

Tree growth is more sensitive than species distributions to recent changes in climate and acidic deposition in the northeastern United States

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Summary

1. Tree-growth responses to environmental change could provide early detection of shifts in forest composition and help facilitate ecosystem management and conservation.
2. We studied forest tree responses to recent trends in climate and acidic deposition using analyses of tree rings and long-term climate, deposition and forest plot data along an elevational climatic gradient in the northeastern United States. We analysed how (i) individual growth of dominant species (*Picea rubens*, *Abies balsamea*) and (ii) spatial distributions of all species, changed with elevation over time due to changing environment.
3. We observed a mean 220 m upslope shift of temperature envelopes since the 1960s, consistent with regional climate warming, but found no evidence of synchronous upslope shifts in species abundance. Species' ranges were stable although some leaned upslope or downslope, suggesting species-specific migration lags or controls on species' ranges.
4. Compared to species distributions, the growth of dominant species was more responsive to environmental change. Although the basal area of *P. rubens* declined within its range since the 1960s, its growth has increased recently with increasing precipitation pH and to a lesser extent with warming climate. *Abies balsamea* has gradually increased in both basal area and density since the 1960s, with its growth responding to precipitation pH but not climate. Historically, *P. rubens* grew better at lower and *A. balsamea* at higher elevations, but these elevation effects appeared to be mediated primarily by moisture, and have disappeared over time.
5. *Synthesis and applications.* Mean tree-growth responses to changing climate (temperature, moisture) and precipitation chemistry were more consistent and more clearly detectable than shifts in tree species' ranges, suggesting that monitoring tree growth across climatically controlled species' ranges (e.g. along elevational or latitudinal gradients) may provide a powerful tool for early detection of potential future changes in forest composition in a changing environment.

Key-words: basal area increment, climate–vegetation relations, environmental change, growing degree-days, migration lags, precipitation pH, spruce-fir, tree growth

Introduction

Climate is a major determinant of vegetation distribution and productivity, and recent climate warming has been implicated in plant distribution shifts to higher elevations (Beckage *et al.* 2008; Kelly & Goulden 2008). Despite

some documented upslope shifts in plant distributions, evidence of widespread climate driven change is mixed (e.g. Foster & D'Amato 2015) presenting a challenge for forest management decisions and for predicting forest ecosystem services (Mina *et al.* 2016). Tree ranges may not track climate perfectly due to other environmental change factors such as air pollution (Driscoll *et al.* 2001), land management (Rasche *et al.* 2011; Wason & Dovciak 2016) or species migration lags (Zhu, Woodall & Clark

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2012). Understanding how individual plants respond to complex environmental change, and how these responses relate to species distribution shifts, is important for predicting and managing plant communities in changing environments (Smith, Knapp & Collins 2009).

Temperature is considered a primary control on tree species distributions in mountainous regions (Siccama 1974; Beckage *et al.* 2008). In the northeastern US, temperature has risen 0.25 °C per decade since the 1970s and it is expected to increase by 2.9–5.3 °C by the end of this century, while trends in annual precipitation are less clear (Huntington *et al.* 2009). A warmer climate should increase tree growth and survival at upper elevation range limits and decrease them at lower elevation range limits (when accounting for changes in competition), but seed-rain limitations and long life spans may delay migration (Zhu, Woodall & Clark 2012). Tree growth is sensitive to climate (Fritts & Swetnam 1989) and changes in growth trends may be detectable earlier than species migrations; thus, monitoring tree growth could represent an efficient monitoring tool that avoids population demography delays, such as dispersal and establishment, enabling earlier adjustments in management actions.

High-elevation spruce-fir forests of the northeastern US occur in areas with cooler temperatures, greater precipitation and more acidic deposition (acid rain) than low-elevation northern hardwood forests (Siccama 1974; Aleksic *et al.* 2009). For some species, acid rain-induced calcium depletion reduces cold tolerance of needles, thereby increasing needle death during extreme cold weather (winter injury; Kosiba *et al.* 2013). Coincident with warming, acid rain has been reduced from peak levels mid-century (Driscoll *et al.* 2001) to preindustrial levels (Likens & Buso 2012). Similar to warming, reduced acid rain should increase tree growth and survival at high elevations, but it may have less effect at low elevations where spruce-fir forest trees may be more sensitive to temperature and moisture stress (Koo *et al.* 2014).

Responses of spruce-fir forests to changing climate and acid rain depend on responses of their dominant species: *Picea rubens* Sarg. growth can increase with temperature (growing degree-days, GDD; Gavin, Beckage & Osborne 2008) and decline with acidic deposition (DeHayes *et al.* 1999) – two factors implicated in regional decline of this species in 1970s (Hamburg & Cogbill 1988) detected by monitoring tree-growth trends (cf., McLaughlin *et al.* 1987); while *Abies balsamea* (L.) Mill. is thought to be less sensitive to these factors (Fitzgerald & Raynal 1991) but likely responsive to competitive release following *P. rubens* decline. The lower elevation margin of spruce-fir forests is expected to move upslope with warming (Beckage *et al.* 2008), even when accounting for reductions in atmospheric deposition (i.e. Koo *et al.* 2014), but downslope shifts were observed in some post-logging landscapes (Foster & D'Amato 2015; Wason & Dovciak 2016). Thus, a better understanding of tree responses to

climate warming and declining acid pollution is needed for forest management and conservation strategies (e.g. thinning to increase resistance to moisture stress; Kerhoulas *et al.* 2013).

To determine how tree growth and forest structure may be effected by warming climate and declining acid rain, we assembled a long-term (>50-year) dataset on climate, precipitation chemistry, forest structure and tree growth in a 'hot-spot' of regional warming (Beier *et al.* 2012) and declining acidic deposition (Lawrence *et al.* 2015) to test the following hypotheses:

H1. Climatic warming since the 1960s has shifted temperature envelopes to higher elevations.

