The demography of tree species response to climate: seedling recruitment and survival

CHARLES D. CANHAM† AND LORA MURPHY

Cary Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA

Abstract. Seedling recruitment and survival are critical bottlenecks in tree population dynamics and are likely to play central roles in shifts in species distributions under climate change. We use data from the Forest Inventory and Analysis program to quantify the relationships between two key climate variables—mean annual temperature and growing season water deficit—and rates of seedling recruitment and survival for the 50 most common tree species in the eastern United States. Our statistical models include the positive effects of conspecific adult abundance on recruitment and the potentially negative competitive effects of total canopy abundance on seedling survival. The tradeoff between these two effects creates a range from positive to negative conspecific density dependence, depending on the absolute and relative abundance of conspecific vs. heterospecific adults in a plot. Variation along the climate gradients mirrors patterns found previously in adult distributions. The clearest signal is in variation in the presence/absence of seedlings, while seedling density when present is only weakly related to local climate. The relatively narrow niche breadths for the presence of both seedlings and adults suggest that the frequency of occurrence of species within the landscape, rather than their relative abundance when present, will show the greatest response to climate change. Our analyses predict seedling survival as a function of mean annual temperature independent of the effects of competition and water deficit and thus provide an indication of the fundamental niche for seedling distribution along the temperature gradient. For more than half of the 50 species, their realized seedling niches are displaced to warmer climates. This reflects the prevalence of species in which survival declines with increasing temperature across a significant portion of at least their southern range. Our results show that when the effects of warmer climates are taken into account, seedling survival generally increases with increasing water deficit in the generally humid climates of the eastern United States. This result is consistent with recent global surveys of the relationship between net primary productivity and forest turnover rates, but contrasts with recent studies highlighting the potential impact of drought stress on tree mortality in more arid climates.

Key words: biogeography of temperate trees; climate niche breadth; climatic range limits; conspecific negative density dependence; drought effects on mortality; eastern United States; Forest Inventory and Analysis; fundamental vs. realized niche; seedling recruitment; seedling survival.

† **E-mail:** canhamc@caryinstitute.org

INTRODUCTION

Models of forest response to climate change fall into three general classes: (1) process models based on ecophysiology and biogeochemistry, usually at the level of biome or plant functional type, rather than species (e.g., Smith et al. 2001, Sitch et al. 2008, Tang and Beckage 2010), (2) largely empirical niche-based models that use a variety of statistical methods to relate spatial and

temporal variation in climate to variation in species distribution and abundance (e.g., Iverson and Prasad 1998, Manthey and Box 2007, McKenney et al. 2007), and (3) models of tree population and community dynamics that incorporate the effects of climate on the demography of component tree species (e.g., Bugmann 1996, Scheller and Mladenoff 2005). Both ecophysiological process models and correlative niche-based models predict large and rapid shifts in tree species ranges and generally positive responses in productivity and carbon storage in temperate forests of the eastern United States under predicted climate change (Iverson and Prasad 1998, Tang and Beckage 2010). In effect, species are assumed to track climate change with little in the way of time lags. But these models typically ignore demographic processes and species interactions that may result in strong inertia in community composition under climate change, and they ignore the expected transient successional dynamics that have been triggered by past land use and disturbance.

Despite a pressing need to be able to predict the effects of climate change on the distribution and abundance of temperate tree species, we still have only rudimentary understanding of how demographic processes determine the current geographic distributions of those species, and how different aspects of climate influence key demographic rates that determine recruitment, growth, and survival (Holt et al. 2005, Parmesan et al. 2005). It seems clear that climate must play a preeminent role in at least the range boundaries of temperate tree species (Simova et al. 2015), but it is much less clear how important climate is in determining the spatial distribution and abundance of a species within its range, particularly given the myriad other factors that influence the presence and abundance of tree species within a stand (Morin et al. 2007). There is also growing recognition that temperate tree species distributions are likely to be in disequilibrium with current climate, given long generation times for temperate trees and pervasive human impacts and natural variation in climate over the past millennium (Canham 2014, Jackson and Blois 2015).

Seedling recruitment and survival are a critical bottleneck in tree population dynamics and are likely to play central roles in shifts in species distributions under climate change (Ibanez et al.

2007, Vanderwel et al. 2013). Ecologists have increasingly relied on networks of national forest inventory plots as a source of data for the analysis of the distribution and dynamics of tree species (e.g., Iverson and Prasad 1998, Canham and Thomas 2010, Lichstein et al. 2010, Thomas et al. 2010). Here, we use data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to quantify the relationships between two key climate variables and rates of seedling recruitment and survival for the 50 most common tree species in the eastern United States, across the full range of climatic conditions present within that region.

Methods

Study region, plots, and species

Plot, tree, and seedling data were obtained from the website of the U.S. Forest Service Forest Inventory and Analysis (FIA) program (http://apps.fs.fed.us/fiadb-downloads/datamart.html, data downloaded in September 2012) for the 31 eastern U.S. states (all states west to Minnesota in the north and Louisiana in the south). We used data from plots censused under the nationally standardized (annualized) protocols established in 1999 (Woudenberg et al. 2010), although some states used effectively the same design with reference to seedling plots prior to that, so the census years in our compiled data set ranged from 1998 to 2012. For each state, we selected the two most complete consecutive census cycles conducted using the new national standard plot design, to allow determination of plot and tree conditions at the time of the first census. We then used seedling count data, by species, at the time of the second census as our primary response variable. For most states, this allowed use of seedling count data from the two most recent censuses in each plot, with a typical remeasurement interval of 5–7 years. Plots that were not classified as "forestland" were excluded from the data set. We also excluded plots in southern pine forest types as the focus of our broader research effort is on the deciduous and mixed deciduous/conifer forests of the eastern United States. True plot locations were obtained from the U.S. Forest Service under a security memorandum.

While there is a rich literature relating plant performance to a wide range of climatic variables

(e.g., Thuiller et al. 2003), we have chosen a priori to focus our analyses on two primary climate variables: annual mean temperature and growing season water deficit. Our reasons are based on both pragmatism and principle. Within our study region, mean annual temperature has an extremely high correlation with both mean monthly temperatures for all months of the year, and with various metrics based on growing degree-days. The correlation between mean annual temperature and monthly mean temperatures averaged 0.986 (range 0.967–0.996). The correlation with growing degree-days (5 degree basis) was 0.983, and the correlations with January minimum temperature and July maximum temperature were 0.980 and 0.944, respectively. And much of the scientific and policy debate about the effects of climate change has been couched in terms of changes in mean annual temperature. While plant growth may be more closely related to water supply than water deficit, the analyses presented here focus on seedling survival, and, again, we chose a priori to focus on an integrated measure of drought stress (water deficit) rather than some permutation of simply the supply of water (in precipitation).

We compiled average annual and monthly temperature and precipitation data for each plot using bilinear interpolation of the 800-m resolution PRISM climate data (http://www.prism.oregonstate.edu/), using only data from the specific years and months between the current and previous censuses of a given plot. We used the National Elevation Dataset compiled by the U.S. Geological Survey at 1/3 arc-second resolution for digital elevation data to calculate incident solar radiation, by month, for each plot location, using solar radiation routines in ArcGIS version 10 (ESRI 2011). Available water storage capacity in the top 100 cm of soil at each plot location was extracted from U.S. Department of Agriculture Soil Survey Geographic (SSURGO) database. The monthly solar radiation data and soil water storage capacity data were then combined with monthly temperature and precipitation data to calculate monthly potential and actual evapotranspiration (PET and AET) using the Turc method (Lu et al. 2005, Dyer 2009). The cumulative difference between PET and AET over the year was summed as a measure of growing season water deficit.

