

Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change

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Abstract

Climate change impacts tree species differentially by exerting unique pressures and altering their suitable habitats. We previously predicted these changes in suitable habitat for current and future climates using a species habitat model (DISTRIB) in the eastern United States. Based on the accuracy of the model, the species assemblages should eventually reflect the new quasi-equilibrium suitable habitats (~2100) after accounting for the lag in colonization. However, it is an open question if and when these newly suitable habitats will be colonized under current fragmented landscapes and realistic migration rates. To evaluate this, we used a spatially explicit cell-based model (SHIFT) that estimates colonization potentials under current fragmented habitats and several estimates of historical migration rates at a 1 km resolution. Computation time, which was previously the biggest constraint, was overcome by a novel application of convolution and Fast Fourier Transforms. SHIFT outputs, when intersected with future suitable habitats predicted by DISTRIB, allow assessment of colonization potential under future climates. In this article, we show how our approach can be used to screen multiple tree species for their colonization potentials under climate change. In particular, we use the DISTRIB and SHIFT models in combination to assess if the future dominant forest types in the north will really be dominated by oaks, as modelled via DISTRIB. Even under optimistic scenarios, we conclude that only a small fraction of the suitable habitats of oaks predicted by DISTRIB is likely to be occupied within 100 years, and this will be concentrated in the first 10–20 km from the current boundary. We also show how DISTRIB and SHIFT can be used to evaluate the potential for assisted migration of vulnerable tree species, and discuss the dynamics of colonization at range limits.

Keywords: cell-based simulation model, convolution, eastern United States, fast fourier transforms, long-distance dispersal, oak forest types, range-limit dynamics, tree species migration

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Introduction

Rapid climate change is forecast by the Intergovernmental Panel on Climate Change (IPCC, 2007) for all major biomes on earth. The estimates vary from ~2 °C by the year 2100 under a conservative carbon emission scenario (B1) up to ~4 °C under our current fossil fuel intensive pathway (A1FI). The implications of such a rapid change for the earth's biota can be staggering. A reassortment of suitable habitats and creation of novel ones are expected for various plant and animal species (Williams & Jackson, 2007). However, species range limits are dynamic and subject to local, regional and global processes that show complex interplay between ecological and evolutionary processes. The crucial

question for tree species, the subject of our study, is whether they adapt, migrate, or go extinct under rapid climate change (Aitken *et al.*, 2008). Historically, tree species niches have remained relatively constant in the face of historical climatic change (niche conservatism), causing them to migrate in line with their native climatic-niches, although adaptive changes have co-occurred as evidenced by changes in population's fitness optimum throughout the species' range (Jackson & Overpeck, 2000; Davis & Shaw, 2001; Wiens & Graham, 2005). Evidences of local adaptations, however, do not point to change in the absolute climate tolerances of species (Parmesan, 2006).

Trees are capable of a wide range of local adaptation via phenotypic plasticity despite low evolutionary rates and are sufficiently long lived to have survived rare and extreme events at various points throughout their evolutionary history; these characteristics partly explain

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their ecological success. Their high genetic variability and abundant fecundity enable extensive gene flow and are therefore capable of rapid microevolution – but low levels of mutation, nucleotide substitution, and speciation rates allow only slow rates of macroevolution (Petit *et al.*, 2004; Petit & Hampe, 2006). Genetic constraints on adaptation and impediment to both gene flow and dispersal by current landscape fragmentation could pose a twin threat to some tree species in the era of rapid climate change. Also, because tree species are subject to differential (perhaps novel) environments and interspecific interactions, the adaptive expression of phenotypic plasticity can be curtailed via ecological constraints (Valladares *et al.*, 2007).

Reid's paradox (Clark *et al.*, 1998; Phillips *et al.*, 2008), which noted the apparent disparity between the relatively slow dispersal capacity of trees and their rapid spread in the early Holocene era, has been a challenge for several generations of climate change and vegetation ecologists. Recently, there have been revisions in the dispersal estimates due to the role of ice-free microrefugia (retention of low-density founder populations) during the Holocene. These refugia appear to have played a larger role in tree species advancing without the need for rapid migration speeds that are needed to reconcile pollen data with actual distributions (McLachlan & Clark, 2004; McLachlan *et al.*, 2005; Anderson *et al.*, 2006; Parducci *et al.*, 2012). McLachlan *et al.*, (2005) explain the discrepancy between the pollen record and current boundaries as a result of local dispersal by isolated persisting populations (refugia) during the early Holocene and migration rates may not have exceeded 10 km/century for many species (Pearson, 2006; Loarie *et al.*, 2009), although other species could have far exceeded this rate in certain periods due to favorable conditions (Davis & Shaw, 2001; Cole, 2010).

In spite of the disparities in historical migration rates, there is widespread recognition of the role of long-distance dispersal (LDD) in the formation of current range boundaries of tree species (Higgins & Richardson, 1999; Hardy, 2009). Traditionally, phenomenological models that use various leptokurtic (fat-tailed) probability density distributions, or combinations of them (Kot *et al.*, 1996; Clark *et al.*, 1998, 1999; Levin *et al.*, 2003), have been used to fit broad-scale distribution patterns – ignoring details of the dispersal process. More recently, mechanistic models that incorporate parameters affecting seed dispersal, and define their effects mathematically, have been used to predict (rather than fit) the dispersal curve independently of the data (Katul *et al.*, 2005; Nathan *et al.*, 2008, 2011). The mechanistic approach, while a promising development, has limitations, including the necessity of simplifying assump-

tions to make it mathematically tractable, the need for large amounts of empirical data to estimate parameters, and the current and future uncertainties of the estimated parameters. They also require extensive and intensive simulations of wind statistics which would be very difficult to obtain for multiple species, thus suggesting the need for a simpler approach.

Material and methods

SHIFT background

One of the criticisms of niche-based species distribution models is that modelled *suitable habitats* are often used to mistakenly depict *actual colonization and establishment* (Botkin *et al.*, 2007; Thuiller *et al.*, 2008). Not all habitats available in the future for the trees will result in colonization and establishment because of time lags involved, intra and interspecies interactions, and other ecological constraints. The DISTRIB model that we built previously, predicts and maps current and future-climate tree habitats for 134 tree species in the eastern United States via changes in relative importance values (IV) (Prasad *et al.*, 2006; Iverson *et al.*, 2008). To address the colonization potential of these suitable habitats, due to species dispersal and migration, we employ the SHIFT model.

