

RESEARCH  
PAPER

# How fast and far might tree species migrate in the eastern United States due to climate change?

Louis R. Iverson\*†, M. W. Schwartz‡ and Anantha M. Prasad†

†USDA Forest Service, Northeastern Research Station, Delaware, OH 43015, USA. E-mail: liverson@fs.fed.us and ‡Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

## ABSTRACT

**Aim** We describe and use a model, SHIFT, to estimate potential migration due to climate change over the next 100 years.

**Location** Eastern United States.

**Methods** Five species, currently confined to the eastern half of the United States and not extending into Canada, were used to assess migration potential: *Diospyros virginiana* (persimmon), *Liquidambar styraciflua* (sweetgum), *Oxydendrum arboreum* (sourwood), *Pinus taeda* (loblolly pine), and *Quercus falcata* var. *falcata* (southern red oak). SHIFT is a matrix simulation model using simple inverse power functions to provide a distance decay of seed dispersal and is driven primarily by the abundance of the species near the boundary, the forest density within and beyond the boundary, and the distance between cells. For each cell outside the current boundary, the model creates an estimate of the probability that each unoccupied cell will become colonized over a period of 100 years. SHIFT is a 'fat-tailed' migration model that allows rare very long distance dispersal events and colonization could occur up to 500 km beyond the current distribution boundary. Model outputs were analysed using transects through sections showing relatively low and high colonization probabilities as a result of low and high densities of target trees (high source strength) as well as high densities of forest (high sink strength). We also assess migration potential for species by concentric rings around the current boundary.

**Results** Model outputs show the generally limited nature of migration for all five species over 100 years. There is a relatively high probability of colonization within a zone of 10–20 km (depending on habitat quality and species abundance) from the current boundary, but a small probability of colonization where the distance from the current boundary exceeds about 20 km. Whether biologically plausible or not, rare very long distance migration events are not sufficient to rescue migration. Species abundance (the source strength of migration) near the range boundary carried relatively more influence than percentage forest cover (sink strength) in determining migration rates.

**Main conclusion** The transect evaluation revealed the importance of abundance of the species near the boundary, indicating that rare species may have much more difficulty in unassisted northward migration due to climate change. The concentric rings analysis of the model outputs showed that only the first 10–20 km of area would have a reasonably high probability of colonization. Rare, long-distance events permit colonization of remote outliers, but much more needs to be understood about the likelihood of these rare events to predict the frequency of outlier establishment.

## Keywords

Climate change, *Diospyros virginiana*, fragmented habitat, global warming, *Liquidambar styraciflua*, migration, *Oxydendrum arboreum*, *Pinus taeda*, *Quercus falcata*, United States.

\*Correspondence: Louis R. Iverson, USDA Forest Service, Northeastern Research Station, Delaware, OH 43015, USA.

## INTRODUCTION

There is now ample evidence that the earth is warming and will continue to warm at unprecedented rates (Melillo, 1999). Climate change already may be influencing species physiology, distribution, and phenology (Hughes, 2000). Recent climate models used by the US National Assessment for Climate Change (National Assessment Synthesis Team, 2000) include the Hadley model (Hadley Centre for Climate Prediction and Research; Mitchell *et al.*, 1995) and the CCC model (Canadian Climate Centre; Boer *et al.*, 2000). They predict potential increases, over the next century, of 2.5° and 6.6 °C, respectively, for January and 2.3° and 5.0 °C for July when averaged for the eastern United States (Iverson & Prasad, 2001). Changes of this magnitude can have dramatic effects on ecological systems (Pastor & Post, 1988; Melillo *et al.*, 1996; Shriner & Street, 1998; Kirschbaum, 2000; National Assessment Synthesis Team, 2000; Schimel *et al.*, 2000; Watson *et al.*, 2000; Yates *et al.*, 2000; Hansen *et al.*, 2001; McCarthy *et al.*, 2001).

Using five scenarios of climate change, Iverson & Prasad (2002) evaluated potential changes in suitable habitat (assuming no barriers to migration) for 80 tree species in the eastern United States. For the Hadley scenario (the least severe), 30 species were modelled so that their 'optimum' latitude of suitable habitat moved > 100 km north (5 of these could move > 200 km). With the more severe CCC scenario, the habitats of 35 species were predicted to move > 100 km (24 of these could move > 200 km north).

The predicted rate of climate warming likely will initiate a potential response that is substantially faster than plants historically shifted their distribution (e.g. Overpeck *et al.*, 1991; Schwartz, 1993; Kirilenko *et al.*, 2000). Rates of past migrations suggest that even relatively rapid changes in range limits will be insufficient to keep pace with predicted future climatic change (Gear & Huntley, 1991), although it remains unclear whether past migrations were limited by rates of climate change or by dispersal capacity of trees (Clark, 1998). Nonetheless, it has been argued that even if trees were not migrating at maximum rates possible during the Holocene, they were probably close to the threshold of being dispersal limited (Huntley *et al.*, 1995). Coupled with this potential climatic lag is the fact that, compared to the Holocene, habitat loss and fragmentation could substantially reduce the ability of certain tree species to migrate (Peters, 1990; Schwartz, 1993; Dyer, 1994, 1995; Malanson & Cairns, 1997; Iverson *et al.*, 1999b). Fragmented landscapes have fewer individuals producing propagules and fewer sites for those propagules to colonize. Schwartz (1993) simulated tree migration through hypothetical landscapes based on an average rate of 50 km per century, near the maximum rate in the palaeoecological literature (e.g. Davis, 1989; DeHayes *et al.*, 2000). Schwartz (1993) found that highly fragmented habitats reduced the simulated migration rate to as low as 1–10 km per century. Similarly, Dyer (1995) predicts bird-dispersed trees to migrate at rates well under 15 km/century with climatic release. Subsequent research by our group has confirmed this highly reduced migration rate (Iverson *et al.*, 1999b; Schwartz *et al.*, 2001). Past and likely future migration rates are driven largely by long-distance dispersal events (Shigesada & Kawasaki, 1997; Clark, 1998; Higgins

& Richardson, 1999). Toward this end, understanding the source strength of propagules has become an important issue and a research priority in predicting 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 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 for tree migration is to understand the relative importance of source and sink strength.

