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Predicting the Potential Future Distribution of Four Tree Species in Ohio Using Current Habitat Availability and Climatic Forcing

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ABSTRACT

We investigated the effect of habitat loss on the ability of trees to shift in distribution across a landscape dominated by agriculture. The potential distribution shifts of four tree species (*Diospyros virginiana, Oxydendron arboreum, Pinus virginiana, Quercus falcata* var. *falcata*) whose northern distribution limits fall in the southern third of Ohio were used to assess possible distribution shift scenarios as a result of global warming. Our predictions derive from the results of simulations using (a) forest inventory based estimates of current distribution and abundance of target species; (b) a satellite-based estimate of forest habitat availability; and (c) a tree migration model (SHIFT). The current distribution and abundance of trees was estimated using USDA Forest Service's Forest Inventory Analysis data and distribution maps from the late 1960s; pre-European settlement forest–nonforest maps were used to represent the fully forested condition for calibration and comparison. Habitat-availability estimates in Ohio were estimated using classified Landsat Thematic Mapper (TM) data from 1994. Tree abundance, forest availability and migration were modeled using a 1-km^2 pixel size. Forest availability was estimated as the proportion of forested TM pixels within each cell. The probability of a migrating species colonizing an unoccupied cell is modeled as a function of forest availability and distance to occupied cells. The results of the migration models suggest that the species studied are capable of colonizing virtually any forested location within Ohio over the next 100 years if climatic controls over the current distribution that may currently inhibit northward movement are relaxed. The contiguous distribution of these species, however, is not likely to shift more than 10 km during the next century regardless of the magnitude of the climate change. Examining the sensitivity of our simulations by varying critical model attributes, we found that whereas the variables controlling the amount of long-distance dispersal have strong effects on migration rates in the fully forested 1800 situation, they have significantly lesser effects on projections of future migration into highly fragmented forests. The low forest availability that characterizes much of the current Ohio landscape, along with the low likelihood of long distance dispersal, result in potential distribution shifts that are concentrated within the principally forested corridors in southeastern Ohio. We propose that in contrast to the past, future tree migrations are likely to be spatially and temporally correlated as a result of large climatic forcing and channelization through limited regions of available habitat. With respect to the management of biodiversity, this result suggests that it may be very difficult to discern plant

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migrations of native forest species owing to exceedingly slow rates of movement.

Key words: migration; climate change; trees; oak; pine; distribution; habitat loss.

INTRODUCTION

Over the past decade, a great deal of attention has been paid to making predictions about the effects of future climatic change on ecological systems (for example, see Iverson and others 1999a; Melillo and others 1990, 1996; Shriner and Street 1998; Schimel and others 2000; Yates and others 2000). With respect to the ecological effects on native plants, two features emerge as critically important: the inevitable doubling of atmospheric carbon dioxide (CO_2) concentration and climatic warming driven by these atmospheric changes (Kattenberg and others 1996). Both effects have the potential to change ecosystem functions, species interactions, population biology, and the distribution of plants (for example, see Melillo and others 1990). A further complication is that habitat loss and fragmentation can reduce the ability of natural systems to respond to global change effects (Peters 1990; Schwartz 1993; Iverson and others 1999b). In this paper, we use the current distribution of four tree species, along with the distribution of forested habitats in and around their ranges, to model the potential rate of species distribution shifts in the face of warming. We focus this study on species with current northern distribution limits in southern Ohio.

Predictions of climate change for Ohio have varied over the past 10 years. Global Circulation Models (GCM) initially suggested a 3–5°C increase in global mean temperature as a result of doubling atmospheric CO_2 (Mitchell and others 1990). A more recent modification of these climate models incorporated the cooling effects of atmospheric pollutants such as SO_x and NO_x to predict a lesser level of warming to 1.4–2.6°C in global temperature through a doubling of CO_2 (Kattenberg and others 1996). Two newer transient climate models that also include the effects of sulfate aerosols, have been developed by the Hadley Centre for Climate Prediction and Research (Hadley model) (Mitchell and others 1995) and the Canadian Climate Center (CCC) (Laprise and others 1998). These models predict potential increases 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 and Prasad Forthcoming). Even though there are still large uncertainties associated with climate change, the question of how trees will respond to a climatic change remains very important given the increasing evidence of ongoing warming (MacCracken 1995; Melillo 1999), continued predictions of warming by numerous GCM (Kattenberg and others 1996); the trend toward decreasing atmospheric pollution (Holland and others 1999), and hence a potential diminution of cooling effects (Kattenberg and others 1996); and a likely scenario of tripling or even quadrupling atmospheric CO_2 within 150 years (Schimel and others 1997).

The magnitude of climatic change from earlier reports (see, for example, Mitchell and others 1990) was estimated to be sufficient to initiate a release of northern distribution limits of trees and eventually displace distributions of some species 300–800 km northward (Woodward 1987; Davis and Zabinski 1992; Graham and others 1990). Using five scenarios of climate change, Iverson and Prasad (Forthcoming) evaluated potential changes in suitable habitat (assuming no barriers to migration) for 80 species from the eastern United States. For the Hadley scenario (the least severe), 30 species were modeled to move more than 100 km north, while five of these could move more than 200 km. With the more severe CCC scenario, 35 species were predicted to move more than 100 km; moreover, 24 of them could move more than 200 km north.

Historical analogues of plant species distribution shifts suggest that future rates of change may be very slow relative to the predicted rate of climatic warming (for example, see Overpeck and others 1991; Huntley 1991; Davis and Zabinski 1992; Schwartz 1993; Kirilenko and others 2000). Predictions of tree responses remain uncertain in part because it is unclear whether historically documented migrations were limited by rates of climate change or by maximum rates of dispersal into new territory (Davis 1981; Huntley and Birks 1983; Davis and others 1986; Schwartz 1992; 1993; Clark 1998). If we presume that past migration rates were limited by rates of climate change, then we know less regarding potential maximum migration rates for trees. There is reason to believe, however, that plants were migrating at, or near, maximum migration rates for at least part of the Holocene (Coope 1977,1979; Davis and others 1986; Davis 1989; Huntley 1991). An examination of these rates of past migrations suggests that even relatively rapid changes in range limits are insufficient to keep pace with predicted future climatic change (Gear and Huntley 1991).