Each FIA plot consists of four circular 7.32 m radius subplots, with 36.6 m between subplot centers. All trees ≥12.7 cm diameter at breast height (dbh) are censused in the subplots. For each subplot, we summed the basal area of conspecific trees and all species combined for use in the analyses as measures of the abundance of both potential local parent trees and as a measure of local canopy neighborhood competitive effects.

Our analyses focus on the 50 most common tree species in our plot data set (Table 1), with separate analyses for each of the 50 species. Seedlings are counted in a single 2.07 m radius microplot located in each subplot. The FIA methods define seedlings as individuals < 2.54 cm dbh and taller than 15.24 cm for conifers and taller than 30.48 cm for angiosperms. Because of the wide spacing between subplots, and because neighborhood-scale canopy tree abundance (of both conspecific and heterospecific individuals) is used in the analyses described below, we treat each subplot (and its associated seedling microplot) as an independent sample. In a very small number of microplots, the record for the count of seedlings of a species was given as the three-digit numeric code used by FIA to identify the species (a total of 30 of >18 million records). These were treated as erroneous counts and excluded from the data set. In practice, this meant that any microplot with a seedling count >200 was treated as missing. Mean seedling densities for even common species were typically <10 seedlings per microplot. Final sample sizes ranged from 369,402 to 369,408 microplots per species. Average seed mass of each of the 50 study species was compiled from literature sources (Bonner and Karrfalt 2008).

A maximum-likelihood inverse model of seedling recruitment and survival

The count of number of seedlings present in the microplot at the time of a census reflects the cumulative effects of input ("recruitment") of individuals greater than or equal to the minimum size counted for that species over some undefined prior number of years, plus the cumulative effects of the subsequent mortality of those cohorts of seedlings. In principle, the count also reflects "outgrowth" as individuals grow beyond the maximum size recorded as a seedling, but given the wide range of

Table 1. The 50 study species, with the percent of microplots in which the species was present, mean density (no. seedlings/10 m²), and the minimum and maximum mean annual temperature of plots where seedlings occurred.

Species	Common name	Percentage of plots present	Mean density when present (no./10 m²)	Minimum temperature (°C)	Maximum temperature (°C)
Abies balsamea	Balsam fir	9.2	4.5	1.5	9.1
Acer rubrum	Red maple	19.5	3.3	2.1	23.5
Acer saccharum	Sugar maple	12.8	6.2	2.3	18.4
Betula alleghaniensis	Yellow birch	2.7	2.9	1.9	16.5
Betula lenta	Sweet birch	1.2	3.3	5.0	17.4
Betula papyrifera	White birch	1.9	2.8	1.5	10.5
Carya alba	Mockernut hickory	3.6	1.4	7.0	21.7
Carya cordiformis	Bitternut hickory	2.2	1.4	4.7	19.8
Carya glabra	Pignut hickory	3.6	1.3	6.5	22.6
Carya ovata	Shagbark hickory	1.3	1.3	6.4	18.8
Cornus florida	Flowering dogwood	5.4	2.0	3.5	22.7
Fagus grandifolia	American beech	9.2	3.0	2.2	20.9
Fraxinus americana	White ash	10.2	3.1	2.8	20.1
Fraxinus nigra	Black ash	1.1	4.3	2.6	14.1
Fraxinus pennsylvanica	Green ash	3.9	2.9	3.2	22.4
Juglans nigra	Black walnut	0.5	1.0	5.0	19.0
Juniperus virginiana	Eastern redcedar	3.8	1.7	5.3	22.5
Liquidambar styraciflua	Sweet gum	4.9	2.2	10.3	22.6
Liriodendron tulipifera	Yellow poplar	3.0	2.5	6.1	19.9
Nyssa sylvatica	Black gum	6.0	1.8	7.0	20.5
Ostrya virginiana	Eastern hop hornbeam	6.9	2.9	2.7	22.1
Oxydendrum arboreum	Sourwood	1.7	1.6	8.7	19.6
Picea glauca	White spruce	1.1	1.7	1.6	9.9
Picea rubens	Red spruce	2.9	3.2	1.5	11.5
Pinus echinata	Shortleaf pine	0.4	2.0	11.5	19.8
Pinus resinosa	Red pine	0.2	1.4	3.9	9.7
Pinus strobus	Eastern white pine	3.4	2.7	2.7	16.2
Pinus taeda	Loblolly pine	2.1	2.3	11.8	21.9
Pinus virginiana	Virginia pine	0.6	2.2	9.4	19.6
Populus balsamifera	Balsam poplar	0.3	3.6	2.6	12.0
Populus grandidentata	Bigtooth aspen	0.9	3.4	3.2	14.9
Populus tremuloides	Quaking aspen	3.4	4.7	2.3	12.0
Prunus serotina	Black cherry	11.5	2.4	1.5	22.5
Quercus alba	White oak	7.5	2.1	3.8	19.8
Quercus coccinea	Scarlet oak	1.2	1.4	6.7	19.7
Quercus falcata	Southern red oak	1.9	1.4	9.6	21.9
Quercus macrocarpa	Bur oak	0.3	3.7	4.9	14.2
Quercus nigra	Water oak	3.1	2.0	13.2	22.8
Quercus prinus	Chestnut oak	1.9	2.1	7.2	19.6
Quercus rubra	Northern red oak	6.1	1.8	3.7	18.5
Quercus stellata	Post oak	1.6	1.8	6.5	21.8
Quercus velutina	Black oak	4.6	1.7	5.0	19.9
Robinia pseudoacacia	Black locust	0.5	1.9	5.4	19.2
Sassafras albidum	Sassafras	6.0	2.5	6.7	20.3
Thuja occidentalis	Northern white cedar	1.2	4.3	1.9	9.8
Tilia americana	American basswood	1.0	1.8	3.9	20.3
Tsuga canadensis	Eastern hemlock	2.3	2.5	3.0	16.3
Ulmus alata	Winged elm	3.4	1.9	11.1	21.4
Ulmus americana	American elm	3.0	2.0	3.2	22.3
Ulmus rubra	Slippery elm	2.0	2.4	2.7	19.8

Note: The minimum mean annual temperature in the data set was 1.5°C, and a number of the species have range distributions that extend well north of the geographic extent of the Forest Inventory and Analysis data.

sizes treated as seedlings by FIA methods, we assume that this is a small number and is subsumed in the estimate of mortality. In order to account for the combined effects of both recruitment and subsequent survival, we have developed an inverse model, fitted using maximum-likelihood methods, that seeks to integrate the two processes.

The recruitment term in the model (i.e., the average annual input of new individuals into the seedling size class) is assumed to be a simple linear function of the basal area of conspecific canopy trees (i.e., stems ≥ 12.7 cm dbh) within the 7.32 m radius subplot:

$$\text{recruitment} = r_a + r_b \times \text{BA}_c \tag{1}$$

where r_a and r_b are estimated parameters and BA_c is the basal area of conspecific trees in the subplot. The slope parameter (r_b) could be either positive or negative.

