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EXPLOITING TEMPORAL VARIABILITY TO UNDERSTAND TREE RECRUITMENT RESPONSE TO CLIMATE CHANGE

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Abstract. Predicting vegetation shifts under climate change is a challenging endeavor, given the complex interactions between biotic and abiotic variables that influence demographic rates. To determine how current trends and variation in climate change affect seedling establishment, we analyzed demographic responses to spatiotemporal variation to temperature and soil moisture in the southern Appalachian Mountains. We monitored seedling establishment for 10 years in five plots located along an elevational gradient of five dominant tree species: *Acer rubrum, Betula* spp., *Liriodendron tulipifera, Nyssa sylvatica,* and *Quercus rubra*. A hierarchical Bayes model allowed us to incorporate different sources of information, observation errors, and the inherent variability of the establishment process. From our analysis, spring temperatures and heterogeneity in soil moisture emerge as key drivers, and they act through nonlinear population demographic processes. We found that all species benefited from warmer springs, in particular the species found on dry slopes, *N. sylvatica*, and those dominant at higher elevations, *Betula* spp. and *Q. rubra*. This last species also benefited from dry environments. Conversely, *L. tulipifera*, which is abundant on mesic sites, experienced highest establishment rates at high moisture. The mechanisms behind these results may differ among species. Higher temperatures are apparently more important for some, while dry conditions and reduced pathogenic attacks on their seeds and new seedlings have a large impact for others. Our results suggest that only communities found at higher elevations are in danger of regional extinction when their habitats disappear given the current climatic trends. We conclude that the recruitment dynamics of the communities where these species are dominant could be affected by minor changes in climate in ways that cannot be predicted using only climate envelopes, which use different variables and miss the nonlinearities.

Key words: climate change; climate envelopes; establishment; hierarchical Bayes; recruitment; seedlings; Southern Appalachians.

INTRODUCTION

Some of the most profound consequences of climate change in North America are predicted for the southeastern United States (National Assessment Synthesis Team 2000). Doubled atmospheric CO_2 concentrations could cause a mean annual temperature rise of 3–5°C and a summer precipitation decline of 20–30% (Mearns et al. 2003). As of 2004, six of the 10 highest recorded mean July temperatures for the region had occurred in the previous 15 years (1993, 1999, 2002, 1991, 1998, and 2000). Late 21st-century forecasts for the southeastern United States predict plant communities characteristic of xeric sites expanding their ranges, and those restricted to high elevations facing regional extinction (Bachelet et al. 2001, Hansen et al. 2001). A major restructuring of most communities will result on the emergence of savanna-like vegetation in this region. Anticipating the response of biodiversity to such subcontinental scale climate shifts is a goal of global change research.

There are at least two ways to study potential forest responses to climate change: climate envelopes and process models that are applied to interannual climatic variation. The climate-envelope approach is most commonly applied to population range boundaries and is based on correlations. The future distributional range is identified with predicted climates that match the current range (e.g., Fleishman et al. 2001, Lasch et al. 2002, Thomas et al. 2004). Additional niche axes might be included, such as soils, hydrology, and disturbance (Iverson and Prasad 1998, Iverson et al. 1999). Models sometimes include dynamic considerations, such as scenarios for dispersal and migration (e.g., Schwartz et al. 2001, Iverson and Prasad 2002). Limitations of the

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TABLE 1. Stand descriptions.

Stand variables	Stand 1	Stand 2	Stand 3
Altitude (m) and exposure	775, SW	830, N	870, N
Type of vegetation	ridge	cove	mixed oak
Dominant tree species	*P. rigida, Q. coccinea, A. rubrum, C. glabra*	*L. tulipifera, A. rubrum, C. glabra, Q. prinus, B. lenta*	*Q. prinus, A. rubrum, C. glabra, O. arboreum, N. sylvatica*
Light level (% full sunlight)†	7.59 ± 3.74	4.26 ± 1.97	3.82 ± 2.08
Mean air temperature (°C)‡	21.4, 3.5	21.1, 2.3	21.8, 2.7
Mean soil moisture (% water content)§	17.8	31	23.9

Note: Species are *Pinus rigida, Quercus coccinea, Acer rubrum, Carya glabra, Liriodendron tulipifera, Quercus prinus, Betula lenta, Oxydendron arboreum, Nyssa sylvatica, Betula alleghenienss,* and *Acer saccharum.*

† Light measurements (mean ± SD) from 50 canopy photos taken at each stand in a 10 × 10 grid (see *Methods*).

‡ Mean July and January temperatures recorded at each stand (see *Methods*).

§ Average soil moisture content at each stand during the studied period (see *Methods*).

approach include the fact that current combinations of climate, soils, and other variables often do not include those expected for the future (Pacala and Hurtt 1993, Pearson and Dawson 2003, Ibáñez et al. 2006). Moreover, different life history stages of different species respond to a rich interaction of biotic and abiotic variables that are missed by this method (Ibáñez et al. 2006).

A second and complementary approach, more often employed by ecosystem ecologists, involves process-based models for the effects of temporal variation in weather or climate on water, carbon and energy balances (e.g., Kumagai et al. 2004, Novick et al. 2004, Boisvenue and Running 2006). Process-based studies could contribute more than they have to understanding population and community responses to climate change, provided several obstacles can be overcome. Interannual variation has long been used to analyze climate regulation of tree growth (Graumlich 1991, Clark et al. 2003*a*, Stevens et al. 2006) and fecundity (McKone et al. 1998, Schauber et al. 2002, Hampe 2005, Mutke et al. 2005). But dynamics of tree populations are highly dependent on recruitment (e.g., Clark et al. 1998, Houle 1998, Hubbell et al. 1999, Brown and Wu 2005, Stephenson and van Mantgem 2005, Matthes and Larson 2006), which has been studied primarily at fine spatial scales, involving biotic interactions and microsite variation (Beckage et al. 2000, Connell and Green 2000, Harms et al. 2000, Hille Ris Lambers et al. 2002, Wright et al. 2005), rather than variation in time. Experiments involving atmospheric effects on recruitment are expensive and, thus, rare (but see DeLucia et al. 1999, Körner 2004, Mohan et al. 2007). Yet, landscapes can provide a diversity of microclimatic settings with superimposed temporal variation that, together, could be exploited for understanding population- and community-level change, just as ecosystem ecologists have done at broad spatial scales.

The challenges for a process-based approach to climate effects at the population level involve complexity, limited control, and limited observability. Specifically, (1) data must span a range of local settings and a substantial number of years during times of climate variation, (2) sample sizes must be sufficiently large to identify relationships, and (3) inferential models must accommodate the many unmeasurable factors that affect demographic process and the data that derive from them. In other words, we require population dynamic models as the basis for inference, combined with sophisticated data models and large data sets.

To identify potential consequences of climate change for tree diversity we combined the demographic techniques that have been traditionally applied to tree population- and community-level processes, with models that include spatiotemporal climate variation. We departed from the design-based inference (ANOVA) that has long been the framework for such analyses, and adopted model-based inference, using demographic process models combined with hierarchical Bayes (Clark 2005). The hierarchical Bayesian framework allowed us to incorporate several demographic processes into the model. We analyzed dynamic responses to climatic variability at the recruitment stage, for dominant tree species growing in five representative communities of the Southern Appalachians. To understand dynamics, more than a decade of spatiotemporal data on each stage, from seed production, through the seed bank, to germination were assimilated in population dynamic models that allowed us to evaluate how environmental influences, light availability, and seed density affected recruitment success (e.g., Kobe et al. 1995, Beckage et al. 2000, Harms et al. 2000, Hille Ris Lambers et al. 2002, Hille Ris Lambers and Clark 2003) and, thus, might interact with climate change.

The approach provides insight concerning spatiotemporal variation in climate and interactions. Specifically, we wanted to identify (1) species most sensitive to climate variability, (2) whether or not species dominant on xeric sites might be more or less sensitive to variation in moisture availability, and (3) to what extent species in moist microsites will be affected by predicted decrease in precipitation. As is the case for any available approach, including climate envelopes, the analysis of responses to the currently changing climate is no substitute for direct observations of response that will occur decades from today. However, climate is changing rapidly now. Responses of contemporary forests to current climate

Table 1. Extended.

Stand 4	Stand 5
1100, NE	1480, NE
mixed oak	northern hardwood
Q. prinus, A. rubrum, Q. rubra, O. arboreum, N. sylvatica	*Q. rubra, B. allegheniensis, B. lenta, A. saccharum*
4.61 ± 1.91	3.03 ± 1.92
19.7, 2	18.4, 0.4
21	25.3

change are arguably the most relevant indication of climate sensitivity. We used these results to consider the potential value of climate envelopes (a correlative approach), process-based data modeling (from in situ observations) used here, and combinations for better anticipating potential consequences of climate change.

Site description and species

The southern Appalachian Mountains include a mosaic of forests expected to respond to climate change in different ways. Five major eastern forest types are represented in the region, mixed hardwoods and hemlock hardwoods in mesic sites, red oak and chestnut oak on slopes, white oak and pignut hickory on north faces of hill tops, and pitch pine and scrub oak on the southern faces (Whittaker 1956).