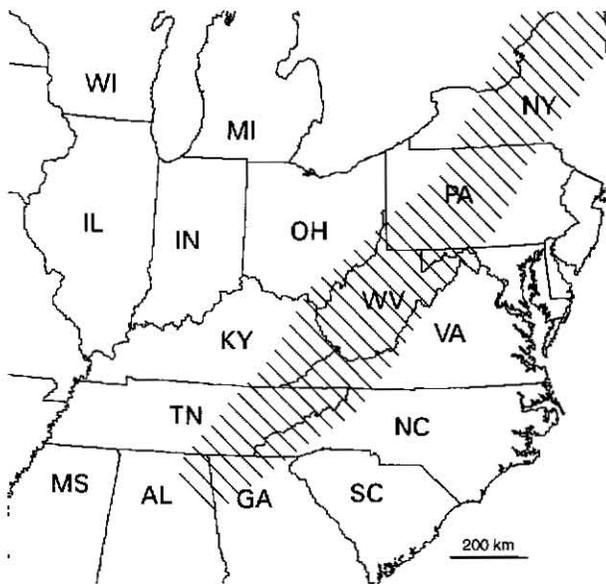
In this paper, we further refine and use a cell-based migration simulation model, SHIFT, to create a spatially explicit prediction of shifts in tree distribution given climatic release (i.e. the release of climatic restrictions to tree growth). Simulated distribution shifts are based on spatially explicit cellular simulations (Schwartz, 1993) by which the landscape is parsed into cells. Each cell is characterized by a unique location, a forest availability scalar, and an initial abundance of the target species. Colonization of initially unoccupied cells is estimated as a function of recipient cell forest availability and the sum of the probability of each occupied cell sending a propagule to that cell. We use the current distribution of five tree species along with the distribution of forested habitats in and around their ranges to model the potential rate of species distribution shifts due to climate warming. We focused on species with current northern distribution limits in the middle latitudes of the eastern United States, and examined the spatial patterns of colonization probability for these five species with respect to proximity to the current range boundary and the relationship of migration to current abundance and distributions of forest cover.

## METHODS

### Species

The five tree species selected for this study were *Diospyros virginiana* (persimmon), *Liquidambar styraciflua* (sweetgum), *Oxydendrum arboreum* (sourwood), *Pinus taeda* (loblolly pine), and *Quercus falcata* var. *falcata* (southern red oak). These species represent a range of life history characteristics and their current or potential future northern limit (following two scenarios of climate change) does not extend to the Canadian border. The distributional and ecological attributes of these five species are discussed in Iverson *et al.* (1999a) and Prasad & Iverson (1999).

Efforts to model global warming responses of trees through migration have varied in terms of either specifying detailed life history attributes in order to create a highly specified model with respect to life history attributes (e.g. Dyer, 1994; Higgins *et al.*, 2003a) or creating a model with few parameters that relies on historical precedents as guides to potential future migration (e.g. Schwartz, 1993). Both types of efforts are important to discern critical factors driving the models and variations in possible outcomes. The latter, more generalized model is justified by the



**Figure 1** Study area of the eastern United States, with state boundaries and the Appalachian Mountains (hatching) delineated. State abbreviations: WI, Wisconsin; IL, Illinois; MI, Michigan; IN, Indiana; OH, Ohio; NY, New York; PA, Pennsylvania; KY, Kentucky; WV, West Virginia; VA, Virginia; TN, Tennessee; NC, North Carolina; MS, Mississippi; AL, Alabama; GA, Georgia; SC, South Carolina.

observation that there is little historical evidence to support the hypothesis that differences in life history have had a large effect on past rates of tree migration (e.g. Portnoy & Willson, 1993). Large uncertainties concerning the impact of dispersal syndrome on seed dispersal curves (Portnoy & Willson, 1993), as well as relatively poor ecological information on interspecific differences in seed production, germination and establishment, suggest that a lightly parameterized model that uses historical migration as a model for future migration, and does not include assumption-laden life history parameters for poorly understood ecological phenomena, is an appropriate means to model future migration. In order to link migration models with landscape data and to predict future distributions of tree species in the eastern United States (Fig. 1), we adopt this lightly parameterized migration model approach.

### SHIFT

A cellular model called SHIFT calculates the probability of an unoccupied cell becoming colonized during each generation (also used as one model iteration):

$$P_{\text{colonization},i} = HQ_i \left( HQ_j * F_j * \left( CID_{i,j}^X \right) \right)$$

where  $P_{\text{colonization},i}$  is the probability of unoccupied cell  $i$  being colonized;  $HQ_i$  and  $HQ_j$  are habitat quality scalars for unoccupied cell  $i$  and occupied cell  $j$ , respectively, that are based on the percentage of forest cover of each  $\text{km}^2$  cell as assessed through LANDSAT images, as described below;  $F_j$ , an abundance scalar, is related to the current estimated importance value (IV) (= abun-

dance) 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 is summed across all  $n$  occupied cells at each generation. Although probabilities are calculated in the range of 0–1, data are reported and mapped in this paper as percentages (0–100) for ease in reading. 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/century is on the upper end of observed Holocene migration rates among trees migrating into forested environments (Davis, 1981).

The value of  $X$ , the dispersal exponent, determines the rate at which seed dispersal declines with distance. As an exponent of  $D_{i,j}$  in the denominator, it decreases colonization with distance as an inverse power function; that is, increasing  $X$  leads to decreasing long-distance dispersal while decreasing  $X$  increases long-distance dispersal. For most simulations we use a value of  $X = 3$  because it fits empirical data (Portnoy & Willson, 1993). The model and associated assumptions are discussed in Iverson *et al.* (1999b) and Schwartz *et al.* (2001). Other dispersal kernels are plausible (e.g. Clark, 1998), though computationally much more difficult within this model structure. These more recent Weibull functions and our model result in ‘fat tails’ of accelerating migration rates with time, and a large fraction of dispersal events at distances > 1 km.

SHIFT was run with a grain size of  $1 \text{ km}^2$  and with an extent of the eastern United States, for several generations, equivalent to 100 years of migration under climate release. Each run was replicated 50 times so that each time the model simulated a cell to become occupied, a 2% chance of colonization was accrued. After 50 runs, the total likelihood of colonization was summed for each cell. The number of generations in the 100-year period varied by species according to their approximate time to maturity: 3 for southern red oak, 4 for persimmon and sweetgum, 5 for sourwood, and 6 for loblolly pine (Burns & Honkala, 1990a,b; Iverson *et al.*, 1999a). Thus, generation time is the primary interspecific life history attribute that varied among models.

