

Montane forest ecotones moved downslope in northeastern USA in spite of warming between 1984 and 2011

JANE R. FOSTER¹ and ANTHONY W. D'AMATO^{1,2}

¹Department of Forest Resources, University of Minnesota, 115 Green Hall 1530 Cleveland Ave. N., St. Paul, MN 55108, USA,

²Rubenstein School of Environment and Natural Resources, University of Vermont, 204E Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA

Abstract

Ecotones are transition zones that form, in forests, where distinct forest types meet across a climatic gradient. In mountains, ecotones are compressed and act as potential harbingers of species shifts that accompany climate change. As the climate warms in New England, USA, high-elevation boreal forests are expected to recede upslope, with northern hardwood species moving up behind. Yet recent empirical studies present conflicting findings on this dynamic, reporting both rapid upward ecotonal shifts and concurrent increases in boreal species within the region. These discrepancies may result from the limited spatial extent of observations. We developed a method to model and map the montane forest ecotone using Landsat imagery to observe change at scales not possible for plot-based studies, covering mountain peaks over 39 000 km². Our results show that ecotones shifted downward or stayed stable on most mountains between 1991 and 2010, but also shifted upward in some cases (13–15% slopes). On average, upper ecotone boundaries moved down -1.5 m yr^{-1} in the Green Mountains, VT, and -1.3 m yr^{-1} in the White Mountains, NH. These changes agree with remeasured forest inventory data from Hubbard Brook Experimental Forest, NH, and suggest that processes of boreal forest recovery from prior red spruce decline, or human land use and disturbance, may swamp out any signal of climate-mediated migration in this ecosystem. This approach represents a powerful framework for evaluating similar ecotonal dynamics in other mountainous regions of the globe.

Keywords: climate migration, decline, disturbance, ecotones, forest dynamics, global change, *Picea rubens*, species range shifts

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Introduction

Transition zones where forests of boreal and temperate tree species meet, called ecotones, are sensitive to changes in climate. In montane regions, this forest ecotone is compressed over a steep vertical gradient, like tree line, and offers the potential to detect climate response in the form of elevational range shifts. Subalpine boreal forests are expected to contract upslope in temperate regions, as climate changes to favor hardwood species with more southerly distributions (Beckage *et al.*, 2008; Iverson *et al.*, 2008). Yet unlike a wide range of taxa that appear to be shifting upward, and also downward, based on occurrence data (Lenoir *et al.*, 2008; Crimmins *et al.*, 2011), the rate at which montane forest composition will change remains in question. Forest dynamics play out over decades or centuries under small-scale disturbance regimes (Foster & Reiners, 1983) and do not always track changes in climate (Zhu *et al.*, 2012). These ongoing forest dynamics complicate both

identification of local compositional shifts and their attribution to climate change alone (Gehrig-Fasel *et al.*, 2007; Lenoir *et al.*, 2010).

The climate attribution problem arises from the fact that several drivers change forests beyond just the biophysical factors that affect performance of individual trees (Lenoir *et al.*, 2010). These factors are difficult to differentiate because they are often confounded in space and time. Recent species distribution patterns, from which we infer climatic tolerance (Iverson *et al.*, 2008), have also been shaped by natural and human disturbances that are both stochastic and systematic in nature (Gehrig-Fasel *et al.*, 2007; Nowacki & Abrams, 2014). If climate is the main driver of changes in forest ecotones, then those changes should be evident across regional spatial scales and show some independence from patterns of human disturbance.

Ecotonal shifts should be observed at spatial scales over which climate is autocorrelated, yet many empirical studies are severely limited in spatial extent. A widely cited example of the rate and direction of montane ecotone change reported that boreal forests dominated by red spruce (*Picea rubens*), balsam fir

Correspondence: Jane R. Foster, tel. +608 215 9957, e-mail: jrfoster@umn.edu

(*Abies balsamea*) and paper birch (*Betula papyrifera* var. *cordifolia*) receded upslope at an alarming rate of 2.13–2.77 m yr⁻¹ from 1965 to 2005 in the Green Mountain Range in Vermont (VT), USA (Beckage *et al.*, 2008). Yet this rate was calculated from aerial photographs for narrow transects (6 m wide) on only two peaks (Beckage *et al.*, 2008). While much of the species' demographic change occurred in the decade after plots were established in 1964 (Siccama, 1974; Beckage *et al.*, 2008), image analysis determined that most of the vertical movement in the ecotone occurred in recent decades (1995–2005), which suggests a migration rate more rapid than typically thought possible in forest ecosystems. These changes foretell habitat loss for many taxa, as the Appalachian extension of the boreal forest shrinks in extent.

Other empirical studies over larger spatial scales have reported increases in the same boreal species in the neighboring White Mountains of New Hampshire (NH) (Fig. S1a). Landsat detected that subalpine conifer forests appeared to be expanding at lower elevations between 1987 and 2010 (Vogelmann *et al.*, 2012), rather than receding upslope, possibly due to increase of *A. balsamea*, a boreal species that has been restricted to higher elevations in this region (Foster & Reiners, 1983; Craig & Friedland, 1991; Vadenboncoeur *et al.*, 2011). Over a similar time frame (1995–2005), recruitment to canopy size classes was higher for *P. rubens* and *A. balsamea* than for all species other than *Fagus grandifolia* in Hubbard Brook Experimental Forest (NH) (van Doorn *et al.*, 2011). These studies suggest spruce–fir abundance either has increased in ecotone elevations or has not changed significantly in recent decades. If this is the case, drivers other than climate must be at play in shaping the ecotone.

