

RESEARCH PAPER

Population dynamics has greater effects than climate change on tree species distribution in a temperate forest region

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Abstract

Aim: Population dynamics and disturbances have often been simplified or ignored when predicting regional-scale tree species distributions in response to climate change in current climate-distribution models (e.g., niche and biophysical process models). We determined the relative importance of population dynamics, tree harvest, climate change, and their interaction in affecting tree species distribution changes.

Location: Central Hardwood Forest Region of the United States.

Major taxa studied: Tree species.

Methods: We used a forest dynamic model, LANDIS PRO that accounted for population dynamics, tree harvest, and climate change to predict tree species' distributions at 270 m resolution from 2000 to 2300. We quantified the relative importance of these factors using a repeated measures analysis of variance. We further investigated the effects of each factor on changes in species distributions by summarizing extinction and colonization rates.

Results: On average, population dynamics was the most important factor affecting tree species distribution changes. Tree harvest was more important than climate change by 2100 whereas climate change was more important than harvest by 2300. By end of the 21st century, most tree species expanded their distributions irrespective of any climate or harvest scenario. By 2300, most northern, some southern, and most widely distributed species contracted their distributions while most southern species, some widely distributed species, and few northern species expanded their distributions under warmer climates with tree harvest. Harvest accelerated or ameliorated the contractions and expansions for species that were negatively or positively affected by climate change.

Main conclusions: Our results suggest that population dynamics and tree harvest can be more important than climate change and thus should be explicitly included when predicting future tree species' distributions. Understanding the underlying mechanisms that drive tree species distributions will enable better predictions of tree species distributions under climate change.

KEYWORDS

colonization, competition, dispersal, disturbance, extinction, forest landscape model, shift

1 | INTRODUCTION

Tree species' distributions change in response to endogenous and exogenous forces and controls operating at different scales. Abiotic controls act at broad regional scales through climate, soil, terrain, and geology, delimit species' potential distributions, and ultimately determine where species can potentially occur (Chase & Leibold, 2003). Population dynamics including demography and biotic interactions (e.g., competition) act at local site scales and interact with biogeochemical processes to determine species' realized distributions and local abundance (Araújo & Luoto, 2007; Boulanger, Taylor, Price, Cyr, & Sainte-Marie, 2018; Ettinger & HilleRisLambers, 2017). At intermediate landscape scales, dispersal process occurs from hundreds of meters to a few kilometers per year and links species' abundance (seed location and abundance), dispersal capability (e.g., distance), and abiotic and biotic suitability at site scales to determine the upper limits of distribution shift at regional scales (García, Klein, & Jorsano, 2017; Nathan et al., 2011; Thuiller et al., 2008). Disturbances (e.g., harvest, fire, and insect) also act at landscape scales (Turner, 2010) and interact with site- and regional-scale processes to modify species' abundance and competitive balance, provide opportunities for seedling establishment, and consequently are important in affecting species distributions (García-Valdés et al., 2015; Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018; Vanderwel & Purves, 2014).

Several kinds of models have been developed to predict tree species distribution at regional scales. Niche models rely on statistical relationships between the observed distributions and abiotic controls to predict the species' fundamental niches (Guisan & Thuiller, 2005). Niche models do not predict realized niches because they do not usually account for the underlying mechanisms at finer scales (Elith & Leathwick, 2009). Biophysical process models predict vegetation distributions by incorporating demography, biotic interactions, and biophysical processes (Scheiter, Langan, & Higgins, 2013). They should, in theory, be better equipped for predicting species responses to novel environment conditions than niche models by simulating mechanisms affecting species (Morin & Thuiller, 2009). However, biophysical process models do not explicitly simulate individual species demography, species interactions, and variation in disturbance impacts among tree species and age classes, and postdisturbance regeneration dynamics (McMahon, Harrison, & Armbruster, 2011; Scheiter et al., 2013). Recent efforts have investigated whether inclusion of biotic interactions, dispersal, and disturbance processes improves predictions by niche and biophysical process models (e.g., Ettinger & HilleRisLambers, 2017; Meier, Lischke, Schmatz, & Zimmermann, 2012; Saltré, Duputié, Gaucherel, & Chuine, 2015; Snell, 2014). No effort, however, has directly compared the contribution of population dynamics, disturbance, and climate change on changes in regional tree species' distributions.

