

Tree demography suggests multiple directions and drivers for species range shifts in mountains of Northeastern United States

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Abstract

Climate change is expected to lead to upslope shifts in tree species distributions, but the evidence is mixed partly due to land-use effects and individualistic species responses to climate. We examined how individual tree species demography varies along elevational climatic gradients across four states in the northeastern United States to determine whether species elevational distributions and their potential upslope (or downslope) shifts were controlled by climate, land-use legacies (past logging), or soils. We characterized tree demography, microclimate, land-use legacies, and soils at 83 sites stratified by elevation (~500 to ~1200 m above sea level) across 12 mountains containing the transition from northern hardwood to spruce-fir forests. We modeled elevational distributions of tree species saplings and adults using logistic regression to test whether sapling distributions suggest ongoing species range expansion upslope (or contraction downslope) relative to adults, and we used linear mixed models to determine the extent to which climate, land use, and soil variables explain these distributions. Tree demography varied with elevation by species, suggesting a potential upslope shift only for American beech, downslope shifts for red spruce (more so in cool regions) and sugar maple, and no change with elevation for balsam fir. While soils had relatively minor effects, climate was the dominant predictor for most species and more so for saplings than adults of red spruce, sugar maple, yellow birch, cordate birch, and striped maple. On the other hand, logging legacies were positively associated with American beech, sugar maple, and yellow birch, and negatively with red spruce and balsam fir – generally more so for adults than saplings. All species exhibited individualistic rather than synchronous demographic responses to climate and land use, and the return of red spruce to lower elevations where past logging originally benefited northern hardwood species indicates that land use may mask species range shifts caused by changing climate.

Keywords: climate change, forest soils, land-use legacy, northern hardwood forest, spruce-fir forest, tree distributions

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Introduction

Recent climatic changes have altered geographical species distributions (Parmesan & Yohe, 2003; Lenoir *et al.*, 2009) and future climate warming is widely expected to force even more dramatic changes in species ranges over time (Iverson *et al.*, 2008; Lenoir & Svenning, 2015). Understanding responses of forest canopy tree species to changing climate is particularly important because trees are foundational organisms (cf., Ellison *et al.*, 2005) affecting emergent ecosystem properties such as nutrient cycling (Likens *et al.*, 1970), productivity (Beck *et al.*, 2011), or microclimate (Dovčiak & Brown, 2014), and they provide habitats for other species (Halpern *et al.*, 2014). However, responses of tree species distributions to climate warming are variable (Lenoir *et al.*, 2010; Zhu *et al.*, 2012) and often modified

by moisture stress (Pederson *et al.*, 2015), land-use legacies (Lenoir *et al.*, 2010; Nowacki & Abrams, 2015), soil conditions (Lafleur *et al.*, 2010), atmospheric deposition (Koo *et al.*, 2014), and migration lags (Renwick & Rocca, 2015; Wu *et al.*, 2015) – factors that should be included in studies of climate change impacts on plant distributions.

The location and character of the transitions between forest types in mountainous regions tend to be driven by well-defined elevational climatic gradients making mountain ecotones particularly sensitive to climate change and suitable for providing early evidence of ongoing shifts in species distributions (Allen & Breshears, 1998; Beckage *et al.*, 2008). Although mountain ecotones tend to be driven mainly by climatic variables related to temperature (e.g., growing season length; Siefert *et al.*, 2015) or moisture (e.g., Boucher-Lalonde *et al.*, 2012), their location or character can be modified also by tree species responses to soil heterogeneity (Lee

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et al., 2005) or past disturbance (e.g., logging; Sundqvist *et al.*, 2013). For example, historic logging in low elevations may have in some cases moved lower boundaries of species distributions to higher elevations (cf., discussion in Foster & D'Amato, 2015), while shallow infertile soils in high elevations may limit upper range margins of some species to relatively lower elevations (Lee *et al.*, 2005). Some boundaries between low-elevation temperate northern hardwood forest and high-elevation conifer forest in the northeastern United States have moved upslope over the last 30 years, while the majority moved downslope inconsistently with the regional warming trend (Foster & D'Amato, 2015), suggesting that drivers other than climate affected ecotone locations across this broad region.

In the absence of historical data, population demography can be used to infer ongoing changes in geographical distributions of long-lived organisms such as tree species (Lenoir *et al.*, 2009; Woodall *et al.*, 2009; Zhu *et al.*, 2012), and especially so in transitional zones (ecotones) between plant community types (Dovčiak *et al.*, 2005, 2015). Considering changes in the demography of individual tree species along climatic gradients can increase our understanding of climatic and other environmental drivers on ongoing changes in tree species distributions and ecotone locations (Leak & Graber, 1974; Lenoir *et al.*, 2009; Bell *et al.*, 2014). The distribution of juvenile trees is likely to be more closely related to current climate compared to the distribution of adults which may lag behind recent climatic changes (Woodall *et al.*, 2009). Thus, a species moving to a higher latitude or elevation with climate warming (cf., Parmesan, 2006) should show a greater recruitment of juveniles near the upper range margins of the adult distribution and less juvenile recruitment near the lower range margins of the adult population (cf., Lenoir & Svenning, 2013), resulting in an elevation mismatch between sapling and adult distributions sometimes assumed to be synchronous across different species affected by the same degree of climate warming (e.g., species march or lean upslope; Breshears *et al.*, 2008).

In this study, we collected spatially extensive field demographic and environmental data to examine the ongoing demographic elevational range shifts in unmanaged populations of common tree species in a four-state region of the northeastern United States while simultaneously investigating the relative roles of environmental drivers such as climate (temperature, moisture), past (historical) land use, and soils on tree species distributions. Our objectives were to (1) determine whether the demography of tree species varies across elevational climatic gradients in a manner

consistent with recent climate change and (2) examine the extent to which climate shapes tree species' distributions and demography relative to other environmental factors. To address these objectives, we tested the following four hypotheses: (H1) Juvenile (sapling) distributions have shifted to higher elevations (upslope) relative to adult distributions of the same species, resulting in an elevation mismatch of these demographic classes consistent with climate warming; (H2) sapling distributions shifted relative to adults more in warmer and drier regions than in cooler and more mesic regions; (H3) compared to adult distributions, sapling distributions were more sensitive to climate than to land-use legacies and soils; and (H4) tree species exhibited variable individualistic rather than synchronous responses to climate, land-use legacies, and soils.

