Understanding Northeastern US Alpine Mountains: Context, Causal Agents of Treeline, and Meteorology to Approximate their Response to Climate Change

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Abstract - Understanding climate change and air pollution impacts on the northeastern region's restricted alpine ecosystems is complex. Reduced in size and spatial distribution post deglaciation, these alpine ecosystems survived the Hypsithermal warming period with less change than lower-elevation ecosystems. They are low for their latitude and below physiologically limited treeline. More-recent data support and expand on earlier researchers' hypotheses that wind and moisture, not temperature, explains the continued existence of alpine ecosystems in the Northeast. Shifts in species composition and abundance may occur, but frequency of free troposphere exposure, wind, clouds, and rime-icing events, and related topographic, aspect, and microhabitat may maintain resistance to major alpine-treeline ecotone boundary shifts in this century. Under scenarios assuming high levels of emission of greenhouse gases, future predictions become less clear.

Background

In the public media and scientific forums, an outstanding question remains: are northeastern alpine mountains the regional canary in the coal mine for climate change? Today these alpine ecosystems are biotic "islands in the sky". They have no perennial snow zone (the nival zone) to allow for upward migration of the alpine in elevation. The scientific literature contains examples of upward migration of the alpine into the nival zone in other parts of the world in response to ongoing climatic warming (Cannone et al. 2007).

Natural factors such as plate tectonics, glacial and interglacial periods, volcanic activity, sunspot cycles, and variations in the earths orbit, tilt, and wobble (Eusden et al. 2013) have and will continue to influence climate by varying degrees over time. Over geologic time frames, the northeastern mountains' climate has and will continue to change, and these mountains will not last forever due to natural processes. During the past 3 centuries in the short time frame of human history, anthropogenic actions have superimposed new and strong climate drivers on top of these natural climate change drivers. These factors include rapid land-use changes and loss of sequestered carbon in forests, intensive agricultural and animal husbandry practices, and the emission of greenhouse gases into the atmosphere from synthetic chemicals and geologically sequestered carbon through combustion of

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fossil fuels. These human-derived changes have contributed to the warming of the planet's climate, and modified the atmosphere, though not universally or homogenously across the planet.

Even as this region warmed since the last glacial period, northeastern alpine ecosystems have survived. The alpine flora, adapting to abiotic stresses, is short in stature with minimal to no understory. Today, the region's alpine areas occur on the high-elevation mountains that are cool, windy, and wet. They have short growing seasons and frost-free periods, and are above the forest-line ecotone boundary. Ecotones are transition zones that form where distinct habitats meet across an environmental gradient.

Dissimilarities between temporally close fossil pollen samples suggest abrupt climate changes at times can and have occurred in less than 500 years (Shuman et al. 2009). The magnitude and abruptness of these events may have created bottlenecks that contributed to the reduced composition of the alpine and sub-alpine flora and fauna in the White Mountains, NH (Cwynar and Spear 2001, Miller and Spear 1999, Spear 2000), and the region. However, the region's alpine ecosystems still host relict tundra biota, though reduced in species composition, that survived these climatic excursions.

Inconsistencies in scientific literature terminologies can lead to misunderstandings. Treeline and forest line are terms frequently interchanged in meaning (Daubenmire 1954, Richardson and Friedland 2009). In the true sense, treeline on the mountains is the highest elevation that trees can grow based on their physiological limits, including krummholz, whereas the forest line in the Northeast is where dominant tree growth shifts from vertical to stunted, horizontal growth of low stature (~2.0 to 2.5 m in height; Kimball and Weihrauch 2000, Richardson and Friedland 2009, Richardson et al. 2004, Spear 1989). To be consistent with many published papers (e.g., Cogbill and White 1991, Kimball and Weihrauch 2000, Richardson et al. 2004), we will refer to the alpine and forest ecotone boundary by using the abbreviated term "alpine–treeline ecotone boundary", or "ATL", understanding that trees can and have grown to the highest elevations in our analysis region for at least the last century (Adams, et al. 1920, Antev 1932) and likely much earlier. *Abies balsamea* (L.) Mill. (Balsam Fir) can be found growing at the highest elevations in protected micro niches on northeastern mountains' summits, e.g., immediately below the summit of Mount Washington, NH, at 1917 m (D.M. Weihrauch pers. observ.), and on Mount Marcy, NY (Adams et al. 1920), at 1628 m. Spear's (1989) pollen and plant macrofossil records from his White Mountain, NH, sites suggests the ATL may have been higher than today from 10,300 to 5000 yr BP.

Today northeastern alpine ecosystems occupy only a tiny fraction of New England, New York, and Quebec south of the St Lawrence River. These alpine ecosystems are scattered on more than 60 mountains (Fig. 1). Different authors have used slightly different criteria to define northeastern alpine ecosystems. At most, there are 35 km^2 of this habitat in the northeastern US, with an additional 45

km² in the Chic Choc Monts on the Gaspé Peninsula of Québec (Capers et al. 2013, Jones and Willey 2012, Kimball and Weihrauch 2000, Martin and Germain 2016). The majority of the area is on the Presidential Range in New Hampshire, Mount Katahdin in Maine, and the Chic Choc Monts in Quebec, Canada. Compared to the narrow ridgeline and patch alpine habitats, these largest units have a smaller ratio of ATL ecotone boundary to alpine surface area and larger ATL ecotone elevational ranges of up to 600+ m. More numerous, though only a small percentage of this habitat type's area and limited to several hundred to 1 ha or less in size, are narrow ridgeline strips (Fig. 2) of alpine habitat (e.g., Franconia Ridge, NH; Mount Mansfield, VT; and Saddleback Mountain, ME), heath balds (Mahoosuc Range, ME), or tiny patches (Fig. 3) on mountain summits (e.g. Camel's Hump, VT; Algonquin Mountain, NY; Shelburne Moriah Mountain, NH; and Moxie Bald, ME). Their ATL ecotone elevational range is typically less than one hundred to just ~10 m in elevation, and their ATL ecotone boundary to alpine surface area ratio is large.

More extensive are subalpine forest above ~823 m that cover 314,263 ha in this region (Publicover et al., in press [this issue]) Of the 765 identified units that are greater than 4 ha in size, 83% of them are less than 405 ha in size.