In this study, we investigated the effects of population dynamics, tree harvest, and climate change on tree species distribution changes in the Central Hardwood Forest Region of the United States (CHFR),

one of the most extensive temperate deciduous forests in the world. Most forests in this region are recovering from heavy exploitation in the 19th and early 20th centuries and are at intermediate successional stages and under rapid changes as a result of population dynamics (Johnson, Shifley, & Rogers, 2009). Tree harvest, primarily in the form of partial harvest within the private forest lands is the primary disturbance in this region, where 75% of forests are privately owned (Shifley et al., 2012). Tree harvest is believed to interact with climate change to have great synergistic effects on how tree species respond to climate change (García-Valdés et al., 2015; Vanderwel & Purves, 2014). Recent studies suggest that tree harvest may play greater effects on tree distributions than climate change (Liang et al., 2018; Wang et al., 2015). Accordingly, we hypothesized that tree harvest would accelerate tree species colonization rates through providing colonization opportunities but ameliorate extinction rates through reducing competition under climate change. We used a spatially explicit, species-specific, forest dynamic landscape model, LANDIS PRO to predict changes in tree species' distributions under climate change at 270 m resolution, at which population dynamics, dispersal, and tree harvest can be realistically represented (Wang, He, Fraser, Thompson, & Spetich, 2014). Specifically, we asked: (a) how will tree species' distributions change under climate change with current tree harvest regimes, and (b) what is the relative importance of population dynamics, tree harvest, climate change, and the interaction of climate and tree harvest on future tree species' distributions?

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area included a large portion of the CHFR and comprised 125 million hectares spanning from Oklahoma to Pennsylvania, New York to Arkansas (Figure 1). It covered 14 ecological sections, 100 ecological subsections, and a variety of vegetation, terrains, soils, and climates (Cleland et al., 2007). Approximately three-quarters of the region were forested, while the remaining area was dominated by agricultural and urban land use. This area encompasses the dissected Appalachian Plateaus in the east, relative flat Central Till Plains, open hills and irregular plains of Interior Low Plateau in the mid-west, and Ozark Mountains in the west (Figure 1). The soil types are mostly Alfisol, Inceptisols, Mollisols, and Ultisols. The climate is continental with hot summer and cold winter. Mean annual temperatures vary from 4° to 18 °C with the warmer temperatures in the south. Annual precipitation occurs mostly in spring and fall and ranges from 50 cm in the northwest to 165 cm in the southeast.

2.2 | Modeling approach and experimental design

We designed a factorial simulation experiment resulting in six different scenarios based on three climate projections (current climate, RCP 4.5, and RCP 8.5) and two levels of tree harvest (no harvest