Annual survival of a given cohort of new recruits was assumed to be the product of three terms: a negative exponential function of total canopy tree basal area in the subplot (as an index of competition and shading effects from canopy trees in the immediate neighborhood) and a Gaussian function of both mean annual temperature and water deficit:

$$\text{survival} = \exp\left[\begin{array}{c} \left(-c_a \text{BA}_t{}^{c_b}\right) - \frac{1}{2}\left(\frac{\text{MAT} - t_a}{t_b}\right)^2 \\ - \frac{1}{2}\left(\frac{\text{WD} - w_a}{w_b}\right)^2 \end{array} \right] \tag{2}$$

where BA_t is total canopy tree basal area and MAT and WD are plot mean annual temperature (°C) and growing season water deficit (mm), and c_a, c_b, t_a, t_b, w_a, and w_b are estimated parameters.

The total expected count of seedlings from a given number (n) of cohorts is then:

$$\text{count} = \text{recruitment} \times \sum_{i=1}^{n} \text{survival}^i \tag{3}$$

The absolute values of the estimated parameters are sensitive to the assumed number of cohorts represented by the total seedling count. But the effect of the choice of n on the parameter estimates becomes negligible for values > 10, and given the wide range of sizes represented by the seedling counts (individuals taller than 15.24 cm

for conifers and taller than 30.48 cm for angiosperms, and < 2.54 cm dbh), it is reasonable to assume that the seedling counts include the input of individuals over at least a 10-year period. We tested models with $n = 5$ and $n = 15$ to determine sensitivity of the results to the choice of n. In both cases, while absolute values of individual parameters varied slightly, the shapes of the responses to competition, temperature, and water deficit were similar.

We also tested several more complex variants of Eqs. 1 and 2, but rejected them because of strong parameter tradeoffs in some species. In particular, we tested models in which the recruitment term (Eq. 1) was also a function of mean annual temperature. But there was strong tradeoff with the temperature sensitivity of survival in those models, and the models for some of the species had difficulty converging. We also tested for conspecific negative density dependence (i.e., Janzen–Connell effects) in the survival term by including separate competition parameters for conspecific vs. heterospecific adult basal area. But again, this led to tradeoffs between the effects of conspecific basal area in the recruitment term vs. the survival term. As will be pointed out in the results, a form of conspecific negative density dependence is present phenomenologically in the observed seedling counts for some species, particularly at low relative abundance, simply because the canopy can only contain a finite total basal area, and the effects of shading outweigh any positive effects of higher abundance of parent trees.

Examination of the data showed that the seedling count distributions for all of the species were zero-inflated (i.e., a variable but much larger number of plots with zero counts than would be expected under either a Poisson or negative binomial distribution). Thus, we partitioned the analysis of seedling counts into two components: (1) "presence", that is, the probability that a species was present in a plot, and (2) the expected seedling density when present. Zero-inflated likelihood functions have been widely used for overdispersed count data where there are more zero observations than expected by a traditional Poisson or negative binomial distribution (Welsh et al. 1996). Zero-inflated regression models often estimate a single (constant) parameter for the zero-inflation term, but visual examination of

our data revealed that the fraction of plots with zero abundance for a given species did indeed vary along the temperature gradient. Thus, we modeled the zero-inflation term (P_z) as a Gaussian function of temperature:

$P_z = 1 - \text{Prob(presence)}$, where

$$\text{Prob(presence)} = p_a e^{-0.5\left(\frac{(\text{MAT} - p_m)}{p_b}\right)_2} \qquad (4)$$

where MAT was the annual mean temperature in the plot and p_a, p_m, and p_b were estimated parameters.

The overall likelihood function was thus

$$\text{Prob}(y|\theta) = \begin{cases} P_z + (1 - P_z)\,\text{Poisson}(0|\theta) & \text{if } y = 0 \\ (1 - P_z)\,\text{Poisson}(y|\theta) & \text{if } y > 0 \end{cases}$$
$$(5)$$

where y was the observed count of seedlings of a given species in a plot, P_z was the estimated zero-inflation term and Poisson($y|\theta$) is the probability of observing an abundance of y given a Poisson distribution and the estimated parameters of the model (θ) (Eqs. 1–4). Note that in Eq. 5, the probability of observing a zero count combines both the structural zeros (P_z) and the sampling zeros [$(1 - P_z) \times \text{Poisson}(0|\theta)$], that is, the probability of observing a zero count given the parameters of the model for abundance when present (Eq. 4).

We used simulated annealing to find the maximum-likelihood estimates of the parameters of the full model for each of the 50 species, using our likelihood package version 1.7 in R version 3.1.0 (R Core Team 2014). We used two-unit support intervals to evaluate strength of evidence for the maximum-likelihood parameter estimates. Goodness of fit was evaluated both graphically (for presence along the temperature gradient) and with a pseudo-R^2 that takes into account the zero inflation.

Results

Seedling vs. adult distribution along temperature gradients

Variation along the temperature gradient in seedling frequency (i.e., presence/absence in a microplot) and abundance (density when present in a microplot) mirrors patterns found previously in adult frequency and abundance (Canham and Thomas 2010): The clearest signal is in variation in the presence/absence of seedlings, rather than in average density when present (graphical results for all 50 species presented in Appendix S1). The patterns of frequency are approximately Gaussian, with a mode estimated by the p_m parameter, breadth estimated by the p_b parameter, and peak frequency estimated by the p_a parameter in Eq. 4 (Appendix S1). We interpret these parameters as measures of the realized temperature niches for seedlings of the 50 species. On that basis, the species differ widely in seedling niche breadth, and there is some modest support for the prediction that seedling niche breadth is wider for species with modes at higher (colder) latitudes (Rapoport's rule; Fig. 1A). But with the exception of five species with exceptionally broad temperature ranges—including *Acer rubrum* and *Acer saccharum*, the two most common tree species in our data set—the rest have seedling niche breadths that are in a fairly narrow range. The data clearly reflect the well-known latitudinal gradient in diversity of woody plants, with the greatest number of species having seedling niche modes in climates with mean annual temperature > 10°C (Fig. 1A).

Adult trees have very slightly broader niche breadths than conspecific seedlings, although the difference in plot size (and therefore detection thresholds) for the two different life history stages could account for the difference (Fig. 1B). Across the full set of 50 species, there was no consistent difference in the median temperatures of subplots containing adults and microplots containing seedlings: The median temperature for adults was on average 0.04°C higher (range = 1.43–1.81°C) than for microplots containing seedlings. This is in agreement with other recent analyses that have found no clear evidence that seedling distributions are currently displaced northward relative to adults in response to recent climate change (e.g., Zhu et al. 2012).

