Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures

Nicholas A. Fisichelli, Lee E. Frelich and Peter B. Reich

N. A. Fisichelli (nfisichelli@gmail.com), L. E. Frelich and P. B. Reich, Dept of Forest Resources, Univ. of Minnesota, 1530 Cleveland Avenue North, St Paul, MN 55108, USA. NAF also at: Climate Change Response Program, National Park Service, 1201 Oakridge Drive, Fort Collins, CO 80525, USA. PBR also at: Hawksbury Inst. for the Environment, Univ. of Western Sydney, Penrith, NSW 2753, Australia.

Temperate and boreal forests are forecast to change in composition and shift spatially in response to climate change. Local-scale expansions and contractions are most likely observable near species range limits, and as trees are long-lived, initial shifts are likely to be detected in the understory regeneration layers. We examined understory relative abundance patterns of naturally regenerated temperate and boreal tree species in two size classes, seedlings and saplings, and across two spatial scales, local stand-scale ecotones (tens of meters) and the regional temperate–boreal transition zone (~250 km) in central North America, to explore indications of climate-mediated shifts in regeneration performance. We also tested for the presence of strong environmental gradients across local ecotones that might inhibit species expansion. Results showed that tree regeneration patterns across ecotones varied by species and size class, and varied across the regional summer temperature gradient. Temperate tree species regeneration has established across local ecotones into boreal forest patches and this process was facilitated by warmer temperatures. Conversely, boreal conifer regeneration exhibited negative responses to the regional temperature gradient and only displayed high abundance at the boreal end of local ecotones at cool northern sites. The filtering effects of temperature also increased with individual size for both boreal and temperate understory stems. Observed regeneration patterns and the minor environmental gradients measured across local ecotones failed to support the idea that there were strong barriers to potential temperate tree expansion into boreal forest patches. Detectable responses, consistently in the directions predicted for both temperate and boreal species, indicate that summer temperature is likely an important driver of natural tree regeneration in forests across the temperate–boreal transition zone. Regeneration patterns point toward temperate expansion and reduced but continued boreal presence in the near-future, resulting in local and regional expansions of mixed temperate-boreal forests.

Understanding and detecting compositional and spatial shifts in ecological communities has become a pressing task given recent and predicted rates of anthropogenic climate change. Numerous studies have detected species-level responses, especially for mobile species with short generation times such as insects and birds (Walther et al. 2002, Parmesan and Yohe 2003). Tree species have much longer generation times and thus evidence of present-day tree-range shifts are only beginning to appear (Beckage et al. 2008, Lenoir et al. 2009, Woodall et al. 2009, Feeley et al. 2011). Species composition of the tree regeneration layer in temperate-boreal forests in central North America can be partially explained by climate, although numerous other variables such as effects of neighboring plants on microenvironmental factors have similar or greater explanatory power (Fisichelli et al. 2013), and it remains unclear whether species are already exhibiting signs of range expansions or contractions. Furthermore, sharp environmental gradients at range boundaries, such as variation in understory light availability, seedbed type, and extant competing vegetation may inhibit temperate species from rapidly expanding as the climate becomes more

suitable to them. Several modeling efforts predict considerable climate-driven forest shifts by the end of the 21st century (Iverson and Prasad 1998, Scheller and Mladenoff 2005), and field-based research aimed at early detection of species level responses is needed to assess the direction of forest change and the ability of species to shift their ranges.

Vegetation boundaries have been proposed as one of the most likely places to detect early signs of climate-mediated community shifts (di Castri et al. 1988, Parmesan et al. 2005). Indeed, there is a growing body of evidence for shifts in tree species distributions along altitudinal range margins (Beckage et al. 2008, Feeley et al. 2011, Jump et al. 2012); however, evidence for latitudinal changes is sparser (Jump et al. 2009). Additionally, documentation of tree expansion at leading edge range limits is far more common than that of contraction at trailing edges (Jump et al. 2009). Seedling establishment beyond the range limit of adult trees can occur relatively rapidly, whereas detectable range shifts of trailing edge populations likely will be slower to develop, due to the longevity of overstory trees (Peñuelas et al. 2007, Crawford 2008). Given the paucity of long-term data to

detect latitudinal shifts in overstory composition, comprehensive studies of understory performance are needed to reveal initial tree species responses and likely range shifts due to a changing climate.

Within the upper Great Lakes region in North America, temperate and boreal tree species reach their northern and southern range limits, respectively, and can be found growing together over a relatively narrow temperature gradient (Goldblum and Rigg 2010). The transition zone is a mosaic of temperate and boreal dominated stands with local ecotones separating these overstory types (Fig. 1). Because tree seedling establishment and growth into the sapling layer are vital first steps towards capturing future canopy space (Pacala et al. 1996), tree regeneration trends across local ecotones, compared across the regional transition zone, may provide initial indications of spatial shifts in forest composition. Additionally, the filtering effects of and sensitivities to temperature may increase with individual size, though many previous attempts to examine regeneration performance have only utilized a single understory size class (Kharuk et al. 2007, Lenoir et al. 2009, Woodall et al. 2009). This research examines regeneration responses using two size classes, seedlings (≤ 1 m height) and saplings (> 1 m height and < 10 cm diameter), for ten co-occurring temperate and boreal tree species.

