

Land use and life history limit migration capacity of eastern tree species

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Abstract

Aim: Temperate tree species overwhelmingly responded to past climate change by migrating rather than adapting. However, past climate change did not have the modern human-driven patterns of land use and fragmentation, raising questions of whether tree migration will still be able to keep pace with climate. Previous studies using coarse-grained or randomized landscapes suggest that dispersal may be delayed but have not identified outright barriers to migration. Here, we use real-world fragmented landscapes at the scale of forest stands to assess the migration capacity of eastern tree species.

Location: Eastern U.S.A.

Time period: Present day to 2100.

Major taxa studied: Eastern U.S. trees.

Methods: We simulated dispersal over 100 years for 15 species common to the mid-Atlantic region and that are predicted to gain suitable habitat in the northeast. In contrast to previous studies, we incorporated greater realism with species-specific life histories and real-world spatial configurations of anthropogenic land use. We used simulation results to calculate dispersal rates for each species and related these to predicted rates of species habitat shift.

Results: Our simulations suggest that land use in the human-dominated east-coast corridor slows species dispersal rates by 12–40% and may prevent keeping pace with climate. Species most impacted by anthropogenic land use were often those with the highest predicted species habitat shifts. We identified two major dispersal barriers, the Washington DC metropolitan area and central NY, that severely impeded tree migration.

Main conclusions: Patterns of anthropogenic land use not only slowed migration but also resulted in effective barriers to dispersal. These impacts were exacerbated by tree life histories, such as long ages to maturity and narrow dispersal kernels. Without intervention, the migration lags predicted here may lead to loss in biodiversity and ecosystem functions as current forest species decline, and may contribute to formation of novel communities.

KEYWORDS

climate change, dispersal barrier, dispersal simulations, eastern tree migration, fragmentation, land use, species distribution models

1 | INTRODUCTION

Temperate forests provide essential ecosystem services and important economic benefits (Iverson, Prasad, Matthews, & Peters, 2008; Millar & Stephenson, 2015; Scheller & Mladenoff, 2005). Identifying forest

vulnerabilities to climate change is therefore crucial for developing adaptive management strategies that minimize losses to ecosystem services and biodiversity as forests respond to climate change (Millar & Stephenson, 2015; Scheller & Mladenoff, 2005). Species distribution models (SDMs), which are often used to evaluate potential species

responses to climate change, have predicted major declines of important species, such as *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg., by the end of the century in the northeastern U.S.A. (Iverson et al., 2008; Scheller & Mladenoff, 2005; Tang & Beckage, 2010). In addition, broadleaf species, such as *Quercus* L. and *Carya* Nutt. species, are predicted to gain substantial suitable habitat in the northeastern U.S.A. (Iverson et al., 2008; Tang & Beckage, 2010; Scheller & Mladenoff, 2005). Although SDMs are valuable for assessing potential species vulnerabilities to climate change, traditional SDMs fail to address the migration process to arrive at a new habitat, including species-specific life-history traits (e.g., dispersal ability) that will determine the likelihood of species migrating into the newly suitable habitat (Dawson, Jackson, House, Prentice, & Mace, 2011; Prasad, Gardiner, Iverson, Matthews, & Peters, 2013; Travis et al., 2013; Zhu, Woodall, & Clark, 2012). Although recently developed modelling approaches do incorporate migration into SDMs (e.g., KISSMig; Nobis & Normand, 2014), they have yet to be applied to the northeastern U.S.A. and at the fine resolution of our study. Given the SDM predictions for the northeastern U.S.A., and knowing that eastern tree species overwhelmingly responded to past climate changes by shifting their distributions (Clark et al., 1998; Corlett & Westcott, 2013), examining the migration capacity of eastern tree species and identifying potential dispersal barriers across the landscape are key to understanding forest vulnerabilities to climate change and informing adaptive forest management (Prasad et al., 2013; Rogers, Jantz, & Goetz, 2017; Scheller & Mladenoff, 2005; Travis et al., 2013).

Previous studies have used simulations to examine the role of dispersal and land use on species' response to climate change and have consistently predicted migration lags for temperate tree species (Lazarus & McGill, 2014; Prasad et al., 2013; Rogers et al., 2017; Snell, 2014). However, few studies have incorporated fine-scale, realistic spatial configurations of land use and habitat fragmentation while also covering a large regional scale, nor have studies identified regions of intensive anthropogenic land use that represent major dispersal barriers. For example, studies have either simulated fine-scale patterns of anthropogenic land use (Lazarus & McGill, 2014) or used a large grid size (e.g., 800 m to 18 km; Prasad et al., 2013; Snell, 2014; Rogers et al., 2017), thereby preventing the ability to examine the influence of local land use patterns on stand-level tree dispersal across the majority of a species' range. In addition, previous work often lacked taxonomic resolution, such as only simulating dispersal for a generic species (Lazarus & McGill, 2014), using identical dispersal kernels across species (Prasad et al., 2013; Rogers et al., 2017) or focusing on only a few tree species to examine migration capacity (Prasad et al., 2013; Snell, 2014).

In this study, we conducted spatially explicit simulations of tree dispersal over the next 100 years across the eastern U.S.A. using species-specific life histories along with current land use patterns to assess the migration capacity of 15 eastern tree species. We selected species that are common to the mid-Atlantic region of the U.S.A. and are predicted to gain significant suitable habitat in the northeastern U.S.A., and that range in dispersal modes (e.g., wind and animal dispersed), age to maturity (5–25 years), extent of current range, dispersal kernel (Clark, LaDeau, & Ibanez, 2004; Clark, Silman, Kern, Macklin, &