In this paper, synthesizing from the literature and our research, we address the following topical questions for northeastern US mountains:

(1) How has the alpine–treeline ecotone boundary changed during this last interglacial period?
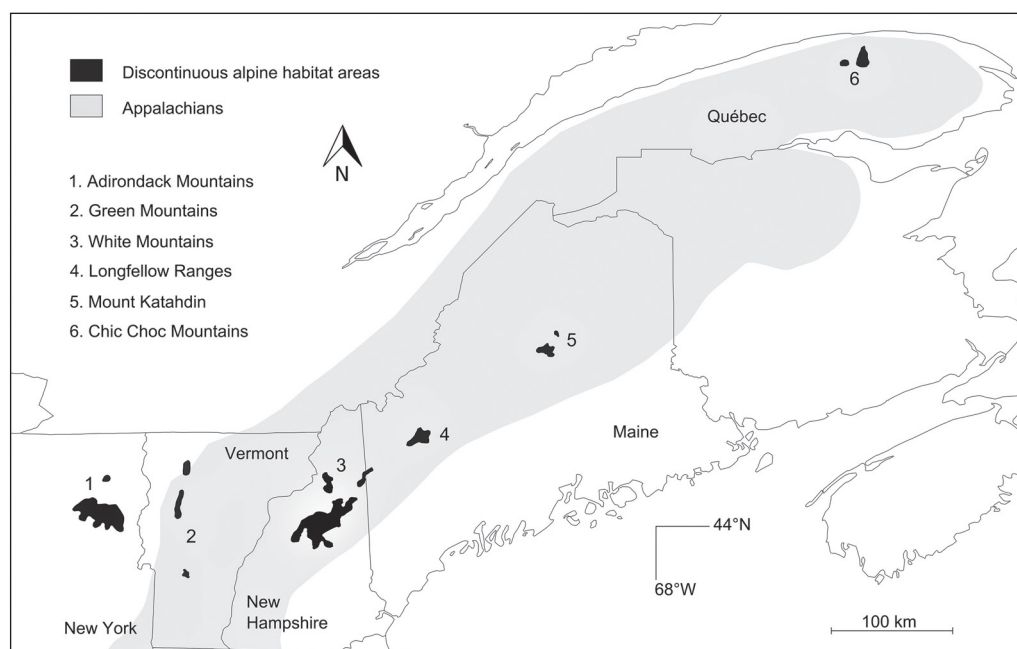

Figure 1. Alpine habitat in northeastern North America. The black-filled areas show the areas in which peaks with alpine communities on their summits occur and represent multiple peaks in most cases (from Capers et al. 2013).

Figure 2. Most of the 80 northeastern alpine ecosystems are small patches or narrow ridge-line bands. Their alpine-treeline (ATL) ecotone elevational range is typically <100 m and their ATL ecotone boundary to alpine surface area ratio is large. Looking south on Franconia Ridge, NH, note that the contiguous krummholz zone reaches the ridgeline on the eastern slope, with only a narrow ribbon of alpine ecosystem on the western windward exposed slope.

(2) What can we discern from the current alpine–treeline ecotone boundaries across northeastern mountains?

(3) Does the current makeup of the northeastern mountain alpine flora indicate what biotic changes we might predict with ongoing regional climate warming?

(4) How does mountain meteorology affect variability in the rate and responses to climate change by elevation on northeastern mountains?

(5) Based on current knowledge, what changes to the northeastern alpine ecosystems might we predict by the end of this century? and

(6) What are current management and research needs?

Topical Questions

How has the alpine–treeline ecotone boundary changed during this last interglacial period?

Palaeobotanical studies in the Northeast (e.g. Jackson and Whitehead 1991, Miller and Spear 1999, Shuman et al. 2009) reveal both major warming and cooling periods during the Holocene following glacial ice recession across the region, starting almost 12,000 years before the present (BP). Tundra-like conditions and

Figure 3. Summit patch alpine habitat of only 0.8 ha on Mount Algonquin/North Boundary, NY, at 1559 m asl, which represents 46% of this habitat type in the Adirondacks (Carlson et al. 2011). Note the presence of Balsam Fir krummholz in protected micro-topography.

biota dominated, followed by boreal conifers. During this interglacial period, the Hypsithermal period (Holocene Climatic Optimum) from ca. 9000 to 5000 yr BP possibly was as warm as today. This period was followed by the onset of the Holocene's neoglacial cooling trend that appears to have been reversed by the 20th century. Even within these periods there were shorter, lower-magnitude fluctuations in temperature. Spear (1989) and Miller and Spear (1999) used plant macrofossil and pollen records in the White Mountains, NH, to show that subalpine fir forests were established by 9000 yr BP and fir trees were more abundant and treeline slightly higher than present from 10,300 to 5000 yr BP. Of their 3 subalpine fir forest sites, the lower elevations showed larger evidence of a warmer interval in the early Holocene. With warming after the glacial retreat, deciduous forests of different compositions came to dominate much of the mid-elevation landscape. The zones of present vegetation became established ca. 2000 yr. BP when *Picea rubens* Sarg. (Red Spruce) and Balsam Fir expanded at 750–1220 m during the more recent neoglacial cooling period (Miller and Spear 1999, Spear 1989). Palaeobotanical results from the Adirondacks suggests similar changing spatial patterns of forest vegetation along elevational gradients during the Holocene in response to climatic, biotic, and other changes (Jackson and Whitehead 1991).

Recent studies covering the past century show conflicting evidence of elevational ecotone shifts on the region's mountains. With ongoing rapid climate change regionally (Murray et al. 2021 [this issue]), high-elevation boreal forests could be expected to migrate upslope into the alpine, with northern hardwood species moving up behind. Some research supports the upslope forest ecotone migration concept, e.g., Balsam Fir and *Betula cordifolia* Regel (Heart-leaved Paper Birch) migrated upslope at an alarming rate of 2.13–2.77 m yr^{-1} from 1965 to 2005 in the Green Mountains, VT (Beckage et al. 2008). However Foster and D'Amato (2015) using Landsat imagery to observe change at spatial scales not possible for plot-based studies such as used by Beckage, showed that forest ecotone boundaries shifted downward or stayed stable on most mountains between 1991 and 2010, but also shifted upward in some cases. They found on average, boreal and northern hardwood forest ecotone boundaries moved down 1.5 m yr^{-1} in the Green Mountains, VT, and 1.3 m yr^{-1} in the White Mountains, NH, suggesting that processes of boreal forest recovery from prior Red Spruce decline, or human land use and disturbance, may swamp out any signal of climate-mediated migration in this ecosystem. Fortin and Pilote (2006) found no definable upslope advancement of the forest line on Mont Jacques Cartier, QC, Canada.