Within a forest stand, composition is driven in part by local resources and conditions (Maycock and Curtis 1960). Local ecotonal boundaries may reflect shifts in environmental variables including soil properties, seedbed conditions, and the composition and cover of competing vegetation layers that may inhibit the establishment and growth of particular tree species (di Castri et al. 1988). For example, Demers et al. (1998) found a strong shift in soil substrate type at the elevational limit of sugar maple *Acer saccharum* with unfavorable substrates dominating at higher elevations. Thus, advance regeneration establishment of temperate species across ecotones in response to climate may be inhibited by these local environmental factors, such as soil development, which itself will strongly lag behind climate shifts (Pennington 1986).

The goal of the present study was assess whether climate-mediated shifts in temperate and boreal species regeneration performance could be detected. To do this, we investigated tree regeneration relative abundance patterns of major temperate and boreal tree species across a number of local ecotones, located across the broader regional temperature gradient. We tested whether local expansion or contraction patterns were detectable, mediated by the regional temperature gradient, and in line with predictions for species near their northern and southern range limits. Warming across the Great Lakes region over the past half century has been above the global mean (Christensen et al. 2007) and may be facilitating forest change. If temperate expansion and boreal contraction are indeed occurring, initial signs should be evident in the regeneration layer. Specifically, we expect to find temperate tree regeneration established across local stand-scale ecotones into boreal forest patches and this expansion should be greater at warmer sites along the regional temperature gradient. Conversely, boreal tree regeneration will be confined to the boreal end of local ecotones and overall performance will be poorest at the warm southern end of the transition zone. Additionally, we sampled environmental variables across local ecotones to assess whether conditions shift dramatically at the fine scale with overstory composition and thus may be barriers to local tree range expansions.

Material and methods

Study sites

The locations of the 125 ecotone study sites, including a total of 456 plots, span 3 degrees of latitude and 7 degrees of longitude and are spread across a 170 000 km² area of northern Minnesota, Wisconsin and the western end of Michigan's Upper Peninsula, USA (Fig. 1). Climate data for each study site were extracted from PRISM 4 km² resolution climate surfaces (Daly et al. 2008). Annual precipitation (655–986 mm) generally increases from west to east and mean annual temperature (2.5–5.6°C) from north to south (1978–2007 averages). Mean summer temperature (June–August, 15.8–19.4°C) has a more complex pattern with increasing temperatures from north to south in Wisconsin and Michigan and increasing temperatures from northeast to southwest in Minnesota.
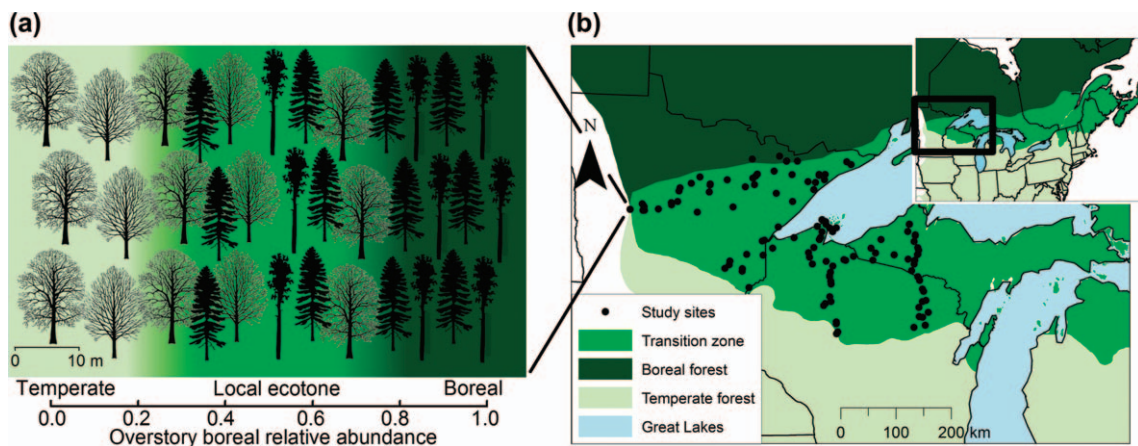

Figure 1. Temperate to boreal transitions across (a) local ecotones and (b) the regional transition zone. Local ecotones, on the scale of tens of meters, were defined by a gradient in overstory composition, while the regional transition zone was defined by the overlapping range limits of temperate and boreal species, as mapped by Little (1971).

Table 1. Common tree species presence by size class in ecotonal temperate-boreal forests of the upper Great Lakes region, USA. Trees are ≥ 10 cm dbh (diameter at 1.3 m above ground level), saplings are ≥ 1 m in height and < 10 cm dbh, and seedlings are > 1 yr old (not germinants) and < 1 m in height. Data are based on 456 plots at 125 sites.

Species	Biome	Leaf-type	Plot frequency by size class (percentage)		
			Tree	Sapling	Seedling
Betula papyrifera	Boreal	Broadleaf	232 (51%)	58 (13%)	33 (7%)
Populus tremuloides	Boreal	Broadleaf	213 (47%)	100 (22%)	188 (41%)
Abies balsamea	Boreal	Conifer	341 (75%)	301 (66%)	328 (72%)
Picea glauca	Boreal	Conifer	220 (48%)	85 (19%)	50 (11%)
Acer rubrum	Temperate	Broadleaf	329 (72%)	162 (36%)	356 (78%)
Acer saccharum	Temperate	Broadleaf	264 (58%)	219 (48%)	298 (65%)
Fraxinus nigra	Temperate	Broadleaf	45 (10%)	55 (12%)	118 (26%)
Ostrya virginiana	Temperate	Broadleaf	43 (9%)	93 (20%)	85 (19%)
Prunus serotina	Temperate	Broadleaf	32 (7%)	44 (10%)	100 (22%)
Quercus rubra	Temperate	Broadleaf	60 (13%)	37 (8%)	110 (24%)