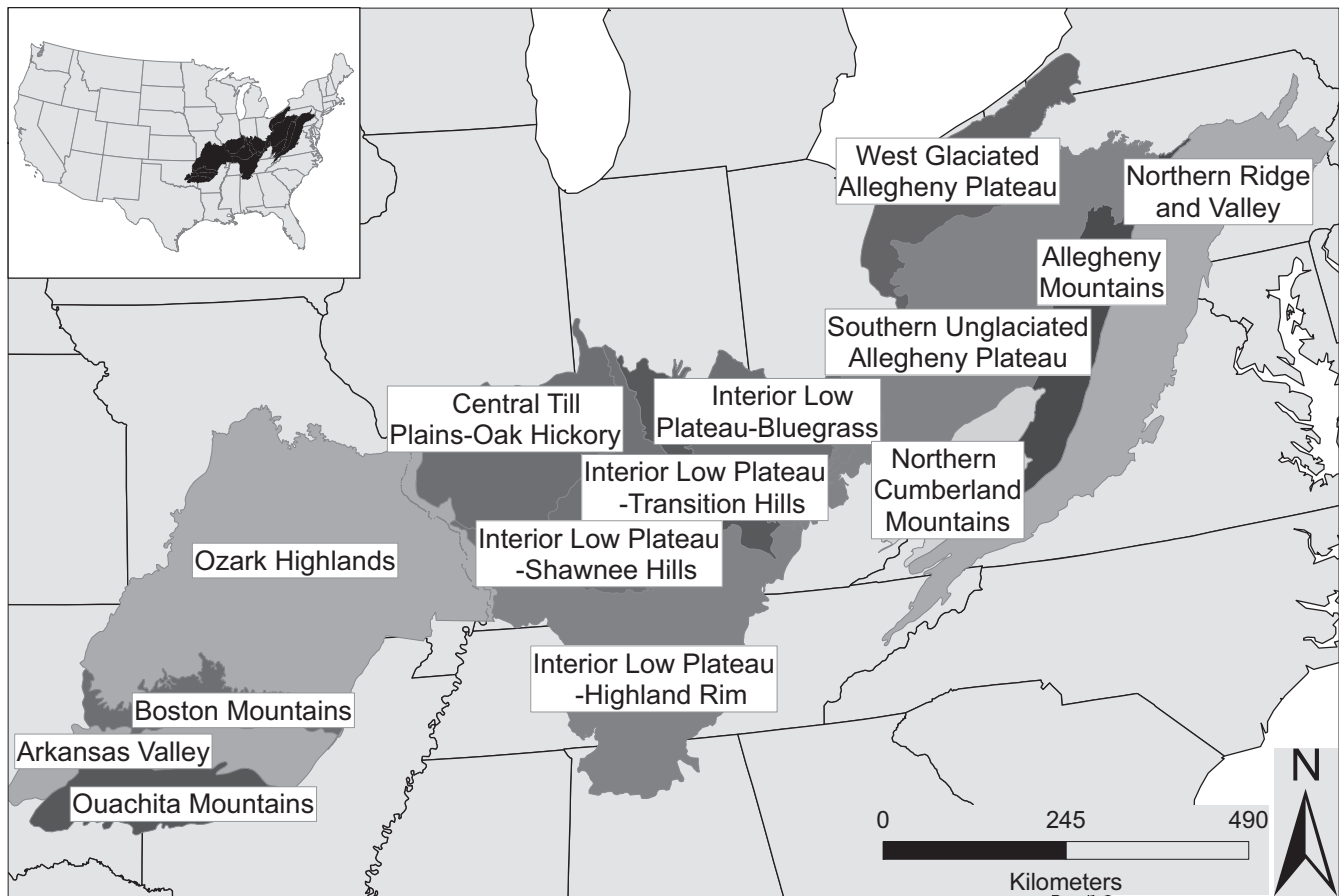


FIGURE 1 The study area covered 14 ecological sections and 125 million hectares, in which we predicted tree species distribution changes under three climate scenarios with and without harvest in the Central Hardwood Forest Region, U.S.A., 2000–2300

and current partial harvest). We modelled the most prominent 23 tree species in this region including oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.), yellow poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), black cherry (*Prunus serotina* Ehrh.), white ash (*F. Americana* L.), and pines (*Pinus* spp.) (Appendix S1).

We used a coupled modelling approach that included the forest dynamic landscape model LANDIS PRO (He, Wang, Shifley, Fraser, & Larsen, 2012; Wang et al., 2013) and the ecosystem process model LINKAGES 3.0 (Dijak et al., 2017) to predict tree species' distributions incorporating the initial tree species distribution and abundance, individual species biological traits, population dynamics, windthrow, harvest, and abiotic controls. We used LINKAGES 3.0 to simulate the physiological effects of abiotic controls on species fundamental niches driven by soil moisture, nitrogen availability, atmospheric conditions, and daily climates. The physiological responses of tree species fundamental niches simulated in LINKAGES 3.0 were characterized using tree species establishment probability (SEP) and maximum growing capacity (MGSO). The estimated SEP and MGSO from LINKAGES 3.0 model under alternative climate scenarios were inputted into LANDIS PRO to regulate tree species demography and link tree harvest and climate change. We then used LANDIS PRO model to simulate population dynamics (including growth, ageing, fecundity,

dispersal, establishment, and competition-caused stem mortality) and tree harvest from 2000 to 2300 (Wang et al., 2013).

Because tree species need long temporal scales (e.g., hundreds of years) to respond to novel climates, thus we simulated 300 years to let species' responses to novel climates unfold. We fixed climate and harvest after 2100 to investigate the equilibrium vegetation state and lag effects due to population dynamics. It was also important to note that our model predictions 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, harvest) allow greater realism than many current alternatives.

