

How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change

Yu Liang^{1,2}  | Matthew J. Duveneck² | Eric J. Gustafson³  | Josep M. Serra-Diaz^{2,4} | Jonathan R. Thompson²

¹CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, The Chinese Academy of Sciences, Shenyang, Liaoning, China

²Harvard Forest, Harvard University, Petersham, MA, USA

³Institute for Applied Ecosystem Studies, Northern Research Station, USDA Forest Service, Rhinelander, WI, USA

⁴Ecoinformatics and Biodiversity Section, Department of Biosciences, Aarhus University, Aarhus C, Denmark

Correspondence

Yu Liang, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, The Chinese Academy of Sciences, Shenyang, Liaoning, China.
Email: liangyu@iae.ac.cn

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Abstract

Climate change is expected to cause geographic shifts in tree species' ranges, but such shifts may not keep pace with climate changes because seed dispersal distances are often limited and competition-induced changes in community composition can be relatively slow. Disturbances may speed changes in community composition, but the interactions among climate change, disturbance and competitive interactions to produce range shifts are poorly understood. We used a physiologically based mechanistic landscape model to study these interactions in the northeastern United States. We designed a series of disturbance scenarios to represent varied disturbance regimes in terms of both disturbance extent and intensity. We simulated forest succession by incorporating climate change under a high-emissions future, disturbances, seed dispersal, and competition using the landscape model parameterized with forest inventory data. Tree species range boundary shifts in the next century were quantified as the change in the location of the 5th (the trailing edge) and 95th (the leading edge) percentiles of the spatial distribution of simulated species. Simulated tree species range boundary shifts in New England over the next century were far below (usually <20 km) that required to track the velocity of temperature change (usually more than 110 km over 100 years) under a high-emissions scenario. Simulated species' ranges shifted northward at both the leading edge (northern boundary) and trailing edge (southern boundary). Disturbances may expedite species' recruitment into new sites, but they had little effect on the velocity of simulated range boundary shifts. Range shifts at the trailing edge tended to be associated with photosynthetic capacity, competitive ability for light and seed dispersal ability, whereas shifts at the leading edge were associated only with photosynthetic capacity and competition for light. This study underscores the importance of understanding the role of interspecific competition and disturbance when studying tree range shifts.

KEYWORDS

climate change, competition, disturbance, Land Use Plus (LU⁺), LANDIS-II, PnET-Succession, seed dispersal, tree range shift

1 | INTRODUCTION

Numerous studies have predicted climatically suitable locations (potential range) of tree species (Iverson, Prasad, Matthews, & Peters, 2008; Parmesan & Yohe, 2003; Svenning & Skov, 2004; Thuiller, 2003; Thuiller et al., 2008). It is assumed that climate change will directly affect tree species' establishment, growth, mortality, and interspecific competition, and trees will migrate to follow the climate conditions where they can best compete (Chen, Hill, Ohlemuller, Roy, & Thomas, 2011; Lenoir, Gégout, Marquet, De Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003; Van der Putten, 2012). Climate-induced tree migration changes spatial patterns of species' abundance (Ehrlen & Morris, 2015; Murphy, VanDerWal, & Lovett-Doust, 2010; VanDerWal, Shoo, Johnson, & Williams, 2009), often resulting in a shift in the boundary of a tree species' range (Monleon & Lintz, 2015; Serra-Diaz et al., 2016). Tree species range boundaries have shifted in response to altered climatic conditions in past millennia (Davis & Shaw, 2001), but the expected rate and spatial properties of future range boundary shifts in the next century will be affected by interacting processes of seed dispersal, disturbance regimes, and land use patterns (Higgins, Lavorel, & Revilla, 2003; Ibanez, Clark, & Dietze, 2008; Iverson & Mckenzie, 2013; Serra-Diaz et al., 2016; Vanderwel & Purves, 2013), many of which are not well understood because they have seldom been studied at appropriate spatial and temporal scales.

Tree species range expansion into newly suitable habitat by migration may not keep pace with the speed of future climate change, resulting in a migration lag (Bertrand et al., 2011; Woodall et al., 2013; Zhu, Woodall, & Clark, 2012). Climate-induced tree species range shifts usually depend on (i) how far seeds disperse to new sites at a given timeframe, (ii) how readily arriving seeds can produce established cohorts, (iii) how quickly newly established cohorts reach sexual maturity, (iv) competition with resident and other migrating species, and (v) natural and anthropogenic disturbances (e.g., harvest, wildfire, insects, and disease) that interact to affect competition for light and water (Angert et al., 2011; Ibanez, Clark, Ladeau, & Hille Ris Lambers, 2007; Moran & Ormond, 2015). Because trees need time to reach reproductive maturity (10–40 years) and then disperse seeds that establish new cohorts, tree migration rate is not constant through time (Boulangeat, Gravel, & Thuiller, 2012; Loehle, 1998, 2000; Solomon & Kirilenko, 1997). Even when migrants are suitable in new regions, they face competition with established species, especially for light (Corlett & Westcott, 2013; Svenning, Gravel, Holt, & Al, 2014; Van der Putten, 2012; Xu, Gertner, & Scheller, 2012). Thus, tree range boundary shifts are expected to be slow and episodic, and under a changing climate, most established populations may occur where the climate is suboptimal (Davis & Shaw, 2001; McGill, 2012; Vanderwel, Lyutsarev, & Purves, 2013; Zhu et al., 2012). These factors also partially explain lagged responses of forests to environmental shifts (Bertrand et al., 2016). Understanding such lagged responses and comparing them to available abiotic metrics of the pace of climate change (e.g., velocity of climate change; Loarie

et al., 2009) constitute a major challenge in ecology and conservation.

Disturbance is expected to interact with climate change and influence the rate and characteristics of future range shifts (Caplat & Anand, 2009; Dale, Joyce, McNulty, & Neilson, 2001; Running, 2008; Serra-Diaz, Scheller, Syphard, & Franklin, 2015; Vanderwel, Coomes, & Purves, 2013). Moderate and low intensity disturbances create canopy gaps, increasing light levels and opportunities for establishment of new cohorts (Caplat & Anand, 2009; Caplat, Anand, & Bauch, 2008; Lugo & Scatena, 1996). Frequent or high intensity disturbances could reduce establishment by removing reproductive adults, and also modify the abundance of some resources (e.g., light and water) for new arrivals, particularly benefitting early successional species (Moran & Ormond, 2015). In addition, attributes of disturbance regimes (i.e., patch size, frequency and intensity) alter the spatial pattern of dispersal barriers and bridges, further complicating the prediction of future range boundary shifts. Previous studies have shown that disturbances interacting with climate change can modify species composition (Brown & Wu, 2005; He, Mladenoff, & Gustafson, 2002; Scheller & Mladenoff, 2005), but there is little consensus on how such interactions will affect tree range boundary shifts, making this an important topic for research. Studies have shown that disturbances could either accelerate forest regeneration and migration (Johnstone & Chapin, 2003; Vanderwel & Purves, 2013; Vanderwel, Coomes et al., 2013), impede them (Boulangeat et al., 2014; Everham & Brokaw, 1996; Lugo & Scatena, 1996; Munier, Hermanutz, Jacobs, & Lewis, 2010; Thom et al., 2017), or both (Hanberry & Hansen, 2015; Moran & Ormond, 2015; Serra-Diaz et al., 2015), through their influence on tree population dynamics (e.g., size and age composition of population) and forest recovery rate. Given the importance of canopies in determining the abiotic conditions that control forest regeneration (Dobrowski et al., 2015), it is crucial to understand how various intensities of disturbances may enhance or hinder species range shifts.

Improving our understanding of how climate change and disturbances interact with local demographic and ecological processes (e.g., dispersal and competition) to affect species range boundary shifts is important for predicting future forest responses to global change (Higgins et al., 2003). Here, our objective was to understand the interactive effects among forest disturbance, tree species competition, and seed dispersal to better understand the potential for climate-induced tree species migration (quantified by range boundary shifts) in the New England region of the northeastern United States. Some northern tree species (i.e., balsam fir [*Abies balsamea*], red spruce [*Picea rubens*]) have only a southern range border within New England, while more southerly species (i.e., Northern red oak [*Quercus rubra*], American basswood [*Tilia americana*]) have only a northern range border within New England. Thus, we considered the northern boundaries for southerly species to be the leading edges of species distribution, and the southern boundaries for northerly species as the trailing edges. We designed a series of disturbance scenarios to evaluate the effect of disturbance, represented as gradients of disturbance extent and intensity. These scenarios were simulated

in the context of climate change (under a high-emission scenario) using a process-based forest landscape model that uses physiological first principles to mechanistically account for the effects of temperature, light, and water availability on photosynthesis (competition and growth), and includes simulation of seed dispersal and establishment. Our approach was to: (i) drive the growth, establishment and competition of the current forest communities in New England with the temperature and precipitation of a high-emission climate future and evaluate the velocity of the associated boundary shifts in tree species' ranges at their leading and trailing edges under the alternative disturbance scenarios, and (ii) further evaluate how competition-related life-history traits (e.g., competitive ability for light, drought tolerance) and seed dispersal characteristics (e.g., distribution of seed dispersal distances) interact with climate change and disturbance regimes to determine range boundary shifts. We hypothesized that the velocity of range shifts will be slower than the velocity of climate change, disturbance will accelerate the range shifts by increasing recruitment rates of migrants, and that boundary shifts at both leading and trailing edge will be larger for species with longer seed dispersal capability.

2 | MATERIALS AND METHODS

2.1 | Study area and species

The study area was the 13 million hectares of forest in the northeastern United States (i.e., the states of Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, and Vermont, collectively known as New England). Average annual temperature in New England increased by 0.8°C or more during the 20th century (Lindsay & Stephen, 2014), and is predicted to rise by another 4.9–6.2°C by 2100 under high-emissions climate change scenarios based on data derived from the United States Geological Survey (USGS) climate data portal (<https://cida.usgs.gov/gdp/>, Accessed 6/30/2016). Within the region, observed mean annual precipitation ranges from 79 to 255 cm with the greatest precipitation found at high elevations (Daly & Gibson, 2002). Under most climate change scenarios, precipitation is expected to increase in winter and spring; fall and summer future precipitation is projected to be more variable (Kunkel et al., 2013). Lengthened growing seasons, driven by increased temperature in the next century, are expected to increase net forest productivity (Duveneck & Thompson, 2017; Keenan, Gray, & Friedl, 2014), although Gustafson, de Bruijn, Miranda, Sturtevant, and Kubiske (2017) found that an increase of 6°C caused productivity to decrease because of elevated respiration rates.