HilleRisLambers, 1999; Martínez & González-Taboada, 2009) and life-form (i.e., conifer and broadleaf). We used current range and predicted suitable habitat data from the U.S. Forest Service Climate Change Tree Atlas (CCTA; Iverson et al., 2008) to represent current and future suitable habitat. Although the CCTA current ranges may not capture the full range of each species, they are a realistic representation of where species occur, along with the landscape setting through which each species must migrate. Future suitable habitat was based on the high-emissions scenario and average of three general circulation models (GCMs). We used the 2011 National Land Cover Database (NLCD 2011; Homer et al., 2015) to characterize the landscape conditions that species will disperse through by classifying land use into natural habitat (e.g., forest and wetland) and anthropogenic land use (e.g., human developed and agricultural land). This approach assumes that anthropogenic land use configurations will remain the same throughout the 100-year simulation, which is likely to be an optimistic scenario, as conversion of natural land cover to anthropogenic land use has been predicted to increase in the study area over the next half century (Ordonez, Martinuzzi, Radeloff, & Williams, 2014). However, the dispersal function that we used, and limitations in computer processing and virtual memory, allowed for only a single barrier layer. Both the CCTA and NLCD 2011 data were rescaled to a 90 m grid size to simulate dispersal and impacts of land use within the scale of a forest stand. Dispersal kernels followed fat-tailed density functions that incorporate rare long-distance dispersal (LDD) events and that better approximate past migration rates and observed seed shadows than Gaussian or exponential density functions (Bullock et al., 2017; Clark et al., 1998, 1999). We used a range of maximal LDDs to approximate the dispersal kernel in our simulations, including the commonly reported 1 and 10 km maximal LDDs (Clark, 1998; Clark et al., 1999; Nathan et al., 2002; Ordonez & Williams, 2013a). We also ran simulations using 50 km as the maximal LDD to incorporate non-standard LDD events that are difficult to detect in field studies but that biogeographical studies of isolated populations indicate are possible and that may help to explain early Holocene rates of tree migration (Higgins, Nathan, & Cain, 2003; Lesser & Jackson, 2013). We ran simulations with anthropogenic land use as a dispersal barrier layer and also ran simulations without a dispersal barrier layer as a null model to quantify the effect of land use on the migration capacity of each species. We used the simulation results to estimate species dispersal rate and related these results to the predicted rates of species habitat shift by calculating the centre of gravity (VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2014; VanDerWal et al., 2012) of current and suitable habitat ranges for each species. We also related the dispersal rates to predicted rates of climate velocity for the study area throughout the 21st century (Hamann, Roberts, Barber, Carroll, & Nielsen, 2015; Loarie et al., 2009) to determine how likely migration lags will be for the species in our study. This is the first study we are aware of that uses spatially explicit dispersal simulations covering a large area of the eastern U.S.A., while also using a scale that is consistent with stand-level dispersal and land use patterns and incorporates complex species-specific dispersal kernels. Using this approach, our main objectives are to (a) determine the migration capacity of eastern tree species, (b) quantify impacts of anthropogenic

land use on migration capacity, and (c) identify potential dispersal barriers on the landscape.

2 | METHODS

2.1 | Data preparation

We adapted the MigClim.migration function in the MigClim package (Engler, Hordijk, & Pellissier, 2013) in R (R Core Team, 2016) for our dispersal simulations. MigClim is a cell-based model that incorporates species-specific dispersal parameters and habitat suitability to simulate dispersal across a landscape and over a given time period. The MigClim simulation requires raster files that represent current habitat and future suitable habitat, and an optional dispersal barrier raster. For our simulations, we used CCTA rasters (Iverson et al., 2008) to represent current and future suitable habitat, and the NLCD 2011 raster (Homer et al., 2015) for the dispersal barrier. Although the CCTA SDMs also included land use predictors, they were incorporated at much larger scales than our simulations (20 km vs. 90 m) and were used to identify future suitable habitat, rather than modelling the process of tree migration as in our study.

We selected species whose furthest northern extent was largely (in most cases entirely) within the lower 48 states to avoid niche truncation of the SDMs. We used the CCTA actual range (i.e., not the current modelled range) for each species to represent current range, and the CCTA average of three general circulation models (GCMs) for the high-emissions scenario (A1FI) to represent the future suitable habitat. It is important to note that the CCTA future suitable habitat predictions are not based on the most recent Intergovernmental Panel on Climate Change (IPCC) scenario for high emissions (e.g., RCP 6.0; IPCC, 2014), and instead used the A1FI high-emissions scenario (IPCC, 2007). However, we are primarily using the CCTA future suitable habitat models as potential areas for species to disperse into to examine species-specific migration capacity, rather than using the future suitable habitat models to make predictions on where species will migrate. The CCTA models are also the basis for many planning efforts for climate change adaptation on managed lands (Fisichelli, Abella, Peters, & Krist, 2014; Janowiak et al., 2017). Therefore, we believe the CCTA future suitable habitat predictions are appropriate for the purposes of our dispersal simulations. The values of the CCTA rasters are importance values (IVs), which are based on the relative number of stems and basal area of each species per grid cell (Iverson et al., 2008). For the dispersal barrier, we converted the NLCD 2011 to a binary dataset, with zero corresponding to natural land cover (land classes: 41 = deciduous forest; 42 = evergreen forest; 43 = mixed forest; 52 = shrub/scrub; 90 = woody wetlands; 95 = emergent herbaceous wetlands), and one corresponding to anthropogenic land cover for the dispersal barrier (land classes: 11 = open water; 21 = developed open space; 22 = developed low intensity; 23 = developed medium intensity; 24 = developed high intensity; 31 = barren land; 71 = grassland/herbaceous; 81 = pasture/hay; 82 = cultivated crops).

