

EVALUATING THE SOURCES OF POTENTIAL MIGRANT SPECIES: IMPLICATIONS UNDER CLIMATE CHANGE

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Abstract. As changes in climate become more apparent, ecologists face the challenge of predicting species responses to the new conditions. Most forecasts are based on climate envelopes (CE), correlative approaches that project future distributions on the basis of the current climate often assuming some dispersal lag. One major caveat with this approach is that it ignores the complexity of factors other than climate that contribute to a species' distributional range. To overcome this limitation and to complement predictions based on CE modeling we carried out a transplant experiment of resident and potential-migrant species. Tree seedlings of 18 species were planted side by side from 2001 to 2004 at several locations in the Southern Appalachians and in the North Carolina Piedmont (USA). Growing seedlings under a large array of environmental conditions, including those forecasted for the next decades, allowed us to model seedling survival as a function of variables characteristic of each site, and from here we were able to make predictions on future seedling recruitment. In general, almost all species showed decreased survival in plots and years with lower soil moisture, including both residents and potential migrants, and in both locations, the Southern Appalachians and the Piedmont. The detrimental effects that anticipated arid conditions could have on seedling recruitment contradict some of the projections made by CE modeling, where many of the species tested are expected to increase in abundance or to expand their ranges. These results point out the importance of evaluating the potential sources of migrant species when modeling vegetation response to climate change, and considering that species adapted to the new climate and the local conditions may not be available in the surrounding regions.

Key words: climate change; climate envelope; migration; seedling recruitment; source of migrant species; survival; transplant experiment; tree species.

INTRODUCTION

Predictive modeling of biodiversity response to global warming attempts to describe a displacement of species from low to high latitudes, and, in mountainous regions, from low to high elevations. Most such models involve calibration of the current species range and climate variables, coupled with a scenario of future climate, the so-called “climate envelope” approach (e.g., Thuiller 2003, Araujo and Pearson 2005, Guisan and Thuiller 2005). Predictions thus rely on a direct connection between climate and species ranges. The added complexity of dispersal has been included in a number of models, usually with caveats concerning limited understanding of current fecundity and dispersal (Eriksson and Jakobsson 1999, Ouborg et al. 1999) and how they

might differ from those under changing climate scenarios (Etterson 2004, Dullinger et al. 2005). Realization that novel storm frequencies and intensities that determine long-distance dispersal are largely unknown has motivated a focus on the two extreme scenarios of “no dispersal” (Midgley et al. 2002) vs. “immediate occupancy” of new sites (Thomas et al. 2004, although see Harte et al. 2004, Thuiller 2004) or both (McKenney et al. 2007), and more realistic approaches have also been suggested (e.g., Iversen et al. 2004, Pearson and Dawson 2005, Midgley et al. 2006).

Despite widespread belief that actual impacts will be more complex than a simple climate envelope model, it has been difficult to include such non-climate-related effects in the predictive-modeling framework. Where additional “niche” variables are included in climate envelopes, the “direct” modeling approach is still typically applied: simple regressions between niche variables are used to project current correlations to the future (Peterson and Cohoon 1999). Again, the limitations are well known (Pacala and Hurtt 1993, Pearson and Dawson 2003, Ibáñez et al. 2006), but remain unresolved due to a perception that mechanistic studies at relevant geographic scales require elaborate and costly infrastructure, and are necessarily limited to

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scattered small plots (e.g. Davidson et al. 2000, Majdi and Ohrvik 2004), although new studies attempting more mechanistic approaches are also emerging (Thuiller et al. 2008).

As a specific example, by mid-century in the southeastern United States, regional climate models predict a mean annual temperature increase of 1–7°C, with a 30% decrease in summer precipitation and a 25% increase in spring rainfall (Mearns et al. 2003). Increased aridity could result in a dramatic shift from temperate deciduous forest to southern mixed forest or even savanna, with increased importance of species from lower latitudes and elevations (Iverson et al. 1999, Bachelet et al. 2001). Climate-envelope assumptions suggest that immigrants will come from warmer regions (more southerly and lower elevation). Thus, predicted immigrants to the southeastern Piedmont are situated today in the Coastal Plain, and those to the Southern Appalachians now reside on the Piedmont (Fig. 1).

In terms of future species composition, the climate-envelope predictions do not provide much guidance. The predicted climate does not agree with that of any potential source area, and certainly not with any area within reach of dispersal scenarios (Ibáñez et al. 2006, 2007). Forecasts for the southeastern United States resemble current conditions in the Caribbean and Central America for January, while predicted July temperatures and precipitation are more like deserts in southwestern North America. These issues are fundamentally unanswerable with climate-envelope models.

In addition, the climate of the Coastal Plain may be more like predicted climates than anything else and more likely to be reached by dispersal. But the Coastal Plain contrasts with the Piedmont and Southern Appalachians in terms of soils, topography, and disturbance regime. Coastal Plain soils are dominated by sand and peat, with low nitrogen availability, high water tables, and historically high fire frequency (Christensen 2000). Species adapted to these conditions may not thrive on the clay-rich soils of the Piedmont and mountains, where fire does not play a role in the dynamics of the community. With these differences in soils come different pathogens and herbivores. The specifics for the southern United States illustrate elements of general biogeographic issues that will affect almost all regions.

Together, these concerns suggest a need for mechanistic studies that focus on the currently changing climate, the natural settings that prevail in the areas that will change, and the species that might invade given the current climate changes. The southeastern United States may see a combination of a new climate (Williams et al. 2007), with soil and land-cover changes best suited to species that are not currently anywhere in the Southeast (or anywhere else). Under such a scenario, is there a source of potential immigrants into the North Carolina Piedmont and the Southern Appalachians? By providing insight into the species that could invade

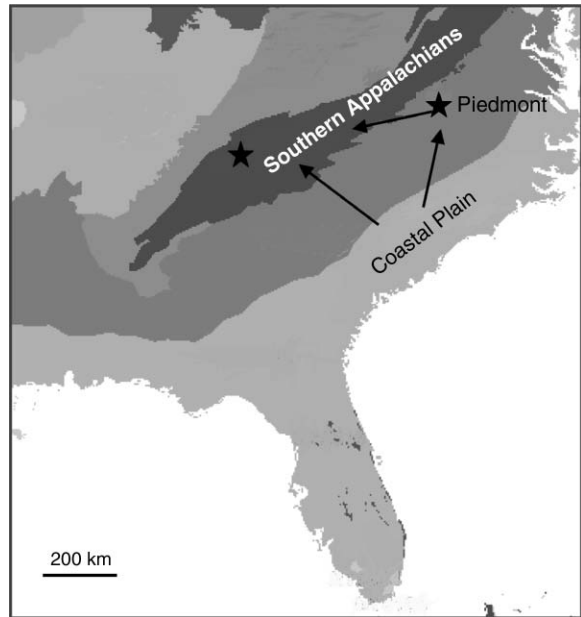


FIG. 1. The study region in the southeastern United States, location of the plots (stars), and potential migratory sources (arrows).

under the currently changing climate, mechanistic studies help us anticipate the redistribution of species and the composition of communities at regional and local scales under plausible climate scenarios.

Several observations led us to suggest that a broader range of mechanistic studies could complement climate-envelope-based modeling. First, we do not have to wait for future climate change to happen or to create future climates artificially. Climate is changing now. Its immediate and future implications can be assessed in intact communities by taking advantage of spatial and temporal environmental gradients. Second, the unanswerable questions regarding dispersal—which immigrants will arrive and when—does not preclude assessment of whether or not potential immigrants could invade the contemporary communities predicted by climate-envelope models. The immediate and relevant questions are not “When will specific species arrive at specific locations?” (Clark et al. 2003a), or “What will be the equilibrium communities under specific and static climate scenarios (because climate does not stop changing)?” Rather, “If propagules arrive in the current changing climate, could they establish?” and, “If so, what local conditions would be required?” A design is needed that evaluates the recruitment of potential immigrants relative to the performance of resident species across a range of the different microsites that affect recruitment success. It needs to be sufficiently long term and controlled to permit evaluation of factors that determine success. Due to high variability in recruitment, it requires a massive sample size. In addition, by growing plants in the actual site we are making

TABLE 1. Species planted, together with years and locations of planting.

