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Climates on the move: Implications of climate warming for species distributions in mountains of the northeastern United States

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ABSTRACT

Mountains contain steep but constricted climate gradients that can provide climate warming refugia often overlooked in coarse-scale models of species migrations. With continued climate warming, the potentially important role of mountains in maintaining suitable climate for migrating species is still not clear. To determine if mountains in the northeastern U.S. can continue to serve as refugia for species in high-elevation spruce-fir forests under warming climate, we studied climate and climate-vegetation relations along elevational gradients across 76 sites on 11 mountains in four states of this region. We calculated (a) fine-scale temperature lapse rates using *in situ* climate loggers on each mountain, and (b) regional long-term temperature trends using 36 meteorological stations, in order to determine (c) recent and expected future shifts in species temperature envelopes along elevational gradients by linking lapse rates with regional temperature trends and climate warming scenarios for 2100 (+1, 3, and 5 °C). Since 1960, temperature regimes have shifted upslope on average by 377 m and 133 m for the monthly mean of daily minimum (T_{min}) and maximum (T_{max}) temperatures, respectively, although climate did not warm equally for all months. By 2100, mid-range warming of 3 °C may shift monthly temperature regimes upslope relative to their 1960s locations on average by 986 m for T_{min} (580 m for 1 °C, and 1393 m for 5 °C scenario) and 588 m for T_{max} (285 m for 1 °C, and 891 m for 5 °C scenario). We confirmed that spruce-fir forest distribution in the northeastern U.S. is strongly related to temperature, particularly October T_{max} that has surprisingly differed from the overall warming trend as it cooled slightly since the 1960s and thus possibly contributed to the recent downslope shifts in some species ranges documented across the region in other studies. However, the vast majority of monthly temperature variables suggest considerable climate warming since the 1960s, and, given the expected future warming, the temperature regimes characteristic of the lower range margin of spruce-fir forests are unlikely to be present on many mountains in the region by 2100. Consequently, mountains in the northeastern U.S. may not provide long-term climate refugia for species dependent on the climate currently found in spruce-fir forests unless they can adapt to warmer temperatures.

1. Introduction

Mountain regions cover ~25% of the global terrestrial land area (Kapos et al., 2000) and can provide refugia from global warming for many species, because highly heterogeneous mountain landscapes contain steep climatic gradients that reduce migration distances needed to track changing climate (Isaak et al., 2016; Jump et al., 2009; Loarie et al., 2009). Studies of climate impacts on regional species distributions and migrations are often limited by available coarse-scale datasets (usually ranging from 1 to 20 km resolution; Iverson et al., 2008; Winter et al., 2016) that may miss ground-level microclimate variation (De Frenne et al., 2013) and related fine-scale population dynamics leading to species spatial spread across landscapes (e.g., Dovčiak et al., 2005). For example, a single grid cell at 20 km resolution can incorporate elevations that vary by > 1500 m in mountains of the northeastern United States (e.g., Mt. Washington, New Hampshire), corresponding to temperature differences of ~7.5 °C between the low and high elevations within the same cell (cf. conservative lapse rate of 0.5 °C per 100 m; Richardson et al., 2004). Even at a 1 km resolution, a single grid cell can still include ~400 m range of elevations and ~2 °C range of temperatures (cf. Winter et al., 2016). Given the magnitude of climate warming (Loarie et al., 2009) relative to the climatic gradients observed in mountains, we need to better understand if and how mountains can serve as species refugia under climate warming at finer

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scales relevant to species biology (Lenoir and Svenning, 2015).

As climate warms, many species may require rapid migration to higher latitudes and elevations to track suitable temperatures (Davis, 1989; Loarie et al., 2009; Williams et al., 2007). However, spatial distributions of long-lived sessile species, such as forest trees, are expected to lag rapid climatic changes (Corlett and Westcott, 2013; Iverson et al., 2004; Urban et al., 1993) and thus potentially make dispersal distances to new climatically suitable areas prohibitively large. Mountains could act as species refugia particularly for the long-lived sessile species since steep climatic gradients can reduce dispersal distances that species need to track their shifting climatic envelopes (Jump et al., 2009; Loarie et al., 2009). Trees are foundational organisms in forested ecosystems, but climate warming can also impact species in more mobile taxonomic and trophic groups directly by altering temperature regime or indirectly by altering species vegetative habitat (e.g., Parmesan, 2006) as shown for example for many bird species (Devictor et al., 2008; Stralberg et al., 2015), insects (Addo-Bediako et al., 2000; Wiezik et al., 2015), and cold-water stream organisms (Isaak et al., 2016). Despite the potentially crucial role of mountains as species' refugia under warming climate, a general lack of fine scale climatic data from mountain regions makes it unclear if mountains can retain suitable climate for temperature-sensitive species and for how long.

