

Effects of species biological traits and environmental heterogeneity on simulated tree species distribution shifts under climate change

Wen J. Wang^{a,b,*}, Hong S. He^b, Frank R. Thompson III^c, Martin A. Spetich^d, Jacob S. Fraser^b

^a Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China

^b School of Natural Resources, University of Missouri, 203 ABNR Bldg, Columbia, MO 65211, USA

^c USDA Forest Service, Northern Research Station, 202 ABNR Bldg, Columbia, MO 65211, USA

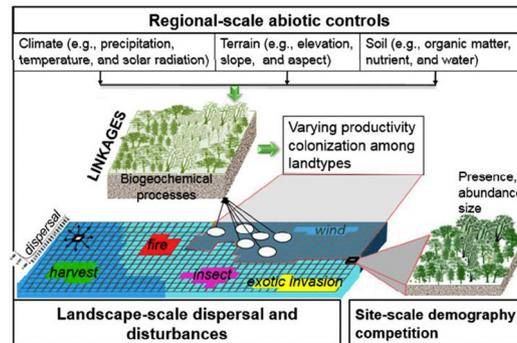
^d Arkansas Forestry Science Laboratory, USDA Forest Service, Southern Research Station, P. O. Box 1270, Hot Springs, AR 71902, USA



HIGHLIGHTS

- Effects of biological traits and heterogeneity on species distribution shifts were investigated.
- Biological traits were important for determining tree species distribution shifts.
- Environmental heterogeneity slowed down tree species distribution shifts.
- Shift rates of tree species were low and may not be able to keep up with climate change.
- Distribution models should include demography and heterogeneity to improve shift predictions.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 19 October 2017

Received in revised form 28 March 2018

Accepted 29 March 2018

Available online xxxx

Editor: Elena PAOLETTI

Keywords:

Dispersal

Demography

Landscape modeling

Species distribution modeling

LANDIS PRO

ABSTRACT

Demographic processes (fecundity, dispersal, colonization, growth, and mortality) and their interactions with environmental changes are not well represented in current climate-distribution models (e.g., niche and biophysical process models) and constitute a large uncertainty in projections of future tree species distribution shifts. We investigate how species biological traits and environmental heterogeneity affect species distribution shifts. We used a species-specific, spatially explicit forest dynamic model LANDIS PRO, which incorporates site-scale tree species demography and competition, landscape-scale dispersal and disturbances, and regional-scale abiotic controls, to simulate the distribution shifts of four representative tree species with distinct biological traits in the central hardwood forest region of United States. Our results suggested that biological traits (e.g., dispersal capacity, maturation age) were important for determining tree species distribution shifts. Environmental heterogeneity, on average, reduced shift rates by 8% compared to perfect environmental conditions. The average distribution shift rates ranged from 24 to 200 m year⁻¹ under climate change scenarios, implying that many tree species may not be able to keep up with climate change because of limited dispersal capacity, long generation time, and environmental heterogeneity. We suggest that climate-distribution models should include species demographic processes (e.g., fecundity, dispersal, colonization), biological traits (e.g., dispersal capacity, maturation age), and environmental heterogeneity (e.g., habitat fragmentation) to improve future predictions of species distribution shifts in response to changing climates.

© 2018 Elsevier B.V. All rights reserved.

* Corresponding author at: Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China.
E-mail address: wangwenj@missouri.edu (W.J. Wang).

1. Introduction

There is mounting evidence that many tree species shift their distributions in response to climate change. Paleo-ecological studies demonstrate that tree species distributions tracked climate change during past glaciations (Jump and Peñuelas, 2005) and shifted hundreds to thousands of meters per year during the recent glacial retreat (King and Herstrom, 1997). Recent studies generally agree that tree species distributions are shifting in response to recent climate change (Kharuk et al., 2007; Ralston et al., 2016; Vayreda et al., 2016). For example, Woodall et al. (2009) used region-wide forest inventory data to estimate tree species shifts in the eastern United States and found that many tree species are currently shifting northward at rates approaching 100 km/century. Predictions of future tree species distributions under changing climates suggest that many tree species will shift northward and upward in elevation (Nathan et al., 2011; Zolkos et al., 2015; Wang et al., 2015, 2016). Estimates from Dynamic Global Vegetation Models (DGVMs) indicate that the shift rates in boreal and temperate biomes may be higher than those in tropical biomes with the northernmost species shifting at a rate of 100 km/century (Malcolm et al., 2002). The niche model SHIFT suggests there is a high probability for tree species colonization within a zone of 10–20 km from species current boundaries over 100 years (Iverson et al., 2004). Recent studies suggest that many species may not move fast enough to track the changing climates and consequently might go extinct at the trailing edges and be replaced by subdominant local species or migrants from other locations, leading to population declines and ecosystem composition changes (Zhu et al., 2012; Corlett and Westcott, 2013; Wang et al., 2015, 2016; Sittaro et al., 2017). The changes in tree species distribution and composition have important consequences for biodiversity and ecosystem services such as carbon sequestration (Dawson et al., 2011; Garcia et al., 2014).

Species distribution shifts are a result of multi-scale demographic processes: fecundity, dispersal, colonization, growth, and mortality (Neilson et al., 2005; Thuiller et al., 2008). Fecundity occurs at site scales and is dependent on species biological traits such as maturation age and seed production (Clark, 1998). Dispersal occurs from hundreds of meters to a few kilometers per year and is regulated by dispersal mechanisms (e.g., wind, animal) and habitat connectivity, and ultimately determines the upper limits of distribution shifts and species' ability to track environmental changes in space and time (Schurr et al., 2007). Site-scale colonization and growth are regulated by site-scale biotic (e.g., competition) and regional-scale abiotic controls (e.g., temperature, precipitation, soil, terrain) (Wang et al., 2013; Liang et al., 2015). Among these processes, dispersal is important for inherently linking site-scale demography and competition, landscape-scale heterogeneity (e.g., habitat fragmentation), and regional-scale abiotic controls on tree species distribution shifts (Nathan and Muller-Landau, 2000; García et al., 2017).