The study site is located at the Coweeta Hydrological Laboratory (35°03′ N, 83°27′ W). Five 80 × 80 m sample plots were established in stands at a range of elevations and soil moisture levels for long-term research studies in 1991. These sites represent the dominant natural communities that vary with well-known environmental gradients of the region (see Table 1 for specific site descriptions). Mesic sites are represented by the cove and northern hardwood stands, the mixed-oak stand at lower elevation and the ridge stand account for the driest types of vegetation found in the area, and the mixed-oak stand at higher elevation represents an intermediate moisture level.

Although all tree species were monitored, we focus our analysis on the five taxa having high densities of seeds and seedlings, including *Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*, *Nyssa sylvatica*, and *Quercus rubra*. *Acer rubrum* L., (red maple) is present in all stands except at the highest elevation northern hardwood stand, and dominates in the driest stand, the ridge. Red maple has seeds that average 0.17 g and remain viable in the seed bank for several years (Haywood 1994, Peroni 1995). *Betula* spp. (birch, including *B. lenta* L. and *B. alleghaniensis* Britton) occurs mainly at the high-elevation northern hardwood stand, but seeds and seedlings have been recorded in all of our stands. We did not differentiate between the two species, because young seedlings are not distinguishable in the field. *Betula* seeds average 0.0006 g and survive in the soil seed bank several years (Houle 1995). *Liriodendron tulipifera* L. (yellow poplar) is a fast growing species and dominant in moist sites, in our study at the cove stand. Seeds average 0.02 g, have low viability, but can survive in the soil seed bank for at least five years (Clark and Boyce 1964, Haywood 1994). In our study region, *Nyssa sylvatica* Marsh, (black tupelo) mainly grows on dry slopes, it is representative of the mixed-oak stand at low elevation. Fleshy fruits average 0.2 g, and they persist in the soil seed bank (Hille Ris Lambers et al. 2005). *Quercus rubra* L., northern red oak, although common in all of our sample stands, dominates in the mixed oak at high elevation and in the northern hardwood stands. Its large 8.7 g seeds do not persist in the seed bank. With the exception of *A. rubrum,* these species set seed in the fall and germinate the following spring.

Methods

To understand how recruitment responds to year-to-year climate variation in the context of spatiotemporal fluctuations in seed density and resources, we conducted a study involving three elements: (1) long-term documentation of climate variation and germination success from sites spanning a range of elevations and local moisture availabilities, (2) population dynamic models that link life history stages, and (3) a hierarchical Bayes modeling framework that allowed us to integrate data with full accommodation of uncertainty at the process stage, limited observations, and spatiotemporal context at the parameter stage (Clark 2005). Environmental data, temperature, soil moisture, and light, together with demographic data, seed rain, seed bank, and seedling establishment of most common trees, were monitored at each stand from 1994 to 2003. Extensive observational data was available on the number of seeds reaching the ground within study plots (Clark et al. 2004) and on seed bank dynamics (Hille Ris Lambers et al. 2005). Understanding the environmental controls of germination rates requires that they be assimilated into the process model in appropriate ways. A hierarchical structure allowed us to link information and processes at different levels (Lavine et al. 2002, Berliner et al. 2003, Clark et al. 2003*b*, Wikle 2003, Clark 2005), where data sets differed in scale and are not independent. This framework allowed us to capture the full dynamics that unfold from the time of seed dispersal through seed bank survival to germination from the seed bank. At each stage we assimilated different types of data, allowing for the errors associated with sampling and the fact that simple stage transition models can be expected to capture only part of the dynamic process. Only by treating parameters as stochastic variables were we able to combine these data; this was one of the advantages of using a Bayesian approach. Furthermore, the Bayesian framework permitted us to use prior knowledge obtained from previous studies at those sites. In cases where prior information was not available we used non-informative priors. Here we describe data sets, followed by the population dynamic model that incorporates them.

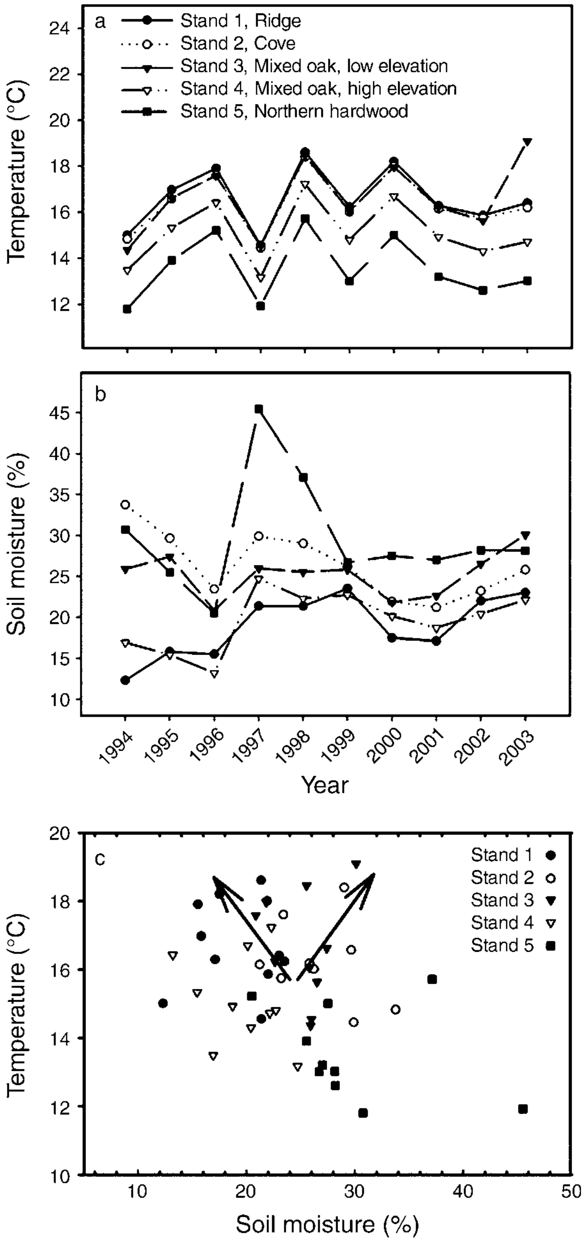

FIG. 1. Environmental variables during the month of May from 1994 to 2003 at each of the five stands (Table 1): (a) mean air temperature, from stand hourly measurements; (b) mean soil moisture, from stand hourly measurements; (c) combined temperature and soil moisture data for each stand. Arrows in panel (c) indicate the direction of forecasted climate change for the region (National Assessment Synthesis Team 2000): warmer and drier (left arrow, Canadian transient climate model CGCM1 [Boer et al. 2000]), and warmer and more humid (right arrow, Hadley model HADCM2SUL [Mitchell et al. 1995]).

Environmental data

Air temperature and soil moisture were recorded hourly at each stand throughout the year. For this study we concentrated on fluctuations in these variables in May (Fig. 1), when seed germination and seedling establishment takes place for the species included in our analysis. In preliminary versions of our analysis, we also considered environmental data taken at different times during the growing season, e.g., June and July temperature and soil moisture. Our final analysis and results reflect the combination of environmental data we believe had the most impact on establishment. Temperature was measured 1.3 m above the forest floor within each stand. Soil moisture data was collected for the upper 30 cm at two locations in each stand. Mean monthly values are used for this analysis (data and methods are *available online*).[7]

We estimated the proportion of full sunlight penetrating the forest canopy, the global site factor (GSF) from canopy photos (Rich et al. 1993) taken in July 2000 (M. Dietze, *unpublished data*). Light levels were calculated from hemispherical photographs taken at 1.15 m above ground using an 8-mm fish-eye lens. We obtained one photograph at each 10 × 10 m grid location in each stand. The GSF combines direct radiation, based on the annual solar track, and diffuse radiation estimated on a uniform overcast sky model. Hemispherical photographs were analyzed using Hemiview (Delta-T, Cambridge, UK). From GSF values we constructed a prediction grid of light level for each seedling plot with Bayesian kriging (GeoBUGS; Bayesian Inference Using Gibbs Sampling, program *available online*).[8]

Seed rain, seed bank, and seedling censuses

Bayesian predictive intervals of seed rain were constructed for all seedling plots in all years (Clark et al. 2004). Both model and data assume spatial scales of 1 m^2, referenced as plot i, nested within stand j, and temporal scales of one year t. Thus, all state variables have units of number per square meter per year. Data to estimate seed rain s_{jit} were collected from 20 seed traps deployed in each of the five stands beginning in 1991. Traps were arranged in two parallel transects, 30 m apart, in the central area of the stand. Three times a year, traps are emptied and seeds are identified, counted, and archived (Clark et al. 1998). For this analysis we incorporated the full uncertainty of data and model with the Bayesian predictive distributions of Clark et al. (2004).

Posterior estimates of the seed bank at each plot, B_{jit}, stand seed bank viability v_j, which determines viable seeds b_{jit} and stand seed mortality d_j come from studies of soil cores located adjacent to seed traps (Hille Ris Lambers et al. 2005).