H2. Growth of *P. rubens* and *A. balsamea* increased at their upper range margins and decreased at their lower range margins over time, consistent with an expected upslope range shift.

H3. Growth of *P. rubens* and *A. balsamea* was influenced primarily by growing season temperature, and also by precipitation pH, moisture stress and winter injury events.

H4. Elevational ranges of spruce-fir and northern hardwood tree species have shifted consistently with elevational shifts in temperature envelopes.

Materials and methods

STUDY AREA

We studied tree growth and distributions on Whiteface Mountain in the northeastern US (44°21'57"N, 73°54'10"W; summit elevation 1483 m above sea level, a.s.l.) using two long-term (50- and 30-year) datasets created by resampling forest plots established in the 1960s and 1980s (Holway, Scott & Nicholson 1969; Battles *et al.* 1992). Vegetation, climate and acidic deposition on Whiteface Mountain were well studied (e.g. Holway, Scott & Nicholson 1969; Fitzgerald & Raynal 1991; Battles *et al.* 1992; Miller *et al.* 1993) and they are broadly representative of the region (Cogbill & White 1991). Mean annual temperature ranges from 5.1 ± 0.2 °C at 610 m elevation to 0.27 ± 0.36 °C at 1483 m elevation (2001–2011 data from SUNY Albany, Atmospheric Sciences Research Center, Wilmington, NY). The growing season extends from June through September and varies with elevation (Miller *et al.* 1993). Annual precipitation ranges from 97 cm year⁻¹ at 600 m to 152 cm year⁻¹ at 1350 m with ~30% occurring as snow (Miller *et al.* 1993). Much of the forest below ~900 m was clear-cut with slash burned by the early 1900s (Scott, Battles & Buckelew 1993). Across the region, spruce-fir forests occur above ~800 m elevation covering 625 000 ha on 242 peaks (Cogbill & White 1991) dominated by *P. rubens* and *A. balsamea* with a minor component of *Betula papyrifera* Marshall var. *cordifolia* (Regel) Fernald. Northern hardwood forests dominated by *Acer saccharum* Marshall, *Fagus grandifolia* Ehrh. and *Betula alleghaniensis* Britton occur below ~800 m (Holway, Scott & Nicholson 1969).

STUDY DESIGN

We resurveyed vegetation on 47 historical plots established for long-term monitoring of spruce-fir and northern hardwood forest responses to environmental change – 24 Forest Response Program (FRP) plots established in 1986–1987 (Battles *et al.* 1992) and 23 Atmospheric Sciences Research Center (ASRC) plots established in 1964–1966 (Holway, Scott & Nicholson 1969). Plots were selected to represent mature forests in all survey periods (i.e. avoiding early successional species composition and stand structure) to minimize the influence of succession and stand development on observed changes. We collected *in situ* microclimate measurements on 35 plots (FRP and additional plots at lower and higher elevations) to characterize the climatic gradient across elevations (from ~410 m to the summit), and we collected tree cores from *P. rubens* and *A. balsamea* at a subset of FRP plots. Due to logistical constraints, plots with forest structure, microclimate and tree core data overlap only partially and each dataset was analysed separately (Fig. S1a–c, Supporting Information).

FIELD METHODS AND TREE CORE PROCESSING

To characterize potential shifts in temperature envelopes due to warming (H1), we quantified the elevational temperature lapse rate by deploying iButton sensors (models DS1923 and DS1921G, 0.5 °C resolution; Maxim Integrated Products, Inc., Sunnyvale, CA) at the 35 microclimate plots (Fig. S1c, see Study design). Sensors logged temperature every 2 hours from 4 June to 31 December 2012 and were suspended in white plastic radiation shields (Dovčiak & Brown 2014) fastened 1-m above the ground on the north-facing sides of tree trunks (Fridley 2009).

To examine changes in tree growth relative to elevation (H2) and environmental factors (H3), we analysed both relatively short- and long-term changes in tree growth. To assess short-term changes in tree growth, we resurveyed 24 FRP plots in 2012, adding to the previous surveys of 1986–1987 and 2001–2002 (hereafter referred to as 1986, 2002 and 2012 surveys; Battles *et al.* 1992, 2003). Each FRP plot is 20 × 20 m large and all trees ≥5 cm diameter at breast height (DBH) were tagged and measured (DBH, to the nearest 0.1 cm) during each survey, allowing us to calculate the growth rate of individual trees between the surveys (1986–2002 vs. 2002–2012 growth) in order to assess potential changes in growth.

To assess long-term changes in tree growth, we collected increment cores (2 radii per tree ≥20 cm DBH) from 55 *P. rubens* (26 plots) and 57 *A. balsamea* (22 plots) across each species' elevational range, thus sampling across many sites to minimize site effects on tree growth (e.g. release events; Fritts & Swetnam 1989). For each species, we cored up to three canopy trees, defined as trees with at least the top of their crowns exposed to full sunlight. Selected trees were within 20 m of the FRP plot and cores were taken 1.3 m above the ground parallel to the elevation contour (Fig. S1b). Cores were processed using standard dendrochronology procedures including cross-dating (Holmes 1983). Ring widths were measured using scanned digital images at 1200 dots per inch (CooRecorder 7.7; Cybis Elektronik & Data AB., Saltsjöbaden, Sweden) on *A. balsamea* and using a sliding scale micrometer (Velmetex, Inc., Bloomfield, NY) and Acu-Rite encoder (Heidenhain Corp., Schaumburg, IL) on *P. rubens* to improve measurement accuracy (0.001 mm accuracy)

on its narrower rings. Mean age (at breast height) of cored individuals was 114 years for *P. rubens* (mean DBH = 31.4 cm) and 70 years for *A. balsamea* (mean DBH = 23.9 cm).