In our simulations, both animal- and wind-dispersed species are given the same colonization function because there is little empirical evidence suggesting that these two forms of dispersal created significant differences in characteristics of seed dispersal. Historical evidence of past migrations shows no systematic differences between dispersal mode and migration rate: animal- and wind-dispersed trees seemed to migrate at similar rates (Davis, 1981; Pitelka & the Plant Migration Workshop Group, 1997; Clark *et al.*, 1999). Also, neither Portnoy & Willson (1993) nor Clark (1998) found systematic differences between the shapes of curves that best fit animal- and wind-dispersed species. In reality, we may find that some animal-dispersed species (e.g. those dispersed by large birds) respond very differently to fragmentation as a result of directed dispersal. Nonetheless, there is no procedure to model these differences explicitly. A heavily 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.

### Tree-species data

The data needed for this effort included an estimate of IV (the  $F$  term in the equation) for each species and an estimate of the percentage forest (the HQ factors) in each 1-km<sup>2</sup> cell. We used two sources of information to characterize current distribution and abundance within the eastern United States: Little (1971) range boundaries and IVs derived from plot data generated by the USDA Forest Service's Forest Inventory and Analysis (FIA) units (Hansen *et al.*, 1992). Little's (1971) provided binomial maps of the distribution of various tree species within the United States that were based on empirical observations and FIA data available at that time. The range boundaries were digitized from the Little distribution maps. In one instance for loblolly pine, we modified the Little range boundary slightly based on the IVs that extended beyond the Little boundary. These were used as the *smooth range boundary from which to migrate the species*; by contrast, the IVs usually created a ragged boundary.

We estimated species abundance for each cell by summarizing FIA plot data for the area. Based on the relative basal area and number of stems of nearly 3 million measured trees for the eastern United States, these FIA data were used to calculate IVs as a measure of abundance (Iverson & Prasad, 1998; Iverson *et al.*, 1999a). The IVs were calculated at the scale of the county (as reported and released by FIA) and ranged from 0 to 200, with 200 indicating single species stands. We smoothed county-level IVs using an inverse distance weighted algorithm in Arc/Info Grid to avoid abrupt county boundaries and distribution gaps. We then assigned the predicted abundance value to all cells that indicated species presence from Little's range maps.

### Distribution of forested habitat

Habitat quality for each cell was estimated as the percentage of forest within each grid cell. This estimate was derived from a modified classification of an AVHRR data set by Zhu & Evans (1994). Thus, habitat quality was scaled from 0 (nonforested) to 1 (100% forested). We further modified the percentage forest map by downgrading some of the Midwest 'corn belt' area for which percentage forest had been overestimated (see Iverson *et al.*, 1989, 1994). We made no attempt to sort sites into forest type, stand age, or current dominance within individual cells, i.e. a simplifying assumption was that all forested habitat was suitable habitat for colonization by each species. As a result, our forest availability map overestimates actual habitat available for colonization by migrating tree species. This simplification will bias our results toward overestimating migration potential.

### Individual species analysis

The output from SHIFT produces estimates of colonization probability over a period of 100 years in the area outside that currently occupied by a species. The 0–100% colonization

probability scores were divided into five 20-percentile groups and mapped. To analyse in more detail the colonization probability trends extending from the boundary, two transects of 90 × 270 km were placed across the range boundary for each species, with 90 km of length inside and 180 km of length outside the boundary (Fig. 2, first column of maps). The inside portion was used to assess the abundance ( $F$ ) of the species near the boundary, while the outside was broken into ten strips of 18 × 90-km to evaluate both percentage forest (HQ) and colonization probability outputs ( $P_{\text{colonization}}$ ) incrementally distant from the range boundary. Transects were chosen to sample relatively low (labelled 'L') and high ('H') colonization probabilities, which usually included low and high initial IV within the distribution (source strength) and low and high forest availability outside the initial range limit (sink strength). Mean colonization probabilities were calculated within each strip, and were plotted in conjunction with forest density on line graphs to show variation as a function of distance from the boundaries.

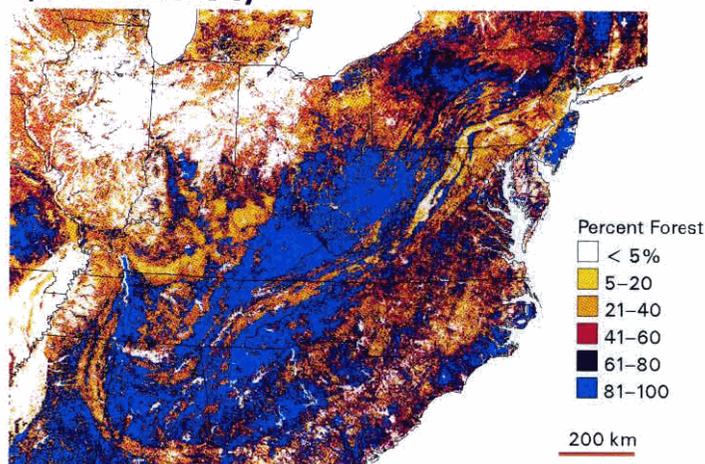
### Source and sink strength analysis

To get an overall idea of the contribution of source and sink strength, additional transects were placed across the northern and western range boundaries of the five species. Outside the current range for each species, to the north or west, were placed six 50 × 50-km boxes to sample the sink strength and resulting colonization probability, while matching 200 × 200-km boxes were placed to the inside of the range to sample source strength (Fig. 2, second column of maps). Sink strength and colonization probability were simply calculated as the mean forest density and mean probability, respectively, within each 50 × 50-km box. For source strength, the forest density and importance value grids were multiplied so that the product of the two was sampled and averaged for each of the 200 × 200-km boxes. The resultant 30 values for sink and source strength were then plotted together with colonization probability to capture overall trends.