MigClim simulation requires that every raster has an identical grid size and projection, and stores the rasters used during the simulation in

virtual memory. For the large spatial extents and fine resolution that we used this study, virtual memory was a limiting factor. To balance virtual memory limits [32 gigabytes of random access memory (RAM)] with spatial extent and resolution, we used a 90 m grid size for rasters and clipped the rasters to cover the mid-Atlantic region up to central New England. We primarily used functions in the raster package (Hijmans, 2016) in R to prepare the rasters for the simulation, including projecting the CCTA rasters to match the NLCD 2011 raster (projection: Albers conical equal area; datum: NAD83), cropping the rasters to a smaller area and reclassifying rasters as binary (i.e., presence or absence). We upsampled (aggregated) and summed the binary NLCD 2011 raster from 30 to 90 m grid size. We then reclassified the aggregated raster into binary with cells values ≤ 4.5 classified as zero for non-barrier (i.e., forest land cover) and cells > 4.5 classified as one for barrier (i.e., anthropogenic land cover). We downsampled (resampled) the CCTA rasters from the original 20 km grid to a 90 m grid using binary interpolation. By using the downsampled CCTA current ranges, our simulations might miss small, isolated populations that exist outside the CCTA current range and that might be important for quantifying tree migration rates (McLachlan, Clark, & Manos, 2005). However, many of the species in our simulation had isolated populations represented in the current range (e.g., *Carya glabra* (Mill.) Sweet, *Quercus prinus* L.), allowing us to examine the influence of isolated populations on the migration capacity. After downscaling to 90 m grids, we then converted the IV in the CCTA rasters to binary using species-specific breakpoints that provided the closest resemblance between the range of the original raster and the 90 m resampled raster. For most species, we used a breakpoint IV of < 0.5 to indicate absent (0) and ≥ 0.5 to indicate present (1). Exceptions include *Pinus taeda* L. and *Pinus virginiana* Mill., which had a breakpoint of one for their current range owing to relatively high IVs near their range boundaries. Species with low IVs near their current range boundaries were *Quercus falcata* Michx. and *Nyssa sylvatica* Marshall, which had breakpoints of 0.25 and 0.1, respectively. All future suitable habitats used a 0.5 breakpoint, except *N. sylvatica*, which used 0.2 as the IV breakpoint for absent and present.

We provide the R code used to process the original raster files and a mock species dataset to run through the R code as supplementary material (Supporting Information Appendices S1 and S2). Note that simulations took 5–10 days to complete a single species run using a high-end laptop [e.g., 32 gigabytes of RAM, i7-4810MQ (2.80 GHz) quad core processor]. To ensure users without access to high-end equipment can run through the provided code, we clipped the mock dataset to cover roughly half of the extent that was used in our analysis, and that only requires a computer with 16 gigabytes of RAM to run.

2.2 | Dispersal simulation

The MigClim function simulates dispersal events at user-specified intervals, in our case 1-year intervals, and up to 99 intervals (i.e., years). The dispersal kernel is a vector of probabilities by distance that determines the probability for a source cell to colonize an empty cell given the distance between both cells and conditional on whether the dispersal

event successfully landed in suitable habitat (i.e., not in a barrier). We adapted the MigClim.migrate function to incorporate species-specific dispersal kernels based on the student DT distribution (Clark et al., 1999, 2004) or a mixture distribution (Martínez & González-Taboada, 2009; Supporting Information Table S1) up to 50.040 km (i.e., 556 bins of 90 m distances), rather than the default negative exponential distribution up to 450 m (i.e., five bins of 90 m distances). In cases where species did not have a published dispersal kernel (e.g., *Carya tomentosa* (Lam.) Nutt.), we used published dispersal kernels for species in the same genus and with a similar life history (e.g., *Carya glabra*). Compared with the default dispersal kernel, the kernels in our study significantly increased time required for simulation runs. Using the full dispersal kernel to 50 km required c. 3–5 weeks to complete a single run with 99 dispersal steps. To cut down on run time for the widest dispersal kernel (50 km LDD), we specified the dispersal kernel probabilities for each 90 m bin up to 9.990 km (111 bins). We used the same LDD probability for cells from 10 to 50 km (from 112 to 556 bins), which was the sum of probabilities from 10 to 50 km. This approach meant that each distance from 10 to 50 km had an equal but very low probability of dispersal and resulted in run times of 5–10 days per simulation. For the narrower dispersal kernels (1 and 10 km LDD), we specified the full dispersal kernel probabilities, which took up to 24 h for the 1 km LDD kernel and 3–5 days for the 10 km LDD kernel.

To simulate dispersal over the next 100 years, we specified the age to maturity, which is the time required for a newly dispersed cell to disperse again in the simulation, as the minimal age reported for a species to germinate from a seed and mature to produce another seed (Burns & Honkala, 1990). Although the MigClim.migrate function allows propagule production potential to increase over time to reflect higher seed production as trees mature, we chose to keep the propagule production potential constant to reduce model complexity. For each species, we ran a simulation with anthropogenic land cover as a dispersal barrier, and a null model that did not include a dispersal barrier. The barrier dataset was specified as weak, which allowed cells to disperse across a barrier cell but did not allow cells to disperse into a barrier cell. Finally, we ran separate simulations for 1, 10 and 50 km maximal LDD for each species. The MigClim function also includes an option to replicate the simulations. However, owing to the length of time required to run individual simulations and the disk space required to save the results of each simulation (500 megabytes raster file per simulation), we did not replicate the simulations.

2.3 | Analysis

We summarized the simulation results using a combination of raster- and vector-based approaches. We used the zonal.stats function in spatialEco (Evans, 2016) to calculate the proportion of suitable habitat that was dispersed into for both the barrier and null model within 10 km consecutive buffers that extended from 10 up to 150 km beyond the current species range and followed the shape of each species' current range based on the CCTA. We also calculated the proportion of suitable habitat that was not dispersed into and that was a dispersal barrier using this approach. Results were summarized for all

three dispersal kernels (i.e., 1, 10 and 50 km LDD) with barrier and null models, although we focus primarily on the 10 km LDD kernel as the most realistic scenario.