Materials and methods

Study area

We studied tree species distributions along elevational gradients on 12 mountains in four states of the northeastern United States (New York, Vermont, New Hampshire, and Maine; Fig. 1). Vegetation in this region is typically arranged along elevational gradients (Holway *et al.*, 1969; Siccama, 1974; Lee *et al.*, 2005): northern hardwood forests with sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), paper birch (*Betula papyrifera* Marshall var. *papyrifera*), and striped maple (*Acer pensylvanicum* L.) typically occur at elevations <800 m above sea level (a.s.l.), while spruce-fir forests comprised mostly of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.) with mixed in cordate birch (*Betula papyrifera* Marshall var. *cordifolia* (Regel) Fernald) occur at higher elevations. The elevation of the ecotone between northern hardwood and spruce-fir forest tends to decrease by 100 m (± 80 m) per degree of latitude (mean \pm SD) across the eastern United States and it occurs in our study region between 690 and 910 m a.s.l. (Cogbill & White, 1991). Tree lines in the region occur between 1,100 and 1,400 m a.s.l. (Cogbill & White, 1991) and are formed by balsam fir (Holway *et al.*, 1969; Siccama, 1974; Lee *et al.*, 2005).

Across the 12 mountains, mean daily minimum temperatures range from -3.0 to -0.6 °C, mean daily maximum temperatures from 5.6 to 10.7 °C, and mean annual total precipitation from 100 to 166 cm (based on 1984–2013 climate data, 4 km resolution, PRISM Climate Group, Oregon State University, Corvallis, OR; www.prism.oregonstate.edu; Table S1). Within the region, climate varies considerably with elevation; for example, as elevation increased from 550 to 1160 m a.s.l. in the Green Mountains of Vermont, mean annual temperature decreased from 5.2 to 1.3 °C, frost free days decreased from ~ 150 to ~ 80 days per year, maximum snow depth increased from 60 to 120 cm, and precipitation during vegetation season increased from 40 to

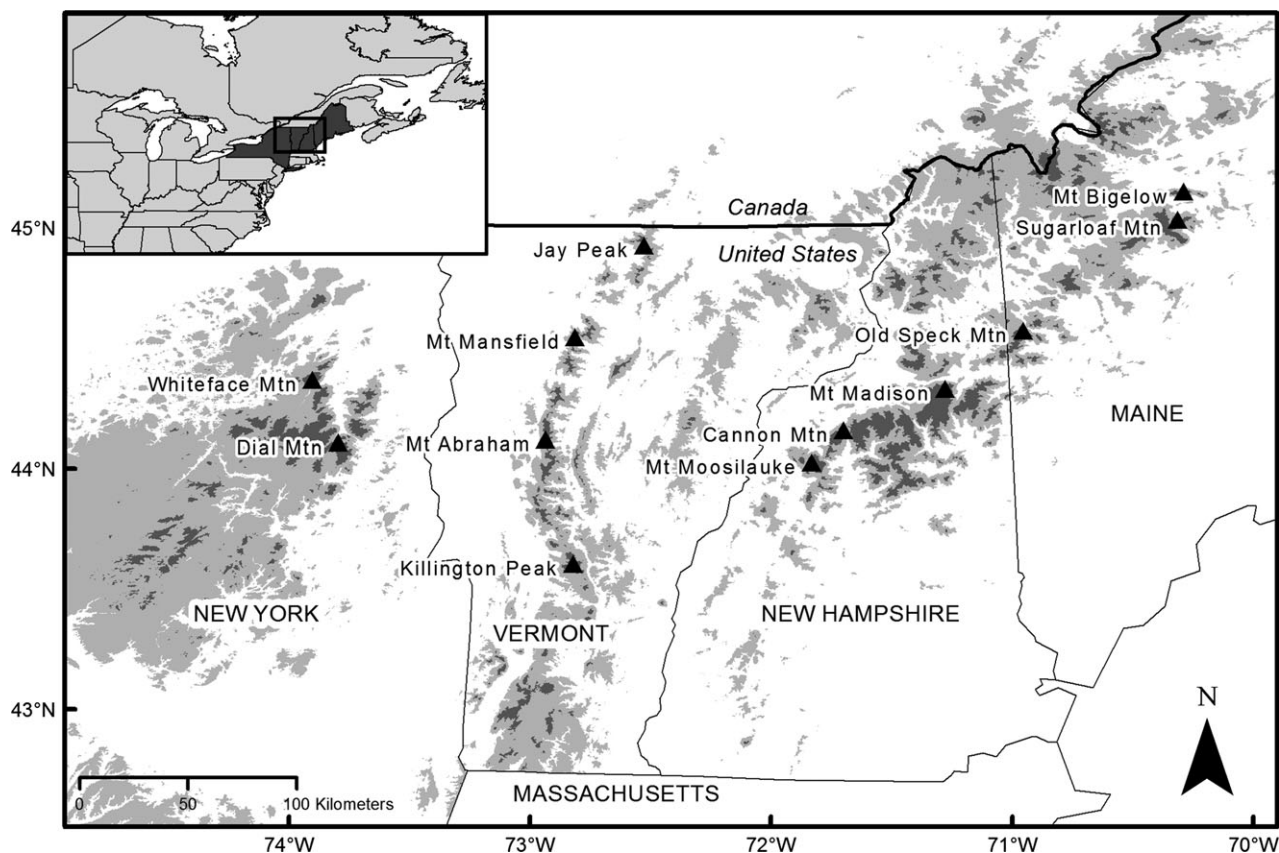


Fig. 1 Locations of 12 studied mountains across four states in the northeastern United States. Light gray areas represent elevations of 500 to 800 m above sea level (lower elevation deciduous northern hardwood forests) and dark gray areas represent elevations > 800 m above sea level to indicate mountainous terrain with transitions (ecotones) to high-elevation spruce-fir forests. Thick lines indicate national and thin lines indicate state boundaries.

60 cm (Siccama, 1974). The cloud ceiling often extends down to ~800 m a.s.l. with condensation on vegetation as much as doubling the effective annual precipitation at high elevations (Siccama, 1974; Miller *et al.*, 1993). Recent evidence suggests that acid deposition, that once influenced ecosystem health in the region (Driscoll *et al.*, 2001), is now approaching pre-industrial levels (Likens & Buso, 2012) although its effects on soils may be longer lived (Lawrence *et al.*, 2015). Soils are primarily spodosols with pH ~5 to 6 at low elevations, and they are shallower and more acidic (pH ~ 4) >800 m a.s.l. (Siccama, 1974).