Faced with conflicting examples of change in the montane forests of the northeastern USA, we are left asking whether the ecotone has moved over the past 20–30 years and can truly serve as a harbinger of contemporary climate impacts. If this ecotone has shifted, what are the drivers and implications for our understanding of forest response to a changing climate? Forests in the Green and White Mountains have experienced similar trends in climate (Richardson *et al.*, 2003; Beckage *et al.*, 2008; Seidel *et al.*, 2009; Hamburg *et al.*, 2013); mean annual temperatures rose 0.19–0.29°C·decade⁻¹ across a range of sites between 1966 and 2005 (Hamburg *et al.*, 2013). Yet disparate forest changes suggest a need for comprehensive analysis of ecotone location and movement across the region.

We developed a method to systematically map the subalpine boreal-hardwood forest ecotone (simply called 'ecotone' hereafter) from leaf-off Landsat imagery that is conceptually similar to prior approaches

(Beckage *et al.*, 2008), but that samples the entire elevational zone between 650 and 1000 m (A.S.L.) throughout these mountain ranges (covering ~39 000 km² region), including peaks from prior publications (Siccama, 1974; Beckage *et al.*, 2008). We fit logistic models to Landsat canopy reflectance to predict the abundance of boreal species across contiguous mountain slopes. This allowed us to estimate ecotone elevation at both the local scale of individual slopes (median area of 132 ha) and at larger scales across mountain ranges. We demonstrate the validity of our remote sensing approach with published forest inventory data from Hubbard Brook Experimental Forest (HBFEF) (Schwarz *et al.*, 2003; van Doorn *et al.*, 2011). We derive inflection points from fitted models that represent the upper and lower ecotone boundaries and tested whether they changed significantly in spring leaf-off imagery over 19 years (1991–2010) and fall imagery over 27 years (1984, 2000 and 2011). We used linear mixed-effects models to quantify how latitude, aspect, slope, year and mountain range influence ecotone elevation. This approach represents a powerful framework for evaluating similar ecotonal dynamics in other mountainous regions of the globe.

Materials and methods

Study area

Our analysis spans the northern portion of the Green Mountains in VT and all of the White Mountain range in NH (Fig. S1), stretching from 43.75°–44.75° N and 70.77°–73.33° W. The Green Mountains consist of ridges that run along a north–south axis with five peaks higher than 1219 m a.s.l. (Siccama, 1974). The White Mountains reach higher elevations, Mt. Washington is the highest peak in the eastern USA at 1914 m a.s.l., and are more clumped in their morphology and orientation. The climate in the study area is continental and becomes more maritime to the east; mean annual temperatures rise from west to east by +0.29 °C·°longitude⁻¹ over this region (Richardson *et al.*, 2004). Mean July temperature at tree line was 14 °C on Mt. Mansfield in the Green Mountains and 13 °C on Mt. Moosilauke in the Whites (Richardson *et al.*, 2004). Mean annual temperatures have risen significantly between 1966 and 2005 (+0.19–0.29 °C·decade⁻¹) (Hamburg *et al.*, 2013), but these trends appear to be less significant at the highest elevations on Mt. Washington (Seidel *et al.*, 2009).

Forest species composition in both mountain ranges varies strongly with elevation, inspiring a long history of ecological inquiry (Siccama, 1974; Foster & Reiners, 1983; Cogbill & White, 1991; Leak & Yamasaki, 2012). Higher elevations are dominated by coniferous forests consisting of *P. rubens*, *A. balsamea* and the deciduous *B. papyrifera* var. *cordifolia*. We use the term 'boreal' to describe these subalpine forests for consistency with past work in the region (Siccama, 1974; Beckage *et al.*, 2008); however, these montane systems contain climatic

and disturbance regimes that are distinct from boreal spruce–fir systems found at higher latitudes (Cogbill & White, 1991). Northern hardwood forests below the ecotone are dominated by *Acer saccharum* (sugar maple), *Betula alleghaniensis* (yellow birch) and *Fagus grandifolia* (American beech).

Remote sensing analysis

We analyzed leaf-off multispectral Landsat Thematic Mapper imagery to map the forest ecotone across the White and Green Mountains, USA. We screened Landsat imagery (Path 13 and Row 29) available from NASA's Landsat Climate Data Surface Reflectance Record (CDR) that is georegistered and atmospherically corrected to surface reflectance using the standard LEDAPS processing stream (Masek *et al.*, 2006; <http://earthexplorer.usgs.gov/>). This free archive is processed to enable accurate comparison among scenes. The mountain ranges in our study area often lack suitable cloud- and snow-free leaf-off imagery. We found high-quality spring images from May of 1991 and 2010 in which leaf-out of deciduous forests had not advanced too high in elevation (> 650 m), and no snow remained at higher elevations (<1000 m) (Table S1). We also tested late fall images from October 1984, 2000 and 2011. Reflectance of senescent deciduous leaves that have not yet dropped contrasts strongly with overstory conifers, but may obscure detection of understory conifers. We used spring leaf-off imagery to map the forest ecotone including both overstory and understory trees and relied on fall imagery to represent overstory trees only. We also tested leaf-on imagery from summer 1991 and 2009, but reflectance patterns differed too much from leaf-off imagery to make formal comparisons (Fig. S5). We report only leaf-off data, although leaf-on results were consistent with the magnitude and direction of reported changes (Fig. S6).

Differences in solar illumination angle can create shadows in remotely sensed images of mountainous terrain that complicate change detection. We selected images taken close to the same day of year (DOY) to ensure comparability (Table S1). We further corrected reflectance data for different solar incidence angles using the C-correction technique (Teillet *et al.*, 1982), which uses solar azimuth, solar elevation and a digital elevation model (DEM from NED, 30 m resolution (Gesch *et al.*, 2002)). This produced Landsat scenes in which topographic illumination and shadows were removed.

