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Research article

Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species

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Abstract

We used a combination of two models, DISTRIB and SHIFT, to estimate potential migration of five tree species into suitable habitat due to climate change over the next 100 years. These species, currently confined to the eastern half of the United States and not extending into Canada, are *Diospyros virginiana* (persimmon), *Liquidambar styraciflua* (sweetgum), *Oxydendrum arboreum* (sourwood), *Pinus taeda* (loblolly pine), and *Quercus falcata* var. *falcata* (southern red oak). DISTRIB uses a statistical approach to assess potential suitable habitat under equilibrium of $2 \times CO_2$. SHIFT uses a cellular automata approach to estimate migration and is driven primarily by the abundance of the species near the boundary, forest density inside and outside of the boundary, and distance between cells. For each cell outside the current boundary, SHIFT creates an estimate of the probability that each unoccupied target cell will become colonized over 100 years. By evaluating the probability of colonization within the potential 'new' suitable habitat, we can estimate the proportion of new habitat that might be colonized within a century. This proportion is low ($<15\%$) for all five species, suggesting that there is a serious lag between the potential movement of suitable habitat and the potential for the species to migrate into the new habitat. However, humans could hasten the migration of certain species by physically moving the propagules, especially for certain rare species that are unable to move sufficiently through fragmented landscapes, or even more common species, e.g., beech, that have lost many of their animal dispersers.

Introduction

Evidence continues to mount that the Earth is warming as most of the hottest years on record occurred during the past decade, and global temperatures increased by 0.6 °C during the 20th century (NAST 2000). Evidence also is mounting that climatic change over the past several decades already may be influencing species physiology, distribution, and phenology (Hughes 2000). The potential effects of future warming have been studied at the global, national, and regional level. The Intergovernmental Panel on Climate Change has published several documents outlining potential climate changes and the resulting consequences (e.g., Houghton et al. 1996; Watson et al. 2000; McCarthy et al. 2001). Also, more than 1000 scientists and stakeholders completed a thorough review of potential impacts of global climate change on the United States (NAST 2000, 2001).

Two transient climate models used by the US National Assessment for Climate Change (NAST 2000) that also include the effects of sulfate aerosols were the Hadley model (Hadley Centre for Climate Prediction and Research; Mitchell et al. 1995) and the CCC model (Canadian Climate Center; Boer et al. 2000). They predict potential increases of 2.5 and 6.6 °C for January and 2.3 and 5.0 °C for July, respectively, when averaged for the eastern United States (Iverson and

Prasad 2002). Consequently, most research indicates that the more severe impacts on health, sea level, and ecosystems would occur should the CCC scenario be realized.

Much attention has thus been directed toward predicting the effects of future climatic change on ecological systems (e.g., Aber et al. 1995; Box et al. 1999; Devall and Parresol 1998; Iverson et al. 1999a; Melillo et al. 1996; Pastor and Post 1988; Shriner and Street 1998; He et al. 1999; Guisan and Theurillat 2000; Kirschbaum 2000; Joyce and Birdsey 2000; Malcolm and Pitelka 2000; NAST 2000; Schimel et al. 2000; Sykes and Prentice 1996; Yates et al. 2000; Hansen et al. 2001). Both the projected doubling of atmospheric CO_2 concentration and changes in temperature and precipitation patterns could alter ecosystem functions, species interactions, population biology, and plant distribution (e.g., Melillo et al. 1990; Hughes 2000; Kirschbaum 2000). On the basis of paleoecological record and various simulation and statistical models, the changing climate likely will have a profound effect on the suitable habitat for many tree species. Simulations to the year 2100 using biogeography models such as MAPPS and BIOME2, biogeochemistry models such as BIOME-BGC, CENTURY, and TEM, as well as linked biogeography and biogeochemistry models such as BIOME3 and MC1 show possible major shifts in biomes (Neilson 1995, VEMAP Members 1995, Neilson et al. 1998; Aber et al. 2001; Bachelet et al. 2001a,b; Hansen et al. 2001).

Historical analogs of shifts in the distribution of plant species suggest that future rates of distribution change may be slow relative to the predicted rate of climatic warming (e.g., Overpeck et al. 1991; Davis and Zabinski 1992, Schwartz 1993; Huntley et al. 1995; Kirilenko and Solomon 1998; Kirilenko et al. 2000; Malcolm et al. 2002). Rates of past migrations suggest that even relatively rapid changes in range limits are insufficient to keep pace with predicted future climatic change (Gear and Huntley 1991). Therefore, the northward shift in the ‘optimum’ latitude of suitable habitat likely will outpace the actual northward migration of the species. This differential between movements of suitable habitat vs. actual migration rates of particular species is the focus of this paper.