The presentation of these demographic processes and their interactions with environmental changes is limited in current climate-distribution models such as niche models (e.g., BIOMD, SHIFT-DISTRIB) and biophysical process models (e.g., DGVMs, ED) (Ehrlén and Morris, 2015; Zurell et al., 2016; Urban et al., 2016). This is because niche and biophysical process models usually operate at relatively coarse spatial resolutions with grid cells ranging from 10 to 50 km and thus they are limited in their ability to spatially simulate the site- and landscape-scale processes associated with distribution shifts (Neilson et al., 2005; Thuiller et al., 2008). For example, although niche models efficiently account for regional-scale abiotic controls on species distribution using statistical methods, there is a lack of representation of underlying mechanisms (e.g., demography) driving distribution shifts (Guisan and Thuiller, 2005). Biophysical process models predict vegetation distribution by simulating biophysical processes, demography, and biotic interactions (Keenan et al., 2011), whereas they highly simplify site- and landscape-scale processes within each grid cell (McMahon et al., 2011). Individual tree species are grouped into plant functional

types and abiotic factors (e.g., soil, temperature, and precipitation) are assumed the same within each grid cell in biophysical models. Currently, no dispersal, unlimited dispersal, or uniform dispersal are commonly assumed in niche and biophysical process models when predicting future species distribution shifts (Iverson et al., 2011; McMahon et al., 2011). Recent efforts incorporate one or few factors limiting dispersal in niche and biophysical process models, such as density, dispersal, habitat fragmentation or biotic interactions (e.g., Meier et al., 2012; Boulangeat et al., 2014; Snell, 2014). Meier et al. (2012) assessed the influence of competition and habitat connectivity on species migration rates under climate change using a species distribution model; Snell (2014) simulated long-distance dispersal in a dynamic vegetation model. However, factors that affect dispersal and associated fecundity and colonization that are not accounted for constitutes a large uncertainty in projections of future species distribution shifts (Thuiller et al., 2008; Lurgi et al., 2015; Urban et al., 2016).

Species-specific, forest dynamic models, such as gap models (Pacala, 1996) and landscape models (Lischke et al., 2006; Wang et al., 2014a, 2014b) ideally have the potential to address these uncertainties through improving the predictions of future tree species distribution shifts. This is because they operate at fine scales (e.g., 10–500 m) and predict the response of individual tree species to environmental conditions by explicitly incorporating species demography and competition and the effects of environmental change on these processes (Shifley et al., 2017). Although these models have been extensively used to explore the species composition changes at site and landscape scales, the use of these forest dynamics models to make predictions of tree species distribution shifts is still rare especially at large scales (e.g., regional, continental) (Morin and Thuiller, 2009; He, 2011; Gutiérrez et al., 2016). Their use at large scales has been limited because they usually require a large amount of data and knowledge for parameterization, restricting their applications to a relatively small set of well-known tree species (Jektsch, 2008). In addition, it is computationally demanding to model fine-scale processes (e.g., individual species demography) at large scales (Strigul et al., 2008; Wang et al., 2013).

In this study, we demonstrate the applicability of a spatially explicit forest dynamic landscape model, LANDIS PRO for predicting tree species distribution shifts at leading edges. LANDIS PRO predicts tree species population and community dynamics as a result of site-scale tree species demography and competition, landscape-scale dispersal and disturbances, and regional-scale abiotic controls (Wang et al., 2014a). Extensive forest inventory data have been directly applied to parameterize over 50 common tree species in the eastern United States (e.g., Wang et al., 2013; Brandt et al., 2014; Luo et al., 2014; Wang et al., 2015, 2016, 2017; Xiao et al., 2017; Iverson et al., 2017; Jin et al., 2017, 2018). Specifically, we address 1) how do tree species biological traits and environmental heterogeneity affect tree species distribution shifts at leading edges and 2) how climate change will affect species distribution shift rates?

2. Material and methods

2.1. LANDIS PRO model

LANDIS PRO tracks number of trees and size of each age cohort for each tree species within each raster cell (Fig. 1, He et al., 2012; Wang et al., 2013). Species demography including growth, fecundity, dispersal, establishment, and mortality is mainly driven by species biological traits, such as maturation age, longevity, shade tolerance, dispersal distance, maximum size, maximum stand density index, minimum sprouting age, and maximum sprouting age. Growth occurs at each time step and is simulated using growth rates (age-DBH relationship) that vary among ecoregions to capture the environmental heterogeneity in soil, terrain, and climate. Trees cohorts generate seeds after reaching their maturation age and total seeds for each species in given raster cell are determined by mature tree density and fecundity capacity.

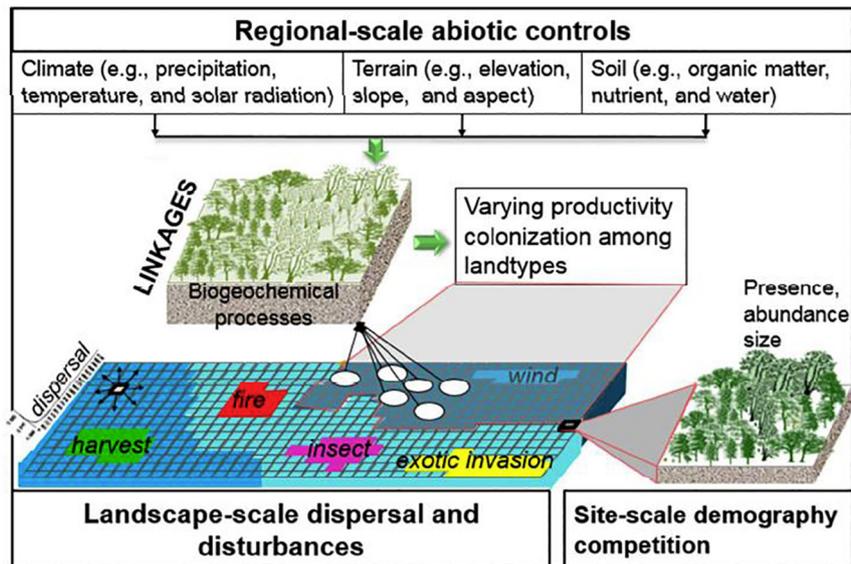


Fig. 1. Overall design of the spatial forest dynamic modeling approach for simulating tree species distribution shift in LANDIS PRO.

Seeds dispersal is determined by dispersal capacity and habitat connectivity. LANDIS PRO simulates dispersal using a generic dispersal kernel proposed by Clark (1998), where the probability (k) of seed travelling a specific distance (x), is:

$$k(x) = \left(\frac{c}{2\alpha\Gamma(1/c)} \right) \exp\left(-\frac{|x|^c}{\alpha}\right) \quad (1)$$

where c is a shape parameter (e.g. $c = 1.0$ was exponential curve, $c = 2.0$ was Gaussian curve, and $c < 1.0$ was fat-tailed curve). A value of 0.5 is used for all tree species to create fat-tailed kernels to capture the long-distance dispersal. $\Gamma(\cdot)$ is the gamma function, and α is a species-specific dispersal distance parameter compiled from the literature (e.g., Clark, 1998; Clark et al., 2005). The total seeds reaching a given forest site are accumulated from all mature trees within the dispersal kernel. Seedling establishment is determined by abiotic controls at each raster cell. Seedling colonization is regulated by seedling establishment probability (SEP), species shade tolerance, and available growing capacity. Trees die as a result of aging, competition, or disturbance. Competition is initiated once maximum growing capacity (MGSO) is reached. Competition-caused mortality is simulated using Yoda's self-thinning theory, where the number of trees decreases with increasing average tree size on the stand and follows the $-3/2$ rule and bigger trees and higher shade tolerance species generally have lower mortality rates (Yoda, 1963; Wang et al., 2013).