We delineated our sample areas through a multistage topographic analysis of the 30 m DEM. First, we delineated all areas that fall between 650 and 1000 m (Fig. S1). Eastern hemlock (*Tsuga canadensis*), a low-elevation conifer that could confuse our models, generally occurs below 650 m (Leak & Yamasaki, 2012), and any remnant snow cover occurred above 1000 m. We derived transformed aspect from the DEM using Beers transformation (Beers & Dress, 1966). We then subdivided our sample area based on two transformed aspect classes, SW (0–1) and NE (>1–2), to create subsets on contiguous mountain slopes with a minimum size of 500 pixels, or 45 ha. The result was a set of 175 subset areas in the Green Mountains and 450 subset areas to sample the White Mountain

topography, which ranged in size from 45 to 3897 ha (median = 132 ha).

We extracted reflectance data and elevation for all pixels that fell within each sample polygon from five Landsat image dates and the DEM. To ensure a consistent comparison among scenes, we masked them simultaneously for clouds, snow (using the FMASK band) and nonforest cover classes from the National Landcover Dataset (2011). Thus, we fit models to sample data from identical pixel locations across years. We excluded outliers from reflectance data in the red, NIR and SWIR (bands 3–5) that had z-scores larger than 3 or unreasonable reflectance values [outside of (0–1)]. We randomly balanced the remaining data across the elevation range such that each 50 m band in elevation was represented by the same number of observations. This was necessary because lower slopes typically cover a larger area than mountain peaks. Balanced subsets with fewer than 100 observations (<9 ha) or that failed to span the elevation range were excluded from analysis. A total of 299 forest subsets did not span the elevation range, while 35 subsets had too few usable observations. We ended with 245 forest subsets suitable for ecotone modeling in the White Mountains and 145 in the Greens, or 54% and 83% of the total number of potential subsets.

We converted reflectance data to two vegetation indices that distinguish between green vegetation canopies and leaf-off forest areas. We tested the normalized difference vegetation index ($NDVI = (B4 - B3)/(B4 + B3)$, where B stands for reflectance in the corresponding Landsat TM band), a common proxy for vegetation greenness, and the normalized difference infrared index [$NDII = (B4 - B5)/(B4 + B5)$] which is a proxy for canopy water content that shows strong contrast between conifer and leaf-off forests. For both indices, higher index values correlate with higher abundance of green vegetation. We normalized vegetation index data to z-scores by mountain to ease comparison of fitted models. NDII produced models with lower uncertainty in parameter fits that agreed with boreal species abundance in forest plot data (details below, Fig. S4b). We selected NDII as our proxy for boreal species relative abundance and present results from NDII models only.

Forest inventory data

We compared our Landsat models and results to forest inventory data from 371 plots in Hubbard Brook Experimental Forest (HBEF) that were established and remeasured in approximately 1995 and 2005 (Battles *et al.*, 1998; Schwarz *et al.*, 2003; van Doorn *et al.*, 2011; Hubbard Brook data archives <http://www.hubbardbrook.org/>). Most of these circular inventory plots covered 0.05 ha ($n = 364$), with the remainder sampling 0.0314 ha in denser, high-elevation forests (van Doorn *et al.*, 2011). Within each plot, tree diameter, species and demographic change were measured for all trees whose diameter at breast height exceeded 10 cm. We fit similar models to predict plot-based relative basal area (RBA) of boreal species measured in 1995 and 2005 from elevation (models described below) to ground-truth, validate and interpret our approach for detecting and mapping the montane ecotones from Landsat NDII data.

Ecotone model derivation

We fit nonlinear four-parameter logistic models to predict conifer relative abundance (measured by NDII) as a function of elevation for each data subset (Fig. 1, Appendix S1) using generalized least squares in R (R Package nlme, Pinheiro *et al.*, 2014). We fit logistic models with spatially correlated errors that followed an exponential model (Fig. S3). Modeling spatially correlated errors is computationally expensive.

Therefore, we capped the sample size of reflectance data to a maximum of 1400 pixels (~126 ha or 30% of largest subset and 95% of median subset size), which corresponded to 200 observations per 50 m rise in elevation. We defined the inflection points occurring at the maximum and minimum of the second derivative of the fitted logistic curves to represent the upper and lower boundaries of the transition zone between spruce–fir and northern hardwood forests (Fig. 1a). These inflection points agreed well with forest inventory data of boreal species