It is important to note that tree migrations during the Holocene period resulted largely from plants moving through nearly fully forested landscapes in the eastern United States. Habitat loss and fragmentation reduce the ability of natural systems to respond to changes in global climate because fewer individuals produce propagules and there are fewer sites for these propagules to colonize (Peters 1990; Schwartz 1993; Dyer 1995). And disturbance can prevent the dispersal and reintroduction of species for a century or longer (Matlack 1994). Schwartz (1993) investigated the role of habitat loss on the ability of trees to migrate through hypothetical landscapes with the assumption that the dispersal-limited maximum migration rate for species moving through fully forested landscapes was about 50 km per century, an average maximum rate in the paleoecological literature for the Holocene (e.g., Delcourt and Delcourt 1988, Davis 1989, DeHayes et al. 2000). He suggested that migration rates of 1 to 10 km per century might be the maximum future rates in highly fragmented habitats; this rate was confirmed by subsequent research (Iverson et al. 1999b, Schwartz et al. 2001). Migration rates are driven largely by rare long-distance dispersal events (Shigesada and Kawasaki 1997; Clark 1998; Higgins and Richardson 1999). However, the bulk of the migration occurs near the current boundary and is dependent on the abundance of the species within the boundary as well as the proximity of forest patches. Toward this end, understanding the source strength of propagules has become an important issue and a research priority in predicting future range shifts (Higgins et al. 2003a, b). Source strength is a function of both the propagule production and dispersal of individual species as well as the density of trees at or near species distribution boundaries. In addition, the regional abundance and proximity of forest patches may play a large role in predictions of potential future migrations. The abundance of available sites, and their invasibility by migrating trees, can be considered a sink strength in terms of plant migration. Thus, an appropriate focus of research to better understand potential consequences of global warming toward tree migration is to understand the relative importance of source and sink strength (Iverson et al., 2004).

We are evaluating potential changes in tree species in the eastern United States with the models DISTRIB and SHIFT. Using five scenarios of climate change, we used DISTRIB to evaluate potential changes in suitable habitat by the year 2100 (assuming few barriers to migration) for 80 tree species common in the eastern United States east of the 100th meridian (Iverson and Prasad 1998; Iverson et al. 1999a) and for forest types in the region (Iverson and Prasad 2001). For the Hadley scenario, the optimum latitude of suitable habitat moves at least 100 km north for 30 species and more

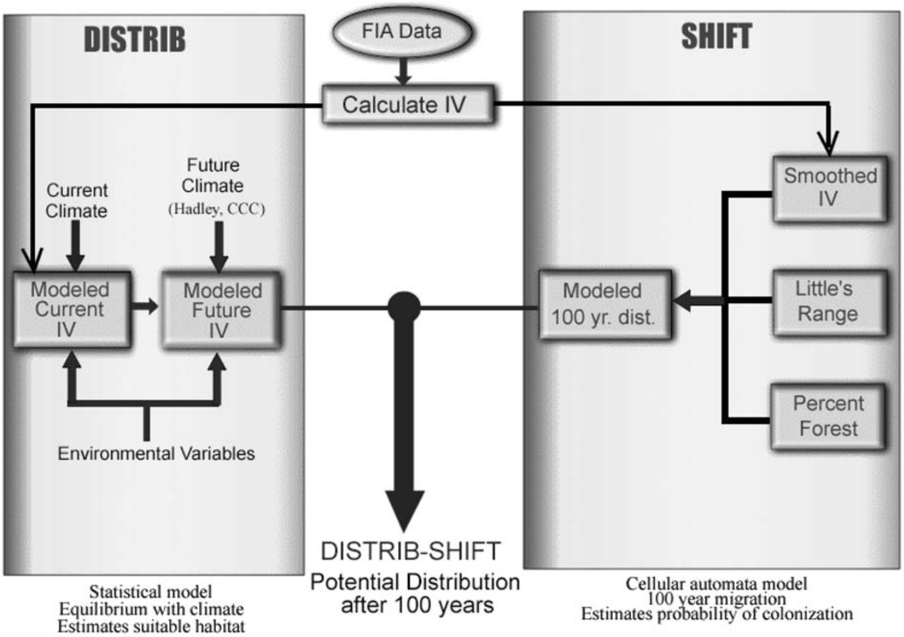

Figure 1. Flow diagram showing inputs and outputs of the DISTRIB and SHIFT models.

than 200 km for five of these. With the more severe CCC scenario, the optimum latitude moves more than 100 km north for 35 species, 24 of which could move at least 200 km north (Iverson and Prasad 2002).

With the cellular automata model, SHIFT, the probability of colonization over the next 100 years (Figure 1) is estimated for each grid cell distant from the current distribution boundary (Schwartz 1993; Schwartz et al. 2001). The combination of these two models yields a mapped estimate of the probability of colonization of certain species within new suitable habitat by the year 2100. This paper expands on a case study of *Pinus virginiana* by Iverson et al. (1999b). Compared to this earlier work, the current paper describes the DISTRIB-SHIFT combination with updated input data, an enhanced modeling algorithm, and a finer resolution of modeling and analysis (1 km vs. 3 km). Also, we tested this combination on five new species with various life characteristics such as distribution and physiological attributes.

Our approach is substantially different from others in the recent literature using dispersal kernels to predict potential migration rates (Higgins et al. 2003a). The dispersal kernel approach uses highly parameterized models that rest on weighty and sometimes unsupported assumptions regarding seed production, dispersal and establishment success. By contrast, our approach uses historical information on rates of past migration events as a model for future potential migration. This approach has its own limitations, such as the uncertainties related to how life history influenced past migration events. We use this approach because we feel that it more accurately reflects our true state of knowledge and allows us to better link a spatially explicit distribution model to a real landscape to create plausible future species distribution scenarios.