Relationships between seedling survival and species distribution along the temperature and water-deficit gradients

The parameters t_a and t_b in Eq. 2 predict expected seedling survival as a function of mean annual temperature—independent of the effects of competition and water deficit—and thus provide an indication of the fundamental niche for seedling distribution along the temperature
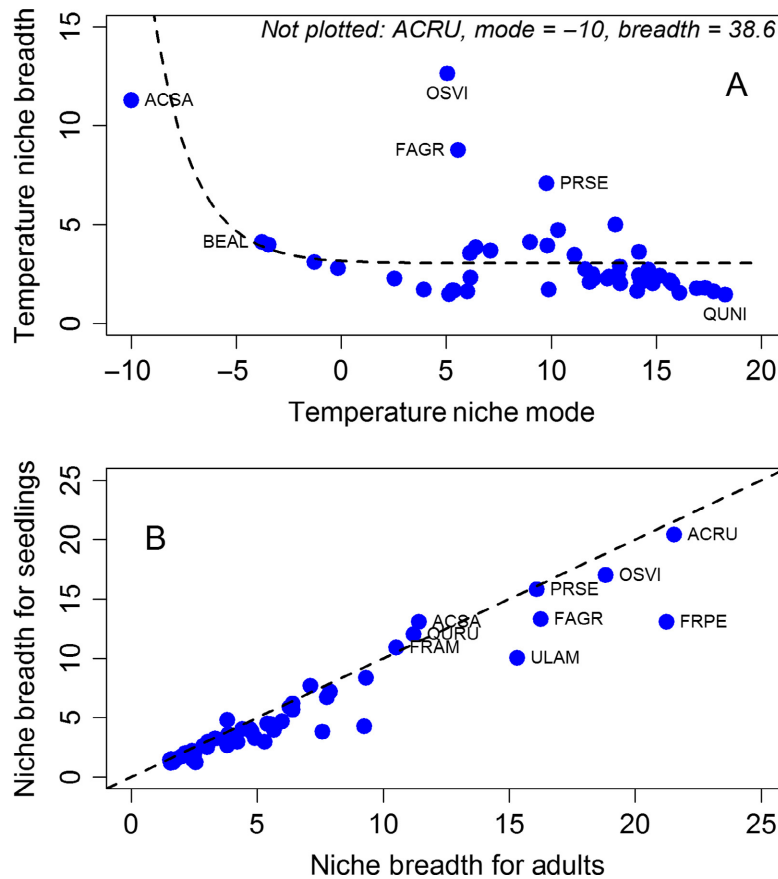
Fig. 1. (A) Temperature niche breadth (parameter p_b in Eq. 4) vs. niche mode (parameter p_m in Eq. 4) for seedlings of the 50 species. Dashed line is a maximum-likelihood fit of an exponential function. (B) Seedling vs. adult tree niche breadth along the temperature gradient. For comparison with adult tree data, this panel uses an alternate measure of niche breadth calculated as the variance in the mean annual temperature of microplots in which seedlings were present, vs. the variance in mean annual temperature of full Forest Inventory and Analysis plots in which conspecific adults were present. Dashed line is a 1:1 relationship. Distinctive species are labeled using standard acronyms (first two letters of genus and specific epithet). All axes are in units of °C.

gradient. Comparison of the shape of the seedling survival function with the shape of the distribution of seedling presence (Fig. 2 and Appendix S2) can therefore suggest the nature of any displacement between fundamental and realized seedling niche distributions along the temperature gradient. Of 12 representative northern species, four—*Picea rubens, Pinus strobus, Betula alleghaniensis,* and *Prunus serotina*— have their highest survival in climates that are slightly warmer than the climates where the seedlings most frequently occur (Fig. 2). For at least these four species, this suggests that an increase in mean annual temperature would

result in higher seedling survival across at least the northern portion of their ranges and that their realized seedling niches are displaced slightly to colder climates. The other eight species, however, occur with greatest frequency in climates that are either warmer than or approximately equal to the predicted temperature with maximum seedling survival (Fig. 2), suggesting either no displacement between fundamental and realized seedling niche distributions or displacement of their realized niches to warmer climates. For these species, an increase in mean annual temperature could be expected to result in a decrease in seedling survival over most if not all of their
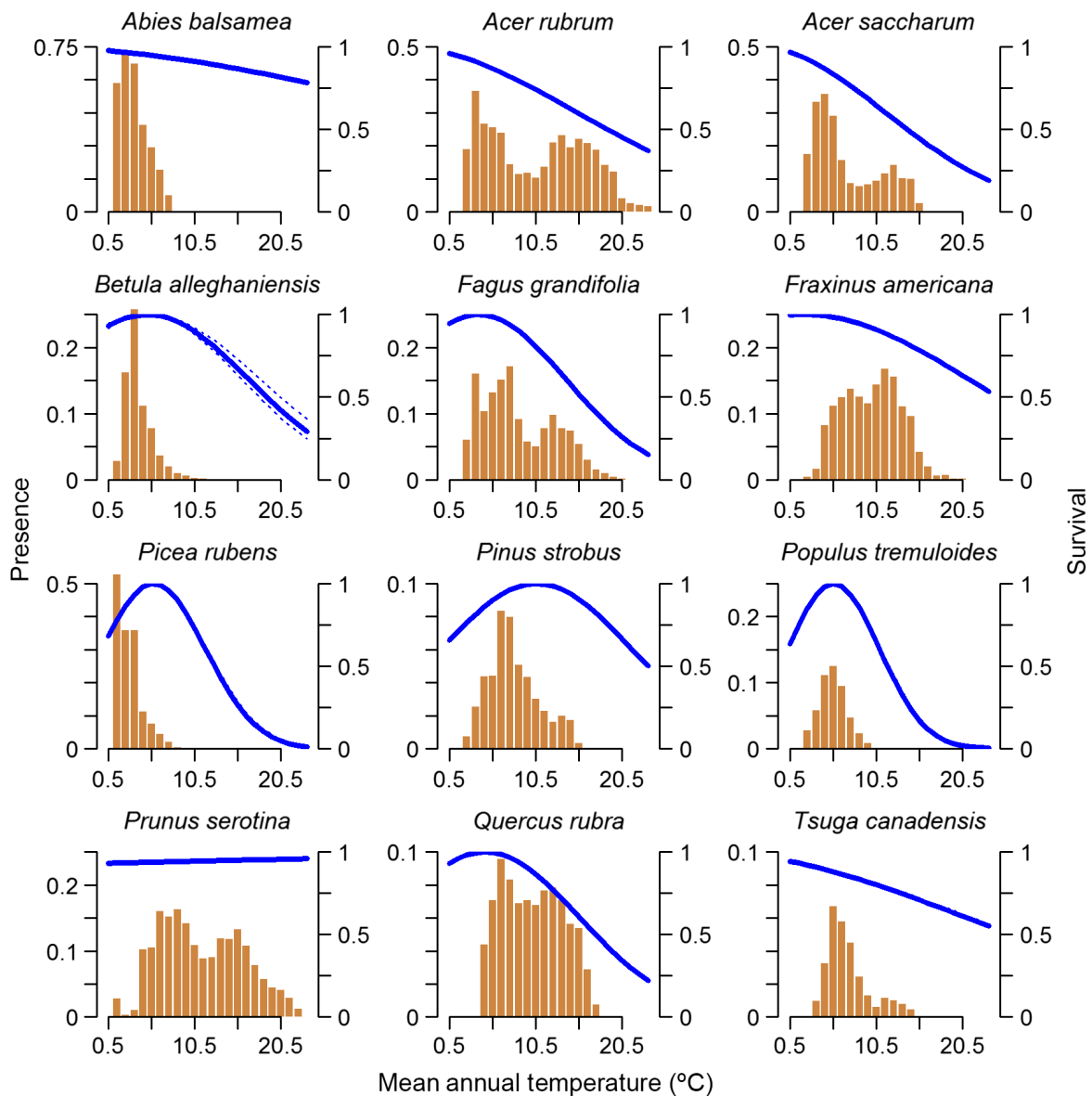
Fig. 2.   Observed presence (fraction of microplots in which seedlings occurred, brown bars) in 1°C intervals of mean annual temperature, and predicted annual seedling survival (blue lines) as a function of mean annual temperature. Two-unit support intervals around the predicted survival curves are shown in dotted lines, but in most cases are too close to the predicted curve to display.

current distribution along the temperature gradient. Five of the six late successional dominant species of northern forests show this pattern (*Abies balsamea, Tsuga canadensis, Acer rubrum, Acer saccharum,* and *Fagus grandifolia*).