Seedling censuses produced counts of new-established seedlings N_{jit} from 1994 through 2003. Transects of continuous 60 1-m^2 plots were established in 1994 in the center of each stand. In July of each year, first-year

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[7] ⟨http://coweeta.ecology.uga.edu⟩

[8] ⟨http://mrc-bsu.cam.uk/bugs⟩

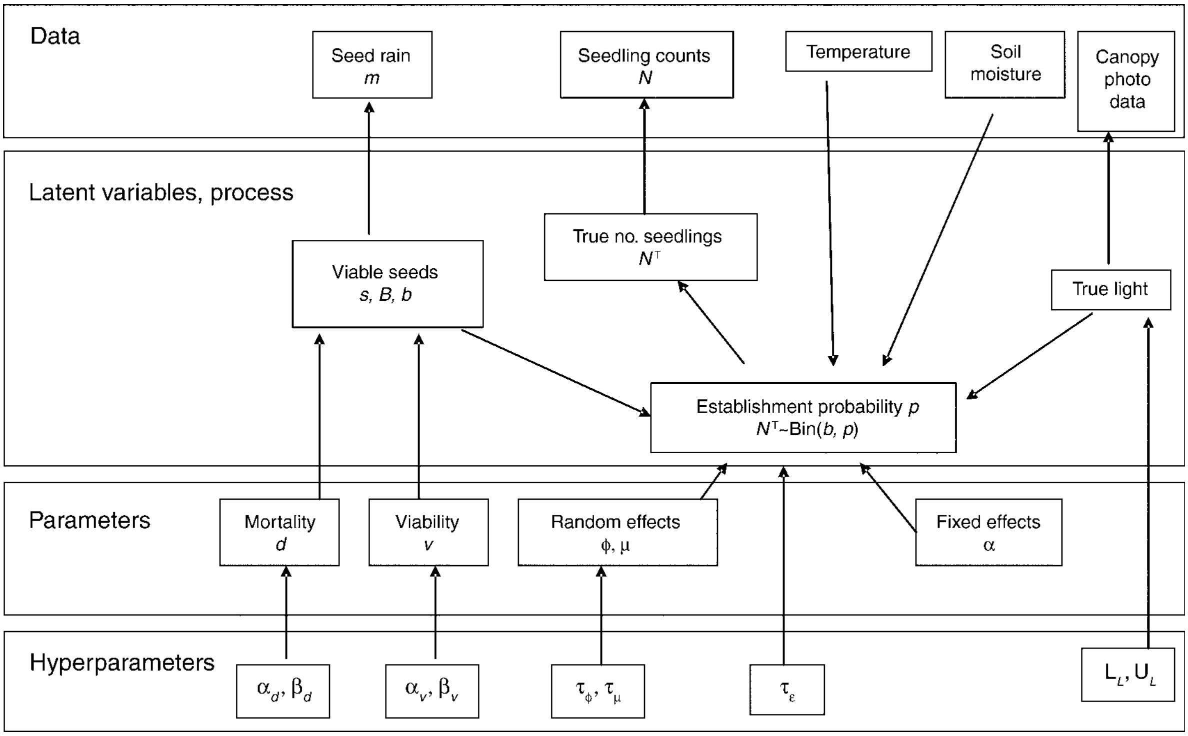

FIG. 2. Graphical representation of the hierarchical model. See Clark et al. (2004) for seed rain predictions and Hille Ris Lambers et al. (2005) for seed bank parameter values and model. Definitions: s, estimated no. seeds from last crop; b, no. viable seeds from last crop; B, estimated no. seeds available for germination (last crop and seed bank); α, fixed effects coefficients associated with each of the covariates affecting establishment; μ, stand random effects associated with seed density in a mixed model; ϕ, plot random effects associated with seed density in a mixed model; τ, error precision term (1/variance); L_L, lower limit for light values; U_L, upper limit for light values.

seedlings were identified by the presence of cotyledons or by the absence of lignified stems.

Model development

Our model involves likelihoods, or data models, process models, and parameter models (Fig. 2). The first stage data model includes the probability that a new seedling will be correctly identified, which depends on the true number of new seedlings and on observation error. At the second "process" stage, the true number of new seedlings depends on the number of seeds and on the probability of establishment. This last parameter, establishment potential, depends on climate (temperature and soil moisture), seed density, which will influence recruitment if the species is affected by negative density dependent mechanisms, and light levels, which are expected to have greatest impact on recruitment of shade-intolerant species. Parameter models allow for process level variation in establishment, in the form of random effects. Here we summarize our treatment of each of these levels.

Data models

Data enter our model as posterior predictive distributions for seed rain s_{jit} from the analysis of Clark et al. (2004) and as seedling demographic data from long-term plots in the five study locations, N_{jit}. The previous analysis of seed banks yielded posterior densities for parameters associated with seed viability and mortality. These were estimated for the same stands and species studied here (Hille Ris Lambers et al. 2005), we used these values for this analysis.

The data model, or likelihood, for counts of newly established seedlings is a conditional Poisson process, having mean value taken to be the true number of established seedlings. Observation error results from incorrect identification or from germination of seedlings late in the year, after the annual census is completed, the error could occur on both directions, under- and over-estimating the number of seedlings. The number of observed newly established seedlings is N_{jit} during the census year $t = 1, \ldots Y$ over $Y = 10$ years, in plot $i = 1, \ldots P$, where the total number of plots $P = 60$, in each stand $j = 1, \ldots S$, where the number of stands $S = 5$. The observed number is drawn from an underlying "true" number of new seedlings N^{true} as $N_{jit} \sim \text{Poisson}\ (N_{jit}^{\text{true}})$. The likelihood for the full seedling data set N is

$$p(N) = \prod_{j=1}^{S} \prod_{i=1}^{P} \prod_{t=1}^{Y} \text{Poisson}(N_{jit} | N_{jit}^{\text{true}}). \tag{1}$$

Observations are not independent, deriving from underlying true values that covary in space and time. We therefore make the underlying process stochastic, which allows us to directly model the interdependence. The next section describes the dynamics that result in production of new seedlings.

The dynamic process model

The process we model follows several state variables over time and space, including seed rain s_{jit}, only b_{jit} of which are viable and enter the seed bank B_{jit}. Some of B_{jit} seeds may survive to the next year, others may germinate, depending on environmental conditions that vary among locations and can change from year to year. The process model is anchored not only by observations of seedlings (previous section), but also by information obtained from other studies at these sites, including annual inputs of seed into plots (Clark et al. 2004), and seed viability and survival in the seed bank (Hille Ris Lambers et al. 2005).

Seeds available for germination.—We estimate annual inputs of seed into each plot from a seed dispersal model parameterized from seed trap data collected in the same years, plots, and stands as our seedling establishment data. The hierarchical Bayes model that generated these estimates is described in detail by Clark et al. (2004). In our model, seed input into plots (s_{jit}) is distributed as a Poisson:

$$s_{jit} \sim \text{Poisson}(m_{jit}) \tag{2}$$

where m_{jit} is the mean of the predictive distribution of seed rain in plot i in stand j in year t (Clark et al. 2004: Fig. 13). For species lacking a seed bank the sole source of seeds in spring of year t is the fall crop from year $t - 1$ (i.e., autumn-dispersed species, such as *Q. rubra*).

Not all s seeds are viable. The number of viable seeds is

$$b_{jit} \sim \text{Binomial}(s_{ji*}, v_j) \tag{3}$$

where v_j is the stand-specific seed viability for seeds of a given species, taken to be the product of the fraction that is viable and the survival probability from the time of seed fall until germination. s_{ji*} is equal to s_{jit-1} for species that dispersed seeds in autumn of the previous year. s_{ji*} is equal to s_{jit} for species that disperse seeds in spring of the current year (*A. rubrum*). Our estimates of v_j come from a previous study of seed survival at our sites (Hille Ris Lambers et al. 2005). We mix over uncertainty in v_j by sampling from posterior estimates (mean ± SD) derived from the same years, plots, and stands as described in that study (Hille Ris Lambers et al. 2005, Appendix A). We do not have prior information for two species, *N. sylvatica* and *Q. rubra*. For these species we used the approach of Hille Ris Lambers et al. (2005) to estimate v_j, with a prior and initial values that were non-informative:

$$v_j \sim \text{Beta}(\alpha_{v_j}, \beta_{v_j}). \tag{4}$$

Because seeds enter and leave the seed bank each year, the full model includes this demographic process. The seed bank process is a critical aspect of the model, providing the information needed to estimate the number of seeds available for germination. For species having a persistent seed bank, estimates of emergence from the seed bank were obtained from Hille Ris Lambers et al. (2005), based on a Bayes model of interannual survival and emergence from the soil. For some species (*A. rubrum*, *L. tulipifera*), they found that, in years of low seed production, the seed bank could contribute up to 75% of the new seedlings. For these species, the number of seeds available for germination in the spring of year t, β^{spr}_{jit}, is the sum of two sources: (1) viable seeds from the most recent seed crop, b_{jit}, which fell in either autumn or winter of $t - 1$ (e.g., *L. tulipifera, Betula*) or in spring of t (*A. rubrum*; Eq. 3), and (2) seeds that survived from the previous year's seed bank, $\beta^{\text{fall}}_{jit-1}$:

$$B^{\text{spr}}_{jit} = b_{jit} + B^{\text{fall}}_{jit-1} \tag{5}$$

where B^{fall} is the number of seeds in the seed bank that neither germinated in the spring nor died during the summer. B^{fall} is drawn from

$$B^{\text{fall}}_{jit} \sim \text{Binomial}\Big(B^{\text{spr}}_{jit}, (1 - p_{jit})(1 - d_j)\Big) \tag{6}$$