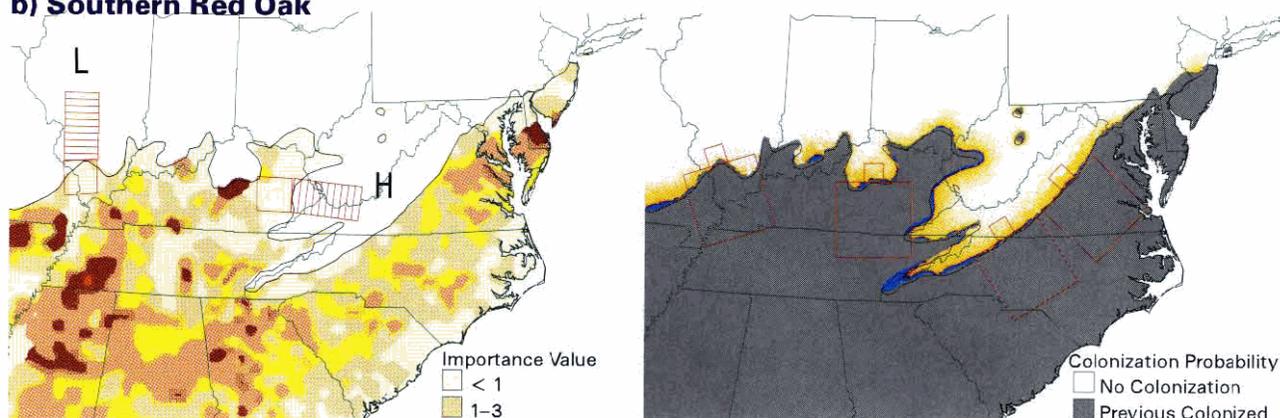
### Concentric rings analysis

We conducted an additional analysis of the spatial outputs by buffering the current range boundary by concentric rings (distances 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200, 300, 400 and 500 km from the species boundary), and then evaluating the average and maximum colonization probability within that ring. These metrics were calculated for all land within the rings, and for only that land which is currently forested. The rings were truncated on the east coast and the western boundary so that only the northern components of the rings were used in the calculations. Finally, the outputs were evaluated to calculate the percentage forest area potentially colonized at a 2%, 5%, 10%, 20% and 50% probability of colonization, again by ring. This analysis also gives an indication of the maximum distance any pixel was observed to incur some probability of colonization north of the present boundary. Therefore it is an attempt to assess those rare events of long-distance dispersal, which may be responsible for much of the rapid migration recorded in the palaeo record (Clark, 1998).

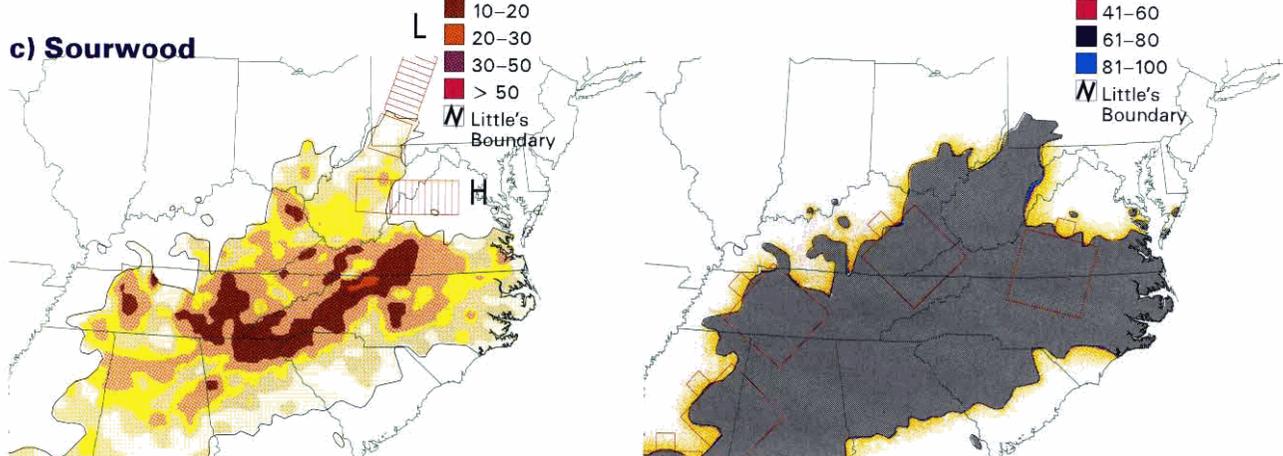
**a) Forest Density**



**b) Southern Red Oak**



**c) Sourwood**



**Figure 2** Inputs and outputs of the SHIFT model: (a) percentage forest by 1-km pixel, used for all five species; (b–f) importance value within the current range (left map) and modelled colonization probability (right map) for (b) *Quercus falcata* var. *falcata* (southern red oak) (c) *Oxydendrum arboreum* (sourwood) (d) *Liquidambar styraciflua* (sweetgum) (e) *Diospyros virginiana* (persimmon), and (f) *Pinus taeda* (loblolly pine). Transects with relatively higher (H) or lower (L) colonization probabilities, for individual species analysis, also are displayed in the left hand maps, whereas boxes for overall analysis of sink and source strength are pictured in the right hand series of maps.