The region experienced climate warming of 0.25 °C per decade since 1970, with greater warming in winter than in summer leading to longer growing seasons (Cooter & Leduc, 1995; Hayhoe *et al.*, 2007; Kunkel *et al.*, 2013), and with climate projections for continued warming (Hayhoe *et al.*, 2008; Kunkel *et al.*, 2013). Annual precipitation trends are less clear but generally suggest slight increases in total precipitation (Hayhoe *et al.*, 2007; Kunkel *et al.*, 2013) with less precipitation falling as snow in winter (Huntington *et al.*, 2004). Extensive logging occurred until the early 1900s across the region, but many higher elevation stands were avoided or logged only selectively for spruce (White & Cogbill, 1992).

Study design and site selection

We selected 12 mountains across the region (two to four mountains per state) that included elevations representing the full elevational range of spruce-fir forest and a portion of the adjacent northern hardwood forest (i.e., from ~ 500 to ~1200 m a.s.l.) (Fig. 1). Satellite images and digital aerial photographs (1992–2012; Google Inc., 2013) were used to select mountains that lacked clear evidence of recent forest management (i.e., we selected mature or maturing forests without logging roads, sharp stand boundaries due to logging, and buildings) on at least one aspect. The majority of selected mountain areas were located in protected areas (such as state parks) that further minimized the possibility of current or relatively recent forest management activities. We selected relatively smooth mountain slopes without distinct ridges or valleys to avoid topographic effects on climate that were not attributable to elevation (Fridley, 2009). Ability to obtain permits, site accessibility, and land ownership was also considered during the selection.

On each mountain, we established sampling sites systematically at 100-m intervals in elevation, starting in the northern hardwood forest and ending at the highest available elevation in spruce-fir forest, thus yielding five to eight sites per

mountain (depending on the upper and lower elevations of spruce-fir forests) and 83 sites in total (Table S1). At each site, we established a 225-m-long transect parallel to a contour line with 15 sampling points spaced 15 m apart along the transect (i.e., sampling points were nested within sites which were nested within mountain). We characterized tree demography, climate (temperature, humidity), land-use history, topography, and soils (slope, aspect, soil depth) at each site either on every sampling point or on a smaller subset of sampling points (see Field methods and measurements) in 2012 (Whiteface Mtn.) and 2013 (all remaining mountains). We selected seven sites on Whiteface Mountain from a larger resurvey of historical vegetation plots so that the selected sites were on the same aspect and spaced ~100 m apart to match the sampling design on the other 11 mountains; these sites were included in the elevation mismatch analyses (hypotheses H1 and H2) but not in species distribution models (hypotheses H3 and H4) because not all model variables were measured on Whiteface Mtn. in 2012 (cf., Holway *et al.*, 1969).

Field methods and measurements

Tree demography. To quantify juvenile (sapling) and adult tree distributions along the elevational environmental gradients (hypotheses H1 through H4), we characterized sapling (diameter at breast height, DBH > 2.5 and ≤10.2 cm) and adult (DBH > 10.2 cm) populations of all tree species at each sampling point at each site using the point-centered-quarter method following the original methods used for historical vegetation surveys on Whiteface Mountain (Cottam & Curtis, 1956; Holway *et al.*, 1969).

Climate. We characterized climate (temperature and humidity) of all sites relative to each other using *in situ* measurements that provided input for models of tree species distributions (hypotheses H3 and H4). We deployed one iButton Hygrochron temperature and humidity logger (model DS1923; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) at the central sampling point of each site to measure air temperature and relative humidity every two hours from spring 2013 to spring 2014 (all iButtons deployed by June 4, 2013, and collected after April 19, 2014). All loggers were suspended in a white plastic radiation shield with ventilation holes and attached 1 m above the ground on the north side of trees to avoid direct solar radiation (Fridley, 2009).

Land-use history. Although we selected sites to avoid forest stands that may have been managed within the last ~100 years to the extent possible based on aerial photography and known recent land-use history (see Study design and site selection), at each site we also characterized any historical land-use legacies due to previous past logging such as the presence of cut stumps and the absence of large coarse woody debris (CWD, naturally downed trees) on the forest floor. At each sampling point, we established a 7.5-m-radius circular search area, and in each half of this area, we located the nearest cut stump or base of a naturally downed tree (with estimated DBH *ca.* 10 cm or larger) if they were present and recorded their species (if discernable).

The presence of cut stumps and the lack of large naturally downed trees would indicate past logging (removal of timber), while the lack of cut stumps and the presence of naturally downed large trees would indicate gap phase dynamics typical of mature temperate forests (Gore & Patterson, 1986; Goodburn & Lorimer, 1998) characterized by large accumulations of coarse woody debris and large dead or decaying trees on the forest floor (Harmon *et al.*, 1986; Sturtevant *et al.*, 1997; McGee *et al.*, 1999). The residence time of downed tree boles and coarse woody debris of dominant tree species in this region is typically around 70 years, with hardwood trees decaying slightly faster than conifers (Foster & Lang, 1982; Russell *et al.*, 2014); thus, the presence of naturally downed large trees (and the absence of cut stumps) in our study should indicate sites that have not experienced land management within the last ~100 years (cf., CWD accumulation in maturing and old-growth northern hardwood forests; McGee *et al.*, 1999).

Soil and topography. We characterized mountain slope steepness, aspect, and soil depth at four of the established sampling points at each site (points 1, 5, 10, and 15). Slope and aspect were measured for the area within 7.5 m of the sample point using a clinometer (Suunto, Vantaa, Finland) and a standard compass. Soil depth was measured using a 1.22-m-long steel rod inserted into the soil twice at each of the four sample points (0.5 m up- and downslope of each point) until an impenetrable object was encountered (adapting methods from Dovciak *et al.*, 2003). Soils on our study sites were relatively shallow and depths >1.22 m were very rare (<0.01% of all measurements, considered conservatively to be 1.22 m).

Data processing and derived variables

To test whether species shifts vary along the regional climatic gradient (hypothesis H2), we characterized longer term climate of each study mountain using PRISM data available for the last 30-year period (1984–2013) prior to our field vegetation surveys; we calculated 30-year averages of monthly means for daily minimum temperature (T_{\min}) and daily maximum temperature (T_{\max}) and of total annual precipitation (Ppt) to describe the regional climate gradient ranging from cool and moist (typically higher latitudes and closer to coast) to relatively warmer and drier climate (southerly and further from coast).