where p_{jit} is the establishment potential, and d_j is the annual mortality in the soil seed bank during the growing season. Mortality in the seed bank is estimated for each stand, d_j, and it is sampled from densities based on posterior estimates (mean ± SD) from Hille Ris Lambers et al. (2005) (Appendix A). For the species lacking prior information on this parameter, *N. sylvatica*, we estimated it according to Hille Ris Lambers et al. (2005), from prior and initial values that were non-informative:

$$d_j \sim \text{Beta}(\alpha_{d_j}, \beta_{d_j}). \tag{7}$$

Seedlings establishing.—The true number of established seedlings N^{true} is binomial. For species having a seed bank (*A. rubrum*, *Betula* spp., *L. tulipifera,* and *N. sylvatica*), germination comes from the seed bank:

$$N^{\text{true}}_{jit} \sim \text{Binomial}(B^{\text{spr}}_{jit}, p_{jit}) \tag{8a}$$

with establishment probability p_{jit}. It is the connection between seed rain and the establishment process that is the focus of this analysis. For species lacking a seed bank (*Q. rubra*), germination comes solely from the current seed crop:

$$N^{\text{true}}_{jit} \sim \text{Binomial}(b_{jit}, p_{jit}). \tag{8b}$$

Establishment probability.—The factors affecting establishment probability p_{jit} are of particular interest, represented as a generalized linear model with logit link (Berkson 1951). Because understanding the effects of environmental variables on establishment potential is the principal goal of this analysis, we tested competing models that represent different assumptions for effects, both fixed and random. For this description, we focus on the models that eventually proved most appropriate, but we summarize the range of models that we considered in Appendix B. We began our analysis by modeling the probability that a seedling establishes in year t, at plot i, in stand j, p_{jit}, as a function of temperature (Temp_{jt}), soil moisture ($\mathrm{Soilm}_{\mathrm{jt}}$), and light availability (Light_{ji}). We used values of temperature and soil moisture collected at various times during the growing season (May to September). Based on the model selection criterion (predictive loss) we subsequently limited climatic covariates to May, the month when most species make the transition from seed to seedling in our study region (I. Ibáñez, *personal observation*). Exploration of residuals indicated the need to allow for random plot effects and the effects of seed density s_{jit} as part of the germination process itself. Still, covariates might not have fully captured stand- and plot-level variation, so we included random effects for either stand (μ_j) or plot (ϕ_{ji}), or for both. Here, we discuss in detail one of the submodels we tested:

$$\ln\left(\frac{p_{jit}}{1-p_{jit}}\right) = \alpha_0 + \alpha_1\mathrm{Temp}_{jt} + \alpha_2\mathrm{Soilm}_{jt} + \alpha_3\mathrm{Light}_{ji} + \alpha_4 s_{jit} + \mu_j + \phi_{ji} + \varepsilon_{jit} \qquad (9)$$

where $\varepsilon_{jit} \sim \mathrm{Normal}(0, \tau_\varepsilon^{-1})$. Temperature and soil moisture data are available for all years, at all stands (see *Methods*).

Light data.—Light observations are available from canopy photos for all stands and plots, obtained in the year 2000. Given the uncertainty in light measurements, this latent variable was estimated as part of the model. Because light estimates are uncertain, light was treated as a latent variable and therefore estimated together with other parameters in the model (Mohan et al. 2007). Light estimation would then been part of the data models. Light availability is taken to be

$$\mathrm{Tlight}_{ji} \sim \mathrm{Uniform}(L_{1ji}, L_{2ji}) \qquad (10)$$

where Tlight denotes "true light."

We chose the lower and upper limits L_{1ji} and L_{2ji} to cover observed variability in light measurements taken in the same place at the same time (e.g., Clark et al. 2003*b*, Mohan et al. 2007). These limits are ±6% from the observed values, this range is based on pairs of photos taken at the same location and time for 15 plots.

Random effects.—These include a vector of stand random effects, one for each of the five stands, μ_j, where $\mu_j \sim \mathrm{Normal}(0, \tau_\mu^{-1})$. We also considered adding a vector of plot random effects, one for each of the 60 plots at each of the five stands, ϕ, being $\phi_{ji} \sim \mathrm{Normal}(0, \tau_\phi^{-1})$. And we added an error term, ε, that accommodated residual uncertainty among plots in each stand and year, $\varepsilon_{jit} \sim \mathrm{Normal}(0, \tau_\varepsilon^{-1})$.

The precision parameters, τ_μ, τ_ϕ, and τ_ε, were drawn from gamma distributions. We used different combinations of more or less informative priors for this distribution, with values ranging from 1 to 0.001. Overall results were similar for the prior combinations we tried, and final runs were then done with priors for the gamma distribution equal to 0.01.

The full model.—The joint posterior distribution for the full model is

$$\begin{aligned}
&p(N_{jit}^{\mathrm{true}}, v_j, d_j, \mathrm{Tlight}_{ji}, \tilde{\alpha}, \tilde{\mu}_j, \tilde{\phi}_{ji} | N_{jit}, m_{jit}, L_{1ji}, L_{2ji}) \\
&\propto \left\{ \prod_{j=1}^{S}\prod_{i=1}^{P}\prod_{t=1}^{Y} \mathrm{Pois}(N_{jit}|N_{jit}^{\mathrm{true}}) \right\} \\
&\times \left\{ \prod_{j=1}^{S}\prod_{i=1}^{P}\prod_{t=1}^{T} \mathrm{Bin}(N_{jit}^{\mathrm{true}}|B_{jit}, p_{jit})\mathrm{Bin}(b_{jit}|s_{ji*}, v_j)\mathrm{Pois}(s_{ji*}|m_{ji*}) \right. \\
&\qquad \left. \times\, N(\varepsilon_{jit}|0, \tau_\varepsilon^{-1}) \right\} \\
&\times \left\{ \prod_{j=1}^{S}\prod_{i=1}^{P} N(\phi_{ji}|0, \tau_\phi^{-1})\mathrm{Unif}(\mathrm{Tlight}_{ji}|L_{1ji}, L_{2ji}) \right. \\
&\qquad \times \prod_{j=1}^{S} N(\mu_j|0, \tau_\mu^{-1})\mathrm{Beta}(v_j|\alpha_v, \beta_v)\mathrm{Beta}(d_j|\alpha_d, \beta_d) \\
&\qquad \times N_5(\tilde{\alpha}|\tilde{\alpha}_m, V_\alpha^{-1})\mathrm{Gam}(\tau_\mu|0.01, 0.01)\mathrm{Gam}(\tau_\phi|0.01, 0.01) \\
&\qquad \left. \times\, \mathrm{Gam}(\tau_\varepsilon|0.01, 0.01) \right\}
\end{aligned}$$

where the three expressions in braces denote the likelihood, priors, and hyperpriors, respectively. This would be for the most complicated submodel we tested, a fall-dispersed species with a seedbank, where we do not have prior information on v and d and they are estimated, and a model that includes all random effects, μ, and ϕ.

We used non-informative priors (Appendix A) for most of the parameters. In the case of seed viability and seed mortality, prior values for three of the species were based on information for these species and stands from previous studies (Appendix A).

Model implementation and diagnostics

Posterior densities of the parameters were obtained using Gibbs sampling, a type of Markov chain Monte Carlo (MCMC) simulation. Model simulations were run in WinBUGS 1.4 (Spiegelhalter et al. 1996). Convergence was assessed from several chains with different initial conditions and Gelman and Rubin's convergence statistic, as modified by Brooks and Gelman (1998). Convergence required 1000–30 000 iterations. These preconvergence "burn-in" iterations were discarded and an additional 100 000 iterations were saved for analysis. Model selection was based on predictive distributions of the data, by minimizing posterior predictive loss function (residual sum of squares;

TABLE 2. Model selected for each species.

Species	Model variation
Acer rubrum, Betula spp., *Lirodendron tulipifera, Nyssa sylvatica*	submodel A (only fixed effects): logit(p_{jit}) = $\alpha_0 + \alpha_1\mathrm{Temp}_{jt} + \alpha_2\mathrm{Soilm}_{jt} + \alpha_3\mathrm{Light}_{ji} + \alpha_4 s_{jit} + \varepsilon_{jit}$
Quercus rubra	submodel F (fixed effects and stand random effects for seed density): logit(p_{jit}) = $\alpha_0 + \alpha_1\mathrm{Temp}_{jt} + \alpha_2\mathrm{Soilm}_{jt} + \alpha_3\mathrm{Light}_{ji} + (\alpha_4 + \mu_j)s_{jit} + \varepsilon_{jit}$

Note: Model selection was based on their posterior predictive loss (Gelfand and Ghosh 1998).

Gelfand and Ghosh 1998). The cost of selecting the wrong model is the error sum of squares, G, and the penalty term is the predictive variance, P. We selected the model with the lowest value of posterior predictive loss D, $D = G + P$.

RESULTS

Climate variation

The range of temperature and soil moisture at our sites (Table 1) during the years this study took place (Fig. 1) spans the range of trends predicted by climate models under doubled atmospheric CO_2 concentrations. Mean May temperatures varied within each stand from 4° to 5°C and among stands within a given year from 3° to 4°C. Soil moisture content fluctuated among stands, and within a stand among years by as much as 20–25%. Thus, there is substantial climatic variation represented by the stands and years included within our data sets. This variation is basis for inference on effects of climatic variation and tree recruitment.