This breakdown is mirrored in the full set of 50 species (Appendix S2). There is a set of seven species for which predicted seedling survival is a monotonically increasing function of mean annual temperature (*Carya glabra, Fraxinus nigra, Juglans nigra, Populus balsamea, Prunus serotina, Quercus falcata,* and *Thuja occidentalis*), although in most of these species the increase is very modest (Fig. 2 and Appendix S2). Survival is predicted to decline monotonically across the current temperature range for a much larger set of 20 species
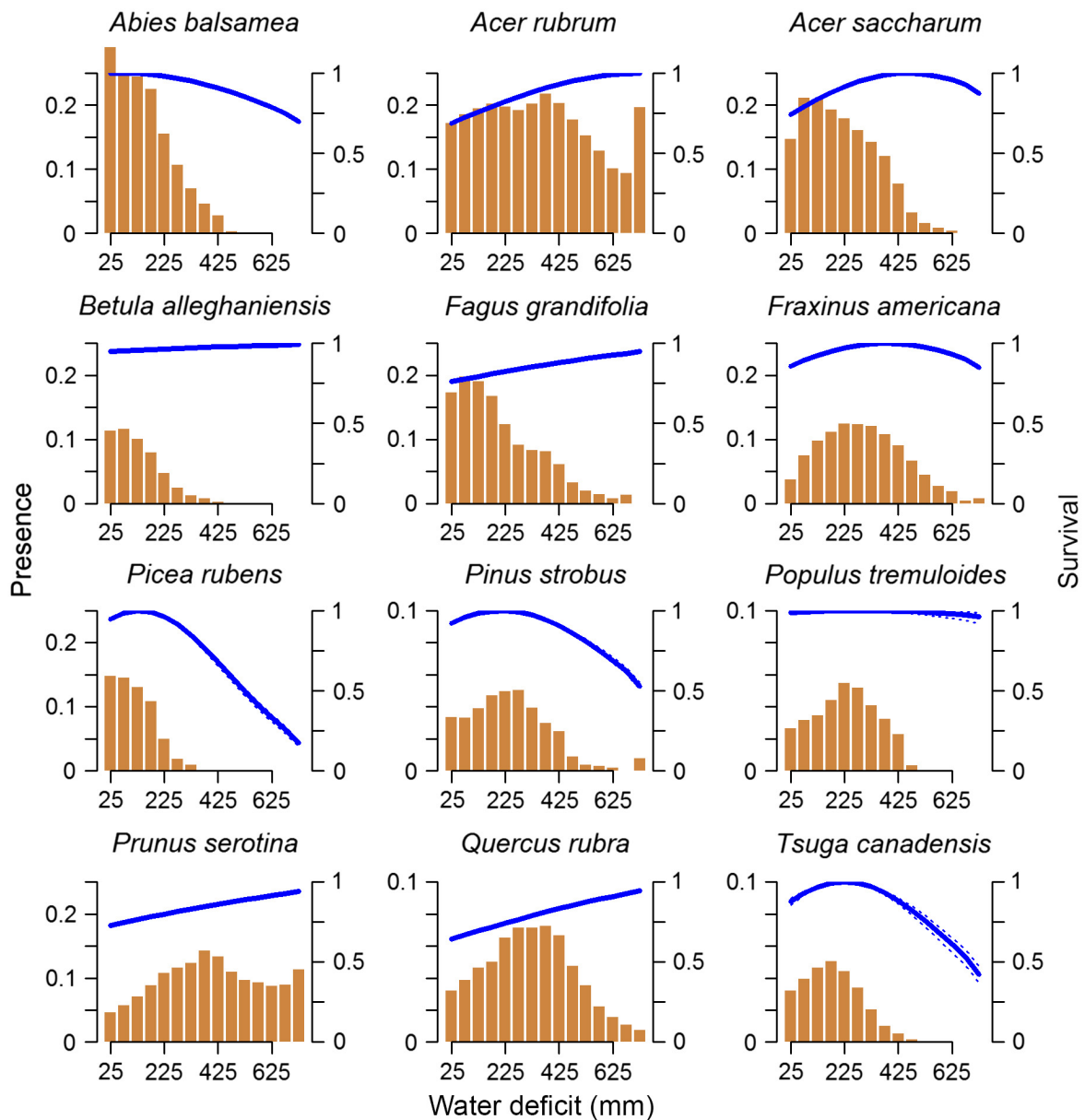
Fig. 3. Observed presence (fraction of microplots in which seedlings occurred, brown bars) as a function of water deficit (mm), and predicted annual seedling survival (blue lines) as a function of water deficit. Two-unit support intervals around the predicted survival curves are shown in dotted lines, but in most cases are too close to the predicted curve to display.

(Fig. 2 and Appendix S2); for these species, greatest survival occurs in climates much colder than their current peak frequency. This includes such common northern species as *Abies balsamea*, *Acer rubrum*, *Acer saccharum*, *Fraxinus americana*, *Tsuga canadensis*, and *Picea glauca*, but also includes species with more southern distributions (e.g.,