SHIFT is a lightly parameterized model that uses historical tree migration rates as a backdrop for estimating future colonizations. It makes use of the relative importance of source and sink strengths at range boundaries to enable colonizations. Sink cells are forested habitats beyond the current range into which the species could migrate. The source strength is a function of both the propagule production and dispersal of individual species. In our case, we use the relative abundance and frequency of the species inside the current range boundary to define the source strength. Sinks are typically fragmented forests or woodlots that become available as suitable habitats under current and future climates.

Model data preparation

The SHIFT model simulates LDD via a fat-tailed inverse power function under current fragmented landscapes (Schwartz, 1993; Iverson *et al.*, 2004). It can evaluate multiple species in a macro-ecological context, under a range of paleoecological rates of spread in current fragmented landscapes using simple but robust techniques that do not rely on many parameters. SHIFT calculates the likelihood of colonization based on the abundance of the species and habitat quality of 1 km² cells in the eastern United States. Each cell informs the model of the location, initial abundance of the species, and the habitat quality (principally by forest or non forest).

The source region of the species was defined by the range boundary created by E. Little from multiple sources in the late 1960s to early 1970s (Little, 1971), updated to reflect current abundance based on the USDA Forest Service's Forest Inventory and Analysis (FIA) data (Smith, 2002; Woudenberg *et al.*, 2010). To fill the source region with species abundance, we

used a combination approach. To inform the cells within the source region of the actual distribution of abundance, we used importance values (IVs), a relative measure of abundance based on the basal area and number of stems of the overstory and understory trees, from the over 100 000 plots of FIA data (Iverson *et al.*, 2008). However, there were still areas within the source region that did not have abundance estimated from FIA because FIA obviously does not sample extensively in all zones (especially with few forests – like the Corn Belt of the Midwestern US). To fill some of these gaps, we used the DISTRIB model which predicts the IVs (a surrogate of suitable habitats) of the tree species based on climate, soil, and landscape predictors (Prasad *et al.*, 2006; Iverson *et al.*, 2008). Filling gaps using modelled IVs will add some uncertainty, but is much more realistic than leaving them as unoccupied, or filling them artificially with a low value of IV. The modelled IVs correspond to the suitable habitat of the species for SHIFT modelling. However, because the DISTRIB model can predict suitable habitats in regions not currently having vegetation, we filtered out cells with very low amounts of vegetation using United States Geological Survey's (USGS), 2006 National Land Cover Data (NLCD), (originally based on 30 m resolution). Even with the DISTRIB filling some gaps, there were still areas within the source boundary that did not have abundance values. We assumed that these are most likely to be areas where the species is absent.

The habitat quality of cells beyond the current boundary (sinks) is based on the NLCD, from which we classify the 1 km² cell as forest or non forest based on the analysis of the percent forest in each cell. We generously define a cell as a colonizable sink if it were 10% or more forested. Colonization of initially unoccupied cells is estimated as a function of recipient cell forest availability and the sum of the likelihood of each occupied cell sending a propagule to that cell. For each cell outside the current occupied boundary, the model estimates the likelihood that each unoccupied cell will become colonized over a period of 100 years (which depends on the number of generations the species requires to achieve 100 years). SHIFT is a 'fat-tailed' dispersal model that allows rare long-distance dispersal events up to 500 km beyond the current distribution boundary and assumes the release of climatic restrictions to tree growth. Although the 500 km is arguably an overly generous window where the colonization can occur, the inverse power function makes the likelihood of colonization decay rapidly from the species front. We use the 500 km window to account for those rare, long-dispersal events over historical periods that can potentially seed colonizations far from the source.

Our approach uses historical information on rates of past migration events as a guide for future potential migration. Our framework has the advantage of taking into account the structure of the landscape, via fragmentation of habitat quality, which can influence both demography and dispersal distances. In contrast, phenomenological and mechanistic dispersion kernel-based models normally ignore landscape structure, or use a very simple heterogeneous landscape consisting of alternating suitable/unsuitable patches, for mathematical tractability (With, 2002; Kawasaki & Shigesada, 2007;

Samia & Lutscher, 2010). This is an important consideration because even though extant species did not go extinct during rapid climate fluctuations in the past, it may no longer hold true under current fragmented landscapes (Lyford *et al.*, 2003; Hof *et al.*, 2011).

SHIFT model

SHIFT calculates the likelihood of an unoccupied cell becoming colonized during each generation (one model iteration), as a function of habitat quality (in occupied cells and potentially future occupied cells), abundance of the species, and a search-distance function as follows:

$$P_{colonize}(i,j) = Q(i,j) \times \sum_k \sum_n \left(Q(k,n) \times F(k,n) \times \frac{C}{\left(\sqrt{(i-k)^2 + (j-n)^2} \right)^x} \right)$$

where $P_{colonize}(i,j)$ is the likelihood of an unoccupied cell being colonized; $Q(i,j)$ and $Q(k,n)$ are habitat quality of unoccupied cell (i,j) and occupied cell (k,n) respectively, (based on the percentage of forest cover of each 1 km² cell according to the NLCD landcover map; $F(k,n)$, an abundance parameter, is the current estimated importance value (IV) for the migrating species in the occupied cell (k,n); $D(i,j;k,n)$, represented by $\left(\sqrt{(i-k)^2 + (j-n)^2} \right)^x$ is the distance between unoccupied cell (i,j) and an occupied cell (k,n) within the search-window distance; x is the dispersal component; and C is a calibration constant. The likelihood of colonization for each unoccupied cell is summed across all n occupied cells at each generation. To add stochasticity, a random number (RN) is drawn from an even distribution (0–1) and compared with the likelihood of colonization to determine if the cell will get colonized (i.e., if $RN \leq P$). The value of C is derived independently for each species through trial runs to achieve migration rates ranging from approximately <25 to >100 km per century (depending on criteria of model runs) of that species under high forest availability (80% cover, representing nearly fully forested conditions, which more closely approximate Holocene conditions), but with the current level of species abundance. Even though 100 km/century is the upper end of observed Holocene migration rates among trees migrating into forested environments (Davis, 1981; Woodall *et al.*, 2009), we include the range of ~25–100 km/century to incorporate other suggested estimates based on species and environmental variations (McLachlan *et al.*, 2005; Cole, 2010). The value of x , the dispersal exponent, determines the rate at which seed dispersal declines with distance. As an exponent of $D(i,j;k,n)$ in the denominator, x 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 simulations reported here, we use a value of $x = 3$ because it fits empirical data (Portnoy &

Willson, 1993) and we vary the migration rate as a function of the calibration constant C to avoid confounding the two factors. The singularity at the origin which is a problem with inverse power functions has no effect because a cell cannot colonize itself. Generation time equivalent to 100 years of migration varied with species (for the four oaks in this study, it is three generations). Each 100 year run was replicated 100 times so that each run corresponded to a 1% chance of colonization.