Germination models

From the different combinations of fixed and random effects (Appendix B) we selected the model for each species that minimized predictive loss (Table 2). A model with only fixed effects α (submodel A) best predicted recruitment for *A. rubrum, Betula* spp., *L. tulipifera*, and *N. sylvatica*. For *Q. rubra,* a mixed model that included stand random effects associated with seed density best predicted recruitment (submodel F).

Models satisfactorily fitted the data (Fig. 3). The total amount of information available for each species, including seedlings, seed rain, and priors, influenced the fits. Predictions for all species tend to underestimate establishment in years and plots with higher than average seed densities, probably because fits are dominated by the overwhelming number of observations at low densities and, perhaps, a tendency to underestimate seed during mast years. It is further possible that seed viability increases with pollen density for some wind pollinated species (Nilsson and Wästijung 1987), resulting in higher viability during mast years. For vertebrate-dispersed *N. sylvatica* drupes and *Quercus* acorns, seed predictions based on locations of trees could underestimate the true inputs. In spite of potential bias, seedling establishment was accurately predicted by the model.

Effects of interannual climatic variability on seedling establishment

All species recruited best during warm springs, with four of the five species affected by high temperatures, their 95% credible interval (CI) around the temperature coefficient estimate did not include zero (Tables 3 and 4, Fig. 4). The effects of soil moisture on seedling recruitment ranged from strongly positive for *L. tulipifera* to negative for *Q. rubra*, again their 95% CI around the soil moisture coefficient did not include zero (Tables 3 and 4). *A. rubrum* recruitment seems to be favored in warm and slightly dry springs. *Betula* spp., despite being at the southern limit of its range at our study site, established best in warm, moist years. Recruitment of *L. tulipifera* was highest in wet springs. Warm temperatures strongly benefited recruitment of *N. sylvatica*. Successful establishment of *Q. rubra* seedlings occurred in warm and dry springs. The extent to which the estimates of establishment probability p varied as a function of the posterior values for the fixed effects is shown in Fig. 5. The range of variation (mean and 95% prediction interval) incorporates the uncertainty in the data and in the parameters we have estimated.

The role of light and seed density

The two species that showed a particularly strong response to light availability at the germination stage, *Betula* spp. and *L. tulipifera* (Tables 3 and 4, Figs. 4 and 5), are shade intolerant (Kelty 1988, Beck 1990, Walters and Yawney 1990). *Acer rubrum* seedlings have the ability to compete as a pioneer on disturbed sites in this part of its distributional range (Johnson et al. 1987, Walters and Yawney 1990). The only species that seemed to establish best at low light is *N. sylvatica*. Two possible explanations for this reduced seedling establishment at high light levels would be an escalation on the risk of desiccation, an increase on exposure to predators, or competition with other species that recruit well at high light levels.

Previous analysis revealed that density dependence affects seedling survival near parent trees (Hille Ris Lambers et al. 2002). Our results suggest that density dependence also operates at the germination stage. With the exception of the small-seeded *Betula* spp. and *L. tulipifera*, all species experienced density dependence at seedling establishment (Tables 3 and 4, Figs. 4 and 5). Plots with highest seed densities experienced the greatest reduction in probability of establishment. This influence

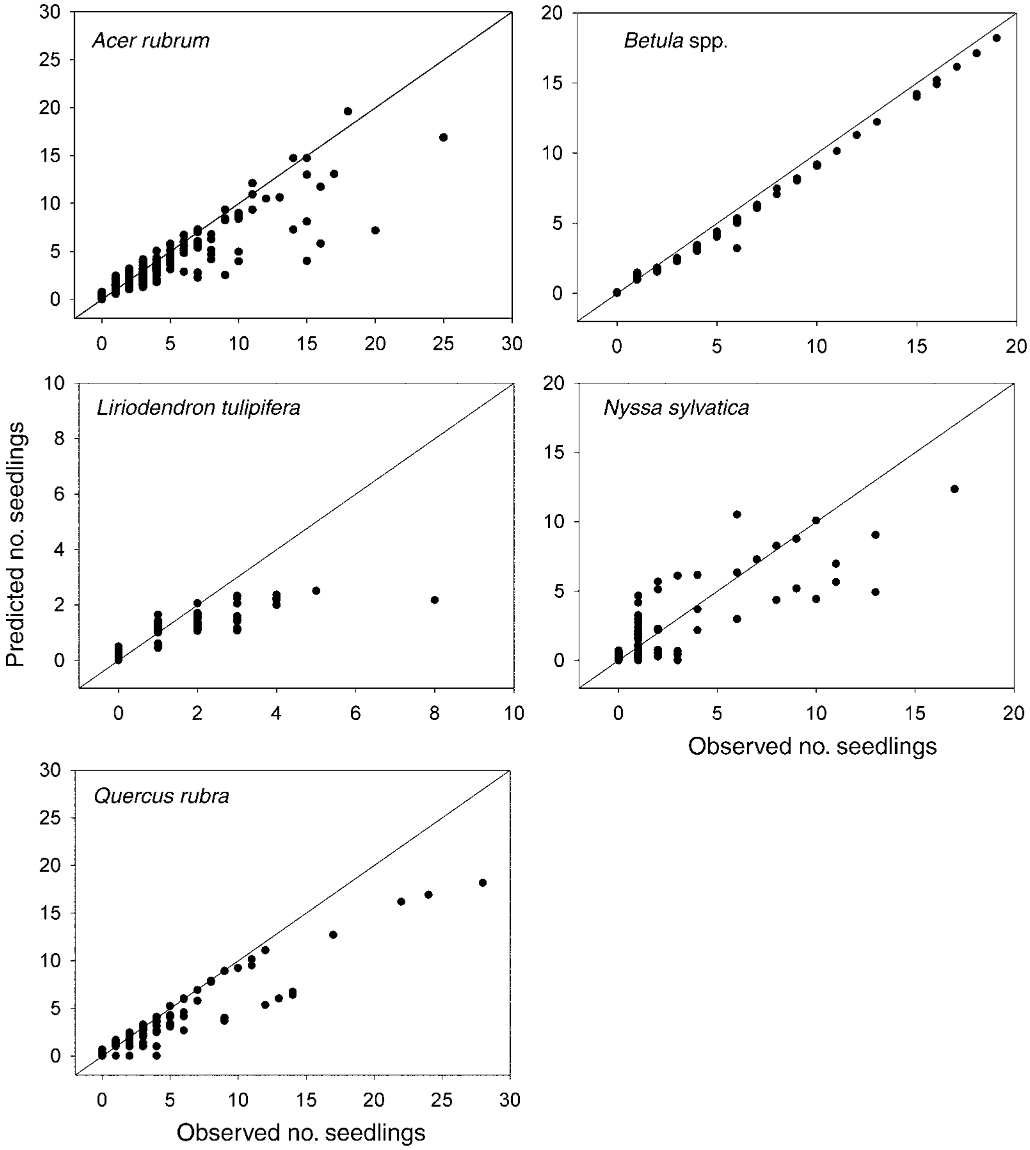

Fig. 3. Model fit for the predicted number of seedlings established vs. the number of observed new seedlings (dots).

is probably due to predation (Beckage and Clark 2005), plots with high densities of seeds attracting more predators, thus reducing the percentage of germinating seeds. The model that best described *Q. rubra* establishment included a stand random effect associated with seed density (Table 2). Values of this parameter were lowest in stands with highest seed densities (seed data not shown).

Discussion

Model-based inference on demographic responses to climate variation did not support projections that have

Table 3. Posterior parameter values (mean ± SD) for fixed effects.

Species	α_0 (intercept)	α_1 (temperature)	α_2 (soil moisture)	α_3 (light)	α_4 (seed density)	τ_ε
Acer rubrum	**−6.97 ± 1.89**	**0.16 ± 0.08**	−0.06 ± 0.03	**41.01 ± 7.46**	**−0.002 ± 0.0002**	0.59 ± 0.08
Betula spp.	**−19.28 ± 2.37**	**0.35 ± 0.11**	0.06 ± 0.03	**54.96 ± 7.37**	**0.0002 ± 0.00005**	0.13 ± 0.02
Liriodendron tulipifera	**−14.22 ± 1.57**	0.04 ± 0.07	**0.18 ± 0.02**	**61.43 ± 7.2**	0.0006 ± 0.0003	11.57 ± 8.74
Nyssa sylvatica	−28.35 ± 11.43	**1.26 ± 0.65**	0.19 ± 0.27	**−180.7 ± 84.93**	**−0.015 ± 0.006**	0.35 ± 0.1
Quercus rubra	**−12.7 ± 2.57**	**0.49 ± 0.12**	**−0.07 ± 0.04**	53.69 ± 22.52	**−0.17 ± 0.12**	0.1 ± 0.03

Note: Bold fixed-effect values were significantly different from zero (based on 95% CI).

TABLE 4. Posterior parameter values (mean ± SD) for random effects, seed viability, and seed mortality in stands 1–5.