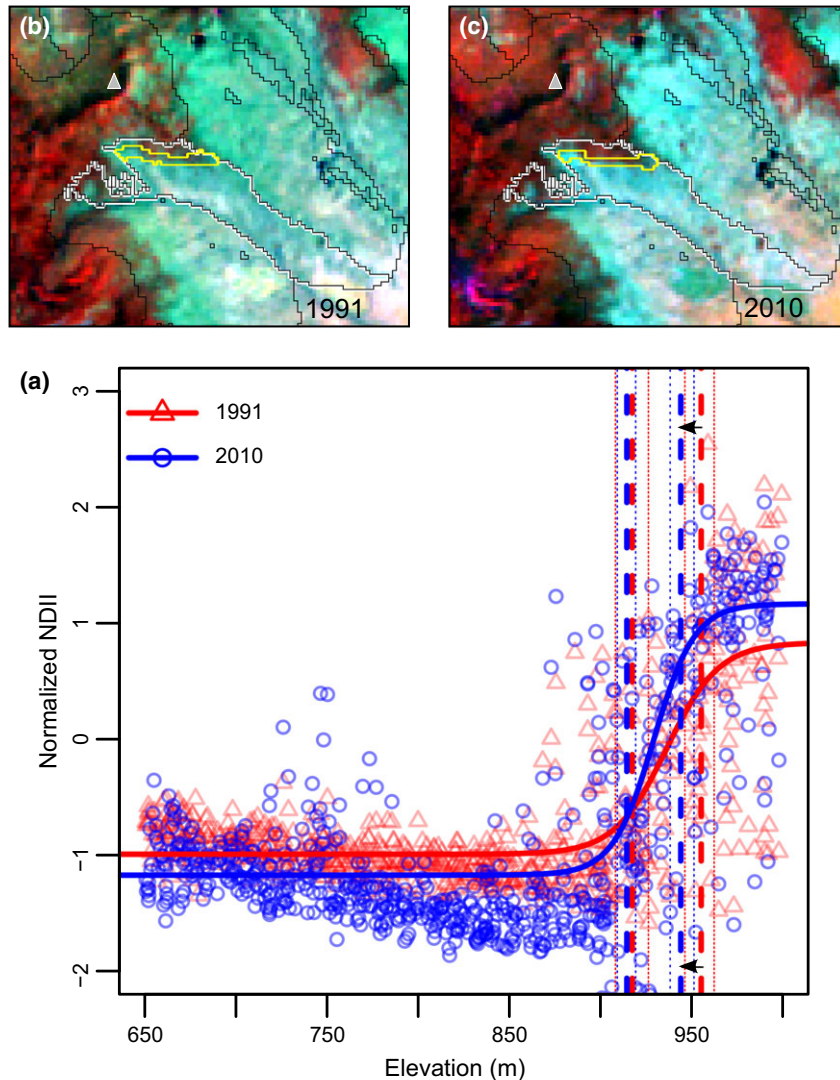


Fig. 1 Example of model fits and derivation of inflection points to locate montane ecotone edges for one Landsat subset located on a SW slope of 'The Horn' (gray triangle, b and c), a peak in the Pilot Range, NH. Solid lines (a) show logistic models fit to normalized NDII data (points/symbols) extracted for pixels in this subset. The subset area is outlined with a combination of fine black over heavy white lines, b and c, while adjacent subsets are outlined by fine black lines only. Heavy dashed lines in (a) show elevations of upper and lower inflection points for each model. Fine dotted lines show 95% CIs for derived boundary edges and arrows show direction of change in ecotone elevation over time. Modeled ecotones (heavy yellow lines, b and c) overlain on spring Landsat imagery from 1991 and 2010 show downward trend of subalpine conifer species over 19 years (conifer vegetation appears in dark and red tones in RGB images of Landsat bands 4, 5 and 3). Much of the elevation range in this subset is dominated by northern hardwood forests, which appear light blue in leaf-off Landsat images (b and c) corresponding to low NDII (a). Increases in subalpine conifer species are also evident in areas above 1000 m around the peak of 'The Horn' (b and c). See Fig. S2 for example with both spring and fall ecotones models.

abundance from HBEF in the White Mountains (measured in 1995, compared to Landsat models from 1991) (Fig. S4c), as well as informal estimates of ecotone location from prior research (Siccama, 1974; Foster & Reiners, 1983; Cogbill & White, 1991; Leak & Yamasaki, 2012). In the HBEF inventory data, these limits corresponded roughly to the elevation zone where boreal species made up 25% to 75% of relative basal area, although boreal species occur at lower elevations (Fig. S4c). To calculate 95% confidence intervals (CIs) for the model estimates of ecotone elevation, we drew 80 random samples from normal distributions of fitted parameters and derived inflection points for each random draw. We compared empirical bootstrapped distributions of ecotone edge elevations among years within each subset using Tukey's HSD test. Tukey's HSD comparisons with adjusted p-values greater than 0.05 were assigned a change in elevation of zero (no change) when summarizing results, while CIs were left unchanged. Negative change values represent ecotone shifts to lower elevation, while positive values show ecotones moving higher.

To infer the geographic drivers of ecotone elevation, we fit linear mixed-effects models with spatial errors using the NLME package in R (Pinheiro *et al.*, 2014). We predicted ecotone boundary elevation (upper or lower) as a function of fixed effects of mean latitude, slope, transformed aspect and year and allowed intercepts to vary randomly via random effects by mountain range (Green or White Mountains). We expected ecotone elevation to decrease with latitude and slope (Cogbill & White, 1991) and to increase with year, if ecotone boundaries have been migrating upward in response to recent climate change (Beckage *et al.*, 2008). We expected ecotones to be higher on SW aspects, where warmer conditions should favor growth of hardwood competitors.

Results

Movement and characteristics of the montane forest ecotone

Movement of the boreal-hardwood forest ecotone varied among individual mountain slopes between 1991 and 2010, with the ecotone moving upward on some slopes, downward on others or staying stable (Fig. 2). Downward shifts occurred more frequently than upward shifts. Ecotone edges on 56% and 42% of slopes (upper and lower edges, respectively) moved downward, while only 13% and 15% of slopes had edges that shifted higher. When changes in ecotone elevation were summarized across mountain ranges, both the upper and lower boundaries shifted downward at rates that averaged -1.5 and -2.0 m yr⁻¹, respectively, in the Green Mountains, while only the upper boundary in the White Mountains showed a mean downward trend of -1.3 m yr⁻¹ (Table 1, Fig. 3, spring models). The ecotone extended from 809 to 921 m on average in the Green Mountains and 782 to 894 m in the Whites, although the distribution of local ecotone elevations