2.3 | Climate data and LINKAGES 3.0 model parameterization

We included a current climate and two climate change scenarios that were ensemble climate change projections for two emission scenarios (RCP 4.5, RCP 8.5) based on four GCMs (ACCESS1-0, CanESM2, GFDL-ESM2M, and MIROC5) (Table 1). These four GCMs credibly projected historical climates but projected different future climate patterns. Thus, by modelling these four GCM-emission scenario

TABLE 1 Changes in average annual and seasonal temperature (°C) and precipitation (mm) of future climates (2070–2099) from four GCMs (ACCESS1-0, CanESM2, GFDL-ESM2M, MIROC5) under RCP 4.5 and RCP 8.5 emission scenarios compared to current climates (1980–2009) in the Central Hardwood Forest Region, USA

	Emission scenarios	Annual	Spring	Summer	Fall	Winter
Temperature	RCP 4.5	3.5	2.8	3.0	3.6	2.8
	RCP 8.5	5.6	5.3	5.5	6.5	5.2
Precipitation	RCP 4.5	−5.1	5.2	−3.2	−15.9	29.8
	RCP 8.5	26.0	−7.6	−16.5	−14.0	38.1

combinations, we generated a range of predictions that incorporated uncertainties in future climate projections.

We created 600 landtypes by intersecting 100 ecological subsections and six landforms derived from DEM to capture region-wide abiotic controls in vegetation, soils, terrains, precipitation, and temperature. We assumed resource availability (MGSO) and species potential habitats (SEP) were uniform within a landtype but different among landtypes. We obtained measures of soil organic matter, nitrogen, wilting point, field moisture capacity, and percent clay, sand and rock for soil polygons in the Natural Resources Conservation Service soil survey (Soil Survey Staff, <http://soils.usda.gov/>). We used a combination of individual species biological traits in LINKAGES 3.0, values from other studies and new calculated values (Dijak et al., 2017; Wang et al., 2013, 2015; Wang, He, Thompson, & Fraser, 2016; Appendix S2).

In LINKAGE 3.0, we used daily climate data (minimum and maximum temperature and precipitation, mean surface wind speed, and incident solar radiation) under each climate scenario, which was able to capture the effects of climate change extremes on SEP and MGSO. With respect to drought, in LINKAGE 3.0, a given tree was characterized as drought-stressed on the given growing day if the potential evapotranspiration exceeded the actual evapotranspiration. If the drought-stressed proportion of the growing season for the given tree exceeded the maximum proportion of growing season this species can withstand drought, trees would have mortality and thereby result in reduced MGSO. The reduced MGSO would result in stem mortality due to competition for growing space in LANDIS PRO.

We obtained the current climate data (1980–2009) including daily maximum and minimum temperature, daily precipitation, and daily wind speed at a 1/8-degree resolution and daily solar radiation and day length for each ecological subsection at 1 km resolution from DAYMET (Thornton et al., 2017). We obtained the down-scaled climate change projections (2070–2099) for each ecological subsection from the Coupled Model Intercomparison Project phase 5 (CMIP5). Compared with the current climates (1980–2009), the four GCMs all projected the mean annual temperature to increase by 3.5°C and 5.6°C in 2070–2099 across the region under the RCP 4.5 and RCP 8.5 emission scenarios, respectively. There was great variation in precipitation projections among four GCMs with more precipitation in the east region but less precipitation in the west region; Precipitation on average decreased 5.1 mm under RCP 4.5 emission scenario and increased 26 mm under RCP 8.5 emission scenario (Table 1).

We estimated SEP by simulating each individual tree species using LINKAGES 3.0 for 30 years with 20 replications for each of 600 landtypes for current climate at year 2000 and the three climate change scenarios at year 2100 based on above soil, climate, and species data in each landtype. The simulated biomass at simulation year 30 was used to derive SEP for each species in each landtype and climate scenario (He, Mladenoff, & Crow, 1999; Wang et al., 2015). We estimated MGSO as the maximum biomass for each climate scenario at year 2100 by simulating 23 species together in LINKAGES 3.0 for 300 years with 20 replications for each of 100 ecological subsections based on above soil, climate, and species data (Wang et al., 2015).