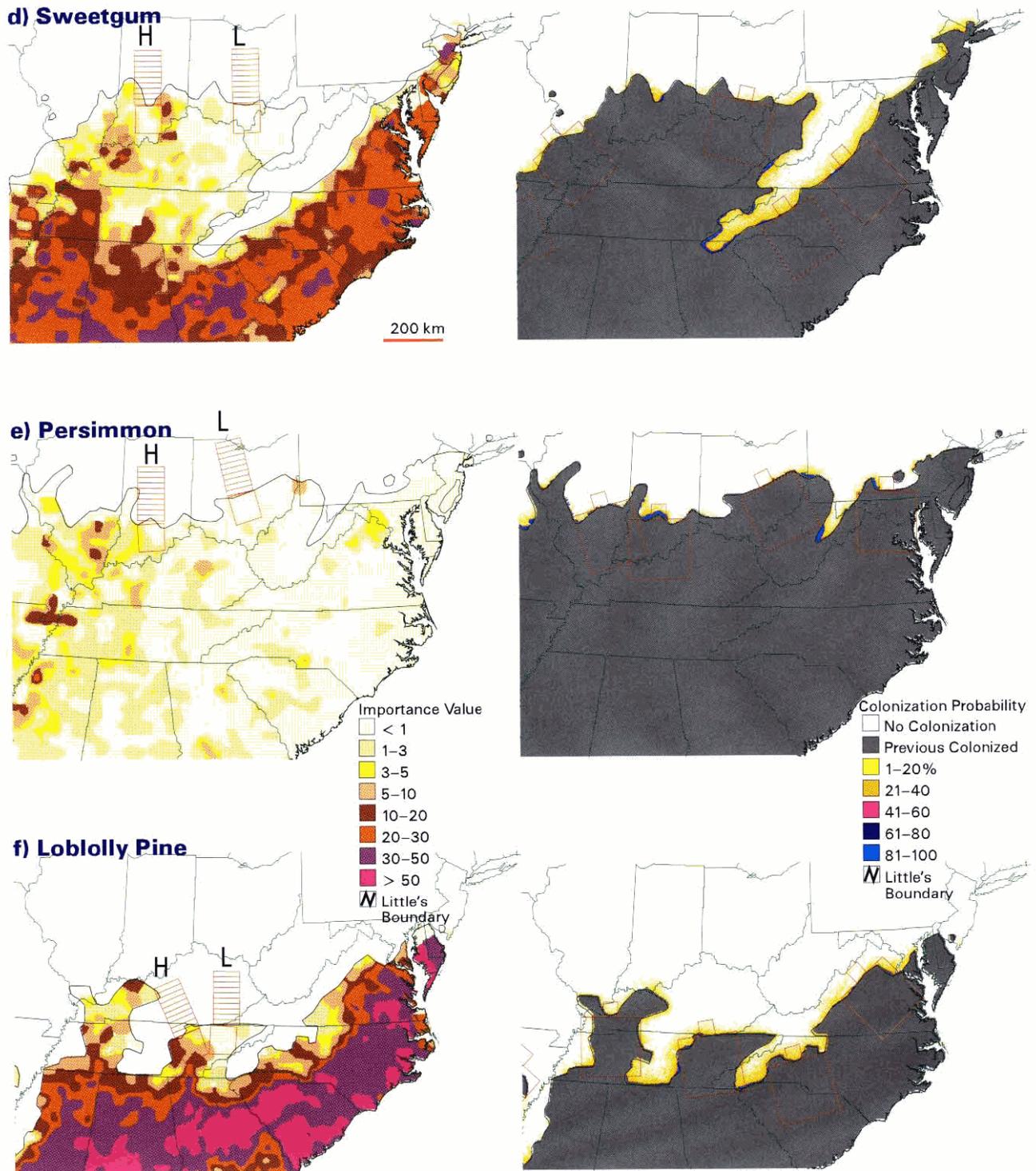


Figure 2 Continued.

## RESULTS

### Individual species analysis

In this analysis, the two transects that were placed across the boundary in zones with relatively low (L) or high (H) migration

rates allowed evaluation of colonization probability and forest cover in 10, 18 × 90-km increments into the new territory, as well as the current abundance (IV) and forest cover in a 90 × 90-km block just inside the boundary (Fig. 2, Table 1).

Results for southern red oak (Figs 2b and 3, Table 1) demonstrate the importance of forest density as a component of both

source and sink strength. In this case, abundance (IV value) inside the range boundary was 1.12–1.14 for the two transects, while the forest cover inside was nearly 3 times higher in the H than in the L transect (Table 1). Outside the current boundary, forest cover averaged 93.5% for the H transect and 15.8% for the L transect for the first 90 km distant from the boundary (Table 1). Consequently, colonization probability was highest of all species (55%) in the first 18-km section for the H transect, with at least a 1% probability of colonization out to 72 km (Fig. 3). The SHIFT output (Fig. 2b) showed some patches of higher colonization probability but mostly a yellow band, indicating 1–20% probability 10–30 km north of the current distribution.

Sourwood (Figs 2c and 3, Table 1) showed negligible migration on the L transect, primarily due to low abundance near the boundary. The H transect had both a higher forest cover (inside and outside) and higher abundance than the L transect (Table 1). As a result, the colonization probability was 25% in the first 18 km, 8% in the second, and 2% in the third 18-km block of the transect (Fig. 3). SHIFT outputs showed only a small area in West Virginia where colonization probabilities exceeded 20% (Fig. 2c).

Sweetgum (Figs 2d and 3, Table 1) was unlike all other species, in that the higher migration rate (transect H) occurred in a zone with lower forest cover (compared to transect L) both inside and outside the range boundary (Table 1). Species abundance was most important, and was 3 times higher for the H transect (2.27 vs. 0.72, Table 1). Migration of sweetgum was negligible on the L transect (Fig. 3). The SHIFT output (Fig. 2d) showed maximum colonization probability in the southern Appalachians, increasing in elevation as the climate warms.

Persimmon (Figs 2e and 3, Table 1) had low abundance throughout and therefore low colonization probability except for a small Appalachian region in West Virginia and Pennsylvania and a small strip of land in southern Indiana (Fig. 2e). Only the H transect showed significant colonization probability and only for the first 18 km from the boundary (Fig. 3). The L transect, with extremely low abundance near the boundary, recorded essentially no migration even though there was forest land within which to migrate.

For loblolly pine (Figs 2f and 3e, Table 1), colonization probability on the H transect was relatively high (> 8%) for the first 36 km and then dropped nearly to zero. For the L transect, colon-

ization probability was about 3% for the first 18 km (highest among all species for this transect) and then dropped. Loblolly had the highest level of abundance near the boundary of all species, and forest cover was fairly high for both transects; in fact it was higher outside in the slower migrating (L) transect (92.2%) than in the H transect (66.3%, Table 1, Fig. 3). However, the abundance of loblolly was several times higher for the H transect and this took on greater relative importance than forest density.

### Source and sink strength analysis

A 3d graph of sink and source strength relative to colonization probability reveals an apparent threshold of source strength needed to achieve significant colonization probability (Fig. 4). Nearly a third of the samples have essentially no colonization probability because of low source strength, regardless of sink strength. At moderate to high source strength (generally, IV > 2.0 with > 75% forested), colonization probability rapidly increases and can then be regulated by sink strength. This explanation is also borne out by a simple regression tree diagram, which shows source strength as the higher level factor and sink strength as the secondary level factor (Fig. 5).

### Concentric-rings analysis

The probability of colonization and a summary of the area potentially colonized over 100 years, by concentric ring, are exemplified for the southern red oak in Table 2 (data for the other four species follow similar patterns and are available from the authors). The mean probability of colonization within the 10-km ring ranged from 10.8% (loblolly pine) to 29.8% (southern red oak) when all land was considered, and from 14.4% to 32.9% (same species) when only land currently forested was considered. Immediately apparent is the rapid reduction in mean probability of colonization as one moves from the 10- to 20-km ring and beyond (Table 2). No species had more than a 1% average probability of colonization beyond 30 km. However, all species had a small probability of colonization even 400–500 km distant from the current boundary.