Forests in New England are still recovering from widespread lumbering and clearing for agriculture in the colonial era (Thompson, Carpenter, Cogbill, & Foster, 2013). Forest cover is approximately 80% of land area in New England and forest types span a gradient from northern temperate hardwood forest in the south to boreal conifer forest in the north (Duveneck, Thompson, & Tyler Wilson, 2015). We simulated competitive interactions among 32 tree species (Table 1). Ten species are widely distributed throughout and beyond

New England (i.e., north and south range limits are outside of New England). Twelve species are found only in southern New England and have only a northern range border in the study area (Figure 1), which we term a leading edge species (e.g., Northern red oak, black cherry [*Prunus serotina*] and sweet birch [*Betula lenta*]). Ten species are found only in northern New England and have only a southern range border in the study area (Figure 1), and are termed a trailing edge species (e.g., balsam fir, red spruce, and paper birch [*Betula papyrifera*]). Range boundaries for both the leading and trailing edge species are consistent with Little's tree species range boundaries (Little, 1971) (Figure 1), which was downloaded from <http://esp.cr.usgs.gov/data/little/>.

2.2 | Calculation of the velocity of climate change in the next century

To evaluate how species movement compared to climate movement, we calculated the latitudinal velocity of temperature and precipitation changes across New England (km/year) using methods modified from Loarie et al. (2009) in each pixel of the study area (250 m resolution). We calculated the velocity of climate change as the ratio of temporal and spatial gradients of annual mean temperature ($^{\circ}\text{C year}^{-1}/^{\circ}\text{C km}^{-1} = \text{km year}^{-1}$) and total annual precipitation ($\text{mm year}^{-1}/\text{mm km}^{-1} = \text{km year}^{-1}$) within each 250 m pixel. The temporal gradient of climate change describes how the climate is expected to change over time while the spatial gradient of climate describes the rate of observed climate is expected to change in space. We calculated the temporal gradient as the change in projected climate from 2000 to 2100 using the Intergovernmental Panel on Climate Change high-emission future (RCP 8.5) (Riahi et al., 2011) coupled to the National Center for Atmospheric Research (NCAR) COMMUNITY CLIMATE SYSTEM MODEL v4.0 (CCSM4). We accessed these climate data downscaled to 12 km grids from the USGS climate data portal. Area weighted annual temperature and precipitation were derived for 25 previously delineated homogenous but noncontiguous climate regions throughout New England (Duveneck, Thompson, Gustafson, Liang, & de Bruijn, 2016). Using each annual time series spatial layer of climate change, we calculated the temporal gradient of changing temperature ($^{\circ}\text{C}/\text{year}$) and precipitation (mm/year) within each climate region with linear regression using all the annual climate change layers to calculate a "predicted" annual rate of change for each climate region.

We calculated the spatial gradient of climate using historical (1981–2010) average annual temperature and precipitation derived from PRISM (Daly & Gibson, 2002). Specifically, we calculated the spatial gradient using a 9×9 moving window (81 pixel kernel). Within the moving window, we calculated the maximum difference between the centroid and its neighbor grid cells as the spatial gradient on an algorithm from generalized and separable Sobel operators (Danielsson & Seger, 1990). To avoid infinite velocities caused by flat spatial gradients, we introduced uniformly distributed random noise (between -0.016 and 0.016°C for temperature and between -0.16 and 0.16°C for precipitation). As expected, mountainous regions had

TABLE 1 Selected species life-history traits, and current (the initial year) and projected (the simulated year 100) mean latitude for each species' range boundary under the succession-only scenario

Representative species		FoIN ^a (% wt.)	H3/H4 ^b (m pressure head)	HalfSat ^c ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Effective seed dispersal distance ^d (m)	Current latitude (°)	Projected latitude (°)
Leading edge species	Northern red oak (<i>Quercus rubra</i>)	2.5	111/152	437	30	44.202	44.224
	Black cherry (<i>Prunus serotina</i>)	2.8	111/152	519	100	44.616	44.707
	Sweet birch (<i>Betula lenta</i>)	2.26	105/145	250	100	42.446	42.459
	White oak (<i>Quercus alba</i>)	2.5	118/160	519	30	42.696	42.733
	Black oak (<i>Quercus velutina</i>)	2.7	111/152	437	70	42.196	42.229
	American basswood (<i>Tilia americana</i>)	2.6	111/152	356	75	44.587	44.613
	American elm (<i>Ulmus americana</i>)	2.3	105/145	437	90	44.775	44.809
	Scarlet oak (<i>Quercus coccinea</i>)	2	118/160	519	50	41.443	41.492
	Gray birch (<i>Betula populifolia</i>)	2.26	105/145	519	100	45.078	45.091
	Pignut hickory (<i>Carya glabra</i>)	2.6	111/152	519	50	41.453	41.462
	Pitch pine (<i>Pinus rigida</i>)	2.3	118/160	437	90	42.723	42.676
	Chestnut oak (<i>Quercus prinus</i>)	2.39	111/152	437	50	41.697	41.711
Trailing edge species	Balsam fir (<i>Abies balsamea</i>)	1.4	105/145	356	30	43.547	43.452
	Red spruce (<i>Picea rubens</i>)	1.2	118/160	437	80	43.588	43.593
	Paper birch (<i>Betula papyrifera</i>)	2.3	105/145	519	100	43.064	43.193
	White spruce (<i>Picea glauca</i>)	1.4	118/160	437	30	44.042	44.039
	Northern white-cedar (<i>Thuja occidentalis</i>)	1.3	105/145	437	45	43.994	44.106
	Black spruce (<i>Picea mariana</i>)	1.2	118/160	437	79	43.971	43.974
	Black ash (<i>Fraxinus nigra</i>)	2.7	111/152	519	200	43.175	43.238
	Balsam poplar (<i>Populus balsamifera</i>)	2.4	100/140	600	100	44.116	44.124
	Tamarack (native) (<i>Larix laricina</i>)	2.3	118/160	600	100	43.555	43.682
	Red pine (<i>Pinus resinosa</i>)	1.7	118/160	519	100	43.087	43.089

Both the leading edge species and the trailing edge species are ordered by species' occurrence (number of cells occupied on the landscape).

^aFoliar nitrogen; represents photosynthetic capacity.

^bDrought tolerance parameters; represents competitive ability for water.

^cLight level when photosynthesis is half of its full sunlight rate; represents competitive ability for light.

^dEffective seed dispersal distance; represents seed dispersal ability.

greater spatial variation in both temperature and precipitation, and flat regions had less spatial variation.

2.3 | Simulation of tree species range shifts

We used the LANDIS-II (v6.0) spatially explicit forest landscape modeling framework (Scheller et al., 2007) to dynamically simulate forest

range shifts as a function of tree species dispersal, establishment and competition in response to climate inputs. LANDIS-II tracks species as individual age cohorts and simulates their establishment and growth as a function of seed dispersal from mature cohorts on nearby cells, establishment probability (calculated dynamically as a function of light and soil water on a site), growth and intercohort competition, with succession dynamics being an emergent property

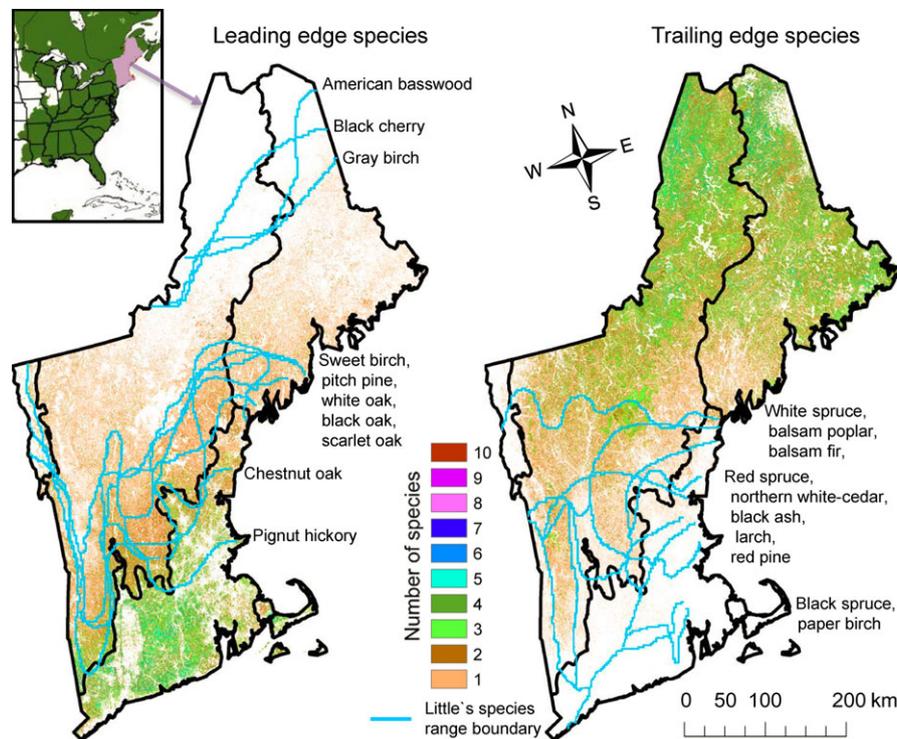


FIGURE 1 Species richness in New England and Little's range boundaries for the leading and trailing edge species. New England study area (purple) within forested areas of eastern North America (dark green) (inset); and species richness for leading (12 species) and trailing (10 species) edge species [Colour figure can be viewed at wileyonlinelibrary.com]

at landscape scale (Scheller et al., 2007). LANDIS-II uses a probability decay function to simulate seed dispersal from surrounding cells (i.e., the probability of arriving seeds decreases with increased seeding distance (He & Mladenoff, 1999), with distance drawn from two negative exponential distributions defined by a species' effective and maximum seed dispersal distances, and the total probability that seed will be present is equal to the sum of the probabilities from each source cell (Ward, Scheller, & Mladenoff, 2005).

Because our study investigates novel conditions of climate and species migration, we used a LANDIS-II succession extension with very direct links between climate drivers and species establishment and growth (Gustafson, 2013). The PnET-SUCCESSION v2.0 extension (de Bruijn et al., 2014) uses the physiological first principles incorporated in the PnET-II ecophysiology model (Aber et al., 1995). In PnET-Succession, cohort photosynthesis and growth is simulated as competition for light and water among all the cohorts at each grid cell with a monthly time step (de Bruijn et al., 2014; Gustafson et al., 2015). Specifically, competition for light is simulated by allocating incoming radiation within stacked layers of the canopy using a standard Lambert-Beer formula (Aber & Federer, 1992). Available soil water depends on soil texture, inputs from precipitation, and losses from interception, evaporation, runoff, transpiration by cohorts, and percolation out of the rooting zone. Species establishment requires the presence of seeds, and is stochastically simulated monthly as a function of available soil water and light. Photosynthetic capacity is determined by species foliar nitrogen, with actual photosynthesis

rate reduced as light, water, and temperature depart from species-specific optimal values, and increased as atmospheric CO₂ concentration increases. Respiration increases with temperature using a Q₁₀ relationship, where a 10°C increase in temperature results in a ten-fold increase in respiration rate (Atkins, 1978). Each species has a minimum temperature for photosynthesis, causing its phenology to respond to the climate inputs each year. Cohort mortality occurs when carbon reserves are depleted when respiration exceeds photosynthesis. Senescence is simulated as a reduction of photosynthetic rate with age, with net photosynthesis reaching zero as cohorts approach longevity. These physiologically meaningful parameters in PnET-Succession extension can be estimated from empirical studies published in the literature and calibrated using forest inventory and other empirical data. Complete details of the PnET-Succession extension are found in de Bruijn et al. (2014) and Gustafson, de Bruijn, Miranda, and Sturtevant (2016).