Table 1. Critical Life History Attributes of Target Species for Migration Projections within Ohio

Species	Pollination	Seed Dispersal	Age of 1st seeding (yr)	Max. Longevity (yr)	Max. Height (m)
Virginia pine	Wind	Wind	20	200	23
S. red oak	Wind	Vertebrate	33	200	25
Sourwood	Insect	Wind	20	120	24
Persimmon	insect	Vertebrate	25	>80	24

Sources: Burns and Honkala 1990a, b; Iverson and others 1999

Schwartz (1993) investigated the role of habitat loss on the ability of trees to migrate through hypothetical landscapes predicated on the assumption that the dispersal-limited maximum migration rate for species moving through fully forested landscapes was about 50 km per century. He suggested that migration rates of 1–10 km/century may be the maximum future rates in highly fragmented habitats. Past and future migration rates are driven by long-distance dispersal events (Shigesada and Kawasaki 1997; Clark 1998). Empirical research on long-distance seed dispersal suggests that populations on the order of 1 km apart are effectively isolated at the scale of gene flow across 1000-year intervals (Greene and Johnson 1995). Thus, the proximity of forest patches plays a large role in predictions of potential future migrations.

In this paper, we combine a modification of a cell-based migration simulation model (Schwartz 1993) with empirical data on current tree species abundances and distributions to create a spatially explicit prediction of tree distribution shifts given climatic release (that is, the release of climatic restrictions to tree growth). Simulated distribution shifts are based on spatially explicit cellular automata (Schwartz 1993) where 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 then overlay projected potential migration onto maps of potential future distribution as a result of climatic release. Finally, we analyze the sensitivity of these simulations by assessing the degree to which the choice of model parameters alters forecasts of future migration through fragmented habitats.

METHODS

Site and Species Selection

To assess potential distribution shifts within a real landscape, we selected a geographical setting that met several criteria. First, we sought a site located east of the Mississippi and at mid-latitudes such that predicted future distribution shifts could be interpreted within the context of historical data on past tree distribution shifts. Further, the region must be characterized by (a) available satellite coverage of forest habitat availability, (b) known tree distributions and abundances through Forest Inventory Analysis plots, (c) a minimum of 300 km in north-to-south and east-to-west dimensions, and (d) variability in the relative amount of forest availability. Ohio met all of these criteria.

Within Ohio, we selected a suite of four tree species whose northern distribution limits occurred within the southern third of the state (Table 1). The species selected for this model were Virginia pine (*Pinus virginiana*), southern red oak (*Quercus falcata* var. *falcata*), sourwood (*Oxydendrum arboreum*), and persimmon (*Diospyros virginiana*). These species vary with respect to several critical life history attributes that may affect their ability to migrate across fragmented landscapes (Table 1). All landscape analysis and map production was conducted using Arc/Info (ESRI 1993). Ohio was divided into 1-km^2 cells for site characterization, species presence and absence, and simulation runs. Our use of a 1-km^2 cell size resulted in a total of 148,400 (400 × 371) cells for analysis.

Characterization of Current Distribution

We used two sources of information to characterize current distribution and abundance within Ohio. Based on empirical observations and inventory data available at that time, Little (1971) created binary maps of the distribution of various tree species within the United States. Presence or absence for 1-km^2 grid cells in Ohio was determined by digitizing the Little distribution maps. To estimate the abundance for each species within each grid cell, we aggregated the USFS Forest Inventory Analysis (FIA) (Hansen and others 1992) plot data for Ohio and the counties bordering southern Ohio. The FIA data was used to calculate importance values (IV) based on relative basal area and number of stems of both the understory and the overstory trees (Iverson and Prasad 1998; Iverson and others 1999b). The IV were calculated at the scale of the county and ranged from 0 to 200, with 200 indicating single-species stands. We smoothed county-level IV using an inverse weighted distance algorithm in Arc/Info Grid. We then assigned the predicted abundance value to all cells that indicated species presence from Little's range maps. Each species is currently restricted to the southern third of Ohio and the species vary considerably in relative abundance.

The Distribution of Forested Habitat

Landsat's thematic mapper (TM) images, with a pixel resolution of 30 × 30 m, were classified into vegetation types by Schaal and Motsch (1997). This classification was used to derive a percent forest map by aggregating to the 1-km^2 resolution. Forest availability for each cell was estimated using the percent abundance of forested pixels within each grid cell. This value was used to scale forest availability from 0 (nonforested) to 1 (100% forested). Owing to the limited ability to classify species composition or stand age using the TM data in this region, we made no attempt to sort sites into forest type, stand age, or current dominance within individual cells. We also did not use variations in soil, topography, or climate to vary the probability of colonization; those factors will be accounted for by the accompanying DISTRIB model, discussed elsewhere (Iverson and Prasad 1998; Iverson and others 1999b). Briefly, DISTRIB provides the overall habitat suitability for a particular species under a changed climate. In contrast, another model, which we call SHIFT, provides the migration simulations into that suitable, but fragmented, habitat. We describe SHIFT in the next section.

In this paper, however, we do not include the DISTRIB component, and all portions of Ohio are assumed to be similar in habitat suitability in terms of soil, topography, and climatic variables. We thus used a simplifying assumption that all forested habitat was suitable for colonization by each species. Hence, our forest availability map overestimates actual habitat available for colonization by migrating tree species. This simplification will bias our results toward an overestimate of migration potential. The distribution of pre-European settlement forests, estimated from Land Office Survey data (Gordon 1969), suggests that Ohio was 95% forested around 1800 (Figure 1a). Current forest cover is considerably reduced from the 1800 condition, which is now estimated at 30% (Griffith and others 1993), with the highest density of forested habitat remaining in southeastern Ohio (Figure 1b).

Tree Distribution Shifts

Location and forest availability are fixed attributes of cells and do not vary within or between runs of any species. Simulation runs were initiated by filling cells initially occupied by the target species for that simulation. Migration projections for each species were run independently under a variety of different scenarios. The single-species, cellular automata model (SHIFT) then calculates the probability of an unoccupied cell becoming colonized during each generation based on the following equation:

$$P_{\text{colonization, i}} = FA_i \ (3 \ FA_j \times F_j \times (C/D_{ij}^X)) \quad (1)$$

where $P_{\text{colonization, i}}$ is the probability of unoccupied cell i being colonized by the species being modeled; FA_i and FA_j are forest availability scalars for unoccupied cell i and occupied cell j, respectively, and based on the percentage of forest cover of each cell; F_j is an abundance scalar for the migrating species in the occupied cell j; and D_{ij} is the distance between unoccupied cell i and an occupied cell j. The colonization probability for each unoccupied cell is summed across all unoccupied cells. The value of C, a rate constant, is derived at the beginning of the simulation to achieve a migration rate of approximately 50 km/century when forest availability is high, simulating the 1800 condition. To set this baseline migration rate, we ran a series of simulations where 80% of cells had a forest availability of 0.8 and the remainder had a forest availability of zero. Using this baseline, we derived a calibration constant of 1 for Virginia pine. Values for each species were estimated independently and are reported in the results.