Providing insight into the near future is that the region's alpine ecosystems were reduced in size and spatial distribution by subalpine forest expansion by 10,000 yr BP. However they then survived through the Hypsithermal warming period filter as refugia, and varied considerably less compared to the lower-elevation montane forests (Miller and Spear 1999, Spear 1989). Northeastern mountains today are relatively low in elevation and still host alpine habitats, compared to other northern latitude mountains in the world, whose treeline extends to much higher elevations (Martin and Germain 2016, Richardson and Friedland 2009). The question then

becomes why didn't these northeastern mountains' alpine ecosystems at such low elevations succumb to forest during the Hypsithermal warming period?

What can we discern from the current alpine-treeline ecotone boundaries across northeastern mountains?

The ATL boundary in the US differs significantly from east to west at latitudes just a few degrees north or south of the 45th parallel. The White Mountains, NH, are at 44°N, and Wyoming's Teton Range is at 43°N. Though it varies by hundreds of meters in elevation, the ATL ecotone boundary averages ~1480 m in the Adirondack Mountains, NY, ~1490 m in the White Mountains, NH, ~1280 m on Mount Katahdin, ME, and ~1160 m on the Chic Choc Monts, QC, declining ~83 m for each 1 degree increase in latitude (Cogbill and White 1991). In the Tetons, the ATL is at ~3000 m. The same discrepancies exist when comparing the ATL in the northeastern US with many of their European counterparts. At higher latitudes in Europe, the ATL is typically much higher in elevation, the opposite of what one would expect. The larger question then becomes why do low-elevation alpine ecosystems still survive in Northeastern US and Canada? Comparatively, their maximum elevations are well below where the ATL exists at other similar latitudes, and temperature regimes are not sufficiently cold (Capers et al. 2013) to suggest they should impede forest development.

The 3 largest northeastern alpine ecosystem units are the Presidential Range, NH, Mount Katahdin, ME, and the Chic Choc Monts, QC. Their highest elevations respectively are 1917 m, 1605 m, and 1268 m asl. Their intra-mountain alpine-treeline ecotone boundary is ragged and ranges considerably in elevation, respectively by 573 m, 661 m, and 293 m (Capers et al. 2013, Kimball and Weihrauch 2000). The rate that air cools with elevation in conditions of thermal equilibrium, the adiabatic lapse rate, in dry air is 1.0° C/100 m and in wet air is 0.6 °C/100 m). Like the ATL, studies have shown that measured lapse rates are quite variable with elevation on mountains (Cogbill and White 1991, Richardson et al. 2004). We conclude that theoretical adiabatic lapse rates are an inappropriate tool to predict or model regional ATL elevations, both because of its low accuracy in modeling actual temperatures by elevation and its assumption that temperature is the controlling factor of the region's ATL.

Aspect, slope, shape (concave or convex), and regional topography are important features in understanding the distribution of the ATL. The extent of treeline on the Presidential and Katahdin Range reaches its higher elevations in the more protected valleys, e.g., Great Gulf – Presidential Range, and its lowest elevations on the more exposed ridges, e.g., Boott Spur – Presidential Range, NH (Kimball and Weihrauch 2000). Similarly, the distribution and elevation of the 25 ha of alpine in the Adirondack Mountains, NY differ between summits reflecting overall summit morphology. The shift from arboreal to non-arboreal vegetation occurs at lower elevations on windward slopes with northerly and northwesterly aspects; on leeward slopes this shift occurs at higher elevations (Carlson et al. 2011). New York's alpine habitat decreases from the northwest to southeast, suggesting that

mountains upwind along the prevailing winter wind vector shield downwind summits, underscoring the role of exposure in limiting the upward growth of trees (Carlson et al. 2011). Antevs (1932) and Griggs (1940) hypothesized, and Spear (1989) more conclusively presented evidence that temperature is a poor indicator of the regional treeline, whereas wind and moisture are the dominant factors determining its position.

Does the current make-up of the northeastern mountain alpine flora indicate what biotic changes we might predict with ongoing regional climate warming?

We divide the region's alpine flora today into 3 general groups: the non-arctic, transitional, and arctic (relict tundra). The first group is commonly found at lower elevations and is exemplified by *Cornus canadensis* L. (Bunchberry); their ranges extend much further south, they are not necessarily new invaders, and they require protected micro-habitats, e.g., topographic irregularities and depressions or rocks, and snow cover to survive in the alpine. Transitional species like *Rhododendron groenlandicum* (Oeder) Kron & Judd (Labrador Tea) and krummholz species Balsam Fir and *Picea mariana* (Mill.) Britton, Sterns & Poggenb (Black Spruce), many of which are woody and shrubby, are the major component of the region's alpine flora, excluding the fell field habitat that is dominated by lichens on rocks (Kimball and Weihrauch 2000). These transitional species' ranges include being common in certain non-alpine habitats at lower elevations, and further to the south as well.

The relict arctic (tundra) species are for the most part limited to the region's extreme alpine habitat, the combination of a cooler environment and strong abiotic stresses like wind, moisture, and icing on convex topography in the cloud zone. And they are at the southern end of their range. Though spatially making up the least amount of the alpine zone, alpine meadows (e.g., *Carex bigelowii* Torr. ex Schwein. [Bigelow's Sedge] and *Juncus trifidus* L. [Highland Rush]) and cushion-tussock communities (e.g., *Diapensia lapponica* L. [Diapensia], and *Rhododendron lapponicum* (L.) Wahlenb. [Lapland Rosebay]) occupy these most extreme exposure environments (Kimball and Weihrauch 2000). Though most arctic species are not rare globally, these ones are commonly found on state rare and endangered species lists due to their regional rarity. The fluctuating climate with major cooling and warming events after the last glaciation has greatly reduced the presence of the relict arctic flora on the region's mountains (Miller and Spear 1999, Spear 2000). Additionally, the region's alpine habitats, being isolated islands today, only support few remnant arctic fauna species, principally invertebrates (Jones and Willey 2012). This fauna's fate will likely be determined by how the flora responds to future climatic conditions.