To determine long-term changes in the distribution and abundance of tree species across the elevational climatic gradient (H4), we resampled 23 ASRC plots established in the 1960s between 457 and 1372 m a.s.l. Plot locations were marked on contour maps by the original authors (Holway, Scott & Nicholson 1969) and converted to geographic coordinates digitally. Plots were relocated in 2009 or 2012 and resampled following the original methods (Holway, Scott & Nicholson 1969). Each ASRC plot consisted of a 225-m-long transect along the elevation contour resampled with 15 regularly spaced subplots using a combination of Bitterlich prism and point-centred-quarter (for mature trees >10.2 cm DBH and saplings 2.5–10.2 cm DBH). Because ASRC plots were not permanently marked, we treated the two surveys as separate (rather than paired) samples.

QUANTIFYING TEMPERATURE SHIFTS WITH ELEVATION

All statistical analyses and figures were conducted in R (R Core Team 2015).

To determine potential warming-induced upslope shifts in temperature envelopes over time (between the 1964 and 2012 vegetation surveys; H1), we calculated annual GDD (4 °C base) at each plot using *in situ* temperature measurements following Gavin, Beckage & Osborne (2008). We then (i) examined how GDD from the field measurements changed with elevation (β ; lapse rate) using linear regression and (ii) tested for a long-term GDD trend using local long-term data (Lake Placid 2 S climate station, NY; 1949–2012) and generalized least squares regression with first-order serial autocorrelation (10 missing GDD values were interpolated; see Fig. 1a). The change in GDD between the two vegetation surveys was calculated as the change in predicted GDD from 1964 to 2012 (Δ GDD). Finally, we calculated the corresponding shift in temperature envelopes with elevation (Δ Elev) during the past c. five decades as

$$\Delta\text{Elev} = \frac{\Delta\text{GDD}}{\beta} \quad \text{eqn 1}$$

where Δ GDD is the change in GDD over time (based on the Lake Placid data) and β is the change in GDD over elevation (i.e. lapse rate, based on field measurements). Note that field temperature measurements (from iButton loggers) covered less than a full year; however, GDD values derived for this shorter period were strongly related to full-year GDD calculations based on the Lake Placid time series ($\rho = 0.90$, $P < 0.0001$).

QUANTIFYING CHANGES IN TREE GROWTH

To determine if tree growth improved at high elevations and declined at low elevations, consistent with expected upslope range shifts (H2), we analysed individual tree-growth trends by elevation from re-measured trees at FRP plots and from tree cores. For live trees on FRP plots that were ≥20 cm DBH (in 2012) and present in all surveys (65 *P. rubens* and 54 *A. balsamea* individuals), we calculated annual basal area increment (BAI, mm² year⁻¹) following Biondi & Qeadan (2008) for the two intervals defined by the surveys (1986–2002 and 2002–2012) as

$$\text{BAI} = \pi(r_n^2 - r_{n-x}^2)x^{-1} \quad \text{eqn 2}$$

where r is the radius at the end of year n , and x is the number of years since the previous measurement. We then quantified changes in tree growth over time by calculating the site-level mean change in individual tree BAI (ΔBAI) between the two periods (1986–2002, 2002–2012) for each species. Furthermore, we examined if changes in tree growth (ΔBAI) of each species were affected by competition using a plot level competition index (CI) calculated as

$$\text{CI} = \frac{(\text{BA}_{2012} - \text{BA}_{1986})}{\text{BA}_{1986}} \quad \text{eqn 3}$$

where BA is the total plot basal area representing competition in either 2012 or 1986 surveys (Lines, Coomes & Purves 2010). In forests, plot basal area represents a meaningful measure of crowding as it includes both the number of trees and the size of trees. We used weighted linear regression (weights corresponding to the number of trees per plot) to first test if mean species ΔBAI per plot was different from zero (intercept only model) and then to relate mean species ΔBAI per plot to elevation and CI.

To extend tree-growth analysis further back in time and to gain a finer resolution of individual tree growth, we used annual raw ring widths from tree cores extending the analysis to 1900s (*P. rubens*) or 1940s (*A. balsamea*). The annual raw ring widths were converted to annual BAI of each individual tree using formula (2) above. To determine how tree species growth varied over time by elevation (H2), annual tree-level BAI was regressed against elevation in each year, yielding multiple coefficient estimates (one regression slope per year) describing the elevation effect on growth each year. The elevation effect was positive when tree growth improved with elevation and negative when it declined with elevation. Tree age or DBH did not vary with elevation to affect growth patterns across elevations (tested with linear regression). Unlike in the growth analysis on the FRP plots, we were unable to assess the influence of competition in tree core analysis because cores were often collected outside the FRP plots where basal area data were not available.

ASSESSING ENVIRONMENTAL EFFECTS ON TREE GROWTH

To determine if mean tree growth and the elevation effect on growth were consistent with changing environment (H3), we examined how each species (mean annual BAI, annual elevation effect) responded to GDD, winter injury, Palmer Drought Severity Index (PDSI) and precipitation pH (Fig. 1). GDD was derived from Lake Placid temperature data as described above (Fig. 1a). Winter injury is a binary variable derived for well-documented winter injury events in the region identified by large numbers of trees with dead foliage in the spring (Curry & Church 1952; Johnson, Friedland & Dushoff 1986; Hadley *et al.* 1991; Kosiba *et al.* 2013; Fig. 1b). Winter injury is likely caused by acid rain reducing the cold tolerance of needles and severe cold weather events resulting in high needle mortality (Kosiba *et al.* 2013). As tree-growth reductions following a winter injury event can last for 4 years (Kosiba *et al.* 2013), we defined the winter injury period as a 4-year window following a winter with a documented injury event. Annual PDSI (New York Climate Region 3, ncdc.noaa.gov) indicates periods of moisture availability (positive