Species and stand	Random effects, μ_j	Seed viability, v_j	Seed mortality, d_j
Nyssa sylvatica			
Stand 1		0.73 ± 0.11	0.51 ± 0.18
Stand 2		0.57 ± 0.13	0.56 ± 0.14
Stand 3		0.86 ± 0.05	0.92 ± 0.02
Stand 4		0.89 ± 0.05	0.27 ± 0.13
Quercus rubra			
Stand 1	0.05 ± 0.12	0.02 ± 0.004	
Stand 2	**12.69 ± 6.32**	0.06 ± 0.006	
Stand 3	5.86 ± 6.72	0.01 ± 0.002	
Stand 4	**0.16 ± 0.12**	0.19 ± 0.009	
Stand 5	**0.17 ± 0.12**	0.04 ± 0.005	

Notes: Stand 1, ridge; stand 2, cove; stand 3, mixed oak, low elevation; stand 4, mixed oak, high elevation; stand 5, northern hardwood. Bold random-effect values were significantly different from zero (based on 95% CI). Viability and mortality were only estimated for the two species for which we did not have prior information, *N. sylvatica* and *Q. rubra*. For the rest of the species we sample the parameter, without calculating posterior values, from previous estimates for those species and stands (Hille Ris Lambers et al. 2004; see Table 3). For *Q. rubra*, $\tau_\mu = 0.03 \pm 0.03$.

come from the climate envelope approach. By combining seed rain, seed bank, and germination dynamics with long-term environmental data within a heterogeneous landscape, we estimated how recruitment of the dominant tree species is affected by ten years of climatic variability. This approach contrasts with predictions of future ranges of plant species derive almost exclusively from climate correlations (e.g., Iverson and Prasad 1998, Iverson et al. 1999). Their predictive capacity is limited if factors other than climate have important effects on species survival (Pacala and Hurtt 1993, Ibáñez et al. 2006). Both approaches have merit, and we should learn most from the instances in which they disagree. Specific advantages of our approach include the fact that we include the actual distribution of spatiotemporal change in climate, in the biological and physical setting in which

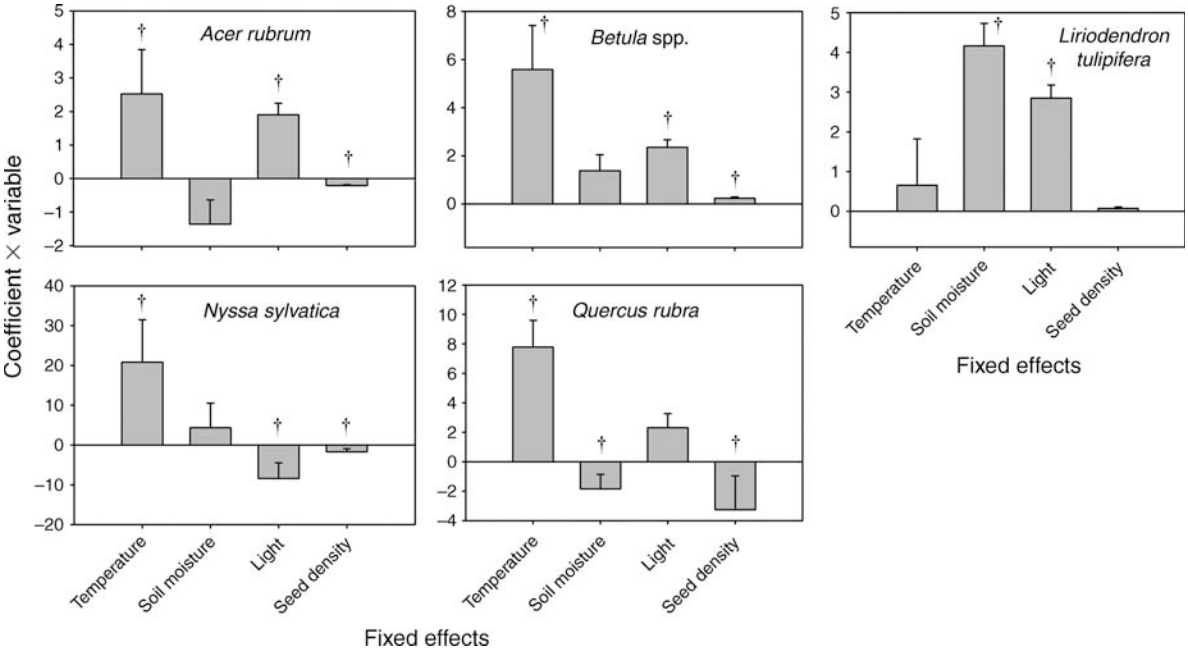

FIG. 4. Posterior means and standard deviations for effects of the predictor variables on seedling recruitment for each of the five species studied. To allow for comparisons across both explanatory variables and species, histograms represent the fitted parameter values for each fixed effect (mean ± SD) scaled by the mean values for each of the associated explanatory variables. A 95% credible interval that does not include zero is indicated by a dagger. In these cases, we considered the associated explanatory variable to have significantly affected survival.

it occurs. The response variables are demographic rates, a tractable level of complexity that is typically employed for population dynamics. This context is made possible by assimilation of multiple sources of information. By accounting for the variability in seed rain and seed soil bank dynamics and the effects of light availability and seed density on seedling establishment, we were able to identify the climate variables likely to be important for specific species.

Which species are most sensitive to climate variability?

Recruitment of all species benefited from warm springs, including the species that are dominant at high elevations in our study region, *Betula* spp. and *Q. rubra*. These two species are near the southern limit of their distribution ranges, and a "climate envelope" approach would predict a northward shift in response to climate warming (e.g., Iverson et al. 1999). This disparity would indicate a seedling–adult conflict that could have larger repercussions on the local survival of these species. *Liriodendron tulipifera*, common on mesic sites, experienced highest establishment rates under the most mesic conditions. On the other hand, *Q. rubra* benefited from dry environments. Again, this was an unexpected finding. The future distribution range of this species is associated with regions that will maintain levels of precipitation similar to those found at its current range, but not lower (e.g., Iverson and Prasad 2002). Clearly, the recruitment dynamics of these species could be affected by minor changes in climate even if those changes do not affect the adult tree populations. More importantly, these responses may not be accurately predicted by the climate these species experience in their current distributions.

Will species found in xeric sites be most sensitive to drought?

Moisture availability for seedlings is likely to decrease with climate change, despite potentially higher spring precipitation. Increased temperatures are likely to result in increased evapotranspiration and thus, lower soil moisture (National Assessment Synthesis Team 2000). The communities we studied span a soil moisture gradient representative of both warmer and drier (Fig. 1c, left arrow) and the warmer and wetter forecasts (Fig. 1c, right arrow). For two species dominant at dry sites (*A. rubrum* in the ridge stand and *N. sylvatica* in the stand of mixed oak), the variability in soil moisture among stands and years was not of sufficient magnitude to affect establishment; thus, these two species might maintain, or even expand, in terms of seedling success. In contrast, *Q. rubra* (a dominant species in the mixed-oak stand at high elevation) may benefit from dry years, potentially due to a reduction on pathogenic attacks on seeds and seedlings in more arid conditions (Packer and Clay 2000, 2003, Reinhart et al. 2003). If this is the case, an increase in spring precipitation may cause seedling establishment to strongly decrease in response to pathogenic infections. On the other hand, if spring precipitation remains the same or decreases, *Q. rubra* populations could expand in the region. Thus, our results suggest that the dominant species in our dry sites will have idiosyncratic responses to decreases in soil moisture as a result of complex interactions between biotic and abiotic factors affecting establishment.

Species in mesic microsites with decreased precipitation

Our results suggest that species in moist microsites may be particularly sensitive to changes in climate. *Betula* spp. and *L. tulipifera* are the prevailing species in the two most mesic stands, the northern hardwood stand and the cove, respectively. *L. tulipifera* required wet springs for successful recruitment. Predicted higher spring precipitation will favor recruitment. However, considering that most of its seedlings die of desiccation during their first summer (I. Ibáñez, *personal observation*) xeric summers will have a negative effect on the long-term survival of the seedlings. And *Betula*, primarily *B. lenta*, a species that benefits from warmer springs at the high elevation stand, will likewise suffer reduced recruitment success during dry years. The majority of its germinating seedlings die after a few weeks at higher rates than observed for any of the co-occurring tree species (I. Ibáñez, *personal observation*), further studies would be necessary to elucidate on the processes taking place during the first few weeks in the life of these seedlings. A reduction in soil moisture, either due to lower precipitation or increased evapotranspiration with increased temperature, will have a large effect on these two species. Reduced recruitment of these important species is expected to fundamentally change dynamics. The response of these two species and possibly others in mesic sites, suggests that the unique vegetation in these locations is at risk under future climate scenarios.

Integrating the evidence for climate sensitivity

Our results suggest that the predictions from simplistic models could be misleading. As a predictive tool, our approach has limitations of its own. The advantage it provides is complementary to climate envelope models. It takes into consideration species response to annual climatic changes that are well underway now, indicating how dynamic responses will vary across the diversity of local settings in real competitive environments.

