

The demography of tree species response to climate: sapling and canopy tree survival

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Abstract. Traits affecting survival from seedling through adult stages are key elements of tree life histories, and it is widely assumed that variation in survival of adult trees plays an important role in the distribution of species along climate gradients. We use data from plots censused by the U.S. Forest Service Forest Inventory and Analysis program during the years 2000–2011 to quantify relationships between two key aspects of climate—mean annual temperature and growing season water deficit—and rates of sapling and canopy tree survival for the 50 most common tree species in the eastern United States. Our analyses include consideration of the effects of tree size, competition, and nitrogen deposition to avoid confounding effects and to provide context for the importance of variation in climate relative to other factors. Tree size and competitive effects, including the effect of tree size on sensitivity to competition, had the greatest impact on observed variation in survival for all of the species. Survival varied as a function of nitrogen deposition in 20 of the 50 species, and responses were stronger in saplings than in canopy trees. Despite clear sorting of the presence of the tree species along regional gradients of temperature and water deficit, there was only modest evidence that either sapling or canopy tree mortality varied systematically along those gradients. For 24 of the 50 species, the most parsimonious models did not include either temperature or water deficit variables. The exceptions to this were for several species of colder climates in which survival declined significantly in warmer climates. In 40 of the 50 species, there was no significant variation in survival as a function of either average growing season water deficit or the most extreme individual growing season water deficit during the 20 yr preceding the end of the census interval. The frequency of all but the most xeric of our study species declines at some point along a water deficit gradient. But it is seedling survival (reported in earlier work), rather than survival of saplings and canopy trees, that varies systematically along water deficit gradients.

Key words: climate responses of temperate trees; competition; eastern United States; Forest Inventory and Analysis; nitrogen deposition; sapling and canopy tree survival; temperature; water deficit.

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INTRODUCTION

Despite a pressing need to be able to predict the effects of climate change on the distribution and abundance of tree species, we have only a limited understanding of how different aspects of climate influence the demographic processes

that in turn determine the current distribution and abundance of those species (Holt et al. 2005, Parmesan et al. 2005). It seems obvious that climate plays a pre-eminent 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 of other factors that influence the presence and abundance of tree species within a stand (Morin et al. 2007, Canham and Thomas 2010).

Traits affecting survival from seedling through adult stages are key elements of tree life histories. Interspecific differences in seedling and sapling survival as a function of light are the foundation for shade tolerance rankings, and have enormous impact on successional dynamics within forests (Kobe et al. 1995, Pacala et al. 1996, Kobe and Coates 1997). There are also well-documented patterns of geographic variation in the relationship between adult tree mortality and net primary production in forests (e.g., Stephenson et al. 2011). But it is less clear whether—and in what life history stages—variation in survival is a major factor in the climatic distributions of tree species. Schenk (1996) and Loehle and LeBlanc (1996) reviewed early models of climate change impacts on tree species and questioned assumptions that range limits were defined by climatic limits on adult tree survival. Dietze and Moorcroft (2011) and Vanderwel et al. (2013) have examined effects of climate on mortality patterns of species grouped into a limited number of plant functional types, and have found variable but modest effects of climate, and evidence from model simulations that those differences are sufficient to play a role in the geographic distributions of some boreal and northern plant functional types. More recently, Canham and Murphy (2016a) have examined variation in seedling survival as a function of temperature for the 50 most common tree species in the eastern United States. For more than half of the species they examined, greatest survival occurred in climates that were colder than the species' current peak frequency of occurrence, reflecting patterns in which seedling survival declined across a significant portion of the southern end of a species' geographic distribution.

Forest inventory networks provide an important source of data for analysis of the distribution and dynamics of tree species (e.g., Ruiz-Benito et al. 2013, Canham and Murphy 2016a, b). Here, we use data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to extend the analyses of Canham and Murphy (2016a) and quantify the relationships between two key

aspects of climate—mean annual temperature and growing season water deficit—and rates of sapling and canopy tree survival for the 50 most common tree species in the eastern United States. Our analyses include consideration of the effects of tree size, competition, and nitrogen deposition both to avoid confounding effects and to provide context for the importance of variation in climate relative to other factors known to influence survival.

METHODS

Study region, plots, and species

We have analyzed survival for saplings and canopy trees using the same study region, plots and set of 50 tree species used in previous analyses of seedling recruitment, and sapling and canopy tree growth (Canham and Murphy 2016a, b; Table 1). These species represent the most common tree species in the 31 eastern U.S. states (all states east of and including Minnesota, south to Louisiana), based on plot and tree data obtained from the website of the FIA program (<http://apps.fs.fed.us/fiadb-downloads/datamart.html>, data downloaded in September 2012). For each state, we selected census cycles for which both the current and previous censuses were conducted using the national standard plot design, to allow determination of plot and tree conditions at the time of the previous census. The second census years for the plots ranged from 2000 to 2011 (mean = 2007), and average remeasurement intervals, by species, varied from 4.4 to 5.0 yr. Plots that were not classified as “forestland” were excluded from the dataset, as were plots that had been logged during the census interval. “Forestland” is FIA's broadest definition of forest and includes land that has (or is in a land use that could support) at least 10% stocking or canopy cover, including plantations (O'Connell et al. 2014). We also excluded plots in southern pine forest types since the focus of our broader research effort is on the deciduous and mixed deciduous/conifer forests of the eastern United States. This left us with observations on 182,249 saplings and 691,251 canopy individuals of the 50 tree species (Table 1). True plot locations were obtained from the U.S. Forest Service under a security memorandum.

Each FIA plot consists of four circular subplots, with 36.6 m between subplot centers. All

Table 1. Sample sizes for saplings and adults of the 50 study species.