With respect to the maximum probability of colonization exhibited by individual cells, all species had at least some cells with 100% probability of colonization within the first 10 km,

**Table 1** Species importance values (abundance) and percentage forest cover inside the current range as well as average forest cover in a 90- × 90-km block outside the current boundary. Data are for two transects for each species, one with a relatively higher (H) migration rate than the other (L). Importance Values were equally weighted for number of stems (> 2.5 cm d.b.h.) and total basal area relative to all stems in each plot

	Importance value inside range boundary		Forest cover (%)			
			Inside		Outside	
	H	L	H	L	H	L
Southern red oak	1.12	1.14	93.3	34.3	93.5	15.8
Sourwood	3.30	0.56	93.6	50.2	69.0	51.9
Sweetgum	2.27	0.72	53.0	69.5	35.7	52.0
Persimmon	1.61	0.10	53.7	45.0	27.6	20.3
Loblolly pine	7.48	1.25	71.1	55.0	66.3	92.2

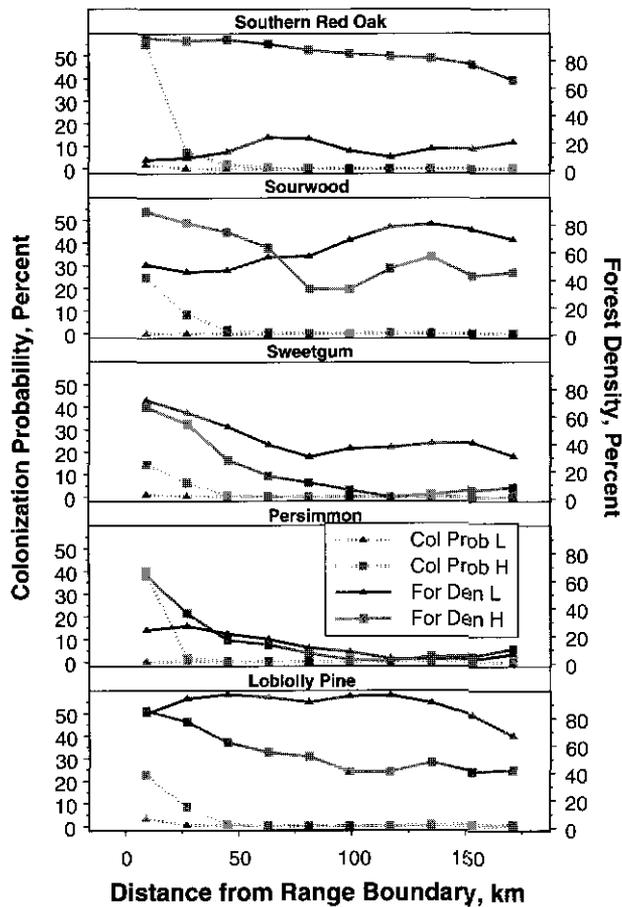


Figure 3 Trends in colonization probability (-----) and forest cover (——) for the L (▲) and H (■) transects for each 18- × 90-km increment distant from the current boundary of southern red oak, sourwood, sweetgum, persimmon, and loblolly pine.

and three species did within the first 20 km (Table 2). Beyond 50–70 km, the model showed only a maximum of 6% probability of colonization for any pixel, for any species.

We also evaluated, by concentric ring, the percentage of forest area with various probabilities (2–50%) of being colonized (again tabulated here only for southern red oak, Table 3). For all species except persimmon (which had extremely low abundance near the boundary), at least 50% of the forest in the first 10-km concentric ring had at least a 2% chance of being colonized within 100 years (Table 3). Even at 50% probability, at least 6% (loblolly and sourwood) and as much as 20% (southern red oak) of the forested landscape within 10 km could be colonized. However, beyond 10 km, the percentage of the landscape with a high (> 10%) probability of colonization dropped dramatically. For example, in the 10–20-km ring, only 2.4% of forest land had at least a 10% probability of being colonized by persimmon, while 16.4% of land could be colonized by southern red oak. No species had forest land beyond 20 km with at least a 50% chance of being colonized over 100 years. However, all species had some area, even as far as 500 km, with at least a 2% chance of being colonized.

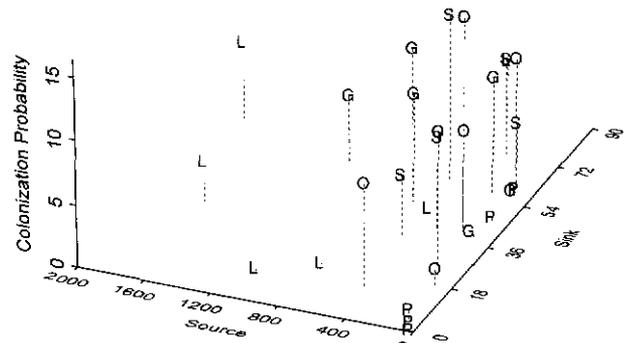


Figure 4 Overall sink (% forest cover) and source (% forest cover × average importance value) strength vs. colonization probability (%) for southern red oak (O), sourwood (S), sweetgum (G), persimmon (P), and loblolly pine (L).

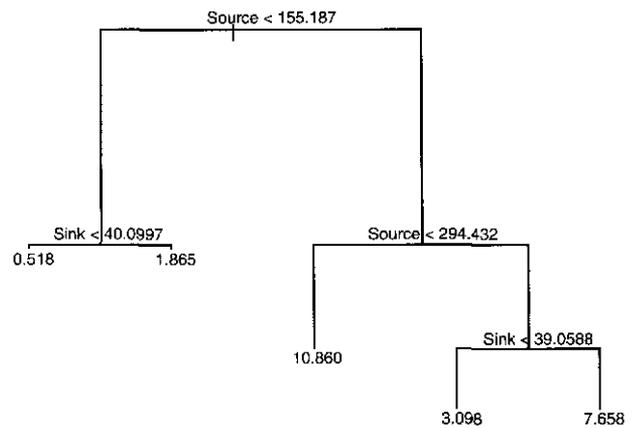


Figure 5 Regression tree diagram displaying influence of sink (% forest cover) and source (% forest cover × average importance value) strength. Terminal nodes express colonization probability (%).

### DISCUSSION AND CONCLUSIONS

Results show the generally limited nature of likely migration over the first 100-year period following climatic release. There is a relatively high probability of colonization within a zone of 10–20 km (depending on habitat quality and species abundance) of the current boundary, but a small probability of colonization as the distance from the current boundary exceeds about 20 km. Nonetheless, the model allows long-distance dispersal on rare occasions, even as far as 500 km from the current range boundary. This is a very generous, arguably unrealistically generous, upper dispersal boundary for tree seeds.