We stratified the regional abiotic controls in soil, terrain, and climate of the whole geographic region into land types to capture their effects on tree species population and community dynamics. Regional-scale abiotic controls mainly determined tree species fundamental niches; Demography, competition, and disturbances further modified species fundamental niches and ultimately determined species realized niches. Climate change affected tree species distribution and abundance. The effects of climate change were triggered by changes to tree species fundamental niches, which were simulated in LINKAGE III, an ecosystem model that modeled species' physiological responses to abiotic factors including climate, soil, and atmospheric conditions (Dijak et al., 2017) (Fig. 1). The fundamental niches from LINKAGE III were characterized as seedling establishment probability (SEP) and the maximum growing capacity (MGSO) (He et al., 1999; Wang et al., 2016). The MGSO and SEP were the same within a land type and different among land types. The estimated MGSO and SEP were then input into LANDIS PRO as model parameters to regulate species demography and competition at site scale (raster cell) within given land types (Fig. 1); for further details

on these parameter estimation processes for LANDIS PRO see Wang et al. (2015, 2016) and Dijak et al. (2017).

2.2. Test tree species with distinct biological traits

We identified four representative tree species in the eastern United States to simulate their dispersal and distribution shifts: red maple (*Acer rubrum*), loblolly pine (*Pinus taeda*), white oak (*Quercus alba*), and white ash (*Fraxinus americana*). We included these four tree species because their species-specific distance parameters (α) of dispersal kernel and reconstructed shift rates during past glaciations have been published (e.g., Clark, 1998; Delcourt and Delcourt, 1987). They also have distinct biological traits representing different life history strategies. Red maple has the youngest maturation age, highest fecundity, and longest dispersal distance by wind. White oak has the oldest maturation age, shortest dispersal distance by animal (e.g., squirrels, blue jays), and second highest fecundity. White ash and loblolly pine have intermediate maturation age, fecundity, and dispersal distance, but white ash has relatively longer dispersal distance and older maturation age than loblolly pine. Recent studies suggest that the four tree species will respond differently to climate change because of different species biological traits and breadth of climatic niches. From example, southern tree species, loblolly pine and widely distributed tree species, red maple may benefit from climate change, shift northward, and thus expand their distribution ranges; However, northern tree species, white ash may fare worse and contract their distribution ranges under future climates (Iverson et al., 2008; Wang et al., 2016). We compiled biological traits for each tree species including maturation age, longevity, shade tolerance, dispersal parameter α , age-size relationship, maximum size, and maximum stand density index from previous studies and literature (Table 1, Burns and Honkala, 1990; Wang et al., 2014b, 2015, 2016, 2017; Clark, 1998; Clark et al., 2005).

2.3. Experiment design

Multi-scale factors (e.g., demography, competition, climate change, habitat fragmentation) act synergistically to drive tree species distribution shifts in a real landscape. To disentangle the synergetic effects, we used a theoretical landscape (44,100 ha) to simulate tree species dispersal and distribution shifts at leading edges (Fig. 2). We divided the landscape into 3×3 grid of nine equal-sized zones. Each zone was comprised of 350×350 raster cells with a cell size of 60 m (Fig. 2). To represent species limited seed sources and low seed density at leading

Table 1

Species biological traits used in the LANDIS PRO model to predict tree species distribution shifts in a representative forest landscape in the Central Hardwood Forest Region, USA, compiled from previous studies and literature (Burns and Honkala, 1990; Wang et al., 2014b, 2015, 2017; Clark, 1998; Clark et al., 2005).

Common name	Species	Maturation age	Longevity	Shade tolerance	Dispersal distance parameter α	Vegetative probability	Maximum DBH (cm)	Maximum Stand density index (trees/ha)
Red maple	<i>Acer rubrum</i> L.	10	150	4	30.8	0.9	65	700
White oak	<i>Quercus alba</i> L.	40	300	4	12.9	0.6	75	570
White ash	<i>Fraxinus americana</i> L.	30	250	3	19.3	0.6	65	570
Loblolly pine	<i>P. taeda</i> L.	20	150	3	15.1	0.4	70	1100

edges, we located a single seed source for each tree species consisting of 100 mature trees at 40 years old in each of the corner raster cells of center zone. The rest of area was not populated with trees but was available for seed dispersal and colonization. The dimensions of each zone (21,000 m) guaranteed that the fastest dispersing species (e.g., red maple) could not disperse into the other three corner zones within 100 years to affect other species' dispersal through competition. We used the landscape for three experimental scenarios.

We parameterized a scenario under perfect abiotic controls without environmental heterogeneity (PNEH) by assuming that abiotic controls in soil, terrain, temperature, precipitation, solar radiation, and wind speed were 100% favorable for seedling establishment of four tree species across the landscape (SEP values were 1.0 for four tree species). There were no changes in abiotic conditions over the simulations (e.g., no climate change, disturbance, and land use change) (Fig. 2). In other words, seedlings were able to colonize any area where seeds could disperse and thus distribution shifts were driven by tree species demography.

We parameterized a scenario with current climate conditions and environmental heterogeneity (CCEH) by using a representative landscape from the central hardwood forest region of United States (CHFR). Environmental heterogeneity was the result of spatial variation in abiotic controls including soil, terrain, climate, and habitat fragmentation. The landscape was mostly forested but moderately fragmented by water, farmland, grassland, and urban areas (Fig. 2; Wang et al., 2015). The non-forested areas resulted in habitat fragmentation and barriers

for seed dispersal. We assumed there was no climate change, disturbance, and land use change in the landscape over the simulations. Tree species distribution shifts were potentially affected by species demography and environmental heterogeneity.

We parameterized a scenario with future climates and current environmental heterogeneity (FCEH) by using the same representative landscape in CHFR under GFDL A1FI climate conditions (IPCC, 2007) from 2000 to 2100 and was held constant hereafter (Fig. 2). On average, mean annual temperature was projected to increase by 6.0 °C and mean annual precipitation was projected to decrease by about 15 cm by end of the 21st century in this landscape under the GFDL A1FI climate change scenario. In this scenario, tree species distribution shifts were driven by tree species demography, environmental heterogeneity, and climate change.