One major issue with our previous attempts at computing this algorithm was that it was too slow to implement for multiple species under a range of historical migration rates. We address this issue using a very different mathematical approach borrowed from digital image processing techniques.

The computationally intensive part of the calculation is the double sum in the above equation. Defining this

$$f(k, n) = Q(k, n) \times F(k, n)$$

and

$$g(k, n) = \frac{C}{\left(\sqrt{(k)^2 + (n)^2}\right)^x}$$

we can write the double sum, as calculated for $P_{colonize}(i, j)$, as

$$h(i, j) = \sum_k \sum_n f(k, n) \times g(i - k, j - n)$$

This construct is a two-dimensional convolution, a technique used routinely in digital image processing. Our grid can be processed as an image, with each grid cell as one pixel in the image. The brightness of each pixel is proportional to the habitat quality times the species abundance in the cell. Then the likelihood of the species spreading can be viewed as a blurring of that image. Each bright spot in the image spreads out, and fades with distance (called the point spread function or PSF – which is the search-window distance operator). This recognition is crucial to converting the most computationally intensive part of the inverse power function to a convolution model that is solvable using Fast Fourier Transforms (FFT), greatly increasing the algorithmic efficiency.

To implement convolution using FFT, we use the property of the convolution theorem which states that if $f(x)$ and $g(x)$ are two functions with Fourier transforms $F(u)$ and $G(u)$, then the Fourier transform of the convolution $f(x)*g(x)$ is simply the product of the Fourier transforms of the two functions, $F(u)$ and $G(u)$ (Fig. 1). Because multiplication is much simpler than convolution, this property, when implemented via FFT, leads to enormous increase in computation speed for large grids (Bovik, 2009). Evaluating the two-dimensional FFT as a series of $2N$ single dimensional transforms decreases the computation time from $O(n^4)$ (i.e., proportional to n^4 —as in the original implementation of the SHIFT algorithm) to $O[n^2 \log_2(n)]$. This is a significant reduction in speed for large values of n ($\sim 10^7$ cells for the eastern United States).

The SHIFT algorithm was implemented in multithreaded 64-bit MATLAB®, a technical computing environment that has built-in support for FFTs. The FFT version of the SHIFT algorithm is fast, but it requires much more memory than the original implementation because the FFT of the point spread function (PSF) is computed and stored explicitly. Consequently, the memory requirement is the limiting factor instead of CPU computation time (which is handled quite efficiently in the multithreaded MATLAB environment). The memory problem can be readily solved with 64-bit operating systems and large memory (16 GB in our case).

Application of SHIFT for four oak species

The ultimate goal of SHIFT is to assess the colonization potential of the suitable habitats predicted by DISTRIB for 134 tree species in the eastern United States – to obtain a more realistic assessment of how these habitats may be colonized with future climates. This goal has become realizable with the resolution of computational constraints associated with tackling multiple species. However, for the purposes of this article and brevity, we will focus on four oak tree species – black oak (*Quercus velutina*), post oak (*Quercus stellata*), chestnut oak (*Quercus prinus*), and white oak (*Quercus alba*). We chose these four oak species because they are strongly climate driven and

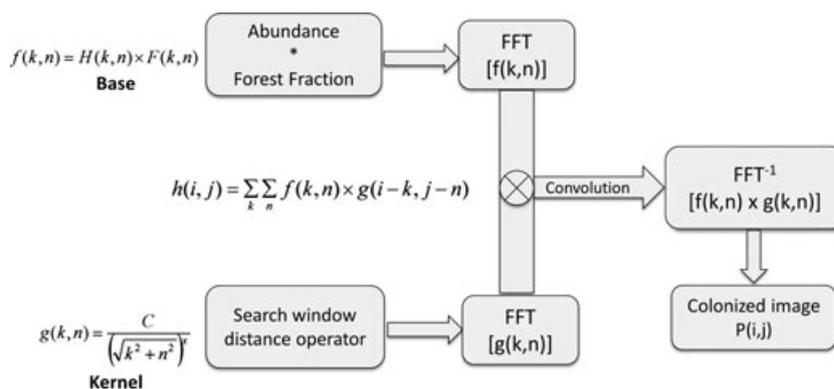


Fig. 1 This schematic shows how the SHIFT model can be expanded to a base and kernel function to make it amenable to convolution. The base represents the abundance and forest fraction multiplication and the kernel represents the search-window distance operator. The base and the kernel can be convoluted using fast Fourier Transform (FFT) and converted back to the original image, making it computationally very efficient.

future warmer climates will have substantial impact on their habitat distribution. The degree to which a species is climate driven was determined by running DISTRIB with: (i) only climate predictors; (ii) full model with climate, soil and landscape predictors, and comparing the variability explained by (i) with (ii). The most strongly climate-driven species was post oak followed by white oak, black oak, and chestnut oak. We also wanted to evaluate how much of the projected large increases in potential oak-dominated forest type habitat in the north and northeast, as predicted by the DISTRIB model (http://www.nrs.fs.fed.us/atlas/tree/ft_summary.html), could be colonized by the end of the century (Iverson *et al.*, 2008, 2011). In this process, we illustrate the utility of our approach in producing various outputs to help understand species dispersal response, evaluate migration corridors for managed relocation, and lay the groundwork for further analysis, and modelling strategies.

Because of uncertainty with respect to historical migration rates in the literature, we chose to target our evaluation for the rate of 50 km/century – although we evaluated the historical ranges from <25 km/century to >100 km/century by varying the calibration constant, *C*, from 0.5 to 4 at steps of 0.5 for a hypothetical historical landscape of 80% forested area in the eastern US (to reconstruct the Holocene vegetation). The rate of 50 km/century is at the middle of the range suggested by the literature: 10 km/century (McLachlan *et al.*, 2005), 30 km/century (Yansa, 2006), 50 km/century (Davis, 1989), and 100 km/century (Woodall *et al.*, 2009; Chen *et al.*, 2011). Recent molecular analyses show that because of glacial refugia effects, the range is likely to be at the lower end (10–25 km/century for most species) (Petit *et al.*, 2003; McLachlan *et al.*, 2005; Svenning & Skov, 2007; Dobrowski, 2011). For our purposes, we chose the rate of 50 km/century to deliberately keep the colonization potential at a higher level (the reasons outlined in the Discussion section). However, the range of eight calibration constants from 0.5 to 4 at steps of 0.5 that we explored accommodates rates of 10–25 km/century at the

lower end to 100–150 km/century at the higher end for most species, and was only possible because of the tremendous speed gains with the convolution-FFT method.