To determine the impact of climate, land use, and soils on species distributions (hypotheses H3 and H4), we characterized each of these broader predictor categories using several proximal variables. Climate was characterized using growing degree days (GDD) to represent growing season length and warmth (cf., Gavin *et al.*, 2008), and vapor pressure deficit (VPD) to represent relative moisture stress at sites (Anderson, 1936). GDD were calculated for each site from iButton data from June 4, 2013, through December 31, 2013, following Gavin *et al.* (2008) and McMaster & Wilhelm (1997) as

$$\text{GDD} = \sum \left(\frac{T_{\max} + T_{\min}}{2} - T_{\text{base}} \right) \quad (1)$$

where T_{\max} and T_{\min} are the daily maximum and minimum temperatures (°C) and T_{base} is the minimum temperature

below which GDD do not accumulate; we used 4 °C as the base temperature (Gavin *et al.*, 2008). VPD (kilopascals, kPa) was also calculated for each site from the iButton data following Ward & Trimble (2003) as

$$VPD = VP_{\text{sat.}} - VP_{\text{act.}} \quad (2)$$

where $VP_{\text{sat.}}$ is the vapor pressure at saturation (maximum amount of water the air can hold at a particular temperature) and $VP_{\text{act.}}$ is the actual vapor pressure (actual amount of water in the air, calculated from relative humidity and temperature) when the temperature is above 0 °C. $VP_{\text{sat.}}$ and $VP_{\text{act.}}$ were calculated following Ward & Trimble (2003) as

$$VP_{\text{sat.}} = \exp\left(\frac{16.78 \times T - 116.9}{T + 237.3}\right) \quad (3)$$

$$VP_{\text{act.}} = VP_{\text{sat.}} \times \frac{RH}{100} \quad (4)$$

where T is the temperature (°C) and RH is the relative humidity (in percent) at the time of observation. We summarized VPD for each site as the seasonal (June–October) mean of monthly maximum VPD to provide a field estimate of relative moisture stress during the growing season. Of 76 iButtons set out in 2013, 13 were displaced or damaged by animals or malfunctioned and we replaced the missing data with their predicted values using a simple linear model of GDD or VPD as a function of elevation separately on each mountain.

Land-use legacy variables used in the analyses to indicate past logging at each site were the probability of encountering cut stumps (calculated as the proportion of points with stumps present) and the probability of absence of large downed trees (calculated as the proportion of points without large downed trees). Topographical and soil variables included in the analyses were mean slope steepness (range = 7–41 degrees) and mean soil depth (range = 9–67 cm) of each site. All predictor variables (Table 1) were screened for collinearity, and we checked variance inflation factors (VIF; our maximum VIF = 2.3, well under the recommended level <10; Neter *et al.*, 1989).

Statistical analyses

To determine differences between species sapling and adult distributions along regional elevational gradients (i.e., demographic elevational mismatch; hypothesis H1), we built logistic regression models to predict the probability of species site (elevation) occupancy separately for saplings and adults as a function of elevation on each mountain (cf., Lenoir *et al.*, 2009). Probability of species site occupancy was calculated as species relative frequency (the proportion of points out of 15 on each site occupied by the species) recommended for characterizing tree species distributions over climatic gradients (Canham & Thomas, 2010). We characterized species distributions on each individual mountain by building logistic regression models for four widely distributed canopy tree species with distributional peaks or range margins on the studied mountains. The demographic elevational mismatch was calculated for each species and mountain when (i) the species was present on at least two sites per mountain, and (ii) the species

Table 1 Summary of the predictors (categories and individual variables) used to model tree species distributions along elevational gradients across the northeastern United States. Each predictor variable was calculated for each site (See Data processing and derived variables for additional details). Species distributions were characterized by species importance values (IV) calculated by size class (i.e., for saplings and adults separately) as an average of species relative frequency, basal area, and density (Holway *et al.*, 1969)

| Category | Variable | Description |
|-----------|-----------------------|--|
| Climate* | GDD, GDD ² | Growing degree days (°C) |
| | VPD, VPD ² | Average maximum monthly vapor pressure deficit (kPa) |
| | Cut use† | Probability of sampling points with cut stumps |
| Land use† | Absent | Probability of sampling points without decaying downed trees |
| | CWD‡ | Mean soil depth |
| Soil | Depth | Mean surface slope |
| | Surface slope | |

*Climate variables included quadratic terms to account for known peaks in the distributions of some of the species (e.g., red spruce) along the regional climatic gradients (cf., Canham & Thomas, 2010). Land-use and soil variables did not require quadratic terms.

†Land-use variables characterize past logging. Other land uses were uncommon in the studied forests.

‡CWD = coarse woody debris (decaying downed tree trunks on forest floor).

exhibited a distributional peak (red spruce) or upper or lower range margin (i.e., probability of species site occupancy declined from or increased to ≥ 0.5 with elevation; American beech, sugar maple, and balsam fir).

To compare the general distributions of adults and saplings of each species over elevation, we compared their logistic models adapting the approaches of Lenoir *et al.* (2009) and Foster & D'Amato (2015). For each species and size class, we calculated their main distributional attribute on each mountain, either (i) the elevation of species peak probability of site occupancy, $Elev_{pk}$ (for red spruce which had a distributional peak), or (ii) the elevation where species probability of occupancy was 0.5, $Elev_{0.5}$ (for species gradually increasing or decreasing with elevation: American beech, sugar maple, and balsam fir). For each species i on each mountain j , we calculated the demographic elevational mismatch between distributions of adults and saplings, $\Delta Elev_{ij}$, by subtracting the elevation of adults from that of saplings (either $Elev_{pk}$ or $Elev_{0.5}$). Thus, positive values of $\Delta Elev_{ij}$ indicate upslope shifts in the distribution of saplings relative to adults of species i on mountain j (as hypothesized in H1), while negative values of $\Delta Elev_{ij}$ would suggest a downslope shift in the distribution of saplings relative to adults (inconsistent with H1). For each species, we tested whether the mean demographic

elevation mismatch across all studied mountains was significantly different from zero (hypothesis H1) using one sample t-tests to determine whether species demography suggested upslope, downslope, or no consistent elevational shift across the northeastern United States. To test whether the demographic elevation mismatch between saplings and adults of each species was greater in warmer and drier regions than in cooler and moister regions (hypothesis H2), we modeled species elevation mismatch across the mountains as a function of regional climatic predictors (T_{min} , T_{max} , and Ppt, see Data processing and derived variables) using simple linear regression.