For species habitat shift, we calculated the centre of gravity of the original (i.e., uncropped) CCTA rasters for species current and future suitable habitats using the COGravity function in SDMTools (VanDerWal et al., 2014). Species habitat shift represented the distance between centres of gravity for the current and future suitable habitat, converted to kilometres per decade. We calculated the maximal dispersal distance and dispersal rate for each species and for both the barrier and the null model by first converting the cells colonized in year 99 (i.e., the end) of the simulation to points and measuring the nearest straight-line distance between the points and the current range boundary. We then calculated the maximal dispersal distance as the maximal distance a point dispersed from the current range boundary. For dispersal rate, we calculated the upper 95th percentile of dispersal distances and converted this to kilometres per decade. It is important to note that species habitat shift was calculated at a different scale and extent from the dispersal rate and quantifies different processes (i.e., shift in core habitat versus migration at the leading edge). Therefore, care must be taken when making comparisons between the two metrics. For example, a dispersal rate that is equal to or faster than the species habitat shift does not mean that a species will be able to keep pace with climate change, as other factors, such as competition or lack of mycorrhizal associates in the newly dispersed habitat, may also limit tree migration. However, dispersal rates that are consistently slower than species habitat shifts suggest that dispersal limitations could lead to migration lags.

3 | RESULTS

Migration capacity varied widely among species, although no species filled the majority of its predicted newly suitable habitat by the end of the 100-year dispersal simulation for any of the dispersal kernels (Figure 1). Dispersal rates for the simulations that used a 1 km LDD dispersal kernel were especially slow, ranging from 0.2 to 1.0 km/decade (Table 1), and dispersal was largely restricted to the first 10 km beyond current species' ranges (Figure 2). The impacts of anthropogenic land use were less severe for the 1 km LDD simulations than for the wider dispersal kernels (e.g., 10 and 50 km LDDs), but mostly because dispersal was already greatly limited by the narrow kernel. Anthropogenic land use impacts were more prevalent in the simulations with the wider dispersal kernels, with an average of 27% slower dispersal rates than the null for the 10 km LDD kernel (range 12–40%) and an average of 24% slower dispersal rate than the null for the 50 km LDD kernel (range 7–42%).

Animal-dispersed species with delayed age to maturity and comparatively narrow dispersal kernels, such as *Quercus* spp., *Liquidambar styraciflua* L. and *N. sylvatica*, had the lowest dispersal rates, ranging from 2.1 to 3.4 km/decade for 10 km LDD (Table 1). These simulated dispersal rates were consistently well below predicted species habitat shifts and were consistently slower than null

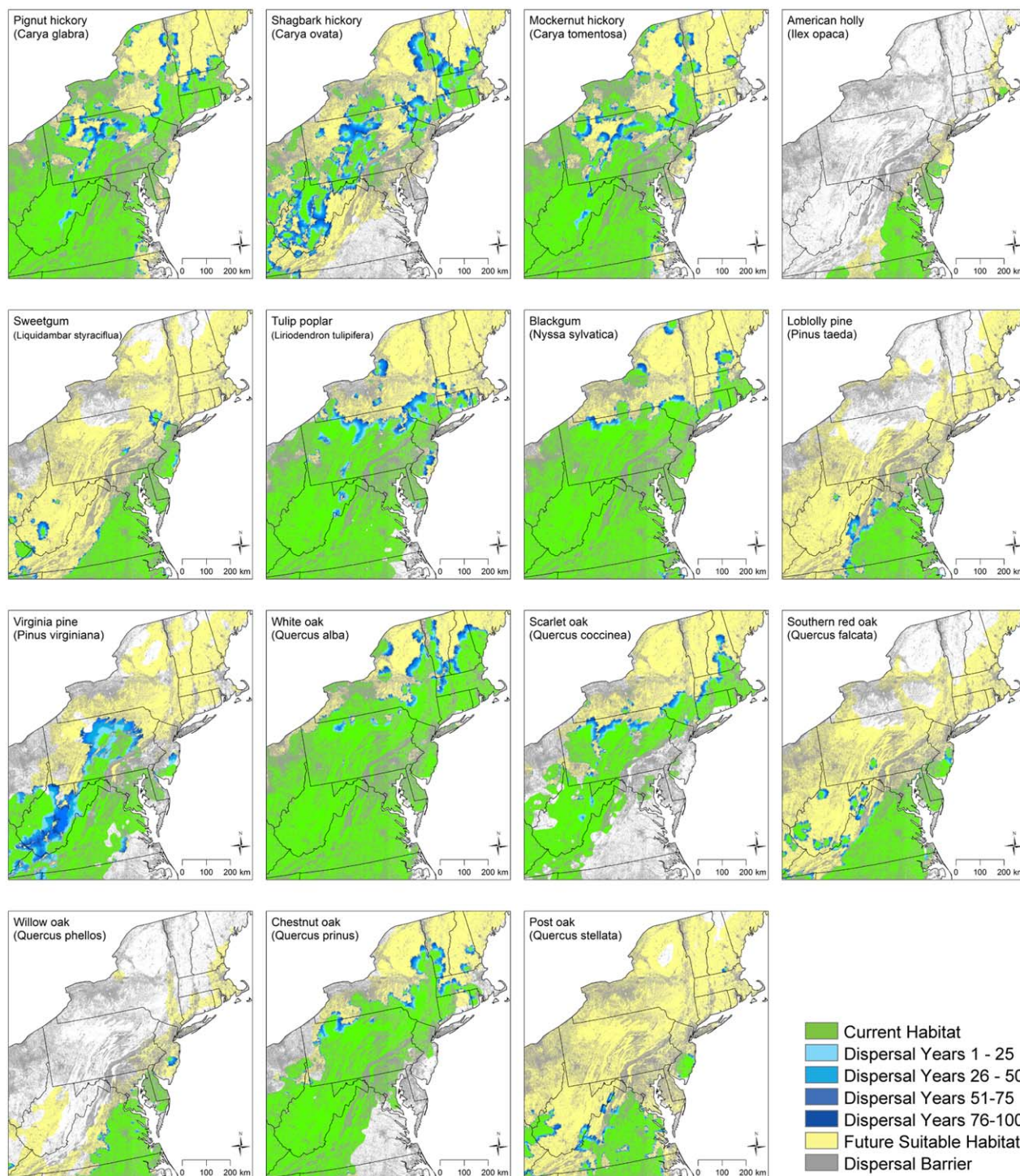


FIGURE 1 Dispersal maps using 10 km as the maximal long-distance dispersal (LDD) for 15 eastern tree species, showing current habitat (green), predicted future suitable habitat (yellow) and non-forest land use as a barrier (grey). Dispersal steps are broken into 25-year intervals (blue)