The value of X, the dispersal exponent, determines the rate at which seed dispersal falls off with distance (inverse power function). For our standard runs, we use a value of $X = 3$. Increasing X leads to a decrease in long-distance dispersal, whereas decreasing X increases long-distance dispersal. Three was chosen because it fits the empirical data from a variety of species analyzed by Portnoy and Willson

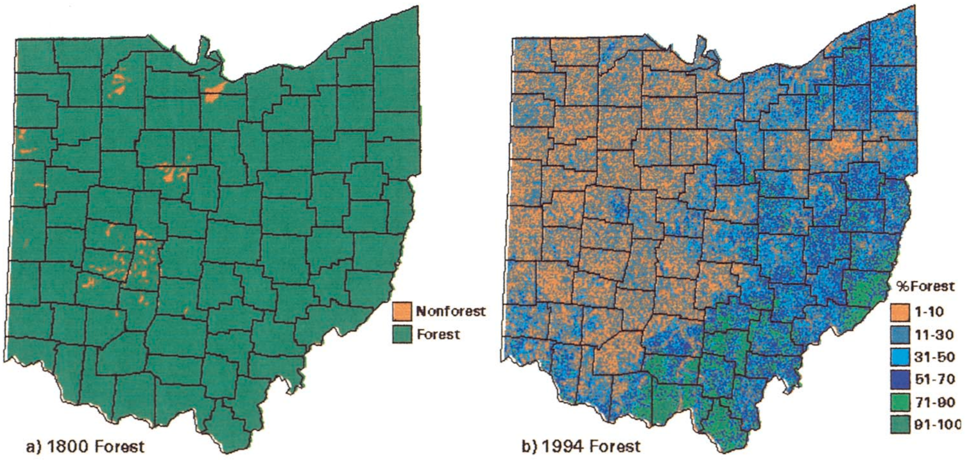


Figure 1. 1800 and current forest abundance in Ohio. **a** 1800 forest abundance is estimated from land survey records for Ohio (Gordon 1969). **b** Current forest abundance is based on TM data with a pixel size of 30 m^2 where all cells classified by Schaal and Motsch (1997) as forested.

(1993). There are several ways by which one may describe the importance of long-distance migration in plant migration. Harper (1977) summarized the results of numerous seed dispersal experiments and found that most experiments fall somewhere between an inverse power and negative exponential functions. Portnoy and Willson (1993) modeled the tails of seed dispersal experiments and found there to be no strong evidence to differentiate between inverse power and negative exponential functions. Schwartz (1993) used both inverse power and negative exponential functions in the original derivation of the model used in this paper and found little difference in that set of scenarios.

Greene and Johnson (1996) assert that the tail of the dispersal curve is best fit by a negative exponential. The exponential curves result in very little long-distance dispersal. Our initial results from these simulation runs, where forest availability varied continuously between 0 and 1, revealed that exponential functions require a very high colonization probability over distances of up to 10 km to ensure a migration rate of 50 km/century. As a result, all cells within 10 km of the species front get colonized as long as forest availability exceeded 0. To make a negative exponential model realistic with respect to past migration events, we needed to incorporate a nonlinear (for example, exponential) function of colonization with forest availability. Although this modification may reflect reality, we have no empirical basis for setting such a function. Initial experimental simulations using exponential and inverse power models suggested that setting colonization as a nonlinear function of forest availability resulted in predictions that were very similar to those generated by modeling dispersal as negative power functions of distance.

Negative power functions also fit many observations of seed density by distance (Portnoy and Willson 1993; Greene and Johnson 1995; Bullock and Clarke 2000) and allow a much higher probability of long-distance dispersal than the negative exponential function. The higher rate of outlier establishment results in more appealing predictions with respect to reflecting our understanding of the pattern of past tree migration and outlier establishment (for example, see Davis and others 1986).

Clark (1998) uses a "fat-tail" distribution to capture long-distance dispersal events in tree migrations. Clark's method sorts seeds into two pools. The short-distance pool fits a negative exponential shape of seed density across distance. The pool of seeds that disperse long distances are lumped into a group that is relatively distance invariant where the probability remains low out to some arbitrary maximum distance. Clark analyzes the behavior of such functions to determine that historical migration rates can be supported by as little as 5% of seeds entering the long-distance pool of propagules. Our model is slightly more conservative than that of Clark (1998) with respect to the proportion of propagules dispersing distances greater than 1 km, but it allows propagules to disperse longer distances by setting no maximum distance. Our migration simulations were sufficiently "fat-tailed" to result in outlier formation and appear to match well with our understanding of outlier formation in other tree species. Further, our model is likely to be optimistic with respect to long-distance colonization because of our use of an instantaneous climatic change rather than a gradual warming.

Once the probability of colonization for an unoccupied cell is calculated, a random number is drawn from an even distribution (0–1). If the random number is less than or equal to the colonization probability, then the cell is colonized.

As a result of these rules, cells of high forest availability in close proximity to other occupied cells may have colonization probabilities greater than 1. These cells are colonized by definition. Cells far from the front of occupied cells have low colonization probabilities.

Life history attributes ought to have strong effects on dispersal ability (Brubaker 1986; Clark 1998). Despite this, animal-dispersed and wind-dispersed species are given the same colonization function in our simulations. We do this 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 approximately the same rate (Davis 1981; King and others 1997). Second, Portnoy and Willson (1993) could find no systematic difference between the shapes of curves that best fit animal- and wind-dispersed species. Thus, empirical observations do not indicate differences in seed-dispersal characteristics between these life histories.

Simulation Assumptions

This forecasting model for future tree migration carries several assumptions. Obviously, we adopt the assumption that climate will change as projected. We assume that current climatic limits to tree species distributions have a physiological basis and are fixed. As a result, climatic parameters associated with the distribution limits of species at present are assumed to accurately project the future potential distribution under climatic warming. We assume that forest abundance within cells is linked to colonization probability. We assume no upper limit to the distance propagules may disperse. One could enumerate several additional assumptions (for instance, no changes in dispersal ability based on different disperser abundances or wind speed and direction, no direct effect of increased CO_2 on plant growth that relates to migration potential). Although these may be important assumptions, we chose to restrict our analyses so as to not speculate too broadly on attributes of global change for which there are limited data.