To determine the drivers of tree species distributions for each size class at the forest tree community level (hypotheses H3 and H4), we expanded our analysis to include four additional species that were not sufficiently common for a regional analysis of elevational mismatch on individual mountains (i.e., species with probability of site occupancy <0.5 on many mountains; yellow birch, paper birch, cordate birch, and striped maple). All eight species combined represented 96% of all live trees with DBH > 10.2 cm measured across all sites. We built linear mixed models for species importance value computed as the site-level average of species relative frequency, relative basal area, and relative density (Holway *et al.*, 1969; Siccama, 1974) to test the effects of the climate, land-use, and soil variables (Table 1) on each individual tree species by size class. In order to determine the influence of the broad predictor categories (climate, land use, and soil) on the elevational distributions of each species size class, we compared the variance explained by fixed effects (marginal R^2 ; Nakagawa & Schielzeth, 2013) in the full model (all climate, land-use, and soil variables included as fixed effects) to a reduced model without the variables from the predictor category of interest (e.g., climate) using likelihood ratio tests (alpha = 0.05; Nelder & Wedderburn, 1972; Bolker, 2008). To account for the nested structure of our sampling design (several sampling elevations nested within each mountain), all models included a random intercept for mountain. To facilitate comparison of coefficient estimates, all variables were scaled (mean = 0, SD = 1) prior to model fitting. In addition, we report the significant (alpha = 0.05; approximated using Wald's 95% confidence intervals) coefficients of each individual variable from the best model (i.e., the model including only those variables from each predictor category that were significant). Finally, we summarized and compared the strengths of the broad predictor categories (in terms of variance explained) pooled across all species (by size class) using ANOVA; when overall F-tests were significant (alpha = 0.05), Tukey's Honestly Significant Difference (HSD) was used to determine significant differences between predictor categories. All statistics and figures were run using the R statistical language (R Core Team, 2015).

Results

Demographic evidence of species range shifts

Sapling and adult distributions along elevational climatic gradients suggest ongoing species-level region-

wide shifts for three of the four most common canopy species but not consistently toward higher elevations (hypothesis H1). For American beech, saplings were always more frequent at higher elevations than adults (with mean elevational mismatch of 71 m; $P < 0.01$), sugar maple saplings tended to be less frequent at higher elevations than sugar maple adults (lagging below the adults by 99 m on average; $P = 0.01$), and red spruce saplings tended to be distributed at lower elevations than adults of this species (by 76 m on average; $P < 0.01$) (Fig. 2). Balsam fir saplings and adults did not significantly differ from each other with respect to elevation on average across all mountains ($P = 0.74$; Fig. 2), but balsam fir did show a range of demographic shifts on the individual mountains that included upslope shifts, downslope expansion, and no change with elevation (Fig. S1).

The elevation mismatch between adults and saplings varied along the regional climatic gradient for only one of the four most common species (cf. hypothesis H2). For red spruce, the elevation

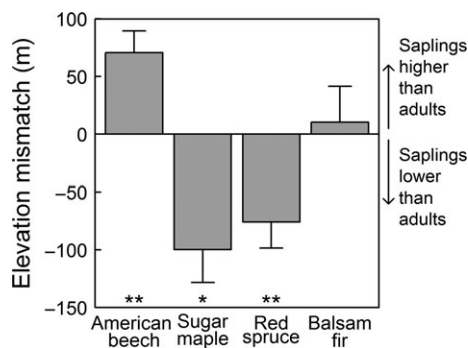


Fig. 2 Elevation mismatch (mean and standard error) in the distributions of saplings and adults of the four common canopy tree species on mountains in the northeastern United States. Elevation mismatch was calculated from logistic models representing sapling and adult probability of site occupancy relative to elevation on each individual mountain (see Fig. S1). Elevation mismatch > 0 indicates that saplings are relatively more common (have higher probability of site occupancy) than adults at higher elevations, suggesting a potential upslope shift in species distribution over time. Elevation mismatch < 0 indicates that adults are relatively more common at higher elevations than saplings, suggesting a potential downslope shift in species distribution over time. Observed elevation mismatch was tested against the null expectation of no demographic mismatch for each species i (i.e., $\sum A Elev_j = 0$; where j is a mountain) using one sample t-test with significance reported as $P < 0.05$ (*) or $P < 0.01$ (**). Species distribution models used to calculate elevation mismatch between adults and saplings on each mountain are given in Fig. S1. Number of mountains per species: American beech = 7, sugar maple = 8, red spruce = 11, balsam fir = 11.

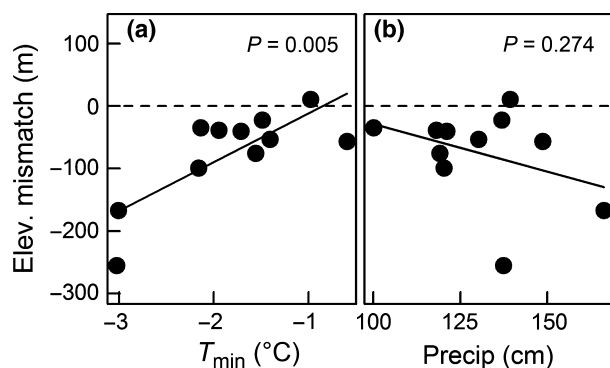


Fig. 3 The effects of regional climatic gradients in (a) temperature and (b) precipitation on elevation mismatch of red spruce on mountains in the northeastern United States (●). Regional climate gradient (T_{\min} : 30-year mean monthly minimum temperature; Precip: 30-year average total annual precipitation) was based on PRISM climate data averages from 1984 to 2013 at each mountain. Dashed lines represent the null hypotheses of no elevational mismatch between species saplings and adults across the regional climatic gradient, while solid lines represent regression slopes (suggesting climatic effects on elevation mismatch; slope P -values reported).

mismatch became more negative on mountains with colder minimum temperatures (T_{\min}) where saplings were more frequent even further downslope from adults (Fig. 3a; slope = 77.8, $P = 0.005$); the elevation mismatch did not vary with regional precipitation (Ppt, Fig. 3b; slope = -1.5 , $P = 0.274$) or T_{\max} (not shown). The elevation mismatch for American beech, sugar maple, and balsam fir did not vary with T_{\min} , T_{\max} , or precipitation (not shown).