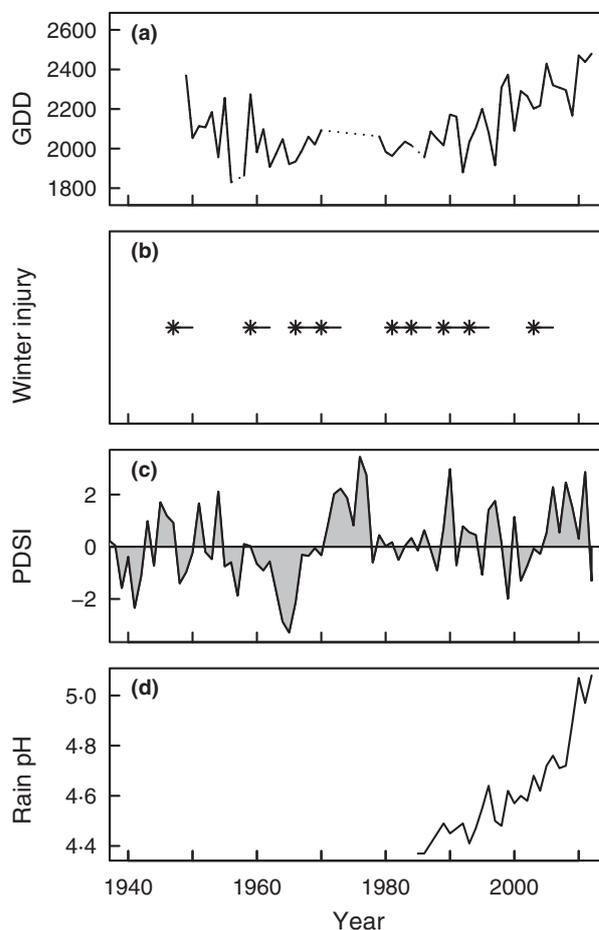


Fig. 1. Environmental variables used to model tree growth, and elevation effect on tree growth, on Whiteface Mountain in the northeastern US. (a) Growing degree-days (GDD) from Lake Placid, NY. (b) Winter injury events (*) with a following 4-year period of reduced growth. (c) Palmer Drought Severity Index (PDSI) for New York Climate Region 3 (negative values indicate drought). (d) Precipitation pH at Whiteface Mountain (610 m a.s.l.). Dotted lines in (a) are interpolated missing values that were used only to test for long-term warming trend (H1). For details see Assessing environmental effects on tree growth.

values) and moisture stress (negative values; Fig. 1c). Precipitation pH was acquired from the National Atmospheric Deposition Program at the base of Whiteface Mountain (1985–2011, site NY98, 610 m a.s.l.; nadp.isws.illinois.edu; Fig. 1d).

For each species (*P. rubens* or *A. balsamea*) and response variable (mean growth or elevation effect on growth), we ran linear models including all variables (without interactions) using generalized least squares, including a first-order autoregressive term to account for temporal autocorrelation (Bolker 2008). Scaled coefficients (mean = 0, variance = 1) were used to compare variables and 95% confidence intervals were used to assess significance. Due to a shorter period with available pH data, we ran the analysis both with pH (1985–2011) and without pH (1949–2011).

ANALYSING POPULATION AND COMMUNITY CHANGES OVER TIME

Finally, we used generalized linear models to examine stand-level changes for all common tree species in spruce-fir forests

(*P. rubens*, *A. balsamea* and *B. papyrifera* var. *cordifolia*) and lower elevation northern hardwood forest (*A. saccharum*, *F. grandifolia* and *B. alleghaniensis*) using the 1960s ASRC plots re-measured in 2009–2012 surveys ($n = 23$; H4). Density and basal area of each species (trees ≥ 2.54 cm DBH) were modelled as a function of elevation (including a quadratic term) and year with Poisson error to capture the increase in variance with the mean (Bolker 2008). If the year variable (indicating the 1960s or 2009–2012 survey) was significant ($P \leq 0.05$), then separate models by year were reported, otherwise we report only the 2009–2012 model.

Results

CLIMATIC SHIFTS WITH ELEVATION

Climate warming (Fig. 1a) resulted in an increase in GDD by 204 degree-days from 1964 to 2012, or 42.5 degree-days per decade ($P = 0.0027$). This rate of increase translated to an estimated 220 m upslope shift in climate (GDD) envelopes. This shift represents substantial portions of the species' range widths (43% for *P. rubens* and 38% for *A. balsamea*; Fig. 2; H1).

CHANGES IN TREE-GROWTH RATES

On FRP plots, *P. rubens*' annual growth increased during the recent period (2002–2012) compared to the previous period (1986–2002) by $248 \text{ mm}^2 \text{ year}^{-1}$ on average per tree (Fig. 3; intercept only model $P = 0.027$) regardless of elevation (Fig. 3; elevation coefficient $P = 0.8$) and

