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Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America

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Abstract. There have been many attempts to model the impacts of climate change on the distributions of temperate tree species, but empirical analyses of the effects of climate on the distribution and abundance of tree species have lagged far behind the models. Here, we used forest inventory data to characterize variation in adult tree abundance along climate gradients for the 24 most common tree species in the northeastern United States. The two components of our measure of species abundance—local frequency vs. relative abundance—showed dramatically different patterns of variation along gradients of mean annual temperature and precipitation. Local frequency (i.e., the percentage of plots in a given climate in which a species occurred) varied strongly for all 24 species, particularly as a function of temperature. Relative abundance when present in a plot, on the other hand, was effectively constant for most species right up to their estimated climatic range limits. Although the range limits for both temperature and precipitation were quite broad for all of the species, the range of climates within which a species was common (i.e., high frequency) was much narrower. Because frequency in sites within a given climate shows a strong sensitivity to temperature, at least, this suggests that the processes determining canopy tree recruitment on new sites also vary strongly with climate.

Key words: biogeography of temperate trees; climate niche breadth; climatic range limits; Forest Inventory and Analysis (FIA); northeastern United States; realized niches of temperate trees; relative abundance vs. local frequency.

INTRODUCTION

Much of the recent research on the potential implications of climate change for the distribution and abundance of tree species has focused on coarse, continental-scale distributions of species as a function of climate, often based solely on presence–absence data across the current geographic ranges of tree species (i.e., Thuiller et al. 2003, McKenney et al. 2007). The resulting "climate-envelope" models have been widely used (e.g., Huntley et al. 1995, McKenney et al. 2007) and their merits widely debated (Loehle and LeBlanc 1996, Jeschke and Strayer 2008), but even the criticisms of climate-envelope models typically do not seek to change the scale of interest from very coarse patterns of presence–absence at a continental scale. As a result, there has been much less focus on finer-scale patterns of frequency of occurrence and relative abundance at sites within a given climate (Iverson and Prasad 1998, Rehfeldt et al. 2008).

There has been considerable recent interest in the use of niche theory as a foundation for predicting climate change impacts on the distribution and abundance of tree species (e.g., Pulliam 2000, Manthey and Box 2007). There are a number of challenges, including distinguishing between fundamental and realized niches (Vetaas 2002, Canham et al. 2006), identifying operationally defined climate variables (Thuiller et al. 2003), and assessing the degree to which geographic distributions can track climate change due to limitations in plant migration rates (Clark et al. 2003, Holt et al. 2005). In many cases, range limits are treated as realized climate niches (i.e., Thuiller et al. 2003, Manthey and Box 2007), without consideration of the dynamic, metapopulation structure of plant distributions at the landscape scale.

In this study we used forest inventory data to characterize variation in two distinct components of adult tree species distribution along climate gradients: average relative abundance when present, and the

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frequency of sites within a particular climate where a species occurred. We were specifically interested in how these two very different metrics of abundance responded to variation in climate, and whether there was evidence of functional groups of species with similar niche dimensions, or whether there was a more individualistic distribution of species along the climate gradients.

MATERIALS AND METHODS

Our analyses are based on data from the USDA U.S. Forest Service Forest Inventory and Analysis (FIA) program. We selected a 19-state region of the northeastern United States for study, from Maine in the north to Virginia and Kentucky in the south and to longitude 90° west in the states of Wisconsin and Illinois. The study area contains a range of continental and maritime climates, with annual mean temperatures ranging from ~0° to 16°C and average annual precipitation from 600 to 2000 mm during the period of the censuses. Although there is a slight positive covariance between temperature and precipitation within this region, there is a wide range of precipitation regimes for any given annual mean temperature, and vice versa.