For both the CCEH and FCEH scenarios, the representative landscape in CHFR was composed of 36 land types. The land type map (including 600 land types) was previously created for the whole CHFR by intersecting 100 ecological subsections (delineated by evaluation and integration of climate, physiography, lithology, soils, and potential natural communities) and 6 landforms (derived from digital elevation model) (Wang et al., 2015). We used the estimates of the maximum growing capacity (MGSO) and seedling establishment probability (SEP) for the 36 land types under current climate and GFDL A1FI climate scenarios from previous studies using the LINKAGES III ecosystem model (Wang et al., 2015, 2016). Inputs to LINKAGES III included soil data (e.g., organic matter, nitrogen, wilting point, field moisture

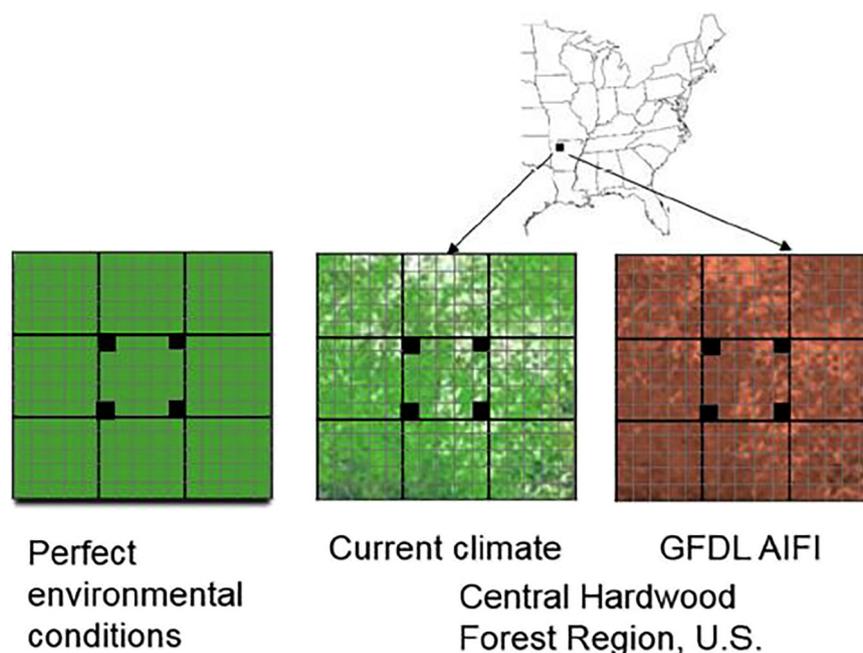


Fig. 2. Three scenarios for simulating tree species distribution shifts at leading edges based on theoretical landscape representing perfect environmental conditions (left), current climate conditions (middle), and GFDL A1FI climate conditions (right) for a representative landscape of the Central Hardwood Forest Region, U.S. A single seed source for each tree species with 100 mature trees at 40 years old was located in each of the corner raster cell of center zone (shown as four single black solid cells).

capacity) from the National Resources Conservation Service Soil Survey (<http://soils.usda.gov/>), wind speed data from the National Oceanic and Atmospheric Administration-National Climatic Data Center (NOAA-NCDC, 2002), current climate data (1980–2009) including daily precipitation at a 1/16th degree resolution and daily maximum and minimum temperature (Maurer et al., 2002), daily solar radiation at 1-km resolution from DAYMET (Thornton et al., 2014), and the downscaled daily climate data for the period 2080–2099 under GFDL A1FI scenario from the U. S. Geological Survey Center for Integrated Data Analysis (USGS CIDA) Geo Data Portal (Stoner, 2011).

2.4. Model simulation and data analysis

We conducted model simulations under the three scenarios for 200 years from 2000 to 2200 at 10-year time step with five replicates for each scenario to capture the stochasticity in the model. The distribution shift rates [m/year = total shift distance (m) / simulation years] for each individual species were calculated before tree species met without competition (about the first 100 simulation years). We reported the average distribution shift rates from five replicates and mapped the seed dispersal and distribution shifts from one replicate simulation because of extremely small variation among replicates. It was important to note that our emission scenario AIFI was not realistic because none of the emission scenarios represented a best guess of the future emissions (IPCC, 2007). Likewise, our simulation results were not to be interpreted as forecasts of futures, because complex interactions and feedbacks in the coupled human and natural systems make true predictions impossible (Liu et al., 2007). However, we believed some features (e.g., demography, competition) allow greater realism than many current alternatives.

We analyzed how shift rates were affected by tree species' biological traits, environmental heterogeneity, and climate change. We used one-way analysis of variance (ANOVA) to determine if environmental heterogeneity (PNEH vs. CCEH) or climate change (CCEH vs. FCEH) was statistically significant on the average distribution shift rates for each species. We also estimated the effects of environmental heterogeneity and climate change on distribution shifts for each individual species by calculating the percentage difference in shift rates between the PNEH and CCEH scenarios, CCEH and FCEH scenarios, respectively.

3. Results

The average distribution shift rates for red maple, loblolly pine, white ash, and white oak under the PNEH scenario within the first 100 simulation years were 200, 59, 56, and 30 m year⁻¹, respectively; The distribution shift rates for red maple, loblolly pine, white ash, and white oak in the CCEH and PCEH scenarios were 192, 54, 53, and 27 m year⁻¹ and 197, 56, 48, and 24 m year⁻¹, respectively (Fig. 3). Shift rates were relatively low in the first few decades for four tree species under three scenarios with very similar distance ranging from 800 m to 1000 m, followed by increases later in the simulation (Fig. 3). As a result of high shift rates red maple spread across the entire landscape under perfect environmental conditions by year 2150 and much of the landscape under current climate and GFDL A1FI climate conditions by year 2200 (Fig. 4). In contrast, loblolly pine, white ash, and white oak had much lower shift rates and their distributions never expanded very far from their initial seed sources, especially in the early decades under the three scenarios (Fig. 4).

Environmental heterogeneity (CCEH), on average, reduced shift rates by 8% compared to perfect environmental conditions (PNEH scenario) ($p < 0.05$ for four species, Table 2) and decreases were greater early in the simulation (13% in 2100) then later in the simulation (6% in 2100; Fig. 5a). The decreases resulting from environmental heterogeneity varied across species and were 12, 10, 6, and 4% for white oak, white ash, red maple, and loblolly pine, respectively.

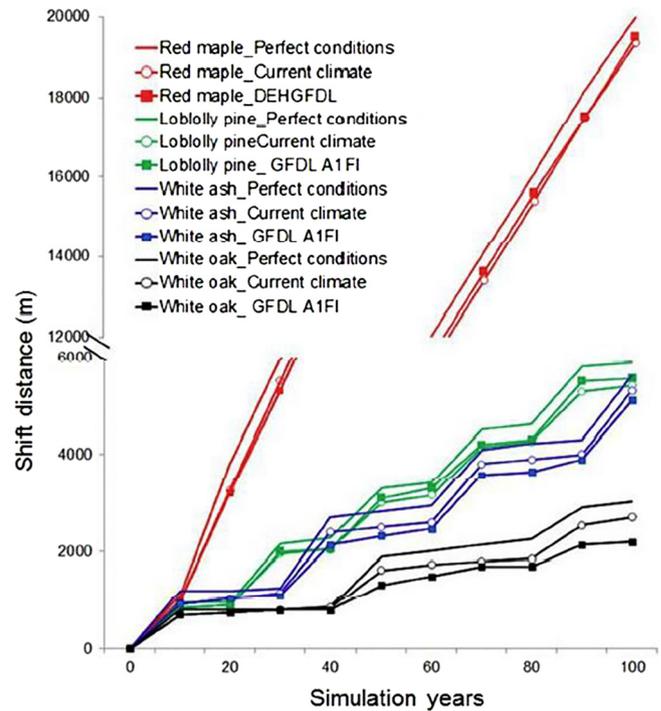


Fig. 3. Simulated distribution shift rates for red maple, white ash, white oak, and loblolly pine under perfect environmental conditions (solid lines), current climate (solid lines with hollow circle markers), and GFDL A1FI (solid lines with solid rectangle markers) climate conditions.