The dominance of woody and shrubby species (e.g., *Empetrum nigrum* L. [Black Crowberry], Labrador Tea, *Vaccinium uliginosum* L. [Alpine Bilberry], and *Vaccinium vitus-idaea* (L.) [Mountain Cranberry]) in this region's alpine zone is the norm, not the exception. Snowbeds occur in sheltered depressions on leeward sides where snow can accumulate to greater depths. Protected from abrasive blowing snow and rime icing, their large plant diversity includes both rare species (e.g.,

Vaccinium cespitosum Michx. [Dwarf Bilberry]) along with many common lower-elevation boreal species (e.g., *Maianthemum canadense* Desf. [Canada Mayflower] and *Trientalis borealis* Raf. [Starflower]).

As a generalization, this region's frequent cloud-base zone (Roberti 2011, Ryerson 1990, Siccama 1974) on its mountains corresponds with the northern hardwood and spruce–fir ecotone boundary at ~800 m. The dominance of alpine species of short stature occurs at elevations 300–700 m higher (Cogbill and White 1991, Kimball and Weihrauch 2000) where topography and microhabitat protects them from greater wind and cloud exposure, winter icing, and abrasive blowing snow. These strong abiotic stresses hinder vertical growth and forest development. These abiotic factors have also allowed the less prevalent relict arctic flora to maintain a foothold in the most exposed sites (Bliss 1963, Kimball and Weihrauch 2000). Climatic changes in wind and moisture regimes, parameters lacking robust climatic records, will likely continue to be dominant factors in determining the future fate of the alpine zone and its floristic composition and stature.

Changes in species composition are influenced by a changing climate, but can also be altered by air pollutants derived from the combustion of fossil fuels and other sources that are the major contributors to global warming. The region's higher elevations receive greater deposition of air pollutants, relative to proximate lower elevations, due to long-distance pollutant transport and increased dry, cloud, and rain deposition, and anthropogenic air pollutants greatly increased acidic and nitrogen deposition to the alpine zone (Keene 2002; Murray et al. 2009, 2013). Alpine areas experimentally have been shown to be sensitive to nitrogen additions (Bowman et al. 2006), which can lead to shifts of arctic community dominance from graminoids to shrubs (Shaver et al. 2001). Ongoing decadal shifts from coal to natural gas to renewables for electric power generation are now altering and reducing the magnitude of acidic and nitrogen additions to the region's alpine ecosystems [(Murray et al. 2013). Furthermore, regional weather fronts, orographic lower-elevation air mass uplift, and the diurnally shifting nocturnal boundary layer that puts the alpine zones in and out of the mixed layer, likely contributes to the complex diurnal and inter-annual variability in pollutant concentrations as measured on Mount Washington (Murray et al. 2013).

By the 1970s, levels of nitrogen deposition were 5–10 times greater than that of the pre-industrialization era (Galloway et al. 1984). Though not verified in the northeastern alpine, warming soil temperatures have the potential to increase the rates of nitrogen cycling (Loomis et al. 2006) and further fertilize alpine habitats. Unlike ever increasing greenhouse gas emissions and global warming trends, sulfur dioxide (SO_2) and nitrogen oxides (NO_x) emissions rates that peaked in the 1970s to 1990s, have since steadily decreased due to legislative mandates, e.g., Clean Air Act Amendments of 1990-Phase 1 from 1995 to 1999, and the more stringent Phase II beginning in 2000. A marked reduction in atmospheric nitrogen loading in the northeastern US has resulted (Strock et al. 2014), though still well above conditions during the pre-industrial era. This region's alpine areas receive higher pollutant deposition rates due to greater precipitation (cloud plus rain) and

dry deposition from winds, declining regionally on a west to east gradient (Driscoll et al. 2001). Though not well understood or studied, reversals in high rates of atmospheric nitrogen loading could negatively impact alpine species benefited by earlier atmospheric N fertilization.

Capers and Stone (2011) reported an increase in a boreal woody species (Alpine Bilberry), possibly at the expense of herbs in the Bigelow Mountains, ME, over a 3-decade period. This study relied on just 2 points in time and therefore cannot detect how these transitions took place. Robinson et al. (2010) measured significant vegetation composition changes over a 23-year period in the Adirondacks, NY, with an overall decrease in bryophytes/lichens and an increase in vascular plants. Community similarity was high among all transects, and increased with time for vascular plants as they became more abundant, indicating a successional convergence. We observed an increase in Alpine Bilberry since 1983 on our permanent alpine transects on Mount Washington and Franconia Ridge, but overall the trend has been a dynamic shifting mosaic with reversion to bare ground first after vegetation loss, as opposed to competitive species displacement. The remnant arctic (tundra) species do not appear to be replaced by transitional or non-arctic origin species (D.M. Weihrauch, unpubl. data). Deciphering the causal agents—natural variation, climate warming, nitrogen fertilization, or other—for the observed changes in these studies remains speculative in the absence of experimentation paralleling long-term monitoring.

Extrapolating climate-change explanations from the tundra to the northeastern US alpine, (e.g., Capers and Stone [2011] explaining shifts to more woody species on the Biglow Mountains, ME) requires caution. Arctic conditions differ considerably by growing season photoperiod due to their higher latitudes, receive much less precipitation and cloud exposure, topographically are much flatter and poorly drained, and have different land-use histories. Wookey et al. (2009) also point out that the effects of global change on alpine and arctic ecosystems and potential climate-change feedbacks are not predictable from simple empirical relationships between processes and driving variables. The effects of changes in species distributions and dominances on key ecosystem processes and properties must also be considered.