Species planted		No. of seedlings included in final analysis, <i>N</i>	Planting locations			
			Piedmont		Southern Appalachians	
Name	Code		Years planted	Type planted	Years planted	Type planted
<i>Acer barbatum</i>	Acba	109			2002, 2004	PI
<i>A. rubrum</i>	Acru	556	2002, 2003, 2004	R	2002, 2004	R
<i>A. saccharum</i>	Acsa	270	2004	R	2001, 2004	R
<i>Carya glabra</i>	Cagl	432	2001, 2002, 2003, 2004	R	2002	R
<i>C. illinoensis</i>	Cail	228	2002	PI	2003, 2004	PI
<i>Fagus grandifolia</i>	Fagr	287	2001, 2003	R	2001	R
<i>Liquidambar styraciflua</i>	List	723	2001	R	2001, 20002, 2003, 2004	PI
<i>Liriodendron tulipifera</i>	Litu	683	2001	R	2001, 2002, 2003, 2004	R
<i>Magnolia grandiflora</i>	Magr	112	2002, 2004	PI	2004	PI
<i>Pinus rigida</i>	Piri	353			20001, 2003	R
<i>P. taeda</i>	Pita	1268	2001, 2002	R	2001, 2002, 2003, 2004	PI
<i>Quercus alba</i>	Qual	257	2002, 2004	R	2002	R
<i>Q. falcata</i>	Qufa	677	2001, 2003	R	2001, 2003	PI
<i>Q. phellos</i>	Quph	1020	2001, 2002	R	2001, 2002, 2003, 2004	PI
<i>Q. prinus</i>	Qupr	176			2002	R
<i>Q. rubra</i>	Quru	1198	2001, 2002, 2003, 2004	R	2001, 2002, 2003, 2004	R
<i>Q. virginiana</i>	Quvi	273	2001, 2002, 2003, 2004	PI		
<i>Tsuga canadensis</i>	Tsca	90			2001	R

Note: Key to abbreviations: R = resident, PI = potential immigrant; *N* = number of seedlings included in the analysis.

predictions for, we ensure their exposure to the whole array of environmental conditions, biotic and abiotic, inherent to the area.

To identify the potential sources of colonizing species into the North Carolina Piedmont and the Southern Appalachians, we carried out experiments of resident (R) and potential immigrant (PI) tree species. Combining large, long-term manipulative experiments with transplantation of more than 13 000 seedlings, we analyzed these two groups of species planted side by side over a diverse range of sites, both natural and manipulated. Within a region, using natural environmental gradients that involve altitude, slope, exposure, and soil types, we assessed colonization success of potential immigrant species relative to that of native plants. Manipulations of the canopy and large mammal-proof enclosures were superimposed on these gradients and provided information on the role of canopy gaps, as they affected light availability, soil moisture, and herbivory in seedling survival. To fully exploit both experimental and observational data at different scales, we developed a hierarchical Bayes model of environmental variation and recruit survival (Clark and LaDeau 2006). From the range of environmental variables analyzed, we report impacts of soil moisture, light availability, winter conditions, and herbivory on survival. Soil moisture and winter conditions emerged as the most important variables that can be directly related to climate-change scenarios. And light availability is affected by the canopy and disturbance regime, which in the southeastern United States is driven by frequent hurricanes.

Our experiments address hypothesized recruitment to Piedmont and Southern Appalachians sites by Coastal

Plain and Piedmont species, respectively. Specifically, we ask how the establishment potential of species from neighboring regions compares to that of residents, i.e., the species with which they will compete for microsites (Table 1). We sought to answer the following questions: (1) Will resident and potential migrant species be able to establish under the future climate? (2) Will these potential colonizers be able to recruit under the particular set of conditions found in these regions?

METHODS

The overall design of the transplant experiments spans a broad range of conditions that directly involve climate variables or are expected to have effects that interact with climate. We use model-based inference (Clark and LaDeau 2006; Cressie et al. 2009), but in the context of experimental manipulations that both extend the range of variation and help isolate some of the effects. Thus, the “environmental template” of soils, elevation, and microclimate provides a backdrop on which we superimpose (1) canopy manipulations, because canopy gaps are recognized as critical for establishment of many species, and (2) herbivore exclosures, because large mammals consume large numbers of seeds and seedlings in this system. Representative “resident” (R) tree species of the local flora and of “potential immigrants” (PI) were grown side by side. We developed a hierarchical Bayes model that integrated survival data with the history of environmental conditions experienced by each individual seedling.

Species

The selection of resident species (R) was done on the basis of their local dominance in the Piedmont and

Southern Appalachians (Table 1). Many are predicted to respond to climate change, some expanding in range and abundance, others declining regionally (e.g., Iverson et al. 1999, Schwartz et al. 2001). For some species (e.g., *Quercus rubra*, *Acer saccharum*) our study sites are near their southern range limit, while for others (e.g., *Acer rubrum* and *Liriodendron tulipifera*) our region is central to it. Potential immigrant species were selected to be representative of Coastal Plain and Piedmont species. They have been predicted to invade our region under mid-21st century climate-change scenarios (Iverson and Prasad 1998, Iverson et al. 1999), and some have already been introduced (e.g., *Magnolia grandiflora* in the Piedmont, *Liquidambar styraciflua* in the Southern Appalachians) (Table 1). For these species, our experiments were aimed at determining the potential to establish natural populations and increase in abundance.

Field sites

Transplant experiments were carried out in the North Carolina Piedmont (Duke Forest; description *available online*)⁶ and in the Southern Appalachians (Coweeta LTER; description *available online*).⁷ We took advantage of the spatial heterogeneity of the landscape and planted seedlings under a range of naturally occurring and relevant conditions. We measured key environmental variables (e.g., soil moisture and light) at each of the planting locations. Of a total 121 plots, 51 plots were in the Southern Appalachians and 70 plots in the Piedmont. In the Piedmont, soils have low organic-matter content and medium to slow permeability; they mainly differ in their water-holding capacity (Orange County Soil Survey 1977). Plots were spread within a 30-ha area that covered several soil types (Tables 2, 3; Fig. 2). In the Southern Appalachians, plots were established at elevations from 685 m to 1500 m with a range of exposures, temperatures, and soil moisture regimes (Table 2, Fig. 2).

Seedling transplants

Transplants were established in each of four consecutive years, from 2001 to 2004, totaling more than 13 000 seedlings. Seeds were germinated and grown in the greenhouse for six weeks and then transplanted into the field early in the summer (late June). Five individuals of each species were planted in rows 25 cm apart within a 5 × 5 m plot, seedlings were also 25 cm apart within a row (see Table 1 for years and locations each species was planted and Tables 2 and 3 for overall characteristics of the plots).

Survival censuses were completed at the end of the winter season (early May), and at the end of the summer (late August) until August 2005. To avoid transplant effects, we did not include the first year in our analysis.

⁶ <http://www.env.duke.edu/forest>

⁷ <http://coweeta.ecology.uga.edu>

TABLE 2. Distribution and characteristics of the experimental plots, southern Appalachians.

Southern Appalachians†			
Elevation (m)	Number of plots		
	Total	N-NE exposure	S-SW exposure
1500	2	1	1
1170	2	1	1
1140	19	11 (5 canopy, 6 gap)	8 (4 canopy, 4 gap)
1030	26	18 (9 canopy, 9 gap)	7 (4 canopy, 3 gap)
685	2	no slope	no slope

Note: Key to abbreviations: Canopy = plots under the forest canopy; gap = plots in canopy gaps.

† The 51 plots in the Southern Appalachians are grouped by elevation.

The number of seedlings included in the final analyses is noted in Table 1.