We evaluated the change in colonization likelihoods with distance from the range boundaries using longitudinal and radian transects. The longitudinal transects were created in GIS simply as 4 km wide belts of the geographic longitudes at 0.5 degree intervals (Fig. 2a). The radian transects were created using the mean center of distribution of IVs (the IV-weighted geographic center of each species' distribution, obtained via the 'MeanCenter' command in ArcGIS) and buffered to 4 km wide strips, at five degree angles from each other (Fig. 2b). Because the radian transects emanated from the mean center of distribution, they frequently emerged perpendicular to the actual distribution, while the longitudinal strips occurred strictly in the N–S directions. The portion of each transect in the sink region was used to record the decline of colonization likelihoods with distance and also to select the appropriate calibration values to realize migration rates of 50 km/century.

Results

Assessment of colonization potentials for four oaks

To avoid manually picking the colonization constant corresponding to migration of 50 km/century via tedious map inspection and measurement, we constructed series of graphs (Fig. 3) that show the mean colonization plotted against the transect distances from Little's boundary at various calibration constants. We used a loess smoother (a locally weighted polynomial regression) to fit the observations and a horizontal line at 5% colonization likelihood to determine the migration distance based on where the line intersects the loess curve. The value of the calibration constant was noted for approximately 50 km distance on the graph



Fig. 2 (a) Longitudinal transect bands buffered to 4 km wide strips at an interval of 0.5 degree. The core area (gray) is Little's boundary for post oak (*Quercus stellata*). (b) Radian transects from the mean center of distribution of post oak (*Quercus stellata*) importance value distribution. The transects are buffered to 4 km strips.

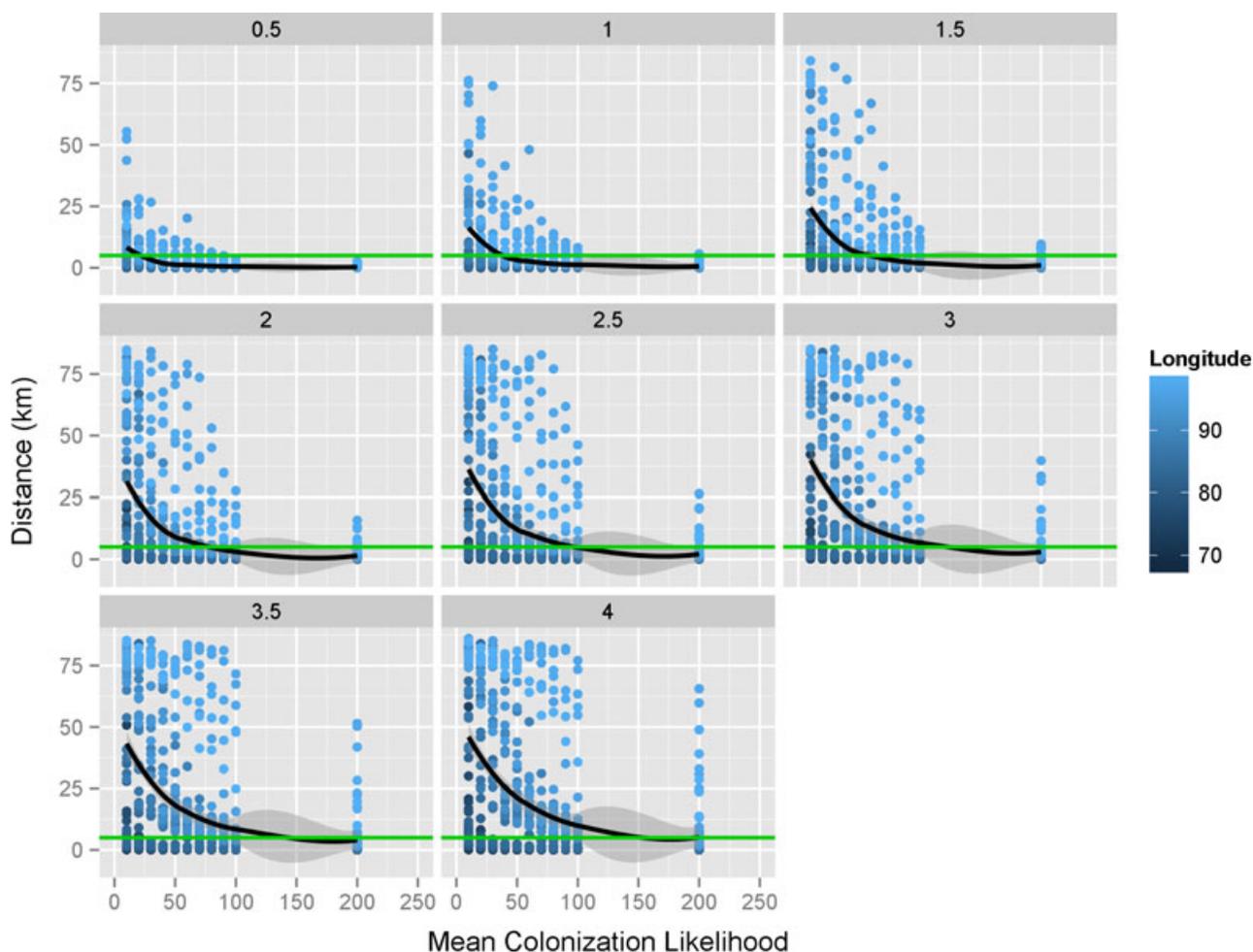


Fig. 3 The co-plots of mean colonization potential plotted against longitudinal transect distances for ‘all’ transects for SHIFT calibration constants (C) from 0.5 to 4 at steps of 0.5 (top panel of each graph), depicting different historical migration rates for post oak (*Quercus stellata*). Notice that the loess smoother intersects the 5% likelihood line at 50 km/century for $C = 1.5$ (see online supplementary material for the longitudinal and radian transect coplots for all the four oak species).