In PnET-Succession, species-specific life-history traits reflect the competitive ability for resources (e.g., light, water), which have implications for simulated tree species range boundary shifts (Table 1). For example, foliar nitrogen content (FolN) is linearly related to maximum photosynthetic capacity, and various reduction factors that vary monthly to reflect stressors and competitive ability are applied to this maximum. HalfSat (light level at which photosynthesis is half its level in full sunlight) reflects competitive ability for light. Two drought tolerance parameters reflect species' competitive ability to access soil water, which is quantified by using species-specific water

pressure thresholds: H3 represents the water potential below which photosynthesis begins to decline, and at H4, photosynthesis stops.

We used the Land Use Plus (LU⁺) extension (Thompson, Simons-Legaard, Legaard, & Domingo, 2016) to create experimentally controlled patterns of a generic disturbance, which integrated the spatial and temporal effects of disturbance into the simulations of species range shifts. Disturbances affect species range shifts through direct effects (e.g., species cohorts removed by disturbance) and indirect effects (e.g., changes in light and water availability that affect establishment and competition).

Forest inventory plots from the U.S. Forest Service, Forest Inventory and Analysis (FIA) program (Bechtold & Patterson, 2005) were used to generate initial species-age cohorts for LANDIS-II (Duveneck et al., 2016). Our map of initial forest conditions (250 m resolution) was generated by imputing the FIA plots to each cell using a gradient nearest neighbor technique based on the spectral signature of MODIS imagery in conjunction with biophysical data (Duveneck et al., 2015; Wilson, Lister, & Riemann, 2012). For each experimental scenario, we produced 10 replicate simulations of 100 years of forest dynamics (2000–2100) at a monthly time step and evaluated modeled species spatial changes at a 10 year interval.

2.4 | Disturbance scenarios

We simulated nine disturbance scenarios, plus a reference “Succession-only scenario” (only minimal gap disturbances), all incorporating the CCSM4 RCP8.5 climate change scenario. To develop the disturbance scenarios, we initially varied extent of landscape disturbed (e.g., number of ha), disturbance intensity (e.g., the amount of biomass removed in the disturbed area), minimum disturbed patch size (e.g., the minimum amount of cells were disturbed in a disturbance patch), and spatial pattern (aggregation). We found that the relative importance of extent and intensity was more than 99% (Fig. S1). Thus, the disturbance scenarios we used included three levels of disturbed extent area: 10%, 30%, and 60% of the study area every ten years; and four levels of disturbance intensity: 10%, 30%, 60%, and 100% of aboveground forest biomass removal in each disturbance patch (minimum patch size is 1 cell with 40% of spatial aggregation). The disturbance scenarios were not designed to emulate any specific disturbance regime, but rather to span a wide range of potential disturbances so as to best understand their effects. But, for comparison, the dominant disturbance agent in the region is timber harvesting. On corporate-owned lands in New England, 36% of the forest area is subject to some level of harvest per decade, and removes a median of 40% of the live tree biomass per harvest event (Thom et al., 2017).

For convenience, we abbreviate the scenarios based on the extent and intensity (e.g., the scenario with 10% disturbance extent and 30% disturbance intensity is referred to D_Ext10Int30). To avoid completely unrealistic disturbance scenarios, we removed three scenarios: D_Ext30Int100, D_Ext60Int60, and D_Ext60Int100 and, thus, our factorial design is not complete. D_Ext10Int100 is the most intense disturbance scenario, and D_Ext60Int30 is the largest extent

disturbance scenario. None of the simulated disturbances was species-specific (i.e., for a given intensity, live biomass of all species in a disturbed cell was reduced equally). Scenarios with less than 100% intensity resulted in disturbed cells retaining some biomass (“seed trees”), whereas 100% intensity resulted in the removal of all seed sources from disturbed cells. The model does not simulate seed banks, so in the absence of seed sources, species-specific sprouting is the only regeneration mechanism following disturbance.

2.5 | Boundary shift analysis

To quantify boundary shifts, we first determined the current boundary of species' spatial distribution and then quantified how far that boundary moved during the 100 simulated years. In recent studies (Vanderwel & Purves, 2013; Woodall et al., 2013; Zhu et al., 2012), species' range boundary was often quantified as the absolute limit of a species' distribution (maximum or minimum latitude of species' distribution) or at the location of a percentile of species' distribution (e.g., 95th or 5th percentile of latitude occurrence). Different definitions of a species boundary can exert a strong influence on the quantification of boundary shifts. Ideally, quantification of a boundary should have a small variance in repeated experiments, so that changes reflect trends in boundary shifts rather than the influence of stochastic processes. We evaluated the 100th, 95th, 90th, and 80th of latitude occurrence for the leading edge, and 0th, 5th, 10th, and 20th of latitude occurrence for the trailing edge respectively by running ten repetitions for one century (Fig. S2). The 95th, 90th, and 80th percentile of latitude occurrence had similar trends of boundary shifts and small variance, as did the 5th, 10th, and 20th percentile. We therefore report changes in the 95th percentile of latitude occurrence to quantify the movement of the leading edge and the 5th percentile for the trailing edge.

To allow for longitudinal variation in boundary shifts over the course of a century for each species, we used a band analysis (revised longitudinal band analysis sensu Zhu et al., 2012; Figure 2). We first delineated the study area into 25-km wide (100 cells) longitudinal bands. Within each band, we calculated the 95th percentile of latitudinal occurrence for each leading edge species and the 100th percentile as the absolute limit of its leading edge. Similarly, we calculated 5th percentile of latitudinal occurrence for each trailing edge species and the 0th percentile as the absolute limit of the trailing edge. Complete leading or trailing edges and their absolute limits in the entire study area were formed for each species by connecting the corresponding spatial locations across bands. We calculated these boundaries for each species for all scenarios at year 10 and year 100. The mean distance for each species' boundary shift was calculated for the appropriate (xth) latitudinal percentile by:

$$LD_{j,x} = q_{j,x}^{(\text{year } 100)} - q_{j,x}^{(\text{year } 10)}$$

where $q_{j,x}$ is the latitude corresponding to percentile x in band j . For both leading and trailing edges, positive $LD_{j,x}$ is consistent with northward movement, because it implies that the boundary at the

simulated year 100 was further north than at year 10. The mean of LDs of all bands along the boundary summarized the mean latitudinal difference (i.e., boundary shift) in the next century.

2.6 | Data analysis

To evaluate how tree species migration was affected by only climate, we calculated the mean boundary shifts from our 10 simulation replicates for each species under climate change and the succession-only scenario (no disturbance). To evaluate the additional effect of disturbance, we compared boundary shifts of all species between the succession-only scenario and each disturbance scenario using two-way ANOVA with multiple comparisons (post hoc Tukey's HSD test). We also compared the projected changes in species presence-absence to explicitly explore the effect of disturbance on species' recruitment. To evaluate how species life-history traits contributed to boundary shifts, we investigated correlations (Pearson's r) between the boundary shifts and four species-specific life-history traits: photosynthetic capacity (FoN), competitive ability for light (HalfSat), competitive ability for water (H3), and seed dispersal ability (Effective_Seed_dispersal_distance), and tested the significance (p value) of each correlation coefficient. We further investigated relative importance of these four species traits for species' boundary shifts, which was assessed by the averaging over orderings method proposed by Lindeman, Merenda and Gold (lmg) (Lindeman,

Merenda, & Gold, 1980) in the multiple linear regression. For all analyses, we used the R statistical software (RCoreTeam, 2013), the *raster* package (Hijmans et al., 2014) and *relaimpo* package for R (Grömping, 2006).

3 | RESULTS

The velocity of climate change under the high-emission climate future (Figure 3), especially temperature change, was far greater than tree species' range boundary shifts (Figure 4). The velocities of temperature and precipitation varied spatially across New England as a function of spatial variation in the temporal and spatial gradients, with higher velocities in flatter areas and relative lower velocities in mountainous areas. The velocity of change in annual mean temperature ranged from 0.01 to 11 km/year, and the geometric mean velocity across all of New England was 1.13 km/year (Figure 3d). The geometric mean velocity of total annual precipitation was 0.26 km/year (0.001–5 km/year, Figure 3h). This indicates that the projected mean horizontal shifts in temperature and precipitation contours in New England will be about 110 and 26 km over the next century, respectively. By contrast, the simulated boundary shifts for both leading and trailing edges (quantified by the 95th and 5th percentile) showed relative stability (generally less than 20 km over the next century under the succession-only scenario),

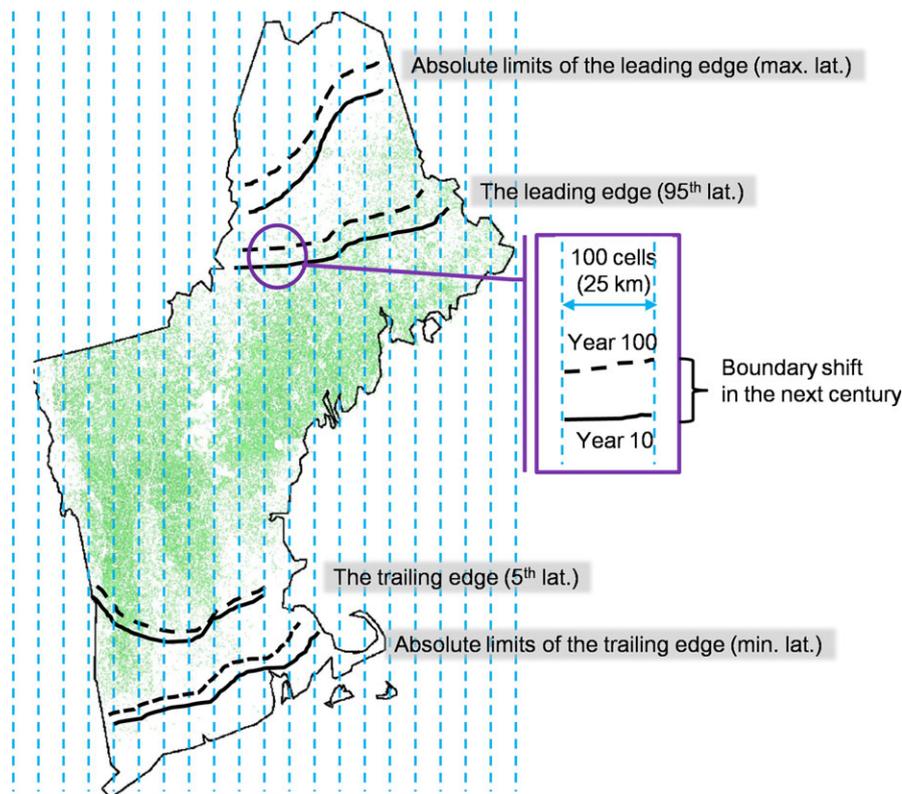


FIGURE 2 Conceptual basis of the boundary shift analysis for the leading and trailing edges (5th or 95th of latitude occurrence) and their absolute limits (the minimum or the maximum latitude). An example of a hypothetical species distribution at year 2100, which is assumed to have both the leading and trailing edges in the study area, is shown in green [Colour figure can be viewed at wileyonlinelibrary.com]

with just a slight northward shift (Figure 4). The absolute trailing edge limits (0th percentile) had a greater shift to the north than did the trailing edges (5th percentile). For example, the absolute limit of the trailing edge of paper birch shifted further (~50 km) than the trailing edge (~14 km) (Figure 4). The leading edge species showed contrasting patterns, with a northward shift of the leading edges, but a southward shift in the absolute limits of the leading edges (Figure 4).

