-25	10-25	0.77
<i>Vaccinium vitis-idaea</i>	65	50	0.90	45	45	0.45	0.12	0.10		1-5	1-5	0.50
<i>Vaccinium uliginosum</i>	55	52	0.59	52	42	0.88	1	0.01		10-25	50-75	<0.01
<i>Vaccinium angustifolium</i>	5	20	0.02	2	12	0.05	0.68	0.53		1-5	25-33	0.04
<i>Juncus trifidus</i>	8	46	<0.01	5	26	<0.01	0.52	0.57		5-10	5-10	0.62
<i>Sibbaldiopsis tridentata</i>	9	61	<0.01	4	35	<0.01	0.56	0.78		1-5	1-5	0.88
												0.83
												0.48

found that four of seven arctic/alpine plants at or near the southern limits of their ranges in Montana had declined from 1989 to 2002, while none increased. The difference between our results may be related to how widespread the species are. The Montana species have severely limited geographic distributions and/or are regionally rare, while the Northeast species are globally widespread and sometimes abundant in the region (Bliss, 1963). Narrow geographic ranges and small population sizes are known to make species vulnerable to climatic warming (Sætersdal and Birks, 1997). Our results suggest that having a small niche or geographic range makes species more vulnerable than does having a northern distribution. Two other northern species, *Carex bigelowii* and *Huperzia appalachiana*, occur primarily in areas that have not been colonized by trees and shrubs—*Carex* in two level areas on the top of Avery Peak that are swept free of snow by winter winds, and *Huperzia* in wet cracks at the base of rock faces. *Hierochloa alpina* occurred in 11 samples in 1976 but only one in 2009. It and *Vahlodia atropurpurea*, of which only two plants were found in 2009, appear to be the most vulnerable species on Avery Peak.

Our study found that the structure of the alpine plant community on one mountain in the Northeast has changed since 1976, with woody plants becoming increasingly frequent and abundant. The only other study that considered change among functional groups in the Northeast also found that the frequency of shrubs increased between 1984 and 2007 on four mountains in the Adirondacks of New York (Robinson et al., 2010). The mountains in these studies are like many in the Northeast in that they have alpine communities at relatively low elevation. Many of the herbaceous plants on these mountains occur in open areas where they are exposed to dry winter winds but also full sun during the brief growing season. These species are not usually found in the shade under trees and shrubs and are secure only as long as the mountains have open alpine habitat. If trees and shrubs continue to become more widespread and abundant, species requiring open habitat may become increasingly restricted to disturbed areas and eventually could disappear, following the pattern observed at some altitudes in an arctic alpine site in Sweden (Wilson and Nilsson, 2009). Additional surveys are needed to determine if other mountains in the region are undergoing similar changes that could threaten the persistence of the region's alpine ecosystems.

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