Seeds came from local parent trees, supplemented where necessary by commercial sources. Local seeds were available in sufficient numbers for *Acer rubrum* (Piedmont), *Liquidambar styraciflua* (Piedmont), *Liriodendron tulipifera* (Piedmont and Southern Appalachians), *Magnolia grandiflora* (Piedmont garden), *Pinus taeda* (Piedmont), and *Tsuga canadensis* (Southern Appalachians). For *L. styraciflua*, *L. tulipifera*, and *P. taeda*, we used seeds from a combination of local collections and commercial sources. Commercially purchased seeds were used for the remaining species. Seedlings from these two sources were planted side by side (five individuals for each group at each plot), and a seed-source effect was included in the model to evaluate if survival rates differed between seed sources.

Canopy manipulation and herbivore enclosures

For any study involving natural variation in environmental variables, interventions can provide an opportunity to break up correlations among variables and help to isolate effects of specific covariates. However, in large-scale studies such as this, there will always remain correlated variation that cannot be fully controlled or observed. Thus, care must be taken in the analysis and interpretation to acknowledge the potential for complex responses.

We supplemented natural variation in a key covariate, light availability, with controlled canopy manipulation. Large (40 m diameter) and small (20 m diameter) gaps were created in March 2002, with a total of four 40 m diameter (large) and four 20 m diameter (small) gaps at the Piedmont site, and six large gaps and four small gaps at the Southern Appalachians location. From previous canopy manipulation, we knew that nontrivial changes in soil moisture, soil temperature, and air temperature attend gap creation (Beckage et al. 2000), so all of these variables were monitored. Following one full growing season of pretreatment data collection, gaps were created by pulling all canopy-status trees with a skidder. Most trees were uprooted, although some snapped along the bole and many of the smaller saplings were knocked

TABLE 3. Distribution and characteristics of the experimental plots, Piedmont.

Piedmont†							
Soil type	No. plots	Soil classification and description				Available water capacity	Shrinks welling potential
		Order	Suborder	Organic matter	Permeability		
Herdon	17 (9 canopy, 8 gap) (2 enclosures canopy)	Udisols	Udults	low	moderate	medium	low
Enon	50 (25 canopy, 25 gap) (6 enclosures canopy)	Alfisola	Udalfs	low	low	medium	high
Iridell	3 (3 canopy)	Alfisols	Udalfs	very low	low	low	very high

Note: Canopy = plots under the forest canopy; gap = plots in canopy gaps.
† The 70 plots in the Piedmont are grouped by soil type.

down. As in naturally formed gaps, our experimental gaps resulted in large spatial heterogeneity (M. C. Dietze and J. S. Clark, unpublished manuscript).

At the Piedmont site, where deer populations have recently expanded a set of eight plots under the forest canopy were enclosed within a wire mesh (2.5 cm wide) from the ground to 165 cm in height. This treatment excluded deer but not small mammals or insects.

Soil moisture and light availability

Volumetric soil moisture was measured for the top 15 cm at each plot of our sites using TDR (time domain reflectometry, Tektronic 1502B; Tektronix, Beaverton, Oregon, USA). Measurements were obtained within 5 m of each plot, from two paired points, every two weeks during the growing season. For this analysis we used the mean of seven measurements for each growing season.

Fractional light transmission was estimated using the global site factor (GSF) obtained from canopy photos

(Rich et al. 1993; M. C. Dietze, unpublished data) or from PAR sensors calibrated to the GSF. For most plots (109) GSFs were calculated from hemispherical photographs taken early in the day, before sun exposure, during the month of July at 1.15 m above the ground using an 8-mm fish-eye lens. From these photographs the proportion of full sunlight reaching the forest floor was calculated using the software package Hemiview (Delta-T Devices, Cambridge, UK). The range of variation among measurements taken at the same point and time, repeated photographs, was 6%. This variability inherent to the method was incorporated in our model. For eight plots in the Southern Appalachians and four plots at the Piedmont site we measured photosynthetically active radiation (PAR) using a light sensor (LI-200 pyranometer; LI-COR, Lincoln, Nebraska, USA). Measurements were taken at mid-day during clear conditions. PAR measurements were calibrated with GSF as: $GSF = 0.088PAR + 6.11$, $R^2 = 0.35$, from a

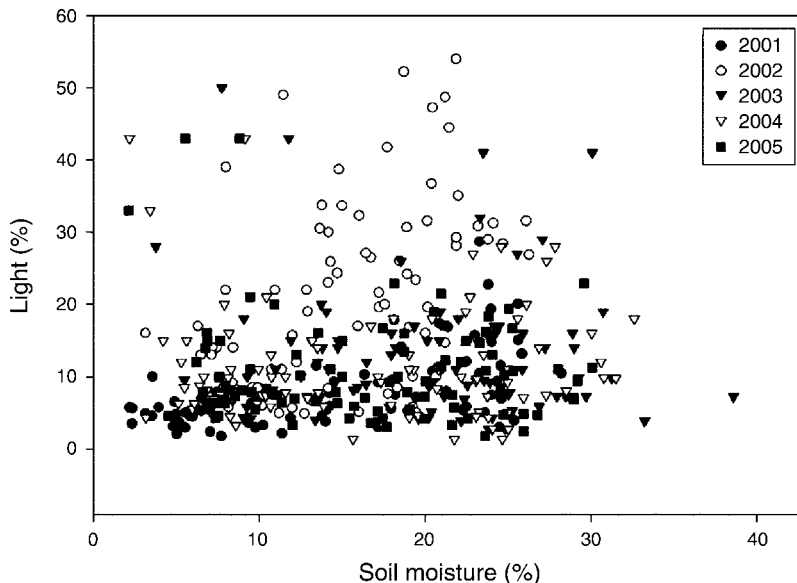


FIG. 2. Summer environmental variability at the 121 study plots during the years the experiment took place (2001–2005). Each point indicates the soil moisture–light combination at each particular plot.

set of 25 measurements taken using both methods. Both GSF and PAR data contain substantial uncertainty, which we accommodate explicitly as part of the process model (Clark et al. 2003b).

Hierarchical modeling

Although five replicate seedlings of each species (and seed source) were planted at each of the 121 plots and years, plot-level survival was not the response variable of interest. Instead, we estimated each individual’s response to the specific environmental conditions to which it was exposed. From these individual-based analyses we evaluated the overall species performance to specific environmental gradients. We modeled seedling survival as a function of environmental variables known to have a critical impact (Grubb 1977, Harper 1977). Seedling census and covariate data were combined in hierarchical models, which allows us to link information and processes at different levels (Gelfand and Smith 1990, Lavine et al. 2002, Clark 2003, 2005, Wikle 2003). To fully explore and exploit the information available from natural spatio-temporal variation and from manipulations, we constructed data models for each and used model-based inference to assess impacts. This involved selection among a large number of competing models, which are summarized in the Appendix. For clarity, the description here focuses on the final model we used in the analyses.