2.4 | LANDIS PRO model parameterization

We derived the initial forest composition map for the LANDIS PRO at year 2000 from 1995–2005 the U.S. Forest Service Inventory and Analysis (FIA) data using Landscape Builder, which stochastically assigned a representative FIA plot to each raster cell based on landform, land cover, and size class (Dijak, 2013). The initial map for each raster cell contained the initial tree species distribution (absence/presence) and abundance (number of trees and diameter at breast height (DBH) by species age cohort and also captured seed sources (mature trees location and abundance) and habitat fragmentation (e.g., forest, urban, water body, and agricultural land) (Wang et al., 2013). We inputted the landtype map as well as SEPs and MGSO estimated from LINKAGES 3.0 for each climate scenario to LANDIS PRO to capture the climate change effects and its interaction with harvest on tree species' distributions.

In LANDIS PRO, we simulated stem mortality due to competition for growing space (e.g., drought) using Yoda's self-thinning theory (Yoda, 1963). Competition-caused stem mortality was initiated once stands reached MGSO, in which smaller trees and lower shade tolerance species would have larger mortality; for further detailed descriptions of LANDIS PRO see Wang et al., 2013; Wang, He, Fraser, et al. (2014). We mechanistically simulated dispersal accounting for seed sources (mature trees location and abundance), dispersal distance, habitat fragmentation, and abiotic and biotic suitability for establishment and survival (Wang et al., 2013). We compiled individual tree species' biological traits including longevity, maturity, shade tolerance, maximum dispersal distance, sprouting probability, maximum stand density index, and maximum DBH from previous studies and literature (Burns & Honkala, 1990; Wang et al., 2013, 2015;



Wang, He, Fraser, et al. (2014); Wang, He, Thompson, & Fraser, 2017; Wang, He, Thompson, Spetich, & Fraser, 2018; Liang, He, Wang, Fraser, & Wu, 2015; Jin et al., 2017; Iverson et al., 2017; Appendix S3).

We simulated partial harvest using the LANDIS PRO Harvest Module by incorporating multiple management units that incorporated private industrial lands, private nonindustrial lands, and public lands (Fraser, He, Shifley, Wang, & Thompson, 2013). We simulated two levels of partial harvest in each management unit using thinning from above that left 6.8 or 18.4 m²/ha residual basal area. We varied the percent of the unit harvested and species rank priority for harvesting to match the removals to those reported in 1995–2005 FIA data (O'Connell et al., 2015). Harvest in any unit was equally split between the two levels of partial harvest and the percent area treated per decade varied from 3% in Oklahoma, 4% in Illinois, 6% in Tennessee, 7% in Pennsylvania, and 9% in Arkansas. The amount of basal area harvested was controlled by the entering and residual stand basal area parameters. This volume-regulated approach actually represented thinning from above, clearcutting, or partial harvest at the raster cell level, which could capture the variation in harvest regimes across the region (Canham, Rogers, & Buchholz, 2013).

We followed the approach described by Wang et al. (2013) and Wang, He, Spetich, et al. (2014) to evaluate the model predictions under current climate and adjust parameters if necessary to ensure the predicted trends in tree species distribution, basal area, and density were consistent with empirical descriptions of old-growth forests in the region. We then used the initial conditions for 2000 as the starting point to simulate tree distribution changes for 300 years with and without harvest from 2000 to 2300 at 270 m resolution using 10-year time steps with five replicates for each scenario that were sufficient to capture the variability (Murphy & Myers, 2003).

2.5 | Analysis of simulation results

We described changes in tree species' distributions in terms of occurrences for the whole region in the short, medium, and long-term based on simulation results for year 2050, 2100, and 2300, respectively. We calculated species' percent occurrences as the number of raster cells in which a species was present divided by the total of number of forested cells in the region. We determined the relative importance of population dynamics, harvest, climate change, and their interaction on individual tree species' distribution changes in the short, medium, and long-term using a repeated measures analysis of variance (Repeated Measures ANOVA) with time as a repeated effect. The data consisted of species' percent occurrences at year 2000, 2050, 2100, and 2300 along with dummy variable indicating the climate scenario and harvest scenario. We estimated the relative importance as the percentage of total variance explained by population dynamics (time), climate, and harvest while controlling for the other factors. Our explanations focused on trends rather than statistical significance because of minimal random noise in the tightly controlled simulations.