Effects of environmental variables on species distributions

Across all eight common species pooled together, climate generally explained species distributions along the elevation gradient equally well for both adults and saplings, and much more so than land-use legacies or soil variables (Fig. 4), contrary to our expectation (hypothesis H3). At the species level, climate was a significant predictor for all common species in both size classes (Fig. 5a), but species varied in their individual responses to environmental variables (hypothesis H4; Fig. 5a–c). Unlike climate, land use was a significant predictor for a smaller subset of species, including both size classes of American beech, red spruce, and balsam fir as well as adults of sugar maple and yellow birch (Fig. 5b). Soil variables were significant predictors only for saplings of American beech and balsam fir and for adults of striped maple (Fig. 5c). Climate explained most variability in the distribution of most species, except for two species – American beech (saplings and

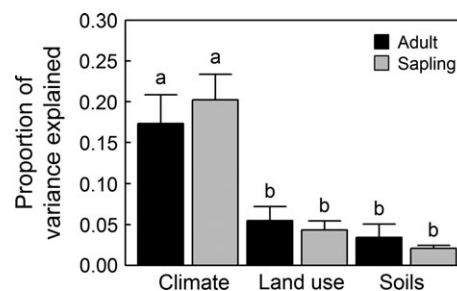


Fig. 4 Mean proportion of variance explained by climate, land-use, or soil variables in models of species distributions for adults or saplings of all tree species common on mountains in the northeastern United States ($n = 8$): American beech, sugar maple, red spruce, balsam fir, yellow birch, paper birch, cordate birch, and striped maple. Species distributions were modeled as species importance values (IV) integrating species relative frequency, basal area, and density (see Statistical analyses). Models were fitted for individual species and size classes, and mean variance explained by fixed effects was calculated across the individual species models (see Fig. 5). Statistically significant differences were determined using Tukey's HSD tests ($\alpha = 0.05$) and indicated by different letters. Error bars are one standard error.

adults) where land-use legacies appeared to be a more dominant predictor, and striped maple (adults) where soil appeared most dominant (Fig. 5a–c).

Growing degree days (GDD) was a significant climate predictor across all species and size classes except for paper birch saplings that were related to moisture stress (VPD) instead and American beech adults that were related to climate in general (Fig. 5a) but not significantly to one individual predictor (Table 2); species increased with GDD (linearly: yellow birch and striped maple, or quadratically: American beech saplings and sugar maple), decreased with GDD (linearly: balsam fir and cordate birch), or they peaked at intermediate values of GDD (red spruce and paper birch adults; Table 2). Species increased with VPD (linearly: balsam fir adults and paper birch, or quadratically: striped maple) or decreased with VPD (linearly: cordate birch adults, Table 2). From land-use legacy variables approximating past logging, only the absence of large CWD (downed trees) was positively related to American beech (adults and saplings) and adults of sugar maple and yellow birch and negatively to red spruce and balsam fir (adults and saplings; Table 2). Soil depth was positively related to striped maple adults and negatively related to balsam fir saplings, while slope steepness was positively related to balsam fir saplings and negatively related to American beech saplings (Table 2).

Species responses to the environmental predictors were individualistic, and for some (but not all) species, they varied by size class; for example, sapling

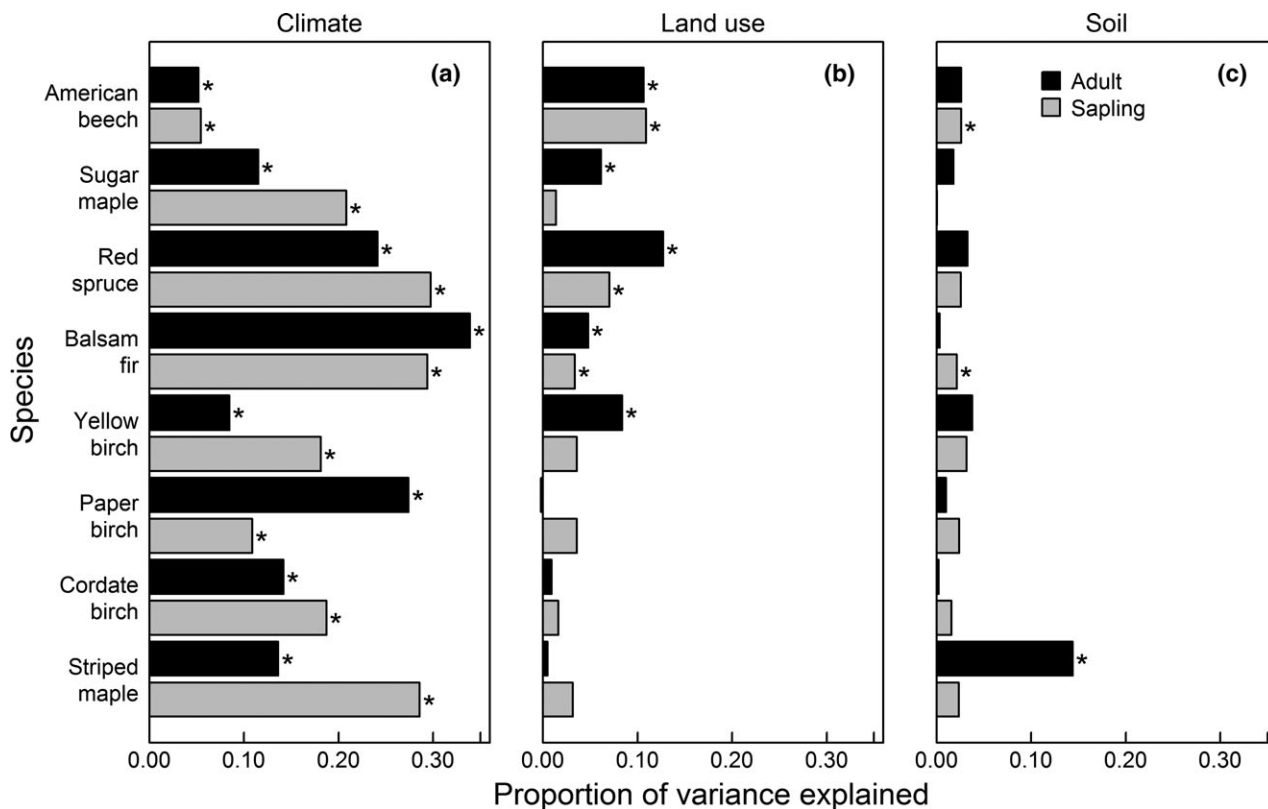


Fig. 5 Proportion of variance explained in the individual species distribution models as a function of climate (a), land use (b), and soil (c) for adults and saplings of tree species common on mountains in the northeastern United States. Species distributions were modeled using species importance values (IV) integrating species relative frequency, basal area, and density (see Statistical analyses). Variance explained and significance (at $\alpha = 0.05$, *) of fixed effects for climate, land-use, and soil variables were determined by likelihood ratio tests of full model against the reduced models.

distributions of red spruce, sugar maple, yellow birch, cordate birch, and striped maple appeared more closely related to climate than adult distributions were (based on percent variance explained), while adult distributions of red spruce, sugar maple, and yellow birch were more closely related to past logging than sapling distributions were (hypotheses H3 and H4; Fig. 5), and all of the species responded differently to individual predictor variables (Table 2).