The model also demonstrates that source strength, the abundance of species near the range terminus, has important impacts on migration rate, and is relatively more important than the forest habitat into which the species would migrate. Simply put, trees have to be present near the range boundary in sufficient numbers in order to drive migration rates. Once source strength is sufficiently high (~ > 2 IV and > 75% forested), sink strength then matters by setting dispersal and colonization barriers that, if low, can slow migration. Our results confirm the importance of higher abundance near the range boundary as a

**Table 2** Probability of colonization (for all land and forested land) and maximum probability of colonization at various probability levels, by distance ring, after 100 years. Only southern red oak model outputs are presented, but the other species follow similar patterns. Calculations are based on a cell size of 1 km square

Distance (km)	Probability of colonization (%)			
	All land (mean)	Forested (Southern red oak)		Area (km <sup>2</sup> × 10 <sup>3</sup> )
		Mean	Max	
10	29.8152	32.8600	100	44.4
20	6.5017	7.2777	100	44.5
30	1.7590	2.0105	38	43.0
40	0.6393	0.7489	14	40.3
50	0.2793	0.3252	14	38.0
60	0.1246	0.1548	6	35.8
70	0.0655	0.0784	6	35.1
80	0.0322	0.0399	4	34.1
90	0.0161	0.0187	2	31.6
100	0.0105	0.0140	4	29.8
150	0.0039	0.0055	4	132.8
200	0.0015	0.0020	2	132.8
300	0.0007	0.0014	2	258.8
400	0.0005	0.0009	2	229.0
500	0.0002	0.0003	2	197.2

**Table 3** Percentage forest area potentially colonized by southern red oak at various probability levels, by distance ring, after 100 years. Only southern red oak results are presented, but the other species follow similar patterns

Distance (km)	Forest area potentially colonized (%)				
	P = 2%	P = 5%	P = 10%	P = 20%	P = 50%
10	56.345	49.816	39.841	31.297	20.354
20	44.338	33.625	16.384	6.671	1.649
30	31.157	17.399	3.230	0.237	
40	17.496	5.934	0.261		
50	9.197	1.864	0.010		
60	4.926	0.524			
70	2.684	0.097			
80	1.388	0.029			
90	0.665	0.008			
100	0.488	0.004			
150	0.194				
200	0.066				
300	0.036				
400	0.017				
500	0.003				

primary driver of species migration. Most species decrease in abundance toward their geographical distribution limits (Brown, 1995); we found that none of the five species evaluated has an exceptionally high level of abundance near the boundary; consequently the migration rates estimated by the SHIFT model are low. Slow migration in response to warming should thus be the expectation for most tree species that taper in abundance toward current distribution boundaries.

Thus, one important finding from this study is the importance of a reasonable abundance of a species near the range boundary to obtain significant colonization probabilities. Transects for any species with low abundances near the boundary had virtually no migration over the 100-year period. If the model approximates reality, it will be difficult for currently rare species to migrate into new suitable habitat as the result of climate change (assuming no assistance from humans). Conservation research and management should consider approaches to deal with this issue. Colonization of new habitat may be facilitated for certain species that are planted outside of their current distribution as ornamental or commercial trees. Examples include persimmon and Virginia pine.

Another important finding is that, because of the narrow bands of higher colonization potential modelled for the next 100 years (< 20 km), it may be nearly impossible to differentiate a no migration response from a realistic expectation of migration based on our current imprecise knowledge of the limits to species distribution. Also, narrowly endemic species, for which there are too few data to model, may face an extinction crisis due to their inability to keep pace with climatic forcing. According to this model, rare species are unlikely to migrate unassisted in response to climate change.

Finally, nontimber forest species, for which sufficient data are also lacking, may suffer from migration lags in response to ongoing warming.

Outputs from SHIFT also indicate that the 'advancing front' of migrating species over the next 100 years likely will be concentrated in the first 10 km from the current boundary. This concentrated front probably would not keep pace with projected rates of climate warming and changes in habitat suitability. However, SHIFT also suggests the possibility, however slight, of colonization over long distances periodically. These rare chance

events may have important implications for migration rates over the long-term (Clark, 1998), and along with the potential dispersal by human activity, will likely have more impact on the overall rate of migration than the movement of the concentrated front. It should be emphasized that SHIFT incorporates numerous simplifying assumptions and thus may not reflect reality. Nevertheless, we contend that our analysis contributes to a better understanding of how tree species may respond to a warming climate and changing climate patterns.

## ACKNOWLEDGEMENTS

We thank Hong He, David Williams, Dan Yaussy, Martin Jones, and the anonymous reviewers for reviewing a previous version of the manuscript, and Mary Boda for additional work on the manuscript. The Northern Global Change Program of the USDA Forest Service provided funding for this research.

## REFERENCES

- Boer, G.J., Flato, G.M. & Ramsden, D. (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.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Burns, R.M. & Honkala, B.H. (Technical co-ordinators) (1990a) *Silvics of North America: 1. conifers*. Agriculture Handbook 654. US Department of Agriculture, Washington, DC.
- Burns, R.M. & Honkala, B.H. (Technical co-ordinators) (1990b) *Silvics of North America: 2. hardwoods*. Agriculture Handbook 654. US Department of Agriculture, Washington, DC.
- Clark, J.S. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, **152**, 204–224.
- Clark, J.S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Davis, M.B. (1981) Quaternary history and the stability of forest communities. *Forest succession: concepts and application* (ed. by D.C. West and H.H. Shugart), pp. 132–153. Springer-Verlag, New York.
- Davis, M.B. (1989) Lags in vegetation response to greenhouse warming. *Climate Change*, **15**, 75–82.
- DeHayes, D.H., Jacobson, G.L., Schaber, P.G., Bongarten, B., Iverson, L.R. & Dieffenbacher-Krall, A. (2000) Forest responses to changing climate: lessons from the past and uncertainty for the future. *Responses of northern forests to environmental change* (ed. by R.A. Mickler, R.A. Birdsey and J.L. Hom), pp. 495–540. Ecological Studies Series. Springer-Verlag, New York.
- Dyer, J.M. (1994) Land use pattern, forest migration and global warming. *Landscape and Urban Planning*, **29**, 77–83.
- Dyer, J.M. (1995) Assessment of climatic warming using a model of forest species migration. *Ecological Modelling*, **79**, 199–219.
- Gear, A.J. & Huntley, B. (1991) Rapid changes in the range limits of Scots pine 4000 years ago. *Science*, **251**, 544–547.
- Hansen, M.H., Frieswyk, T., Glover, J.F. & Kelly, J.F. (1992) *The Eastwide forest inventory data base: users manual*. General Technical Report NC-151. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R. & Bartlein, P.J. (2001) Global change in forests: responses of species, communities, and biomes. *Bioscience*, **51**, 765–779.
- Higgins, S.I., Clark, J.S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J.M.V., Aguiar, M.R., Ribbens E. & Lavorel, S. (2003a) Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology*, **91**, 341–347.
- Higgins, S.I., Lavorel, S. & Revilla, E.E. (2003b) Estimating plant migration rates under habitat loss and fragmentation. *Oikos*, **101**, 354–366.
- Higgins, S.I. & Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, **153**, 464–475.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Huntley, B., Berry, P., Cramer, W. & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, **22**, 967–1001.
- Iverson, L.R., Cook, E.A. & Graham, R.L. (1989) A technique for extrapolating and validating forest cover data across large regions: calibrating AVHRR data with TM. *International Journal of Remote Sensing*, **10**, 1805–1812.
- Iverson, L.R., Cook, E.A. & Graham, R.L. (1994) Regional forest cover estimation via remote sensing: the calibration center concept. *Landscape Ecology*, **9**, 159–174.
- Iverson, L.R. & Prasad, A.M. (1998) Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465–485.
- Iverson, L.R. & Prasad, A.M. (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, **4**, 186–199.
- Iverson, L.R. & Prasad, A.M. (2002) Potential tree species shifts with five climate change scenarios in the Eastern United States. *Forest Ecology and Management*, **155**, 205–222.
- Iverson, L.R., Prasad, A.M., Hale, B.J. & Sutherland, E.K. (1999a) *An atlas of current and potential future distributions of common trees of the eastern United States*. General Technical Report NE-265. US Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA.
- Iverson, L.R., Prasad, A.M. & Schwartz, M.W. (1999b) Modeling potential future individual tree-species distributions in the Eastern United States under a climate change scenario: a case study with *Pinus virginiana*. *Ecological Modelling*, **115**, 77–93.
- Kirilenko, A.P., Belotelov, N.V. & Bogatyrev, B.G. (2000) Global model of vegetation migration: incorporation of climatic variability. *Ecological Modelling*, **132**, 125–133.