How does mountain meteorology affect variability in the rate and responses to climate change by elevation on northeastern mountains?
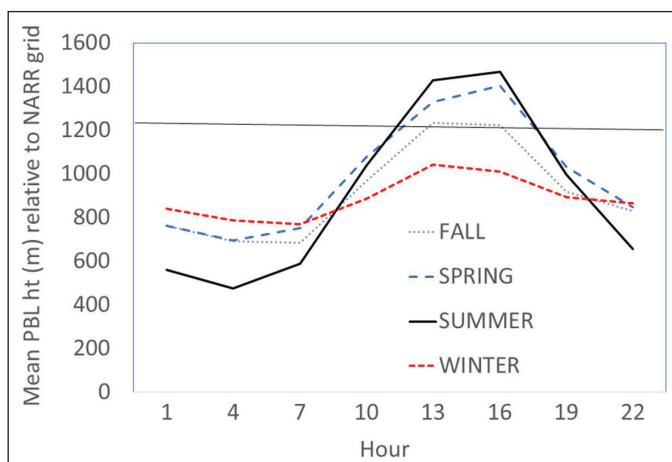
There is considerable disparity between the spatial scale of many climate-modeling efforts and the finer biological scale at which montane organisms experience their temperature environment. For example, most climate models are unable to simulate influencing features in the planetary (atmospheric) boundary layer (Dobrowski et al. 2009), particularly at the finer scale of mountains. The planetary boundary layer (PBL) is the region of the lower troposphere that is heavily influenced by the surface of the earth. The earth's surface holds and releases heat and moisture, and it creates friction for moving air masses. Above the PBL is the free troposphere, an air mass of different origin at times and less affected by ground-

level effects. The PBL top migrates up and down both daily and seasonally, and higher montane elevations in the Northeast can be exposed to free tropospheric air at times and the PBL at other times. At nighttime, and seasonally in the winter, the higher elevations are frequently above the PBL (Fig. 4), meaning they experience higher winds and different air masses (see Murray et al. 2009, 2021 [this issue]) and greater air pollutant exposure from long-distance transport than lower elevations (Fischer et al. 2004). Grant et al. (2005) calculated for Mount Washington's summit that 50% of the days experience free troposphere influence from horizontal air movement (advective), and only 20% of winter and 37% of summer times experience upward (convective) boundary layer influence.

We found in analyzing one of the world's best climate datasets from the Mount Washington Observatory (Murray et al. 2021 [this issue], Seidel et al. 2009) that the summit is warming more slowly than surrounding lower elevations. Similar results have been reported for Mount Mansfield, VT, but its monitoring site and data have been compromised at times, and the period of record is shorter (Kelsey 2018). The free troposphere has experienced a slower warming trend than the PBL at many locations globally (Pepin and Seidel 2005), which could explain the summit's slower warming rates relative to lower elevations during this season since Mount Washington and other higher mountains in the region are more frequently exposed to free tropospheric air in winter (Murray et al. 2021 [this issue]). Climatic warming trends by elevation, mostly due to warming of the daily minimum temperatures, are closer during late spring through early autumn—the seasons when sensible heating grows the convective PBL past the summit elevation routinely (Murray et al. 2021 [this issue]).

Altitudinal lapse rates vary considerably by season, time of day and aspect, compromising their usefulness in extrapolating climate models based on lower-elevation temperature records to predict mountain climate changes. On average, the air is more stable on Mount Washington's summit during nights and in fall

Figure 4. Diurnal pattern of the planetary boundary layer (PBL) on Mount Washington, NH. The horizontal line is the height of the summit relative to the North American Regional Reanalysis (NARR) grid height (1998–2008 NARR data; NOAA 2021). This height is lower than the true summit height as it is based on an average across the 32 km NARR grid. Alpine zone exposure to free tropospheric air is much greater in the nighttime hours and seasonally during the fall and winter. When above the PBL, exposure to long-distantce air pollution transport is greater.

and winter, resulting in the average lapse rates being significantly lower than dry adiabatic predictions. During these times, cold stable air typically resides in the valleys. An unstable atmosphere (i.e., high lapse rates) has significant atmospheric turbulence and vertical mixing. As a result, due to increased solar radiation, spring and summer seasons experience the greatest and deepest mixing of air. The mixing often extends from the valleys up to 2750 m, and lapse rates differ by aspect, being greater on the windward side than the leeward side of the mountain (Kelsey 2018, Wells 2017). Richardson et al. (2004) found similar lapse-rate differences in other NY, VT, and NH mountains.

Orographic effects also greatly increase precipitation and winds with elevation. Prevailing winds are forced upslope when they encounter mountains, resulting in increased wind speeds on ridges and summits, like air passing over an airplane wing. As air is forced up, air pressure drops, cooling the air mass. When the dew point is reached, the air parcel becomes saturated, and further ascent causes super-saturation and precipitation. Due to the proximity of the northeastern mountains to maritime moisture, the higher elevations are more frequently immersed in clouds, (e.g., >57% of the time on Mount Washington's summit; Seidel et al. 2007). The windward side experiences greater precipitation than the leeward sides. To determine the amount of precipitation contributed from cloud moisture, Vogelmann et al. (1968) set out rain gauges equipped with screen coils to intercept and collect cloud droplets along a Green Mountain, VT, mountain slope. The screened rain gauge at 550 m collected slightly less water than the unscreened gauge. At 1100 m, where clouds and fog are frequent, the screened gauge collected 67% more water than the unscreened gauge. Since the regional prevailing winds are typically west too east, the maritime moisture effect relative to the Presidential Range, NH, diminishes to the west in NY's mountains and to the north-northeast in Mount Katahdin, which is further from the ocean.

Importantly, in the spring, fall, and winter, clouds amongst the region's higher-elevations can result in rime ice. Rime ice forms when supercooled droplets of liquid water impact surfaces at temperatures below freezing. The stronger the winds the faster the moisture replenishment rate and resulting rime-ice accretion. Ryerson (1990) measured ice accretion measurement rates on passive, manually operated collection baskets and automatic ice detectors in the Green Mountains, VT, and Mount Washington, NH. Icing rates increased exponentially with elevations above 800 m, with the rate seemingly secondarily controlled by microtopographic relief exposure, i.e., convex versus concave topography. Ryerson's cloud-base elevation roughly corresponds to that reported by Siccama (1974), who correlated the northern hardwood/spruce–fir forest ecotone boundary in the Green Mountains, VT, with the regional cloud base. Though less frequently in the clouds, lower exposed ridges where winds are accelerated have a greater moisture replenishment rate from clouds than higher, more-protected gulfs, which may be in the clouds more frequently. Ryerson (1990) concluded that his measured dependence of icing rate with elevation to be largely a function of New England's high wind and cloud regimes, which differ from many other mountains in the world.