Species	Acronym	No. plots	No. saplings	No. adults	Temperature range	Maximum water deficit (mm)
<i>Abies balsamea</i>	ABBA	4738	21,786	23,017	1.9–8.3	479.2
<i>Acer rubrum</i>	ACRU	16,730	20,485	83,852	2.5–22.8	705.9
<i>Acer saccharum</i>	ACSA	9640	13,246	59,628	2.5–17.9	634.8
<i>Betula alleghaniensis</i>	BEAL	3687	2610	11,563	1.9–15.0	486.5
<i>Betula lenta</i>	BELE	2186	1663	6735	5.3–16.2	631.2
<i>Betula papyrifera</i>	BEPA	4622	4187	17,068	1.9–10.5	486.6
<i>Carya alba</i>	CAAL	4462	1895	8897	7.0–19.8	697.1
<i>Carpinus caroliniana</i>	CACA	1605	3001	1030	4.3–22.3	697.1
<i>Carya glabra</i>	CAGL	4672	1422	9993	6.8–22.1	691.0
<i>Carya ovata</i>	CAOV	3032	951	7475	6.2–18.7	675.7
<i>Cornus florida</i>	COFL	3721	5332	2337	7.6–20.8	705.9
<i>Fagus grandifolia</i>	FAGR	5219	6961	17,615	2.5–20.5	691.4
<i>Fraxinus americana</i>	FRAM	5971	3344	14,829	3.0–19.8	690.6
<i>Fraxinus nigra</i>	FRNI	1568	1611	4211	2.7–14.5	485.9
<i>Fraxinus pennsylvanica</i>	FRPE	2512	1524	5203	3.4–21.8	705.9
<i>Juniperus virginiana</i>	JUVI	2722	2569	9350	6.5–20.6	705.9
<i>Liquidambar styraciflua</i>	LIST	3856	5553	15,041	10.4–22.4	713.3
<i>Liriodendron tulipifera</i>	LITU	5766	3378	21,826	6.6–20.0	705.9
<i>Nyssa sylvatica</i>	NYSY	5429	4446	8351	7.1–21.8	691.4
<i>Ostrya virginiana</i>	OSVI	3642	5800	4063	3.1–20.2	668.3
<i>Oxydendrum arboreum</i>	OXAR	3068	2133	7394	7.4–19.8	691.0
<i>Picea glauca</i>	PIGL	1771	1129	5866	1.9–11.8	482.6
<i>Picea rubens</i>	PIRU	1877	3724	10,392	1.9–11.2	395.6
<i>Pinus banksiana</i>	PIBA	590	322	2516	2.5–10.6	471.9
<i>Pinus echinata</i>	PIEC	2117	406	7376	8.7–19.8	697.1
<i>Pinus resinosa</i>	PIRE	1410	772	17,346	2.5–12.7	519.6
<i>Pinus strobus</i>	PIST	4123	2983	20,476	3.1–16.0	651.0
<i>Pinus taeda</i>	PITA	2637	2493	11,528	9.4–22.3	700.7
<i>Pinus virginiana</i>	PIVI	1654	727	6538	7.8–17.5	654.6
<i>Populus balsamifera</i>	POBA	823	1304	3419	2.7–10.0	476.0
<i>Populus grandidentata</i>	POGR	2434	3417	10,361	2.9–15.6	502.3
<i>Populus tremuloides</i>	POTR	5449	17,609	31,896	2.5–11.7	486.4
<i>Prunus serotina</i>	PRSE	7733	5365	16,623	2.4–22.1	700.7
<i>Quercus alba</i>	QUAL	9877	3342	39,757	4.3–19.8	697.1
<i>Quercus coccinea</i>	QUCO	3260	550	9586	6.8–18.8	679.1
<i>Quercus falcata</i>	QUFA	2402	840	5470	11.4–20.1	697.1
<i>Quercus macrocarpa</i>	QUMA	1242	487	4524	3.2–15.1	557.4
<i>Quercus nigra</i>	QUNI	1847	2665	4727	13.0–22.6	713.3
<i>Quercus prinus</i>	QUPR	3707	1007	21,412	6.0–18.9	669.2
<i>Quercus rubra</i>	QURU	8569	2478	26,775	3.2–18.6	693.0
<i>Quercus stellata</i>	QUST	3289	1131	12,244	10.5–21.8	697.1
<i>Quercus velutina</i>	QUVE	6151	1747	18,345	5.0–19.7	669.6
<i>Robinia pseudoacacia</i>	ROPS	1652	692	4321	5.8–19.2	699.5
<i>Sassafras albidum</i>	SAAL	2751	2235	4885	6.5–19.7	669.6
<i>Thuja occidentalis</i>	THOC	1523	933	8733	1.9–9.1	476.8
<i>Tilia americana</i>	TIAM	3166	1586	11,624	3.3–18.6	599.7
<i>Tsuga canadensis</i>	TSCA	3313	2373	20,269	3.5–16.1	609.4
<i>Ulmus alata</i>	ULAL	2012	1979	2639	10.0–21.4	716.9
<i>Ulmus americana</i>	ULAM	4605	3039	8794	3.6–22.5	705.9
<i>Ulmus rubra</i>	ULRU	2155	1017	3331	5.1–19.0	637.6

Note: Also listed are the number of plots, range of mean annual temperature during the census interval (°C), and the maximum of the average growing season water deficit (mm) during the census interval for plots where a species was present as either a sapling or adult.

trees ≥ 12.7 cm diameter at breast height (dbh) are censused in the 7.32 m radius subplots. Saplings (stems ≥ 2.5 and < 12.7 cm dbh) are censused in a single 2.07 m radius microplot within each subplot. Because of the wide spacing between subplots, and because subplot-scale sapling and canopy tree abundance is used in the analyses to characterize competition, we treat each subplot as a separate sample location. Sample sizes for species ranged from 1030 to 83,852 adults and 322 to 21,786 saplings, in 1072–36,439 subplots.

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 on two primary climate variables: mean annual temperature and growing season water deficit. 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 (Canham and Murphy 2016b), the analyses presented here focus on survival. 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). While drought stress can trigger immediate mortality, it can also initiate a decline syndrome that takes some number of years to eventually result in mortality. Thus, we tested models using two measures of water deficit: (1) the average growing season water deficit for the years between the first and second census and (2) the most extreme water deficit for any year in the 20-yr period up to and including the year of the second census.

We compiled annual and monthly temperature and precipitation data for each plot location using bi-linear interpolation of the 800-m resolution

PRISM climate data (<http://www.prism.oregonstate.edu/>). The calculation of water deficit required estimates of monthly potential and actual evapotranspiration. 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 the 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.

A number of recent studies have documented effects of anthropogenic nitrogen (N) deposition on tree growth and mortality in temperate forests (e.g., Thomas et al. 2010, Dietze and Moorcroft 2011). We used regional maps of total annual wet deposition of nitrate and ammonium generated by the National Trends Network (NTN) of the National Atmospheric Deposition Program (NADP; National Atmospheric Deposition Program 2015). Data for nitrate and ammonium wet deposition were downloaded from the NADP website (<http://nadp.sws.uiuc.edu/ntn/annualmaps/ByYear.aspx>). We then extracted the deposition data for each FIA plot location, using only the data from the years from the beginning to the end of the census interval used for a given plot. Average annual wet nitrate and ammonium depositions ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) were then combined for an estimate of average total annual wet N deposition during the census interval.