(see online supplementary material for the other oaks). To ensure that the calibration constant matches the historical migration distance, we mapped all SHIFT-colonization outputs in GIS and measured the distances at various segments on the map with very good agreement for all four species. The graphs are helpful because with these graphs migration rates can be approximately estimated, even without manually picking transects and measuring distances for each species from the map. In addition, we can assess how the mean colonization varies with distance for each selected transect by producing a co-plot for each transect for the updated Little’s boundary (Fig. 4 – see supplementary material for co-plots for all four oak species and scenarios) which shows the decrease in mean colonization with distance for different transects. It should be noted that only some transects show any measurable drop

reflecting the spatial heterogeneity in the distribution of the percent colonized by SHIFT.

Colonization under future climates

To assess how the species colonization potentials can affect habitat occupancy under changed climate, we intersected the SHIFT colonized maps (corresponding to migration rate of 50 km/century and total generation time of 100 years) with the Hadley High climate scenario’s modelled habitats according to DISTRIB (corresponding to equilibrium conditions by 2100). The corresponding outputs depict the potential colonization of the sink habitats roughly by the year 2100. We will confine our analysis to Hadley High GCM (HadCM3 GCM under carbon emission scenario of A1FI) scenario because the other scenario we analyzed – PCM Low

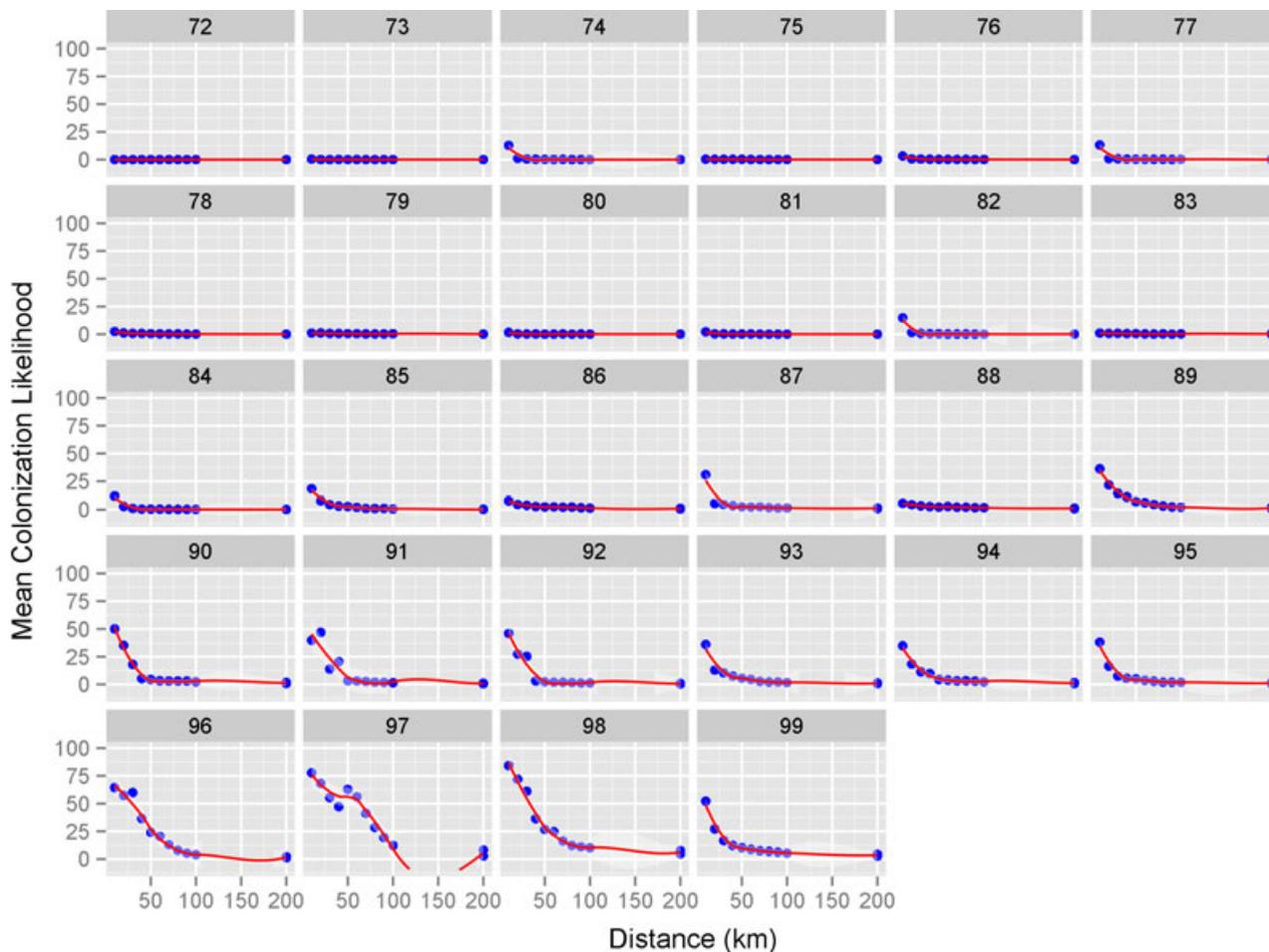


Fig. 4 The co-plots show the change in mean colonization likelihood with distance for 'all' longitudinal transects corresponding to 50 km/century for post oak (*Quercus stellata*). Notice that only some of the many are active transects that show a drop in colonization with distance – illustrating the spatial heterogeneity of colonization potentials (see online supplementary material for the longitudinal and radian transect co-plots for all the four oak species).

GCM (Parallel Climate Model, under carbon emission scenario of B1), is too conservative and does not track current and future carbon emission and climates adequately.