Our results for five dominant tree species showed a continuum of responses to interannual climate variability and environmental conditions during seedling establishment. Although recruitment of all the species was favored by warm spring temperatures, sensitivity varied. The mechanisms behind these responses may differ. Warm springs may mean optimal metabolic conditions for some species while, for others, the

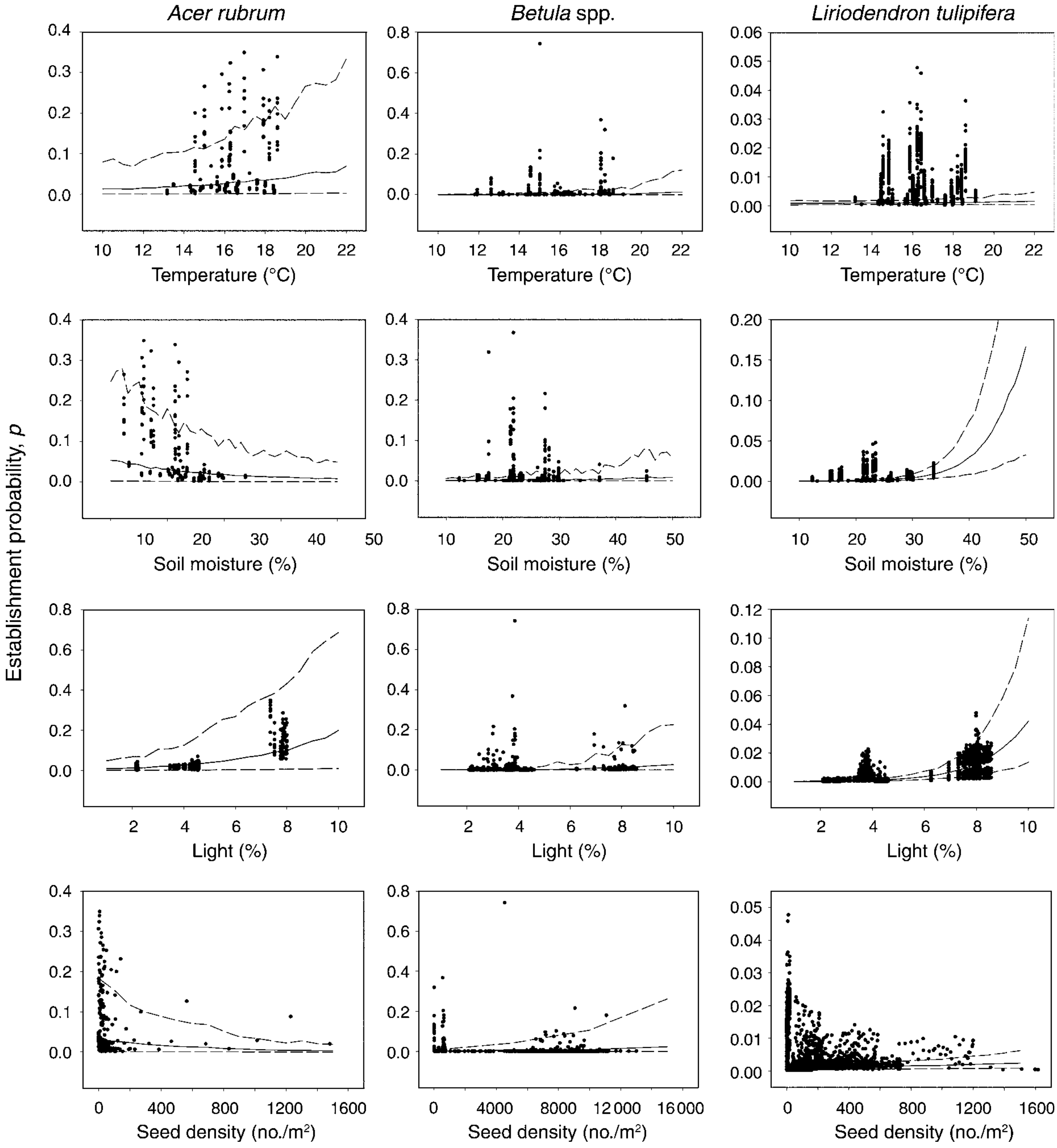

FIG. 5. Predicted probability of establishment, p, for each species as a function of the explanatory variables tested, shown as mean (solid line) and 95% prediction intervals (dashed lines). Individual estimates of p (posterior means) for each plot and year are also shown (dots).

beneficial effects could be due to dry conditions that mitigate pathogenic fungi.

At our sites, each species requires a particular set of conditions to optimize recruitment. For the dominant species in our region, future recruitment appears to hinge on a balance between optimal spring temperatures and sufficient soil moisture, with interactions involving disturbance. Communities like those found at the ridge and low elevation oak stands, where *A. rubrum* and *N. sylvatica* are dominant species, will expand under warm/dry conditions. Proliferation of cove vegetation, where *L. tulipifera* thrives, can only occur if precipitation increases compensate for increased evapotranspiration rates. Mixed-oak communities at intermediate elevations, where oak species dominate, will be influenced by increased spring temperature and precipitation,

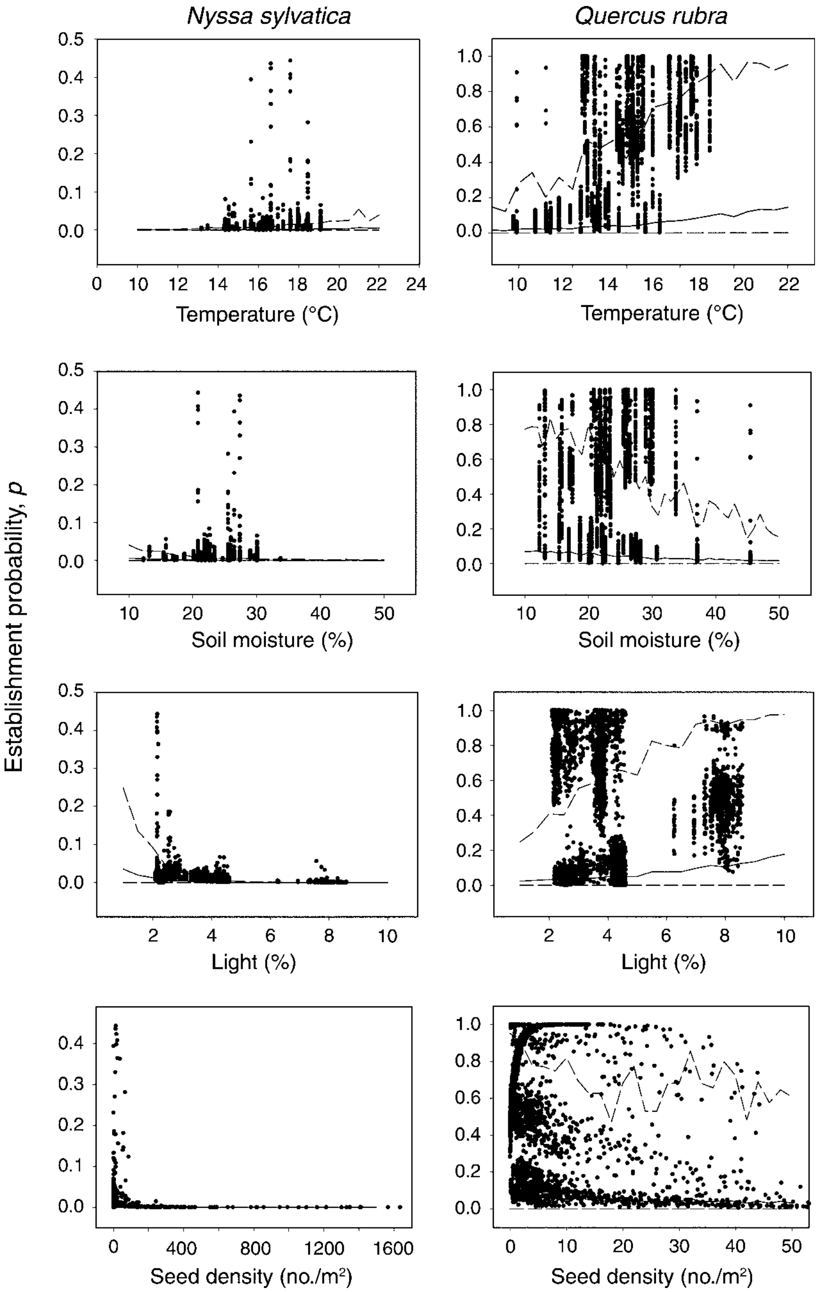

FIG. 5. Continued.

depending on interactions with pathogens. The northern hardwood stand we analyzed will require migration to higher elevations that can still provide optimal conditions for seedlings recruitment of *Betula* species.

Conclusions

We found sensitivity to climate variation at the process level that would not lead to the same predictions as climate envelope models, which are now the commonly used predictive tool. Specifically, spring temperatures and heterogeneity in soil moisture emerge as critical factors. Moreover, the consequences of variation in these factors could not be captured by simple linear correlations. Our process-level approach, based on actual climate changes in natural settings, indicates that climate impacts will be complex, and only by employing a comprehensive approach were we able to discern each species response to climatic variability.

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LITERATURE CITED

Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4:164–185.

Beck, D. E. 1990. *Liriodendron tulipifera* L. yellow poplar. Pages 406–416 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.

Beckage, B., and J. S. Clark. 2005. Does predation contribute to tree diversity? Oecologia 143:458–469.

Beckage, B., J. S. Clark, B. D. Clinton, and B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 30:1617–1631.

Berkson, J. 1951. Why I prefer logits to probits. Biometrics 7: 327–339.