Methods

Species

For the five species selected for analysis, the current or potential future northern limit was the mid-latitudes of the eastern United States below the Canadian border (Iverson et al. 1999a; Prasad and Iverson 1999). They included *Diospyros virginiana* (persimmon), *Liquidambar styraciflua* (sweetgum), *Oxydendrum arboreum* (sourwood), *Pinus taeda* (loblolly pine), and *Quercus falcata* var. *falcata* (southern red oak).

Data required for this evaluation included a spatial estimate of the range and importance for each species. To characterize the current ranges within the eastern United States, we used Little's (1971) binary maps of the distribution of various US tree species. These range boundaries were digitized and are available at http://www.fs.fed.us/ne/delaware/4153/global/littlefia

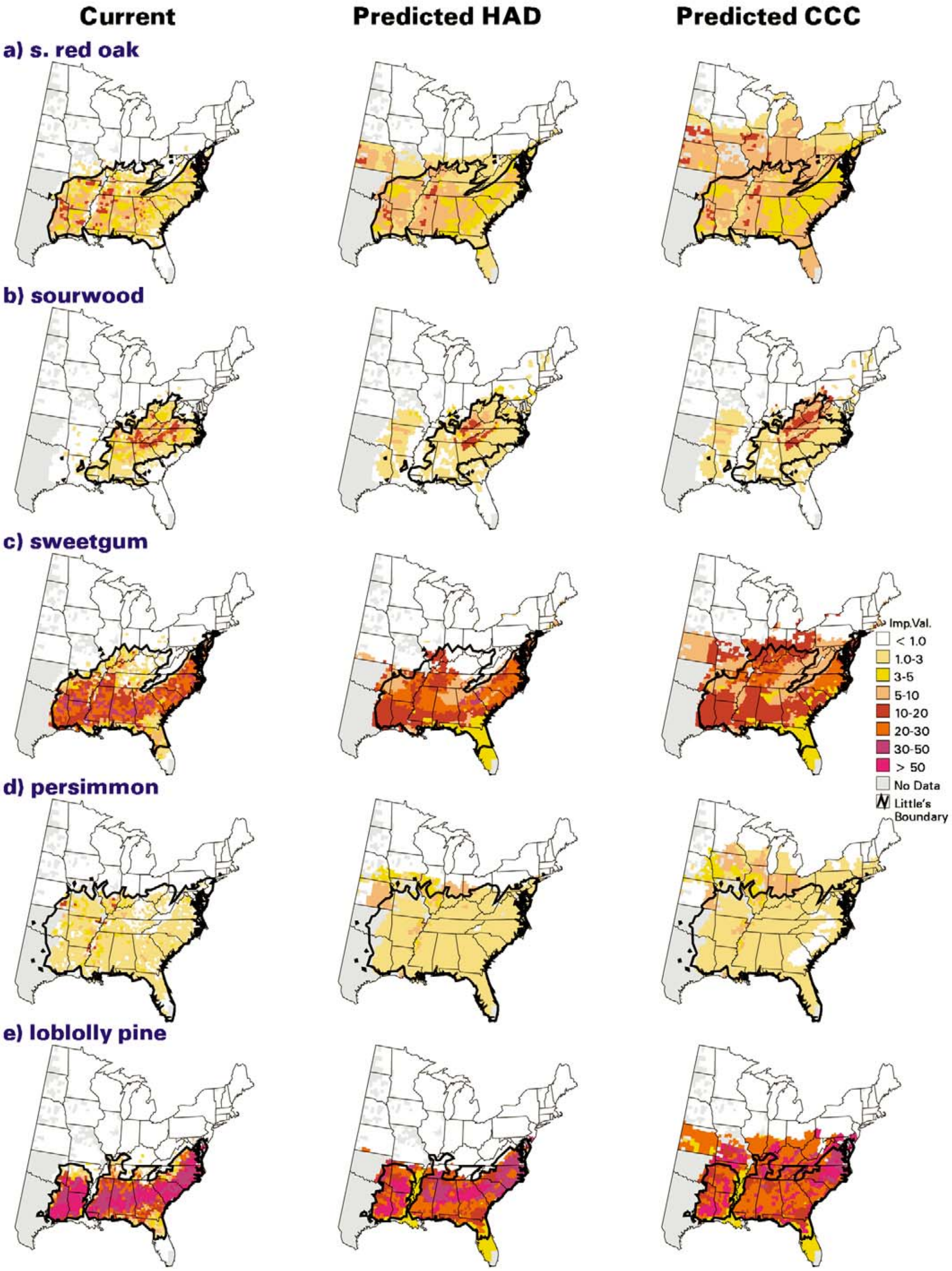

Figure 2. Maps of DISTRIB outputs, showing potential suitable habitat for five species under the Hadley and CCC scenarios.