dispersal models, indicating widespread migration lags. Results were most extreme for *Quercus stellata* Wengen. and *Quercus coccinea* Münch., which exhibited species habitat shifts more than 45 km/decade faster than their dispersal rate. In contrast, wind-dispersed species, such as *P. virginiana*, *P. taeda* and *Liriodendron tulipifera* L., had relatively early ages to maturity, comparatively wider dispersal kernels, and subsequently, the highest dispersal rates. *P. virginiana*

was the only species in this study with a dispersal rate that exceeded its species habitat velocity (15.2 vs. 13.1 km/decade), but only for the 50 km LDD kernel. *P. taeda* and *L. tulipifera* had the next highest dispersal rates, at 8.5 and 7.0 km/decade, respectively, for the 50 km LDD kernel, although dispersal rates were considerably slower than species habitat velocities for these two species (Table 1).

TABLE 1 Species dispersal rate for 1, 10 and 50 km long-distance dispersal compared with species habitat shift

Latin name	Maximal dispersal distance (km)						Dispersal rate (km/decade)						Species habitat shift (km/decade)
	1 km		10 km		50 km		1 km		10 km		50 km		
	Barrier	Null	Barrier	Null	Barrier	Null	Barrier	Null	Barrier	Null	Barrier	Null	
<i>Carya glabra</i> (Mill.) Sweet	3.7	4.1	37.2	38.9	73.7	79.1	0.3	0.3	2.9	3.6	4.3	5.5	16.5
<i>Carya ovata</i> (Mill.) K. Koch	5.0	5.4	51.2	62.7	98.3	106.7	0.4	0.4	3.9	5.3	6.6	8.0	26.5
<i>Carya tomentosa</i> (Lam.) Nutt.	3.5	4.0	36.7	38.8	72.4	79.6	0.3	0.3	2.9	3.6	4.4	5.6	15.3
<i>Ilex opaca</i> Aiton	3.3	3.7	3.2	3.7	3.3	3.6	0.3	0.3	0.3	0.3	0.3	0.3	13.2
<i>Liquidambar styraciflua</i> L.	3.6	3.9	40.7	47.4	62.7	85.2	0.3	0.3	2.7	4.3	4.3	5.6	15.4
<i>Liriodendron tulipifera</i> L.	6.4	6.6	49.6	63.7	93.0	136.6	0.6	0.6	4.0	5.4	7.0	10.1	16.0
<i>Nyssa sylvatica</i> Marshall	3.3	3.6	42.1	48.2	81.8	100.6	0.3	0.3	3.2	4.3	4.7	6.3	9.9
<i>Pinus taeda</i> L.	6.1	6.5	58.2	72.1	125.5	126.8	0.5	0.6	4.1	6.4	8.5	10.0	15.6
<i>Pinus virginiana</i> Mill.	11.9	12.3	96.1	145.0	181.7	225.7	1.0	1.1	8.2	13.1	15.2	19.4	13.1
<i>Quercus alba</i> L.	3.7	2.9	44.7	47.6	66.5	72.6	0.2	0.2	3.4	4.3	4.5	5.5	22.9
<i>Quercus coccinea</i> Münchh.	2.8	3.0	42.3	47.1	54.2	86.9	0.2	0.2	3.4	4.2	3.7	5.3	49.5
<i>Quercus falcata</i> Michx.	2.4	2.7	35.4	39.5	62.9	65.3	0.2	0.2	2.1	3.6	3.2	4.7	19.5
<i>Quercus phellos</i> L.	2.5	2.8	31.8	47.7	44.9	73.6	0.2	0.2	2.6	4.3	3.2	5.5	12.3
<i>Quercus prinus</i> L.	2.8	2.8	39.9	47.6	71.9	73.1	0.2	0.2	3.2	4.3	4.4	5.4	21.2
<i>Quercus stellata</i> Wangenh.	2.5	2.9	37.0	38.8	54.1	67.3	0.2	0.2	2.4	3.5	3.0	4.6	54.2

Note. Maximal dispersal distance is the maximal distance (in kilometres) that each species dispersed to at the end of the dispersal compared with the edge of the current range. Dispersal rate is based on the upper 95% distribution of dispersal distances at the end of the dispersal, converted to kilometres per decade. Species habitat shift represents the shift in the centre of gravity between the current and future suitable habitat, converted to kilometres per decade.

Anthropogenic land use substantially reduced migration capacity for all species, with species ranging from 12 to 40% lower dispersal rates in the 10 km LDD simulations that incorporated land use compared with null models without land use (Table 1). With the exception of *P. virginiana*, high proportions of anthropogenic land use adjacent to the current range boundaries impeded species dispersal from the start of the simulation, particularly in the 10 and 50 km LDD simulations. Therefore, the proportion of suitable habitat most species dispersed into was typically 20–50% lower within the first 50 km of the current range for the model with anthropogenic land use than the null model without anthropogenic land use (Figure 2). In contrast, *P. virginiana* dispersal was most impeded by increases in the proportion of anthropogenic land use starting c. 50 km from its current range.

Simulations revealed a consistent dispersal barrier that originated around the greater Washington, DC metropolitan area and extended into southeastern Pennsylvania and parts of New Jersey. Dispersal for species with northern range boundaries that end south of this DC/PA dispersal barrier were greatly restricted, with impacts most pronounced for *L. styraciflua*, *P. taeda*, *Quercus phellos* L. and *Q. falcata* (Figure 3). A broad east–west stretch of anthropogenic land use located in central NY also served as a dispersal barrier for the more northern species in this study, including *Carya* spp., *N. sylvatica* and *Quercus alba* L. (Figure 4). However, the impacts of the NY barrier were less extreme, as most species that were potentially affected already had populations extending north of the barrier.