We also adopt additional simplifying rules. Generation time, maximum current abundance, and the number of cells initially occupied are the principal drivers of interspecific differences in migration rate. Each time step of the simulation is one generation in length. Generation time was set by silvicultural data (Table 1). Population sizes (that is, importance values, or IV) were divided by the ratio of the maximum IV and the third quartile of IV, when IV exceeded zero.

Population size of newly colonized cells depended on the initial colonization probability. It was set at one-eighth of the third quartile of IV (for IV greater than 0). In all cases, population size in newly colonized cells was doubled in each generation if the resultant IV was smaller than the third quartile of IV (for IV less than 0); if the third quartile value was reached or exceeded, IV was set to the third quartile value.

Abundance within initially occupied cells was held constant through the course of each simulation. In reality, habitat suitability of currently occupied forest may diminish under global warming. We chose not to incorporate these into our simulations to provide the maximum potential of trees to shift northward in response to warming. Populations in newly colonized cells were not allowed to shrink or go extinct. This simplification enhanced the ability of trees to move through the landscape in our simulations. Finally, the border of Ohio was treated as a "hard" edge. That is, no seed dispersal was allowed from cells outside Ohio. As a result, migration along the border cells is somewhat slowed by having a lower colonization probability by virtue of having fewer neighbor cells from which to draw propagules.

Each species was allowed to migrate though Ohio in 50 replicate simulations for both the 1800 and current vegetation coverages of Ohio. We then summarized the colonization probability for each cell in Ohio as a proportion of the times that this cell was colonized through the replicate simulations. Migration rates were summarized graphically by (a) the total number of cells colonized in each of 10 colonization probability categories, and (b) colonization probability along two transects (20 × 100 km) from each species' initial range boundary outward that typify different amounts of modern forest coverage.

Sensitivity Analysis

A sensitivity analysis was conducted using SHIFT, where we varied key parameters reflecting potential peculiarities associated with the individual life histories of the different species (Table 1). For example, persimmon has a large fleshy fruit that may not disperse well. Thus, we ran a variation of the persimmon simulation where we increased the exponent of the dispersal equation by 0.5 to reduce the amount of long-distance dispersal. To do this, we recalibrated the initial migration through unforested habitat to set a new constant. For Virginia pine, we conducted a variant increasing long-distance dispersal. For southern red oak, we set a maximum migration distance to simulate a limit on the distance a bird may fly carrying a seed. Both 50-km and 20-km dispersal limits were tested. Because the 50-km limit was not substantively different than the basic model, we present the results of just the 20-km maximum dispersal limit runs. For persimmon, we also ran a simulation in which we doubled the importance value of the existing populations. This simulates the effect of a species that has an artificially high abundance in the modern landscape. For this variant, we did not recalibrate C, the calibration coefficient. These alternative runs were a means to test the sensitivity of the model to variation in the details of the migration aspect of the simulation.

RESULTS

Colonization Probability

To calculate an exact rate of migration in such simulations, one must choose an occupancy probability to define as the range boundary. For purposes of this paper, we arbitrarily define the newly occupied range as those lands where the probability of colonization exceeds 5%. Using transects periodically distributed across the range boundary in a fully forested condition, we find that our calibration of migration resulted in a greater than 5% occupancy probability at 50 km for most species in most transects (Figures 2 a, c, and 3 a, c). Graphically depicting colonization probabilities throughout Ohio shows that our models allow the colonization of virtually any forested location within Ohio over a 100-year period given a climatic release. These figures present colonization expressed as a probability of occupancy. The 1800 migration models predict that the colonization probabilities within 5–12 km of the initial species front are typically high (more than 40%). These maps indicate that most species will nearly fully occupy potential habitat patches a few kilometers from the current distribution boundary after a century. Probabilities of colonization from 12 to 25 km outside the current species boundary are lower (typically 10%–40%); outside 50 km, they are generally low (less than 5%). The probabilities of reaching the far northern end of Ohio within 100 years are, as expected, very low (less than 2%).

The modern (1994) migration scenario is significantly different from the 1800. The average migration rate, based on a 5% occupancy criterion, is less than 20 km/century across species and transects (Figures 2 b, d, and 3b, d). Typically, migration is less than 5 km/century in the western (that is, highly agricultural) portion of each species' distribution (Figure 4). The spatial pattern of colonization probabilities suggests that future migrations are likely to be similar across species. All species show a propensity to migrate at a faster rate along the heavily forested corridor in southeastern Ohio.

Although a visual assessment of migration is powerful, a comparative analysis of migration potential between the modern scenario and the 1800 one is possible by tabulating, across our series of transects, the mean colonization probability for all cells at a given distance from the initial species boundary. Plotting colonization probability by distance, we observe the effect of habitat loss on potential migration rate, based on the rules established for these simulations (Figure 4). We observe from the colonization probabilities within transects that range boundaries were fairly abrupt. That is, the mean colonization probability within both the 1800 and the 1994 landscapes drops precipitously with distance. We also observe that simulations using 1994 habitat availability yield considerably lower probabilities of colonization and flatter curves of mean colonization probability vs distance. Nonetheless, spatial differences in colonization rate in 1800 habitats are generally maintained in the 1994 habitat availability model. This is because the eastern third of the state was more forested prior to settlement and remains so. In most cases, the 1994 colonization probabilities are less than 10% that of 1800 colonization probabilities at distances up to 50 km from the initial range boundary in the western portion of Ohio, while probabilities fall to between 10% and 90% in eastern Ohio, depending on the distance and species (Table 2).

Sensitivity Analysis

The final point to note in our simulation results is that the model parameters have a strong effect on simulations conducted using 1800 habitat availability (as one would expect), whereas they have markedly smaller effects on migration rates under 1994 habitat availabilities. Increasing the dispersal exponent decreases long-distance dispersal probabilities, while decreasing the exponent increases them. Changing the dispersal exponent had strong effects on migration through the forested 1800 landscape, resulting in changes to the rate of migration. However, these differences did not translate to increased modern dispersal (Figure 5).