Compared to the current climate scenario, on average, the MGSO was decreased by 28%; the SEP values were increased by 60% and 16% for loblolly pine and red maple while they were decreased by 48% and 32% for white ash and white oak, respectively, under the GFDL A1FI climate change scenario. The shift rates on average were increased by 3% for red maple and loblolly pine and were decreased by 7% for white ash and white oak under climate change scenario (FCEH) compared to current change scenario from 2010 to 2100 ($p < 0.05$ for four species, Table 2) (Fig. 5b). Effects of climate change also varied by species and were 4, 3, -8, -5% for loblolly pine, red maple, white oak, and white ash, respectively.

4. Discussion

We investigated the effects of biological traits and environmental heterogeneity on tree species distribution shifts using a species-specific, forest dynamic model LANDIS PRO. Our results showed that distribution shifts lagged behind for all tree species in the early decades mainly because of limited seed sources from their low initial density and limited distribution. The limited mature trees and distributions constrained dispersal to realize their full dispersal ranges. This finding is consistent with the recent studies that suggest that distribution shifts are largely dependent on population density at the species leading edges (Kubisch et al., 2011). Thus, although red maple had the greatest dispersal capacity, it did not achieve long distance dispersal in the early decades because of limited seed sources. However, red maple juveniles quickly matured because of its youngest maturation age (10 years) and thereby increased density to create a larger seed source, leading to increases in shift rates in later decades. We suggest tree species distribution shift at leading edges under warming climates will likely not be rapid especially in early 21st century because of the usual low density near species' northern edges.

We captured the responses of individual tree species through incorporating species demography that was mostly driven by the species-specific biological traits, such as dispersal capacity, maturation age,

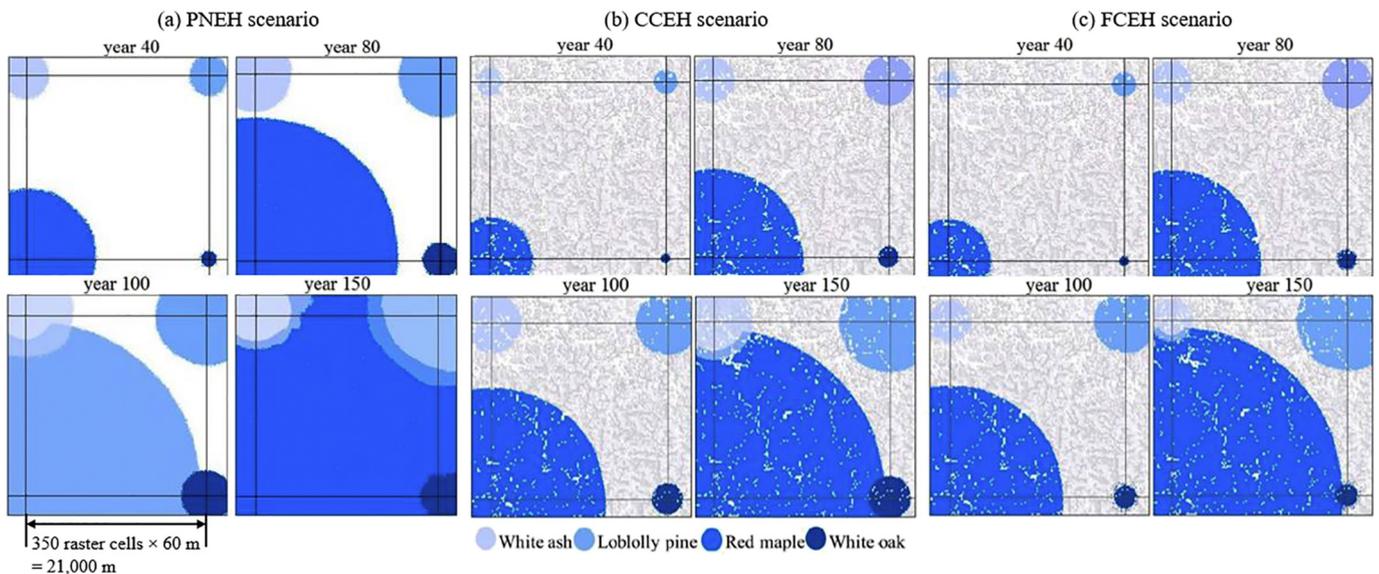


Fig. 4. Distribution shifts for red maple, white ash, white oak, and loblolly pine at year 40, 80, 100, and 150 in a theoretical landscape under perfect environmental conditions (a), in a representative landscape of the Central Hardwood Forest Region, U.S. under current climate conditions (b) and under GFDL AIFI climate conditions (c) (white color represented non-forested area and grey colors represented forested area with different shades of grey colors for different land types).

shade tolerance, vegetative probability, and fecundity. Although we did not vary biological traits to analyze the contribution of individual trait, among these biological traits, our results suggested that dispersal capacity (dispersal distance parameter α) and maturation rate might be the most important biological trait affecting shift rates. Because dispersal capacity determined the potential distance seeds could travel and maturation age determined tree generation time required for juveniles to mature and produce the next generation and thus delayed tree species distribution shifts. For example, wind-dispersed tree species red maple (with the largest dispersal distance parameter α (30.8) and youngest maturation age (10 years)) had the greatest shift rates whereas animal-dispersed tree species white oak (with the smallest dispersal distance parameter α (12.9) and oldest maturation age (40 years)) had the slowest shift rates. Thus, species demography and biological traits are important and should be incorporated to improve prediction of future tree species distributions under climate change.

Our modeling approach reasonably captured the lagged effects of environmental heterogeneity on tree species distribution shifts through affecting tree species demography such as colonization and dispersal. This finding confirms our expectations that abiotic controls are important for predicting tree species distribution shifts (Thuiller, 2004). Although we did not directly investigate the effects of different spatial resolutions on distribution shifts, coarse grid cells (e.g., 10–50 km) without environmental heterogeneity, that are used in niche and biophysical process models, may not capture the effects of the environmental heterogeneity (García-Valdes et al., 2015; Saltré et al., 2015). Our results also suggested that there were interactive effects between environmental heterogeneity and abundance of the seed source. Once

there was a sufficiently large seed source, the effects of environmental heterogeneity decreased and distribution shifts were mainly limited by dispersal capacity and maturation age. In our study, the representative landscape had low level of fragmentation and thus had low effects on distribution shift rates. Because of the non-linearity of threshold effects of fragmentation, with the increasing level of fragmentation and land use change, habitat fragmentation may have greater effects (García-Valdes et al., 2015; Dullinger et al., 2015).