/index.html. In several instances, we modified Little's range boundary based on inventory data that indicated a species now extends beyond his boundary. These served as the boundaries from which to migrate the species. The range boundaries were made at a coarse scale, so outlier populations may extend beyond them. We would expect the migration rate of populations outside of the boundary to be enhanced by backfilling (Clark 1998, Malcolm et al. 2002). Just as likely, however, is that the Little's boundaries encompass most of

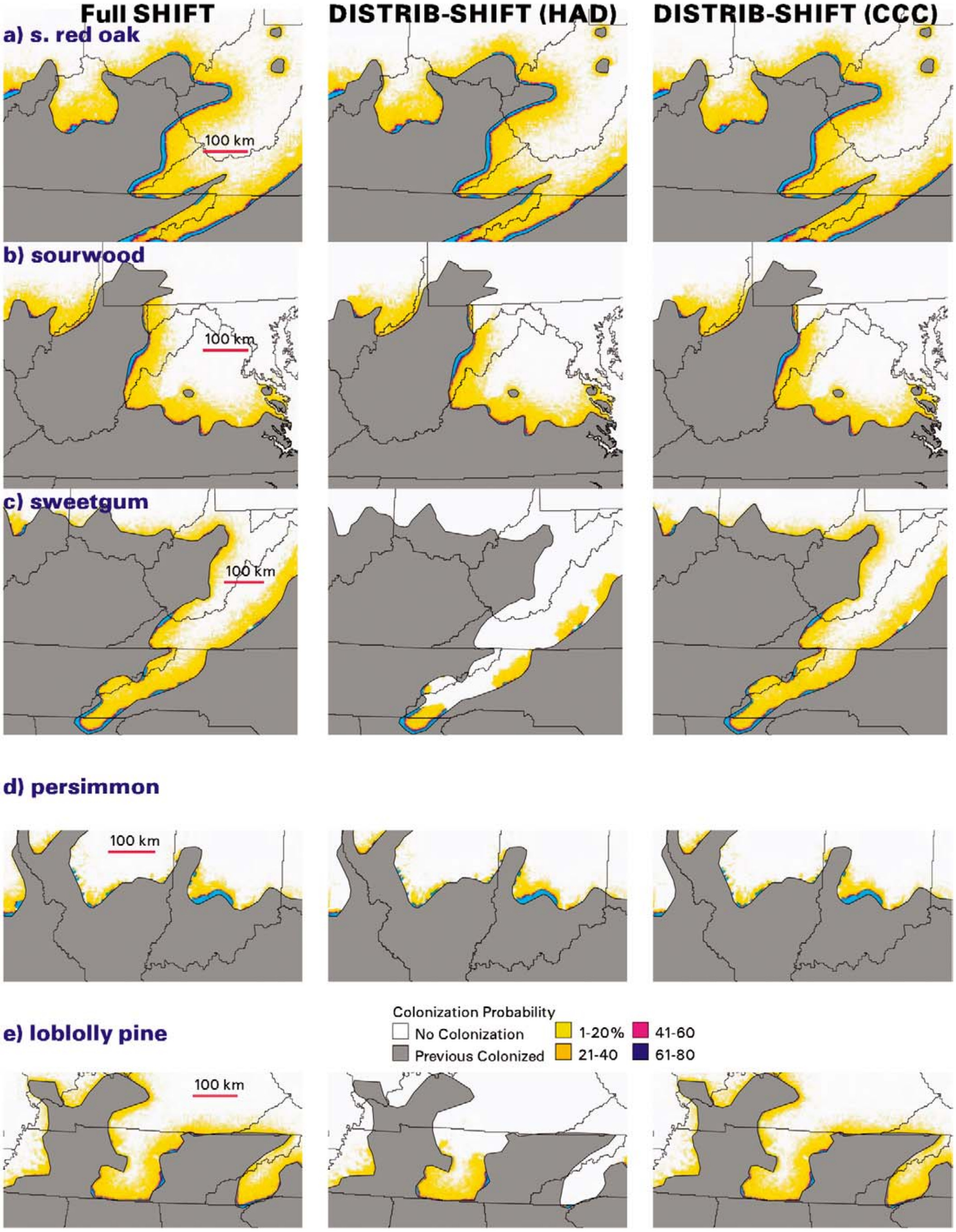

Figure 3. Maps of SHIFT outputs (in the left column of maps), showing the colonization potential of five species after 100 years, apart from the DISTRIB model. The middle and right columns of maps show the intersection of DISTRIB and SHIFT, with suitable habitat considered as well as colonization potential over 100 years.

the outlier populations, as we found that the plot-level inventory data show low average abundance near the range boundaries for many species.

To estimate abundance for each species within Little's range boundaries, we used plot data collected by the USDA Forest Service's Forest Inventory and Analysis (FIA) unit (Hansen et al. 1992). These data consisted of more than 100 000 plots and nearly three million trees measured for the area east of the 100th meridian. FIA data were used to calculate an importance value (IV) for each species, based on relative basal area and number of stems of both understory and overstory trees (Iverson and Prasad 1998; Iverson et al. 1999a). IVs were calculated at the scale of the county and ranged from 0 to 200, with 200 indicating single-species stands. The latter was the predicted variable in the regression tree analysis performed within DISTRIB (Figure 1). As an input to SHIFT, we smoothed county-level IVs using an inverse distance weighted algorithm in Arc/Info Grid. We then assigned the predicted abundance value to all 1 km^2 cells that indicated the presence of species from Little's range maps.