A maximum-likelihood model of sapling and adult tree survival

As in our previous analyses of tree growth using FIA data (Canham et al. 2006, Thomas et al. 2010, Canham and Murphy 2016b), we assume that survival is a multiplicative function of terms representing (1) an ontogenetic effect of plant size, (2) a measure of neighborhood competition, and (3) terms representing abiotic environmental

effects. The latter include explicit measures of (1) nitrogen deposition, (2) temperature, and (3) water deficit. In order to minimize potential parameter tradeoffs inherent in any multiplicative model, the sets of factors above are scalars (0–1) which are multiplied by an estimated potential survival (PS) representing expected survival at optimal levels of all of the factors. Thus, the basic model is:

$$\text{survival} = [\text{PS} \times \text{size} \times \text{competition} \times \text{nitrogen} \times \text{temperature} \times \text{water deficit}]^{R/5} \quad (1)$$

where PS is the probability of surviving for a 5-yr interval and R is the remeasurement interval for the subplot, in years. The other terms are dimensionless scalars (0–1). The FIA plots span the full range of edaphic conditions within the study region, and field crews assign a site class code (an ordinal measure from 1 to 7) based on estimates of growth for individual site trees (O’Connell et al. 2014). We grouped the seven site index codes into three general site index classes (FIA plot variable SITECLCD 1–2 = 1; SITECLCD 3–4 = 2; and SITECLCD 5–7 = 3) to ensure adequate sample sizes within the three classes, and estimated separate PS parameters for each of the three classes.

The ontogenetic effect of plant size on survival was modeled as a 4-parameter compound exponential function of diameter at breast height (dbh), to allow for a U-shaped response:

$$\text{size} = (1 - a \times e^{(b \times \text{dbh})}) \times (e^{(c \times \text{dbh}^d)}) \quad (2)$$

where dbh (in meters) is measured at the beginning of the census interval, and a , b , c , and d are estimated parameters. The size term was fit with a single set of parameters for all stems (adults and saplings).

In previous studies with FIA data, we have used a species-specific and distance-dependent neighborhood competition index (NCI) to model the effects of competition (e.g., Canham et al. 2006). For the current study, we followed the approach used in Canham and Murphy (2016b) and used a simpler competition function based on total tree basal area (m^2) in the subplot where an individual tree was located, and included a term to factor in the size of the target tree relative to the mean size of neighbors:

$$\text{competition} = e^{-\alpha \times \text{BAratio}^\gamma \times \text{totalBA}^\beta} \quad (3)$$

where α , β , and γ are estimated parameters. For adult trees, totalBA is the total basal area of all other trees in the 7.32 m radius subplot at the time of the first census. For saplings, totalBA includes the basal area of all adult trees in the subplot, plus the basal area of all other saplings in the 2.07-m microplot. BAratio is the ratio of the mean basal area of individual trees used in the calculation of totalBA to the basal area of the target tree or sapling, at the time of the first census. The parameters α and β determine the shape of the decline in survival with increasing neighbor abundance. The parameter γ determines whether sensitivity of the target tree to crowding varies as a function of its size relative to the mean size (basal area) of neighbors. When γ is zero, there is no effect of target tree size relative to neighbors. As γ increases, target trees are more sensitive to crowding when they are progressively smaller than the mean size of neighbors. Separate sets of the three parameters were fit for saplings and adults because of prior research supporting the assumption that saplings and adults differ in their responses to crowding, and because initial tests showed that fitting separate competition parameters for saplings and adults yielded superior models (in terms of Akaike’s information criterion [AIC]).

The effects of nitrogen deposition on sapling and canopy tree survival were fit with a simple Gaussian function:

$$\text{nitrogen} = e^{-0.5 \left(\frac{N_{\text{deposition}} - N_0}{N_b} \right)^2} \quad (4)$$

where $N_{\text{deposition}}$ is the average annual wet nitrogen deposition ($\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) at the plot location, and N_0 and N_b are estimated parameters. Again, because of both prior research and initial tests, separate sets of parameters were estimated for both saplings and canopy trees.

There is no consensus in the literature on the most appropriate functional forms for the response of tree survival to variation in either temperature or water deficit. Our approach is to use a functional form that is flexible enough to faithfully fit the data but with parameters that have interpretable effects on the shape of the function. As in our analyses of tree growth (Canham and Murphy 2016b), we did initial tests on a

number of simpler alternatives including Gaussian and lognormal functions, but settled on a compound double logistic function with three parameters that controlled the shape of the function at the low end of the temperature or water deficit gradient and three parameters that controlled the shape of the function at the high end of the gradient. The functional form was flexible enough to allow different non-zero tails at each end of the gradient and different shapes of rising and falling responses, with a broad plateau at intermediate temperature or water deficit if dictated by the data:

$$\text{climate response} = \left[\text{low}_a + \frac{1 - \text{low}_a}{1 + \left(\frac{\text{low}_b}{C}\right)^{\text{low}_c}} \right] \times \left[\text{hi}_a + \frac{1 - \text{hi}_a}{1 + \left(\frac{C}{\text{hi}_b}\right)^{\text{hi}_c}} \right] \quad (5)$$

where C is either water deficit or mean annual temperature, and the other terms are estimated parameters. Temperature was converted to degrees Kelvin to avoid discontinuities in the function at zero degrees Celsius. By inverting the position of the climate variable in the two parts of the function, and making the low_c and hi_c parameters strictly positive, the first half of the function allows for a rising response at the low end of the temperature or water deficit gradient, while the second half of the function allows a falling response at the high end of the gradient. But the low_b and hi_b parameters determine over what range of the climate variable the function either rises or falls, and are allowed to vary enough that Eq. 5 can fit monotonically increasing or decreasing responses within the range of the data. For both the *temperature* and *water deficit* effects in Eq. 1, separate sets of parameters were estimated for saplings and adults, because initial tests showed that models that allowed separate climate responses of juveniles and adults were always superior (in AIC) to simpler models that tried to fit both life stages with a single climate response. While this required a large number of estimated parameters (6 parameters \times 2 climate variables \times 2 life

history stages), the sample sizes for all 50 species were also very large (Table 1).