Berliner, L. M., R. F. Milliff, and C. K. Wikle. 2003. Bayesian hierarchical modeling of air-sea interaction. Journal Of Geophysical Research–Oceans 108: article no. 3104.

Boer, G. J., G. M. Flato, and D. Ramsden. 2000. A transient climate change simulation with historical and projected greenhouse gas and aerosol forcing: projected climate for the 21st century. Climate Dynamics 16:427–451.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity: evidence since the middle of the 20th century. Global Change Biology 12:862–882.

Brooks, S. P., and A. Gelman. 1998. Alternative methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434–455.

Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86:3030–3038.

Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003*a*. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. Proceedings of the National Academy of Sciences (USA) 100:5852–5857.

Clark, F. B., and S. G. Boyce. 1964. Yellow-poplar seed remains viable in the forest litter. Journal of Forestry 62:564–567.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters 8:2–14.

Clark, J. S., S. LaDeau, and I. Ibáñez. 2004. Fecundity of trees and the colonization–competition hypothesis. Ecological Monographs 74:415–442.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecological Monographs 68:213–235.

Clark, J. S., J. Mohan, M. Dietze, and I. Ibáñez. 2003*b*. Coexistence: how to identify trophic trade-offs. Ecology 84: 17–31.

Connell, J. H., and P. T. Green. 2000. Seedling dynamics over thirty-two years in a tropical rain forest tree. Ecology 81:568–584.

DeLucia, E. H., S. L. Naidu, R. B. Thomas, J. A. Andrews, A. C. Finzi, G. R. Hendrey, and W. H. Schlesinger. 1999. Net carbon storage in an intact forest under experimental CO_2 enrichment. Science 284:1177–1179.

Fleishman, E., R. Mac Nally, J. P. Fay, and D. D. Murphy. 2001. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. Conservation Biology 15: 1674–1685.

Gelfand, A. E., and S. K. Ghosh. 1998. Model choice: a minimum posterior predictive loss approach. Biometrika 85: 1–11.

Graumlich, L. J. 1991. Sub-alpine tree growth, climate, and increasing $CO_{2:}$ an assessment of recent growth trends. Ecology 72:1–11.

Hampe, A. 2005. Fecundity limits in *Frangula alnus* (*Rhamnaceae*) relict populations at the species' southern range margin. Oecologia 143:377–386.

Hansen, A. J., R. R. Neilson, V. H. Dale, C. H. Flather, L. R. Iverson, D. J. Currie, S. Shafer, R. Cook, and P. J. Bartlein. 2001. Global change in forests: responses of species, communities, and biomes. BioScience 51:765–779.

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.

Haywood, J. D. 1994. Seed viability of selected tree, shrub and vine species in the field. New Forest 8:143–154.

Hille Ris Lambers, J., and J. S. Clark. 2003. Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. Canadian Journal of Forest Research–Revue Canadienne De Recherche Forestiere 33:783–795.

Hille Ris Lambers, J., J. S. Clark, and B. Beackage. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417:732–735.

Hille Ris Lambers, J., J. S. Clark, and M. Lavine. 2005. Seed banking in temperate forests: implications for recruitment limitation. Ecology 86:88–95.

Houle, G. 1995. Seed dispersal and seedling recruitment: the missing link(s). Ecoscience 2:238–244.

Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula Alleghaniensis*: spatial inconsistency in time. Ecology 79:807–818.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557.

Ibáñez, I., J. S. Clark, M. C. Dietze, K. Feeley, M. Hersh, S. LaDeau, A. McBride, N. E. Welch, and M. S. Wolosin. 2006. Predicting biodiversity change: outside the climate envelope, beyond the species–area curve. Ecology 87:1896–1906.

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.

Iverson, L. R., and A. M. Prasad. 2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecology and Management 155:205–222.

Iverson, L. R., A. M. Prasad, N. J. Hale, and E. K. Sutherland. 1999. An atlas of current and potential future distributions of common trees of the eastern United States. Department of Agriculture, Forest Service, Northeastern Research Station Newtown Square, Pennsylvania, USA.

Johnson, J. E., C. L. Haag, J. G. Bockheim, and G. G. Erdmann. 1987. Soil–site relationships and soil characteristics associated with even-aged red maple (*Acer rubrum*) stands in Wisconsin and Michigan. Forest Ecology and Management 21:75–89.

Kelty, M. J. 1988. Sources of hardwood regeneration and factors that influence these sources. Pages 17–30 *in* H. C. Smith, A. W. Perkey, and W. E. Kidd, editors. Guidelines for regenerating Appalachian hardwood stands. Workshop proceedings, 24–26 May, 1988, Morgantown, West Virginia. SAF Publication 88-03. West Virginia University Books Morgantown, West Virginia, USA.

Kobe, R. K., S. W. Pacala, J. A. Silander, and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5:517–532.

Körner, C. 2004. Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. Philosophical Transactions of the Royal Society of London B Biological Sciences 359:493–498.

Kumagai, T., G. G. Katul, A. Porporato, T. M. Saitoh, M. Ohashi, T. Ichie, and M. Suzuki. 2004. Carbon and water cycling in a Bornean tropical rainforest under current and future climate scenarios. Advances in Water Resources 27: 135–150.

Lasch, P., M. Lindner, M. Erhard, F. Suckow, and A. Wenzel. 2002. Regional impact assessment on forest structure and functions under climate change: the Brandenburg case study. Forest Ecology and Management 162:73–86.

Lavine, M., B. Beckage, and J. S. Clark. 2002. Statistical modeling of seedling mortality. Journal of Agricultural Biological and Environmental Statistics 7:21–41.

Matthes, U., and D. W. Larson. 2006. Microsite and climatic controls of tree population dynamics: an 18-year study on cliffs. Journal of Ecology 94:402–414.

McKone, M. J., D. Kelly, and W. G. Lee. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. Global Change Biology 4:591–596.

Mearns, L. O., F. Giorgi, L. McDaniel, and C. Shields. 2003. Climate scenarios for the southeastern U.S. based on GCM and regional model simulations. Climatic Change 60:7–35.

Mitchell, J. F. B., T. C. Johns, J. M. Gregory, and S. Tett. 1995. Climate response to increasing levels of greenhouse gases and sulphate aerosols. Nature 376:501–504.

Mohan, J. E., J. S. Clark, and W. H. Schlesinger. 2007. Long-term CO_2 enrichment of a forest ecosystem: implications for temperate forest regeneration and succession. Ecological Applications 17:1198–1212.

Mutke, S., J. Gordo, and L. Gil. 2005. Variability of Mediterranean Stone pine cone production: Yield loss as response to climate change. Agricultural and Forest Meteorology 132:263–272.

National Assessment Synthesis Team. 2000. Climate change impacts on the United States. The potential consequences of climate variability and change: overview report. U.S. Global Change Research Program, Washington, D.C., USA.

Nilsson, S. G., and U. Wästijung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. Ecology 68:260–265.

Novick, K. A., P. C. Stoy, G. G. Katul, D. S. Ellsworth, M. B. S. Siqueira, J. Juang, and R. Oren. 2004. Carbon dioxide and water vapor exchange in a warm temperate grassland. Oecologia 138:259–274.

Pacala, S. W., and G. C. Hurtt. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Pages 57–74 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer, Sunderland, Massachusetts, USA.

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

Packer, A., and K. Clay. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. Ecology 84:108–119.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Peroni, P. A. 1995. Field and laboratory investigations of seed dormancy in red maple (*Acer rubrum* L.) from the North Carolina Piedmont. Forest Science 41:378–386.

Reinhart, K. O., A. Packer, W. H. van der Putten, and K. Clay. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. Ecology Letters 6:1046–1050.

Rich, P. M., D. B. Clark, D. A. Clark, and S. F. Oberbauer. 1993. Long-term study of solar radiation in a tropical wet forest using quantum sensors and hemispherical photography. Agricultural and Forest Meteorology 65:107–127.

Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by 18 New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83:1214–1225.

Schwartz, M. W., L. R. Iverson, and A. M. Prasad. 2001. Predicting the potential future distribution of four tree species in Ohio using current habitat availability and climatic forcing. Ecosystems 4:568–581.

Spiegelhalter, D. J., N. Thomas, N. Best, and W. Gilks. 1996. BUGS 0.5: Bayesian inference using Gibbs sampling. Manual (version ii). Medical Research Council Biostatistics Unit, Cambridge, UK.

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

Stevens, L. R., J. R. Stone, J. Campbell, and S. C. Fritz. 2006. A 2200-yr record of hydrologic variability from Foy Lake, Montana, USA, inferred from diatom and geochemical data. Quaternary Research 65:264–274.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Walters, R. S., and H. W. Yawney. 1990. *Acer rubrum* L. red maple. Pages 60–69 *in* R. M. Burns and B. H. Honkala, editors. Silvics of North America. Hardwoods. Agricultural Handbook 654. U.S. Department of Agriculture, Forest Service Washington, D.C., USA

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1–80.

Wikle, C. K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. Ecology 84:1382–1394.

Wright, S. J., H. C. Muller-Landau, O. Calderón, and A. Hernandéz. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology 86: 848–86.

APPENDIX A

Priors and initial parameter values (*Ecological Archives* M077-006-A1).

APPENDIX B

A list of different models tried for each species (*Ecological Archives* M077-006-A2).