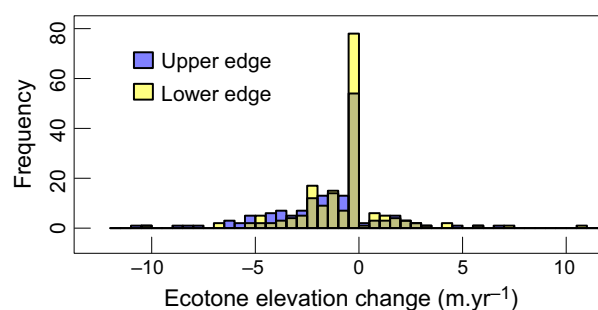


Fig. 2 Distribution of changes in ecotone elevation estimated for 170 individual slopes over 19 years between 1991 and 2010 (spring) for both the White and Green Mountains. Annual rates of elevation change show that the ecotone moved both up and down at local scales, and often remained unchanged. Differences deemed insignificant according to Tukey's HSD multiple comparison tests were assigned to zero change.

varied widely, stretching from the top to the bottom of the examined elevation zone (Fig. 3). Mean lower boundary elevations correspond well to earlier generalized estimates of 790 m (± 15 m) in the Green Mountains and 760 m (± 15 m) in the White Mountains (Cogbill & White, 1991).

Forest inventory data measured in 1995 and 2005 at HBEF illustrate how ecotone changes detected with Landsat relate to changes observed in tree species abundance (Schwarz *et al.*, 2003; van Doorn *et al.*, 2011). Spatial logistic models fit to plot-based relative basal area (RBA) of boreal species (Fig. 4) show that ecotone edges in HBEF shifted downward at rates of -2.5 and -0.2 m yr⁻¹ (upper and lower edge, respectively) between 1995 and 2005, consistent with the direction and magnitude of mean change for the White Mountains (1991-2010) (Table 1). At the same time, the change in plot-based boreal RBA increased with elevation (Fig. 5a), as did the percent of boreal trees that transitioned from subcanopy or intermediate canopy positions to dominant or codominant positions (Fig. 5b). HBEF data confirm that ecotone changes detected by Landsat represent gains in relative abundance by boreal tree species, from a combination of growth and recruitment as reported in van Doorn *et al.* (2011).

The distribution in ecotone elevation suggests that the location and character of the boreal-hardwood forest ecotone vary widely (Mayfield & Hicks, 2010) and are not always constrained between 650 and 1000 m. The logistic model form corresponds to an idealized concept of the ecotone representing an abrupt boundary between climatically distinct forest types. Logistic models converged for 205 of 245 potential subsets (82%) in the White Mountains and 85 of 145 subsets in the Green Mountains (59%), or 92 218 ha and

Table 1 Mean changes in elevation of ecotone edges derived from pairs of spring and fall Landsat NDII images

Season	Ecotone edge	Years	Weighted difference* (m)	No of Subsets	No of Years	Difference (m yr ⁻¹)	95% CI (m yr ⁻¹)
Green mountains							
Spring	Upper	2010–1991	-39.17	52	19	-2.06	-2.94, -1.34
	Lower	2010–1991	-28.90	53	19	-1.52	-2.68, -0.52
Fall	Upper	2000–1984	-18.71	31	16	-1.17	-1.86, -0.37
	Lower	2000–1984	-16.59	33	16	-1.04	-2.07, -0.16
	Upper	2011–2000	-24.45	48	11	-2.22	-3.72, -1.11
	Lower	2011–2000	8.16	49	11	0.74	-0.81, 2.38
White Mountains							
Spring	Upper	2010–1991	-25.27	118	19	-1.33	-2.67, -0.32
	Lower	2010–1991	-9.41	124	19	-0.50	-2.00, 0.80
Fall	Upper	2000–1984	1.45	79	16	0.09	-0.85, 1.27
	Lower	2000–1984	-13.06	84	16	-0.82	-2.31, 0.28
	Upper	2011–2000	-6.85	81	11	-0.62	-2.49, 1.12
	Lower	2011–2000	2.61	89	11	0.24	-1.96, 2.39

*Significant mean differences in bold. Mean changes combined point estimates from all subsets (insignificant changes determined by Tukey's HSD were assigned a value of zero for no change), weighting each estimate and its 95% CI by the number of pixels in the subset model.

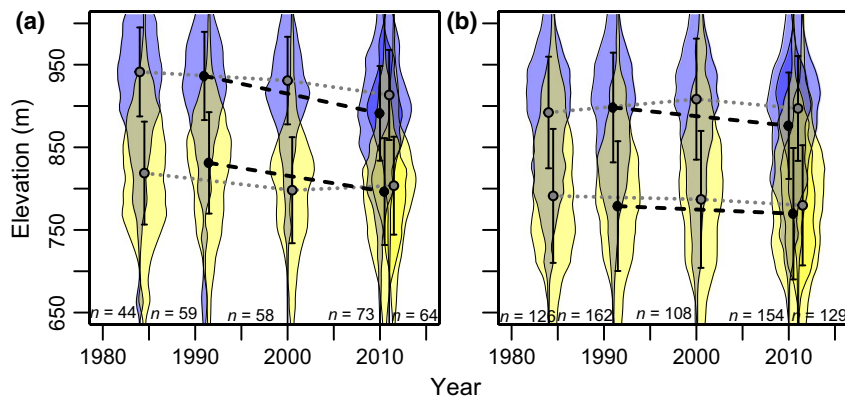


Fig. 3 Violin plots show the distribution of upper (dark shading) and lower (light) boundary elevations for the ecotone between boreal and hardwood forest in the Green Mountains (a) and the White Mountains (b). Black dashed lines and circles show the trend between weighted means of boundary locations detected in spring leaf-off conditions (understory visible to sensor, 1991 to 2010). Dotted gray lines and circles show boundary locations detected in fall conditions (understory less visible to sensor, 1984, 2000 and 2011). Data represented by violin plots vary by year as shown by the number of subset models (*n*) that could be fit in each Landsat date. Lower ecotone boundary distribution is offset +0.5 years for clarity. Error bars show ± 1 SD (variance among subset models).