To illustrate the differentiation in the sink habitats predicted by DISTRIB for Hadley High, we reclassified the IVs to low, medium and high suitability classes. Figure 5 shows the DISTRIB and SHIFT outputs juxtaposed for the four oaks. When the sink habitats predicted by DISTRIB (left map), and the percent colonized according to the SHIFT model for these sink habitats (right map) are compared, there is only a small percentage of the sink habitats that have any chance of getting colonized at higher likelihoods. The colonization potential falls rapidly with distance and is largely determined by the source strength within the range boundary. Table 1 illustrates that for the four oaks

under Hadley High scenario. Focusing only on the habitats that are deemed colonizable (split into low, medium, and high quality habitats), generally only a small percent of the 'potentially' colonizable habitat has much chance of getting colonized at 5%, and even less under 50%. For those with relatively higher percentages – for example white and black oak under high habitat quality, the percentage of habitat occupied (number in square brackets) is quite low. Post oak, being a strongly climate-driven species, has plenty of habitat available northward according to DISTRIB (Fig. 5) – but, as the table shows, only 9% of these habitats have a 5% chance of being colonized, and only 2% have a 50% chance. For the other three oaks, the percentage is higher, but DISTRIB is more conservative in the northward distribution of habitats. If other on-the-ground modifying factors like insects, diseases, and competition from red

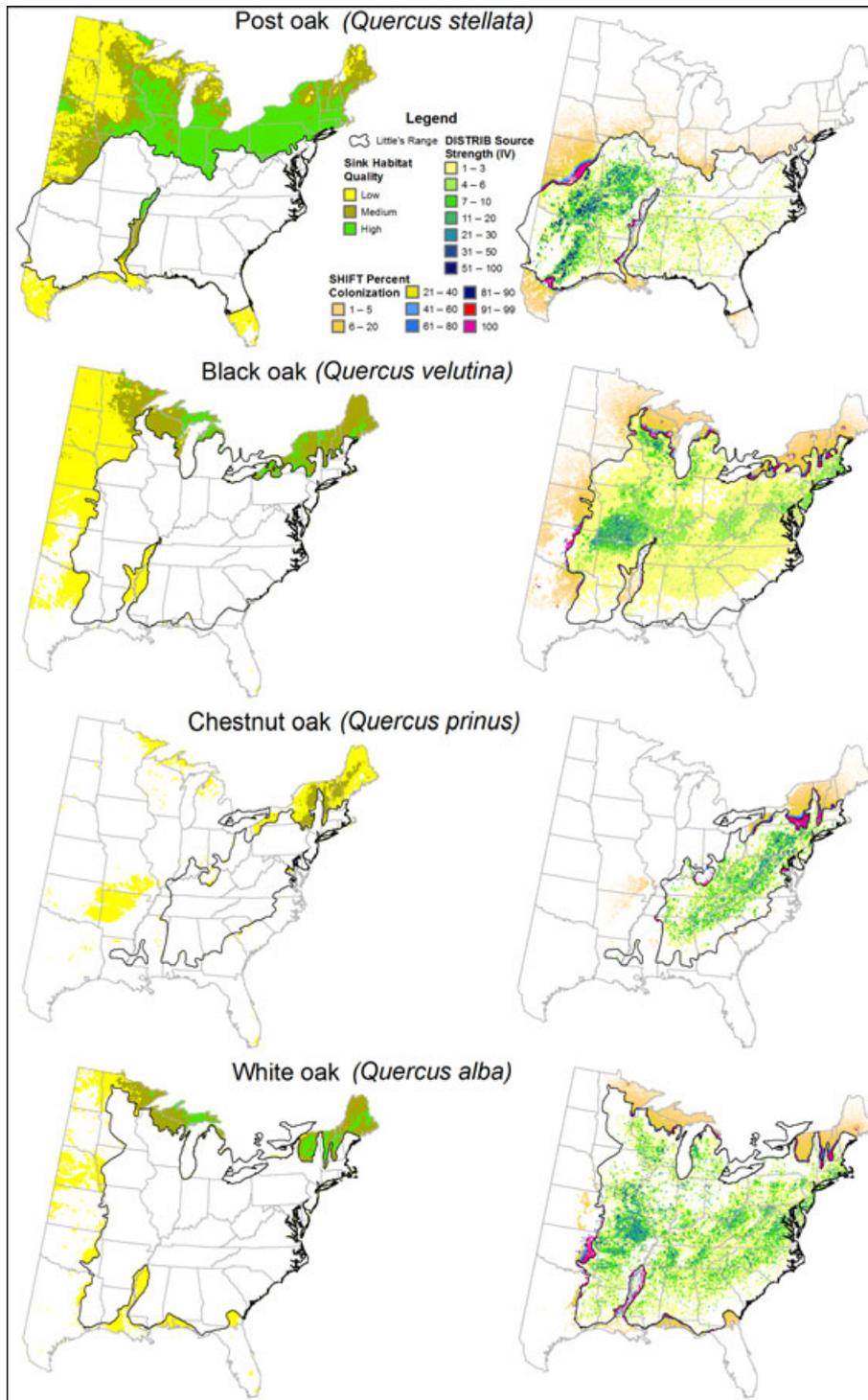


Fig. 5 The sink habitat quality and the corresponding SHIFT percent colonized juxtaposed for the four oaks. The thicker black line is the updated Little's range boundary within which the source strength (IV) is shown. The area beyond the range boundary is the sink – the left map denotes the quality of the sink habitats as predicted by DISTRIB under Hadley High scenario. The right map shows the percent colonized in the sink habitats according to the SHIFT model. The percent colonized correspond to historical migration rate of 50 km/century.

maple are taken into account, there could be even a further decrease in this potential (Matthews *et al.*, 2011). However, it should be borne in mind that if conditions

change sufficiently in the future, these negative pressures can be mitigated by other factors like favorable climatic water balance (oaks being drought tolerant)

Table 1 The percent of sink habitats colonized by SHIFT for all (total), low, medium and high quality habitats, using the Hadley High output from DISTRIB. The percent occupied at or above 5% likelihood and 50% likelihood is comma separated. The item in the square bracket is the percent of suitable habitat – they add up to 100 for low, medium and high habitats. For example, of the total sink area colonized by post oak, only 10% of habitats have $\geq 5\%$ chance of getting colonized and only 3% have $\geq 50\%$ chance of getting colonized – similarly for the high quality habitat, only 6% has $\geq 5\%$ chance and only 1% has $\geq 50\%$ chance. Notice also that only 36% of the available habitat for post oak is of high quality

Habitat	Total (5%, 50%)	Low (5%, 50%)	Medium (5%, 50%)	High (5%, 50%)
White oak (<i>Quercus alba</i>)	25, 9 [100]	21, 11 [53]	30, 6 [34]	38, 10 [13]
Chestnut oak (<i>Quercus prinus</i>)	19, 8 [100]	14, 5 [84]	50, 26 [16]	0, 0 [0]
Post oak (<i>Quercus stellata</i>)	9, 2 [100]	12, 2 [34]	12, 4 [30]	6, 1 [36]
Black oak (<i>Quercus velutina</i>)	21, 6 [100]	14, 3 [61]	34, 9 [30]	42, 15 [9]

that could override the limiting factors and give oaks the competitive advantage to thrive (Dobrowski & Abatzoglou, 2013).