4 | DISCUSSION

The dispersal rates for the narrowest dispersal kernel (1 km LDD) were within the ranges reported by McLachlan et al. (2005), which estimated considerably slower migration rates (< 1 km/decade) than pollen reconstructions by identifying cryptic northern refugia using molecular markers. If the migration rates estimated by McLachlan et al. (2005) prove accurate, then the 1 km LDD simulations in our study suggest that eastern tree migration will be very slow and that translocating populations into new areas and protecting northern refugia of species will be essential to avoid widespread losses in biodiversity.

Dispersal rates with the 10 km LDD dispersal kernel were more in line with the 1–10 km/decade rates reported for early Holocene tree migration using pollen reconstructions (Clark et al., 1998; Ordonez & Williams, 2013a), although dispersal rates were on the low end of that range for all but *P. virginiana*. Dispersal rates for the 10 km LDD simulations were below the range of climate velocity (3.5–14.4 km/decade) predicted for our study area during the 21st century. In addition, species habitat shifts in this study (i.e., 9.9–54.2 km/decade) were often considerably faster than their simulated dispersal rates and higher than the rapid range shifts that have recently been documented for several terrestrial species (16.9 km/decade; Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Species habitat shifts were also higher than estimated rates of climate velocity for the 21st century (3.5–14.4 km/decade) for the eastern U.S.A. (Hamann et al., 2015; Loarie et al., 2009). Although

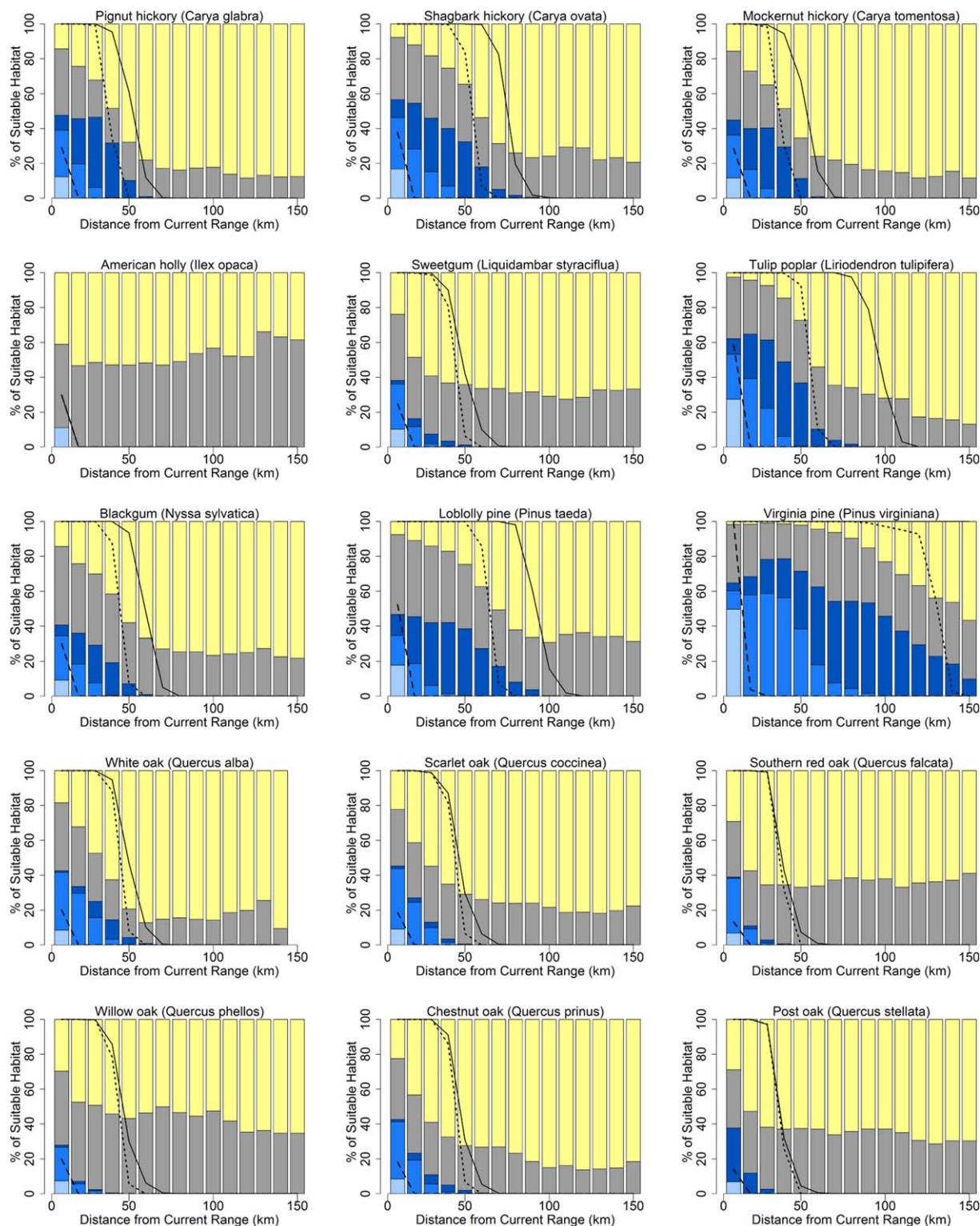


FIGURE 2 Percentage of suitable habitat by 10 km bands from the current range. Grey is the percentage barrier. Light blue is the percentage dispersed into using a 1 km long-distance dispersal (LDD). Medium blue is the additional habitat dispersed into with a 10 km LDD, and dark blue is the additional habitat dispersed into using a 50 km LDD. Yellow is the percentage of suitable habitat that was not occupied by dispersal using 50 km LDD or barrier. The black lines are the percentage of suitable habitat that the null model dispersed into using 50 (continuous line), 10 (dotted line) and 1 km LDD (dashed line)

differences in calculation methods do not allow for direct comparisons between the species shifts reported by Chen et al. (2011), predicted climate velocity, and the species habitat shift and dispersal rates observed

in our study, the consistently and significantly slower dispersal rates that we documented suggest that eastern tree species will be likely to experience migration lags owing to dispersal limitations. Given that