26 789 ha, respectively. In cases where a logistic model fit was not possible (~20–40% of subsets), the structure of the transitional forest varied from dominance of either spruce–fir or hardwood forests across the entire elevational range (i.e., no ecotone), to a linear increase in spruce–fir RBA (gradual gradient), to a wide range of patterns. The reality of the transitional forest often varies dramatically from the conceptual ideal (Appendix S1). This raises the question of how stable the ecotone has been over time or whether its location has always been subject to a natural range of variability characterized by periodic expansion and contraction.

Seasonal effects on ecotone detection

Fall Landsat imagery provided estimates of the ecotone as it is characterized by overstory trees, resulting in ecotone elevations that could be higher than estimates derived from spring leaf-off imagery. Upper ecotone boundaries appeared to be 12.9 m higher than spring estimates in the Green Mountains (95% CI, 0.8–31.6 m), based on comparisons from spring 2010 and fall 2011 (Fig. 3). This is consistent with our assumption that fall images do not represent complete leaf-off conditions, but rather show some retention of senescent leaf cover

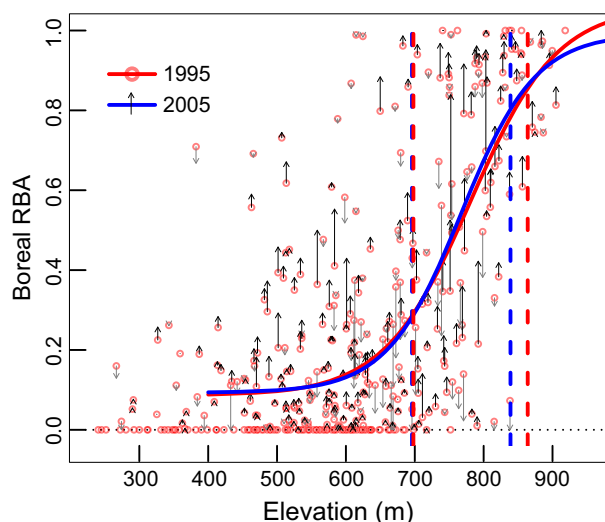


Fig. 4 Downward ecotone shift detected from 371 remeasured forest inventory plots at Hubbard Brook Experimental Forest is consistent with Landsat models. Spatial logistic models (solid lines) fit to plot-measured boreal relative basal area (RBA) from 1995 (circles) and 2005 (arrows) estimated downward movement of -2.5 and -0.2 m yr^{-1} for the upper and lower ecotone edges (vertical dashed lines), similar to Landsat-detected shifts in the White Mountains (Table 1).

that may interfere with the detection of subcanopy conifers. Ecotone edges detected from fall imagery in the White Mountains did not shift on average over 27 years (1984–2011), suggesting that ecotones have been relatively stable when viewed from the overstory (Table 1). More movement occurred in fall ecotone boundaries in the Green Mountains, which shifted downward by approximately -1 m yr^{-1} between 1984 and 2000, with the lower boundary remaining stable between 2000 and 2011. We note that the apparent upward ecotonal shift previously reported for slopes in the Green Mountains (Beckage *et al.*, 2008) could be an artifact of this seasonal effect, as they compared leaf-off to fall imagery in that analysis. We further tested our approach with an image pair from late summer 1991 and 2009 for the Green Mountains (Table S1) and found downward shifts in ecotone elevation that were similar to leaf-off image results (Figs S5, S6), indicating that detection of downward movement was robust across three seasons.

Effects of slope, aspect and latitude on ecotone elevation

Our extensive results allowed us to explore how ecotone elevation varies with latitude, slope, aspect and mountain range (Table S2). We found that the montane boreal forest extended lower on steeper slopes, by -1.1 and -2.0 $\text{m-percent-slope}^{-1}$ (upper and lower edges),

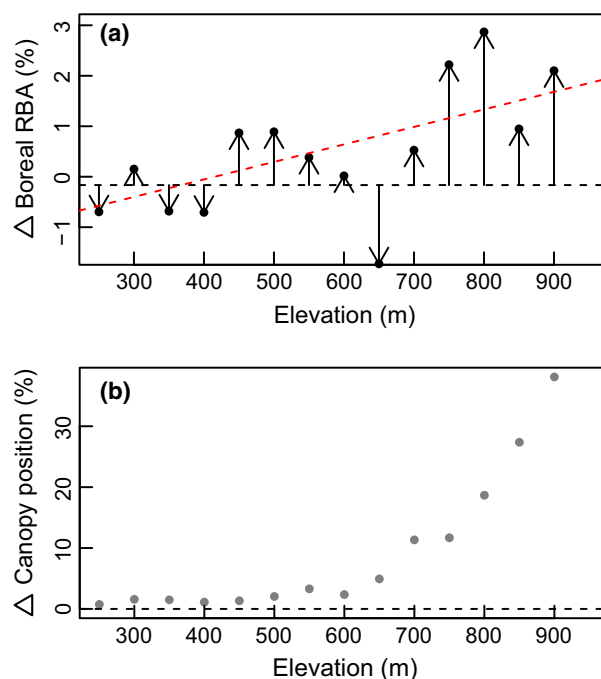


Fig. 5 Mean trends in boreal species abundance change across an elevational gradient derived from remeasured Hubbard Brook Experimental Forest inventory data (Schwarz *et al.*, 2003; van Doorn *et al.*, 2011; <http://www.hubbardbrook.org/>). Between 1995 and 2005, mean change in boreal RBA increased significantly with elevation (a) ($P = 0.013$, $R^2 = 0.34$), with the greatest change occurring within the modeled ecotones (Fig. 4). This corresponds to a proportionate decrease in RBA of northern hardwood species. The proportion of boreal trees that transitioned from sub- and intermediate canopy positions, to dominant and codominant positions, also increased nonlinearly in the ecotone range (b).