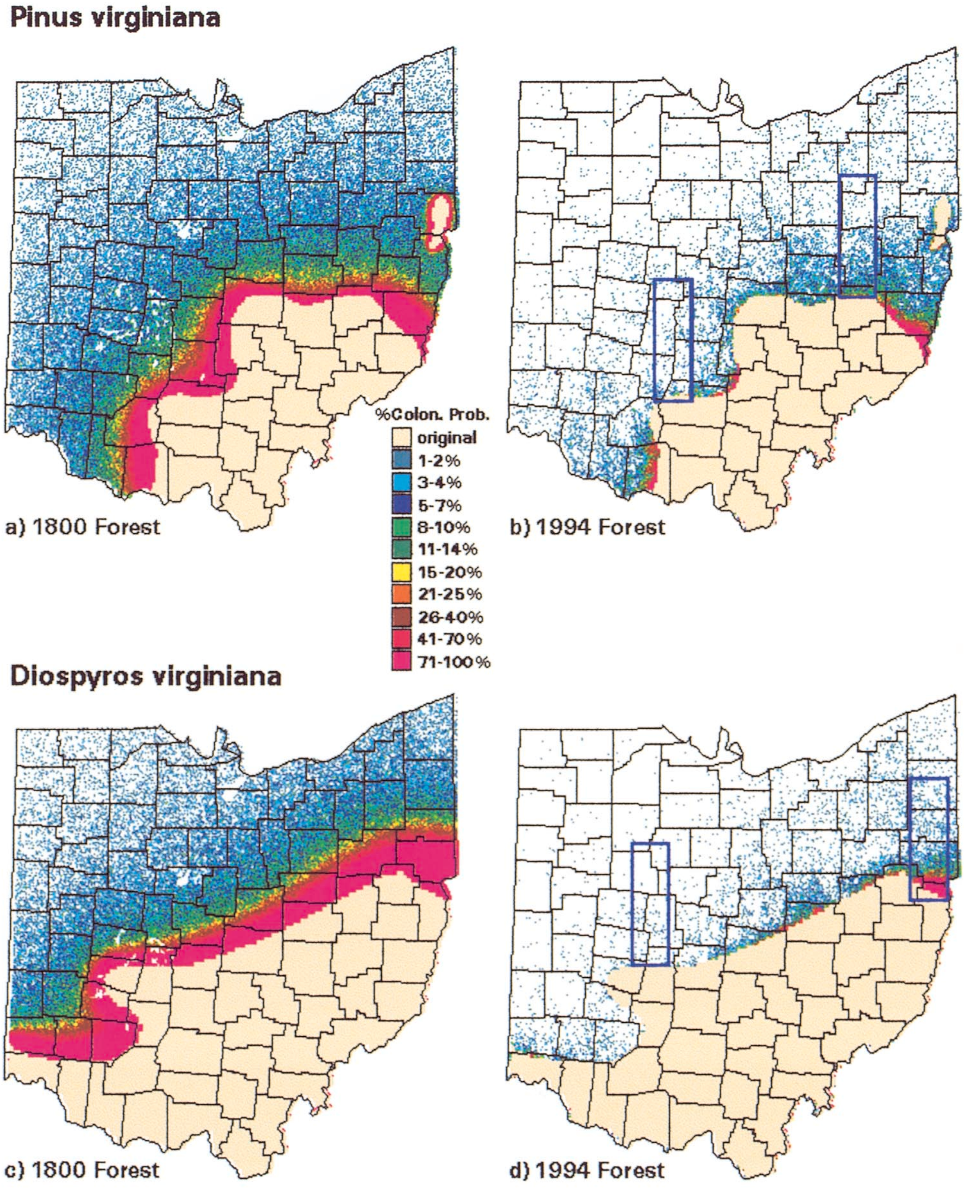


Figure 2. Mean colonization plotted against distance for **a** Virginia pine (*Pinus virginiana*) under 1800 forest conditions, **b** Virginia pine under modern forest conditions, **c** southern red oak (*Quercus faclata* var. *falcata*) under 1800 forest conditions, and **d** southern red oak under modern forest conditions. Blue boxes (50 × 20 km) indicate the position of transects for detailed analysis of migration rates.

Similarly, capping maximum dispersal distance has a relatively strong effect on colonization probabilities at the longer distances from the initial range boundary, but not much effect within the expected migration distance of less than 10–15 km (Figure 4d). Finally, doubling the initial importance value of persimmon for 1994 had a strong effect on estimates of colonization probabilities in the modern landscape (Figure 5b).

These results indicate that current forest abundance has the strongest effect on projected migration, followed by the effect of species abundance (that is, importance value). These results are reassuring because of the uncertainty over the exact shape of the curve that best describes long-distance dispersal in trees. These simulations suggest that habitat availability drives predictions of future migration potential. Exact parameter choice may not matter all that much as long as there is some relatively sharp dropoff in dispersal with distance.

DISCUSSION

These forecasts of future tree migration are speculative for several reasons. First, the magnitude and pattern of future climate remains uncertain. Models of climate change are likely to continue to change, and actual climate may only loosely track these projections. Second, climatic change models do not explicitly track some attributes of climate and the