For each of the 50 species, initial model testing and development was done using the global optimization algorithm in our likelihood package in R (R Core Team 2014). Since the regression model (Eq. 1) is already probabilistic, the likelihood function is simply

$$\log - \text{likelihood} = \sum_{i=1}^n \left\{ \begin{array}{l} \log(P(\text{survival})) \\ \text{if the individual survived} \\ \log(1 - P(\text{survival})) \\ \text{if the individual died} \end{array} \right\} \quad (6)$$

Given the very large sample sizes, large number of parameters, and large number of iterations required for convergence of the optimization routine, the final models were fit using an implementation of the optimization algorithm in Java. This reduced the computational demand by more than an order of magnitude. We also tested variants of Eq. 1 in which either or both of the climate variables were dropped from the model. Alternate models were then compared using AIC to choose the most parsimonious model with or without one or both of the climate variables. Uncertainty in the maximum-likelihood parameter estimates was assessed using 2-unit support intervals. Goodness of fit of the models was assessed with a pseudo- R^2 method in which the data were binned by classes of predicted survival, and the mean predicted survival within a class was compared to the fraction of individuals in the class that actually survived during the census interval. We tested for bias using the slope of the relationship between observed and predicted survival across the binned classes.

RESULTS

The models for the 50 species were unbiased (slopes for adult species: mean = 0.996, range 0.971–1.005; for saplings mean = 0.998, range 0.853–1.017), with relatively high R^2 (adult species mean = 0.809, range 0.348–0.953; saplings mean = 0.5262, range –0.678 to 0.925; Table 2 and Appendix S1). The sapling species with low R^2 were five minor species, in which the bins with lowest predicted survival saw higher-than-expected survival (Appendix S1).

Variation in survival with tree size

While it is widely assumed that survival is lowest in both saplings and the largest canopy tree size classes, robust empirical estimates of ontogenetic effects on survival for large trees have been elusive because of small sample sizes, even in studies using large national inventory datasets (Vieilledent et al. 2009, Lines et al. 2010). The maximum-likelihood estimates for the four species-specific parameters for the size term in our model (Eq. 2) produce the expected steep increase in survival with increasing size from the sapling to small canopy tree size classes, and then a gradual decline in survival in the largest canopy tree size classes, with substantial variation among species in the exact shape of the size dependency of survival (Appendix S2). As expected, the support intervals on the predicted decline in survival with increasing size are quite large for many of the species, reflecting small numbers of very large trees of any of the species, even in this dataset with sample sizes ranging from 1,030 to over 83,000 individuals of a given species.

Interspecific differences in effects of competition on sapling and canopy tree survival

Our analysis uses a very simplified functional form (Eq. 3) to capture the effects of crowding on survival as a function of the total basal area of canopy trees and saplings within the immediate neighborhood of a target tree (i.e., within the 7.32 m radius subplot for neighboring canopy trees, and within the 2.07 m radius microplot for neighboring saplings). The parameters α and β in Eq. 3 determine the shape and steepness of the decline in survival with increasing neighbor crowding (as measured by total basal area of neighbors). In general, support intervals on the maximum-likelihood estimates of α and β were much tighter for adults than for saplings of a given species and were tightest for both saplings and adults in species with the largest sample sizes (Appendix S3).

Among saplings, sensitivity to crowding was closely related to traditional shade tolerance rankings (Appendix S4). For a 2 cm dbh sapling with a mean neighbor dbh of 20 cm (i.e., with $BA_{ratio} = 100$) in a neighborhood with a total basal area of 60 m²/ha, *Fagus grandifolia* was the least sensitive to crowding among the canopy-sized

species, followed by *Tsuga canadensis*, *Acer saccharum*, *Acer rubrum*, and *Abies balsamea*. Two of the understory species (*Ostrya virginiana* and *Carpinus caroliniana*) and one sub-canopy species (*Ulmus alata*) were three of six species least sensitive to crowding while in the sapling size classes (Appendix S4, among only species for which the range of the support intervals for the estimated competitive effect was <10% in absolute units of survival). There were two anomalous species: Neither *Betula lenta* nor *Carya alba* are considered shade tolerant, but there was little predicted variation in sapling survival as a function of overstory basal area for either of these species (Appendix S4). Saplings of the six species of pines (*Pinus* spp.) and the three species of *Populus* were among the most sensitive to crowding (Appendix S4).

Rankings of the sensitivity of canopy trees to crowding were much less closely tied to traditional shade tolerance classifications (Appendix S4). While adults of the three shade-tolerant species—*T. canadensis*, *F. grandifolia*, and *A. saccharum*—were all relatively insensitive to crowding, adults of all three of the hickory species (*Carya* spp.) and the three species of elms (*Ulmus* spp.) were also relatively insensitive to crowding. The most sensitive to crowding were (as with saplings) the *Populus* species. Oaks (*Quercus* spp.), in general, were also very sensitive to crowding (Appendix S4).

The functional form for competition (Eq. 3) also includes an estimated parameter (γ) to allow for variation in sensitivity to crowding as a function of the basal area of the target tree, relative to the mean basal area of neighbors. The effect of the size of an individual target tree (relative to the average size of neighbors) on its sensitivity to crowding was much stronger for adult trees than for saplings (mean γ for adults = 0.96, 25–75% quartiles = 0.71–1.24 among the 50 species; mean γ for saplings = 0.30, 25–75% quartiles = 0.03–0.31). There was no clear relationship between shade tolerance and the effect of target tree size relative to mean neighbor size on sensitivity to crowding for either saplings or adults (Appendix S4). The very shade-tolerant *F. grandifolia* had the lowest estimated γ as an adult, but *T. canadensis*—also very shade tolerant—had a relatively high estimated γ as an adult.

Table 2. Comparison of differences in AIC among five alternate models: the full model in Eq. 1, and models with either mean annual temperature (“mean temp”), average annual growing season water deficit (mean WD), or the most extreme growing season water deficit during the 20 yr up to the year of the second census (LT WD) as the only climate term in the model.