Disturbance did not have a large effect on the direction or rate of range boundary shifts (Figure 5). Two-way ANOVA results show that there was no significant difference among various extent disturbance scenarios, while differences occurred among various intensity disturbance scenarios ($p < .05$) for both leading and trailing edge. Based on multiple comparisons analysis, only the most intense disturbance scenario (D_Ext10Int100) showed a significant difference from the succession-only scenario (Figure 5). Simulated boundary shifts remained relatively stable across various levels of disturbances except the most intense disturbance scenario. In addition, for both the leading edge species and trailing edge species, disturbance had little effect on the correlations between boundary shifts and species life-history traits (Table 2). Disturbance did accelerate regeneration and establishment, with the reduction in shade resulting in greater recruitment opportunities, especially under the highest intensity disturbance scenario (D_E10I100) (Figures 6 and 7), but range shifts did not necessarily follow.

For the leading edge species, species' photosynthetic capacity (FolN) and competitive ability for light (HalfSat) were more important for range boundary shifts than competitive ability for water (H3) and seed dispersal ability (effective seed dispersal distance) (Table 2). Range boundary shifts had a positive correlation with species' photosynthetic capacity and competitive ability for light regardless of the disturbance scenarios (Table 2, Fig. S3). For example, the leading edge shift for black cherry (with higher FolN) was greater than that of white oak (with a lower FolN) (Figure 6). Correlations were weak or even negative between leading edge boundary shifts and the drought tolerance and seed dispersal distance life-history traits (Table 2, Fig. S3). By contrast, trailing edge shifts were positively correlated with multiple species life-history traits, such as species' competitive ability for light (Table 2, Fig. S4). For example, paper birch (with a higher HalfSat) shifted further north than white spruce (with a lower HalfSat) (Figure 7). The correlation was also weak between trailing edge boundary shifts and the drought tolerance (H3) life-history trait (Table 2, Fig. S4). The correlation with seed dispersal distance was statistically significant (Table 2), but examination of the plot of the relationship suggests that the correlation is spurious (Fig. S4). The relative importance of photosynthetic capacity, competitive ability for light, and seed dispersal distance (28%, 57%, 14% under the succession-only scenario, respectively) for boundary shifts were larger than the relative importance of competitive ability for water (just 1% under the succession-only scenario). There was

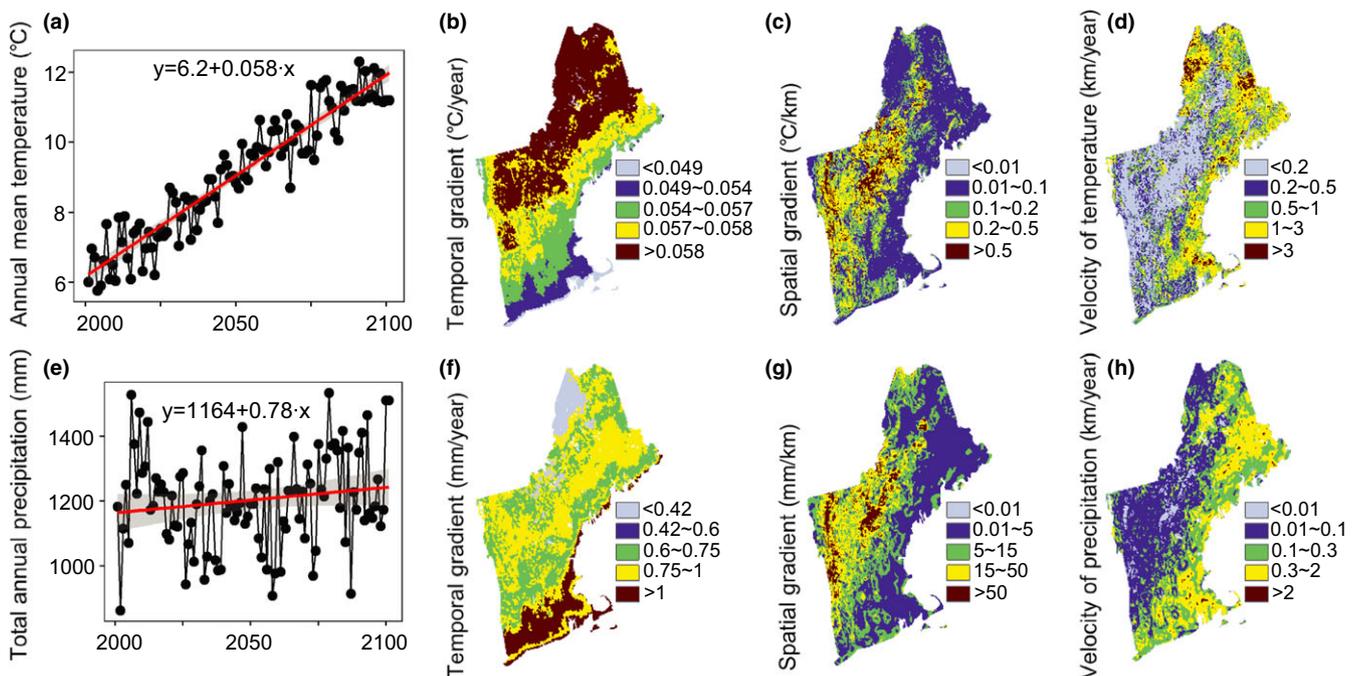


FIGURE 3 The velocity of change in annual mean temperature (a–d) and total annual precipitation (e–h) in New England in the next century under the high-emission scenario (RCP 8.5). (a,e) The mean temperature and precipitation at the landscape level for the period 2000–2100. The red line represents a linear fit for temperature and precipitation as a function of year ($p < .001$); (b,f) temporal gradients from 2000 to 2100, which are quantified by the slope of the associated linear regression line at each pixel; (c,g) Spatial gradients are calculated at each pixel using 9×9 moving window; (d,h) The velocity of temperature change calculated from the quotient of (b) and (c) (unit of the velocity of annual mean temperature: $^{\circ}\text{C year}^{-1}/^{\circ}\text{C km}^{-1} = \text{km year}^{-1}$), and the velocity of precipitation change calculated from the quotient of (f) and (g) (unit of the velocity of total annual precipitation: $\text{mm year}^{-1}/\text{mm km}^{-1} = \text{km year}^{-1}$) [Colour figure can be viewed at wileyonlinelibrary.com]

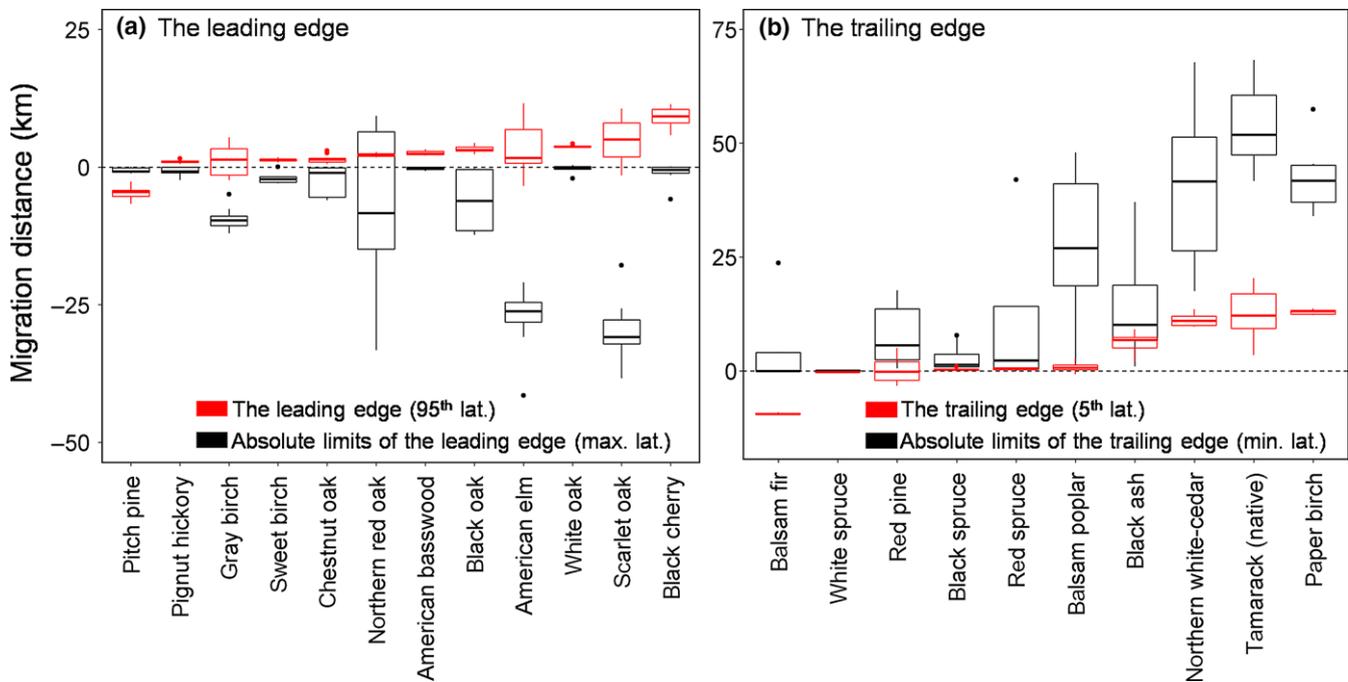


FIGURE 4 Species boundary shifts in the next century under the succession-only scenario. Each box plot represents variation of boundary shifts among 10 simulation replicates of the succession-only scenario. (a) The leading edge and its absolute limits, quantified by the 95th and the maximum latitude of species range, respectively; (b) The trailing edge and its absolute limits, quantified by the 5th and the minimum latitude of species range [Colour figure can be viewed at wileyonlinelibrary.com]

no substantial difference in the correlations of range boundary shifts with species life-history traits among different disturbance scenarios (Figs S3 and S4).