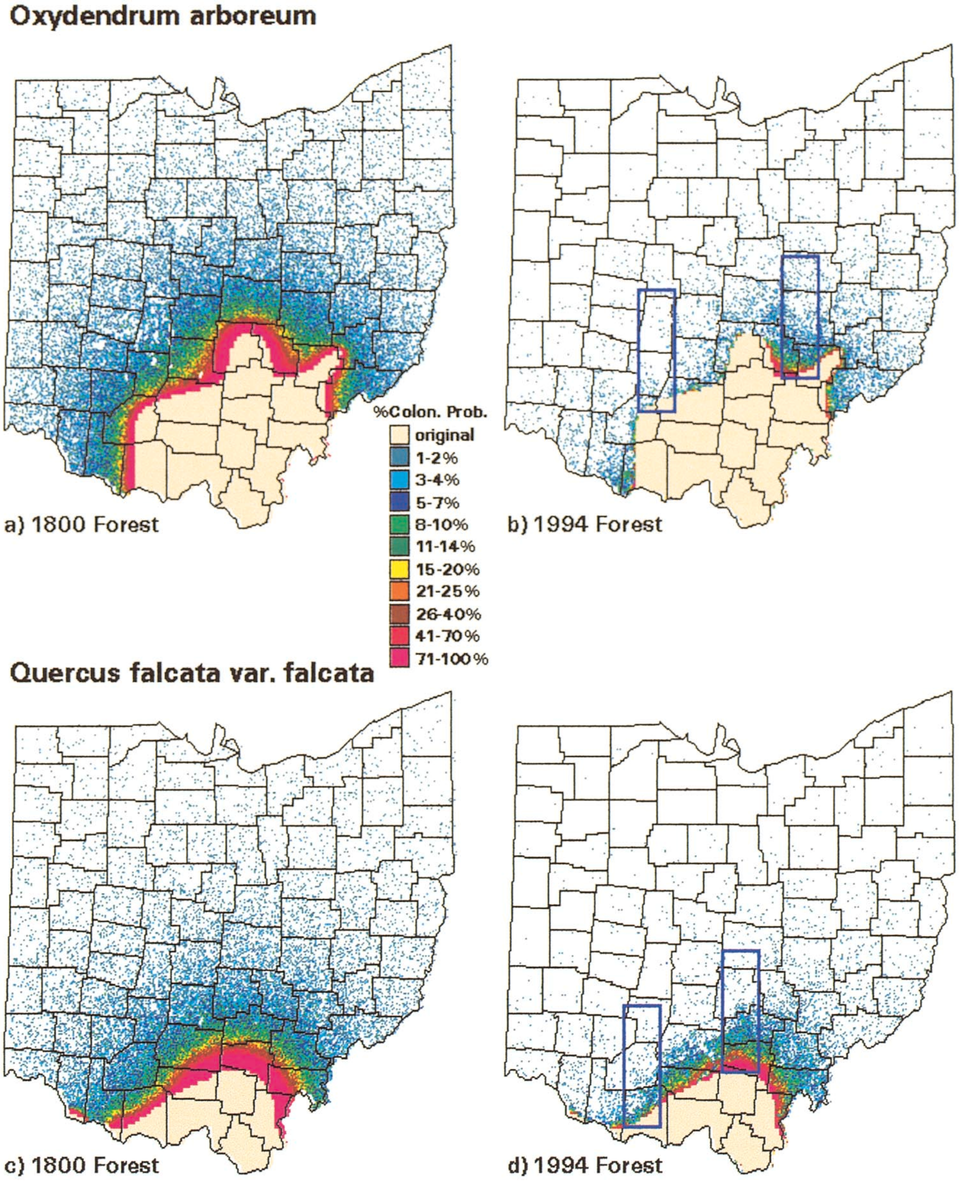
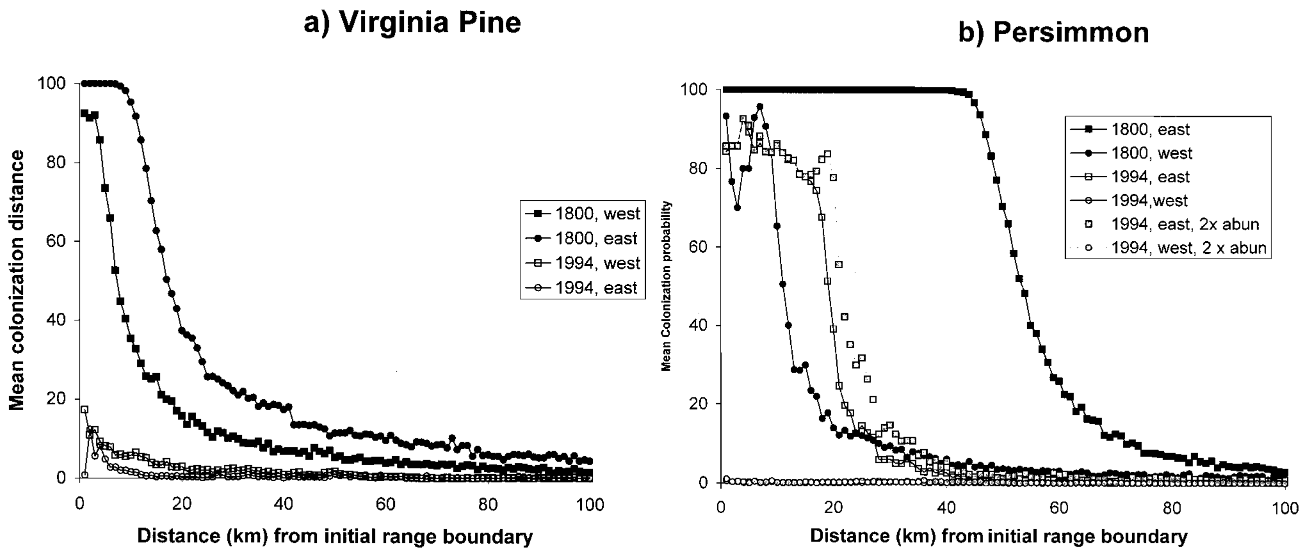


Figure 3. Mean colonization plotted against distance for **a** sourwood (*Oxydendron arboreum*) under 1800 forest conditions, **b** sourwood under modern forest conditions, **c** persimmon (*Diospyros virginiana*) under 1800 forest conditions, and **d** persimmon under modern forest conditions. Blue boxes (50 × 20 km) indicate the position of transects for detailed analysis of migration rates.

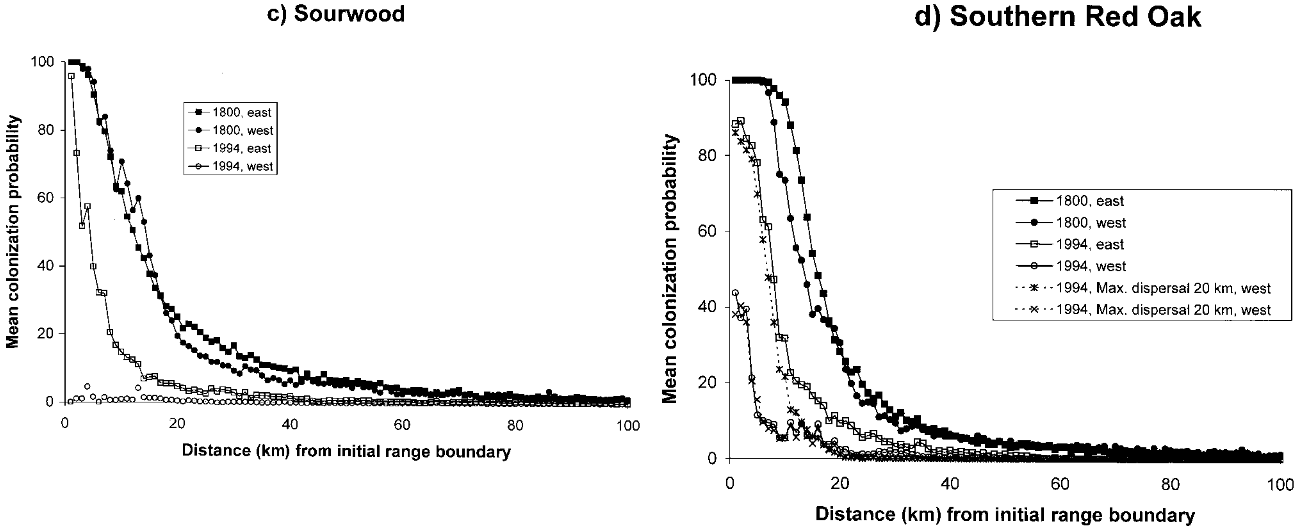
environment that may be critical in determining distribution limits. For example, model outputs generally predict mean temperatures and precipitation. Realistic models may require predicting the distribution of extremes in climate such as minimum winter low temperatures or growing season precipitation during a drought year (Woodward 1987). These parameters are much harder to predict. In addition, climate change is likely to have a significant impact on natural disturbance rates (for example, fire, drought, ice storms, floods) (reviewed in Hanson and others 2001. Disturbances such as fire and drought are expected to increase (Hanson and Weltzin 2000; Flannigan and others 2000), but wind storm damage is too uncertain to predict (see, for example, Peterson 2000; Lugo 2000; Irland 2000). Increased disturbance rates are likely to increase canopy turnover and have the potential to aid migration. Third, we assume an abrupt change in climate that releases trees from current climatic restrictions on their growth. Gradual warming would further slow migration potential. Nor, as we model here, are all forests within Ohio suitable for all species of trees. Thus, our migration projections may be optimistic.