Species	Full model	Mean temp	Mean WD	LT WD	No climate	Sapling R^2	Adult R^2
<i>Abies balsamea</i>	23	168	0	23	163	0.71	0.87
<i>Acer rubrum</i>	0	360	12	34	345	0.88	0.81
<i>Acer saccharum</i>	0	14	38	36	38	0.26	0.93
<i>Betula alleghaniensis</i>	37	23	12	34	0	0.83	0.75
<i>Betula lenta</i>	51	17	21	39	0	0.28	0.84
<i>Betula papyrifera</i>	21	40	0	22	32	0.63	0.85
<i>Carya alba</i>	37	14	23	47	0	0.01	0.73
<i>Carpinus caroliniana</i>	25	21	1	17	0	0.39	0.78
<i>Carya glabra</i>	44	26	23	46	0	-0.68	0.76
<i>Carya ovata</i>	34	24	7	34	0	0.58	0.76
<i>Cornus florida</i>	16	121	0	19	104	0.81	0.87
<i>Fagus grandifolia</i>	18	93	0	31	182	0.76	0.79
<i>Fraxinus americana</i>	43	96	0	48	72	0.74	0.95
<i>Fraxinus nigra</i>	41	18	22	43	0	0.41	0.78
<i>Fraxinus pennsylvanica</i>	31	68	12	0	43	0.59	0.89
<i>Juniperus virginiana</i>	5	0	26	41	55	0.65	0.90
<i>Liquidambar styraciflua</i>	14	21	2	6	0	0.89	0.93
<i>Liriodendron tulipifera</i>	38	21	16	43	0	0.75	0.90
<i>Nyssa sylvatica</i>	24	21	3	28	0	-0.06	0.81
<i>Ostrya virginiana</i>	18	4	21	27	0	-0.23	0.39
<i>Oxydendrum arboreum</i>	48	31	18	38	0	0.78	0.89
<i>Picea glauca</i>	25	42	0	18	19	0.75	0.90
<i>Picea rubens</i>	36	15	18	36	0	0.61	0.35
<i>Pinus banksiana</i>	43	24	21	44	0	0.92	0.72
<i>Pinus echinata</i>	36	45	58	0	53	0.35	0.80
<i>Pinus resinosa</i>	17	72	14	0	73	0.81	0.83
<i>Pinus strobus</i>	1	6	4	30	0	0.64	0.79
<i>Pinus taeda</i>	51	80	33	0	66	0.82	0.92
<i>Pinus virginiana</i>	60	49	34	0	21	0.70	0.94
<i>Populus balsamifera</i>	39	53	0	17	18	0.71	0.92
<i>Populus grandidentata</i>	53	37	29	33	0	0.81	0.90
<i>Populus tremuloides</i>	56	91	0	24	98	0.81	0.84
<i>Prunus serotina</i>	0	67	3	27	60	0.86	0.91
<i>Quercus alba</i>	20	6	8	25	0	0.38	0.63
<i>Quercus coccinea</i>	30	28	0	26	0	0.93	0.86
<i>Quercus falcata</i>	44	27	12	37	0	0.90	0.90
<i>Quercus macrocarpa</i>	45	25	23	49	0	0.74	0.82
<i>Quercus nigra</i>	56	58	0	63	21	0.86	0.92
<i>Quercus prinus</i>	46	19	0	5	21	0.77	0.85
<i>Quercus rubra</i>	20	161	0	4	180	0.35	0.86
<i>Quercus stellata</i>	34	25	16	36	0	0.29	0.80
<i>Quercus velutina</i>	17	122	0	20	134	0.05	0.89
<i>Robinia pseudoacacia</i>	45	28	20	36	0	-0.63	0.90
<i>Sassafras albidum</i>	18	38	0	20	10	0.50	0.91
<i>Thuja occidentalis</i>	21	30	0	22	4	0.91	0.37
<i>Tilia americana</i>	42	18	21	37	0	0.75	0.72
<i>Tsuga canadensis</i>	26	88	0	24	62	0.57	0.61
<i>Ulmus alata</i>	18	23	5	25	0	-0.39	0.84
<i>Ulmus americana</i>	21	89	24	0	107	0.25	0.84
<i>Ulmus rubra</i>	26	34	0	29	22	0.29	0.73

Notes: The fifth model (no climate) does not include any climate terms. The best model has a Δ AIC of zero (in boldface). Also reported is the pseudo- R^2 of the best model for prediction of sapling and adult survival (see text and Appendix S1 for details on calculation of R^2).

Effects of N deposition on sapling and canopy tree survival

Survival did not vary as a function of average annual wet nitrogen (N) deposition for 30 of the 50 species (Appendix S5). Responses to N deposition among the remaining species were more commonly found in saplings than in canopy trees (12 of 20 species as saplings, vs. nine of 20 species of adults), and responses of saplings were typically much stronger than the responses of canopy trees (Fig. 1; Appendix S5). Previous analyses of variation in growth as a function of N deposition have found that endomycorrhizal species were more likely to respond, and respond positively, to N deposition than were ectomycorrhizal species (Thomas et al. 2010, Phillips et al. 2013, Canham and Murphy 2016b). In contrast, in our current results, roughly equal proportions of endo- and ectomycorrhizal species showed survival responses to N deposition as either saplings or canopy species (five of 17 endomycorrhizal species and 11 of 33 ectomycorrhizal species; Appendix S5). And with few exceptions (i.e., *Pinus virginiana* and *Quercus velutina*), survival peaked at intermediate levels of N deposition ($\sim 5\text{--}6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and declined as N deposition increased (Fig. 1; Appendix S5).

Variation in sapling and canopy tree survival along temperature and water deficit gradients

Despite clear sorting of the presence of the tree species along regional gradients of temperature and water deficit, there was little evidence that either sapling or canopy tree mortality varied systematically along those gradients (Fig. 2; Appendix S2). For almost half of the species (24 of 50), the most parsimonious models did not include either temperature or water deficit variables (Table 2). The raw data for sapling and canopy tree survival along temperature and water deficit gradients confirm the disconnect between survival and the frequency of occurrence of most species along those climate gradients (Appendix S6). There was no response to variation in mean annual temperature in just over half of the species (26 of 50). Support intervals on the predicted temperature responses were quite large, particularly for saplings, indicating that sapling survival was particularly insensitive to regional variation in mean annual temperature (Appendix S2). The exceptions to

this general lack of pattern between sapling and canopy tree survival and species distributions along temperature gradients were in three species of colder climates: *A. balsamea*, *Betula papyrifera*, and *Picea glauca*. In all three of these species, canopy tree survival declined significantly in warmer climates (Fig. 2).

In 40 of the 50 species, there was no significant variation in survival as a function of either average growing season water deficit during the census interval or the most extreme individual growing season water deficit during the 20 yr preceding the end of the census interval (Table 2). In six of the remaining 10 species, the most parsimonious model included a response to the most extreme water deficit during the preceding 20 yr, but with a counter-intuitive pattern. Four of the six species were pines that typically occur on dry sites (*Pinus echinata*, *Pinus resinosa*, *Pinus taeda*, and *P. virginiana*), and in all four species, survival was higher in sites that had more extreme water deficits at some point during the preceding 20 yr (Appendix S2).

DISCUSSION

We deliberately excluded plots that had been harvested during the most recent census interval, since analyses of regional variation in logging frequency and intensity require consideration of a much different set of ecological, economic, and social drivers (Canham et al. 2013). The FIA program posts periodic evaluations of the forest inventory data, by state, including data on aggregate rates of removal of timber. It is worth noting that logging is by far the largest single cause of mortality of adult trees (stems $\geq 12.7 \text{ cm dbh}$) in forests of the eastern United States, and exceeds all other causes of mortality combined. For plots censused during the period from 2003 to 2008 in the 19 northeastern states from Kentucky and Virginia north to Wisconsin and Maine, harvesting accounted for 58% (on a volume basis) of annual tree mortality (Canham et al. 2013).