We used the most recent full census of FIA plots in each of the 19 states (see Appendix A for census periods and numbers of plots, by state, and for a list of the 24 most common tree species in the region that were selected for study). Descriptions of sample design and field methods are *available online*.[4] Although FIA methodologies have been standardized nationwide in the past decade, pre-1999 census methods varied among states. In our specific data set, the majority of the states in the study region were sampled using the current protocol of 24-foot radius plots, but several of the states were sampled with variable-radius plots. Because our analyses required knowledge of exact plot location (to extract climate data at the plot level), we had to limit our analyses to plots for which GPS coordinates of exact plot location were available through a security memorandum with the FIA program. We compiled climate data for each plot using bilinear interpolation of the 800-m resolution PRISM climate data (*available online*).[5] We downloaded annual climate data for the period from the previous to the most recent full census in the plot data set, and then for each plot we did the bilinear interpolation using only data from the specific years between the two censuses at that plot. Although there is a rich literature relating plant performance to a wide range of climatic variables that can be derived from data on temperature and precipitation (e.g., Thuiller et al. 2003), we have focused our analyses on two primary climate variables: average annual mean temperature and average annual precipitation. Our reasons are based on both pragmatism and principle. More complex, derived climate variables (i.e., potential evaporation, drought indices, and so forth) clearly have a more direct, mechanistic link to plant performance, although the specific derived climate variables that would provide the best predictive power could vary among species. Much of the scientific and policy debate about the effects of climate change, however, has been couched in terms of changes in annual mean temperature and total rainfall (Schneider et al. 2007).

Statistical analyses

We calculated relative abundance of the 24 focal species in each of the plots, based on their percentage of aboveground adult tree biomass at the time of the second census. Biomass was calculated from stem diameter using dimension analysis equations (Jenkins et al. 2004) for all adult trees (stems $\geq$ 12.7 cm diameter breast height). We omitted plots with no live adult trees (as a result of either harvesting or natural disturbance), leaving 18 546 plots within the study region, with an average of 17.7 live trees per plot for calculation of relative abundance. Examination of the data on relative abundance by plot showed that the distributions for all of the species were both left-skewed and zero-inflated (i.e., a variable, but large, number of plots with zero abundance, and non-normal distributions even for the plots with nonzero abundance). Thus, we partitioned the analysis of relative abundance into two components: (1) "frequency," i.e., the probability that a species was present in a plot, and (2) relative abundance when present. The data also displayed clear evidence of range limits along the temperature and precipitation gradients where the probability of presence was effectively 0. This required that we add a third component to the model to estimate upper and lower range limits; i.e., points along the temperature and precipitation gradients beyond which the probability of presence was effectively zero (and predicted relative abundance = 0).

We used a Gaussian function for predicted relative abundance when present:

$$\mathrm{RA} = \mathrm{ra}_{\max}\exp\left[-0.5\left(\frac{x-\mathrm{ra}_m}{\mathrm{ra}_v}\right)^2\right]$$

$$\text{if } x_{\min} \leq x \leq x_{\max}; \quad \text{otherwise RA} = 0 \tag{1}$$

where x was annual mean temperature or annual precipitation in a plot, and $x_{\min}$ and $x_{\max}$ were the estimated lower and upper range limits for the climate variable, respectively. While the Gaussian function has been widely used in describing niche dimensions of species, our choice of its use here also reflects the very flexible nature of the function. Depending on the values of the parameters ra_m (i.e., the mode) and ra_v (i.e., the standard deviation), the shape of the function can be monotonically increasing, monotonically decreasing, or unimodal within a give range of x. Note that relative abundance was scaled from 0 to 100, so $\mathrm{ra}_{\max}$ was the predicted relative abundance (in percentage of plot aboveground tree biomass) in the optimal environment

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[4] ⟨http://fia.fs.fed.us/⟩

[5] ⟨http://www.prism.oregonstate.edu/⟩

(i.e., when $x = \mathrm{ra}_m$). Given the skew in the data, we used a gamma distribution for the likelihood function.

Eq. 1 is truncated to zero when a plot is outside the estimated climatic range limits for a given species. There has been relatively little work on defining statistical estimation methods for climatic range limits (Parmesan et al. 2005, Platts et al. 2008). In our likelihood framework, we define a climatic range limit as the value along a climate gradient beyond which the probability of observing a nonzero abundance within a plot is set to some arbitrarily defined but very small likelihood. Setting this likelihood threshold to zero (i.e., an absolute limit) is problematic for both computational reasons (generating underflows when taking the log of zero) and from a sampling perspective, because there can be errors in identification of species that result in records outside the true range of a species. More generally, there is a fractal dimension to the problem of range limits that is outside the scope of our study (Fortin et al. 2005). We arbitrarily set the likelihood to 1 in a million (0.000001) for the probability of observing a species present in a plot outside the estimated range limit for the species. We tested alternate thresholds and they did not result in significant changes in the estimated range limits because the thresholds in relative abundance along the temperature and precipitation gradients were quite abrupt.