We further investigated the effects of population dynamics, harvest, and climate change on changes in species distributions by summarizing extinction and colonization rates under three climate scenarios with harvest in the short, medium, and long-term. We classified a species status in a raster cell as extinction if it was present at year 2000 and absent in the future and colonization if it was absent at year 2000 but present in the future with minimum of 108 stems in each raster cell which corresponded to one tree in a FIA plot based on FIA's expansion factor in this region. We calculated the extinction and colonization rates for each species under each scenario as the number of raster cells in each category in the short, medium, and long-term divided by the number of cells a species was present at year 2000. We summarized species distribution changes as expansion when species colonization was greater than extinction and contraction when colonization was less than extinction for the three climate change scenarios with harvest in the short, medium, and long-term.

3 | RESULTS

3.1 | Importance of population dynamics, harvest, and climate change

The relative importance of three factors affecting tree species' distribution changes varied among species and time periods. On average, population dynamics had the greatest effect on species distribution changes and explained 87.1%, 71.2%, and 48.2% of the variation in occurrences in the short, medium, and long-term, respectively (Table 2). Harvest, on average, explained 8.3%–15.3% of the variation in species occurrences and had more consistent effects across time periods. Climate change, on average, explained 1.0% and 8.3% of variation in species occurrences in the short and medium term, respectively, but it explained 31.5% of variation and was more important than harvest in the long-term (Table 2).

By year 2300, climate explained more variation in occurrences than population dynamics for 8 of 23 tree species. Climate change explained a large percentage of variation for northern species such as sugar maple, American beech, and eastern white pine; southern species such as loblolly pine, and yellow poplar; and widely distributed species such as white oak and chestnut oak (Table 2). Harvest generally explained more variation in occurrences for tree species that were harvested, such as white oak, loblolly pine, and eastern white pine; for shade-intolerant tree species such as yellow poplar; and of shade-tolerant tree species such as American beech (Table 2).

3.2 | Cumulative climate and harvest effects

Tree species' occurrences changed progressively under climate change scenarios with harvest and substantially in the long-term. The magnitude of distribution changes varied among species and climate change scenarios, with greater changes under the RCP 8.5 climate scenario. In the short and medium term, most tree species

TABLE 2 The relative importance of population dynamics (P), harvest (H), climate change (C), and their interaction (H*C) in determining variation in tree species occurrences in the Central Hardwood Forest Region, USA, 2000–2300. Relative importance was measured as the percent variation explained in species occurrences based on the repeated-measures ANOVA

	50				100				300			
	P	C	H	C*H	P	C	H	C*H	P	C	H	C*H
White oak	88.5	0.1	8.4	0.0	79.2	4.5	12.5	1.8	57.1	18.5	18.5	2.5
Chestnut oak	87.9	0.2	10.5	0.0	75.0	5.5	14.6	2.4	49.3	26.5	17.6	2.6
Post oak	92.5	0.1	4.6	0.0	84.5	3.1	8.5	1.3	62.9	16.4	15.6	1.8
Northern red oak	82.3	2.7	12.0	0.0	60.1	6.8	28.5	2.6	52.0	18.6	22.5	3.3
Black oak	85.2	1.5	10.3	0.0	59.2	10.2	25.4	3.2	31.5	46.9	13.6	4.5
Scarlet oak	83.3	1.2	13.5	0.0	54.4	9.8	30.2	3.6	25.6	53.2	15.4	4.6
Southern red oak	90.8	0.2	7.0	0.0	78.3	6.7	10.5	2.5	70.2	14.6	8.7	3.2
Red maple	93.1	0.1	4.8	0.0	80.2	8.9	6.8	3.1	76.9	8.9	5.8	3.8
Sugar maple	80.1	3.7	13.0	0.2	65.8	13.5	15.4	4.3	31.0	48.6	12.6	4.6
Yellow poplar	86.7	0.2	9.5	0.0	75.9	7.5	12.5	2.1	60.4	23.8	10.8	3.0
American beech	82.0	0.3	15.6	0.1	50.8	12.8	30.5	3.9	23.0	52.3	16.9	4.5
Black cherry	92.1	0.8	6.2	0.0	65.2	6.8	23.7	2.3	61.5	16.4	15.6	3.2
White ash	87.2	0.3	10.5	0.0	75.3	8.2	12.3	3.2	30.3	51.3	11.3	3.9
Pignut hickory	90.7	0.4	5.9	0.0	82.6	7.2	5.7	2.5	47.1	40.6	6.2	3.0
Mockernut hickory	93.5	0.2	4.3	0.0	83.1	6.3	6.5	2.1	69.2	17.3	7.1	3.2
Shagbark hickory	93.8	1.0	5.2	0.0	82.5	7.9	5.6	2.0	67.0	20.4	6.4	3.0
Sweetgum	92.3	0.3	5.4	0.0	82.2	8.5	5.2	2.1	47.5	37.5	8.5	3.1
Shortleaf pine	93.1	0.1	4.8	0.0	86.6	6.4	3.7	1.3	78.3	9.7	6.7	2.1
Loblolly pine	87.6	1.5	8.5	0.0	66.7	9.1	18.6	3.5	44.8	27.8	20.1	4.1
Eastern white pine	80.9	2.4	15.6	0.1	65.6	10.5	10.7	3.2	9.2	65.3	18.4	3.9
Eastern hemlock	80.5	2.6	14.5	0.2	70.3	11.8	12.3	3.6	20.8	55.2	16.7	4.2
Eastern redcedar	90.4	0.1	6.5	0.0	67.9	3.4	23.5	2.1	68.1	8.6	14.2	2.9
Red spruce	68.3	4.1	23.5	1.1	45.9	15.9	28.7	8.5	49.6	21.2	18.9	10.2
Average	87.1	1.0	9.6	0.1	71.2	8.3	15.3	2.9	49.3	30.4	13.4	3.7