Each study site contained a gradient in overstory composition (ecotone) from temperate to boreal dominated (Fig. 1a). Potential study sites, based on overstory composition, were identified on state and federal GIS vegetation layers and final selection was made during field visits. Dominant overstory species in these dry-mesic to wet-mesic forests included two boreal broadleaf species, *Populus tremuloides* and *Betula papyrifera*, two boreal conifers, *Picea glauca* and *Abies balsamea*, and two temperate broadleaf species, *Acer saccharum* and *Acer rubrum* (Table 1). Selected sites were free from signs of recent human disturbance, especially logging, that might have a biased effect on the composition and density of tree species in the overstory and understory layers. Study sites were typical of stands across the region, generally of second-growth origin from harvesting activities 70–100 yr ago (Friedman and Reich 2005) and now at the understory reinitiation stage (Oliver 1981). Site-level soil pH ranged from 3.14 to 5.48 and soil texture varied from clay loam to loamy sand across the study region.

Sites were sampled during the growing season (June–August) 2008–2010. An average of four plots per site, placed at 50 m intervals, were established across each ecotone to capture the entire available gradient in overstory composition from temperate to boreal dominated. Plots were located a minimum of 30 m from forest edges (e.g. wetland and road boundaries). The number of plots per site varied between two and seven based on the presence of boreal and temperate overstory tree species and the extent of local variation in overstory composition and thus width of the ecotone. Ideally, each site had a boreal dominated, temperate

dominated and mixed composition plot, though the spatial distance across ecotones and magnitude of change in overstory composition dictated the number of plots. Overstory, sapling, and seedling data were collected within nested circular plots. Tree species density and basal area within the overstory neighborhood were determined from all live stems ≥ 10 cm diameter 1.3 m above ground level (dbh) within the entire 10 m radius plot. Sapling stems, > 1 m in height and < 10 cm dbh, were identified to species and tallied in a 5 m radius subplot centered within the 10 m radius tree plot. We sampled seedlings, > 1 yr old (not germinants) and ≤ 1 m in height, in four 1 m radius plots located within the 5 m radius sapling subplot.

Data on 9 environmental variables were collected within each plot (Table 2). Understory light availability, measured as canopy openness, was quantified with a concave spherical densiometer. Four readings, one per cardinal direction, were taken at plot center at 1 m above ground level. Plot slope position was determined based on a four-point scale from 0–1, with 0 for lower terrace/toe slopes, 0.33 for foot slopes, 0.67 for mid to upper slope positions, and 1.0 for shoulder/summit positions. Soil/seedbed conditions included four variables, mineral soil pH, mineral soil sand fraction, fresh leaf litter thickness (Oi layer), and duff or decomposing organic layer thickness (Oe and Oa layers). We measured litter and organic layers within the seedling plots and collected samples of the upper 20 cm of mineral soil for pH and soil texture analysis. In the laboratory, mineral soil samples were sieved to remove roots and the gravel fraction (> 2 mm diameter). We measured soil pH using a 2:1 deionized

Table 2. Summary data for environmental variables in temperate-boreal forests. Values are based on untransformed variables from all plots (n = 456). For analyses, variables were transformed to conform to parametric test assumptions. Plot slope position ranged from 0 for lower terrace/toe slopes to 1.0 for shoulder/summit positions. See 'Methods' for full definitions of the environmental variables.

Transformation	Variable	Units	Mean	SD	Min	Max
ln(x)	Canopy openness	Percent	15.3	6.6	5.2	44.98
	Slope position	Scale 0–1	0.45	0.34	0	1
	Soil pH		4.60	0.47	3.14	6.48
x^2	Soil sand fraction	Percent	67.7	16.6	18	91.4
sqrt(x)	Litter thickness (Oi)	cm	1.5	0.6	0.3	4.0
ln(x)	Organic layer (Oe + Oa)	cm	1.4	1.9	0	10
sqrt(x)	Ground vegetation cover	Percent	36.2	26.9	0.5	100
ln(x)	Shrub density (seedling)	stems m^{-2}	1.1	1.3	0	8.8
ln(x)	Shrub density (sapling)	stems m^{-2}	0.2	0.4	0	2.4

water:soil suspension and mineral soil sand fraction with the hydrometer method.

The abundance of competing understory vegetation was assessed for three functional groups, ground vegetation, shrubs ≤ 1 m in height, and shrubs > 1 m in height. We measured the percent cover of ground vegetation, including herbaceous species and prostrate shrubs, within four quadrants of each seedling plot using a modified Braun-Blanquet (1964) cover class system with 12 classes (0, < 1, 1–5, 6–10, 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80, 81–90, 91–100%). Cover was converted to a continuous variable by taking the midpoint of each cover class and averaging the four quadrants per plot. Tall shrub stems (defined as woody species typically reaching the sapling layer but not tree layer, such as *Corylus cornuta*, *Acer spicatum*, and *Amelanchier* spp.) were counted in the seedling and sapling size classes within the seedling and sapling subplots.