In our study, we only used results in the first 100 simulation years without competition (before tree species met) to quantify species shift rates. Thus, we did not quantify the effects of competition on tree species shift rates (after tree species met), because competition, demography, and environmental heterogeneity acted in synergy, making quantifying the sole competition effects difficult. This was a limitation of our experimental design, which led to overestimates of tree species shift rates. It is important to note the importance of competition in affecting tree species distribution shifts because trees had to compete with the existing tree species for growing space (Meier et al., 2012). For example, red maple was not able to colonize on sites that were already fully-occupied by over 100 years-old white ash, white oak, or loblolly pine trees (e.g., Figs. 4 and 5 at 150 years). However, although our study overestimated the tree species distribution shift rates, our simulated shift rates of 24–197 m year⁻¹ were generally comparable to previous pollen-reconstructed rates and field data-based estimated rates, for example, 126–200 m year⁻¹ for red maple and 22–174 m year⁻¹ for southern pine in Delcourt and Delcourt (1987), 30–200 m year⁻¹ for North American wind-dispersed trees in Nathan et al. (2011), and 36 m year⁻¹ for animal-dispersed trees species in Clark et al. (2005). This finding generally agreed with previous studies that suggested the distribution shifts at leading edges may be largely determined by regional abiotic controls (e.g., temperature, and precipitation) and species biological traits such as dispersal capacity (Thuiller, 2004).

Although our results should not be interpreted to predict real species distribution rates, our overestimated simulated-shift rates of 24–197 m year⁻¹ support the hypothesis that many tree species may not be able to track climate change because the velocity of climate change in the Upper Midwest of United States was >1000 m year⁻¹ (Loarie et al., 2009). Such slow shift rates were mainly because of limited dispersal capacity and long generation time (e.g., decades) as well as environmental heterogeneity such as habitat fragmentation (Zhu et al., 2012; Sittaro et al., 2017). The failure of tree species to keep pace with

Table 2

Results of the analysis of variance (ANOVA) for environmental heterogeneity or climate change effects on the average distribution shift rates for four tree species.

	Environmental heterogeneity		Climate change	
	d.f.	p-Values	d.f.	p-Values
Red maple	1	<0.05	1	<0.05
Loblolly pine	1	<0.05	1	<0.05
White oak	1	<0.05	1	<0.05
White ash	1	<0.05	1	<0.05

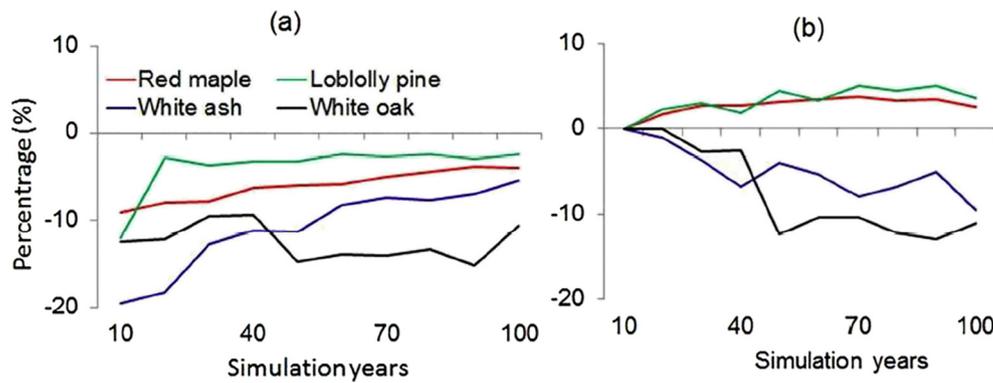


Fig. 5. Effects of environmental heterogeneity and climate change on tree species distribution shifts, which were calculated as the percent difference in shift rates between a landscape with perfect environmental conditions and a representative landscape with environmental heterogeneity (a) and between current climate conditions and climate change under the GFDL A1FI scenario (b).

climate change will lead to significant species distribution and composition changes, and consequently have potential negative consequences for biodiversity and ecosystem services. Forest management that favors tree species that are better adapted to future climates may promote resilience and adaptation to climate change (Buma and Wessman, 2013). For example, planting loblolly pine with limited seed source currently in CHFR may facilitate its adaptation to future climates (Brandt et al., 2014).

Our modeling resulting may be subject to uncertainties in conceptualization, parameterization, and validation, which can affect model simulation results. Our conceptual design was based on well-established ecological theories in population dynamics and stand dynamics. We verified our conceptual design by comparing how tree species shift rates were affected by species biological traits and environmental heterogeneity. Shift rates followed expected patterns among species and scenarios, which provided some verification of our conceptual design. We addressed parameterization uncertainties by evaluating the initial-ized and calibrated parameters against extensive Forest Inventory and Analysis (FIA) data in previous studies (Wang et al., 2014b). We assessed validation uncertainties by comparing the predicted shift rates against reconstructed estimates from pollen and genetic data and an experimental study.

5. Conclusion

We investigated the effects of biological traits and environmental heterogeneity on tree species distribution shifts using a species-specific, forest dynamic model LANDIS PRO. Dispersal capacity and maturation age might be the most important biological trait in determining tree species distribution shifts. Our results suggested that tree species may not be able to keep up with climate change because of limited dispersal capacity, long generation time, and environmental heterogeneity. Although it is unlikely our model can forecast species distribution shifts, we believe it has substantial greater realism than many current modeling approaches based assumptions of no dispersal, unlimited dispersal, or uniform dispersal. We believe our modeling approach can be used to develop more realistic predictions of how tree species will respond to changing climates to guide decision making in natural resource management concerning climate change adaptation and mitigation.

Acknowledgements

This project was funded by the USDA Forest Service Northern Research Station and Southern Research Station, a cooperative agreement from the United States Geological Survey Northeast Climate Science Center, and the University of Missouri-Columbia. Its contents are solely the responsibility of the authors and do not necessarily represent views of the Northeast Climate Science Center or the USGS. This manuscript is

submitted for publication with the understanding that the United States Government is authorized to reproduce and distribute reprints for Governmental purposes.