We modeled the probability that a seedling will survive from a census at time $t - 1$ to the census at time t as a Bernoulli process with probability s :

$$w_{pit} \sim \text{Bernoulli}(s_{pit}) \tag{1}$$

for individual i , on plot p where $w = 1$ if the seedling is alive at time t , and 0 if the seedling is dead. A total of N individuals of each species were included in the analysis (Table 1), with N_p individuals planted on each of $P = 121$ plots. Observations on an individual continued from one year after the transplant date (t_{0i}) until death or the end of the experiment if it was still alive, referenced as t_{0i} to t_{ni} . The two census times for each year (ending May and ending August) constitute seasonal effects that will enter through s_{pit} . There are a total of nine censuses, starting August 2001 and ending August 2005. The likelihood for the full survival data set is

$$p(\mathbf{w}|\mathbf{s}) = \prod_{p=1}^P \prod_{i=1}^{N_p} \prod_{t=t_{0i}}^{t_{ni}} \text{Bernoulli}(w_{pit}|s_{pit}). \tag{2}$$

The probability of a seedling surviving a census interval, s_{pit} , is the logit,

$$\text{logit}(s_{it}) = \mathbf{x}_{pit}\boldsymbol{\beta} \tag{3a}$$

where \mathbf{x}_{pit} is the design vector of factors and covariates, and $\boldsymbol{\beta}$ is the corresponding vector of parameters. We tested a large number of models, represented by different design vectors \mathbf{x} (Appendix). Climate is not the only difference between plots within regions (e.g., across

elevation) and between regions. For example, soils differ between the southern Appalachians and Piedmont. To help understand these interactions, we tested a large number of models with combinations of fixed and random effects (Appendix). For example, climate differences with elevation were included as fixed effects, but we also examined the random plot effects to determine if there were residual plot differences not accommodated by the specific fixed effects included in models. Covariates for this final model are summarized here and included an intercept for each region (β_1 and β_2), summer mean soil moisture percentage (Soilm), herbivore protection vs. control (Herb), light level (Light), season (winter vs. summer), and seed origin (Origin). The final model is

$$\begin{aligned} \text{logit}(s_{pit}) = & \beta_1 SA_p + \beta_2 P_p + \beta_3 x1_t \text{Soilm}_{pt} + \beta_4 \text{Herb}_{pt} P_p \\ & + \beta_5 \text{Light}_{pt} + \beta_6 x2_t + \beta_7 \text{Origin}_{ipt} SA_p \text{ (or } P_p) \end{aligned} \tag{3b}$$

where $SA =$ Southern Appalachians, 1 if the seedling was planted in this location, 0 otherwise; $P =$ Piedmont, 1 if the seedling was planted in this location, 0 otherwise; $\text{Herb} =$ herbivory protection, 1 if inside an enclosure, 0 if control; $x1$ and $x2$ are indicators of census time, if summer census $x1$ is 1, 0 otherwise, and if winter census $x2$ is 1, 0 otherwise; $\text{Origin} =$ origin of the seed, 1 if local, 0 if purchased.

We estimated winter and summer survival separately to specifically target the effects of summer water availability on seedling survival. Winter mortality, from late August to early May, can be caused by several factors for which we have no information (e.g., underground herbivory, frost damage). Minimum temperature during the coldest month, January, did not affect winter mortality, so it was not included in the selected model.

We included soil moisture content in the analysis instead of precipitation, because this variable better relates to seedlings survival. Variability in summer soil moisture is sampled for each plot and year from a normal distribution where the mean (S) is the average soil moisture measured at two paired points nearby the experimental plot during the summer months, and the variance is fixed for all the observations ($\sigma_S^2 = 10$; this value reflects the average variance among the paired measurements):

$$\text{Soilm}_{pt} \sim \mathcal{N}(\bar{S}_{pt}, \sigma_S^2). \tag{4}$$

In the case of the second environmental covariate, light, the uncertainty in our measurements (i.e., what we measured vs. what the seedlings experienced) lead us to treat light as an additional variable that needed to be estimated. Light was therefore modeled to allow for observation error (Clark et al. 2003b, Mohan et al. 2007). The “true” light available to seedlings, Light , was considered a latent variable and estimated based on the

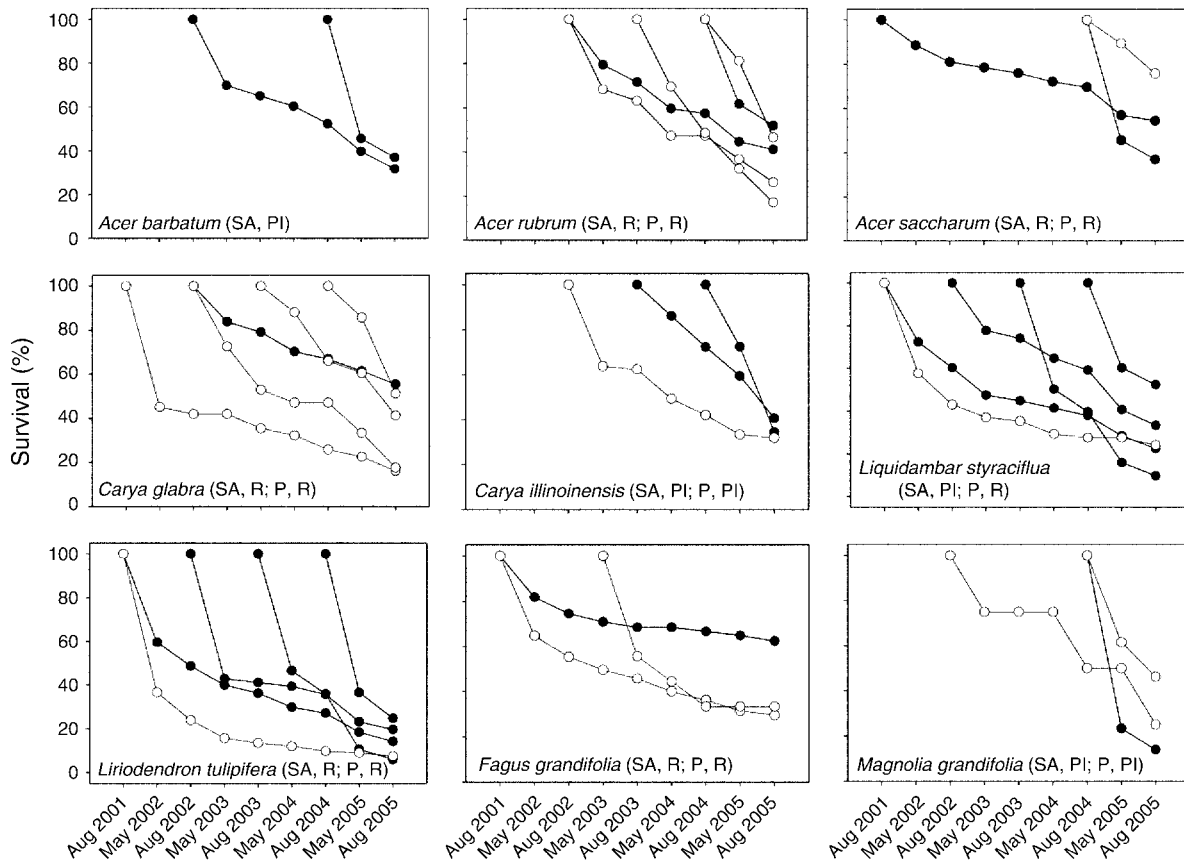


FIG. 3. Time-series data (August 2001–August 2005) on seedling survival during the study period. Key to abbreviations: SA = Southern Appalachians, P = Piedmont; R = native species, PI = potential migrant. Data from the Southern Appalachians are solid circles (●); the Piedmont series are represented by open circles (○).

GSF indices, PAR measurements, and observation error. For sites that did not experience canopy gap formation, differences among GSF indices and PAR data from year to year result primarily from observation error, which is informed by the repeated GSF measurements from that location and time. The data thus enter as a non-informative (uniform) prior bounded by the range of observations,

$$\text{Light}_{pt} \sim \text{Uniform}(a_{pt}, b_{pt}) \quad (5)$$

where lower and upper limits, a_{pt} and b_{pt} , come from repeated photos taken at the same plot and time (see *Methods: Soil moisture and light availability*, above). Therefore, the overall model will contribute to the estimation of light values, with the only constraint that they will be limited by these upper and lower bounds. Light was included as a covariate in both summer and winter survival, for the winter census we used light estimates from the previous summer.

The fixed effects, β , associated with the explanatory variables are modeled as a multivariate normal prior with sufficiently large variance to assure that data dominate:

$$\beta \sim \text{Multivariate } \mathcal{N}(\beta_0, \sigma^2 \mathbf{I})$$

$$\beta_0 = [0, 0, 0, 0, 0, 0, 0]^\top \quad \sigma^2 = 10\,000.$$

Additional models included other covariates, such as percentage vegetation cover, winter minimum temperature, seedling age, seedling size at the time of planting, and light at ground level (calculated as a combination of the light measurements, which were taken at 1.15 m, and the vegetation cover), and different types of random and fixed effects (Appendix).