Zero-inflated likelihood functions have been widely used for over-dispersed count data where there are more zero observations than expected by a traditional Poisson or negative binomial distribution (e.g., Lambert 1992, Welsh et al. 1996). The approach can be generalized to continuous variables in which the data represent a mixture of two processes: one that generates zeroes in the independent variable, and one that determines the expected value when it is nonzero. 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 two climate gradients. Thus, we modeled the zero-inflation term (P_z) again as a Gaussian function:

$$P_z = 1 - \mathrm{Prob(presence)}$$

where

$$\mathrm{Prob(presence)} = p_{\max}\exp\left[-0.5\left(\frac{x - p_m}{p_v}\right)^2\right]. \qquad (2)$$

The overall likelihood function was thus

$$\mathrm{Prob}(y \mid \theta) = \begin{cases} 0.000001 & \text{if } x < x_{\min} \text{ or } x > x_{\max} \\ P_z & \text{if } y = 0 \\ (1 - P_z)\mathrm{Gamma}(y \mid \theta) & \text{if } y > 0 \end{cases} \qquad (3)$$

where y was the observed relative abundance of a given species in a plot, x was the annual mean temperature or annual precipitation in the plot, $x_{\min}$ and $x_{\max}$ were the estimated lower and upper climate range limits for the species, P_z was the estimated zero-inflation term, and $\mathrm{Gamma}(y \mid \theta)$ was the probability of observing an abundance of y given a gamma distribution and the estimated parameters of the model (θ) (Eqs. 1 and 2). Note that in Eq. 3, P_z combines both the structural zeros and the sampling zeros: $\mathrm{Gamma}(0 \mid \theta)$, i.e., the probability of observing a zero value given the parameters of the model for abundance when present (Eq. 1).

We used simulated annealing to find the maximum-likelihood estimates of the parameters of the model for each of the 24 species as a function of either annual mean temperature or annual precipitation. Simulated annealing (Goffe et al. 1994) uses an iterative procedure to search globally for the parameters that maximize the likelihood (Eq. 3). Thus, for instance, the range limits ($x_{\min}$ and $x_{\max}$) are found by simply trying 10 000 iterations with different values for each of the parameters. We calculated two-unit support intervals to evaluate the strength of evidence for the maximum-likelihood parameter estimates. The maximum-likelihood parameter estimates and two-unit support intervals for all of the models are presented in Appendix B. All analyses were done using R version 2.9.0 (R Development Core Team 2009).

Results

The two components of our measure of species abundance, frequency vs. relative abundance, showed dramatically different patterns of variation along the two climate gradients (Fig. 1). Frequency (i.e., the percentage of plots in a given climate in which a species occurred) varied strongly for all 24 species, particularly as a function of temperature (see Plate 1). Relative abundance when present in a plot, on the other hand, was effectively constant for most species right up to their estimated climatic range limits (Fig. 1). In all species where there was measurable variation in relative abundance as a function of temperature, species were more abundant in colder climates (Fig. 1). If the probability of the presence of a species is treated as a measure of the realized climate niche of a species, then the parameter p_v in Eq. 2 is effectively a measure of realized niche breadth, and p_m is a measure of niche mode (Table 1). There have been analyses showing that early-successional species have wider range limits (Morin and Chuine 2006), but two of the most shade-tolerant of the 24 species we examined, *Acer saccharum* and *Fagus grandifolia*, had the highest niche breadths along the temperature gradient (Table 1). The two next highest p_v estimates were for *Acer rubrum* and *Betula papyrifera*, species of intermediate-to-low shade tolerance. *A. rubrum* is known for its very broad distribution along edaphic gradients and its abundance throughout eastern forests. Our results indicate that it also has a broad tolerance of variation in annual mean tempera-