Managed relocation

Even though a short migration response, decaying rapidly with distance will be fairly typical for most species, it is important to estimate how these responses vary spatially for species with differential source strengths as illustrated by the maps of the oaks (Fig. 5). When SHIFT outputs are intersected with future habitats predicted by DISTRIB, they can be used to help plan for managed relocation more systematically for vulnerable tree species. This approach is valuable because tree longevity, gene flow from distant populations and phenotypic plasticity will facilitate the process of local adaptation once a small founder population is established (Petit *et al.*, 2003; Aitken *et al.*, 2008). Therefore, predicted habitat openings and colonization potential indicated by the DISTRIB and SHIFT models can be opportunistically used to initiate new populations to facilitate migration and these populations need not be very large (McLachlan *et al.*, 2007; Richardson *et al.*, 2009). This strategy is especially useful for specialist species with narrow habitat requirements as they are far more likely to face extinction threat as compared to more generalist species (Trakhtenbrot *et al.*, 2005). The DISTRIB and SHIFT models allow exploration in the spatial domain to delineate suitable corridors and patches for facilitating the establishment and migration of tree species. As an illustration, we can explore migration corridors for black oak in the Wisconsin area where there is sufficient source strength and outlier populations – depicting areas of suitable sink patches and corridors near satellite populations

where black oak can be populated to facilitate migration (Fig. 6).

Discussion

Our spatially explicit cell-based simulation approach to estimating the migration potential of tree species described here should be viewed as a complement to phenomenological and mechanistic models. Lightly parameterized simulation models like ours, based on estimates of historical patterns of migration rates, and using an inverse power function to decay the spread with distance, are quite useful when screening multiple tree species under current fragmented landscapes and exploring the interplay of source strength on the colonization of sinks beyond the current species range boundary. When this SHIFT model is combined with the DISTRIB model, which predicts ‘potential suitable’ habitats, they yield ‘potential colonizable’ habitats by the year 2100 (Iverson *et al.*, 2011; Engler & Guisan, 2009; Midgley *et al.*, 2010; Mustin *et al.*, 2009).

The major limitation of simulating migration potential for multiple tree species so far has been the computational constraints that limited our ability to assess more than a few species. With the convolution-based FFT approach, we overcome the computational barrier and can now tackle many species efficiently. In addition, we are able to evaluate multiple scenarios for each species, facilitating the automation of the calibration constant to simulate a range of historical migration rates, and also to derive useful products that enhance our understanding of species dispersal ecology.

It should be stressed that we have deliberately overestimated the migration response by making optimistic assumptions: a fairly generous historical migration rate of 50 km/century; inverse power function with a search window of 500 km; no difference in dispersal

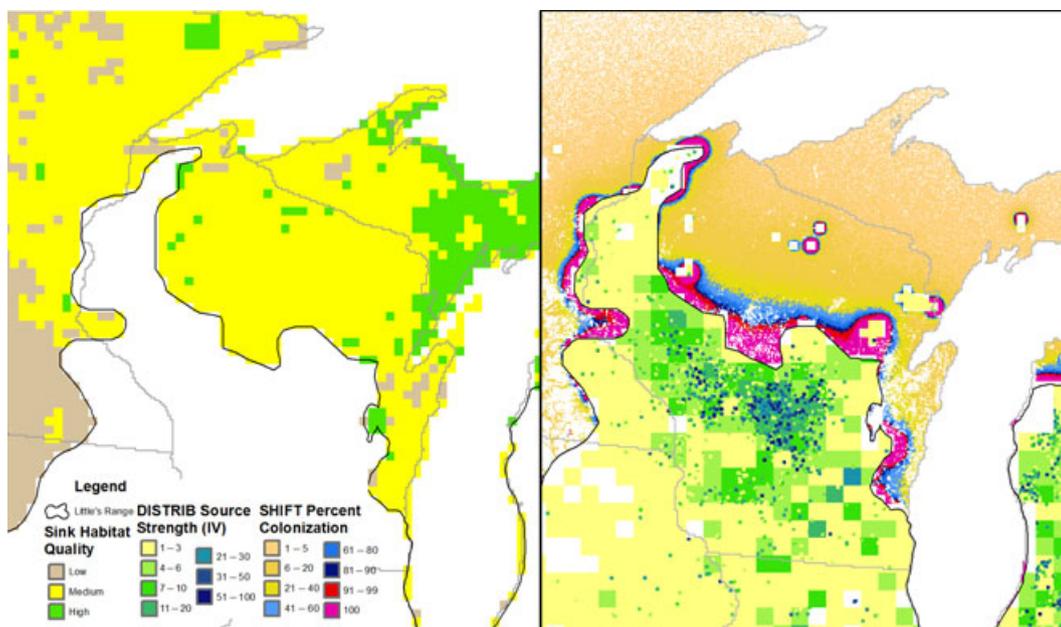


Fig. 6 Evaluating establishment and migration potential for black oak (*Quercus velutina*) for managed relocation in the Wisconsin area. We can evaluate future suitable high quality habitats and outlier populations (islands), source strength, and sink-colonization potential under Hadley High simultaneously using FIA data, and the outputs of DISTRIB and SHIFT models.

rates based on seed characteristics or dispersal modes; no reduction in population of occupied cells; and all sink cells deemed colonizable are equally suitable for colonization. Another factor (not considered in our analysis) that makes our results optimistic is that, in addition to colonization of suitable habitats, the colonized species should be able to overcome competitive exclusion and establish to adulthood (Thuiller *et al.*, 2008). Despite all these deliberately optimistic assumptions, the rate of decline with distance is remarkable and casts doubt whether the dispersal ability of specialized species can compensate under current fragmented landscapes.

In our earlier paper (Iverson *et al.*, 2004), we established that the source strength that is, the abundance of the species near the range terminus was crucial to even get a migration response of ~10–20 km from the boundary, and the habitats the species could colonize (sink strength) is important only after the source strength is sufficiently strong. It should therefore be borne in mind that the advancing front of the colonizing species over the next 100 years will be concentrated in the first 10–20 km from the current boundary according to our model and the percent colonized is quite low (Table 1) – although it allows for rare long-distance dispersal up to 500 km from the current range boundary. This implies that it may be very hard to differentiate dispersal response from no-dispersal response owing to our imprecise knowledge of the limits to species dis-

tributions (Woodall *et al.*, 2009; Zhu *et al.*, 2012). This problem is exacerbated for narrowly endemic species, which may face an extinction crisis due to their inability to keep pace with climate forcing.