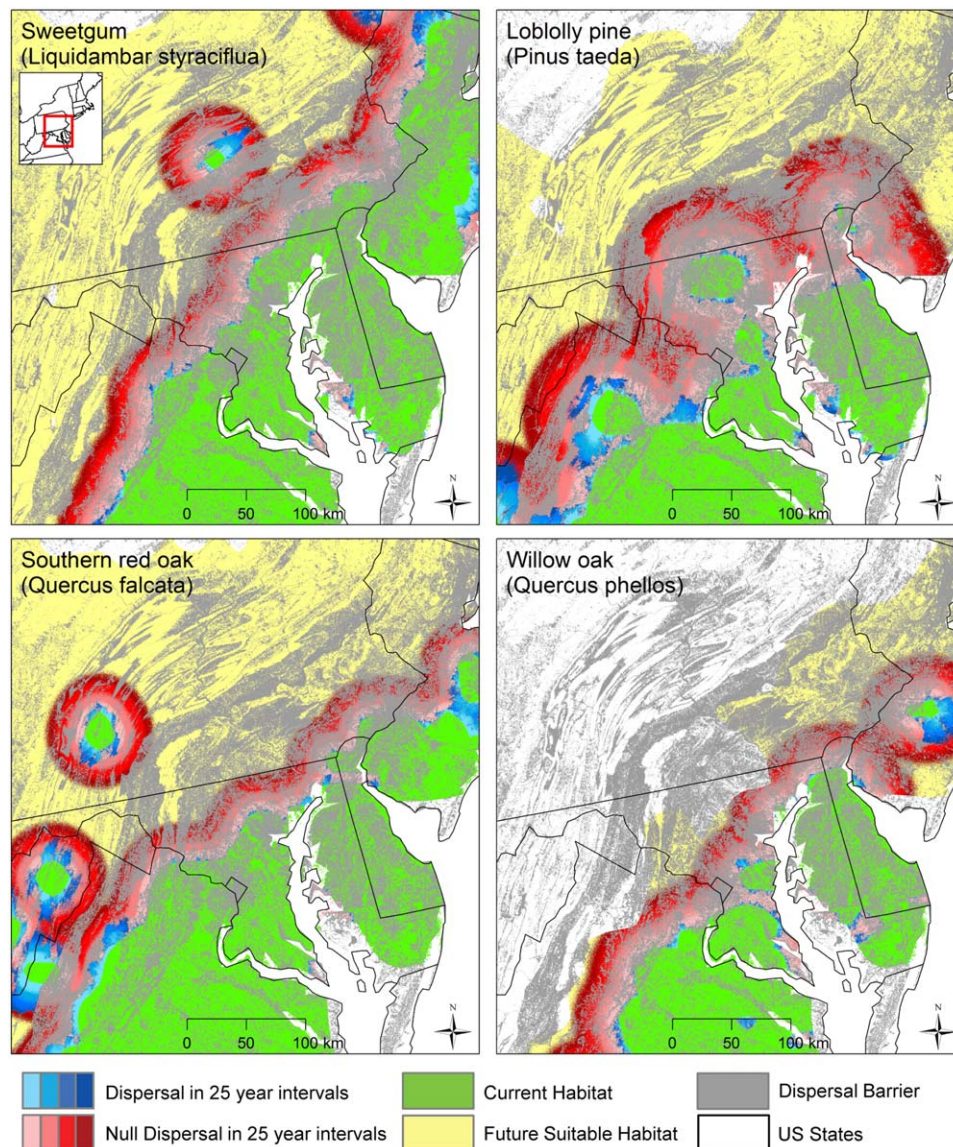


FIGURE 3 Dispersal maps using 10 km as maximal long-distance dispersal (LDD) for the four eastern tree species most affected by the DC/PA dispersal barrier. The dispersal with barrier results (shades of blue) and barrier (grey) are mapped on top of the null dispersal results (shades of red) to demonstrate how the configuration of the anthropogenic land use impeded dispersal and the extent that species dispersed in the absence of anthropogenic land use in the null model

dispersal rates were 12–40% slower when a dispersal barrier was incorporated into the simulations with 10 km LDD, anthropogenic land use is a major driver of these dispersal limitations and the resulting migration lag.

Results of our study are consistent with others that have suggested that dispersal limitations will contribute to migration lags (Clark et al., 1998; Prasad et al., 2013; Zhu et al., 2012). However, this is the first study to quantify the impacts of anthropogenic land use on migration capacity over the majority of each species' range and to identify regional dispersal barriers that consistently suppressed dispersal for multiple tree species. Despite documenting widespread migration lags and large dispersal barriers, our results are optimistic. For age to maturity, we used the minimal time reported in the literature for a germinated seed of each species to grow into a mature individual that

can produce another seed/dispersal event (Burns & Honkala, 1990). Achieving the minimal age to maturity would require a seed to disperse into ideal conditions, which is likely to be a rare occurrence, rather than widespread as specified in our simulations. In addition, our simulations do not consider competition with existing species, which may be less adapted to the changing climate but may create unsuitable conditions for species dispersing into new habitat. Competition with existing species has already been posed as a potential factor behind the current lack of migration signal in eastern forests (Zhu et al., 2012). In our study, the species with the highest dispersal rates, specifically *P. taeda*, *P. virginiana* and *L. tulipifera*, may be most suppressed by the conditions they disperse into because they are not tolerant of shade (Burns & Honkala, 1990). In addition, mycorrhizal strategies and presence or absence of mutualists are likely to influence tree migration dynamics