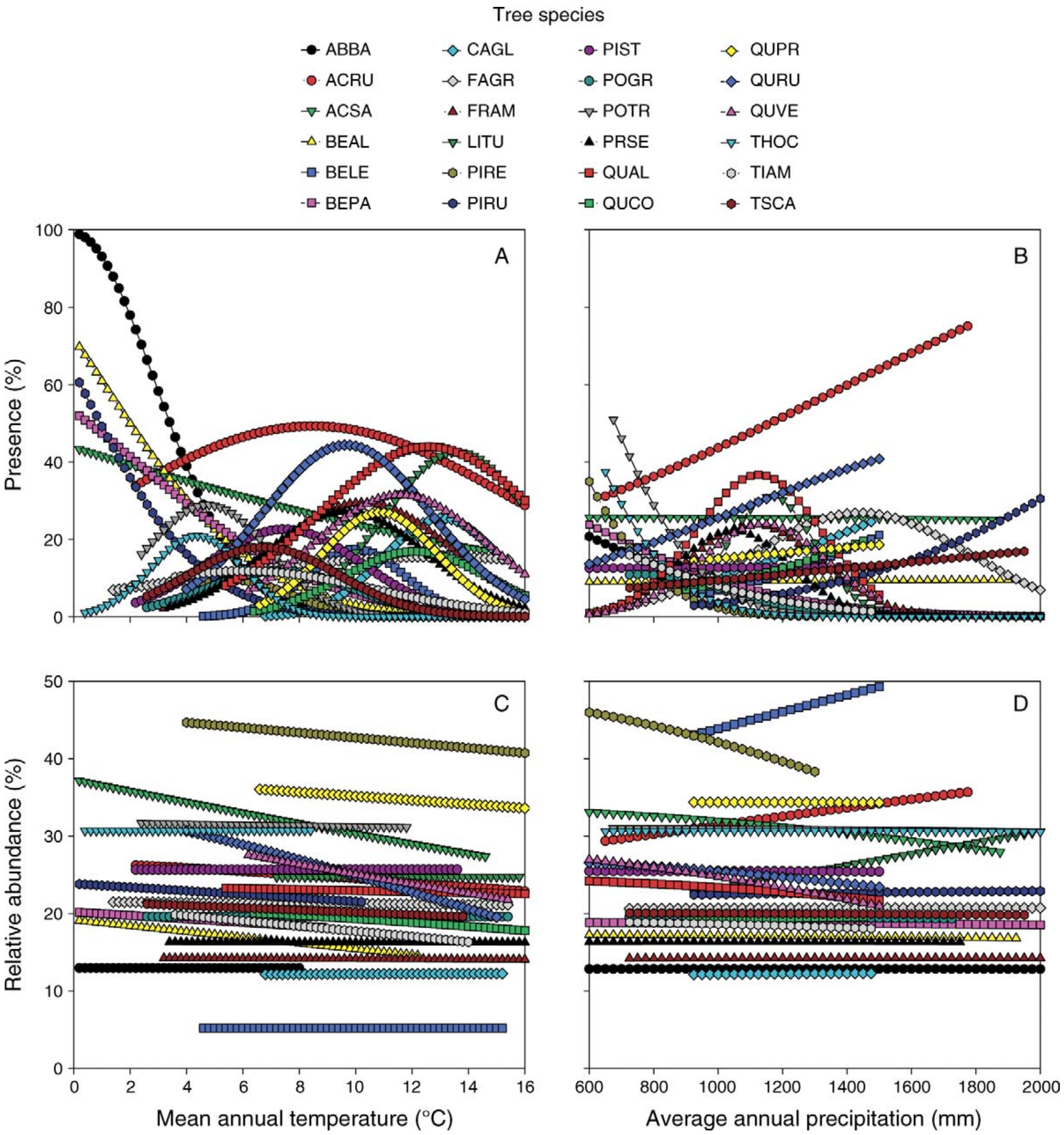

FIG. 1. (A, B) Predicted variation in frequency (presence, the percentage of plots in which the species occurs) and (C, D) relative abundance (percentage of aboveground biomass, when present) for adult trees of the 24 study species, as a function of annual mean temperature and annual precipitation. Maximum-likelihood estimates and two-unit support intervals for the parameters of all of the functions are given in Appendix B. Species abbreviations consist of the first two letters of the genus and specific epithet. The full species names are listed in Table 1.

ture (Fig. 1). The rest of the species had relatively similar (and surprisingly narrow) niche breadths along the temperature gradient (i.e., $2 \leq p_v \leq 3$ for 12 of the remaining 20 species).