Oxydendrum arboretum, *Cornus florida*, *Carya cordiformis*, *Juniperus virginiana*, *Sassafras albidum*, *Quercus alba*, and *Quercus velutina*). The remaining roughly half of the species show highest survival within their current temperature range. For most of these remaining species, however, the modal temperature for survival is still at least
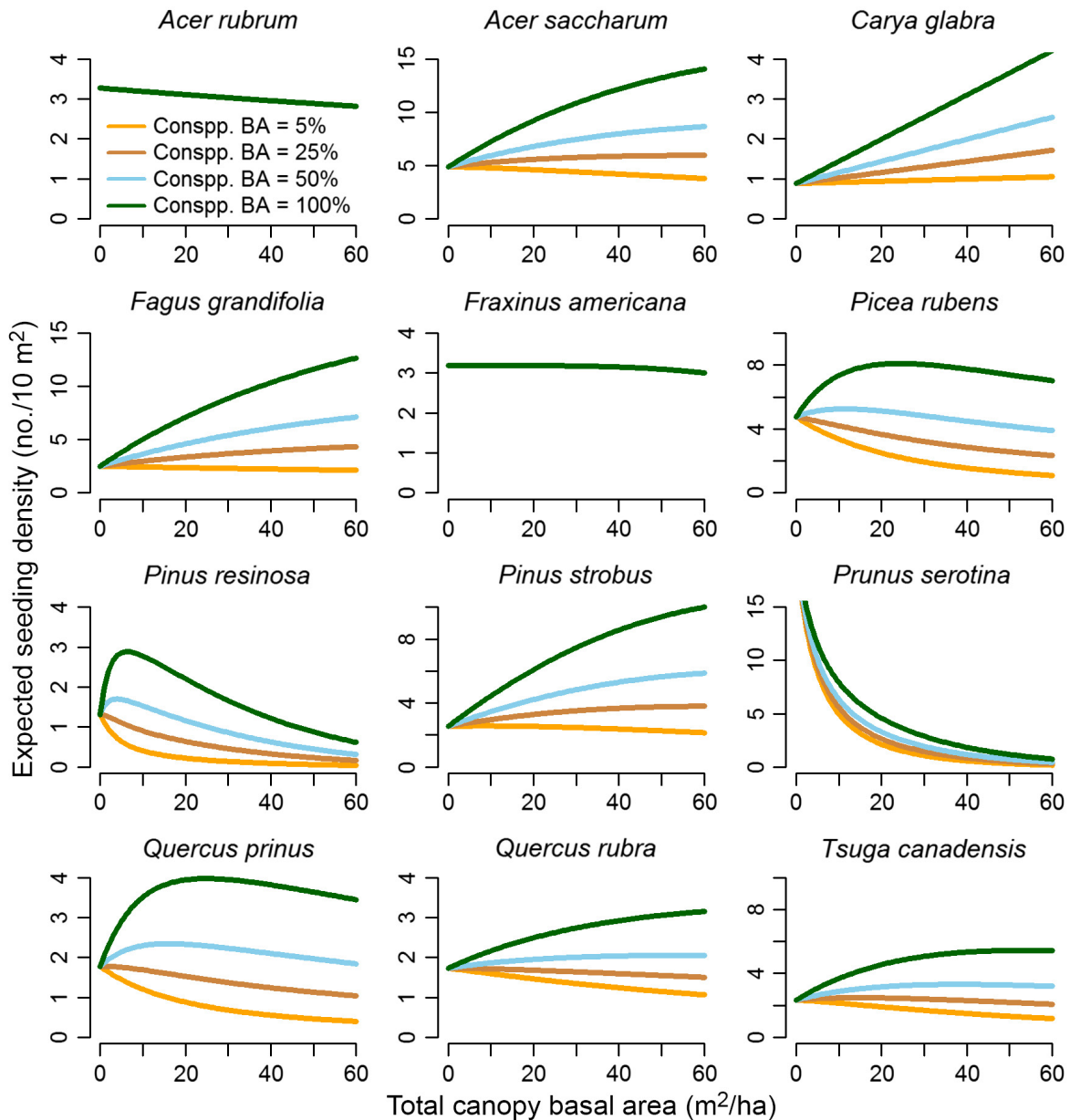
Fig. 4. Predicted seedling density (if present at all) for 12 representative tree species as a function of total canopy basal area, with conspecific adult basal area making up 5%, 25%, 50%, or 100% of canopy basal area.

several degrees (C) colder than the temperature with peak frequency. Thus, for the vast majority of the 50 species, an increase in mean annual temperature would be expected to reduce survival across at least the warmer end of their current distribution.

All but four of the 50 species (*Abies balsamea, Carya cordiformis, Pinus virginiana,* and *Populus*

balsamea) showed a positive relationship between survival and water deficit across at least some portion of the range where they occurred along the gradient (Appendix S1). Of the 12 main northern forest species, the four conifers showed a decline in survival with increasing soil water deficit over at least a significant fraction of their range, while the four most common angiosperms

(*Acer rubrum, Acer saccharum, Betula alleghaniensis*, and *Fagus grandifolia*) showed increasing seedling survival with increasing water deficit across their entire ranges (Fig. 3).

Interspecific variation in per capita seedling recruitment

The r_a and r_b parameters in Eq. 1 relate the expected annual input of new seedlings to the local abundance of conspecific adults. For 12 of the 50 species, there was no relationship between abundance of conspecific adult trees within the local neighborhood (i.e., within the 7.32 m radius subplot) and the estimated average annual input of new seedlings (i.e., maximum-likelihood estimates of the r_b parameter in Eq. 1 were effectively zero, and the expected number of new recruits annually was determined by the r_a parameter; Appendix S3). Note that given the zero-inflated likelihood function, this result applies only to plots in which at least one seedling of a species was present. The 12 species included both species with very light wind-dispersed seeds (i.e., all three species of *Betula*, and *Populus tremuloides*), but also a number of species with larger wind-dispersed seeds, including two species of *Ulmus*, two species of *Fraxinus*, and *Acer rubrum*, the most common tree in the data set (Appendix S3). The remaining species showed a very wide range of per capita seedling recruitment rates (r_b parameter; Appendix S3). This variation presumably reflects species-specific differences in reproductive effort and seed size, but could also reflect differences in shade tolerance, as more shade-tolerant species might generate a higher number of minimum-sized seedlings.

The masses of cleaned seeds of the 50 species span almost five orders of magnitude (from <100 seeds/kg to >8,000,000 seeds/kg). But there was no correlation between seed mass and the predicted (1) average annual input of new seedlings (i.e., recruitment; Pearson correlation coefficient $r = -0.115$, $P = 0.43$), (2) the subsequent annual survival of those seedlings (i.e., shade tolerance; $r = -0.136$, $P = 0.35$), or (3) the expected numbers of all seedlings present in a microplot under a dense canopy of conspecific adults with the climate conditions most favorable for survival ($r = -0.121$, $P = 0.40$). The only clear pattern between seed mass and seedling demography and distribution is a reflection of the fact that the

largest seeded species (species of *Quercus* and *Carya*) reach their greatest frequencies as seedlings in climates with mean annual temperatures >8°C, while the only seedling species reaching their greatest frequency at temperatures <5°C were conifers or angiosperms with small- to moderate-sized seeds (species of *Acer*, *Betula*, and *Populus*). In effect, all of the species with primarily northern distributions have small- to moderate-sized seeds.

Net effects of recruitment and survival on expected seedling density: apparent conspecific density dependence

Although the recruitment function in Eq. 1 is a simple linear model of conspecific basal area, the expected seedling density in a plot is a function of both the potentially positive effects of conspecific adult abundance on the input of new seedlings and the potentially negative effects of total canopy basal area on seedling survival (e.g., due to aboveground and belowground competition, or through host-specific pathogens). The tradeoff between these two effects could in principle create a range from positive to negative relationships between seedling and adult density, depending on both the absolute and relative abundance of conspecific vs. heterospecific adults in the immediate neighborhood. In fact, our results predict a broad range from positive to negative conspecific density dependence among the 50 species, and the strength and sign (positive vs. negative) of the relationship vary as a function of the absolute and relative abundance of the species within a stand (12 representative species shown in Fig. 4, patterns for all 50 species are in Appendix S4). For all 50 species, when the species is a small component of the canopy (e.g., 5% of total stand basal area), the relationship between both total and conspecific adult tree abundance is negative to neutral (Fig. 4 and Appendix S4) because low rates of seedling recruitment are outweighed by competitive effects of canopy trees on seedling survival. When species are dominant in a stand (e.g., >50% of total basal area), conspecific density dependence can vary from strongly positive to negative depending on species (Fig. 4).

The strength and sign of the density dependence varies as a function of (1) the slope of the function for seedling recruitment vs. conspecific

basal area, (2) the sensitivity of survival to the total canopy basal area in the subplot (i.e., sensitivity to competition), and (3) the relative abundance of a species in the subplot (i.e., what fraction of total canopy basal area is made up of conspecific adults). For example, *Acer saccharum* has high per capita seedling recruitment, and as a shade-tolerant species has only a modest decline in survival with increasing total canopy basal area (Fig. 4). The net effect is a very slight negative density dependence when the species is a small fraction of total adult biomass in a stand, but a strongly positive density dependence when the species has high relative abundance (i.e., the effects of competition are offset by high total recruitment). *Pinus resinosa* also had high per capita seedling recruitment, but is shade intolerant and shows a very steep decline in survival with increasing canopy basal area (Fig. 4). For stands with low total biomass made up primarily of *P. resinosa*, predicted seedling density initially rises quite steeply with increasing stand biomass, but once stand basal area exceeds 10 m^2/ha, the strong effects of competition on survival overwhelm high per capita recruitment and lead to rapid declines in expected seedling density with increasing conspecific abundance (and total canopy biomass; Fig. 4).