Statistical analyses

Hypotheses were tested using several parametric tests. In order to analyze environmental gradients and regeneration abundance shifts across local ecotones, we quantified plot ecotonal position by overstory composition. Specifically, boreal overstory relative abundance (boreal RA) was utilized as a continuous explanatory variable reflecting the gradient in overstory composition across local ecotones (Fig. 1a). For example, plots with only temperate species in the overstory received a boreal RA = 0, plots with equal overstory abundance of temperate and boreal species received a boreal RA = 0.5, and plots with only boreal species in the overstory had a boreal overstory RA = 1. For overstory relative abundance we used the importance value, calculated as the average of relative stem density and relative basal area, as it moderates the differences between abundant small diameter trees that dominate the relative density metric and individual large diameter trees that dominate plot basal area. We designated each tree species as 'temperate' or 'boreal' based on northern and southern range limits mapped by Little (1971).

We assessed shifts in environmental variables across ecotones using a linear mixed-effects model with site as a random effect. Slope position and the midpoints of plant cover classes were treated as continuous variables. Environmental variables were transformed as necessary to improve linear relationships and conform to parametric test assumptions (Table 2).

The 10 tree species included in analyses were each present in the understory, on average, in at least ≈10% of plots and in as much as ≈70% (Table 1). This minimum sample size was necessary to ensure a sufficient number of stems distributed across local and regional scales for analyses. For each species, analyses only included plots where the species was present in at least one size class (overstory or understory). The response variables, species' seedling and sapling relative density within a plot (ranging from 0 to 1), were arcsine square root transformed to stabilize the variance (Sokal and Rohlf 1995).

To examine tree regeneration relative abundance patterns across local and regional scales, we assessed the roles of four explanatory variables (Supplementary material Appendix 1, Table A2), conspecific overstory relative abundance, size class, overstory boreal relative abundance (boreal RA), and summer temperature (June–August 1988–2007 average, Daly et al. 2008), as well as two two-way interactions, size class by temperature and boreal RA by temperature. Plot-level conspecific overstory relative abundance was included as a covariate in analyses in order to capture varying propagule pressure across local ecotones due to shifts in overstory abundance. Current overstory composition was the strongest predictor of understory composition in mixed temperate-boreal stands (Fisichelli et al. 2013), and within similar closed canopy forests, seed and seedling densities were generally greatest within 10–15 m of the adult tree (Ribbens et al. 1994). Accounting for differences in conspecific overstory abundance and thus propagule availability permits more accurate comparisons of understory performance across plots and sites. Boreal RA, reflecting the gradient in overstory composition within a site, was included to test for differences in understory relative abundance across ecotones, after taking into account overstory abundance.

Site-level temperature was included to assess shifts in performance across the regional temperate–boreal transition zone. Within site climate data, at the spatial resolution of 10 s of meters, were not available and thus shifts in performance across the regional temperature gradient, as quantified by site-level temperature, were examined. Summer temperature was selected as it closely correlates with the location of temperate–boreal ecotones along elevational gradients (Cogbill and White 1991) and showed the strongest multivariate relationship with regeneration compositional variation across the region (Fisichelli et al 2013). Because the climate data are only available as monthly means, potential climate variables were highly correlated (e.g. growing degree days and summer temperature, r = 0.95). A 20 yr average was selected as this reflects the median age of understory stems of the most common species (data not shown). Other climate windows (e.g. 10 or 30 yr means) were strongly correlated with the 20 yr average and as temperatures are being compared across sites and thus across a roughly 3.5°C temperature gradient, results from analyses using these other intervals of time were very similar. Summer temperature interactions were included in analyses in order to test whether local scale regeneration trends and size class abundance patterns varied across the regional transition zone due to the temperature gradient.

Tree regeneration relative abundance shifts across ecotones were examined with linear mixed-effects models, using site and plot nested within site as random effects to account for the hierarchical sampling structure. For each species, we fit models of varying complexity from a simple model only including the covariate conspecific overstory relative abundance as a predictor to a model with all four main effects and two interactions. Thus, for each species, the response variable was tree regeneration relative abundance and the potential explanatory variables were conspecific overstory relative abundance, size class (seedling/sapling), boreal RA (gradient in overstory composition across local ecotones), summer temperature, size × temperature interaction, and boreal RA × temperature interaction. Model parameters were fit using maximum likelihood estimation which finds the set of parameter values that make the observed data most likely to have occurred. We evaluated the 14 potential models for

each species through comparisons of small sample corrected Akaike information criteria (AIC$_c$), which assesses model performance based on goodness-of-fit and a penalty for the number of model parameters (Burnham and Anderson 2002). Variance inflation factors (VIFs) for variables in final models were < 2 indicating a lack of multi-collinearity (Zuur et al. 2009). For each species, we present results from the model with lowest AIC$_c$. Parameter estimates of top models were assessed via t-values and prediction intervals calculated through model fitting. All analyses were carried out using the 'nlme' package (ver. 3.1) (Pinheiro et al. 2009) in R (ver. 2.12) (R Development Core Team).