- Kirschbaum, M.U.F. (2000) Forest growth and species distribution in a changing climate. *Tree physiology*, **20**, 309–322.
- Little, E.L. (1971) *Atlas of United States trees, Volume 1. conifers and important hardwoods*. Miscellaneous Publication 1146. US Department of Agriculture, Forest Service, Washington, DC.
- Malanson, G.P. & Cairns, D.M. (1997) Effects of dispersal, population delays, and forest fragmentation on tree migration rates. *Plant Ecology*, **131**, 67–79.
- McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S., eds (2001) *Climate change 2001: impacts, adaptation, and vulnerability*. Contribution of Working Group II to the third assessment report of the IPCC. Cambridge University Press, Cambridge, UK.
- Melillo, J.M. (1999) Warm, warm on the range. *Science*, **283**, 183–184.
- Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.-D. & Sala, O.E. (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. *Climate change 1995: the science of climate change. Intergovernmental panel on climate change* (ed. by J.T. Houghton, L.G. Meira Filho, B.A. Callender, N. Harris, A. Kattenberg & K. Maskell), pp. 445–481. Cambridge University Press, Cambridge, UK.
- Mitchell, J.F.B., Johns, T.C., Gregory, J.M. & Tett, S. (1995) Climate response to increasing levels of greenhouse gases and sulphate aerosols. *Nature*, **376**, 501–504.
- National Assessment Synthesis Team (2000) *Climate change impacts on the United States: the potential consequences of climate variability and change*. US Global Change Research Program, Washington, DC.
- Overpeck, J.T., Bartlein, P.J. & Webb, T. III (1991) Potential magnitude of future vegetation change in Eastern North America: comparisons with the past. *Science*, **254**, 692–695.
- Pastor, J. & Post, W.M. (1988) Response of northern forests to CO<sub>2</sub> induced climate change. *Nature*, **334**, 55–58.
- Peters, R.L. (1990) Effects of global warming on forests. *Forest Ecology and Management*, **35**, 13–33.
- Pitelka, L.F. & the Plant Migration Workshop Group (1997) Plant migration and climate change. *American Scientist*, **85**, 464–473.
- Portnoy, S. & Willson, M.F. (1993) Seed dispersal curves: behavior of the tail of the distribution. *Evolutionary Ecology*, **7**, 25–44.
- Prasad, A.M. & Iverson, L.R. (1999) *A climate change atlas for 80 forest tree species of the eastern United States*. [WWW document]. URL [www.fs.fed.us/ne/delaware/atlas](http://www.fs.fed.us/ne/delaware/atlas)
- Schimmel, D., Melillo, J., Tian, H.A., McGuire, D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R. & Rizzo, B. (2000) Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science*, **287**, 2004–2006.
- Schwartz, M.W. (1993) Modelling effects of habitat fragmentation on the ability of trees to respond to climatic warming. *Biodiversity and Conservation*, **2**, 51–61.
- Schwartz, M.W., Iverson, L.R. & Prasad, A.M. (2001) Predicting the potential future distribution of four tree species in Ohio, USA, using current habitat availability and climatic forcing. *Ecosystems*, **4**, 568–581.
- Shigesada, N. & Kawasaki, K. (1997) *Biological invasions: theory and practice*. Oxford University Press, Oxford, UK.
- Shriner, D.S. & Street, R.B. (1998) North America. *The regional impacts of climate change* (ed. by R.T. Watson, M.C. Zinyowera and R.H. Moss), pp. 253–330. Cambridge University Press, New York.
- Watson, R.T., Noble, I.R., Bolin, B., Ravindranath, N.H., Verardo, D.J. & Dokken, D.J., eds. (2000) *Land use, land-use change, and forestry*. Special Report of the IPCC. Cambridge University Press, Cambridge, UK.
- Yates, D.N., Kittel, T.G.F. & Cannon, R.F. (2000) Comparing the correlative Holdridge model to mechanistic biogeographical models for assessing vegetation distribution response to climatic change. *Climatic Change*, **44**, 59–87.
- Zhu, Z. & Evans, D.L. (1994) US forest types and predicted percent forest cover from AVHRR data. *Photogrammetric Engineering and Remote Sensing*, **60**, 525–531.

#### BIOSKETCHES

**Louis Iverson** is a Research Landscape Ecologist with the USDA Forest Service in Delaware, Ohio, and Adjunct Professor with the Ohio State University School of Natural Resources. **Anantha Prasad** is an Ecologist and GIS Specialist with the USDA Forest Service in Delaware, Ohio.

**Mark Schwartz** is a Professor with the Department of Environmental Science and Policy at the University of California at Davis. The authors' research interests include creating a better understanding of the potential impacts of climate change on vegetation, as well as of species-environment relationships at multiple scales and locations. Much of this work requires extensive GIS and statistical modelling.