Variation in frequency along the precipitation gradient was less regular. The 24 species can be visually lumped into three functional groups with respect to distribution of frequency along the precipitation gradient (Fig. 2). The largest group (11 species) showed either little variation or a monotonic increase in frequency at higher levels of annual precipitation. A second group of six species showed a distinct peak in frequency at intermediate precipitation levels, and the final group (seven species) had peak frequency at the dry end of the rainfall gradient (Fig. 2). Membership in the three functional groups was not clearly linked to conventional wisdom on the drought tolerance and distribution of the species along soil moisture gradients; e.g., all of the oak

TABLE 1. Parameter estimates from models for local frequency as a function of either temperature or precipitation.

	Temperature					Precipitation				
	Range limit (°C)		Peak frequency	Niche mode (°C)	Niche breadth	Range limit (mm)		Peak frequency	Niche mode (mm)	Niche breadth
Tree species	Lower	Upper				Lower	Upper			
Abies balsamea	—	8.08	0.99	—	2.97	—	—	0.36	—	575.7
Acer rubrum	2.06	—	0.49	8.48	7.25	647.1	1786.6	1.00	—	1459.0
Acer saccharum	—	14.74	0.94	—	23.87	—	1879.2	0.26	332.7	7324.0
Betula alleghaniensis	—	12.25	1.00	—	5.46	—	1947.9	0.10	—	8244.3
Betula lenta	4.46	15.27	0.17	10.00	1.75	909.1	1512.0	1.00	—	893.0
Betula papyrifera	—	8.83	0.65	—	6.45	—	—	0.39	—	598.1
Carya glabra	6.74	15.22	0.25	13.06	2.06	918.5	1495.6	0.45	—	778.2
Fagus grandifolia	1.37	15.49	0.15	12.78	8.94	722.2	—	0.27	1441.8	338.9
Fraxinus americana	3.19	—	0.29	10.25	3.11	715.9	—	0.24	1109.6	205.2
Liriodendron tulipifera	7.06	15.89	0.43	13.61	2.63	908.3	—	0.31	1165.2	137.0
Picea rubens	—	10.25	0.99	—	4.16	900.2	—	0.99	—	956.8
Pinus resinosa	3.97	—	0.10	5.58	2.07	—	1316.7	1.00	151.0	309.7
Pinus strobus	2.09	13.78	0.23	7.47	2.75	—	1508.1	0.13	3835.1	9995.6
Populus grandidentata	2.44	15.45	0.12	7.31	2.63	701.6	1748.7	0.11	755.1	268.1
Populus tremuloides	2.37	11.84	0.29	4.74	2.17	654.2	—	0.97	336.7	297.0
Prunus serotina	3.32	—	0.27	9.64	2.84	—	1769.7	0.22	1046.2	175.5
Quercus alba	5.30	—	0.44	12.59	3.91	—	1508.0	0.37	1126.3	194.0
Quercus coccinea	6.38	—	0.17	12.13	2.56	895.8	1461.3	1.00	—	1086.4
Quercus prinus	6.45	—	0.27	10.86	2.04	909.6	1504.1	0.25	—	2066.8
Quercus rubra	3.81	15.16	0.44	9.67	2.97	—	1509.3	0.46	1926.3	849.0
Quercus velutina	6.00	15.57	0.31	11.58	3.04	—	1516.4	0.24	1140.5	197.3
Thuja occidentalis	—	8.59	0.21	4.37	1.62	648.6	—	1.00	233.2	297.4
Tilia americana	3.48	14.05	0.12	6.07	4.55	724.4	1478.3	0.35	—	581.3
Tsuga canadensis	2.46	13.86	0.18	6.73	2.65	708.6	1954.8	0.22	—	1657.9

Notes: The lower and upper range limits are $x_{\min}$ and $x_{\max}$, respectively, in Eq. 1. Peak frequency, niche mode, and niche breadth are parameters $p_{\max}$, p_m, and p_v, respectively, from Eq. 2. Cells in the table with "—" indicate cases where the estimated range limit or niche mode was outside the observed range of the data set for a given species. The full set of maximum-likelihood parameters (and two-unit support intervals) from Eqs. 1–3 for are reported in Appendix B.

species showed peak frequency at intermediate or high ends of the rainfall gradient (Fowells 1965).