Results

Environmental variation across local ecotones

Although linear mixed-effects analyses found significant gradients (p < 0.05) in five out of nine environmental variables across local ecotones, these changes were generally minor (Fig. 2, Supplementary material Appendix 1, Table A1). Across local ecotones from temperate to boreal dominated overstories, canopy openness increased on average by 4.2% (absolute increase; t = 4.96, p < 0.0001) and slope position decreased slightly, by 0.1 units (t = –2.90, p = 0.004). Mineral soil pH and percent sand did not exhibit detectable changes across local ecotones (t = –0.41, p = 0.68; t = –0.46, p = 0.65, respectively). Litter layer thickness decreased by 0.4 cm (t = –4.27, p < 0.0001) across ecotones from temperate to boreal overstories, while the organic layer did not show a significant trend (t = 1.59, p = 0.11). Ground vegetation cover increased by 11% (absolute increase; t = 2.99, p = 0.003) and shrub density in the seedling layer increased by 0.4 stems/m² across ecotones (t = 2.05,
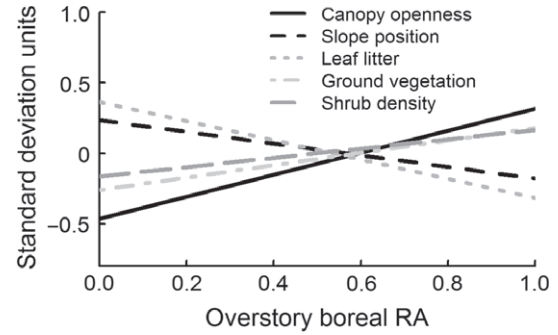

Figure 2. Environmental variables showing significant (p < 0.05) shifts across local temperate–boreal ecotones (based on linear mixed-effects models with 'Site' as the random effect, see Supplementary material Appendix 1, Table A1 for model summaries). The fixed effect (predictor) was overstory boreal relative abundance, varying from 0–1 and reflecting the gradient in overstory composition across local ecotones. For plotting, transformed response variables were standardized (standard deviation units). Shrub density refers to stems in the seedling size class (< 1 m in height). See Table 2 for transformations and 'Material and methods' for further explanation of variables.

p = 0.04), while tall shrubs in the sapling size class did not exhibit a detectable trend (t = 0.81, p = 0.42).

Species relative abundance trends

Tree regeneration relative abundance models indicated shifts in performance across local ecotones and responses to temperature for several species (Table 3). Temperature or temperature interactions were included in top models for 6 out of 10 species. Regeneration relative abundance shifts across local ecotones, after controlling for conspecific

Table 3. Fixed effect parameter estimates (standard errors) for top performing linear models of species' understory relative stem density, with 'Plot' nested in 'Site' as the random effect. RA is relative abundance calculated as the average of relative density and relative basal area. Overstory boreal RA reflects plot location across local ecotones as defined by overstory composition. See Table 1 for size classes. Parameter estimates for the sapling size class are the differences from the seedling size class (Intercept). r² is the squared correlation coefficient between fitted and actual values.

Species	Intercept	Conspecific tree RA	Size class (sapling)	Overstory boreal RA	Temperature	Size × temp	Boreal RA × temp	r²
Betula papyrifera								
	0.054 (0.007)	0.031 (0.028)	0.024 (0.009)					0.54
Populus tremuloides								
	0.164 (0.012)							
Abies balsamea								
	0.237 (0.017)	0.073 (0.051)	0.181 (0.016)	0.102 (0.043)	−0.056 (0.026)	−0.052 (0.025)	−0.150 (0.059)	0.49
Picea glauca								
	0.081 (0.009)	−0.108 (0.031)	0.047 (0.010)		−0.022 (0.011)			0.44
Acer rubrum								
	0.151 (0.015)	0.167 (0.046)	−0.208 (0.014)	0.230 (0.037)				0.60
Acer saccharum								
	0.395 (0.020)	0.194 (0.056)	−0.084 (0.017)	−0.183 (0.052)	0.000 (0.030)		0.195 (0.060)	0.55
Fraxinus nigra								
	0.291 (0.024)	0.268 (0.114)	−0.063 (0.027)	0.210 (0.073)	0.032 (0.039)	0.114 (0.047)		0.76
Ostrya virginiana								
	0.296 (0.018)	0.029 (0.104)	0.142 (0.021)		0.088 (0.034)	0.095 (0.040)		0.63
Prunus serotina								
	0.227 (0.023)	−0.281 (0.093)	0.050 (0.027)	−0.010 (0.053)	0.012 (0.048)	0.093 (0.056)	0.269 (0.119)	0.45
Quercus rubra								
	0.128 (0.011)	−0.127 (0.039)	−0.035 (0.014)					0.64

overstory abundance, were found for 5 out of 10 species. Abundance differences by size class were supported for 9 out of 10 species. Complexity of top performing models varied from no support for any explanatory variables (*Populus tremuloides*) to the inclusion of all four main effects and two interactions (*Abies balsamea*, *Prunus serotina*).