Ontogeny and the importance of plant size

Models of forest structure and dynamics are quite sensitive to accurate representation of the ontogenetic effects of tree size on survival, including the effects of tree size on sensitivity to

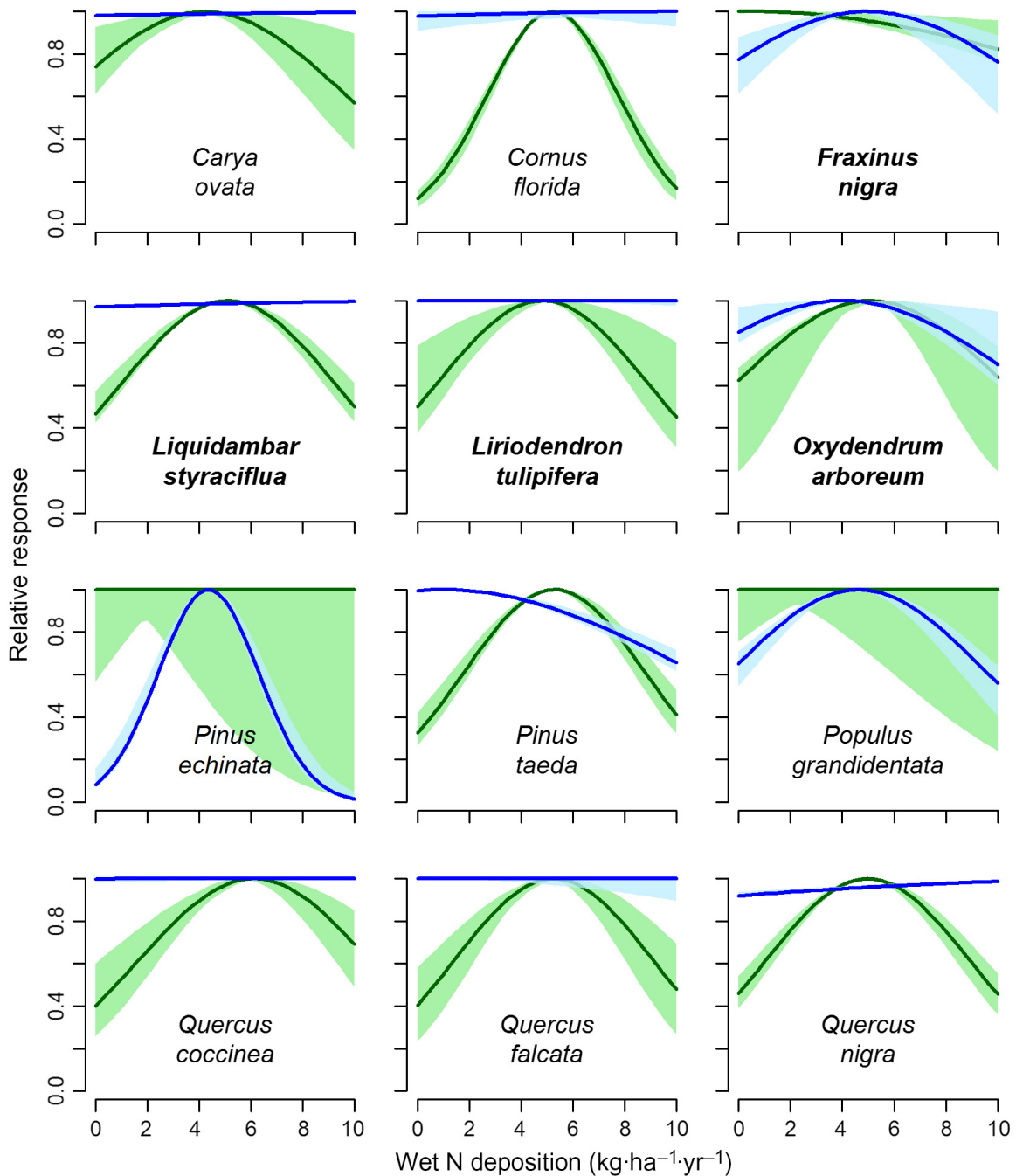


Fig. 1. Predicted relative responses of 5-yr survival of 12 representative species to variation in total wet nitrogen (N) deposition ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) for saplings (stems ≥ 2.54 cm dbh, green) and adult trees (stems ≥ 12.7 cm dbh, blue). The shaded regions are the bounds of 2-unit support intervals around the predicted curves, with green shading for saplings and blue shading for adults. In many cases, the support regions are too narrow to display. Species with endomycorrhizal associations are identified in bold type. For reference, the mean wet N deposition for the plots in the dataset was $4.68 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ and ranged from 2.1 to $10.5 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, with first and third quartiles of 3.9–5.4 $\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$.