Rime-ice accretion mass can be substantial, resulting in major mechanical damage to the forest canopy (Fig. 5). Combined with strong winds, annual winter foliage losses can be up to 20% of the most exposed canopy (Marchand 1995). This foliar loss with elevation during the winter is strikingly visible by its litterfall on the snow's surface when hiking the higher elevations in late winter/early spring. Foster (1988) on Mount Moosilauke, NH, showed that overstory mortality occurs rapidly and synchronously within the exposed dieback zones of subalpine, wave-regenerated Balsam Fir of the northeastern United States. Reductions in leaf area associated with dieback zone formation may cause increases in within-canopy windspeeds and rime-ice deposition rates during winter storms, resulting in further foliage loss. Rime-ice deposition during winter storms and cumulative winter needle litterfall were greatest in the dieback zone, with 1-year-old foliage having 56% lower photosynthetic capacity than current-year foliage. Foster concluded that repeated defoliation each winter may contribute to tree death by reducing whole-tree photosynthetic capacity.

Similarly, Marchand (1979) provided evidence from Mount Lafayette, NH, that the region's low elevation of treeline may result from the suppression of photosynthetic production due to reduced leaf-surface temperature, and lost total leaf area and stored carbon reserves due to exposure to a high-wind regime. Higher-elevation

Figure 5. Rime-ice accretion on Balsam Fir on Mount Mansfield, VT, ridgeline exposed to the highest winds. Note in the background the higher stature trees with minimal rime-ice accretion in a more protected microhabitat off the ridgeline.

trees at treeline had a greater reliance on the mobilization and utilization of metabolites stored over winter in 1-year old foliage compared to lower-elevation, more protected trees. The heavy loss of foliage at treeline during the winter compounds the problem of reduced photosynthetic capacity in these cooler environments (Marchand et al. 1986). We observed Balsam Fir growing vertically in stature in the alpine zone in protected niches on Mount Washington until a winter rime event damaged the cambium and resulted in a loss of leaf area (Fig. 6). Similarly, blowing snow across the surface can be very abrasive, resulting in the loss of mid-stem krummholz foliage growing above their sheltered microhabitat, creating broom-like growths.

The region is predicted to see higher precipitation in the future (MCC 2020). Mount Washington's summit for the 1934–2004 period of record has exhibited an increase in the frequency occurrence of fog annually (0.5% decade^{-1}), with the greatest shift in the summer and particularly the fall months at ~1% decade^{-1} (Seidel et al. 2007). Though the highest elevations are trending warmer annually, the rate is slowest in the winter and comparatively slower than at lower elevations (Murray et al. 2021 [this issue]). Should increased cloud frequency result in more and/or greater magnitude of rime-ice events in the near future, the effects of mechanical damage preventing upward migration of the forest line would be continued or enhanced and, in the extreme, possibly even resulting in downslope advancement of the alpine ecosystem.

We note that Richardson et al. (2003), using data from 24 airport weather stations along the north–south axis (35º–45ºN) of the Appalachian Mountains, showed a significant rising trend in cloud-ceiling height from 1973 to 1999. They suggest potential ecological effects on high-elevation forests, where the transition from

Figure 6. Rime-ice event in the Presidential Range, NH, that degraded the exposed krummholz's vertical growth that occurred during more benign years to heights above its protected microhabitat in a topographic depression (left) by abrasively exposing the cambium and causing needle loss (right).

deciduous to coniferous forest is thought to be controlled by the height of the cloud base. However, Roberti (2011) showed on Mount Washington, NH, that proximate airport data to be inaccurate for comparisons and should not be extrapolated or interpolated to account for clouds within the Presidential Range, NH, particularly since cloud heights fluctuated considerably at different sites on the mountain due to aspect, strong weather fronts, and orographic effects. Kimball and Keifer (1988) found spatially proximate, low-elevation temperature data to underestimate relationships between temperature and montane Red Spruce tree-ring data on Mount Washington, NH, compared to on-mountain temperature data. These studies exemplify the dangers of modeling or extrapolating lower-elevation meteorological data, though more readily available, to the region's mountains.

Based on current knowledge, what change to the northeastern alpine ecosystems might we predict by the end of this century?

Climate changes in the region's alpine habitats this century will be influenced by the rate and magnitude of the ongoing regional warming trend and changes in precipitation by elevation (Murray et al. 2021 [this issue]), as well as shifts in atmospheric circulation (e.g., Arctic amplification) and the greater frequency of extreme weather events (Francis and Vavrus 2012) among others. Current climatic models under varying emission scenarios predict continued global temperature increases. The mid- to high-emissions scenarios predict warming for the Northeast of 2.9–5.1 °C by the end of the century relative to a base period of 1976–2005 (Wuebbles 2017), and the region is expected to continue to warm faster than other regions in the US (Karmalkar and Bradley 2017). Since predicted temperature increases by the end of this century have or will likely surpass regional temperature and precipitation regimes during the Hypsithermal warming period (Jacobson et al. 2009), using the existing palaeobotanical record for guidance is useful, but requires caution.

A modified matrix of 6 trait categories to assess climate change vulnerability of Maine's ecosystems has been proposed by Whitman et al. (2014). We address these in our following assessment.

Habitat specificity. At macro- and meso-scales, the alpine plant communities correlate with environmental parameters such as elevation, aspect, and concavity–convexity (Bliss 1963, Carlson et al. 2011, Kimball and Weihrauch 2000). At the microhabitat level, species heterogeneity typically is the rule. As described earlier, our monitoring transects established in 1983 in the White Mountains, NH (D.M. Weihrauch and K.D. Kimball, unpubl. data), to quantify temporal and spatial changes in alpine species composition and stature suggest that northeastern alpine species do shift in place at the microhabitat level. Sites commonly go back to bare earth when a species is lost from it before being substituted by another species, as opposed to one species directly taking over another. Studies from western mountains suggest similar progressions (Spasojevic et al. 2013). Monitoring alpine species changes in long-term monitoring plots from 6 community types over 20 years in a complex alpine landscape with pronounced gradients in microtopography and consequently large variation in temperatures, snow depths, and nitrogen

availability across small, 10-m scales, Spasojevic et al. (2013) concluded that fine-scale landscape heterogeneity allowed species composition and functional diversity to move in response to directional changes in climate, nitrogen depositions, and grazing over time. These interactions within complex topography create refugia at various scales, which may aid in the persistence of alpine species (Dobrowski 2011, Morelli et al. 2017, Trivedi et al. 2008).