Distribution of forested habitat

An estimate of percent forest in each km^2 cell across the eastern United States also was required for SHIFT. We obtained such an estimate within a cell from a modified classification of an AVHRR data set by Zhu and Evans (1994), who used a calibration method to assign a forest density value on the larger AVHRR pixel based on a collection of smaller Landsat TM pixels within that cell (Iverson et al. 1989, 1994). Thus, habitat quality was scaled from 0 (nonforested) to 1 (100% forested). We made no attempt to sort sites into forest type, stand age, or current dominance within individual cells, though we did downgrade some of the Midwest 'corn belt' area that was overestimated for percent trees. We used a simplifying assumption that all forested habitat was suitable habitat for colonization by each species, so our forest availability map overestimates actual habitat available for colonization by migrating tree species. This simplification will bias our results toward overestimating migration potential. Nonetheless, the use of the real, fragmented landscape allows us to begin to understand the role of fragmentation in migration, which is addressed by few models up until now (Pitelka 1997).

DISTRIB

DISTRIB was first run on the five species to estimate potential future suitable habitat under the Hadley and CCC scenarios (Figure 1). Briefly, DISTRIB uses regression tree analysis to assess 33 environmental variables for relation to the current distribution and abundance of the species (see Iverson and Prasad (1998) for a full description of the model). Environmental variables included county-level data on climate, soils, land use, elevation, and landscape pattern. Once a viable model was created that replicated (by independent testing) the current distribution and abundance of a species, it was used again; this time, present-day climate variables were replaced by Hadley or CCC scenario climate variables to estimate the new locations of suitable habitat and potential abundance (Iverson et al. 1999a; Prasad and Iverson 1999; Iverson and Prasad 2002).

SHIFT

SHIFT calculates the probability of an unoccupied cell becoming colonized during each generation based on percent forest cover in each unoccupied cell (= habitat quality), abundance of the species in each occupied cell (= abundance of seed sources), distance between the occupied and potentially colonized cell, and a typical maximum historic rate of migration for trees of 50 km/century through a fully forested landscape (Iverson et al. 1999b, Schwartz et al. 2001). Thus, SHIFT assumes a 'climate release' in that the species is being pushed to migrate at the high end of historic rates (i.e., the zone of migration extends 50 km with at least a 5% probability of colonization within 100 years). The formula SHIFT uses to calculate the probability of an unoccupied cell becoming colonized during each generation is:

$$P_{\mathrm{colonization},i} = HQ_i \times \Sigma \left[HQ_j \times F_j \times (C/D_{i,j}^X) \right] \quad (1)$$

where $\mathrm{P}_{\mathrm{colonization},i}$ is the probability of unoccupied cell i being colonized by at least one individual and surviving into reproductive status; HQ_i and HQ_j are habitat quality scalars for unoccupied cell i and occupied cell j, respectively, that are based on the proportion of forest cover of each km^2 cell as assessed through LANDSAT images, as described below; F_j, an abundance scalar (0−1), is related to the current estimated importance value (IV) (=abundance), for the migrating species in the occupied cell j (estimation described below); and $D_{i,j}$ is the distance between unoccupied cell i and an occupied cell j. The colonization probability for each unoccupied cell, a value between 0 and 1, is summed across all n occupied cells at each generation. Thus, an unoccupied cell very close to numerous occupied cells may end up with a colonization probability greater than 1.0. These cells are determined to be colonized. For cells with summed colonization probabilities less than one, a random number less than 1.0 is chosen and all cells whose probability of colonization exceeds the random number are colonized in that model step. Newly colonized cells then contribute to the colonization probability of unoccupied cells in the next model time step.

The value of C, a rate constant, is derived independently for each species through trial runs to achieve a migration rate of approximately 50 km per century of that species under high ($> 80\%$ cover) forest availability and moderate species abundance condition. Note that 50 km per century is on the upper end of observed Holocene migration rates among trees migrating into forested environments (Davis 1981).

The value of X, or dispersal exponent, determines the rate at which seed dispersal declines with distance. Being in the denominator, this decreases colonization with distance as an inverse power function. For the simulations reported here, we used a value of $X = 3$ because it fits empirical data (Portnoy and Willson 1993). Further discussion on the dispersal function can be found in Schwartz et al. (2001) Increasing C or decreasing X both increase colonization probabilities. In this model, a fixed value of X was used on all species, while C varied among species as needed to calibrate high migration rates under pristine forest conditions.