The joint posterior distribution is then

$$p(\mathbf{s}, \text{Light}, \beta | \mathbf{w}, \mathbf{a}, \mathbf{b}, \mathbf{X}, \text{priors})$$

$$\propto \prod_{p=1}^P \prod_{i=1}^{N_p} \prod_{t=t_{0i}}^{t_{1i}} \text{Bernoulli}(w_{pit} | s_{pit}) \times \prod_{p=1}^P \prod_{t=1}^T \text{Unif}(\text{Light}_{pt} | a_{pt}, b_{pt}) \text{MVN}(\beta | \beta_0, \sigma^2 \mathbf{I}).$$

Model implementation, convergence, and model selection

Posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman 1984) using Win-

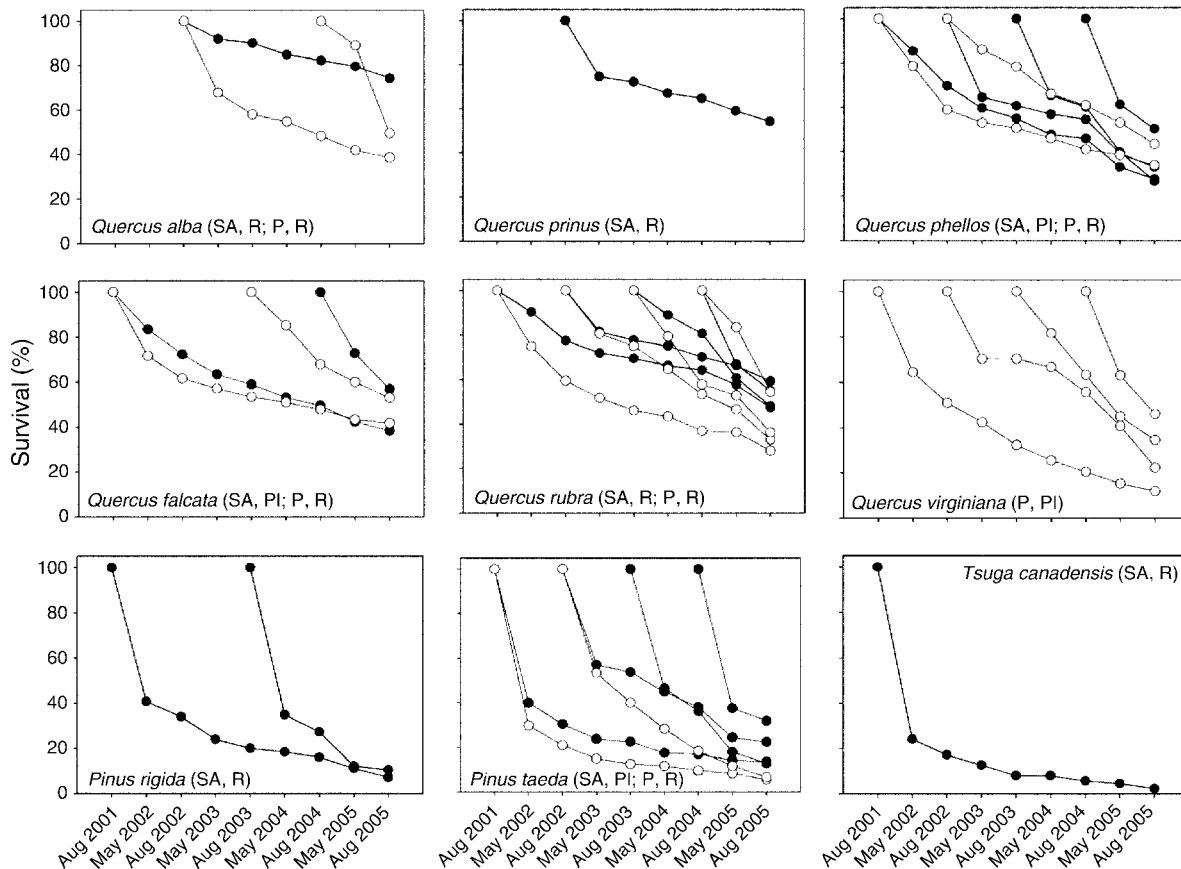


FIG. 3. Continued.

BUGS 1.4 (Spiegelhalter et al. 1996). Simulations were run for 50 000 iterations. Convergence was assessed from multiple chains with different initial conditions and Gelman and Rubin's *R*, as modified by Brooks and Gelman (1998), where convergence is assumed when *R* is close to 1. Convergence required from 1000 to 10 000 iterations. Preconvergence "burn-in" iterations were discarded. Model selection was based on DIC (deviance information criterion; Spiegelhalter et al. 2000). The effective number of parameters is approximated by subtracting the deviance of the posterior means of the parameters from the posterior mean of the deviance. Adding this value to the posterior mean deviance gives a deviance information criterion for comparing models, where the best predictor of the data is the model with lowest DIC. We ran several models for each species, and report results for the model that performed best among most species.

RESULTS

Environmental variability

Substantial spatio-temporal variation in covariates among plots and years provided a basis for modeling environmental effects on survival (Fig. 2). Soil moisture measurements among plots and years ranged between

8.4% and 53.2% in the Southern Appalachian plots, and between 2.13% and 38.6% in the Piedmont. The wettest year was 2003 with mean soil moisture content of 24.8% in the Southern Appalachians, and 13.87% in the Piedmont. The driest year was 2001, where soil moisture means were 19% for the Southern Appalachians and 6.9% for the Piedmont. This environmental gradient provided us with a range of conditions spanning those anticipated for the future. Here, although an increase in precipitation has been forecasted for the region (Solomon et al. 2007), an overall decrease in surface soil moisture has been predicted due to higher temperatures and evapotranspiration rates (Christensen et al. 2007).

Pre-gap-formation light levels average 11% in the Southern Appalachians and 4.8% in the Piedmont. The summer after the gaps were created, 2002, mean light levels rose to 27.8% in the Southern Appalachians, and 14.21% in the Piedmont. For the five years of our study, light ranged from 1.4% to 53.9% in the Southern Appalachians, and between 1.15% and 49.8% in the Piedmont.

Model selection and overall survival

The model that best predicted the data included the covariates soil moisture, herbivory, light, and seed origin

TABLE 4. Parameter estimates, mean posterior values (95% CI), for the fixed-effects coefficients.