4 | DISCUSSION

4.1 | Tree migration lags behind climate change

Our results support the work of others that have shown tree species range shifts driven by local processes (e.g., tree growth, seed dispersal, establishment, and competition) may lag far behind their climate potentials over the next century in New England. Many eastern US tree species have been found to be unable to keep pace with climate change based on long-term inventory plots (Murphy et al., 2010; Sitaro, Paquette, Messier, & Nock, 2017; Woodall et al., 2013; Zhu et al., 2012). These studies estimated tree migration potential by comparing present latitudes of seedlings to those of adult trees, but it is not clear how such estimates can be used to predict actual range shifts in response to future climate change.

Our study highlights the importance of incorporating ecological factors (e.g., species life-history traits) into predictions of range change dynamics. Climate change velocity did not produce concomitant changes in forest species distributions raising caution on the use of climate change velocity such metrics as a proxy for biological conservation decision-making (Dobrowski & Parks, 2016). Advances have been made in similarly fashioned metrics by including climate paths (Dobrowski & Parks, 2016; Serra-Diaz et al.,

2014) and species-specific climate relationships (e.g., bioclimatic velocity) (Serra-Diaz et al., 2014). While the use of such metrics has been successful for mobile organisms (e.g., bioclimatic velocity in fish) (Comte & Grenouillet, 2015), they may only portray general patterns of shifts in climate fitness for trees rather than actual range change projections at the century scale. For instance, Serra-Diaz et al. (2014) estimated higher climate velocity at the trailing edge than bioclimatic velocity at leading edges for several Californian tree species (similar to our results for several species); but the predicted rate of spatial advance may still be optimistic because these projections do not directly incorporate dispersal mechanisms and shifting competition dynamics in a different climate (Franklin, 2010).

Part of the disagreement between the climatic velocities calculated here and the simulated range margins is due to the way climate velocities were calculated, where climate velocities were high in flat areas due to a very small spatial gradient in temperatures (Loarie et al., 2009). In these areas, other biotic and bioclimatic processes may be key to understand how species move, including canopy-mediated microclimates (Lenoir, Hattab, & Pierre, 2016) and biotic interactions (e.g., competition, facilitation). Crucially, our modeling approach based on physiological first principles was able to capture such dynamics by appropriately representing species' level competitive and dispersal dynamics (as opposed to plant functional types in DGVMs) and emerging microclimatic influences through canopy shading, and their feedbacks with disturbance dynamics (Gustafson, 2013), which improves simulation realism and provides insight into

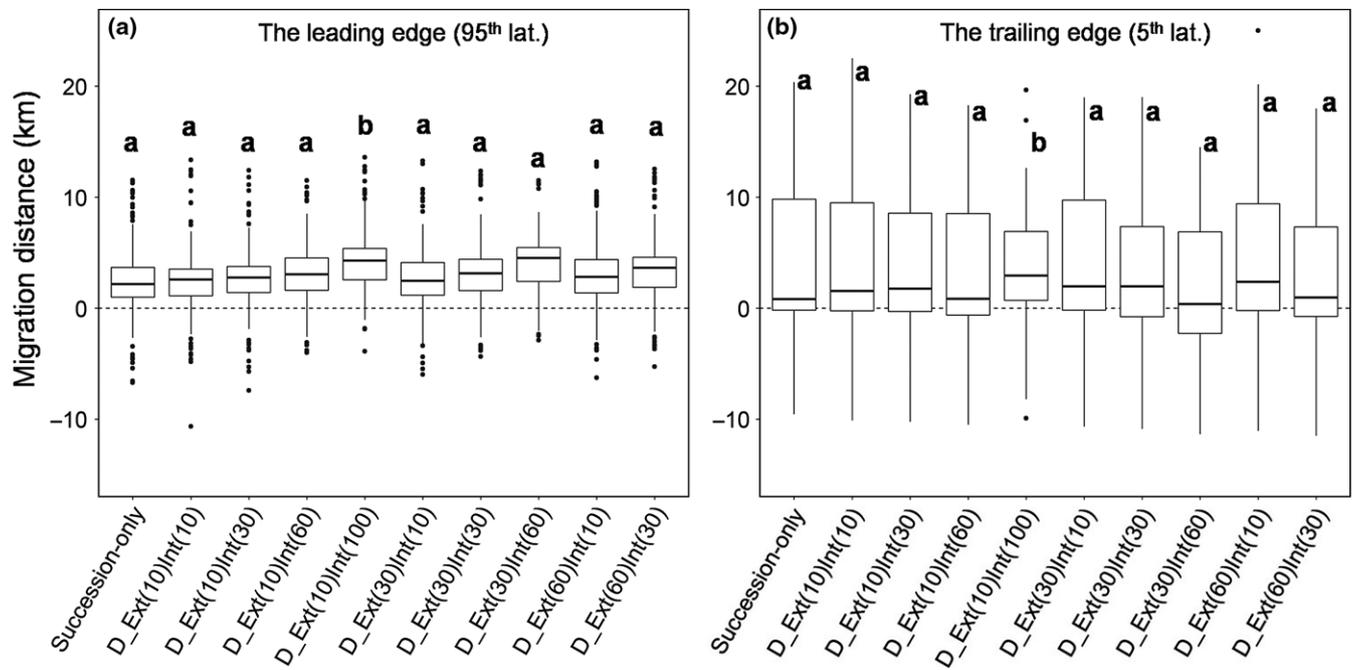


FIGURE 5 Comparison of boundary shifts among the succession-only scenario and various disturbance scenarios in the next century at the leading edge (a) and the trailing edge (b). Each box plot represents the variation of boundary shifts among multiple species, each with 10 simulation replicates. Lowercase letters represent results of multiple comparisons in ANOVA. The same letter represents no significant difference between the succession-only scenario and disturbance scenario, whereas different letters signify a significant difference

TABLE 2 Correlations (quantified by Pearson's correlation coefficient, r) between the magnitude of boundary shifts and four species life-history traits and relative importance of these four species traits (assessed by the averaging over orderings method for multiple linear regression) under the succession-only scenario and the highest intensity disturbance scenario (D_Ext10Int100)

	Photosynthetic capacity (FoIN)		Competitive ability for water (H3)		Competitive ability for light (HalfSat)		Seed dispersal ability (effective seed dispersal distance)	
	Correlation coefficient	Relative importance (%)	Correlation coefficient	Relative importance (%)	Correlation coefficient	Relative importance (%)	Correlation coefficient	Relative importance (%)
Shifts at the leading edge								
Succession-only scenario	.29*	47	-.081*	12	.24*	40	-.03	1
Disturbance scenario	.36*	60	-.15*	12	.17*	22	.11*	6
Shifts at the trailing edge								
Succession-only scenario	.44*	28	-.05	1	.53*	57	.35*	14
Disturbance scenario	.53*	27	.13*	9	.64*	48	.46*	16

For more details of these species life-history traits, see Table 1.

* $p < .05$.

how interactions between climate change and landscape dynamics may produce future shifts in tree species' ranges.

4.2 | Species' range boundary shifts

Our results showed that the simulated leading edge of most species expanded northward slightly and the trailing edge experienced a

contraction from the south. This is consistent with previous studies of eastern US tree species, which indicated expected range contractions in the south and limited expansion in the north (Monleon & Lintz, 2015; Murphy et al., 2010; Serra-Diaz et al., 2016; Zhu et al., 2012) resulting in a northern edge stability (Masek, 2001; Woodall et al., 2013). For the leading and trailing edges (quantified by 5th and 95th percentile of latitudinal occurrence), range shifts are limited

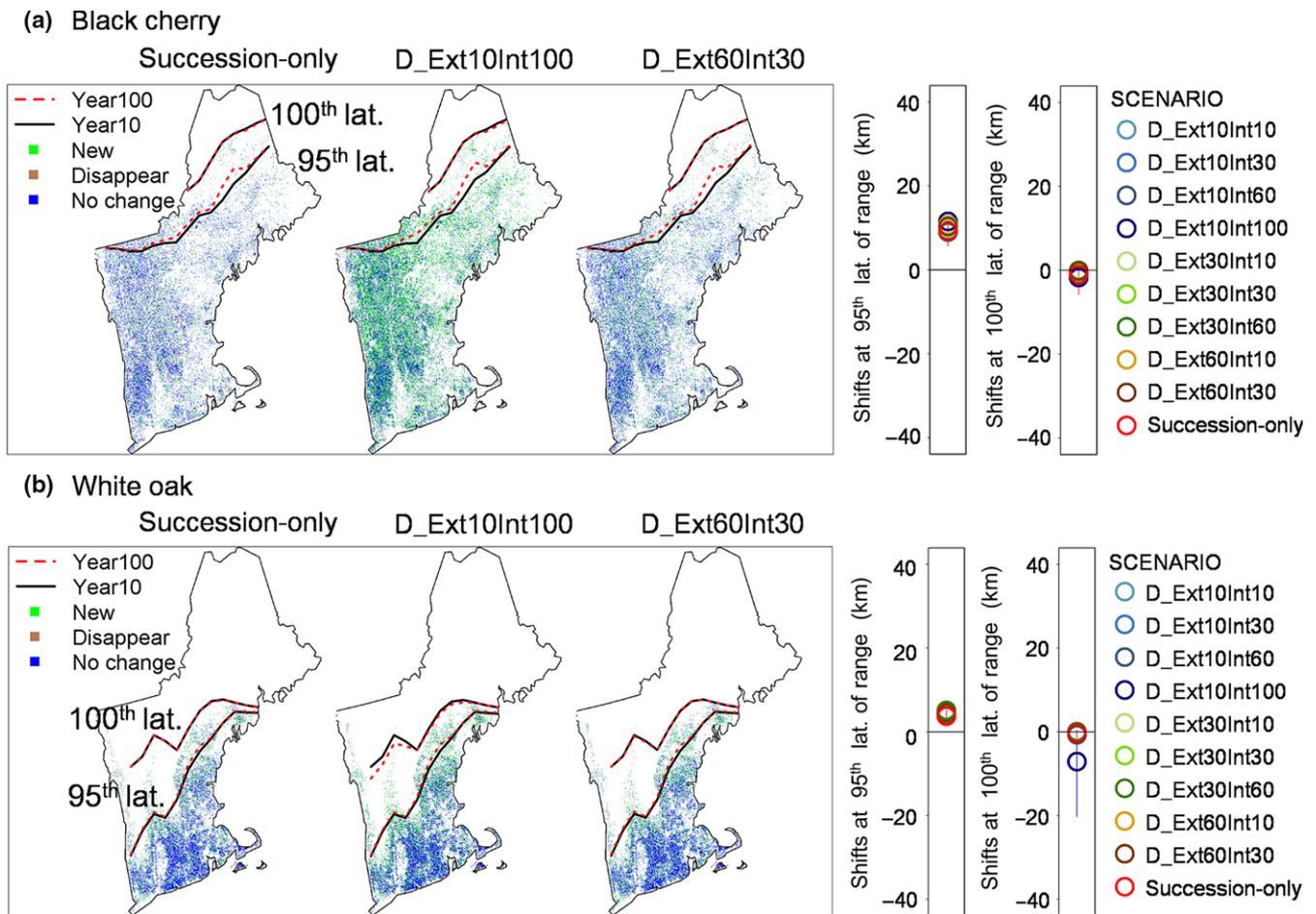


FIGURE 6 Spatial differences in range boundary shifts for the leading edge under the succession-only scenario and selected disturbance scenarios. Two leading edge species are shown as examples: (a) black cherry, (b) white oak. The maps show shifts in species' range boundary (quantified by 95th percentile latitudes of species range) and their absolute limits (quantified by maximum percentile latitudes of species range) in the next century. Colors represent changes in species presence-absence in the next century where green is a new occurrence, brown is a loss, and blue is no change. The quadrant schematic diagram on the right shows migration distances of the species' range boundary (quantified as shifts in the 95th percentile of latitude occurrence) and absolute limits (quantified as shifts in the maximum latitude), where a positive value means a northward boundary shift, and a negative value means a southward boundary shift. Each circle represents a scenario [Colour figure can be viewed at wileyonlinelibrary.com]

and difficult. This is because overlapping leading and trailing edges for most pairs of species of this study are some distance apart (usually >50 km), whereas only a couple species have leading and trailing edges that overlap quite closely, and these species often do not compete directly. Therefore, invaders tend not to be invading sites where another species is clearly vacating, which results in a slow migration.