A number of recent studies have focused on the relationship between the strength and sign of conspecific density dependence (as a species trait) and the commonness or rarity of a species across its range (e.g., Johnson et al. 2012, Zhu et al. 2015). We calculated the slope of the relationship between expected seedling density and total tree biomass in a stand, when a species represented only 5% of total stand biomass (i.e., under the conditions most likely to show conspecific negative density dependence) as a measure of the potential strength of conspecific negative density dependence. All but five species showed evidence of negative density dependence on that basis—the exceptions were an understory species (*Ostrya virginiana*), all three species of hickories (*Carya cordiformis, C. glabra,* and *C. ovata*), and a species of elm (*Ulmus rubra*). But there was no relationship between that measure of conspecific negative density dependence and the average abundance of the 50 species across the 31 eastern United States (Pearson correlation coefficient = 0.022, *n* = 50).

DISCUSSION

Seedling vs. adult distribution and abundance along climate gradients

The patterns of seedling distribution and abundance of these 50 temperate tree species closely mirror patterns of adult distribution and abundance along the temperature gradient (Canham and Thomas 2010). Most of the species have very broad temperature ranges (5.8–21.4°C, with a mean of 13.5°C; Table 1), but relatively narrow ranges within which they occur with high frequency (Fig. 2 and Appendix S2). Both relative abundance of adults and the density of seedlings within plots, on the other hand, show much less predictable variation along the temperature gradient (Appendix S3). These results suggest that relative abundance of a tree species—whether as a seedling or adult—within a site, given that it is present, is controlled primarily by factors other than climate (Canham and Thomas 2010). In contrast, the relatively narrow niche breadths for frequency of both seedlings and adults suggest that the frequency of occurrence of species within the landscape, rather than their relative abundance or even range limits, will show the greatest response to climate change. Previous studies (Woodall et al. 2009, 2013, Zhu et al. 2012, 2014) have compared seedling vs. adult distributions along latitudinal or temperature gradients to test for evidence of northward shifts in species distributions in response to recent climate change. Like those studies, our analysis found little if any evidence that there has yet been detectable northward migration in these temperate tree species.

Fundamental vs. realized seedling niche distribution along the temperature gradient

The parameters t_a and t_b in Eq. 2 predict expected seedling survival as a function of mean annual temperature—independent of the effects of competition and water deficit—and thus provide an indication of the fundamental niche for seedling distribution along the temperature gradient. Comparison of the shape of the seedling survival function with the shape of the distribution of seedling presence (Fig. 2 and Appendix S2) can thus be used to characterize the nature of any displacement between fundamental and realized seedling niche distributions along the

temperature gradient. For more than half of the 50 species, there is evidence that their realized seedling niches are displaced to warmer climates. This reflects the prevalence of species in which survival declines with increasing temperature across a significant portion of at least the southern range of the species, and in which the species has highest frequency in climates with less than optimal survival (Appendix S2).

The observed pattern of lower seedling survival in warmer climates is consistent with a number of other recent studies. Zhu et al. (2014) noted evidence for higher turnover in seedling populations of eastern U.S. tree species at the warmer end of their ranges. Woodall et al. (2009) noted that seedling densities for northern U.S. tree species tend to be higher in the more northern portions of their range—a result consistent with higher seedling survival in colder climates. Fisichelli et al. (2014) noted decreased survival of first-year seedlings with increasing temperature in a field experiment using 15 North American tree species. Vanderwel et al. (2013) observed higher mortality rates with increasing temperature for saplings and adults of eastern U.S. species grouped into a set of plant functional types. All of these studies are consistent with Stephenson and van Mantgem's (2005) global survey, in which forest turnover rates (defined as the average of tree mortality and recruitment rates) paralleled patterns of net primary productivity both across and within biomes.

There is little consensus on the mechanisms that underlie higher mortality across all tree life stages in warmer climates. Stephenson and van Mantgem (2005) offer several nonmutually exclusive hypotheses, ranging from bottom-up mechanisms (more intense competition in more productive environments) to top-down processes (higher secondary production resulting in more intense herbivory and attacks by pests and pathogens). Our analyses explicitly incorporate competitive effects and show higher mortality in warmer climates regardless of the intensity of competition. We know of no synoptic surveys, however, of geographic variation in the importance of herbivores, pests, and pathogens as factors in tree mortality. This may reflect the difficulty in assigning causes of mortality in long-lived plants, where mortality may be the consequence of a multiyear sequence of abiotic stresses and biotic attacks (Manion 1981). Anderegg et al.

(2015) present a framework for assessing the relative importance of insect attack (particularly bark beetles) as a function of drought stress in western U.S. tree species. More broadly, there appears to be increased recognition of the ubiquity of trophic interactions as agents of tree mortality, and as agents of changes in the distribution and abundance of tree species (e.g., Pureswaran et al. 2015).

Our analyses explicitly treat water deficit and temperature as interacting (i.e., multiplicative) factors, so there is little reason to believe that the predicted pattern of higher seedling mortality in warmer climates is due to confounding with higher mortality due to greater drought stress in warmer climates (Allen et al. 2015). And, in fact, for these tree species in a generally humid climate, our results show that when the effects of warmer climates are taken into account, seedling survival generally increases with increasing seasonal water deficit. Thus, for a majority of the 50 species, seedling mortality is higher in both warmer and wetter climates. This result is still consistent with Stephenson and van Mantgem's (2005) global survey of the relationship between net primary productivity and forest turnover rates, but contrasts with recent studies highlighting the potential impact of drought stress on tree population dynamics in more arid climates (Allen et al. 2010, McDowell and Allen 2015).

Apparent density dependence between adults and conspecific seedlings

There is a long history of interest in negative effects of adult trees on conspecific seedlings. Early work focused on spatial patterns in which proximity to adult trees resulted in higher mortality rates for seedlings, presumably due to density dependence in the effects of natural enemies (i.e., Janzen–Connell effects, Janzen 1970, Connell 1970). While early work focused on tropical forests (Wills et al. 1997, Harms et al. 2000), the expected pattern of displacement of older seedlings away from nearby conspecific adults (e.g., Uriarte et al. 2005, Martin and Canham 2010) and the presence of host-specific predators or pathogens as a putative mechanism are also common in temperate forests (Packer and Clay 2000). Recent work has focused more generally on conspecific negative density dependence (CNDD) within seedling populations, regardless of proximity to or local abundance of adults (i.e., Johnson et al.

2012, Bachelot et al. 2015, Zhu et al. 2015). Some studies treat density dependence as a species-specific trait and have sought to determine whether the strength of CNDD could be a factor in the average regional abundance of a species (i.e., commonness vs. rarity; Seri and Shnerb 2015, Xu et al. 2015, Zhu et al. 2015). Our results illustrate that both the strength and the sign of the relationship between adult abundance and density of conspecific seedlings can vary depending on a species' relative abundance within a stand, regardless of its average abundance across its range. More generally, conspecific density dependence is fundamentally phenomenological and can be the product of many different and simultaneous mechanisms. Whether or not Janzen–Connell mechanisms are active, our analyses highlight that conspecific negative density dependence can arise simply from the interplay of tradeoffs between the abundance of adult trees as seed sources vs. their competitive effects (either aboveground or belowground) on seedling survival.