In the northeastern U.S., the elevational distributions of forest tree species have shifted over time with climate (at timescales > 1000 years; Jackson and Whitehead, 1991) with spruce-fir forests occupying high elevations above northern hardwood forests (currently *ca.* > 800 m above sea level, a.s.l.) and below mountain summits (1917 m a.s.l. at Mt. Washington, the tallest mountain in the region, but most summits are lower and often rocky and unsuitable for forest) (Cogbill and White, 1991). Thus, the elevation of the ecotone (transition) between northern hardwood and spruce-fir forests, and the height of mountain summits, determine together the amount of habitat climatically suitable for spruce-fir forests, and the area of this habitat is expected to gradually shrink as climate warming causes upslope shifts of current climate regimes and vegetation zones to higher elevations (Lenoir and Svenning, 2015). Although the elevation of this ecotone is generally thought to be determined by climate, it may also be mediated by local factors such as land-use or soil characteristics (Hayes et al., 2007; Lee et al., 2005; Wason and Dovciak, in press). Importantly, climatic controls on tree species distributions include species responses to finer-scale temporal variation in climate such as monthly maximum or minimum temperatures (Cogbill and White, 1991; Cook and Johnson, 1989; Goldblum and Rigg, 2010; Saxe et al., 2001). Yet, the effects of monthly temperature variables on ecotone locations under climate warming are not well understood due to the lack of fine-scale studies integrating *in situ* measurements of forest vegetation and local climate along well-defined elevational climatic gradients with broad scale climate warming trends.

Given the sensitivity of forest tree species distributions to climate, the predicted warming (between 1 and 5 °C; Collins et al., 2013; Van Vuuren et al., 2011) is expected to rapidly diminish areas with climate associated with spruce-fir forests on broad regional scales in the northeastern U.S. (by 2100; Iverson et al., 2008). Yet, recent finer-scale studies documented both upslope (Beckage et al., 2008; Savage and Vellend, 2015) and downslope (Foster and D'Amato, 2015; Wason and Dovciak, in press) shifts of tree species ranges in this region over the past few decades. While the upslope shifts of species distributions with elevation are consistent with warming climate, the downslope shifts are not. The downslope elevational shifts may be related to other drivers such as land-use change (Foster and D'Amato, 2015; Wason and Dovciak, in press), but may also be linked to climate if climate warming trends vary with the time of year or they are weak when tree species are most responsive; for example (winter months have been warming faster than summer months; Hayhoe et al., 2007; Kunkel et al., 2013) and temperature effects on tree growth vary with month of the year (Cook and Johnson, 1989). However, few studies examined how monthly temperature regimes change with elevation (i.e., monthly lapse rates; Richardson et al., 2004; Siccama, 1974) and how they relate to the broader-scale monthly climate warming trends to affect shifts in species climatic envelopes (and ultimately species distributions) along elevational climatic gradients (Kollas et al., 2014; Lenoir and Svenning, 2015).

To understand the capacity of mountains in the northeastern U.S. to provide species' climate change refugia, and to predict potential elevational shifts of species ranges tracking suitable temperature regimes, we combined forest plot vegetation data (characterized on 76 sites) with regional monthly temperature trends (from 36 meteorological stations) and fine-scale *in situ* temperature measurements (from a network of 63 temperature loggers) distributed across a range of elevations on 11 mountains in the region. Our specific objectives were to: first, quantify the elevation ranges potentially available as a habitat for spruce-fir forests between their ecotone with northern hardwood forests and mountain summits; second, determine if and how temperature and its seasonality relate to the distribution of spruce-fir forests along elevational gradients; third, characterize seasonal (monthly) variation in temperature regimes both along elevational gradients and over time; and ultimately, combine these data to quantify recent and potential future temperature regime shifts with elevation in mountains caused by changing climate while considering different future climate warming scenarios.

2. Materials and methods

2.1. Study area description

We studied climate and vegetation distributions along elevational gradients on mountains in four states (New York, Vermont, New Hampshire, and Maine) in the northeastern United States (Table 1). The

Table 1

Characteristics of 11 mountains studied in the northeastern United States sorted by latitude. Loggers were deployed at 63 sites across all mountains and recorded temperature every two hours from June 4, 2013 to April 19, 2014. Ecotone elevations (where predicted spruce-fir and northern hardwood forest basal areas were equal) were calculated from vegetation data from 76 sites located on these mountains (bootstrapped standard errors in parentheses; Fig. S1).

Mountain	Summit elevation (m)	Aspect	# Sites	Logger elevation range (m)	Ecotone elevation (m)	Latitude (°N)	Longitude (°W)
Mt. Bigelow	1227	N	7	500–1200	621 (± 46)	45.1554	70.2844
Sugarloaf Mtn.	1290	W	6	600–1100	712 (± 51)	45.0416	70.3300
Jay Peak	1148	S	4	800–1100	824 (± 36)	44.9157	72.5217
Old Speck Mtn.	1263	N	7	500–1100	681 (± 50)	44.5806	70.9538
Mt. Mansfield	1337	S	3	900–1100	752 (± 65)	44.5165	72.8023
Mt. Madison	1620	E	6	600–1200	849 (± 34)	44.3128	71.2513
Cannon Mtn.	1228	N	5	600–1100	786 (± 31)	44.1636	71.6870
Mt. Abraham	1207	W	6	700–1200	790 (± 27)	44.1218	72.9455
Dial Mtn.	1215	NW	6	700–1200	725 (± 61)	44.1091	73.8041
Mt. Moosilauke	1468	SE	6	700–1200	734 (± 79)	43.9989	71.8304
Killington Peak	1288	SW	7	600–1200	896 (± 26)	43.5829	72.8345