Compared to boundary shifts at the leading and trailing edges (quantified by 5th and 95th percentile of latitudinal occurrence), species' absolute limits (quantified by minimum or maximum latitude) showed a more complex response to climate change. Leading edges showed a slight northward shift, whereas absolute limits tended to retreat from the north. The cause of this result may be related to competition from resident species. If the northward expansion of these species is not accompanied by a decrease in the abundance of the resident species, they could experience a slower advance. Another possible explanation could be that these specific leading

edge species may have limited dispersal and establishment capabilities and long generation times that result in very slow rates of advance even given a competitive advantage (Hanski & Gyllenberg, 1993; Odum & Allee, 1954).

At the trailing edge, the simulated range boundaries and their absolute limits shifted northward. This is consistent with expectations under warming conditions, where retreat from the trailing edge is expected to follow their optimal climate (Clark, Lewis, & Horvath, 2001; Davis & Shaw, 2001; Neubert & Caswell, 2000; Zhu et al., 2012). For example, more than 80% of eastern North American trees showed a lower abundance and occupancy near their southern range margin (Zhu et al., 2012), indicating range contractions at trailing edges. The fossil record also indicates that population extirpations at the trailing edge were common in the late Quaternary, which could be a result of climatic stress, or because of competition with new arrivals migrating from the south (Davis & Shaw, 2001).

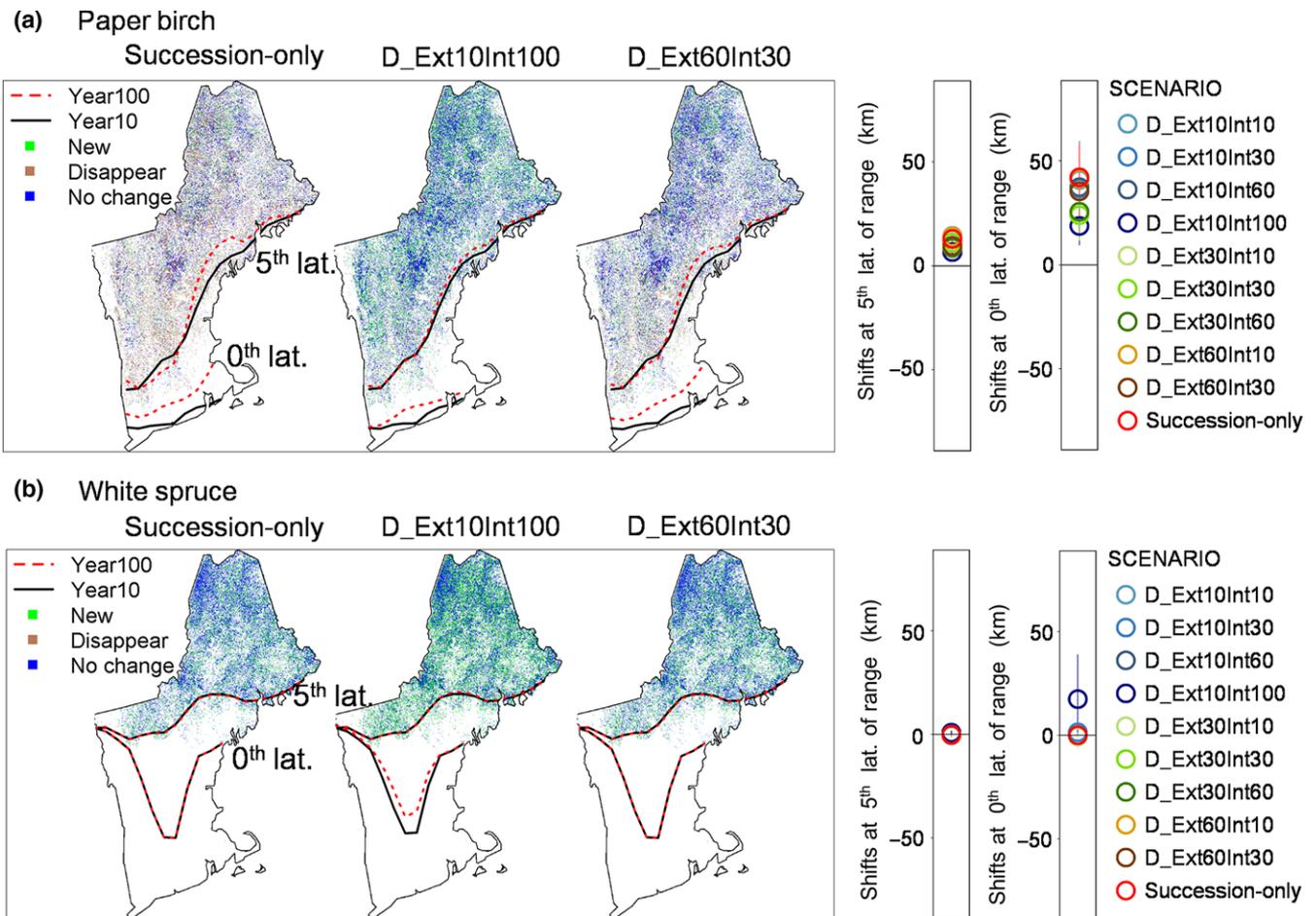


FIGURE 7 Spatial differences in range boundary shifts for the trailing edge under the succession-only scenario and selected disturbance scenarios. Two trailing edge species are shown as examples: (a) paper birch, (b) white spruce. The maps show shifts in species' range boundary (quantified as shifts in the 5th percentile of latitude occurrence) and their absolute limits (quantified as shifts in the minimum latitude) in the next century [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | The effect of disturbance

Disturbance did not substantively accelerate or slow tree range boundary shifts for leading or trailing edges over the next century in New England, although the highest intensity disturbance scenario showed a small effect on species' boundary shifts. However, this should not be interpreted to mean that disturbance has no effect on tree migration. Disturbance scenarios, including disturbance with 100% intensity, had a limited effect on boundary shifts because such disturbances do not completely eliminate competition from the species currently found there, and because many species can re-sprout after disturbance and disturbances do not eliminate nearby seed sources. We expected that the presence of established competitors would hinder the establishment of invading migrants that were superior competitors, but we also expected that disturbance would "level the playing field" so that a new community would result based primarily on the ability of existing and new species to compete for light and water for establishment and growth. This was not the case, even under 100% intensity disturbance, perhaps because recovery of a disturbed site is determined as much by the presence of propagules

(or sprouts) as it is by growth competition. It is worth noting that the model does not include a seed bank, but if it did, resident species would have an even greater advantage. In many cases, disturbance favors the resident species, particularly at the early stage of recovery. For example, thirty years after an experimental disturbance in the Harvard Forest in central Massachusetts, persistent local species have all but excluded the establishment of invaders, despite the opportunity for colonization (Plotkin, Foster, Carlson, & Magill, 2013). Furthermore, the leading edge species are also killed by disturbance, which results in the reduction in propagule pressure. Such reduction may slow or delay range expansion even if the disturbance reduces competition and creates physical conditions more favorable for their recruitment. It should be noted that the LANDIS-II dispersal algorithm we used simulates the probability of seeds arriving from surrounding cells (i.e., presence or absence), but does not explicitly model propagule pressure (i.e., abundance of seeds), assuming that if seeds can reach the site, establishment will be proportional to the suitability of the site for growth of established cohorts. Such an algorithm that models propagule pressure is under development (Lichti, Sturtevant, Miranda, Gustafson, & Jacobs, in prep), but it is

computationally intensive, and would not be feasible at the scale of our study. However, propagule pressure would be expected to be greater for established species than migrants, so, if anything, our results are biased in favor of migrants. Thus, our results suggest that disturbance does not appear to be an important factor in determining the rate of boundary shifts in New England over the next century. Other studies have similarly shown that disturbances have influence on some forest type transitions (Frelich, 2002; Scheller & Mladenoff, 2005), but are unlikely to facilitate ubiquitous forest transitions in the coming decades (Vanderwel, Coomes et al., 2013; Vanderwel, Lyutsarev et al., 2013).

4.4 | The effects of competition and dispersal

Both interspecific competition and seed dispersal characteristics have been highlighted as key mechanisms for tree migration in previous theoretical studies (Caplat et al., 2008; Clark et al., 2001; Kubisch, Holt, Poethke, & Fronhofer, 2014; Moran & Ormond, 2015; Renwick & Rocca, 2015; Serra-Diaz et al., 2015; Thompson & Katul, 2008), but their effects on tree range boundary shifts are not fully understood (Hillerislambers, Harsch, Ettinger, Ford, & Theobald, 2013; MacLean & Beissinger, 2017; Sittaro et al., 2017; Zhu et al., 2012). Our results showed that shifts at the trailing edge tend to be regulated by photosynthetic capacity, competitive ability for light and seed dispersal ability, whereas leading edge shifts tend to be regulated only by photosynthetic capacity and competitive ability for light, but not seed dispersal ability. Leading edge shifts were not correlated with seed dispersal distance as we expected, even for species that are better adapted to the new climate, which suggests that establishment beyond the leading edge is the limiting factor. Pioneer species tend to have high growth rates, high fecundity, and long dispersal distances, and would be expected to advance their range more quickly, especially when there are disturbances to create suitable conditions. Our results suggest that existing species resist such migrants by being more likely to establish new cohorts through greater seed rain and sprouting so that pioneer migrants may face stiff competition, particularly for light. Mid and late-seral species tend to be shade tolerant and therefore should be better able to compete with existing species, but they usually reach reproductive maturity slowly and produce relatively fewer seeds that disperse shorter distances (Feurdean et al., 2013; Lischke, 2005), and are therefore unable to migrate quickly.