as has been observed elsewhere (Cogbill & White, 1991). With typical slopes between 20 and 40%, this effect causes fine-scale variation in ecotone elevation of $\sim \pm 22$ to 79 m. The lower ecotone boundary descends with latitude by -33.5 $\text{m} \cdot \text{degree}^{-1}$. We included year as a fixed effect, treating spring and fall ecotone estimates similarly. This cross-seasonal year effect averaged rates of -0.7 and -0.8 m yr^{-1} for upper and lower boundaries, confirming the downward direction of change. The intercept varied randomly for mountain range. Ecotones in the Green Mountains were 16.2 m (upper edge) and 35.1 m (lower edge) higher than they were in the Whites (Table S2). Aspect had a significant effect primarily on the upper ecotone, which occurred up to 13.3 m higher on northeastern slopes than on southwestern ones. This aspect pattern may be diminishing, however, as the upper ecotone has shifted downward faster on SW slopes than NE slopes in the Green Mountains (by -0.9 m yr^{-1}).

Discussion

Comparing results to previous reports

In addition to Hubbard Brook data, local results on individual slopes also agreed well with published ecotone descriptions, although the extent of published observations (~ 2–20 ha) was typically much smaller than Landsat sample areas (~ 45–126 ha). Models covering old-growth forest at Crawford Notch, NH, located the ecotone between 707 and 927 m in 1991, which agreed well with the ecotone description of 760–955 m from 1980 (Foster & Reiners, 1983). The ecotone was described falling between 800 and 900 m in the 1970s for 'The Bowl' on Whiteface Mountain, NH (Leak & Yamasaki, 2012), which corresponded to the modeled ecotone from 750 to 886 m in 1991. Transition from northern hardwoods to spruce–fir was described to center between 792 and 823 m (Siccama, 1974) in 1965 on western slopes of Camel's Hump and Mt. Abraham, VT. Ecotones modeled for these slopes in 1991 fell between 776 and 950 m (95% CI), and ecotone edges shifted downwards at rates of -2.2 and -1.2 m yr⁻¹ (Mt. Abraham) and -2.0 and -0.8 m yr⁻¹ (Camel's Hump) from 1991 to 2010, similar to means for the Green Mountains, but in contrast to reports of upward shifts on these slopes that were derived at much smaller scales (Beckage *et al.*, 2008).

Our multivariate mixed-effects models found that latitude and aspect affected ecotone elevation in ways that differed from previous studies. Our results showed ecotone elevation descending -33.5 m·°latitude⁻¹, while prior research (Cogbill & White, 1991) reported the ecotone descending -100 m·°latitude⁻¹. These results may differ because previous research was based on univariate models from a broader latitudinal range in the eastern USA (11°, compared to ~1° here). We found upper ecotones in the Green Mountains to be higher on northeastern slopes than on southwestern ones. Others report spruce and fir extending 100–200 m lower on northern slopes than on southern ones (Cogbill & White, 1991), presumably because northern aspects are characterized by colder conditions that favor boreal species, although Siccama (1974) mentions higher ecotones on eastern slopes. Higher ecotones in the Green Mountains, and on southwestern aspects, may reflect higher red spruce mortality rates reported for both these conditions in the decades prior to our analysis (Craig & Friedland, 1991).

Interpreting forest structure from shifts

The characteristics of the Landsat sensor can help us interpret these ecotone changes. The Landsat bands

used in the NDII index measure reflectance in the near-infrared (NIR) and shortwave IR (SWIR) ranges of the electromagnetic spectrum (bands 4 and 5). Light in these wavelengths produces strong signal to noise ratios and tends to scatter deep within forest canopies rather than just bouncing off the top layer of leaves. Each Landsat pixel measures light reflected from the volume of canopy leaves that fall within its field of view. This means that each pixel measures the foliage of several trees, particularly in dense northern forests composed of tightly packed spruce and fir crowns (~ 18–152 trees·pixel⁻¹ based on HBEF densities). When our modeled upper ecotone boundary shifts downward in elevation, it signifies that the density and abundance of conifer foliage have increased in the upper half of the transition zone (Figs 2, 4). We generally saw larger downslope movement for the upper ecotone boundary than for the lower boundary. We speculate that conifer foliage has changed most in subcanopy and understory layers reflecting downslope migration through understory recruitment and growth in this zone.

Equivalent ecotone changes in both spring and fall imagery show forest composition shifting through all layers of the forest canopy (Green Mountains). Yet when ecotones change less in fall imagery, the composition of overstory trees may be more stable (White Mountains). We generally saw more substantial changes in spring leaf-off conditions than in the fall. There may be two processes of change occurring simultaneously: recovery of boreal species to lower elevations in the subcanopy, while northern hardwood species in the overstory are increasing at higher elevations than in the past. Simultaneous but opposite shifts in the ecotone could help explain bidirectional movement by bird species in the White Mountains (1993–2010), where spruce–fir-dependent species have shifted downward, consistent with our results, yet northern hardwood-dependent species have also shifted higher (B. Deluca, D. King, personal communication).

Potential drivers of downward shift in montane forest ecotone

Our analysis demonstrates that the montane boreal-hardwood forest ecotone has shifted downward over the past 20–30 years, rather than upwards, as would be expected if regional climate change was driving species turnover. We turn our attention to other important drivers of recent forest dynamics in the northeastern USA to interpret this result, while also recognizing that species could be responding to climate change in unexpected ways (Lenoir *et al.*, 2010). We consider three processes of forest change: (a) recovery of red spruce from recent decline (Battles *et al.*, 2003), (b) weakening

of hardwood competitors currently under stress (Lenoir *et al.*, 2010) and (c) recovery from past land-use patterns in the region (Gehrig-Fasel *et al.*, 2007).