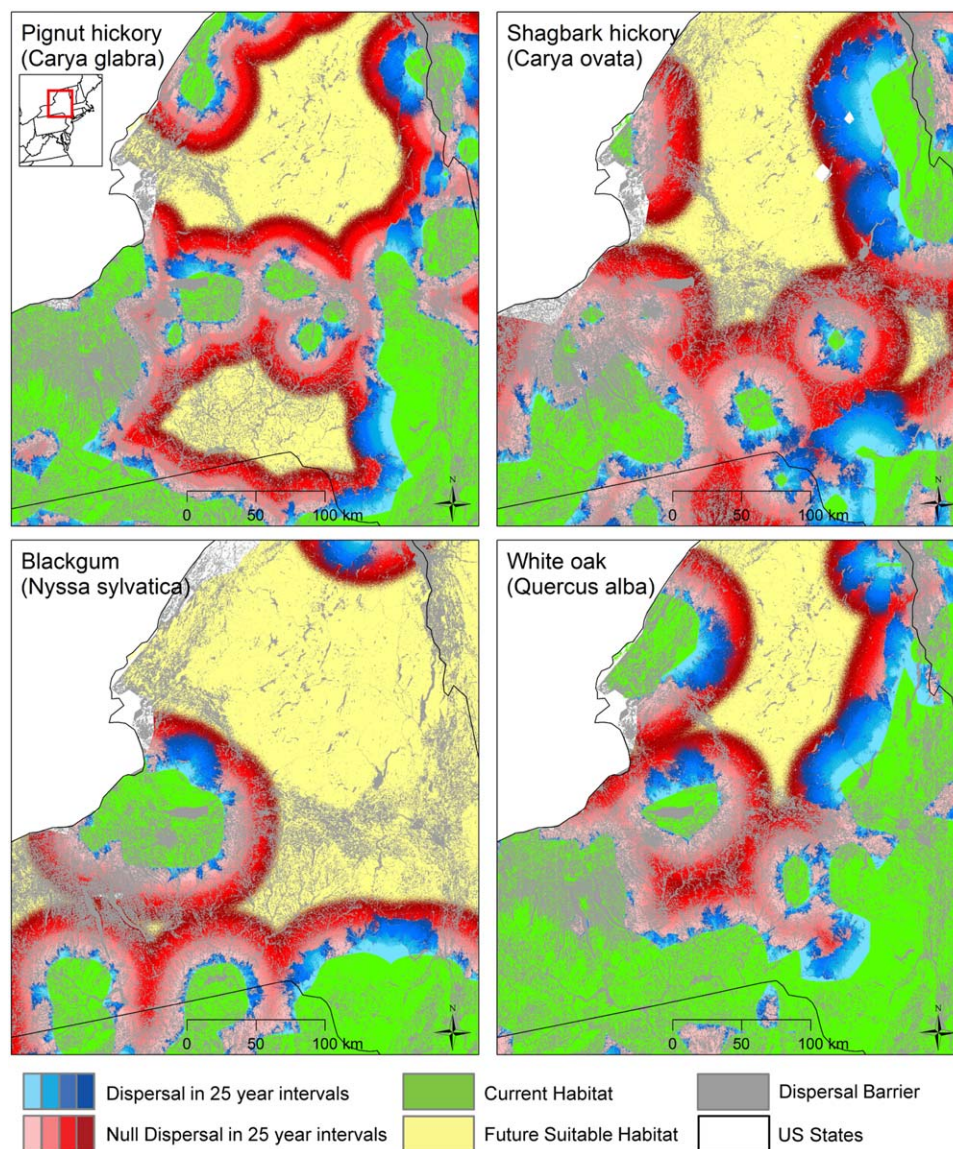


FIGURE 4 Dispersal maps using 10 km as maximal long-distance dispersal (LDD) for eastern tree species that were affected by the central NY dispersal barrier. The dispersal with barrier results (shades of blue) and barrier (grey) are mapped on top of the null dispersal results (shades of red) to demonstrate how the configuration of the anthropogenic land use impeded dispersal and the extent that species dispersed in the absence of anthropogenic land use in the null model

(Lankau, Zhu, & Ordonez, 2015) but are not considered in our simulation. Our simulations also assumed that current land use patterns were static over the 100-year dispersal period, when in fact, conversions of forest to urban and agricultural land use are predicted to increase throughout the region in our study (Ordonez et al., 2014).

The low dispersal rates and regional dispersal barriers documented in our study have important management implications that require immediate attention to reduce potential losses in biodiversity and ecosystem function as northeastern forests respond to climate change (Millar & Stephenson, 2015). Intervention, such as incorporating tree species (e.g., *Q. phellos* and *Q. stellata*) into urban tree planting initiatives, may help to facilitate species migration across dispersal barriers. However, managed relocations of species into newly suitable habitats may ultimately be necessary to maintain diverse and functioning

forests in the northeastern U.S.A. (McLachlan, Hellmann, & Schwartz, 2007; Williams & Dumroese, 2013). Without management intervention, migration lags could lead to declines in biodiversity and ecosystem function (Millar & Stephenson, 2015) and may contribute to the formation of novel communities as northeastern forests respond to climate change (Dawson et al., 2011; Ordonez & Williams, 2013b; Williams & Jackson, 2007).

Although our study focuses on tree species common to the eastern U.S.A., the implications, particularly the migration impacts caused by major metropolitan and/or agricultural lands that are located near species range boundaries, have global relevance. Our results underscore the need for forest management and conservation planning to identify and consider the impacts that dispersal barriers will have on forest response to climate change, and for adaptive management

strategies to consider multiple solutions to deal with the likely migration lags that will occur in forest ecosystems.

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DATA ACCESSIBILITY

The current and future suitable habitat rasters used in this analysis are available upon request from the U.S. Forest Service Climate Change Tree Atlas Program (<https://www.fs.fed.us/nrs/atlas/>). The 2011 National Land Cover Database can be downloaded from the NLCD website (http://www.mrlc.gov/nlcd11_data.php). The dispersal datasets generated during the present study are available from the corresponding author on reasonable request. We provide a mock raster dataset of current and future suitable habitat as supplementary material to run the simulation and analysis code used in this study.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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