The four oak species studied show that in spite of the large availability of suitable habitats to the north according to the DISTRIB model, we cannot expect much ‘natural’ colonization due to habitat fragmentation, limited colonization, and disease, insect, and competition effects. However, it should be noted that in spite of the current limited regeneration ability in the eastern US (Abrams, 2003; Nowacki & Abrams, 2008), there is potential in the future for oaks to colonize under favorable circumstances because they are sufficiently climate driven and would react positively to a deficit in climatic water balance due to their drought tolerance. Also, because SHIFT depicts the spatial heterogeneity of colonization potentials, corridors and patches with higher potential for colonizations can provide crucial information for selecting suitable areas for assisted migration for vulnerable species.

In our simulations, we do not distinguish between animal and wind-dispersed species, because there is not enough empirical evidence suggesting that these two forms of dispersal created significant differences in seed dispersal (Higgins *et al.*, 2003). However, habitat loss in current and future landscapes could likely make the differences between these two types of dispersals more significant. In reality, we may find that some ani-

mal-dispersed species (e.g., those dispersed by birds) respond very differently to fragmentation as a result of directed dispersal (Johnson & Webb, 1989). However, repeated attempts fail to find systematic differences in dispersal rates of trees as a consequence of seed dispersal mechanisms (Portnoy & Willson, 1993; Clark *et al.*, 1998; Higgins *et al.*, 2003). Thus, empirical observations do not indicate significant differences in seed-dispersal characteristics between these life histories despite known differences in dispersal biology.

During the Holocene, which started about 11 700 years ago, the temperatures increased rapidly and continued to rise at a slower rate during the next 1500 years (Cole, 2010). The current projections of climate change by the International Panel on Climate Change (IPCC) are similar to this historical pattern of temperature change. Our model projects changes by about 2100, by incorporating equilibrium conditions. However, this assumption of equilibrium conditions in less than a century raises concerns because the species response is going to be shaped by nonequilibrium conditions of continuing increases in temperature, changes in precipitation patterns and land-use change (Johnstone & Chapin, 2003). It is, however, possible now to simulate transient changes in climate by gradually changing it through time and modelling occupancy rates. Solving the computational barrier opens up possibilities for SHIFT that were hitherto unachievable, and hence other modelling challenges enumerated in this article can be addressed – although they add complexity and assumptions in the process.

SHIFT uses 1 km² cells in the eastern United States. This cell resolution is reasonable to evaluate whether there are enough forest patches for the colonization to happen. However, more local biotic interactions like competition/mutualism, density dependent demographics, herbivory, etc. cannot be reliably estimated at the 1 km scale. Evaluation of these microecological effects goes beyond the scope of our analysis because these would require localized data and analysis for any degree of realism. Currently, our model does not address finer within-cell or among-cell ecological dynamics although these can be addressed via submodels at finer scales.

The influence of range boundary of tree species on dispersal is an area of research that has progressed in recent years. Phillips and colleagues (2008) have argued that dispersal kernels are not static in the expanding front and could drive evolution of dispersal kernels. This implies that the offspring of the individuals on the front could have higher dispersal ability than the offspring of individuals from within the core population. In addition, gene flow from core populations can introduce alleles pre adapted to warmer climate (Davis &

Shaw, 2001). Therefore, it is possible that with climate change, the dispersal capabilities of the species at the front of the range will be more influential compared to the core (Parmesan, 2006; Dytham, 2009; Sexton *et al.*, 2009). On the other hand, there is very often a reduction in species importance near the species boundaries so that there are less individuals from which to disperse – therefore the populations at the range boundaries are under greater biotic and abiotic stress because of lower densities and stiffer interspecific competition, compromising their ability to migrate under climate change (Petit *et al.*, 2004; Bridle & Vines, 2007; Aitken *et al.*, 2008). With our simulation model it is possible to artificially inflate abundances in the leading edge to explore these processes in an approximate manner and compare it to the baseline. In a similar vein, Purves (2009) argued that comparing geographic variation in species demography at the range boundary as compared to the core of the range is necessary to understand the historical and current determinants of species' ranges. In addition to climatic change, tree species are subject to multiple biotic and abiotic stressors that could limit the ability of tree species to adapt, especially narrowly adapted populations with low phenotypic plasticity (Valladares *et al.*, 2007). Based on our argument that source strength is critical in driving the colonization at the boundaries, the fact that it tends to be lower at the margins compared to the core can be a countervailing influence for evolutionary mechanisms. We plan to explicitly explore source-strength mechanisms for most of the major species modelled by DISTRIB in the eastern United States and also explore submodels that will shed light on finer aspects of dispersal at the edges.

We have not explicitly explored the effect of colonization at the trailing edge of the species' in our models. It has been argued that the trailing edge is important to assess the vulnerability of the species to extinction – especially for narrowly endemic species (Davis & Shaw, 2001; Hampe & Petit, 2005; Thuiller *et al.*, 2008). Even though our simulation model calculates the colonization likelihoods at the range boundaries irrespective of the direction, plasticity, and the ecology of meta-population dynamics may be more crucial at the trailing edge, requiring additional investigations (Nicotra *et al.*, 2010).

In summary, it is hoped that our enhanced SHIFT model has laid the groundwork for further analysis of the colonization potential of tree species. The point spread function to speed up the model via convolution and FFT can be generalized to speed up models where similar kernels are involved. In spite of the considerable progress in the application of dispersal models in recent years (Hampe, 2011), multiple modelling strategies will be needed to tackle the complexities of

dispersal, colonization, and establishment owing to various confounding factors (Bullock *et al.*, 2012). Our simulation-based approach, which uses the simple source/sink strength paradigm, is a powerful method to rapidly compute colonization potentials for a large number of tree species in a geographically fragmented area under various estimates of historical migration rates. When combined with the habitat-prediction model DISTRIB, it is possible to evaluate possible trajectories of range changes due to climate change by the year 2100.

Our generalized macro-ecological framework can provide valuable insights into species distribution and colonization potentials and allow model-guided evaluation of assisted migration corridors and patches for vulnerable tree species that may not be able to keep pace with climate change. There is always room for species-specific enhancements based on the analysis of local ecological dynamics at finer scales, and this fine-tuning is encouraged.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The figures and graphs for all four oaks.