Tree regeneration relative abundance responses to temperature followed biome designations (temperate or boreal) for each of the six temperature sensitive species (Fig. 3, 4).
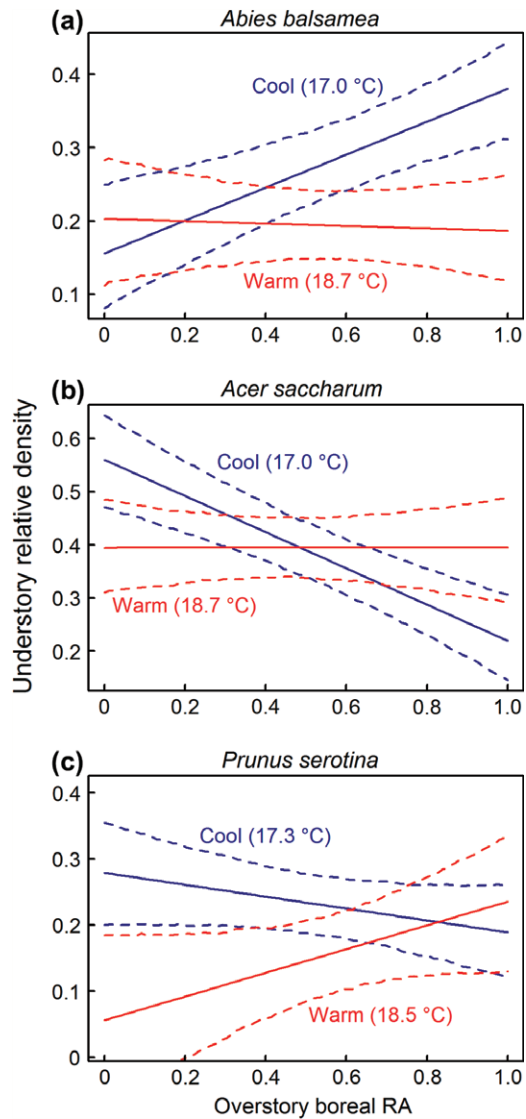
Figure 3. Tree regeneration relative abundance trends across local ecotones varied with summer temperature for the boreal conifer (a) *Abies balsamea* and two temperate broadleaf species, (b) *Acer saccharum* and (c) *Prunus serotina*. Figure panels show the modeled understory relative abundance response from linear mixed-effects models (Table 3), dashed lines represent approximate 95% prediction intervals. The x-axis, overstory boreal relative abundance (RA), reflects the gradient in overstory composition across local ecotones from temperate to boreal forest. To display the interaction between the regional temperature gradient and location across local ecotones, the modeled responses for the 10th percentile (cool, northern sites) and 90th percentile (warm, southern sites) temperature values for each species are shown. Dashed lines represent approximate 95% prediction intervals. Seedlings and saplings were considered jointly.
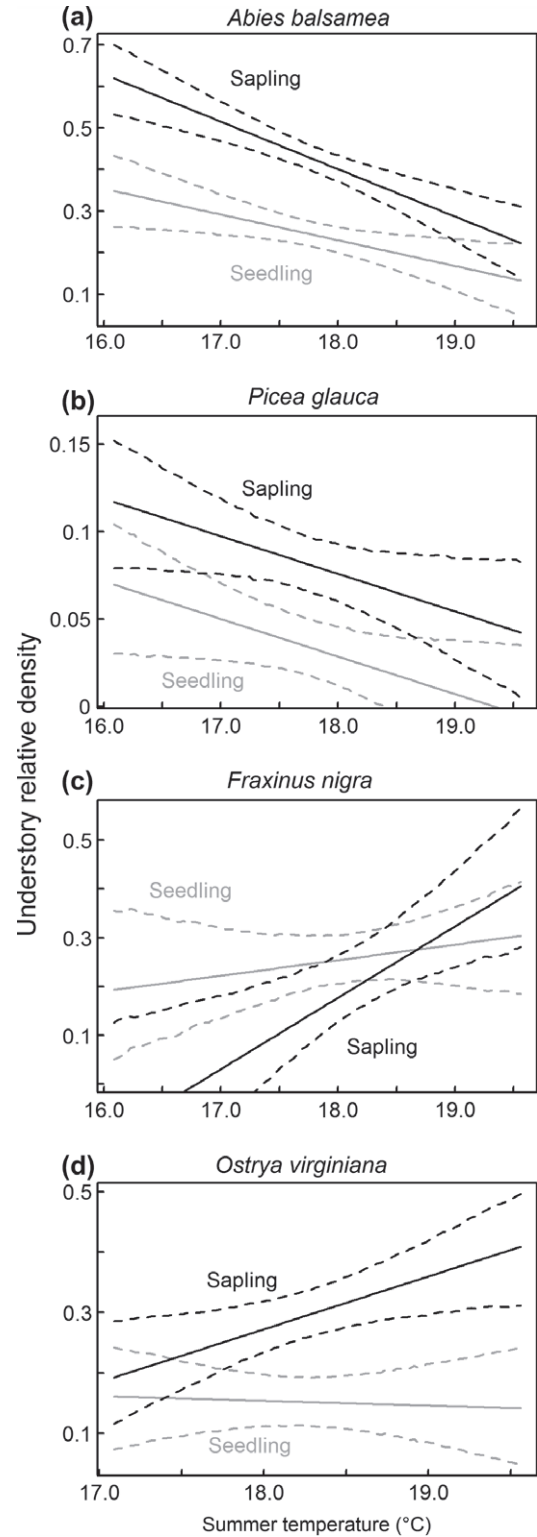

Figure 4. Tree regeneration relative abundance trends varied with size class and summer temperature across the temperate–boreal transition zone. The boreal conifer (a) *Abies balsamea* and two temperate broadleaf species, (c) *Fraxinus nigra* and (d) *Ostrya virginiana*, showed an interaction between size class and temperature, while the two main effects were additive for the other boreal conifer, (b) *Picea glauca*. Seedlings were < 1 m in height and saplings were ≥ 1 m in height and < 10 cm diameter. The modeled understory relative abundance responses are from linear mixed-effects models (Table 3), and dashed lines represent approximate 95% prediction intervals.

Temperature interactions for boreal *A. balsamea* showed that across local ecotones from temperate to boreal overstories, relative abundance of regeneration (seedlings and saplings considered jointly) was consistently low at warm sites close to its southern range margin, but *A. balsamea* regeneration density was much greater beneath boreal than temperate overstories at cool sites nearer the northern end of our study region (Fig. 3a). *Abies balsamea* abundances also exhibited a strong negative response to the regional temperature gradient, with the response of saplings steeper than seedlings (Fig. 4a). Regeneration of the other boreal conifer in the study, *Picea glauca*, showed a similar though weaker negative response to temperature, with size class as an additive effect (Fig. 4b). The only strong trend from the two boreal broadleaf species, *P. tremuloides* and *Betula papyrifera*, was a difference in understory relative abundance by size class for latter (Table 3).