References

- Boulangeat, I., Damien, G., Thuiller, W., 2014. FATE-HD: a spatially and temporally explicit integrated model for predicting vegetation structure and diversity at regional scale. *Glob. Chang. Biol.* 20, 2368–2379.
- Brandt, L., He, H., Iverson, L., Thompson, F.R., Butler, P., Handler, S., Janowiak, M., Shannon, P.D., Swanston, C., Albrecht, M., Blume-Weaver, R., Deizman, P., DePuy, J., Dijak, W.D., Dinkel, G., Fei, S., Jones-Farrand, D.T., Leahy, M., Matthews, S., Nelson, P., Oberle, B., Perez, J., Peters, M., Prasad, A., Schneiderman, J.E., Shuey, J., Smith, A.B., Studyvin, C., Tirpak, J.M., Walk, J.W., Wang, W.J., Watts, L., Weigel, D., Westin, S., 2014. Central Hardwoods Ecosystem Vulnerability Assessment and Synthesis: A Report From the Central Hardwoods Climate Change Response Framework Project. U.S. Department of Agriculture, Forest Service, Northern Research Station. (254 p). Gen. Tech. Rep. NRS-124, Newtown Square, PA.
- Buma, B., Wessman, C.A., 2013. Forest resilience, climate change, and opportunities for adaptation: a specific case of a general problem. *For. Ecol. Manag.* 36, 216–225.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America: 1. Conifers; 2. hardwoods.* Agriculture Handbook. 654. USDA Forest Service, Washington, D.C., USA (tech. Coord.).
- Clark, J.S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.* 152, 204–224.
- Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F., Parker, V.T., 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* 86 (10), 2684–2694.
- Corlett, R.T., Westcott, D.A., 2013. Will plant movements keep up with climate change? *Trends Ecol. Evol.* 28, 482–488.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–58.
- Delcourt, P.A., Delcourt, H.R., 1987. *Long-term Forest Dynamics of the Temperate Zone.* Springer-Verlag, New York.
- Dijak, W., Hanberry, B., Fraser, J.S., He, H.S., Thompson III, F.R., Wang, W.J., 2017. Revision and application of the LINKAGES model to simulate forest growth in Central Hardwood landscapes in response to climate change. *Landsc. Ecol.* 32 (7), 1365–1384.
- Dullinger, S., Dendoncker, N., Gattringer, A., Leitner, M., Mang, T., Moser, D., Múcher, C., Plutzer, C., Rounsevell, M., Willner, W., Zimmermann, N., Hülber, K., 2015. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. *Divers. Distrib.* 21, 1375–1387.
- Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* 18, 303–314.
- García, R.A., Cabeza, M., Rahbek, C., Araújo, M.B., 2014. Multiple dimensions of climate change and their implications for biodiversity. *Science* 344 (6183), 1247579.
- García, C., Klein, E.K., Jorsano, P., 2017. Dispersal processes driving plant movement: challenges for understanding and predicting distribution range shifts in a changing world. *J. Ecol.* 105, 1–5.
- García-Valdes, R., Svenning, J.C., Zavala, M.A., Purves, D.W., Araujo, M.B., 2015. Evaluating the combined effects of climate and land-use change on tree species distributions. *J. Appl. Ecol.* 52, 902–912.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Gutiérrez, A.G., Snell, R.S., Bugmann, H., 2016. Using a dynamic forest model to predict tree species distributions. *Glob. Ecol. Biogeogr.* 25, 347–358.
- He, H.S., 2011. Challenges of forest landscape modeling-simulating large landscapes and validating results. *Landsc. Urban Plan.* 100, 400–402.
- He, H.S., Mladenoff, D.J., Crow, T.R., 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecol. Model.* 114, 213–233.
- He, H.S., Wang, W.J., Fraser, J.S., Shifley, S.R., Larsen, D.R., 2012. LANDIS: A Spatially Explicit Model of Forest Landscape Disturbance, Management, and Succession. LANDIS PRO 7.0 USERS GUIDE. School of Natural Resources, University of Missouri, Columbia, MO, USA.