Where species shifts do occur within microhabitats, even if to more woody species like Alpine Bilberry (Capers and Stone 2011)*, the characteristic low plant form in the alpine governed by protection to resist mechanical damage from wind and icing currently is retained. And topographically complex environmental heterogeneity allows the alpine vegetation to track this finer-scale variability, enhancing its resilience to underlying directional changes in environmental conditions. We hypothesize that this resilience will likely continue this century in the larger alpine units. The role and importance of ongoing changes in atmospheric nitrogen deposition, or other causal agents in this shifting mosaic of species in these microhabitats remains unclear. Also less understood is the fate of alpine snowbank communities, where data are sparse (Capers et al. 2013). Thaw events on Mount Washington are increasing (Murray et al. 2021 [this issue]) and may challenge snowbank communities that host large species diversity (Berend et al. 2020).

The threat of overall loss of the regional alpine is greatest for the narrow ridgeline and pocket alpine habitats. With minimal elevational range, and their large alpine–treeline ecotone boundary to alpine surface area ratio, conditions for the encroachment of spruce–fir krummholz and even the forest line is more favorable.

Edge of range. Are the arctic (tundra) species at the southern edge of their range, whose populations are highly fragmented, more vulnerable to climate change? Much of the region's alpine flora is already dominated by transitional species, many woody, that are adapted to warmer climatic conditions. The relict arctic species now for the most part survive in the region's extreme alpine habitats on convex topography where strong abiotic stresses like wind, moisture, and icing exist. The fluctuating climate with major cooling and warming events after the last glaciation and isolation has greatly reduced the abundance and diversity of the relict arctic flora on this region's mountains (Miller and Spear 1999, Spear 2000) suggesting that this component of the alpine species composition is at greater risk this century. Excluding the large and complex alpine areas (the Presidential Range, NH; Mount Katahdin, ME; and the Chic Choc Monts, QC), the threat of extirpation within the numerous small alpine habitats is even greater. Due to their limited size, they support smaller, more-vulnerable populations (Lande 1993) and have minimal complex alpine topography (micro-refugia) to facilitate on-site resilience (Graae et al. 2018).

Environmental or physiological tolerance. More vulnerable are species restricted to a narrow range of temperature, hydrology, or snowpack conditions, including both edge-of-range species with distributions most likely determined by climate (as opposed to habitat), and specialists with narrow physical-niche tolerance. Since many of the remnant arctic species are adapted to and occupy

some of the most exposed habitat and that exposure factor is likely to continue, their near-term risk may be medium in the larger alpine units. Their ratio of ATL ecotone boundary to alpine surface area is relatively small and their ATL ecotone elevational range of thousand(s) of feet is relatively large. The threat of competitive effects and loss of remnant arctic species is greatest on the small ridgeline and summit patch alpine ecosystems. They have a comparatively large ratio of ATL ecotone boundary to alpine surface area, and a small ATL ecotone elevational range of less than several hundred feet elevation.

Some upward (or downward) migration in the ATL ecotone boundary is possible as this ecotone is not entirely static overtime (Miller and Spear 1999, Spears 1989). Shifts in the ATL will impact the alpine flora since those species cannot tolerate or compete under a forest canopy. Overall, we do not hypothesize in the near-term wholesale shifts in the current transitional and non-arctic species composition due to physiological limitations, though species abundance can be a shifting mosaic within decadal time frames in the White Mountains, NH (D.M. Weihrauch, unpubl. data). Retention of low physical stature, and a continuation of overall resistance to major upward migration of the ATL, a trend exhibited during temperature swings during the Hypsithermal warming period several millennia ago (Spear 1989, 2000), will possibly last into the end of this century. The tenure of this time lag in biotic response to climatic warming becomes more challenged as the timeframe is moved out further, or rates of greenhouse gas emissions remain high or increase.

We note from the limited data available from our successful restoration work with the formally federally listed endangered species *Potentilla robbinsiana* (Lehm.) Oakes ex Rydb. (Robbins' Cinquefoil) that our transplants grown from collected seeds germinated, survived, and reached flowering size multiple years earlier when grown at much lower elevations and latitudes in Framingham, MA, at temperatures likely exceeding those predicted to change this century at its montane locations (Brumback et al. 2004). However, sufficient winter cold for enhanced seed germination appears important. Though higher-elevation sites' greater exposure to the free troposphere results in comparatively slower warming rates, especially in winter, compared to lower-elevation locations (Murray et al. 2021 [this issue], Seidel et al. 2009), seed-germination success rates of the relict arctic flora could be diminished in future decades since the greatest driver in climate warming is higher daily minimum temperatures.

Interspecific or phenological dependence change. Species having high dependencies or requiring special environmental cues or interspecific interactions are more likely to be disrupted by climate change. The degree of genetic variability in the remnant arctic species and their capability to evolve with environmental changes is poorly studied and mostly unknown. The non-arctic and transitional species, through their wide distribution range and current domination of this region's alpine habitat, exhibit their ability to adapt to a wide range of environmental conditions, excluding upward migration of the ATL.

Over time, Antevs (1932) and Spear (1989) on Mount Washington, NH, and Holtmeier and Broll (2010) have all more broadly concluded that discussions of

a potential climatically driven upward shift of the treeline at the landscape and smaller scales require greater attention to the effects of wind and moisture because warming alone cannot compensate for these other factors. We concur and hypothesize, based on prior major temperature swings and the degree of resistance and resilience to climatic variability that the Northeast's alpine ecosystems have exhibited post-deglaciation, that many of the region's larger alpine units will continue to survive to the end of this century, though their species composition and abundance may change.

Frequent exposure to the free troposphere, wind, clouds, and rime icing, and related topography, aspect, and microsite facilitation that provide shelter from these physical events will continue to strongly influence any shifts of the ATL in the next several decades to the end of the century. Based on regional climate model predictions of increased precipitation (Lynch et al. 2016) and ongoing trends in cloud/fog incidence (Seidel et al. 2007), it is reasonable to assume that cloud frequency exposure and subsequent seasonal rime-ice accretion will continue. Consequently its role in mechanical damage and corresponding disruption of a tree's ability to retain sufficient carbon reserves due to needle loss and cambium damage will likely continue to override the role of heat deficiency and lengthening growing season in determining treeline position, spatial pattern, and resulting asymmetric and suppressed growth forms in the near term. Warmer, moister winters, even if less snow and more rain, could increase rime-ice incidence at higher elevations. We have also recorded reproductive phenology of some alpine species, and using temperature data beginning in the 1930s, our modelling results indicate minimal change in phenology of alpine plant flowering, compared to lower elevations (Kimball et al. 2014).