The 24 species represent the most common tree species across the entire study region, so almost by definition they are expected to have broad climatic range limits. Nonetheless, they represent a wide range of average regional abundance (defined as the product of both local frequency and relative abundance when present). There was no clear relationship, however, between regional abundance and niche breadth as defined by distribution of frequency along the temperature gradient (Fig. 1). The majority of these species had either upper or lower estimated climatic limits that were outside the range of annual mean temperatures encompassed in even this very large study region (Table 1). For example, for only four of the 24 species (*Populus tremuloides*, *Pinus strobus*, *Tilia americana*, and *Tsuga canadensis*) did our range of annual mean temperature (~0–16°C) appear to completely encompass their temperature extremes.

DISCUSSION

Our results suggest that relative abundance of a tree species within a site (i.e., given that a species is present in a stand) is controlled primarily by a variety of factors other than climate. Once a species is present within a site, our results suggest that climate per se has relatively little impact on the relative abundance of adult trees within a stand. We must again stress the proviso that our results do not rule out that the interaction between a climate variable (precipitation) and edaphic factors (soil water-holding capacity and topography) may have strong effects on adult tree abundance, growth, and survival. Note also that the lack of response of relative abundance to the two climate variables used in our analysis does not imply that adult tree relative abundance is highly predictable in a given climate: there was considerable residual variation in relative abundance that is presumably due to historical factors, local edaphic conditions, competitive interactions with other species, and other processes.

We were surprised by the relatively narrow range of temperature within which species reached peak local frequency (Fig. 1). Rehfeldt et al. (2008) found similarly narrow distributions of frequency of conifer species along a composite climate gradient in the northwestern United States. The relatively narrow niche breadths for local frequency of tree species along the temperature gradient suggests that the frequency of occurrence of species within the landscape, rather than relative abundance within sites, will show the greatest response to climate change. Although there has been considerable debate about whether climate-envelope models over- or underestimate potential changes in species' ranges under climate change (e.g., Jeschke and Strayer 2008), our results suggest that it will also be important to consider