Discussion

Many studies have emphasized the role of climate (Siccama, 1974; Beckage *et al.*, 2008), land use (Nowacki & Abrams, 2015), and soils (Siccama, 1974; Lee *et al.*, 2005) on tree species distributions. Despite recent climate warming and its potential effects on tree species elevational distributions (e.g., Beckage *et al.*, 2008; Breshears *et al.*, 2008), our results on demography of the common tree species in mountain forests of the northeastern United States do not suggest widespread ongoing upslope shifts in species distributions across

northeastern United States (hypothesis H1) or relative to the regional climatic gradient (H2). Instead, our results support the idea that species distributions may be shifting in variable directions (cf., Boisvert-Marsh *et al.*, 2014; Foster & D'Amato, 2015). Although climate tended to be the most important predictor for sapling and adult distributions of most species (H3), individual species clearly varied in their sensitivity to climate, land-use legacies, and soils (H4) suggesting that global warming fingerprints are likely to be species-specific (cf., Boisvert-Marsh *et al.*, 2014; Rapacciuolo *et al.*, 2014) and that land-use legacies and soils can strongly modify demographic responses of some species to climate warming (Iverson *et al.*, 2008). Although current sapling distributions may not perfectly represent future forest canopies, the individualistic species demographic responses to climate and land use that we observed suggested ongoing downslope expansion (red spruce), no change (balsam fir), downslope contraction (sugar maple), and upslope expansion (American beech), and thus, they stand in contrast to studies that suggest that species respond to environmental change by

Table 2 Coefficients from species distribution models along elevational gradients for adults and saplings of tree species common on mountains in the northeastern United States. Species importance value was expressed as a function of climate, land-use, and soil variables (see Table 1 for variable definitions), with significant coefficients ($\alpha = 0.05$) reported for the best models (determined using likelihood ratio tests, Fig. 5). Sites occupied indicate the number of sites with species present (maximum 76; sites where species did not occur were also included in the models). Coefficients scaled (mean = 0, SD = 1) prior to model fitting to facilitate comparisons

| Species | Size class | Sites occupied | R^2_c | R^2_m | GDD | GDD ² | VPD | VPD ² | Absent CWD | Soil depth | Surface slope |
|----------------|------------|----------------|---------|---------|--------|------------------|-------|------------------|------------|------------|---------------|
| American beech | adlt | 18 | 0.50 | 0.42 | | | | | 0.050 | | |
| | sapl | 22 | 0.70 | 0.52 | -0.583 | 0.635* | | | 0.099 | | -0.048 |
| Sugar maple | adlt | 25 | 0.68 | 0.58 | -0.965 | 1.055* | | | 0.071 | | |
| | sapl | 21 | 0.48 | 0.48 | -0.444 | 0.505* | | | | | |
| Red spruce | adlt | 54 | 0.48 | 0.38 | 0.723 | -0.666† | | | -0.051 | | |
| | sapl | 56 | 0.37 | 0.36 | 1.318 | -1.235† | | | -0.063 | | |
| Balsam fir | adlt | 64 | 0.87 | 0.82 | -0.299 | | 0.080 | | -0.087 | | |
| | sapl | 60 | 0.82 | 0.78 | -0.281 | | | | -0.087 | -0.047 | 0.045 |
| Yellow birch | adlt | 42 | 0.57 | 0.44 | 0.058 | | | | 0.046 | | |
| | sapl | 32 | 0.33 | 0.33 | 0.030 | | | | | | |
| Paper birch | adlt | 38 | 0.47 | 0.24 | 0.569 | -0.550† | 0.031 | | | | |
| | sapl | 11 | 0.32 | 0.11 | | | | 0.004 | | | |
| Cordate birch | adlt | 45 | 0.29 | 0.29 | -0.035 | | | -0.026 | | | |
| | sapl | 28 | 0.33 | 0.20 | -0.029 | | | | | | |
| Striped maple | adlt | 26 | 0.35 | 0.35 | 0.019 | | | -0.054 | 0.055* | 0.017 | |
| | sapl | 35 | 0.52 | 0.49 | 0.070 | | | -0.199 | 0.231* | | |

adlt = adults, sapl = saplings. GDD = growing degree days (°C). VPD = vapor pressure deficit (kPa). CWD = large coarse woody debris. Cut stumps not included in the table because it was not a significant predictor in the best models. R^2_c (conditional) and R^2_m (marginal) represent the variance explained by all effects (fixed and random) or only fixed effects, respectively (Nakagawa & Schielzeth, 2013).

*Quadratic increase with GDD or VPD.

†Hump-shaped response to GDD.

synchronous upslope shifts (e.g., Beckage *et al.*, 2008; Breshears *et al.*, 2008; Kelly & Goulden, 2008) as we discuss below.

The downslope population expansion of red spruce documented in our study on almost all mountains is consistent with the idea that red spruce may be recolonizing lower elevations that it historically occupied (Jackson & Whitehead, 1991), and especially so in the areas that were logged around 1900 (Thompson *et al.*, 2013; Foster & D'Amato, 2015), but it is inconsistent with the upslope red spruce range shift implied by other studies (Beckage *et al.*, 2008). The historical decline (population crash) of canopy red spruce that has been well documented across the region and attributed to acid deposition (McLaughlin *et al.*, 1987) or climate warming (Hamburg & Cogbill, 1988) could cause an upslope shift of the deciduous–coniferous ecotone due to mortality of adult red spruce, but our demographic data suggest a more recent downslope expansion of an advanced regeneration layer of red spruce saplings with their distribution related more to climate and less to historical logging legacies compared to adults. The red spruce demographic shift downslope was more pronounced in colder parts of the region in

our study, suggesting that red spruce recolonization of the lower elevations can be hampered by warmer climate (cf., Hamburg & Cogbill, 1988), although it may be positively affected also by declining acidity of precipitation (Likens & Buso, 2012; Koo *et al.*, 2014; Engel *et al.*, 2016). Interestingly, the documented downslope shifts in red spruce are consistent with the southerly latitudinal shifts of saplings of other spruce species (*Picea glauca*, *P. mariana*) in adjacent eastern Canada (Boisvert-Marsh *et al.*, 2014), which may also be responding to interactions of changing climate and logging legacies.