expanded their distributions (Figure 2) and had greater colonization rates than extinction rates under two climate change scenarios with harvest (Appendix S3, Appendix S4). Extinction rates averaged 1%–5% in the short-term and increased to 3%–15% in medium term whereas colonization rates averaged 10%–40% in the short term and increased to 20%–50% in the medium term. In the long-term, however, tree species had three general types of changes in distribution. The first species group expanded their distributions under two climate scenarios with harvest and included northern species chestnut oak, widely distributed species red maple, and some southern species (loblolly pine, and yellow poplar) and (Figures 2 and 4, Appendix S5). Colonization rates were high ranging from 60% to 80% for red maple, yellow poplar, and loblolly pine (Figure 3). The second species group contracted distributions under two climate scenarios with harvest and included most northern species (e.g., sugar maple, and eastern hemlock, northern red oak, and black cherry), southern species (e.g., shortleaf pine), and most widely distributed species (e.g., shagbark hickory) (Figures 2 and 4, Appendix S5, Appendix S6). Extinction rates were high ranging from 50% to 80% for sugar maple, red spruce, and eastern hemlock

(Figure 3). The third species group expanded their distributions under the RCP 4.5 climate scenarios but contracted under the RCP 8.5 climate scenarios; This group included white oak and American beech (Figures 2–4).

We interpreted shifts in the edges of species distributions in response to climate change from spatial patterns in extinction and colonization in this region. The northern edge of loblolly pine and yellow poplar distributions shifted northward; the southern edge of distributions for tree species such as sugar maple, American beech, northern red oak, black cherry, and eastern hemlock shifted northward and upward in elevation in the Appalachian Mountains (Figure 4, Appendix S5, Appendix S6).

3.3 | Interactive effects

The percent variation in tree species occurrences explained by the interaction between harvest and climate change was minor and averaged <5% (Table 2). However, colonization and extinction rates varied by as much as 10% for some species between harvest and no-harvest scenarios, which corresponded to millions of hectares