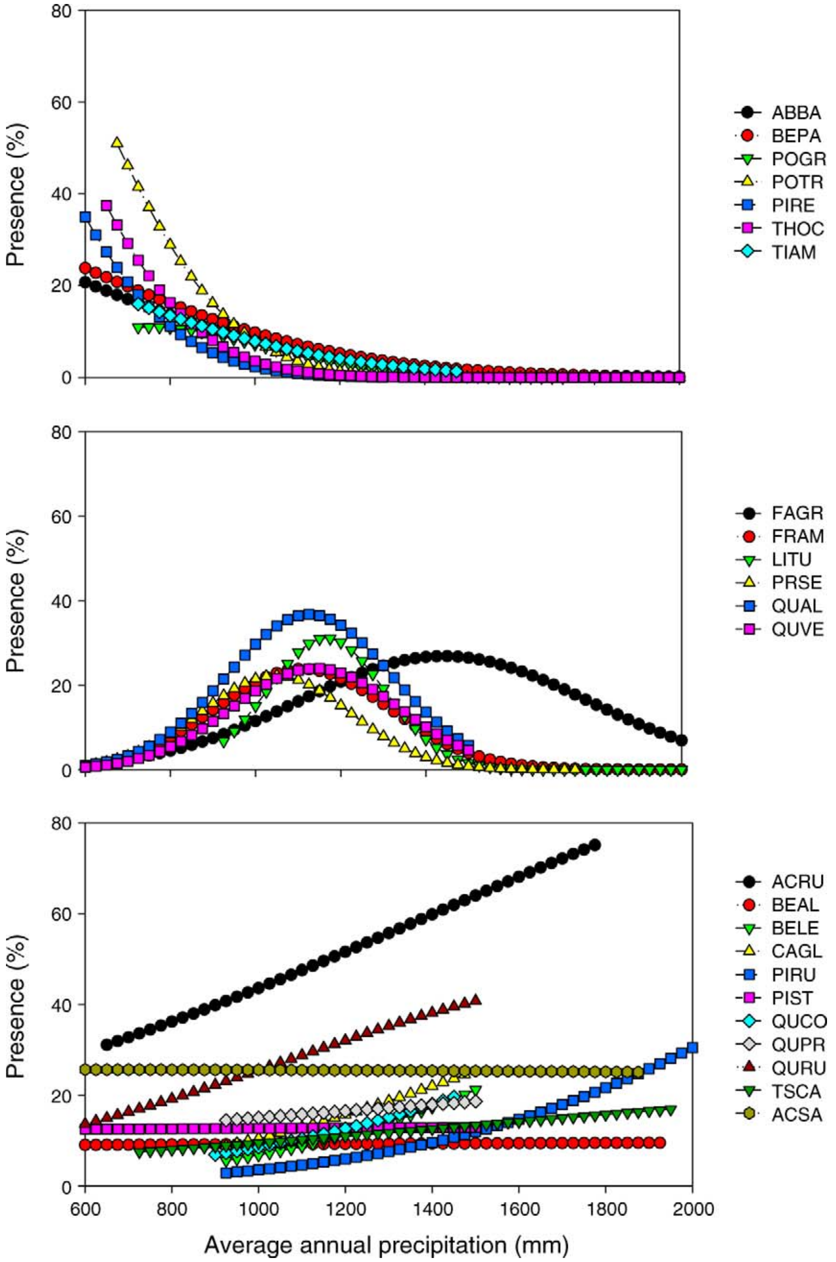

FIG. 2. Predicted variation in presence (the percentage of plots in which the species occurs) for adult trees of the 24 study species, as a function of annual precipitation. Species are grouped visually based on the shapes of their response to the precipitation gradient. Species abbreviations consist of the first two letters of the genus and specific epithet. The full species names are listed in Table 1.

changes in local frequency of occurrence of species within their current or future ranges.

The range limits of temperate trees have been previously reported to conform to Rapoport's rule, i.e., that species at higher latitudes have larger north–south ranges (Morin and Chuine 2006). Our analyses let us examine a potential corollary of the rule: does niche breadth (defined for frequency of occurrence at sites within a species' range) increase for species with niche modes at colder temperatures? The simple answer is that there was no obvious (negative) relationship between niche mode and niche breadth along the temperature gradient (Table 1).

It is not surprising that a relationship describing range limits would not necessarily apply to the prediction of patterns of frequency and relative abundance within a species' range. Much of the literature on both process-based and empirical models of tree species distributions has indeed been focused on predicting range limits, not abundance within ranges (e.g., Holt et al. 2005, Manthey and Box 2007). A number of those studies suggest that

PLATE 1. A forested hillside in the Adirondack Mountains of New York, USA. While relative abundance of northeastern U.S. tree species (when present) is relatively insensitive to variation in annual mean temperature, species showed a relatively narrow range of temperatures in which they were common (i.e. present in high frequency). Photo credit: C. D. Canham.

interactions between climate and phenological processes are important in determining range limits (e.g., Morin et al. 2007). Phenology, however, seems much less likely to serve as a mechanism for variation in frequency within range limits. Holt et al. (2005) argue that the mechanisms responsible for range limits are likely to be as varied as the diversity of species examined. We expect that this is even more likely in the case of specific mechanisms responsible for variation in frequency and relative abundance within a species' range. Like Holt et al. (2005), we suggest that demographic models seeking to identify the life history stages and demographic rates that give rise to observed patterns of variation in abundance along environmental gradients will be quite useful in predicting species' responses to climate change. Such models would also seem to be a promising way to generate hypotheses about the specific mechanisms that are responsible for the patterns of variation in abundance of species within their ranges.

What do our results tell us about the processes that are likely to govern shifts in tree species distribution and abundance under climate change? In general, they suggest that processes that influence the presence of adults of a species (i.e., canopy recruitment and local extinction) will be particularly important. These are perhaps best considered in the context of patch dynamics and/or metapopulation theory (Pickett and Thompson 1978, Hanski 1998), and they highlight processes that include disturbance and canopy tree recruitment at a landscape scale. Our results suggest that species that are characterized by high rates of turnover within sites (particularly early- to mid-successional species) will be most sensitive to climate change. In effect, most of the 24 species are fugitive species, maintained within the landscape by large-scale disturbances that allow colonization of new sites, or persistence within a given site via small-scale disturbance and gap-phase dynamics. Because frequency in sites within a given climate shows a strong sensitivity to temperature, at least, this suggests that the processes that determine canopy tree recruitment on new sites (dispersal, seedling establishment, juvenile growth, and survival) and/or local extinction within sites do indeed vary strongly with climate.

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APPENDIX A

Dates of the FIA censuses for the 19-state study region and a list of the 24 tree species included in the study (*Ecological Archives* E091-244-A1).

APPENDIX B

Parameter estimates and support intervals for models for tree species abundance as a function of temperature and precipitation (*Ecological Archives* E091-244-A2).