Similar to red spruce, balsam fir is a species restricted to cool and moist climate of high elevations (Cogbill & White, 1991). Balsam fir can tolerate extreme cold and is unable to photosynthesize in favorable winter thaws (contrary to red spruce; Schaberg, 2000), and its range suggests that it can tolerate a wider range and more extreme climatic conditions (cf., temperature, moisture, acid deposition, and elevational ranges; Burns & Honkala, 1990; DeHayes *et al.*, 1999; this study). Perhaps due to its greater ecological versatility, balsam fir showed no demographic signal of a range shift (upslope or downslope) on average across northeastern

United States in our study, corroborating the lack of latitudinal range shift documented for this species across the eastern United States (Woodall *et al.*, 2009), but contrasting with both the upslope shift documented in Vermont (Beckage *et al.*, 2008) and the southerly latitudinal shift documented in adjacent eastern Canada (Boisvert-Marsh *et al.*, 2014). However, our study suggests that although the distribution of balsam fir is controlled by climate most, it is also affected by logging legacies and soil depth – variables that may have contributed to a range of demographic shifts of this species observed in our study on individual mountains (from upslope shift to downslope expansion to no change with elevation) and likely also in other studies (cf., Beckage *et al.*, 2008; Woodall *et al.*, 2009; Boisvert-Marsh *et al.*, 2014).

Consistent with the downslope expansion of red spruce (and in some cases balsam fir), sugar maple demography suggested an ongoing consistent downslope shift of this species in our study (range contraction) consistent with the regional sugar maple decline and poor recruitment on acidic soils (Sullivan *et al.*, 2013), which is likely more extreme at higher elevations where soils are less well buffered (Siccama, 1974) and received more acidic precipitation (Aleksic *et al.*, 2009). In addition, our results are also consistent with the studies suggesting that browse by large mammal herbivores (deer, *Odocoileus virginianus*, or moose, *Alces alces*) may limit the recruitment of preferred browse species such as sugar maple more so than it limits the recruitment of less palatable spruce, essentially ‘cooling’ the deciduous–coniferous ecotones experiencing climate warming (McLaren & Peterson, 1994; Fisichelli *et al.*, 2012; Frelich *et al.*, 2012). Although deer densities in mountainous regions may be low due to unfavorable climate, topography, and fewer preferred browse species, we commonly observed browse (likely moose) on many balsam fir saplings (but rarely on spruce). Our results and the regionally documented sugar maple decline contrast with both the upslope shift (range expansion) and increase in sugar maple basal area at its upper elevation range margin in Vermont (Beckage *et al.*, 2008) and with latitudinal studies showing northward demographic shifts for sugar maple saplings in eastern United States (Woodall *et al.*, 2009) and eastern Canada (Boisvert-Marsh *et al.*, 2014). While these other studies did not evaluate the effects of past logging legacies, our data suggest that northern hardwood species including sugar maple, American beech, and yellow birch have responded positively to past logging (at the expense of red spruce and balsam fir) (cf., Thompson *et al.*, 2013) and that the current recruitment into the sapling size class may be reflecting this land-use legacy as red spruce (and in some cases

balsam fir) gradually recolonize some of the areas that they originally occupied prior to logging.

American beech was the only species in our study that showed a consistent upslope demographic shift regardless of the regional climate gradient in agreement with the northward latitudinal expansion of saplings of this species documented in eastern Canada (Boisvert-Marsh *et al.*, 2014). Although beech demography may be complicated by beech bark disease which increases canopy tree mortality and formation of beech sapling thickets (Houston, 1975; Giencke *et al.*, 2014), the disease severity has been found to be proportional to beech basal area and it is not expected to be consistently affected by elevation (Griffin *et al.*, 2003). Although the upslope expansion of beech was closest to trends expected under warming climate, land-use legacies predicted the distribution of this species more than climate did in our study, suggesting that beech dynamics cannot be interpreted with regard to climate alone. Indeed, reduced competition from sugar maple on acidified soils (Halman *et al.*, 2014), past logging (this study), and warmer climate (Beckage *et al.*, 2008; this study), particularly on moderate slopes, could increase the abundance of beech saplings. The increase in beech following logging occurred likely at least partly at the expense of sugar maple recruitment as American beech saplings and sprouts can vigorously compete with sugar maple regeneration (Hane, 2003); however, beech bark disease makes it unlikely that beech saplings will attain dominant canopy positions in the future. Indeed, monitoring both the effects of ongoing forest management and changing climate on species distributions along elevation gradients could provide further insights into the impacts of species interactions (competition) on changes in species ranges (Kellman, 2004; Brown & Vellend, 2014) and potentially help forest managers to design adaptive management approaches to facilitate tree species migration along elevational gradients with changing climate.

In summary, our results indicate that the demography of the dominant tree species in mountain forests of the northeastern United States is not responding to recent climatic or land-use changes with a synchronous upslope species shifts as suggested by some conceptual studies (e.g., Breshears *et al.*, 2008), or by synchronous ecotone shifts across species (up- or downslope) observed in our region (Beckage *et al.*, 2008; Foster & D’Amato, 2015). Instead, species exhibited individualistic demographic responses related to their life-history strategies that stemmed from their unique relationships with climate, land-use legacies, and soil characteristics, corroborating the individualistic character of plant communities (Gleason, 1926) – a critical concept for accurate predictions of species migrations across landscapes under changing climate (cf., Iverson *et al.*, 2008)

that is sometimes overlooked in studies anticipating consistent synchronous species responses to global warming (cf., Parmesan & Yohe, 2003; Breshears *et al.*, 2008). Importantly, our work suggested that land-use legacies can rival climate change effects and cause the unexpected downslope demographic shifts that we consistently documented for red spruce and sugar maple (and balsam fir on some mountains), ultimately leading at times to the downslope ecotone shifts observed in our region (Foster & D'Amato, 2015) and appearing more common in other studies of species range shifts (Lenoir *et al.*, 2010). Future studies of species range shifts need to more explicitly test additional drivers of species distributions that are regionally important (e.g., fire effects in Schwilk & Keeley, 2012; mycorrhizal associations in Lankau *et al.*, 2015) rather than focusing purely on a global warming effect. The effects of land-use (this study) and other disturbance legacies (Kelly & Goulden, 2008; Schwilk & Keeley, 2012) highlight the importance of conservation areas with relatively undisturbed forests as natural laboratories for the study of tree population responses to changing climate that are not constrained by concurrent species responses to land-use legacies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Tree species distribution models for adults and saplings on individual mountains.

Table S1. Site characteristics of the study mountains.