Species code†	β_1 (slope SA)	β_2 (slope P)	β_3 (Soil moisture)	β_4 (Herbivory protection)	β_5 (Light)	β_6 (Winter survival)	β_7 (Origin)
Acba	2.7 (0.41, 5.25)	‡	-0.02 (-0.11, 0.07)	‡	-0.02 (-0.06, 0.03)	-1.62 (-4.12, 0.6)	‡
Acru	0.45 (-0.12, 1.05)	0.16 (-0.29, 0.64)	0.08 (0.05, 0.11)	0.68 (0.08, 1.33)	-0.02 (-0.04, -0.01)	1.07 (0.53, 1.58)	‡
Acsa	1.34 (0.31, 2.42)	1.36 (0.57, 2.22)	0.07 (0.02, 0.12)	0.06 (-0.74, 0.93)	-0.013 (-0.03, 0.01)	0.86 (-0.06, 1.77)	‡
Cagl	1.01 (0.33, 1.67)	0.29 (-0.13, 0.76)	0.06 (0.03, 0.09)	0.28 (-0.18, 0.77)	0.002 (-0.01, 0.01)	1.15 (0.64, 1.62)	‡
Cail	0.53 (-0.39, 1.48)	0.74 (0.11, 1.32)	0.08 (0.04, 0.13)	-0.4 (-1.26, 0.51)	-0.03 (-0.06, 0.009)	1.03 (0.37, 1.7)	‡
Fagr	3.57 (2.67, 4.53)	2.19 (1.42, 3.01)	0.0002 (-0.04, 0.04)	0.51 (-0.09, 1.15)	-0.02 (-0.03, -0.004)	-0.71 (-1.56, 0.071)	‡
List	0.72 (0.05, 1.36)	-2.53 (-8.8, 6.52)	0.03 (0.005, 0.06)	0.55 (-0.01, 1.16)	0.02 (0.005, 0.03)	-0.4 (-1, 0.2)	P: 3.62 (-5.5, 9.9)
Litu	1.17 (0.41, 1.8)	0.36 (-0.37, 1.07)	0.01 (-0.02, 0.04)	1.8 (1.26, 2.35)	0.004 (-0.007, 0.01)	-0.92 (-1.61, -0.21)	SA: 0.19 (-0.1, 0.5) P: -0.72 (-1.27, -0.2)
Magr	-0.71 (-2.72, 1.38)	0.8 (-0.94, 2.64)	0.05 (-0.05, 0.14)	0.93 (-0.06, 2.05)	-0.016 (-0.12, 0.08)	-0.3 (-1.83, 1.16)	‡
Piri	2.05 (0.65, 3.25)	‡	-0.02 (-0.07, 0.004)	‡	-0.001 (-0.01, 0.014)	-2.09 (-3.26, -0.74)	‡
Pita	0.89 (0.46, 1.39)	0.44 (0.03, 0.91)	0.02 (-0.004, 0.04)	0.72 (0.42, 1.02)	0.02 (0.01, 0.03)	-1.06 (-1.52, -0.67)	P: -0.12 (-0.37, 0.13)
Qual	1.15 (0.14, 2.15)	-0.11 (-0.84, 0.58)	0.08 (0.03, 0.13)	0.47 (-0.17, 1.13)	0.0002 (-0.02, 0.02)	1.77 (0.99, 2.57)	‡
Qufa	1.75 (1.25, 2.26)	1.66 (1.27, 2.05)	0.03 (0.004, 0.05)	0.37 (0.001, 0.77)	0.001 (-0.01, 0.01)	-0.02 (-0.42, 0.37)	‡
Quph	0.48 (0.06, 0.91)	1.04 (0.69, 1.4)	0.06 (0.04, 0.08)	0.57 (0.23, 0.93)	0.007 (-0.002, 0.02)	0.53 (0.15, 0.91)	‡
Qupr	2.35 (0.2, 4.88)	‡	0.034 (-0.06, 0.12)	‡	-0.005 (-0.04, 0.03)	-0.53 (-3.12, 1.6)	‡
Quru	1.28 (0.91, 1.66)	0.84 (0.55, 1.17)	0.04 (0.001, 0.06)	0.55 (0.21, 0.89)	-0.007 (-0.02, 0.003)	0.76 (0.45, 1.15)	‡
Quvi	‡	1.32 (0.71, 1.96)	-0.004 (-0.05, 0.05)	0.21 (-0.27, 0.73)	-0.005 (-0.02, 0.01)	-0.28 (-0.89, 0.31)	‡
Tsca	1.45 (-1.8, 4.39)	‡	0.005 (-0.11, 0.14)	‡	-0.02 (-0.05, 0.004)	-1.46 (-4.2, 1.6)	‡

Notes: Bold values indicate that the 95% credible interval for the coefficients did not include zero (β_{3-7}), and in the case of intercepts (β_{1-2}), that the difference between them was different from zero. Key to abbreviations: SA = Southern Appalachians, P = Piedmont.

† For species code key, see Table 1.

‡ The parameter was not calculated for this species.

(Eq. 3b; sub-model B, Appendix); this was the case for most species (16 out of 18 species) and we used this model for all to facilitate comparisons. However, to determine if residual plot differences remained after taking covariates into consideration, we inspected scattered plots of plot random effects, γ_p , from an alternative sub-model, C (see Appendix). We plotted the posterior distributions of γ_p against soil type, exposure, and winter temperature (not shown). These plots did not show residual differences among plots. We then felt confident about excluding these covariates (soil type, exposure, and temperature) from the analysis.

For most species and years, survival was higher in the Southern Appalachians than it was on the Piedmont (Fig. 3). Exceptions were *Quercus phellos* planted in 2002 and *Acer saccharum*, *Magnolia grandiflora* and *Q. rubra* planted in 2004. Not unexpectedly, the highest mortality rates experienced by each cohort occurred within the first year of life. Large seeded species, i.e., *Quercus*,

Carya and *Fagus*, had higher survival (~30%) than species with the smallest seeds, e.g., *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Pinus*, and *Tsuga canadensis* (~10%). The values of fitted coefficients (β) summarize effects of covariates (Eq. 3). Differences between regions that are not explained by covariates are then taken up in the intercept coefficients β_1 for the Southern Appalachians, and β_2 for the Piedmont (Table 4).

Climate impacts

Prediction intervals of survival probability are narrower where soil-moisture data are dense and vice versa. Several trends are apparent. First, for the species planted at both sites (see Table 1) survival probability tended to be higher in the Southern Appalachians. Second, for most species, the probability of survival increased with soil moisture content (Table 4, Fig. 4). Most species had relatively high probabilities of survival