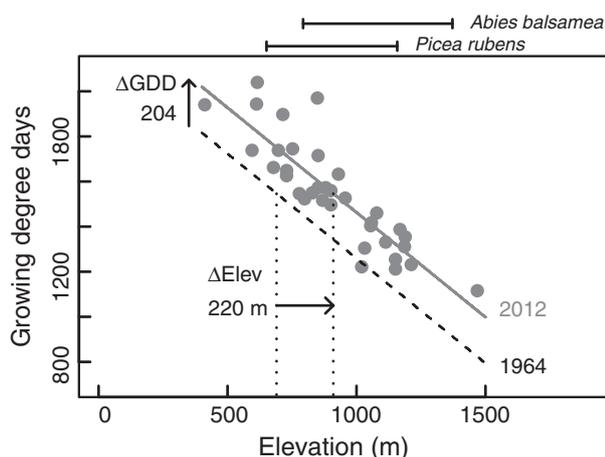


Fig. 2. Upslope shift in temperature envelopes over the last five decades on Whiteface Mountain in the northeastern US. The regression slope between growing degree-days (GDD) and elevation (m) was derived from 2012 field data (●; grey solid line; slope = $-0.929 \text{ GDD m}^{-1}$, $R^2 = 0.77$, $P < 0.0001$). Long-term change in GDD from 1964 (dashed line) to 2012 calculated from long-term climate data (Fig. 1) and plotted relative to elevation by adjusting regression intercepts by the change in GDD since 1964 (ΔGDD ; see Quantifying temperature shifts with elevation). Dotted drop lines indicate how changing climate translated into an upslope shift (ΔElev) of the climate typical of the lower range margin of spruce-fir forest since the 1960s (from 690 m to 910 m a.s.l.). *Picea rubens* and *Abies balsamea* ranges shown for context (predicted basal area $\geq 5 \text{ m}^2 \text{ ha}^{-1}$ in the 1960s; Fig. 5).

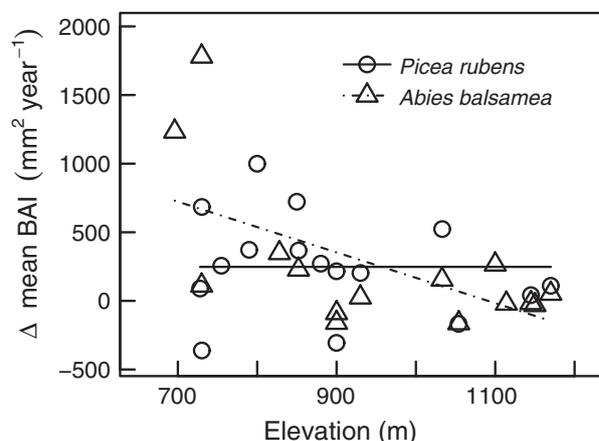


Fig. 3. Change in growth rates of *Picea rubens* and *Abies balsamea* trees with elevation on Whiteface Mountain in the northeastern US. Growth rates expressed as the change in mean annual basal area increment (BAI; $\text{mm}^2 \text{ year}^{-1}$) for each species and Forest Response Program plot calculated by subtracting the mean annual BAI during 1986–2002 from that during 2002–2012; values above zero represent higher growth during 2002–2012 compared to the 1986–2002 period.

competition (not shown; competition coefficient $P = 0.6$). *Abies balsamea* annual growth increased over time by $722 \text{ mm}^2 \text{ year}^{-1}$ on average per tree at low elevations (c. 700 m a.s.l.; Fig. 3; elevation coefficient $P = 0.005$) and it was not affected by competition (not shown; competition coefficient $P = 0.7$).

Tree rings confirmed that *P. rubens*' growth increased over time, with the exception of the decline period in 1960–1980 (Fig. 4a). Tree rings also revealed historically negative effects of elevation on *P. rubens* growth that diminished over time (Fig. 4b); thus, *P. rubens* grew better in low elevations compared to high elevations historically (pre-1960s), but it grew comparably well at low and high elevations since then (consistent with FRP plot results and partially with hypothesis H2). *Abies balsamea* growth increased gradually over time (Fig. 4c) and it was historically greater at high elevations than at low elevations (positive elevation effect); however, *A. balsamea* growth dramatically increased at low elevations over the past decade (Figs 4d and S3) causing the decreasing trend in *A. balsamea* growth with elevation (negative elevation effect) seen also in FRP plots (Fig. 3 contrary to hypothesis H2).

EFFECTS OF ENVIRONMENT ON TREE GROWTH

Growing degree-days, winter injury, moisture stress and precipitation pH were important drivers of tree growth (H3), but their effects varied by species and elevation. For *P. rubens*, mean growth decreased with winter injury, and it increased either with precipitation pH (reduced acid rain; 1985–2011) or with GDD (when pH was not included; 1949–2011; Table 1). The typically negative elevation effect for *P. rubens* (Fig. 4b) became stronger (more negative) during wet years with high PDSI

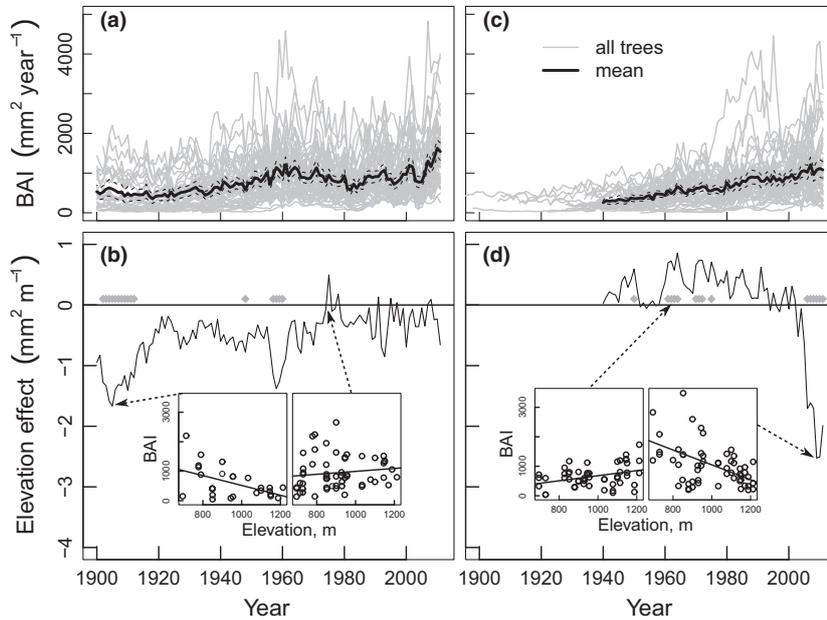


Fig. 4. Mean annual basal area increment over time (BAI, $\text{mm}^2 \text{year}^{-1}$) and elevation effect on tree growth (BAI/elevation; $\text{mm}^2 \text{m}^{-1}$) from tree cores collected on Whiteface Mountain in the northeastern US for *Picea rubens* (a, b) and *Abies balsamea* (c, d). Elevation effect is a regression slope describing the relationship between BAI and elevation (positive when tree growth improved with elevation, negative when it declined with elevation). Insets show years with the highest and lowest elevation effect for each species. Years with significant elevation effect ($P = 0.05$) are marked with grey diamonds in (b) and (d). Decadal elevation effects are given in Figs S2 and S3.