For the six temperate species, inclusion of boreal RA or temperature as explanatory variables of regeneration abundance were each supported in 4 out of 6 top regeneration models and two temperate species displayed boreal RA by temperature interactions (Table 3). At cool sites, *Acer saccharum* dominated temperate patches but decreased in relative abundance with increasing overstory boreal RA, while at warm sites *A. saccharum* regeneration did not vary by location across the ecotone (Fig. 3b). With increasing boreal overstory dominance across local ecotones, relative abundance of *Prunus serotina* regeneration shifted from a decreasing trend at cool sites to an increasing trend at warm sites (Fig. 3c).

Model comparisons of tree regeneration relative abundance also indicated support for size class by temperature interactions for three temperate species (Table 3). *Fraxinus nigra* (Fig. 4c), *Ostrya virginiana* (Fig. 4d), and *P. serotina* showed more positive relative abundance increases with temperature in the sapling than seedling classes. Understory relative abundances of two temperate species, *Acer rubrum* and *F. nigra*, increased with increasing overstory boreal RA (Fig. 5) and *A. rubrum* displayed the largest differences in relative abundance by size class for any species. Mid shade-tolerant *Quercus rubra* was the only temperate species for which no support was found for understory relative abundance responses to either boreal RA or temperature.

Discussion

Establishment and persistence of seedlings and saplings are early, yet crucial steps in forest development and successional change. By specifically sampling multiple local ecotones across the temperature gradient where major temperate and boreal tree species are found growing together, we were able to detect local shifts in understory relative density by species, size class, and summer temperature interactions. Temperate tree species regeneration has established across local ecotones (tens of meters) into boreal forest and this process was facilitated by warmer temperatures. Conversely, boreal conifer regeneration exhibited negative overall responses to temperature and only maintained high abundance in cool northern sites at the boreal end of local ecotones. Size class trends also indicated increasing temperature sensitivity from the
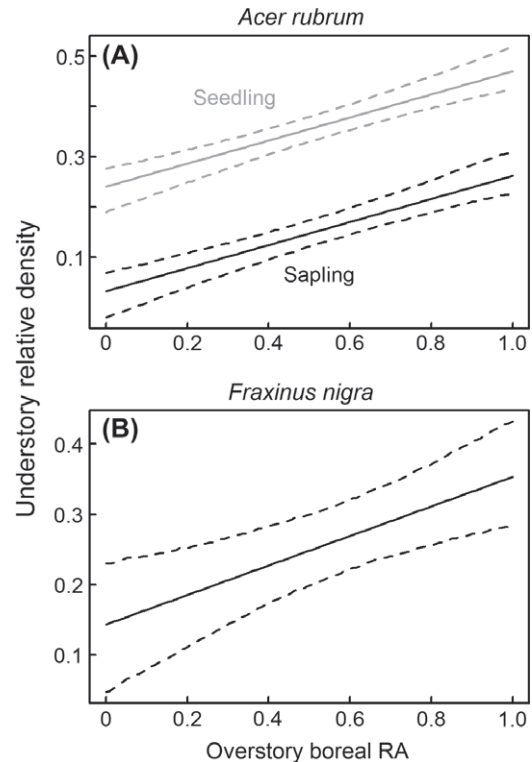

Figure 5. Tree regeneration relative abundance increased from the temperate to boreal end of local ecotones (increasing overstory boreal relative abundance) for two temperate broadleaf species, (a) *Acer rubrum* and (b) *Fraxinus nigra* (seedlings and saplings considered jointly). *Acer rubrum* also showed the greatest difference in relative abundance by size class (additive effect) of any species analyzed. Seedlings were < 1 m in height and saplings were ≥ 1 m in height and < 10 cm diameter. Figure panels show the modeled understory relative abundance response from linear mixed-effects models (Table 3), dashed lines represent approximate 95% prediction intervals.

seedling to sapling size class for both boreal and temperate species. Gradients in environmental conditions across ecotones in this study were generally minor and do not appear likely to strongly inhibit expanding tree species. Temperate-boreal forests are forecast to have dramatic compositional shifts by the end of the current century and this research provides an early indication of likely changes across both local ecotonal boundaries and the regional transition zone.

Regeneration trends found are generally in agreement with predicted climate-mediated changes, including short-term widening of ecotones as temperate species establish in boreal patches, and likely future contraction of the southern boreal range limit as conspecific regeneration fails to replace the current boreal overstory (Jump et al. 2009). The difference in mean summer temperature, 3.5°C, between the cold and warm ends of the temperate–boreal transition zone are at the moderate end of projected warming by century's end (Wuebbles and Hayhoe 2004, Christensen et al. 2007). Under these projections, conditions and associated species level performance observed today at the warm end of the transition zone, including temperate expansion and boreal regeneration failure, could shift 300+ km north to locations

even beyond the current northern limit of ecotonal stands. Reduced densities of boreal species found in the regeneration layer at trailing edges will eventually lead to fewer individuals of a species reaching the canopy layer, although a distinct range contraction will not be detectable until long-lived overstory trees die (Peñuelas et al. 2007, Jump et al. 2009).