In 1982, Siccama *et al.* (1982) reported that red spruce had declined by 50% (basal area) between 1964 and 1979. This marked the start of two decades of research devoted to quantifying and interpreting the decline of red spruce in northeastern mountain ranges (Battles *et al.*, 2003), as well as the start of our time series in 1984. A prevailing explanation for these declines revolved around the impacts of decades of atmospheric deposition on soil calcium availability and corresponding effects on membrane function and prevalence of winter injury in red spruce (Johnson *et al.*, 1988; Hawley *et al.*, 2006). Now, several populations of red spruce across northern New England appear to be growing at unexpectedly high levels, possibly indicating lower incidences of winter injury due to improving air quality and warmer winter temperatures (van Doorn *et al.*, 2011; Kosiba *et al.*, 2013). Although we did not look at patterns of winter injury at these broad spatial scales, it is possible the downward shift in boreal species reflects a favorable response of red spruce to decreased levels of atmospheric deposition. There is also some evidence that balsam fir may have increased growth and recruitment in response to growing space released by declining red spruce (Battles *et al.*, 2003; Beckage *et al.*, 2008; van Doorn *et al.*, 2011), although it is unclear whether fir will persist at the lower elevations historically occupied by spruce (Boyce *et al.*, 2013). The fact that upper ecotones are shifting downward fastest on western slopes in the Green Mountains, where decline mortality was highest (Craig & Friedland, 1991), is consistent with boreal species reclaiming former dominance in this zone.

While multiple lines of evidence support the conclusion that red spruce has been recovering since the 1990s (Battles *et al.*, 2003), would-be competitors among northern hardwood species have been experiencing concurrent stress dynamics. Sugar maple (*A. saccharum*) is a shade-tolerant species that is expected to migrate upslope under warming temperatures (Beckage *et al.*, 2008; Leak & Yamasaki, 2012), yet it has its own vulnerabilities, responding poorly to stress from insect defoliation, soil freezing associated with diminished snow packs, seedling predation at high elevation (Brown & Vellend, 2014) and cation depletion in soils (Hallet *et al.*, 2006). Dynamics of another competitor, American beech (*Fagus grandifolia*), continue to change unpredictably in response to beech bark disease (Beckage *et al.*, 2008; Vadenboncoeur *et al.*, 2011). Abundance of the deciduous component of the montane forest may also be declining in ecotone elevations; paper birch mortality exceeded recruitment in HBEF between 1995 and 2005, reflecting this species' shorter longevity and

limited regeneration under canopy shade (van Doorn *et al.*, 2011). The multiple stresses affecting hardwood competitors in the transition zone suggest that the location and composition of the ecotone could remain unstable for some time.

The final potential driver of the unexpected downslope migration of boreal species is a land-use recovery dynamic reflecting a legacy of selective harvesting of red spruce from the boreal-hardwood ecotone. In particular, red spruce was aggressively harvested from mixed hardwood spruce and spruce–fir communities to satisfy high commercial demand during the mid-19th to early 20th century (Oosting & Billings, 1951; Kelty & D'Amato, 2006). This land use may have effectively truncated the realized breadth of the ecotone, particularly the lower elevation bounds, and generated a false impression of a climatically controlled elevational limit in studies from periods shortly following this era. The downslope migration observed in the present study in many cases may reflect reoccupation of the historically realized climatic niche for red spruce prior to this land-use period (Gehrig-Fasel *et al.*, 2007; Lenoir *et al.*, 2010; Vadenboncoeur *et al.*, 2011). This is consistent with other findings that forest succession following human land use is a primary process driving forest dynamics in New England (Solomon & Leak, 1994; Nowacki & Abrams, 2014).

Detecting downward shifts in subalpine tree species is not unique (Lenoir *et al.*, 2008; Crimmins *et al.*, 2011), yet it was unexpected in this case, given prior reports and the ecophysiology of boreal tree species in the northeastern USA. What is unique in our approach is its ability to capture spatially explicit changes in species abundance, rather than occurrence, thereby avoiding many of the pitfalls encountered when trying to quantify long-term change from presence/absence data in historical datasets (Crimmins *et al.*, 2011; Wolf & Anderegg, 2011). Our approach also reveals whether changes observed at smaller scales are actually representative of a larger region. Our modeling approach could be adapted to measure ecotonal shifts in many montane ecosystems, including questions addressing tree line, as long as differences in the ecotone correlate to differences in Landsat reflectance. Understanding both the magnitude and spatial pattern of ecotonal change brings us closer to a mechanistic understanding of the drivers of elevational range shifts, which will ultimately improve our ability to weight attribution of species movement to climate change or other causes.

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Data accessibility

Extracted Landsat and topographic data, subset boundaries and related results and code: Dryad doi: <http://dx.doi.org/10.5061/dryad.104jj>

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Supporting Information

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

Appendix S1. Materials and methods, additional details on models, calibration and validation.

Figure S1. Location of the study area and illustration of sample subsets based on aspect.

Figure S2. Example of model fits and derivation of inflection points to locate montane ecotone edges in both fall and spring imagery.

Figure S3. Example of spatial dependence in residual errors for logistic models.

Figure S4. Comparison with Hubbard Brook Experimental Forest valley tree inventory plots.

Figure S5. Example of ecotones models using summer, leaf-on imagery 1991–2009.

Figure S6. Violin plots of ecotone distribution estimated from summer growing-season imagery for the Green Mountains, VT.

Table S1. Characteristics of Landsat images used for ecotone mapping and change analysis.