(Table 1). For *A. balsamea*, mean growth was related only to precipitation pH (positively) and the typically positive elevation effect of *A. balsamea* recently shifted to a negative elevation effect during a recent period of high moisture availability and increasing precipitation pH (Table 1).

POPULATION AND COMMUNITY CHANGES

We found no consistent upslope shifts in species elevational distributions since the 1960s contrary to expectations (cf. H4). In spruce-fir forests, *P. rubens* declined significantly since the 1960s across its range in both basal area ($P < 0.0001$; Fig. 5a) and density ($P < 0.0001$; Fig. 5b), while *B. papyrifera* var. *cordifolia* increased in both basal area ($P = 0.0007$; Fig. 5c) and density ($P < 0.0001$; Fig. 5d) as did *A. balsamea* (basal area: $P = 0.008$; Fig. 5e; density: $P < 0.0001$; Fig. 5f). In northern hardwood forests, *A. saccharum* basal area did not

change ($P = 0.37$; Fig. 6a) but density decreased towards its lower range margin ($P = 0.0009$; Fig. 6b), while *F. grandifolia* increased in basal area ($P = 0.04$; Fig. 6c) and density ($P < 0.0001$; Fig. 6d) near its upper range margin and *B. alleghaniensis* did not change in basal area ($P = 0.31$; Fig. 6e) but decreased in density slightly at the upper portions of its range ($P < 0.0001$; Fig. 6f).

Discussion

Despite upslope shifts in temperature envelopes (H1) and changes in tree growth with elevation (H2) and environmental drivers (H3), we did not find strong evidence for upslope shifts in tree distributions (H4). Our results suggest that the distributions of tree species lag behind tree-growth responses to environmental drivers, most likely due to slow migration (dispersal limitations) and long life spans of existing canopy trees. Consequently, low-cost tree growth and microclimate monitoring networks

Table 1. Effects of environmental variables (Fig. 1) on both mean tree growth and the elevation effect on tree growth (Fig. 4) of *Picea rubens* and *Abies balsamea* on Whiteface Mountain in the northeastern US. Scaled coefficients (\pm SE) shown. Bold coefficients are significantly different from zero. Models were run in two configurations: with pH (model coverage: 1985–2011) and without pH (model coverage: 1949–2011) to account for missing pH data prior to 1985. Variable definitions are given in Figs 1 and 4

Variable	<i>Picea rubens</i>		<i>Abies balsamea</i>		Model coverage
	Mean growth	Elevation effect	Mean growth	Elevation effect	
GDD	0.088 (± 0.17)	0.24 (± 0.35)	0.34 (± 0.29)	0.12 (± 0.11)	1985–2011
Injury	-0.44 (± 0.13)	-0.35 (± 0.23)	0.053 (± 0.15)	0.14 (± 0.084)	1985–2011
PDSI	-0.075 (± 0.10)	-0.40 (± 0.20)	0.097 (± 0.16)	-0.18 (± 0.065)	1985–2011
pH	0.57 (± 0.24)	-0.12 (± 0.39)	0.72 (± 0.27)	-0.84 (± 0.15)	1985–2011
GDD	0.37 (± 0.13)	0.27 (± 0.17)	0.068 (± 0.075)	0.054 (± 0.081)	1949–2011
Injury	-0.43 (± 0.10)	-0.23 (± 0.14)	-0.11 (± 0.061)	-0.001 (± 0.066)	1949–2011
PDSI	-0.006 (± 0.088)	-0.31 (± 0.12)	-0.074 (± 0.052)	-0.12 (± 0.056)	1949–2011