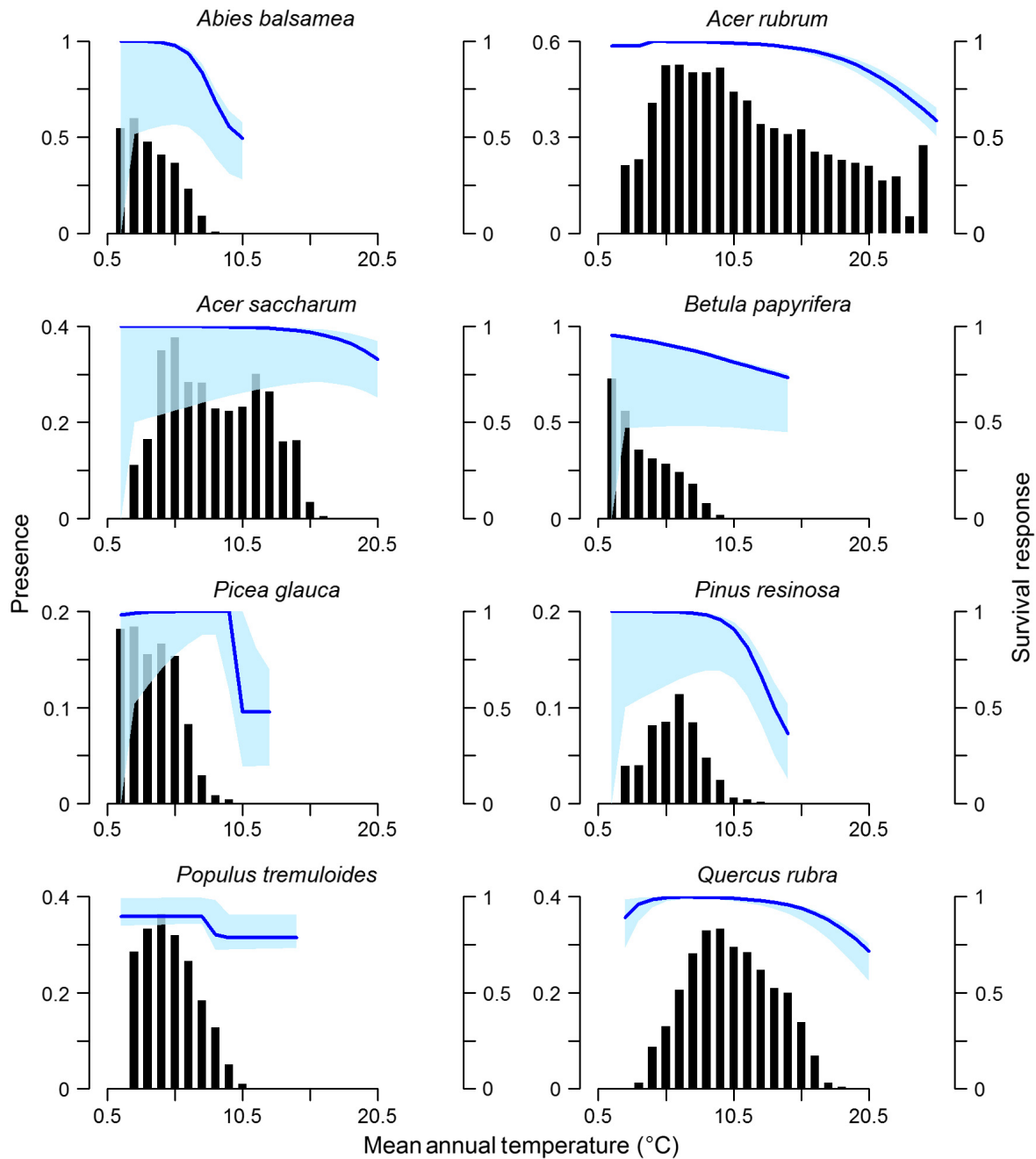


Fig. 2. Expected responses (blue line, fraction of potential 5-yr survival, right-hand axis) to variation in mean annual temperature for canopy trees of eight representative tree species. Lines are plotted only over the range of temperature in which a species occurred. The shaded areas around each line are 2-unit support limits on the predicted responses. The histograms (black bars) show the fraction of plots (left-hand axis) in 1-degree intervals of mean annual temperature in which canopy trees of a given species occurred.

competition and abiotic stress (Pacala et al. 1996, Astrup et al. 2008). And while it is widely assumed that ontogenetic effects on mortality are generally “U-shaped,” with an uptick in mortality rates in very large trees (Uriarte et al. 2004, Vieilledent et al. 2009, Lines et al. 2010), even datasets from large national forest inventories typically contain too few very large trees to provide robust estimates of the relationship between size and survival in large trees. Vieilledent et al. (2009) argue for a semi-parametric approach to estimation of size-dependent mortality to address this issue. Regardless of whether parametric or non-parametric approaches are used in estimation, small sample sizes for very large trees result in considerable uncertainty in the absolute magnitude of any decline in survival among large trees.

Stephenson et al. (2011) argue that true senescence is not common in trees, but note that there are cumulative effects of stress and damage over time that result in an age- and/or size-related increase in mortality. Given well-known life history-related differences in lifespan and mature tree size, that uptick in mortality occurred across very different sizes among our 50 study species (Appendix S2). Size-dependent patterns of mortality in at least a subset of the species also appear to reflect the long-term impact of introduced pests and pathogens. *Fagus grandifolia*, *T. canadensis*, and *Ulmus americana* are all subject to region-wide impacts of introduced pests or pathogens in which mortality is size dependent in at least the early stages of an infestation (Mize and Lea 1979, Orwig and Foster 1998, Marks and Canham 2015).

Competition

We included a term for competition in our analyses to control for the effects of competition and avoid confounding any climate-based differences in the average intensity of competition with underlying direct effects of climate on survival of both saplings and canopy trees. As with our analyses of sapling and canopy tree growth (Canham and Murphy 2016b), the functional form for the competition index used here is simpler than in our previous studies that are spatially explicit and account for species-specific differences in both competitive effects and responses (Canham et al. 2004, 2006). Those more complex formulations of

competitive interactions yield much better goodness of fit (R^2), but do so at the cost of a much greater computational burden in both parameter estimation and implementation of the resulting relationships in forest simulation models. Even the simple formulation for competitive effects used here, however, confirms that the combined effects of crowding and target tree size (including the effects of target tree size relative to the mean size of neighbors on sensitivity to crowding) have the greatest impact on predicted survival of any of the terms in the model (Appendix S2).

Nitrogen deposition

Our analyses of the effects of nitrogen (N) deposition on sapling and canopy tree survival expand on an earlier analysis using FIA data for canopy trees only in a smaller set of species (23 vs. 50) and over a smaller geographic region (19 northeastern and north central states vs. the 31 easternmost states; Thomas et al. 2010). In that earlier study, survival of canopy trees of 11 of 23 species varied in response to N deposition. Eight of those species were ectomycorrhizal, and survival of all eight declined monotonically with increasing N deposition (Thomas et al. 2010). The results from our current analysis of the larger sample of tree sizes and species and across a much larger region confirm the general patterns of the previous study, but with some important differences. Notably, even the endomycorrhizal species that responded to N deposition in the current analysis showed peak survival at intermediate levels of N deposition and declines in survival when deposition exceeded $5\text{--}6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of wet deposition (roughly equal to an area-weighted mean wet deposition for the 31-state region). Moreover, saplings often had different responses to N deposition than canopy trees and, in general, showed stronger responses than canopy trees of the same species (Fig. 1; Appendix S5). A positive response of survival to what is effectively N fertilization is likely to reflect an indirect effect of higher N availability on sapling growth (e.g., Bigelow and Canham 2007), coupled with a positive relationship between growth and survival (i.e., Kobe et al. 1995). The mechanisms behind a decline in survival with increasing N deposition may be more varied and species-specific. For example, Dzedek et al. (2016) reported increased drought sensitivity in two temperate tree species

under nitrogen addition treatments. N fertilization can also increase pest and pathogen attack in temperate trees (e.g., McClure 1991, Latty et al. 2003). Negative effects of chronic N deposition on sapling and canopy tree survival may also reflect the suite of ecosystem changes associated with N saturation (Aber et al. 1998).