SHIFT was run with a grain size of 1 km and with an extent of the eastern United States. Using a grain size of 1 km, as compared to our earlier use of 3 km (Iverson et al. 1999b), represented a large computational increase but also a large theoretical advantage to SHIFT. We are now much closer to representing individual patches, except on the most fragmented landscapes. Because the probability of each unoccupied cell being colonized was based on the distance and species abundance in all surrounding occupied cells, considerable computation is required, in this case, several days of runs on a high-end PC for each species. Each run considered several generations equivalent to 100 years of migration under climate release. The number of generations during this period varied with the approximate time to reproductive maturity for different species: 33 years (3 generations) for southern red oak, 25 years (4 generations) for persimmon and sweetgum, 20 years (5 generations) for sourwood, and 17 years (6 generations) for loblolly pine (Iverson et al. 1999a; Burns and Honkala 1990a,b). After each generation, the newly colonized sites could act as sources for colonization in the next generation. Each run was replicated 50 times so that each time the model simulated the cell to become occupied, a 2% probability of colonization was accrued. After 50 runs, the probability of colonization was summed for each cell so that if a particular cell was simulated to become occupied in each of the 50 runs, the probability of colonization was 100%. The model has some similarity to the cellular automata model DISPERSE (Carey 1996).

Animal- and wind-dispersed species are given the same colonization function in our simulations for two reasons. First, historical evidence of past migrations shows no systematic differences between dispersal mode and migration rate: animal- and wind dispersed trees appeared to migrate at nearly the same rate (Davis 1981; Pitelka 1997; Wilkinson 1977; Clark et al. 1999; Higgins et al. 2003a). Second, repeated attempts fail to find systematic differences in dispersal rates of trees as a consequence of seed dispersal mechanisms (Portnoy and Willson 1993; Clark 1998; Higgins et al. 2003). Thus, empirical observations do not indicate differences in seed-dispersal characteristics between these life histories despite known differences in dispersal biology.

In reality, we may find that fragmentation interacts with dispersal in important ways. For example, seeds distributed by large birds may increase dispersal distance under fragmentation as birds fly further between suitable habitat patches. Conversely, long distance dispersal may break down in other species as their dispersers leave isolated fragments and disperse seeds among patches. Nonetheless, we have chosen our modeling platform because we feel that there is insufficient empirical evidence with which to parameterize such attributes in a model. A fully parameterized model that relies on estimates of seed production, seed dispersal, seed germination rates, and seedling survivorship curves would carry, we feel, too many unrealistic assumptions given our limited knowledge of long-term tree performance. Thus, we feel it preferential to use a minimally parameterized model that carries fewer and more explicit assumptions.

DISTRIB/SHIFT combined

The intersection of the outputs from DISTRIB and SHIFT was used to create an output that estimates the probability of colonization over 100 years along with the suitable habitat estimated to be available in 2100 (Figure 1). The intersection of the two output maps yields maps for which constraints on future distributions are provided by each model. DISTRIB provides the future suitable habitat, which imposes climate, soil, and land-use constraints on the species. SHIFT provides the probability of colonization in the face of spatial constraints of distance and percent forest in each km^2 cell, abundance of the species near the range boundary, realistic generation times for the species, and 100 years of migration time. Thus, we create a plausible scenario for these five species where the region of suitable habitat will shift northward, and identify the extent to which this new habitat could be colonized from species migration over the next 100 years. Of course, our models carry numerous assumptions and uncertainties (see Iverson and Prasad 1998; Iverson et al. 1999a,b). These assumptions, including issues of actual climate change, the actual response of trees to climate, and the efficacy of using historical tree migration as a proxy for future migrations, are further discussed below. Nonetheless, the outputs of our models and others like them need to be viewed as hypotheses of potential future responses rather than absolute, spatially accurate visions of the year 2100.

Analyses

Analyses consisted of calculating the area represented by outputs from DISTRIB, SHIFT, and the intersection of the two models for each of the two climate change scenarios and for each species. These data allowed the percentage calculation of potential new suitable species habitat (as modeled by DISTRIB) that would potentially be occupied within the next 100 years (as modeled by SHIFT). The calculation was performed for three probability levels of colonization: 2, 20, and 50%, and for both the CCC and Hadley scenarios. As one example calculation, what proportion of new habitat modeled by DISTRIB for loblolly pine will have a 20% probability of being colonized by 2100?

Results and discussion

DISTRIB

The DISTRIB mapped outputs for the five species show greater increases in suitable habitat by 2100 for the CCC scenario than for the Hadley scenario (Figure 2). For southern red oak, persimmon, sweetgum, and loblolly pine, it matters a great deal whether the climate changes according to the Hadley against the CCC scenario of climate change. Each species had 2 to 4 times as much suitable habitat created under the warmer, relatively drier CCC scenario than under Hadley. For example, loblolly has nearly 4 times the new suitable habitat with CCC (822 000 km^2) than with Hadley (218 000 km^2) (Table 1). For sourwood, the new habitat was modeled to be equivalent under both scenarios (Table 1). The maps also show current and potential importance values of the species, indicating the degree of suitability of habitat. The new potential habitat often shows relatively high importance values, indicating that the new habitat would be highly suitable for the species (Figure 2).

Considering the overall suitable habitat estimated to be available in 2100, CCC could provide a substantial increase for each species, ranging from 25% for persimmon to 96% for southern red oak (Table 2). With Hadley, habitat expansion is much lower, i.e., increases of 40 to 60% for sourwood and southern red oak, and 5 to 10% for loblolly pine and persimmon, and a decrease of 3% for sweetgum (Table 2).