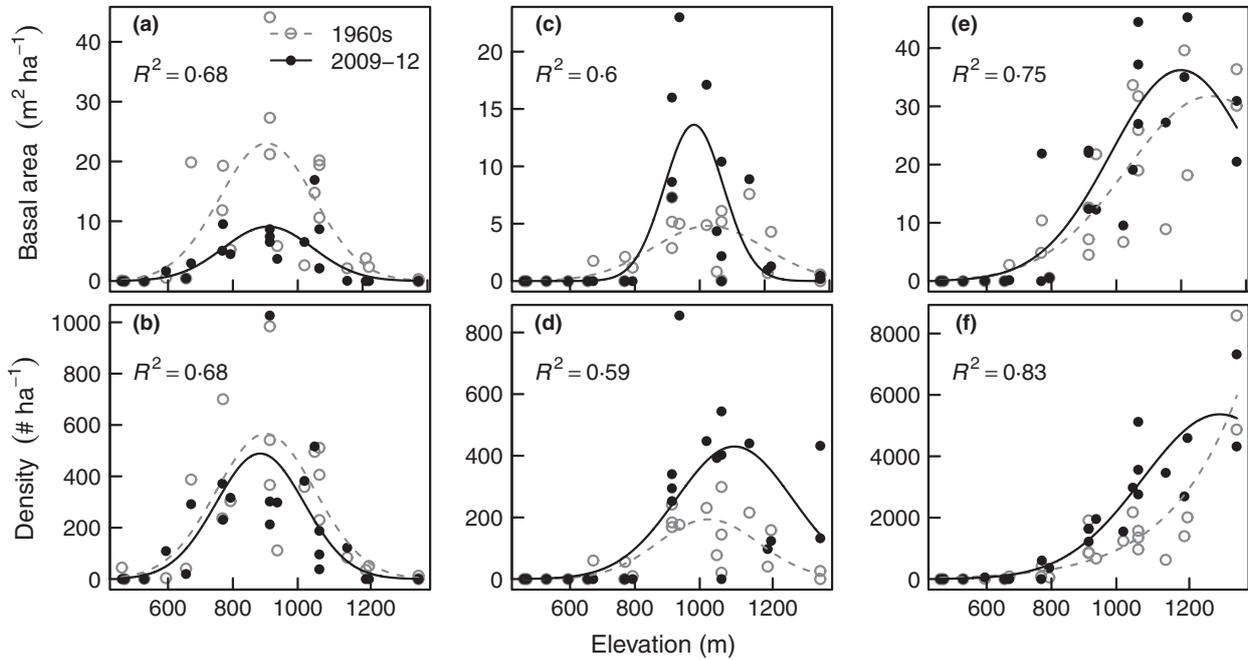


Fig. 5. Changes in stand basal area and density of spruce-fir forest species (≥ 2.54 cm diameter at breast height) on Whiteface Mountain in the northeastern US from the 1960s to 2009–2012: *Picea rubens* (a, b), *Betula papyrifera* var. *cordifolia* (c, d) and *Abies balsamea* (e, f). Symbols represent surveys carried out on Atmospheric Sciences Research Center plots in the 1960s or 2009–2012. If there is a significant year effect, solid lines indicate the 2009–2012 model and dashed lines indicate the 1960s model; otherwise only the 2009–2012 model (solid line) is reported. Per cent deviance explained (R^2) reported for the full model (including the year effect). Note different scaling of y axes.

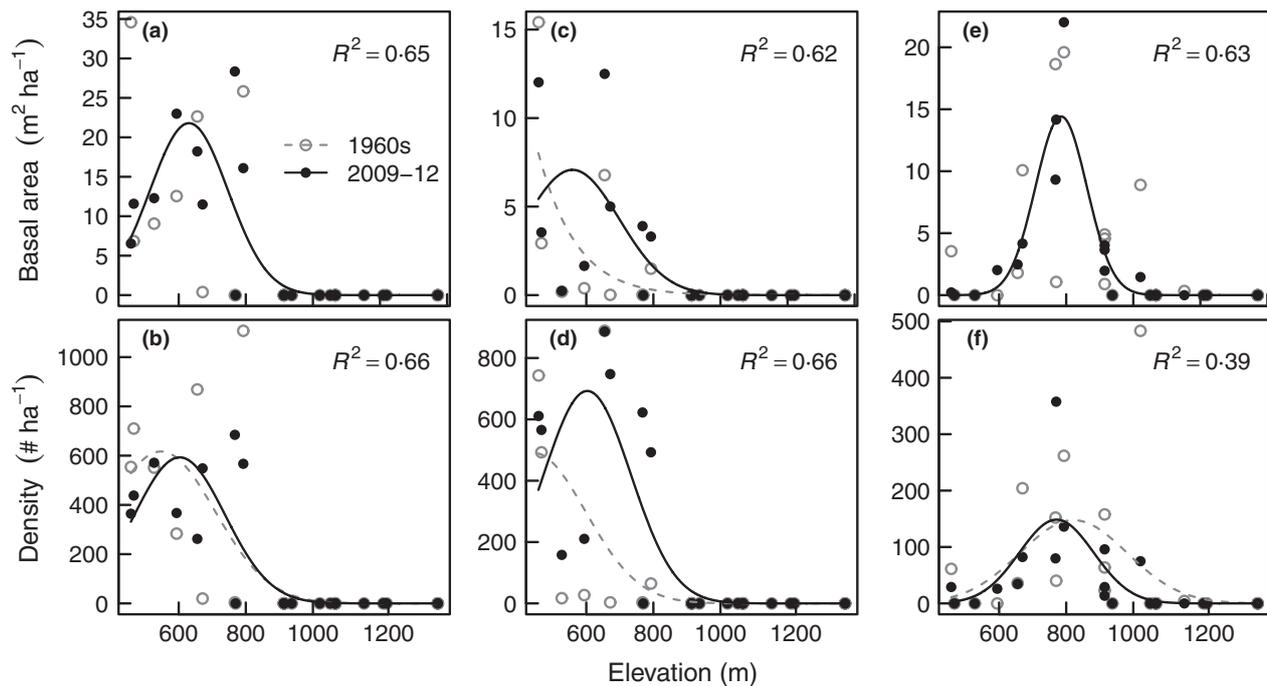


Fig. 6. Changes in stand basal area and density of northern hardwood species (≥ 2.54 cm diameter at breast height) on Whiteface Mountain in the northeastern US from the 1960s to 2009–2012: *Acer saccharum* (a, b), *Fagus grandifolia* (c, d) and *Betula alleghaniensis* (e, f). Symbols represent surveys carried out on Atmospheric Sciences Research Center plots in the 1960s or 2009–2012. If there is a significant year effect, solid lines indicate the 2009–2012 model and dashed lines indicate the 1960s model; otherwise only the 2009–2012 model is reported. Per cent deviance explained (R^2) reported for the full model (including the year effect). Note different scaling of y axes.

established across climatic (elevational or latitudinal) gradients can provide useful tools enhancing forest ecosystem management by allowing early detection of changing forest health and anticipation of future forest responses to environmental change.