Relative abundance patterns across any individual local ecotone are not verification of range shifts; however, trends across 125 sites, which incorporate temperature and overstory neighborhood effects, offer strong indications of initial forest changes. Although comparisons of size distributions alone are insufficient to predict future forest composition (White et al. 1985), regeneration abundance responses in conjunction with other lines of evidence, such as sapling growth responses to temperature (Fisichelli et al. 2012), provide broad evidence of forest sensitivity to climate change and the likely winner and loser species. It must also be noted that shifts in understory performance associated with mean summer temperature may be due in part or whole to more extreme climate events, the severity of which are also correlated with mean temperature (Jentsch et al. 2007).

Results from two long-term local temperate–boreal ecotone studies further bolster our regeneration layer evidence for tree range shifts. Buell and Martin (1961), working in western Minnesota, documented temperate tree regeneration expanding across a local temperate–boreal ecotone. Over a 20 yr period, this resulted in overstory changes and a spatial shift in the ecotone at the study site. Shifts in overstory composition across an altitudinal ecotone in Vermont were observed over a 40 yr period, with temperate species expanding upslope and an overall widening of the ecotone due to persistence of overstory boreal stems at the lower slope boundary (Beckage et al. 2008). Additionally, similar regeneration patterns for *A. saccharum* at a research site 400 km to the east of our study region (Goldblum and Rigg 2002) suggest that local temperate expansion may be occurring across much of the temperate–boreal transition zone of eastern North America.

Temperature interactions, with size class or boreal RA, were found for 5 out of 6 temperature sensitive species, indicating that forest responses to climate change may not always be straightforward, easily detected, or consistent across the landscape (Clark et al. 2011). For example, high overstory and understory abundance of *Acer saccharum* within temperate patches near its northern range limit masked the response to temperature, which was only detectable by looking at regeneration patterns across ecotones. Temperature by size class interactions for 4 out of 6 species suggests that filtering effects of temperature are adding up over multiple life-stages and are most detectable in larger size classes. Simple correlations of temperature with site level data, only utilizing a single understory size class, would have concealed the finer scale expansion and contraction patterns of tree regeneration present in temperate-boreal forests. Also, the two most shade-intolerant species in the study, boreal broadleaf *Betula papyrifera* and *Populus tremuloides*, exhibited overall poor regeneration and no relationship to temperature, illustrating that shady understory conditions may be swamping out responses to temperature for some species.

The type, size, and severity of disturbances opening up the canopy layer will have a major impact on which species are able to ascend into the overstory. The dominant natural disturbances in these forests of the temperate–boreal transition zone are wind and fire. Over the past several centuries, stand replacing events such as intense fires were very infrequent (1000 + yr return interval) while small-scale wind created canopy gaps were more common, occurring every 150–300 yr (MN DNR 2003, Schulte and Mladenoff 2005). Thus, the historic disturbance regime would likely favor gap-phase and shade-tolerant temperate species, such as *Acer rubrum* and *A. saccharum*, able to capture canopy space through small to mid-sized gaps. Large, intense fires are more common to the north of the study region within the boreal forest (Heinselman 1999) and temperate expansion into that region may favor more fire-tolerant species, such as oaks. However, with predicted climate change, frequency of both wildfires and large windstorms might increase during this century.

The ultimate rate and direction of forest responses to climate change will be influenced by a host of biotic and abiotic variables (Fisichelli et al. 2013), and land managers have an opportunity to work with the current advance regeneration to steer successional trajectories and foster healthy and productive forests (Millar et al. 2007, Frelich and Reich 2009). Sample sites in this study included preserved natural areas and lands managed for timber. Thus, management actions such as controlling light availability to advance regeneration through harvest gap size selection or reducing deer populations and browse pressure may be applied to favor tree species also better adapted to a warmer environment (Fisichelli et al. 2012).

Environmental differences

Although we detected gradients in environmental conditions across local ecotones, most variables showed high variance, and tree species did not appear strongly inhibited from establishing across ecotonal boundaries. Somewhat surprisingly, local differences in overstory composition were not attributable to soil pH or texture. Legacy effects from past disturbances or unmeasured variables, such as soil nutrient availability, may have contributed to the existence of local ecotones. Higher light availability beneath boreal overstories may have facilitated the establishment of mid shade-tolerant temperate *Fraxinus nigra* and *Prunus serotina* and tolerant *A. rubrum*. The higher frequency of boreal patches at lower slope positions was potentially in response to proximity to the groundwater table or cooler conditions from cold air drainage (Barnes et al. 1998). More frequent late-spring frost events which more adversely affect temperate broadleaf species (Peters 1992) and lower drought stress at lower slope positions likely promote boreal persistence near southern range margins. However, continued warming will eventually override these lower slope position advantages for boreal species.

Abundance in the understory is controlled by numerous variables and as a regeneration metric integrates performance at many life-history stages, including reproduction, establishment, early growth, and survival. Detectable

and consistent responses, in the directions predicted for both temperate and boreal species, suggest that summer temperature and interactions are indeed important drivers of natural tree regeneration in forests across the temperate–boreal transition zone. Temperate expansion across local ecotones suggests an increase in mixed temperate-boreal forests in the near-future, and temperature sensitivities point toward an eventual northward shift in the regional transition zone as temperate species expand and boreal species fail to regenerate near southern range limits.

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Supplementary material (Appendix ECOG-00197 at <www.oikosoffice.lu.se/appendix>). Appendix 1.