DISTRIB provides for the abiotic variation across landscapes and does not allow the species to colonized in habitats that are climatically or edaphically unsuitable. It assumes that the species will have no barriers to migration and that migration will be instantaneous. It also assumes that the species are in equilibrium with the environmental drivers dictating its range and abundance. As such, DISTRIB outputs can be considered only as potential suitable habitat and not the new species distribution by 2100. Thus, to gain a more realistic picture of the potential distribution of the species at 2100, we need to add SHIFT.

SHIFT

The SHIFT outputs for the five species are shown in Figure 3 (first column). For greater visibility, the outputs were produced at a fine scale, but for only a portion of the northern boundaries of the species. Results show a narrow band (10 to 20 km) of relatively high probability of colonization followed by a larger zone with a low probability as one moves outward from the current range boundary. For some species, this low probability band can extend as far as 500 km from the current boundary. Therefore, on rare occasions, one could expect long-distance dispersal that might result in significantly higher rates of migration.

SHIFT by itself yields the probability of colonization within 100 years apart from any constraints due to climate or edaphic conditions (see Full SHIFT category in Tables 1 and 2). At the $>2\%$ probability level, this represents an increase of range over current of about 24 400 to 111 700 km^2, or 1 to 14% for the five species. These totals are reduced substantially at the 20- or 50% probability levels to as low as an increase of 0.3 percent in colonized area estimated for persimmon with a 50-percent probability of colonization by 2100. This analysis does not account for the fact that the species may not find suitable habitat in the

Table 1. Estimated areas for five species as output by DISTRIB and SHIFT under two climate change scenarios.

	S. Red Oak	Sourwood	Sweetgum $\text{km}^2 \times 1000$	Persimmon	Loblolly
DISTRIB total area					
Current FIA	1252.8	773.7	1340.8	1354.4	1053.1
Smoothed current	1349.3	722.6	1423.7	1933.6	1111.7
Modelled CCC	2648.7	1130.0	2069.5	2424.4	1910.3
Modelled Hadley	1912.8	1131.7	1379.0	2053.3	1220.3
DISTRIB new habitat					
Modelled CCC	1338.8	541.7	687.2	792.3	822.1
Modelled Hadley	602.9	543.4	195.8	303.9	218.4
SHIFT newly colonized					
Full SHIFT > 2%	111.7	101.1	90.4	24.4	77.5
Full SHIFT >20%	27.7	16.6	17.0	7.4	13.0
Full SHIFT >50%	16.3	6.6	9.1	5.3	5.7
DISTRIB-SHIFT newly colonized					
SHIFT-CCC >2%	101.6	68.6	79.5	21.5	68.8
SHIFT-CCC >20%	26.4	13.0	15.4	6.5	11.9
SHIFT-CCC >50%	15.7	5.4	8.3	4.7	5.3
SHIFT-HAD >2%	69.1	44.5	28.9	11.5	21.6
SHIFT-HAD >20%	24.9	11.9	10.0	3.9	7.0
SHIFT-HAD >50%	15.3	5.2	5.8	2.8	3.4

newly colonizable cells. For this, SHIFT outputs must be combined with DISTRIB.

DISTRIB-SHIFT

The intersection of outputs from DISTRIB and SHIFT allows each model to constrain the other so that barriers and migration rates can be accommodated. Most of the potential migration, as deduced from SHIFT, can be accommodated within the new suitable habitat as estimated by DISTRIB with the CCC scenario (Table 2 and Figure 3; middle and right columns of maps). Except for sourwood (68%), at least 88 percent of the area modeled by SHIFT to be colonized with at least a 2% probability can be accommodated by the new potential habitat, as modeled by DISTRIB using the CCC scenario. With Hadley, there was generally less area of new suitable habitat so that a lesser proportion (28 to 62%, Table 2) of the modeled SHIFT area could be accommodated by the new potential habitat from DISTRIB.

With southern red oak, only 1.2 and 2.5 percent of the potential new suitable habitat according to CCC and Hadley, respectively, had at least a 50% probability of being colonized within 100 years (Table 2). At a 2% probability cutoff, those percentages were 7.6 and 11.5, respectively, for CCC and Hadley. The other four species had varying amounts of their suitable habitat potentially occupied within 100 years, ranging – at the 50% colonization probability cutoff – from 0.6% for loblolly pine and persimmon under CCC to 3% for sweetgum under Hadley (Table 2). Even at the smallest probability of colonization level, the percentage of newly suitable habitat potentially occupied never exceeds 15% for any species (Table 2).

These results show that there is a serious lag between the potential movement of suitable habitat and the potential for the species to migrate into the new habitat. According to our models, only a fraction of the potential new habitat will be colonized within 100 years of natural migration at Holocene rates. However, humans could hasten the migration of certain species by physically moving the propagules. This may be a critical management practice for certain rare species that are unable to move sufficiently through fragmented landscapes, or even more common species (e.g., beech), that have lost many of their animal dispersers.

The DISTRIB-SHIFT models do not allow the estimation of range retrenchment over the next 100

Table 2. Percentage of current distribution, as determined by DISTRIB and SHIFT output listed in Table 1, and percentage of new suitable habitat that may be colonized in 100 years.