- IPCC, 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Iverson, L.R., Schwartz, M.W., Prasad, A.M., 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Glob. Ecol. Biogeogr.* 13, 209–219.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *For. Ecol. Manage.* 254, 390–406.
- Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2011. Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14, 1005–1020.
- Iverson, L.R., Thompson, F.R., Matthews, S., Peters, M., Prasad, A., Dijk, W.D., Fraser, J., Wang, W.J., Hanberry, B., He, H.S., Janowiak, M., Butler, P., Brandt, L., Swanston, C., 2017. Multi-model comparison on the effects of climate change on tree species in the eastern US: results from an enhanced niche model and process-based ecosystem and landscape models. *Landsc. Ecol.* 32 (7), 1327–1346.
- Jektsch, F., 2008. The state of plant population modelling in light of environmental change. *Perspect. Plant Ecol. Evol. Syst.* 9, 171–189.
- Jin, W., He, H.S., Thompson III, F.R., Wang, W.J., Fraser, J.S., Shifley, S.R., Hanberry, B.B., Dijk, W.D., 2017. Future forest aboveground carbon dynamics in the central United States: the importance of forest demographic processes. *Sci. Rep.* 7, 41821.
- Jin, W., He, H.S., Shifley, S.R., Wang, W.J., Kabrick, J.M., Davidson, B.K., 2018. How can prescribed burning and harvesting restore shortleaf pine-oak woodland at the landscape scale in central United States? Modeling joint effects of harvest and fire regimes. *For. Ecol. Manage.* 410, 201–210.
- Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8, 1010–1020.
- Keenan, T., Serra, J.M., Lloret, F., Ninyerola, M., Sabate, S., 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO2 matters! *Glob. Chang. Biol.* 17, 565–579.
- Kharuk, V.I., Ranson, K.J., Dvinskaya, M., 2007. Evidence of evergreen conifer invasion into larch dominated forests during recent decades in central Siberia. *Eurasian J. For. Res.* 10 (2), 163–171.
- King, G.A., Herstrom, A.A., 1997. Holocene migration rates objectively determined from fossil pollen data. In: Huntley, B., Cramer, W., Marsa, A.V., Prentice, I.C., Allen, J.R.M. (Eds.), *Past and Future Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*. Springer-Verlag, New York, New York, USA, pp. 91–102 (1997).
- Kubisch, A., Poethke, H.J., Hovestadt, T., 2011. Density-dependent dispersal and the formation of range borders. *Ecography* 34, 1002–1008.
- Liang, Y., He, H.S., Wang, W.J., Fraser, J.S., Wu, Z.W., 2015. The effects of site-scale processes in forest landscape models on prediction of tree species distribution. *Ecol. Model.* 300, 89–101.
- Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S., Löffler, T.J., 2006. TreeMig: a forest landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecol. Model.* 199, 409–420.
- Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., Ostrom, E., Ouyang, Z., Provencher, W., Redman, C.L., Schneider, S.H., Taylor, W.W., 2007. Complexity of coupled human and natural systems. *Science* 317, 1513–1516.
- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. *Nature* 462, 1052–1057.
- Luo, X., He, H.S., Liang, Y., Wang, W.J., Wu, Z.W., Fraser, J.S., 2014. Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China. *Landsc. Ecol.* 29, 1187–1200.
- Lurgi, M., Brook, B.W., Saltré, F., Fordham, D.A., 2015. Modelling range dynamics under global change: which framework and why? *Methods Ecol. Evol.* 6 (3), 247–256.
- Malcolm, J.R., Markham, A., Neilson, R.P., Garaci, M., 2002. Estimated migration rates under scenarios of global climate change. *J. Biogeogr.* 29, 835–849.
- Maurer, E.P., Wood, A.W., Adam, J.C., Lettenmaier, D.P., Nijssen, B., 2002. A long-term hydrologically-based data set of land surface fluxes and states for the conterminous United States. *J. Clim.* 15, 3237–3251.
- McMahon, S.M., Harrison, S.P., Armbruster, W.S., 2011. Improving assessment and modeling of climate change impacts on global terrestrial biodiversity. *Trends Ecol. Evol.* 26 (5), 249–259.
- Meier, E.S., Lischke, H., Schumatz, D.R., Zimmermann, N.E., 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Glob. Ecol. Biogeogr.* 21, 164–178.
- Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90 (5), 1301–1313.
- Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15 (7), 211–219.
- Nathan, R., Horvitz, N., He, Y.P., Kuparinen, A., Schurr, F.M., Katul, G.G., 2011. Spread of North American wind-dispersed trees in future environments. *Ecol. Lett.* 14, 211–219.
- Neilson, R.P., Pitelka, L.F., Solomon, A.M., Nathan, R., Midgley, G.F., Fragoso, J.M., Lischke, H., Thompson, K., 2005. Forecasting regional to global plant migration in response to climate change. *Bioscience* 55 (9), 749–759.
- NOAA National Climatic Data Center, 2002. Enhanced Hourly Wind Station Data for the Contiguous United States, DSI-6421. [indicate subset used]. NOAA National Centers for Environmental Information [access date].
- Pacala, S.W., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Ralston, J., Deluca, W.V., Feldman, R.E., King, D.I., 2016. Population trends influence species ability to track climate change. *Glob. Chang. Biol.* 23, 1390–1399.
- Saltré, F., Duputié, A., Gaucherel, C., Chuine, I., 2015. How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. *Glob. Chang. Biol.* 21, 897–910.
- Schurr, F.M., Midgley, G.F., Rebelo, A.G., Reeves, G., Higgins, S.I., 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. *Glob. Ecol. Biogeogr.* 16, 449–459.
- Shifley, S.R., He, H.S., Lischke, H., Wang, W.J., Jin, W., Gustafson, E.J., Thompson, J.R., Thompson III, F.R., Dijk, W.D., Yang, J., 2017. The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. *Landsc. Ecol.* 32, 1307–1325.
- Sittaro, F., Paquette, A., Messier, C., Nock, C.A., 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Glob. Chang. Biol.* <https://doi.org/10.1111/gcb.13622>.
- Snell, R.S., 2014. Simulating long-distance dispersal in a dynamic vegetation model. *Glob. Ecol. Biogeogr.* 23 (1), 89–98.
- Stoner, A.M.K., 2011. Downscaled climate projections by Katharine Hayhoe. http://cida.usgs.gov/climate/hayhoe_projections.jsp (Accepted 1 Nov 2011).
- Strigul, N., Pristiniski, D., Purves, D., Dushoff, J., Pacala, S., 2008. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecol. Monogr.* 78, 523–545.
- Thornton, P.E., Thornton, M.M., Mayer, B.W., Wilhelm, N., Wei, Y., Devarakonda, R., Cook, R.B., 2014. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2, 1980–2012. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Thuiller, W., 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography* 27, 165–172.
- Thuiller, W., Albert, C.H., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, G., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E., 2008. Predicting global change impacts on plant species distributions: future challenges. *Perspect. Plant Ecol. Evol. Syst.* 9, 137–152.
- Urban, M.C., Bocedi, G., Hendry, A.P., Mhoub, J.B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D., Huth, A., John, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A., Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate change. *Science* 353, 1113.
- Vayreda, J., Martínez-Vilalta, J., Gracia, M., Canadell, J.G., Retana, J., 2016. Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. *Glob. Chang. Biol.* 22, 3984–3995.
- Wang, W.J., He, H.S., Spetich, M.A., Shifley, S.R., Thompson III, F.R., Larsen, D.R., Fraser, J.S., Yang, J., 2013. A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. *Ecosphere* 4 (9), 106.
- Wang, W.J., He, H.S., Fraser, J.S., Thompson, I.I.F.R., Shifley, S.R., Spetich, M.A., 2014a. LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. *Ecography* 37, 225–229.
- Wang, W.J., He, H.S., Spetich, M.A., Shifley, S.R., Thompson III, F.R., Dijk, W.D., Wang, Q., 2014b. Evaluating forest landscape model predictions using empirical data and knowledge. *Environ. Model. Softw.* 62, 230–239.
- Wang, W.J., He, H.S., Thompson III, F.R., Fraser, J.S., Hanberry, B.B., Dijk, W.D., 2015. Importance of succession, harvest, and climate change in determining future forest composition changes in U.S. Central Hardwood Forests. *Ecosphere* 6 (12), 277.
- Wang, W.J., He, H.S., Thompson III, F.R., Fraser, J.S., 2016. Landscape-and regional-scale shifts in forest composition under climate change in the Central Hardwood Region of the United States. *Landsc. Ecol.* 31, 149–163.
- Wang, W.J., He, H.S., Thompson III, F.R., Fraser, J.S., Dijk, W.D., 2017. Changes in forest biomass and tree species distribution under climate change in the northeastern United States. *Landsc. Ecol.* 32 (7), 1399–1413.
- Woodall, C.W., Oswalt, C.M., Westfall, J.A., Perry, C.H., Nelson, M.D., Finley, A.O., 2009. An indicator of tree migration in forests of the eastern United States. *For. Ecol. Manage.* 257, 1434–1444.
- Xiao, J.T., Liang, Y., Thompson, J., He, H.S., Wang, W.J., 2017. The formulations of site-scale processes affect landscape scale forest change predictions: a comparison between LANDIS PRO and LANDIS-II forest landscape models. *Landsc. Ecol.* 32, 1347–1363.
- Yoda, K., 1963. Self-thinning in overcrowded pure stands under cultivate and natural conditions. *J. Biol. Osaka City Univ.* 14, 107–129.
- Zhu, K., Woodall, C.W., Clark, J.S., 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Glob. Chang. Biol.* 18 (3), 1042–1052.
- Zolkos, S.G., Jantz, P., Cormier, T., Iverson, L.R., McKenney, D.W., Goetz, S.J., 2015. Projected tree species distribution under climate change: implications for ecosystem vulnerability across projected areas in the eastern United States. *Ecosystems* 18, 202–220.
- Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Munkemüller, T., Gravel, D., Dullinger, S., Norman, S., Schifffers, K.H., Moore, K.A., Zimmermann, N.E., 2016. Benchmarking novel approaches for modelling species range dynamics. *Glob. Chang. Biol.* 22, 2651–2664.