The role of variation in seedling, sapling, and canopy tree survival in the biogeography of temperate trees

Our results provide very limited evidence that variation in sapling and canopy tree survival plays an important role in the distribution and abundance of these tree species along gradients of mean annual temperature and either the average or the most extreme growing season water deficit at a location. And yet, as previous analyses have documented (Canham and Thomas 2010), and confirmed here (Fig. 2; Appendix S2), the frequency of occurrence of seedlings, saplings, and canopy trees does vary systematically along those gradients. Our previous studies have examined seedling recruitment and survival (Canham and Murphy 2016a) and sapling and canopy tree growth (Canham and Murphy 2016b). Of the three life history stages (seedlings, saplings, and canopy trees) and the three demographic processes (recruitment, growth, and survival), seedling recruitment and survival had the strongest relationships with patterns of species distribution and abundance (Canham and Murphy 2016a). Other recent analyses of FIA data have also noted variation in seedling abundance and recruitment along latitudinal and climate gradients (Johnson et al. 2012, Zhu et al. 2015). There are notable exceptions in our current results, particularly for a limited set of conifer species common in colder climates (e.g., *A. balsamea*, *P. glauca*, and *P. resinosa*, Fig. 2), where adult survival is much lower in warmer climates. These results are in broad agreement with previous studies that have examined geographic variation in sapling and canopy tree mortality in eastern U.S. forests, across either all species lumped together or sorted into broad plant functional types (Brown and Schroeder 1999, Lines et al. 2010, Dietze and Moorcroft 2011, Vanderwel et al. 2013, 2016).

Early studies of the biogeography of temperate trees assumed that competition determined

southern range boundaries, while stress, particularly tolerance of freezing injury due to minimum winter temperatures, determined northern boundaries (e.g., Sakai and Weiser 1973, Loehle 1998). A number of studies have noted that minimum winter temperatures correlate with northern range limits in many temperate tree species (e.g., Thuiller et al. 2003), and early models of responses of temperate forests to climate change often assumed that northern range limits of those species were governed by low adult tree survival due to extreme winter temperatures (e.g., Sykes and Prentice 1995). While we have used mean annual temperature in our analyses, it is highly correlated with both average and the most extreme minimum monthly winter temperatures over the past 30 yr. With very few exceptions, notably two of the southern pine species (*P. taeda* and *P. echinata*; Appendix S2), there was little evidence that sapling and canopy tree survival declined across the colder end of a species' current distribution. In contrast, it was much more common for seedling survival to decline slightly in colder climates (Canham and Murphy 2016a). And more broadly, after accounting for competition, there are stronger temperature effects on survival at the warmer edge of a species' range than at the northern edge (Canham and Murphy 2016a).

Drought stress and canopy tree mortality in mesic temperate forests

Our results also provide very limited evidence that geographic variation in either average or extreme growing season water deficits explains patterns of variation in sapling or canopy tree mortality of the 50 most common tree species in these generally mesic temperate forests. This is in contrast to the occurrence of drought-related mortality in more xeric forests worldwide (van Mantgem and Stephenson 2007, Allen et al. 2010, Anderegg et al. 2015, Moore et al. 2016). Steinkamp and Hickler (2015) addressed the generality of drought stress-related mortality events in forests globally and concluded that it was present primarily in xeric climates. There are clearly many challenges both in measuring drought stress and in a mechanistic assessment of the role of drought stress in tree mortality (McDowell et al. 2008). Our calculation of growing season water deficit would presumably miss short-duration drought

events within a growing season, but should still have a broad general correlation with the likelihood of extreme drought events across sites. The frequency of occurrence of all but the most xeric of our study species declines at some point along the water deficit gradient (Appendix S2). But as with the distributions of these species along temperature gradients, it is seedling survival, rather than survival of saplings and canopy trees, that varies systematically along water deficit gradients (Canham and Murphy 2016a).

Displacement of fundamental vs. realized climate niches across life history stages

By factoring out ontogenetic and competitive effects, our analyses of potential growth and survival of seedlings, saplings, and canopy trees provide an assessment of the fundamental climate niches of the species (Canham and Murphy 2016a, b, and current results). These can be compared to the distributions of abundance of the species along the climate gradients to assess displacement of the fundamental vs. realized climate niches of the species. Two main patterns emerge from those comparisons. First, there is significant displacement of the realized niches (frequency of occurrence) from climates with optimal growth or survival (as measures of fundamental niches; Canham and Murphy 2016a, b). Second, the fundamental climate niches of a given species (i.e., climates with optimal growth and survival after controlling for ontogeny and competition) differed among the three life history stages. For example, seedling survival of most of the 50 species was higher in drier and colder plots than where the species was most frequently found (Canham and Murphy 2016a). In contrast, the most common pattern among the 50 species was for growth of saplings and canopy trees to be higher in warmer plots than where the species was most frequently found (Canham and Murphy 2016b).

Mesoscale vs. local climate and the biogeography of temperate trees

Any examination of the relationship between climate and the biogeography of the temperate tree species of eastern North America has to address the most salient feature of the patterns of distribution of those species. Specifically, species vary systematically in the frequency of their

occurrence (at the stand level) along climate gradients, while their average relative abundance within a stand (when present) shows little variation along those climate gradients (Canham and Thomas 2010, Canham and Murphy 2016a, b; Appendix S2 of this study). This suggests that a general explanation for the climate distributions of these species is best couched in terms of metapopulation dynamics and the factors that control the colonization and local extinction dynamics of species within individual locations. Strong variation in seedling recruitment and survival along temperature and water deficit gradients (Canham and Murphy 2016a) supports this view. But the patterns of variation in the presence of species within stands along the climate gradients are still much more pronounced than the observed variation in demography we have documented at any of the three life history stages (seedlings, saplings, and canopy trees). The climate variables we have used in our analyses combine both mesoscale climate and finer-scale topographic and soil factors that determine plot-level variation in both temperature and moisture regimes. But there are obviously additional local factors such as cold air drainage and upslope contributions to soil moisture that could modify those local temperature and moisture regimes. Thus, while our mesoscale climate variables can define average expected conditions at the plot level, in any given mesoclimate we would expect local variation both above and below mean conditions. One consequence would be that even if the critical demographic processes had effectively “square” functional forms, with little variation within the range of a species but a set of sharply defined demographic limits, the frequency of occurrence of suitable local or microclimate conditions within a given mesoclimate would still be expected to decline as climate varied above or below the optimal conditions for a species, producing the observed roughly Gaussian distributions of presence along mesoclimate gradients.

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