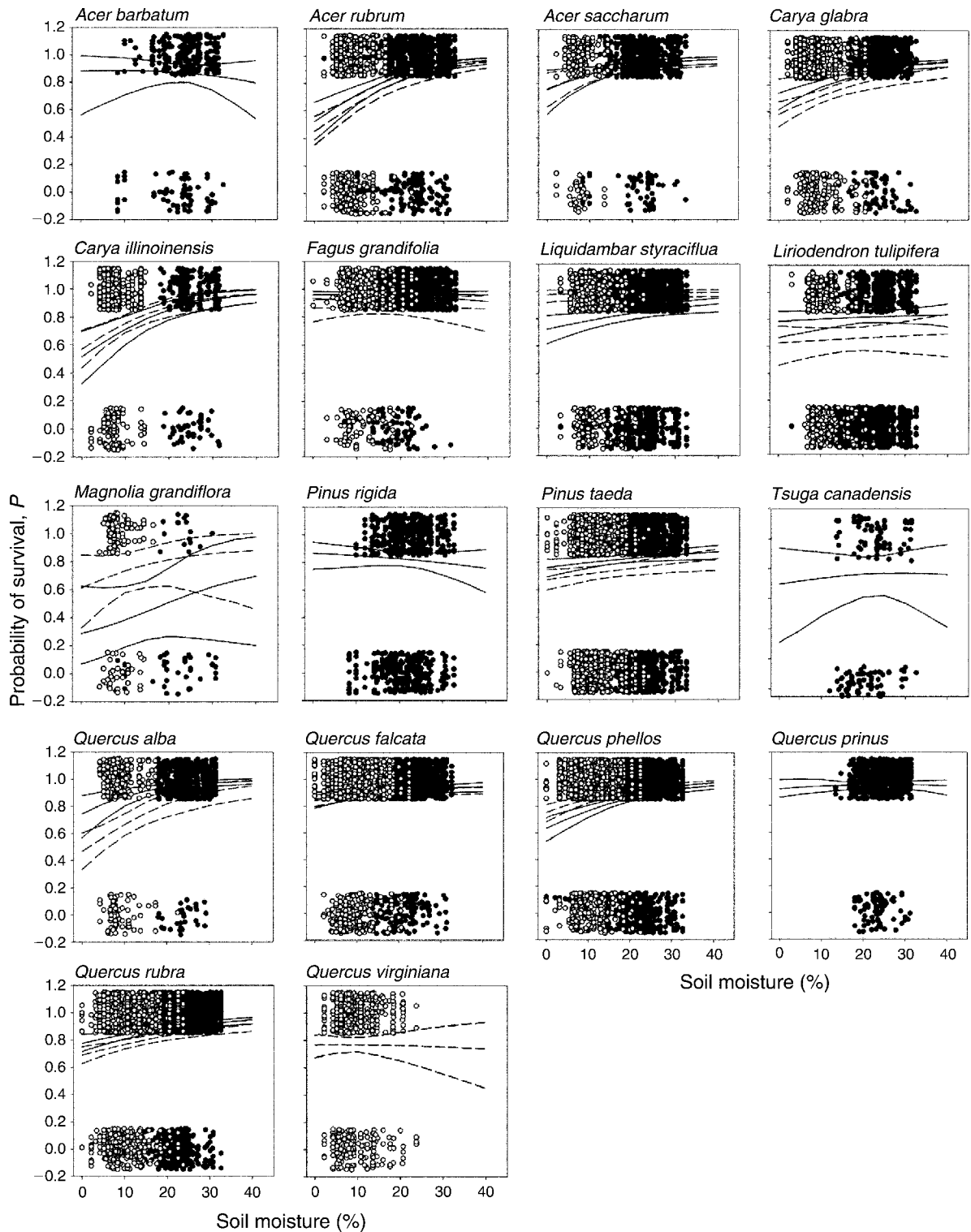


FIG. 4. Seedlings predicted probability of survival (mean and 95% PI, prediction interval) as a function of soil moisture (%). Key to symbols: Southern Appalachians, solid line and solid circles (●); Piedmont, dashed line and open circles (○). Values around 1 in the y-axis are from seedlings that were alive; points close to 0 come from seedlings found dead (note that point values have been jittered around the 1 and 0 lines for better viewing). Predicted survival was calculated at a mean light level of 12%.

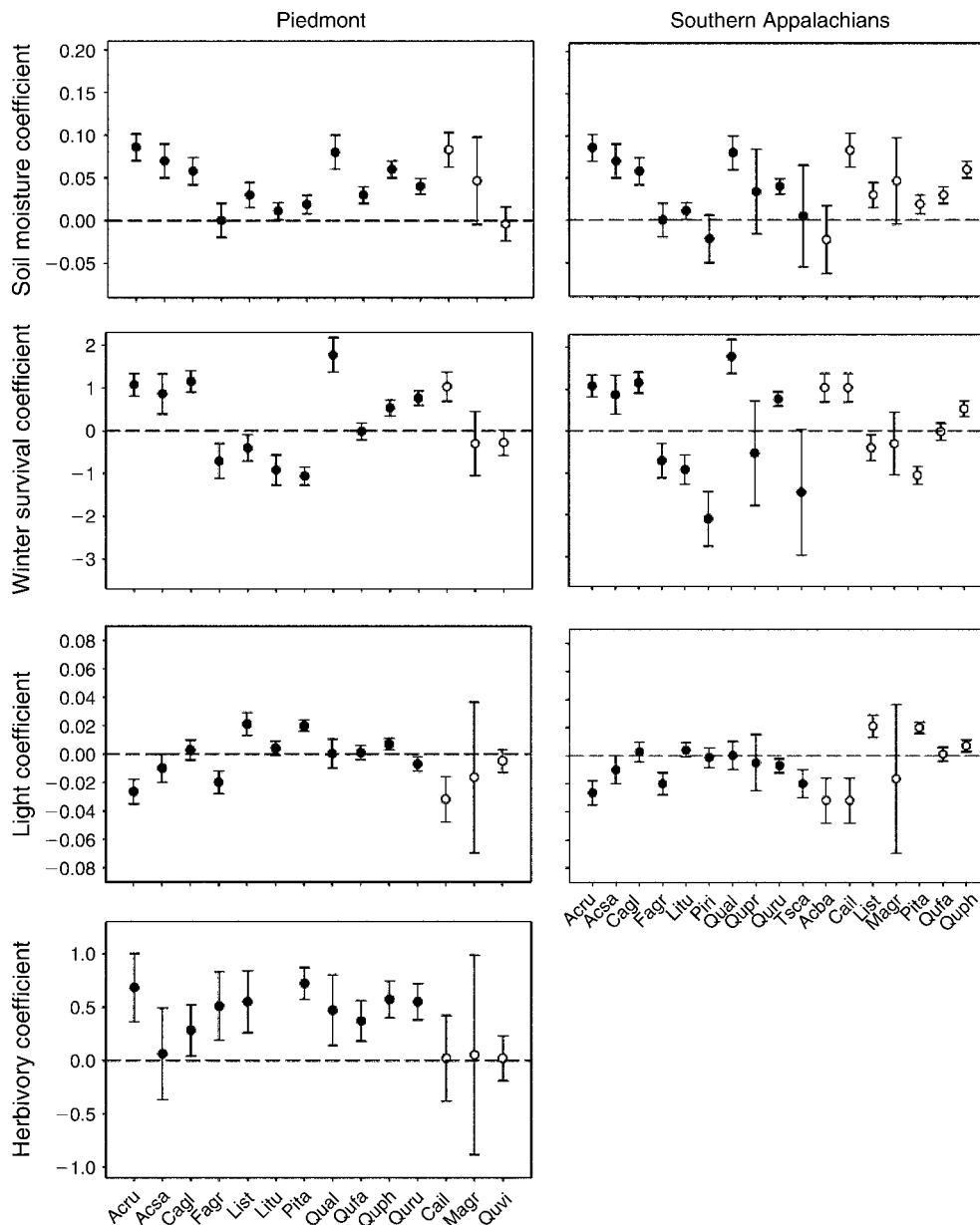


FIG. 5. Posterior values (mean + SD) for the coefficients associated with the covariates. Solid symbols (●) represent resident species; open circles (○) are potential immigrants. For species code key, see Table 1.

at low soil-moisture conditions (Fig. 4), and these probabilities tended to increase under wetter conditions. Potential immigrants to the Southern Appalachian sites tended to require higher soil-moisture levels for enhanced survival than most to the resident species, with four out of the seven species (*Carya illinoensis*, *L. styraciflua*, *Q. falcate*, and *Q. phellos*) being strongly affected by this variable, as evident from posteriors (Table 4, β_3 , Fig. 5). At the Piedmont site, one of the three potential migrant species (*C. illinoensis*) showed high survival in plots and years with high soil moisture (Table 4: β_3 , Fig. 5).

The coefficients associated with winter (β_6) are a rough indicator of how limiting current winters may be for native and potential migrant species. This term applied to survival from late August to early May, therefore mortality due to causes other than harsh winter conditions may have been possible. Species having negative coefficients (β_6) faced lower survival during this season than they do in the summer (Table 4, Fig. 5). Of the seven migrant species into the Southern Appalachians *Pinus taeda* was the only one to experience a significant lower survival during the winter, although four more also had negative coefficients (*A. barbatum*, *L.*

styraciflua, *M. grandifolia*, and *Q. falcata*), and two of the three potential migrants did at the Piedmont site (*M. grandifolia* and *Q. virginiana*).

Environmental interactions

Herbivory.—Nearly all species planted in the Piedmont benefited from growing inside enclosures (β_4), and, therefore, under lower herbivore pressure (Table 4, Fig. 5). For six species, *A. rubrum*, *L. tulipifera*, *P. taeda*, *Q. falcata*, *Q. phellos*, and *Q. rubra*, results were significant, the 95% CI did not include zero.

Light.—With few exceptions, posterior estimates of light availability for each plot and year were close to our measurement (estimated Light vs. light measurements from GSF [global site factors] and PAR [photosynthetically active radiation], results not shown). Light effects were less consistent than those seen for soil moisture. Some species had higher survival in high-light plots (*C. glabra*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *P. taeda*, *Q. alba*, *Q. falcata*, and *Q. phellos*), while other species had lower survival in high-light plots (all *Acer* species, *C. illinoensis*, *F. grandifolia*, *M. grandiflora*, *P. rigida*, *Q. prinus*, *Q. rubra*, *Q. virginiana*, and *T. canadensis*) (β_5 in Table 4, Fig. 5). Positive survival response to light level was estimated only for *Liquidambar styraciflua* and *P. taeda*. Negative coefficients were found for *A. rubrum* and *F. grandifolia*.