In addition to rates and patterns of predicted vs actual future climate change, we have a relatively poor understanding of long-distance dispersal events in plants (Bullock and Clarke 2000). If we extrapolate from curves generated from empirical observations of seed dispersal curves measured over relatively short distances (for example, less than



a) Virginia Pine

b) Persimmon



c) Sourwood

d) Southern Red Oak

Figure 4. Colonization probabilities for SHIFT simulations plotted as a function of distance for each of the four target tree species migrating through the Ohio landscape under 1800 (*closed symbols*) and modern (*open symbols*) forest conditions. Target transects are identified by different symbol shapes: squares = west and circles = east. Mean colonization values are based on 50 replicate simulation runs. For each transect for each species, we observe a very steep decrease in colonization probability in both the modern and 1800 simulations but far lower colonization probabilities in simulations using modern habitat availability.

100 m), then we would predict that trees could not have migrated as fast as we know that they historically did (Greene and Johnson 1995). Pushing the boundaries of this empirical data, Greene and Johnson (1997) have estimated that the wind events required to carry a pine seedling 1 km in southern Ontario happen with a frequency of about 1 min each decade.

In contrast, if we assume that we can segregate seed dispersal into one curve over a measurable distance and a separate curve that describes just that portion of seeds that move long distance (*sensu* Clark 1998; Clark and others 1998), then we have very little empirical data with which to work. We can estimate the proportion of seeds that leave an area via long-distance dispersal (Clark and others 1999), but we do not know where they go. Thus, we are forced to make some educated guesses regarding the steepness of this curve. This is integral in predicting future migration rates and there is no empirical evidence to exclude curves that would support an effectively infinite rate of migration (Clark 1998). However, we do not observe migration rates this high during the Holocene.

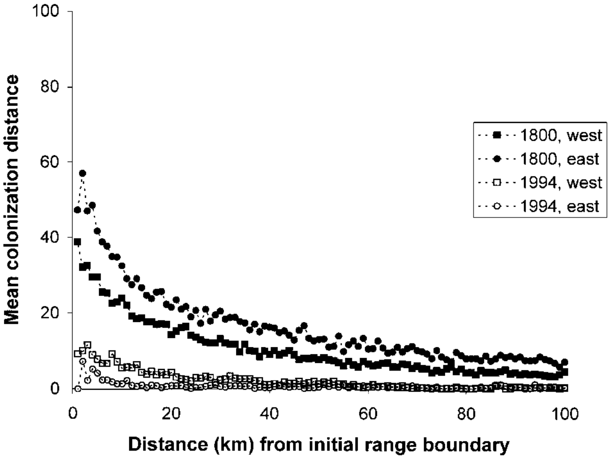
Table 2. Degree to which the Simulated Modern Colonization Probability Saturates the 1800 Colonization Probability, at Varying Distances from the Starting Range Limit, for Four Tree Species Moving through Ohio, Expressed as a Percentage within Transects Sampled across the Species Boundary

Species	Distance (km)	East	West
Virginia pine	5	11.0	4.7
	10	16.1	1.6
	20	18.5	0.8
	50	32.1	9.6
S. red oak	5	78.5	11.4
	10	33.7	7.3
	20	33.1	7.9
	50	36.8	7.7
Sourwood	5	44.0	1.6
	10	23.7	1.3
	20	18.7	2.6
	50	13.2	0
Persimmon	5	89.2	0.4
	10	86.2	0.2
	20	39.1	0
	50	0.4	2.7

With these empirical data, we can legitimately set virtually any set of expectations for long-distance dispersal. Our approach was to use empirical seed shadow data and to calibrate it to match historical migration rates. Owing to its simplicity, this model carries relatively few unwieldy assumptions (for example, seed recruitment rates, adult mortality rates, maximum dispersal distances, fractions of seed rains falling into a long-distance seed pool).

Our model results suggest that the primary factor that significantly affects rates of future tree migration is the availability of forested habitat. For the purposes of these predictions, we assumed forest abundance and distribution to be fixed. However, we realize that forest distribution and abundance have fluctuated widely through time, and there is no reason to expect them to remain constant into the future. Historically, Ohio was 95% forested in 1800, about 12% in 1900, and about 30% in 2000 (Griffith and others 1993). Competing forces of agriculture, forestry, urbanization, and recreation will have spatially varying and uncertain effects over the next 100 years. Forest cover and volume has been increasing over much of the eastern United States for the past several decades (Powell and others 1993). Despite these past patterns, we find no acceptable model for predicting rates and patterns of forest change in the future.