Trailing edge range shifts are driven by the same mechanisms as leading edge shifts, since one species' trailing edge is another species' leading edge. These shifts are determined by interactions among the rate of mortality of existing species caused by senescence and disturbance, the competitive ability of the existing species (both for establishment and growth), and on the dispersal and competitive ability (both for establishment and growth) of the encroaching migrants (Vanderwel, Lyutsarev et al., 2013). However, abiotic conditions of soils, climate, and disturbance regimes differ between the leading and trailing edges of a species, and the specific species

competing with each other differ considerably, resulting in different behavior at the leading and trailing edges. We would expect that short-lived species should experience more rapid erosion at the trailing edge of their range, especially when disturbances are rare and do not kill longer lived species prematurely. Conversely, long-lived species can resist trailing edge erosion even when they are poorly adapted to current climate conditions, especially when disturbances are rare. Our study area is not large enough to contain the entire range of any tree species, and certainly not the entire range of all the species, so our study was unable to detect boundary shifts at both leading and trailing edges of species. Because tree species ranges in eastern US forests are very large and individualistic, advancing species are not aligned with displacing species that are in suboptimal conditions, which helps explain the slow changes in tree ranges.

4.5 | Limitations and implications

Given that some of our results were counter to our expectations, we considered various sources of error to determine our confidence in the model results. Random error, or stochasticity, was assessed by computing confidence intervals from the results of the 10 replicates, which were quite small. This is consistent with results typically obtained using forest landscape models. Model specification error results when reality is formalized into computational algorithms and equations within a simulation model. This process involves simplifications and generalizations to make the model tractable. PnET-Succession uses first principles to simulate growth and competition, and its algorithms are based on the widely used and vetted PnET-II eco-physiology model (Aber et al., 1995). It has among the most direct links between climate and tree species growth and competition of all FLMs, but its use of monthly time step nevertheless averages dynamics that occur at shorter time scales. Furthermore, LANDIS-II does not track individual trees, but species cohorts. The reliance of PnET-Succession on well-vetted algorithms based on first principles, scaled to spatial and temporal scales appropriate for landscape and regional dynamics, enhanced our confidence in its predictions. Nevertheless, the model propagates uncertainty surrounding our understanding of some physiological processes, such as CO₂ acclimation, which is not accounted for. The LU⁺ disturbance extension was used to implement generic disturbance regimes, which did not attempt to mimic any particular disturbance agent or regime. While this allowed for a tightly controlled experiment, it produced uncertainty about whether real disturbance regimes might impact species migration differently. The LANDIS-II dispersal algorithm has robust capabilities to simulate dispersal distances (Ward et al., 2005), but it has no capacity to simulate propagule abundance. However, if there are multiple cells within the maximum dispersal distance, the total probability that seed will be present is equal to the sum of the probabilities of each source cell. If seed is present, then the algorithm essentially assumes that propagules are abundant. This assumption about propagule pressure is perhaps the most important source of uncertainty in our results.

Parameter error reflects uncertainty in the value of input parameters resulting from use of a measure of central tendency in a parameter that varies widely, or because the actual value of the parameter is uncertain. We performed sensitivity analyses of LANDIS-II in our previous studies to evaluate the effect of input parameters on simulation results (Thompson, Foster, Scheller, & Kittredge, 2011; Xiao et al., 2016). These studies show that simulated species distributions and biomass are not overly sensitive to any individual input parameter in LANDIS-II (such as growth shape and mortality parameters) and that parameter sensitivity is not enhanced or diminished over simulation time. Other studies also have shown that PnET-Succession is not overly sensitive to individual parameters (Duveneck et al., 2016; Gustafson et al., 2015, 2016, 2017). Although it uses parameters that can be estimated from the literature, modest calibration of some parameters is required, which introduces uncertainty. We used parameter settings that were successfully calibrated and used for studies in Wisconsin (Gustafson et al., 2016) and Maryland (Gustafson et al., 2017), and validated for this study using eddy-flux data from New England (Duveneck et al., 2016). The climate projections for the study used a single emission scenario coupled with a single Global Circulation Model. This approach allowed us to robustly assess range shifts for that particular climate scenario, but it does introduce uncertainty about how well our results represent other possible climate futures. We conclude that our methods did not introduce unreasonable uncertainty into our results, but they must nevertheless be interpreted in light of the assumptions and uncertainty inherent to our methods. This study is one of the first to apply a mechanistic model that includes the most relevant processes that determine species' range boundary shifts at a scale that is difficult to achieve with such models.

Our results support the hypothesis that tree species ranges will be unable to shift latitudinally fast enough to keep pace with climate change, and suggest that the lag may be even greater than previously thought. This means that most species will be stuck in locations where their growth rates may be suboptimal for considerable time, and this may have important consequences for forest productivity and carbon sequestration globally. Furthermore, suboptimal growth rates may increase stress levels, making some species more susceptible to disturbances such as insect pests and drought (Raffa, Aukema, Erbilgin, Klepzig, & Wallin, 2005) and making forests less resilient (Oliver et al., 2015). Many countries are relying on their forests to help them meet their carbon commitments, and their assumed rates of forest growth and carbon storage may be overly optimistic (Kurz et al., 2009).

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REFERENCES

- Aber, J. D., & Federer, C. A. (1992). A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*, 92, 463–474.
- Aber, J. D., Ollinger, S. V., Féderer, C. A., Reich, P. B., Goulden, M. L., Kicklighter, D. W., ... Lathrop, R. G. (1995). Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research*, 5, 207–222.
- Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chuncu, A. J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, 14, 677–689.
- Atkins, P. W. (1978). *Physical chemistry*. Oxford, UK: Oxford University Press.
- Bechtold, W. A. & Patterson, P. L. (Eds.) (2005). *The enhanced forest inventory and analysis program – National sampling design and estimation procedures (GTR-SRS-80)*. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station.
- Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., ... Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479, 517–520.
- Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., De Ruffray, P., Gégout, J. C., & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications*, 7, 12643.
- Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulkhak, S., ... Thuiller, W. (2014). Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography*, 37, 1230–1239.
- Boulangeat, I., Gravel, D., & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–593.
- Brown, P. M., & Wu, R. (2005). Climate and disturbance forcing an episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*, 86, 3030–3038.
- Caplat, P., & Anand, M. (2009). Effects of disturbance frequency, species traits and resprouting on directional succession in an individual-based model of forest dynamics. *Journal of Ecology*, 97, 1028–1036.
- Caplat, P., Anand, M., & Bauch, C. (2008). Interactions between climate change, competition, dispersal, and disturbances in a tree migration model. *Theoretical Ecology*, 1, 209–220.
- Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.
- Clark, J. S., Lewis, M., & Horvath, L. (2001). Invasion by extremes: Population spread with variation in dispersal and reproduction. *The American Naturalist*, 157, 537–554.
- Comte, L., & Grenouillet, G. (2015). Distribution shifts of freshwater fish under a variable climate: Comparing climatic, bioclimatic and biotic velocities. *Diversity and Distributions*, 21, 1014–1026.
- Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology and Evolution*, 28, 482–488.
- Dale, V. H., Joyce, L. A., McNulty, S., & Neilson, R. P. (2001). Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, 51, 723–734.

- Daly, C., & Gibson, W. (2002). *103-Year high-resolution temperature climate data set for the conterminous United States*. Corvallis, OR: The PRISM Climate Group, Oregon State University.
- Danielsson, P. E., & Seger, O. (1990). Generalized and separable sobel operators. In: H. Freeman (Ed.), *Machine vision for three-dimensional scenes* (pp. 347–379). Orlando, FL: Academic Press.
- Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*, 673–678.
- de Bruijn, A., Gustafson, E. J., Sturtevant, B. R., Foster, J. R., Miranda, B. R., Lichti, N. I., & Jacobs, D. F. (2014). Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II. *Ecological Modelling*, *287*, 44–57.
- Dobrowski, S. Z., & Parks, S. A. (2016). Climate change velocity underestimates climate change exposure in mountainous regions. *Nature Communications*, *7*, 12349.
- Dobrowski, S. Z., Swanson, A. K., Abatzoglou, J. T., Holden, Z. A., Safford, H. D., Schwartz, M. K., & Gavin, D. G. (2015). Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography*, *24*, 917–927.
- Duveneck, M. J., & Thompson, J. R. (2017). Climate change imposes phenological trade-offs on forest net primary productivity. *Journal of Geophysical Research: Biogeosciences*, *122*, <https://doi.org/10.1002/2017JG004025>.
- Duveneck, M. J., Thompson, J. R., Gustafson, E. J., Liang, Y., & de Bruijn, A. M. G. (2016). Recovery dynamics and climate change effects to future New England forests. *Landscape Ecology*, *32*, 1385–1397. <https://doi.org/10.1007/s10980-10016-10415-10985>
- Duveneck, M. J., Thompson, J. R., & Tyler Wilson, B. (2015). An imputed forest composition map for New England screened by species range boundaries. *Forest Ecology and Management*, *347*, 107–115.
- Ehrlen, J., & Morris, W. F. (2015). Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters*, *18*, 303–314.
- Everham, E. M., & Brokaw, N. V. L. (1996). Forest damage and recovery from catastrophic wind. *The Botanical Review*, *62*, 113–185.
- Feurdean, A., Bhagwat, S. A., Willis, K. J., Birks, H. J. B., Lischke, H., & Hickler, T. (2013). Tree migration-rates: Narrowing the gap between inferred post-glacial rates and projected rates. *PLoS One*, *8*, e71797.
- Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, *16*, 321–330.
- Frelich, L. E. (2002). *Forest dynamics and disturbance region*. Cambridge, UK: Cambridge University Press.
- Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software*, *17*, 1–27.
- Gustafson, E. J. (2013). When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology*, *28*, 1429–1437.
- Gustafson, E. J., de Bruijn, A., Lichti, N. I., Jacobs, D. F., Sturtevant, B. R., Foster, B. R., ... Dalglish, H. J. (2017). The implications of American chestnut reintroduction on landscape dynamics and carbon storage. *Ecosphere*, *8*, e01773.
- Gustafson, E. J., de Bruijn, A. M. G., Miranda, A. M. G., & Sturtevant, B. R. (2016). Implications of mechanistic modeling of drought effects on growth and competition in forest landscape models. *Ecosphere*, *7*, e01253.
- Gustafson, E. J., Miranda, B. R., de Bruijn, A. M. G., Sturtevant, B. R., & Kubiske, M. E. (2017). Do rising temperatures always increase forest productivity? Interacting effects of temperature, precipitation, cloudiness and soil texture on tree species growth and competition. *Environmental Modelling and Software*, *97*, 171–183.
- Gustafson, E. J., de Bruijn, A. M. G., Pangle, R. E., Limousin, J. M., McDowell, N. G., Pockman, W. T., ... Kubiske, M. E. (2015). Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology*, *21*, 1–14.
- Hanberry, B. B., & Hansen, M. H. (2015). Latitudinal range shifts of tree species in the United States across multi-decadal time scales. *Basic and Applied Ecology*, *16*, 231–238.
- Hanski, I., & Gyllenberg, M. (1993). Two general metapopulation models and the core-satellite species hypothesis. *The American Naturalist*, *142*, 17–41.
- He, H. S., & Mladenoff, D. J. (1999). Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. *Ecology*, *80*, 81–99.
- He, H. S., Mladenoff, D. J., & Gustafson, E. J. (2002). Study of landscape change under forest harvesting and climate warming-induced fire disturbance. *Forest Ecology and Management*, *155*, 257–270.
- Higgins, S. I., Lavorel, S., & Revilla, E. (2003). Estimating plant migration rates under habitat loss and fragmentation. *Oikos*, *101*, 354–366.
- Hijmans, R. J., Van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., ... Shortridge, A. (2014). raster: Geographic data analysis and modeling. R package version 2.1-16. Retrieved from <http://CRAN.R-project.org/package=raster>
- Hillerlambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R., & Theobald, E. J. (2013). How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, *1297*, 112–125.
- Ibanez, I., Clark, J. S., & Dietze, M. C. (2008). Evaluating the sources of potential migrant species: Implications under climate change. *Ecological Applications*, *18*, 1664–1678.
- Ibanez, I., Clark, J. S., Ladeau, S. L., & Hille Ris Lambers, J. (2007). Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Monographs*, *77*, 163–177.
- Iverson, L. R., & McKenzie, D. (2013). Tree-species range shifts in a changing climate: Detecting, modeling, assisting. *Landscape Ecology*, *28*, 879–889.
- 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. *Forest Ecology and Management*, *254*, 390–406.
- Johnstone, J. F., & Chapin, F. S. (2003). Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology*, *9*, 1401–1409.
- Keenan, T., Gray, J., & Friedl, M. (2014). Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Natural Climate Change*, *4*, 598–604.
- Kubisch, A., Holt, R. D., Poethke, H., & Fronhofer, E. A. (2014). Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos*, *123*, 5–23.
- Kunkel, K. E., Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., ... Dobson, J. G. (2013). *Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 1. Climate of the Northeast U.S.* (87 p.). Washington, DC: US Department of Commerce, National Oceanic and Atmospheric Administration. Retrieved from http://www.nesdis.noaa.gov/technical_reports/NOAA_NESDIS_Tech_Report_142-141-Climature_of_the_Northeast_U.S.pdf
- Kurz, W. A., Flannigan, W. A., Stinson, G., Metsaranta, J., Neilson, E. T., & Dymond, C. D. (2009). Projected forest carbon sinks highly vulnerable to increases in natural disturbances. IOP Conf. Series: Earth and Environmental. *Science*, *6*, 042020.
- Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*, 1768–1771.
- Lenoir, J., Hattab, T., & Pierre, G. (2016). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, *40*, 253–266. <https://doi.org/10.1111/ecog.02788>