MONITORING TREE-GROWTH RESPONSES TO ENVIRONMENTAL CHANGE

Our results confirm that recent increases in tree growth in spruce-fir forests in the northeastern US (cf. Kosiba *et al.* 2013; this study) can be interpreted as complex species-specific responses to winter injury, moisture stress, GDD and precipitation pH (e.g. Johnson, Cook & Siccama 1988; Gavin, Beckage & Osborne 2008). Importantly, our findings suggest that increasing precipitation pH can rival climate as the driver of improved tree growth as corroborated by well-documented sensitivity of *P. rubens* to both temperature and acid rain which predisposes it to winter injury (Cook & Johnson 1989; DeHayes *et al.* 1999). Compared to *P. rubens*, *A. balsamea* is considered more cold tolerant and less sensitive to acidification (DeHayes *et al.* 1999) and we refined this notion by showing its sensitivity to precipitation pH but not to climatic factors (GDD or winter injury) – corroborating the low climate sensitivity of this species observed in other relatively cool mesic settings (cf., wetlands; Raney *et al.* 2016).

Examining growth trends across species ranges proved to be a useful tool to identify potential environmental drivers of growth that can be further studied to anticipate future population changes (Juday, Alix & Grant 2015). Our results revealed that the growth of *P. rubens* decreased more with elevation during wet years, potentially as a result of reduced radiation input and growth at high elevations (cf. cloud ceiling; Siccama 1974). Interestingly, the growth of *A. balsamea* tended to generally increase with elevation until the recent period of higher PDSI that has correlated with increased growth of this species at lower elevations. These changes in the elevation effects for the two species suggest species-specific responses to changing environmental conditions that reflect their different elevational and environmental niches (e.g. Holway, Scott & Nicholson 1969; Siccama 1974; Cogbill & White 1991).

Although our results partly suggest that forest managers can expect enhanced growth of large canopy trees in closed spruce-fir forests in the northeastern US, this growth enhancement is likely to weaken over time as rainfall pH has approached pre-industrial levels (Likens & Buso 2012). Continued warming may lead to growth declines that would likely be detectable first at species' lower range margins and may be indicative of future impacts on trees in other parts of their ranges (Juday, Alix & Grant 2015). We also must consider the potential for interactive effects of climate change with air pollution (Koo *et al.* 2014) or other stressors. For example, Koo *et al.* (2014) noted that growth rates of trees may respond differently to reduced pollution depending on the effect of

climate change across elevation. Therefore, forest health monitoring should focus on range margins for early detection of environmental impacts on forest growth to suggest when manipulating forest canopy structure may increase forest productivity or resilience (e.g. Rasche *et al.* 2011; Kerhoulas *et al.* 2013).

TREE POPULATION AND COMMUNITY RESPONSES TO ENVIRONMENTAL CHANGE

We observed upslope shifts in temperature envelopes exceeding a documented upslope retreat of spruce-fir forests in Vermont (Beckage *et al.* 2008); however, we found no change in the distribution of spruce-fir forests on Whiteface Mountain. Although we found that tree growth responded to recent environmental change (precipitation pH, GDD and moisture stress), the distribution of tree species along the elevational gradient did not shift upslope with these environmental changes that are relatively short term (last ~50 years) compared to tree life span (~100–300 years). The complexity of recent warming trends in the northeastern US, which can vary by season, but are stronger for minimum temperatures relative to maximum temperatures (Beier *et al.* 2012), may play a role in different species-level range shifts across the region. Our study thus corroborates that spruce-fir forests in the northeastern US are not shifting upslope for now (cf. Foster & D'Amato 2015; Wason & Dovciak 2016) and it suggests that monitoring the more responsive tree-growth trends can provide early indications of future vegetation changes in response to complex climate and environmental trends, in order to support management efforts.

The well-documented decline of *P. rubens* in the 1960s was detected and monitored using a combination of growth rates (cf. McLaughlin *et al.* 1987) and permanent forest plots (cf. Battles *et al.* 1992). Red spruce decline, confirmed by our analyses, represented an opportunity for other species to colonize the unoccupied space and increase their density and, in some cases, basal area (Battles & Fahey 2000). *Picea rubens*, in our study, declined mostly in larger size classes, while sapling (DBH 2.5–10.2 cm) density increased since the 1960s (data not shown). Yet, *A. balsamea* expanded within, but not beyond, its historical range (cf. Beckage *et al.* 2008). The apparent upward shift of *F. grandifolia* in our study may be related to *P. rubens* decline, climate warming, reduced acid rain or their interactions with beech bark disease (cf. Giencke *et al.* 2014). Regional growth decline of range-centred *A. saccharum* recently detected at lower elevations (Bishop *et al.* 2015), coupled with the lack of upslope migration that we observed, raise concerns for its ability to adapt to or migrate with further environmental change.

Conclusions

Globally, forest ecosystems are expected to respond to multiple environmental changes, such as climate warming

and reductions in acid pollution in the northeastern US (Huntington *et al.* 2009; Likens & Buso 2012). Predicting forest compositional shifts is important in forest management and conservation, but tree species' distributional responses are often delayed and complex (Rapacciuolo *et al.* 2014). Our results suggest that monitoring tree growth across explicit environmental gradients can provide early detection of the effects of environmental change on forest trees and ecosystems. Forest managers, particularly of range margin tree populations, can use tree-growth monitoring as an additional tool for anticipating future species dynamics and management needs. Moreover, we showed that caution is needed when attributing changes in tree growth or forest structure to warming climate as other ongoing environmental changes, such as increasing precipitation pH, may contribute in complex ways to the observed changes.

Authors' contributions

All authors conceived the ideas and methodology; J.W. and J.B. collected the data; J.W. analysed the data; J.W. and M.D. wrote the manuscript; and all authors contributed critically to manuscript drafts and gave final approval for publication.

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Data accessibility

All data used in this manuscript are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.327t0> (Wason *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Maps depicting research plot locations.

Fig. S2. *Picea rubens* decadal elevation effect on growth.

Fig. S3. *Abies balsamea* decadal elevation effect on growth.