	S. Red Oak	Sourwood	Sweetgum	Persimmon	Loblolly
			Percent		
Percentage smoothed current (DISTRIB not constrained by SHIFT)					
DISTRIB-CCC	196.3	156.4	145.4	125.4	171.8
DISTRIB-HAD	141.8	156.6	96.9	106.2	109.8
Percent of smoothed current (SHIFT not constrained by DISTRIB; assumes no retrenchment)					
Full SHIFT > 2%	108.3	114.0	106.3	101.3	107.0
Full SHIFT >20%	102.1	102.3	101.2	100.4	101.2
Full SHIFT >50%	101.2	100.9	100.6	100.3	100.5
Percent of smoothed current (constrained by both DISTRIB and SHIFT; assumes no retrenchment)					
SHIFT-CCC >2%	107.5	109.5	105.6	101.1	106.2
SHIFT-CCC >20%	102.0	101.8	101.1	100.3	101.1
SHIFT-CCC >50%	101.2	100.7	100.6	100.2	100.5
SHIFT-HAD >2%	105.1	106.2	102.0	100.6	101.9
SHIFT-HAD >20%	101.8	101.6	100.7	100.2	100.6
SHIFT-HAD >50%	101.1	100.7	100.4	100.1	100.3
Percent of Full SHIFT colonizable					
SHIFT-CCC >2%	91.0	67.9	87.9	88.1	88.8
SHIFT-CCC >20%	95.3	78.3	90.6	87.8	91.5
SHIFT-CCC >50%	96.3	81.8	91.2	88.7	93.0
SHIFT-HAD >2%	61.9	44.0	32.0	47.1	27.9
SHIFT-HAD >20%	89.9	71.7	58.8	52.7	53.8
SHIFT-HAD >50%	93.9	78.8	63.7	52.8	59.6
Percent of new suitable habitat colonized (constrained by both DISTRIB and SHIFT)					
SHIFT-CCC >2%	7.6	12.7	11.6	2.7	8.4
SHIFT-CCC >20%	2.0	2.4	2.2	0.8	1.5
SHIFT-CCC >50%	1.2	1.0	1.2	0.6	0.6
SHIFT-HAD >2%	11.5	8.2	14.7	3.8	9.9
SHIFT-HAD >20%	4.1	2.2	5.1	1.3	3.2
SHIFT-HAD >50%	2.5	0.9	3.0	0.9	1.6

years. Although suitable habitat may shrink on the southern ends of the species ranges, we have no way of estimating whether the species would be eliminated from its current range in that period. Most species would be expected to remain, at least in certain microclimatically acceptable refugia, throughout their current range (Loehl 1998). We remain agnostic on the potential for range contraction because it often is less clear whether southern range limits are under climatic control (McArthur 1972). As such, we do not concur with the work of Thomas et al. (2004) who state that 18–37% of species occupying ∼20% of the earth's terrestrial surface may become 'committed to extinction' due to climate change by 2050. However, the potential increase of fire, human, and climatic disturbances (e.g., Dale et al. 2001), coupled with less hospitable conditions for germination and growth would provide opportunities for especially rare species to be eliminated from the portion of range that is marginally suitable or unsuitable for the species.

Conclusions

Clearly, there is great uncertainty associated with these models. Hunsaker et al. (2001) discussed uncertainty as traced to five sources: data collection, data processing, model structure, human intervention, and natural variability. In the work reported here, we have compounding uncertainty from all five sources, so the outputs are best viewed as hypotheses for potential response. Recent work by dispersal biologists attempting to create parameterized models of long distance dispersal have concluded that parametric models of seed dispersal that capture the predominant mode of dispersal do not predict spread well (Clark et al. 2003, Higgins 2003b). Although these authors suggest methods for modeling these important long distance dispersal events, we feel that the best solution remains using historical patterns as a backdrop against which to predict future scenarios. Although we have incorporated current land use, we have not incorporated future land-use change, which can be even more important than climate change for future species distributions (Dale 1997; Pielke 2002). Our method also fails to include the importance of interspecific competition in determining species abundances, another important factor (Davis et al. 1998). Nor does it account for the variation among species in capacity to establish on selected sites. For example, loblolly pine is known to establish readily on bare areas whereas sourwood is more likely to establish in intact forests.

Finally, we do not know the maximum achievable migration rate for trees, particularly in human-altered environments and potentially human-assisted situations. Still, this two-prong method adds credibility to projections of future distribution. We also identify attributes that drive model behavior to facilitate modifications as we learn more about dispersal and drivers of range limit boundaries, and identify abiotic variables that may be current drivers to species importance values. These can be adjusted according to future climate scenarios. In simulating the actual movement of species within the new suitable habitat, we are using realistic estimates of fragmented habitats with varying degrees of habitat quality and species abundance.

The combined models consider the following factors that are important in assessing possible impacts of climate change on forest ecosystems: climate change scenario (Hadley or CCC); climate envelope to which the species is currently adapted; potential barriers to migration that are related to soil, elevation, landscape pattern, or climate; habitat quality or fragmented nature of the unoccupied zone; historic rate of migration; abundance of the migrating species near the range boundary; and distance from the current range boundary. To our knowledge, no other models have incorporated all of these factors.

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