Seed origin.—The sources of the seeds (β_7) did not affect survival for most cases (Table 4). In one case seedlings from a local source had lower survival than did seedlings grown from purchased seeds (*Liriodendron tulipifera* at the Piedmont site).

DISCUSSION

Our major objective was to quantify the colonization potential (potential to establish in a new region) of likely migrant tree species. This work goes beyond the uncertainty of dispersal limitation, asking instead, "If a species arrives, could it invade?" For that, we exploited landscape heterogeneity and temporal variability of the environment to evaluate seedling survival under a wide range of environments. We planted seedlings of native and potential migrant species side by side to assess their relative performance in experimentally created gap and understory environments, accounting for the spatio-temporal variation in environmental changes within and among plots from two regions. In the course of our five-year experiment we observed responses to not only the experimental manipulation, but also to drought and hot years (2001 and 2005, respectively), which had different impacts on plots located in wet and dry sites. These plots and years included climatic conditions (i.e., soil water availability) similar to those anticipated for coming decades. Rising temperatures will translate to increased surface desiccation (Christensen et al. 2007). By estimating survival in the lower range of the soil moisture gradient, we were able to obtain a realistic picture of seedling performance under dry conditions

while still exposed to the full array of other environmental variables characteristic of our many sites and manipulations.

There are caveats to our experimental approach. We could not mimic the entire range of conditions to which plants will be exposed in the future. Increasing atmospheric CO₂ concentrations and nitrogen deposition will influence species response to climate change. In particular, species-specific responses to elevated CO₂ could exacerbate interspecies differences in drought survival (Polley et al. 2002), and on survival at low light (Mohan et al. 2007). Still, this study provides us with information on what might be limiting species recruitment in the next decades at current CO₂ concentrations. Another limitation of this study arises from the number of species tested, in particular at the Piedmont site where we were only able to plant three potential immigrant (PI) species. We chose species on the basis of their role as representative species of their communities, and under the assumption that they would be able to grow in our studied regions. Therefore we avoided selecting species with very specific requirements (e.g., fire, water-logged soils) and instead chose species to represent broad functional groups: pioneer species (e.g., *Pinus*, *Liquidambar styraciflua*), mid-successional species (*Quercus*, *Carya*), and late-successional species (*Magnolia grandiflora*). Despite the limited number of PI species, the scope of this experiment is unusual, in terms of total numbers of species, numbers of individuals, range of environmental variation (both natural variation and experimentally imposed), and duration.

Finally, this study includes a single life-history stage. Germination and early establishment of seedlings will respond to climate change (e.g., Ibáñez et al. 2007), and changing seed production due to climate change will have a large effect on the recruitment rates (Clark et al. 2003a). Also, adult trees will respond in terms of growth and mortality (e.g., Gitlin et al. 2006, Andreu et al. 2007, Buntgen et al. 2007, Sarris et al. 2007). And all these interactions will add to the overall species response to climate change.

Will neighboring species be able to establish under drier conditions?

Even general circulation models that forecast a slight (0–5%) increase in summer precipitation (Christensen et al. 2007, although see Mearns et al. 2003) predict net surface drying due to higher evapotranspiration under warmer temperatures (Christensen et al. 2007). In our studied locations winters will be similar to those in Central America and the Caribbean, but summers will resemble conditions in the southwestern United States. This scenario has no equivalent in the surrounding regions. Given this fact, the simple shift in species distributions from south to north predicted by climate-envelope models may not occur. Species growing at lower latitudes from our study sites could take advantage of warmer winters, but they might not be

able to colonize the region under much drier conditions. In addition, most native species may experience decreasing seedling survival due to growing season aridity.

Although we found seedlings could survive across the whole soil-moisture gradient, for most species the analyses pointed to an increase in performance at the higher end of the soil moisture gradient in both groups, resident and potential migrant species. Taking these results as an indication of the potential to survive under future climatic conditions in these areas, we may expect reduced recruitment given the predicted decline in available water. This suggests that current populations of resident species and future migrants could become increasingly dependent on particularly wet years and moist locations on landscapes. In the Piedmont site, the group of potential migrant species performed remarkably less well than the residents, and at the Southern Appalachians potential migrants, as a group, also experienced lower survival at low soil moisture than did residents.

Moreover, temperatures could increase to a point where residents are lost. These findings highlight one of the scientific challenges of coming decades: with climate warming, and reduced establishment of residents, is there a reliable source of potential migrant species? This possibility, that feasible species do not reside within migratory distances, could take place if changing climate results in a combination of conditions not represented in neighboring regions (Ibáñez et al. 2006).

The implications of these results, that a simple northward displacement of species could be thwarted by novel summer aridity, are suggested by specific responses in our experiment. The potential migrant species for the Southern Appalachians, e.g., *L. styraciflua*, *Q. falcate*, and *Q. phellos*, are predicted to increase considerably both in distribution and abundance (Iverson et al. 2008). In contrast to model predictions, we find a strong positive response of these species to high soil moisture. If seedling survival for these species responds primarily to moisture availability, the decline in effective soil moisture may not ensure colonization and the maintenance of stable populations in sites north of current ranges.

*Will potential colonizers be able to recruit
under these local conditions?*

To account for as many environmental factors affecting recruitment as possible, we carried out the transplant experiments along a large range of conditions. Specifically, we selected plots within a canopy gap–canopy interface to expose seedlings to a realistic range of light levels. Plots were also laid out for different soil types (characterized by different structure and water holding capacity), elevations, slope exposures, and levels of deer herbivory. These arrangements provided a large set of microsites that allowed us to estimate species survival under a variety of local conditions. Through

covariates and examination of plot-level random effects, we did not detect effects of soil type, although we do expect soils to matter.

Herbivory will clearly interact with climate change. Residents and potential immigrants alike benefited from protection from deer herbivory. With the current large deer populations in the Southeast, some of the herbivore pressure will shift to the species that best survive the changing climate. For example, on the basis of simple climate predictions, Coastal Plain oaks are potential immigrants to the Piedmont (Iverson et al. 1999, Bachelet et al. 2001). However, severe herbivore pressure may be among the factors currently limiting the regeneration of the once-dominant oaks in the Piedmont. Acorns are a preferred source of food for a large number of vertebrates (McShea and Schwede 1993), and oaks are heavily browsed by rapidly increasing deer populations (Bryant et al. 1980, Garrott et al. 1993). Herbivores and seed predators already feeding on native oaks could also adopt new hosts, reducing the colonization chances of particular species.

Because most recruitment occurs in canopy gaps, interactions involving climate change and resource levels in gaps, primarily light and soil moisture, could be crucial. Our findings show a strong response to light from species traditionally considered pioneers in the region (Peet and Christensen 1988), e.g., *L. styraciflua* and *Pinus taeda*. On the other hand, *Fagus grandifolia*, a typically shade tolerant species survived better at low light values. And in the case of *Acer rubrum*, a conspicuous species in our sites, a detrimental effect of higher light levels is probably related to a higher risk of desiccation. The natural disturbance regime of the region, i.e., hurricanes, seems to provide suitable microsites for shade-intolerant species to recruit.

Conclusions

In this study, we addressed a challenge faced in many regions where neither current trends nor model predictions provide confident scenarios for future climate and vegetation change. There is no obvious regional species pool for the combination of climate variables predicted by general circulation models. We estimated that potential migrant species into the North Carolina Piedmont and the Southern Appalachians might not be able to establish stable populations under 21st-century climates, raising concerns about simple climate-envelope models. Even if the region offers a range of microhabitats for seedling survival (we explicitly considered variation in soil moisture and canopy gaps), the particularly dry summers predicted for the region may limit establishment of potential migrant populations. In addition, we could also expect resident species to experience a reduction in seedling survival. Together, these results suggest reduction of native species and limited replacement by new ones. Whether or not this would result in overall reductions in biomass and carbon sequestration is unclear, but the changes in biodiversity

alone could cascade to soil fertility, water yield, and ecosystem stability.

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APPENDIX

Description of some of the sub-models tested (*Ecological Archives* A018-056-A1).