a) Virginia Pine



b) Persimmon

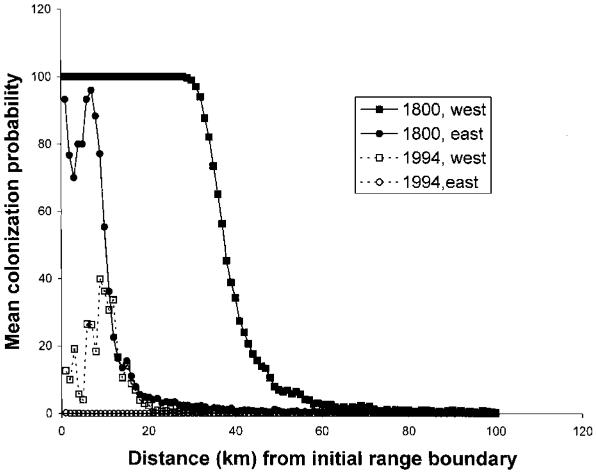


Figure 5. Results of simulations testing model sensitivity by varying model parameters. Mean colonization is plotted against distance for (**a**) Virginia pine (*Pinus virginiana*), and (**b**) persimmon (*Diospyros virginiana*) for 1800 (*closed symbols*) and modern (*open symbols*) SHIFT simulations in each of the target transects. Target transects are identified by different symbol shapes: squares = west and circles = east. Mean colonization values are based on 50 replicate simulation runs. Reducing the dispersal exponent from 3 to 2.5 resulted in increased long-distance dispersal for Virginia pine. This resulted in an increased likelihood of long-distance colonization under 1800 conditions but little change of northward shift using modern habitat availability. Increasing dispersal coefficient from 3 to 3.5 for persimmon resulted in an even sharper dropoff in colonization probability with distance under 1800 conditions, but it had little effect on modern dispersal. Doubling the modern abundance of persimmon resulted in increased migration potential for the species.

For individual species, the types of forests and how they are managed may have critical and driving roles in determining colonization success. If plantations of pine, for example, were heavily managed, including the exclusion of potential migrating species, colonization success and subsequent migration rates would be reduced. On the other hand, management could significantly increase migration rates by planting particularly threatened species in distant locations to serve as "long-distance events". Management could therefore be directed to encourage change to the new species and communities more appropriate for the new environments. Establishing and maintaining major forest corridors could accelerate species migration. For example, the Appalachian corridor, a major forested region including southeastern Ohio, could be closely monitored and periodically "assisted" to migrate the species most threatened by global warming.

The model forecasts presented here must be regarded as hypotheses for what may happen over the course of 100 years following warming. There is considerable uncertainty in these projections. Nonetheless, these results point to several important conclusions. First, the extent of migration may be so low as to preclude detection based on our current limited understanding of specific range boundaries. If we cannot define a species boundary within 5 km—and for most trees species we cannot—then we are unlikely to detect northward migration of that boundary. This is an important conclusion relative to how we monitor for responses of plant communities to climatic change. If we would like to detect change, then we must monitor for change at the appropriate scale. Unfortunately, this scale may be very fine, making it difficult to monitor accurately.

Attempts to observe migration at the appropriate scale are critical because, in the absence of detectable migration, we may be tempted to suggest that changes in CO_2 are somehow compensating for increased warming (for example, increased water use efficiency). For example, Hättenschwiler and Körner (1995) looked specifically at an elevational ecotone and could find no evidence of upslope tree migration in the Alps despite evidence of local warming. These authors concluded that the current distribution limit is partially determined by biotic interactions such that warming has resulted in no upslope distribution shift. The direct effects of CO_2 on tree growth are projected to be substantial (see for example, Melillo and others 1996). We do not incorporate these effects into our models because they also remain somewhat speculative and vary across species. Nevertheless, if species are migrating as fast as possible and we do not detect it, we are likely to come to erroneous conclusions about the net effect of CO_2 increase.

Second, if trees fail to migrate northward at rates commensurate with climate change, then it becomes important to determine the rate that species' southern distribution limits may retract in response to warming. For narrowly distributed species, a large degree of warming may result in a future climatic distribution that is wholly discontinuous with the current distributions (Schwartz 1993). Failure to migrate would thus result in a potential extinction risk for these species. In a more general sense, the slow northward expansion of species ranges, accompanied by the relatively swift northward retraction of southern distribution boundaries (if we assume range retraction is dependent upon climate and species physiology), may result in relatively rapid changes to forest composition. In contrast, MacArthur (1972) first asserted that southern range boundaries are more likely controlled by competition than by environmental factors. If this were true, then we would expect extirpations to be slower than the pace of the northern range expansions of competitors. This would reduce the potential extinction problem substantially. Our forecasts do not consider interspecific competition at any point during model runs. This could substantially slow expansion potential as well as the range retraction rate. We do not as yet have a good model that incorporates the full spectrum of factors (that is, competition, disturbance, climate, management, herbivores, and so on) that could drive altered forest structure and dynamics.

For example, our projections with respect to animal-dispersed species are particularly prone to uncertainty. One can imagine that birds flying between forest patches and carrying seeds would move further in landscapes where forest availability is low. Longer movement rates may thus increase migration potential. Some animal dispersers may also be more common in the modern landscape than under 1800 conditions. As a result, average seed movement could increase for certain types of animal-dispersed species. We do not have an empirical basis for incorporating this aspect of disperser behavior into our model, so we did not venture a guess. Nonetheless, dispersal mechanism is a potentially important attribute to consider for predicting specific migration responses to warming.

In examining the specific outcomes of our models, we can discern a few attributes that provide important lessons for forecasting forest change. First, we observe an acceleration effect of trees migrating across the landscape. In other words, a few outlying colonization events help to drive migration to faster and faster rates. This observation is common to migration models driven by long-distance dispersal (see, for example, Clark 1998). We calibrated our migration runs so as to reach a 50-km migration window over 100 years. If we were to run our models for longer periods over a larger landscape, these baseline migration rates would increase substantially. Similarly, if we presume current distributions to be static as a result of trees being in climatic equilibrium, then we would predict that initial migration rates would be slow relative to potential maximum migration rates. In this sense, our model forecasts may be overly optimistic by driving baseline migration rates to targeted final rates in just 100 years.

Finally, perhaps the most important observation to emerge from these migration scenarios is that sensitivity analysis (that is, increased and decreased long-distance seed dispersal, doubled initial abundance, and truncated maximum dispersal distances) showed much stronger effects on projected migration rates in simulations of 1800 forest availability simulations than migration rates in the 1994 forest availability simulations. For example, flattening the seed dispersal curve increases the potential for long-distance dispersal and increases the migration rate (as for Virginia pine). The shape of the distance–dispersal probability curve altered migration rates in the 1800 scenario but not in the 1994 landscape. This insensitivity of migration to changes in the distance coefficient suggests that low forest availability is a very strong inhibitor of tree migration. Thus, we can expect forest fragmentation to severely decrease potential migration rates.

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