- Lichti, N., Sturtevant, B. R., Miranda, B. R., Gustafson, E. J., & Jacobs, D. F. (in prep). Linking landscapes and demography: accounting for propagule pressure in a forest simulation model.
- Lindeman, R. H., Merenda, P. F., & Gold, R. Z. (1980). *Introduction to bivariate and multivariate analysis*. Glenview, IL: Scott, Foresman.
- Lindsay, R., & Stephen, Y. (2014). Temperature change in New England: 1895–2012. *International Journal of Undergraduate Research and Creative Activities*, 6, 1895–2012. <https://doi.org/10.7710/2168-0620.1024>
- Lischke, H. (2005). Modeling tree species migration in the Alps during the Holocene: What creates complexity? *Ecological Complexity*, 2, 159–174.
- Little, E. L. Jr (1971). Atlas of United States trees, volume 1, conifers and important hardwoods. U.S. Department of Agriculture Miscellaneous Publication, 1146, 9 p., 200 maps.
- Loarie, S. R., Duffy, S. R., Hamilton, H., Asner, G. P., Field, C. B., & Ackery, D. D. (2009). The velocity of climate change. *Nature*, 462, 1052–1056.
- Loehle, C. (1998). Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, 25, 735–742.
- Loehle, C. (2000). Strategy space and the disturbance spectrum: A life-history model for tree species coexistence. *The American Naturalist*, 156, 14–33.
- Lugo, A. E., & Scatena, F. N. (1996). Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica*, 28, 585–599.
- MacLean, S., & Beissinger, S. R. (2017). Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology*, 23, 4094–4105. <https://doi.org/10.1111/gcb.13736>
- Masek, J. G. (2001). Stability of boreal forest stands during recent climate change: Evidence from Landsat satellite imagery. *Journal of Biogeography*, 28, 967–976.
- Mcgill, B. J. (2012). Trees are rarely most abundant where they grow best. *Journal of Plant Ecology*, 5, 46–51.
- Monleon, V. J., & Lintz, H. E. (2015). Evidence of tree species' range shifts in a complex landscape. *PLoS One*, 10, e0118069. <https://doi.org/10.1371/journal.pone.0118069>
- Moran, E. V., & Ormond, R. A. (2015). Simulating the interacting effects of intraspecific variation, disturbance, and competition on climate-driven range shifts in trees. *PLoS One*, 10, e0142369.
- Munier, A., Hermanutz, L., Jacobs, J. D., & Lewis, K. (2010). The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: Implications for treeline advance with climate warming. *Plant Ecology*, 210, 19–30.
- Murphy, H. T., VanDerWal, J., & Lovett-Doust, J. (2010). Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters*, 13, 1233–1244.
- Neubert, M. G., & Caswell, H. (2000). Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, 81, 1613–1628.
- Odum, H. T., & Allee, W. C. (1954). A note on the stable point of populations showing both intraspecific cooperation and disoperation. *Ecology*, 35, 95–97.
- Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., ... Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, 30, 673–684.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–41.
- Plotkin, A. B., Foster, D., Carlson, J., & Magill, A. (2013). Survivors, not invaders, control forest development following simulated hurricane. *Ecology*, 94, 414–423.
- Raffa, K. F., Aukema, B. H., Erbilgin, N., Klepzig, K. D., & Wallin, K. F. (2005). Interactions among conifer terpenoids and bark beetles across multiple levels of scale: An attempt to understand links between population patterns and physiological processes. *Recent Advances in Phytochemistry*, 39, 80–118.
- RCoreTeam (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Renwick, K. M., & Rocca, M. E. (2015). Temporal context affects the observed rate of climate-driven range shifts in tree species. *Global Ecology and Biogeography*, 24, 44–51.
- Riahi, K., Rao, S., Krey, V., Chirkov, V., Fischer, G., Kindermann, G., ... Rafaj, P. (2011). RCP 8.5—A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, 109, 33–57.
- Running, S. W. (2008). Ecosystem disturbance, carbon, and climate. *Science*, 321, 652–653.
- Scheller, R. M., Domingo, J. B., Sturtevant, B. R., Williams, J. S., Rudy, A., Gustafson, E. J., & Mladenoff, D. J. (2007). Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, 201, 409–419.
- Scheller, R. M., & Mladenoff, D. J. (2005). A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Global Change Biology*, 11, 307–321.
- Serra-Diaz, J. M., Franklin, J., Dillon, W. W., Syphard, A. D., Davis, F. W., & Meentemeyer, R. K. (2016). California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography*, 25, 164–175.
- Serra-Diaz, J. M., Franklin, J., Ninyerola, M., Davis, F. W., Syphard, A. D., Regan, H. M., & Ikegami, M. (2014). Bioclimatic velocity: The pace of species exposure to climate change. *Diversity and Distributions*, 20, 169–180.
- Serra-Diaz, J. M., Scheller, R. M., Syphard, A. D., & Franklin, J. (2015). Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landscape Ecology*, 30, 1039–1053.
- 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. *Global Change Biology*, 23, 3292–3301. <https://doi.org/10.1111/gcb.13622>
- Solomon, A. M., & Kirilenko, A. P. (1997). Climate change and terrestrial biomass: What if trees do not migrate? *Global Ecology and Biogeography Letters*, 6, 139–148.
- Svening, J. C., & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecological Letters*, 7, 565–573.
- Svenning, J. C., Gravel, D., Holt, R. D., & Al, E. (2014). The influence of interspecific interactions on species range expansion rates. *Ecography*, 37, 1198–1209.
- Thom, D., Rammer, W., Dirnbock, T., Muller, J., Kobler, J., Katzensteiner, K., ... Seidl, R. (2017). The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology*, 54, 28–38.
- Thompson, J. R., Carpenter, D. N., Cogbill, C. V., & Foster, D. R. (2013). Four centuries of change in northeastern United States forests. *PLoS One*, 8, e72540.
- Thompson, J. R., Foster, D. R., Scheller, R. M., & Kittredge, D. (2011). The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications*, 21, 2425–2444.
- Thompson, S., & Katul, G. (2008). Plant propagation fronts and wind dispersal: An analytical model to upscale from seconds to decades using superstatistics. *The American Naturalist*, 171, 468–479.
- Thompson, J. R., Simons-Legaard, E., Legaard, K. R., & Domingo, J. B. (2016). A LANDIS-II extension for incorporating land use and other disturbances. *Environmental Software and Modeling*, 75, 202–205.
- Thuiller, W. (2003). BIOMOD – Optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9, 1353–1363.

- Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., ... Zimmermann, N. E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, 9, 137–152.
- Van der Putten, W. H. (2012). Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Review of Ecology, Evolution, and Systematics*, 43, 365–383.
- VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Society of Naturalists*, 174, 282–291.
- Vanderwel, M. C., Coomes, D. A., & Purves, D. W. (2013). Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. *Global Change Biology*, 19, 1504–1517.
- Vanderwel, M. C., Lyutsarev, V. S., & Purves, D. W. (2013). Climate-related variation in mortality and recruitment determine regional forest-type distributions. *Global Ecology and Biogeography*, 22, 1192–1203.
- Vanderwel, M. C., & Purves, D. W. (2013). How do disturbances and environmental heterogeneity affect the pace of forest distribution shifts under climate change? *Ecography*, 37, 10–20.
- Ward, B. C., Scheller, R. M., & Mladenoff, D. J. (2005). *Technical Report: LANDIS-II double exponential seed dispersal algorithm*, Madison, WI.
- Wilson, B. T., Lister, A. J., & Riemann, R. I. (2012). A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. *Forest Ecology Management*, 271, 182–198.
- Woodall, C. W., Zhu, K., Westfall, J. A., Oswalt, C. M., D'amato, A. W., Walters, B. F., & Lintz, H. E. (2013). Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *Forest Ecology and Management*, 291, 172–180.
- Xiao, J. T., Liang, Y., He, H. S., Thompson, J. R., Wang, W. J., Fraser, J. S., & Wu, Z. W. (2016). The formulations of site-scale processes affect landscapescale forest change predictions: A comparison between LANDIS PRO and LANDIS-II forest landscape models. *Landscape Ecology*, 32, 1347–1363. <https://doi.org/10.1007/s10980-016-0442-2>
- Xu, C., Gertner, G. Z., & Scheller, R. M. (2012). Importance of colonization and competition in forest landscape response to global climatic change. *Climatic Change*, 110, 53–83.
- Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, 18, 1042–1052.

SUPPORTING INFORMATION

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