Acknowledgments

Literature Cited

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:55.

Anderegg, W. R. L., et al. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytologist 208:674–683.

Bachelot, B., R. K. Kobe, and C. Vriesendorp. 2015. Negative density-dependent mortality varies over time in a wet tropical forest, advantaging rare species, common species, or no species. Oecologia 179:853–861.

Bonner, F. T., and R. P. Karrfalt, editors. 2008. The woody plant seed manual. Agricultural handbook number 727. USDA Forest Service, Washington, D.C., USA.

Bugmann, H. K. M. 1996. A simplified forest model to study species composition along climate gradients. Ecology 77:2055–2074.

Canham, C. D. 2014. Disequilibrium and transient dynamics: disentangling responses to climate change versus broader anthropogenic impacts on temperate forests of eastern North America. Pages 109–128 in D. A. Coomes, D. F. R. P. Burslem, and W. D. Simonson, editors. Forests and global change. Cambridge University Press, Cambridge, UK.

Canham, C. D., and R. Q. Thomas. 2010. Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. Ecology 91:3433–3440.

Connell, J. H. 1970. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 in P. J. den Boer and G. R. Gradwell, editors. Dynamics of population. Proceedings of the Advanced Study Institute, Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Dyer, J. M. 2009. Assessing topographic patterns in moisture use and stress using a water balance approach. Landscape Ecology 24:391–403.

ESRI. 2011. ArcGIS desktop: release 10. Environmental Systems Research Institute, Redlands, California, USA.

Fisichelli, N., A. Wright, K. Rice, A. Mau, C. Buschena, and P. B. Reich. 2014. First-year seedlings and climate change: species-specific responses of 15 North American tree species. Oikos 123:1331–1340.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493–495.

Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: single species approaches. Oikos 108:18–27.

Ibanez, I., J. S. Clark, S. LaDeau, and J. HilleRisLambers. 2007. Exploiting temporal variability to understand tree recruitment response to climate change. Ecological Monographs 77:163–177.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465–485.

Jackson, S. T., and J. L. Blois. 2015. Community ecology in a changing environment: perspectives from the

Quaternary. Proceedings of the National Academy of Sciences USA 112:4915–4921.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

Johnson, D. J., W. T. Beaulieu, J. D. Bever, and K. Clay. 2012. Conspecific negative density dependence and forest diversity. Science 336:904–907.

Lichstein, J. W., J. Dushoff, K. Ogle, A. P. Chen, D. W. Purves, J. P. Caspersen, and S. W. Pacala. 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. Ecological Applications 20:684–699.

Lu, J., G. Sun, S. G. McNulty, and D. M. Amatya. 2005. A comparison of six potential evapotranspiration methods for regional use in the southeastern United States. Journal of the American Water Resources Association 41:621–633.

Manion, P. D. 1981. Tree disease concepts. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Manthey, M., and E. O. Box. 2007. Realized climatic niches of deciduous trees: comparing western Eurasia and eastern North America. Journal of Biogeography 34:1028–1040.

Martin, P. H., and C. D. Canham. 2010. Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. Oikos 119:807–824.

McDowell, N. G., and C. D. Allen. 2015. Darcy's law predicts widespread forest mortality under climate warming. Nature Climate Change 5:669–672.

McKenney, D. W., J. H. Pedlar, K. Lawrence, K. Campbell, and M. F. Hutchinson. 2007. Beyond traditional hardiness zones: using climate envelopes to map plant range limits. BioScience 57:929–937.

Morin, X., C. Augspurger, and I. Chuine. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology 88:2280–2291.

Packer, A., and K. Clay. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404:278–281.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, P. A. Townsend, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58–75.

Pureswaran, D. S., L. De Grandpre, D. Pare, A. Taylor, M. Barrette, H. Morin, J. Regniere, and D. D. Kneeshaw. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. Ecology 96:1480–1491.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Scheller, R. M., and D. J. Mladenoff. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biology 11:307–321.

Seri, E., and N. Shnerb. 2015. Spatial patterns in the tropical forest reveal connections between negative feedback, aggregation and abundance. Journal of Theoretical Biology 380:247–255.

Simova, I., et al. 2015. Shifts in trait means and variances in North American tree assemblages: Species richness patterns are loosely related to the functional space. Ecography 38:649–658.

Sitch, S., et al. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Global Change Biology 14:2015–2039.

Smith, B., I. C. Prentice, and M. T. Sykes. 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Global Ecology and Biogeography 10:621–637.

Stephenson, N. L., and P. J. van Mantgem. 2005. Forest turnover rates follow global and regional patterns of productivity. Ecology Letters 8:524–531.

Tang, G. P., and B. Beckage. 2010. Projecting the distribution of forests in New England in response to climate change. Diversity and Distributions 16:144–158.

Thomas, R. Q., C. D. Canham, K. C. Weathers, and C. L. Goodale. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nature Geoscience 3:13–17.

Thuiller, W., J. Vayreda, J. Pino, S. Sabate, S. Lavorel, and C. Gracia. 2003. Large-scale environmental correlates of forest tree distributions in Catalonia (NE Spain). Global Ecology and Biogeography 12:313–325.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2005. Seedling recruitment in a hurricane-driven tropical forest: light limitation, density-dependence and the spatial distribution of parent trees. Journal of Ecology 93:291–304.

Vanderwel, M. C., V. S. Lyutsarev, and D. W. Purves. 2013. Climate-related variation in mortality and recruitment determine regional forest-type distributions. Global Ecology and Biogeography 22:1192–1203.

Welsh, A. H., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 1996. Modelling the abundance

of rare species: statistical models for counts with extra zeros. Ecological Modelling 88:297–308.

Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. Proceedings of the National Academy of Sciences USA 94:1252–1257.

Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, M. D. Nelson, and A. O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. Forest Ecology and Management 257:1434–1444.

Woodall, C. W., K. Zhu, J. A. Westfall, C. M. Oswalt, A. W. D'Amato, B. F. Walters, and H. E. Lintz. 2013. Assessing the stability of tree ranges and influence of disturbance in eastern US forests. Forest Ecology and Management 291:172–180.

Woudenberg, S. W., B. L. Conkling, B. M. O'Connell, E. B. LaPoint, J. A. Turner, and K. L. Waddell. 2010. The Forest Inventory and Analysis Database: database description and users' manual. Version 4.0 for Phase 2. General Technical Report RMRS-GTR-245. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Xu, M., Y. Wang, and S. Yu. 2015. Conspecific negative density dependence decreases with increasing species abundance. Ecosphere 6:257.

Zhu, K., C. W. Woodall, and J. S. Clark. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18:1042–1052.

Zhu, K., C. W. Woodall, S. Ghosh, A. E. Gelfand, and J. S. Clark. 2014. Dual impacts of climate change: forest migration and turnover through life history. Global Change Biology 20:251–264.

Zhu, K., C. W. Woodall, J. V. D. Monteiro, and J. S. Clark. 2015. Prevalence and strength of density-dependent tree recruitment. Ecology 96:2319–2327.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1424/supinfo