Mobility. Adaptive capacity can take several forms: resistance (persist in place with the capacity to withstand change) and resilience (capacity for recovery of function, including by shifting in place) (Pimm 1984, Tilman and Downing 1994). Major upward migration by the region's alpine flora to climate change is not an option as the region is absent a nival zone of perennial snow. Nor is significant alpine migration to other forested mountain summits in the region likely viable, even if they are anthropogenically altered as has occurred in a few isolated instances due to fire, e.g., Mounts Monadnock and Cardigan, NH, and Baldface Mountain, ME (Jones and Willey 2012).

The rarer, relict arctic (tundra) flora considered most vulnerable and now spatially distant from its origin, has shown considerable resistance by maintaining its existence to date. However, if diminished or lost, particularly on the small summit patches and linear ridge alpine habitats, these species will have immense difficulty in repopulating, with possibly the exception of on the Chic Choc Monts, QC, which are more northern and proximate to these species' wider distribution. The endemic, rarest species with the smallest populations and extremely limited range and ability to disperse have the greatest vulnerability if lost, e.g., Robbins' Cinquefoil.

Exotic pathogens or invasive species. Whether the region's alpine ecosystems are sensitive to exotic pathogens or invasive species that may increase or arrive due

to climate change has minimal evidence to date. Much of the alpine species' composition is and has been dominated by transitional species found at lower elevations, many which are woody shrubs. They are not considered invasive. Since the mid-1800s, when horses and mules carried tourists and supplies up and down Mount Washington, NH, dandelion and other non-native species seeds were deposited—and fertilized—in protected spots along the road and around summit buildings. In 2014, Robert Capers and Nancy Slack (University of Connecticut, Storrs ,CT [retired], and Sage College, Troy, NY [retired], respectively, pers. comm.) found *Taraxacum officinale* F.H. Wigg. (Common Dandelion) thriving near the summit of Mount Washington, NH in a remote, pristine 65-m^2 area with more than 2800 robust dandelion flowers. Volunteers were recruited to remove this invasive cluster. In alpine restoration efforts with exotic grass seed mix on both Franconia Ridge, NH (Guy Waterman (deceased), pers. comm.), and in the Adirondacks, NY (Ketchledge et al.1985), the introduced grass species died out in less than a decade. We expect the threat from exotic pathogens or invasive species to this region's alpine ecosystems due to climatic change to remain low to the end of this century due to the severe abiotic conditions including mechanical degradation from icing and frequent freeze thaw cycles, that will likely persist. The expansion of transition and non-arctic species already in the alpine zone is more likely.

Summary. We hypothesize that northeastern alpine ecosystems under the emission models that predict the lowest to medium degrees of warming scenarios will continue to survive this century, with some shifts in species composition, but typically retaining low physical stature. Upslope movement of the ATL ecotone boundary will continue to be impeded and slowed by wind and rime ice, and slower winter warming rates. Most at risk are the ridgeline and summit patch alpine habitats where only minimal ATL encroachment can result in the demise of these alpine habitats. Relatively stronger climatic and ecological changes may occur at lower montane elevations (Pucko et al. 2011) with their faster warming trends and much earlier spring and later autumn phenology. Under warming scenarios generated by high-emission models, or longer timelines, predictions become much more challenged as major disruptions to current atmospheric circulation, ocean currents, and other dominant climatic factors are quite possible. Such disruptions could trigger sudden, major, and more permanent climatic shifts.

What are current management and research needs?

Except for Saddleback and Sugarloaf mountains in Maine, which host privately owned ski resorts on their alpine ecosystems, all other larger units have varying degrees of conservation management and protection status through state, federal or non-profit ownership. Mount Washington, NH, hosts privately owned cog-railway and auto road corridors, and a State Park facility with a large sewage treatment facility on its summit cone. The Presidential Range, NH, hosts 3 alpine huts operated by the Appalachian Mountain Club. Mount Whiteface, NY, has summit buildings and like Mount Mansfield, VT, alpine ski areas and roads to their alpine ecosystems. All of these alpine areas, except for the Chic Choc Monts, QC, are readily accessible to large human populations. Near term, the major threats to the

relict alpine ecosystems will continue to be from human activities, e.g., ski areas, burgeoning numbers of hikers and backcountry winter recreationists, and externally derived impacts from air pollutants (acidic wet and dry deposition, ozone, nitrogen fertilization, etc.). State and federal land managers are currently challenged to just address ongoing high-volume recreational impacts to their alpine ecosystems. Their expertise and legislative mandates to influence impacts originating outside of their jurisdictional boundaries are much more limited, as has been exhibited by impacts from air pollution. A shift to climate change being an increasingly severe and much more dominant threat is foreseeable if greenhouse gas emissions are not reduced dramatically below current emission rates in the next decades, as wide oscillations beyond known climatic conditions then become more likely. For state and federal land managers who oversee the region's alpine ecosystems to have an effective and meaningful voice in addressing air pollutant and climate-change impacts that originate outside of their designated management boundaries will require a paradigm shift in their staff's scientific expertise, legislated mandates, and resources allocated to them.

Future research needs to better predict responses of northeastern alpine ecosystems to ongoing changes in climate and air-pollutant deposition are described in Capers et al. (2013) and Wookey et al. (2009) and for brevity are not repeated here. Very problematic is the scarcity of continuous weather and climatic data on this region's mountains. Of the 347 active National Oceanic Atmospheric Administration (NOAA) meteorological stations in northern New York, Vermont, New Hampshire, and Maine, only 2 are above 650 m asl; the longest and most complete quality data sets are from the summit (1917 m asl) and base (650 m asl) on Mount Washington, NH, starting in 1935 (Murray et al. 2021 [this issue]). Though the most thorough and comprehensive ecological, palaeobotanical, and climatic data are from Mount Washington and the Presidential Range, NH, other less comprehensive data sets from the region's alpine ecosystems appear to be in general alignment with the assumptions that are heavily drawn from this better-studied mountain. A priority research need is to confirm these assumptions, which, in part, will require state and federal land managers to be more flexible in permitting the necessary monitoring equipment and research needs.

Acknowledgments

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