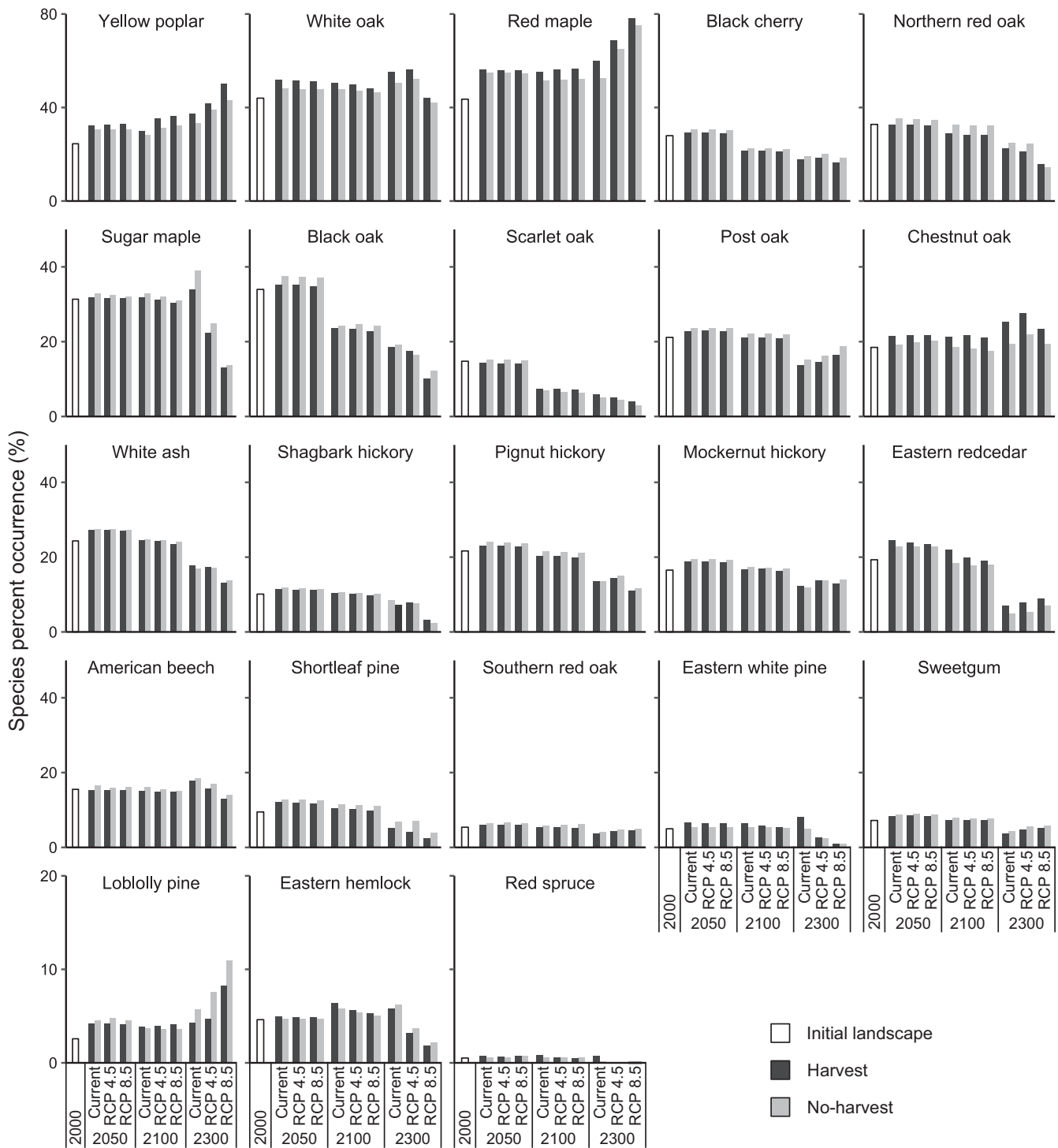


FIGURE 2 Predicted percent occurrences for all 23 tree species under three climate scenarios with and without harvest at year 2000, 2050, 2100, and 2300 in the Central Hardwood Forest Region, U.S.A

across the region. The added effects of harvest generally accelerated the contractions for tree species that were negatively affected by climate change such as sugar maple and American beech (Figures 3 and 4). Harvest also accelerated the species expansions that were positively affected by climate change such as loblolly pine and yellow-polar under climate change scenarios (Figures 3 and 4). For example, extinction rates for sugar maple under RCP 8.5 climate

scenario was 64% with harvest and 55% without harvest; colonization rates for yellow poplar under RCP 8.5 climate scenario was 100% with harvest and 90% without harvest (Figure 3). However, harvest ameliorated contractions for tree species such as black oak, white ash, and eastern white pine under climate change (Figures 2 and 4). For example, the extinctions rates for white ash under the climate change with harvest scenarios (e.g., 51% under RCP 8.5-

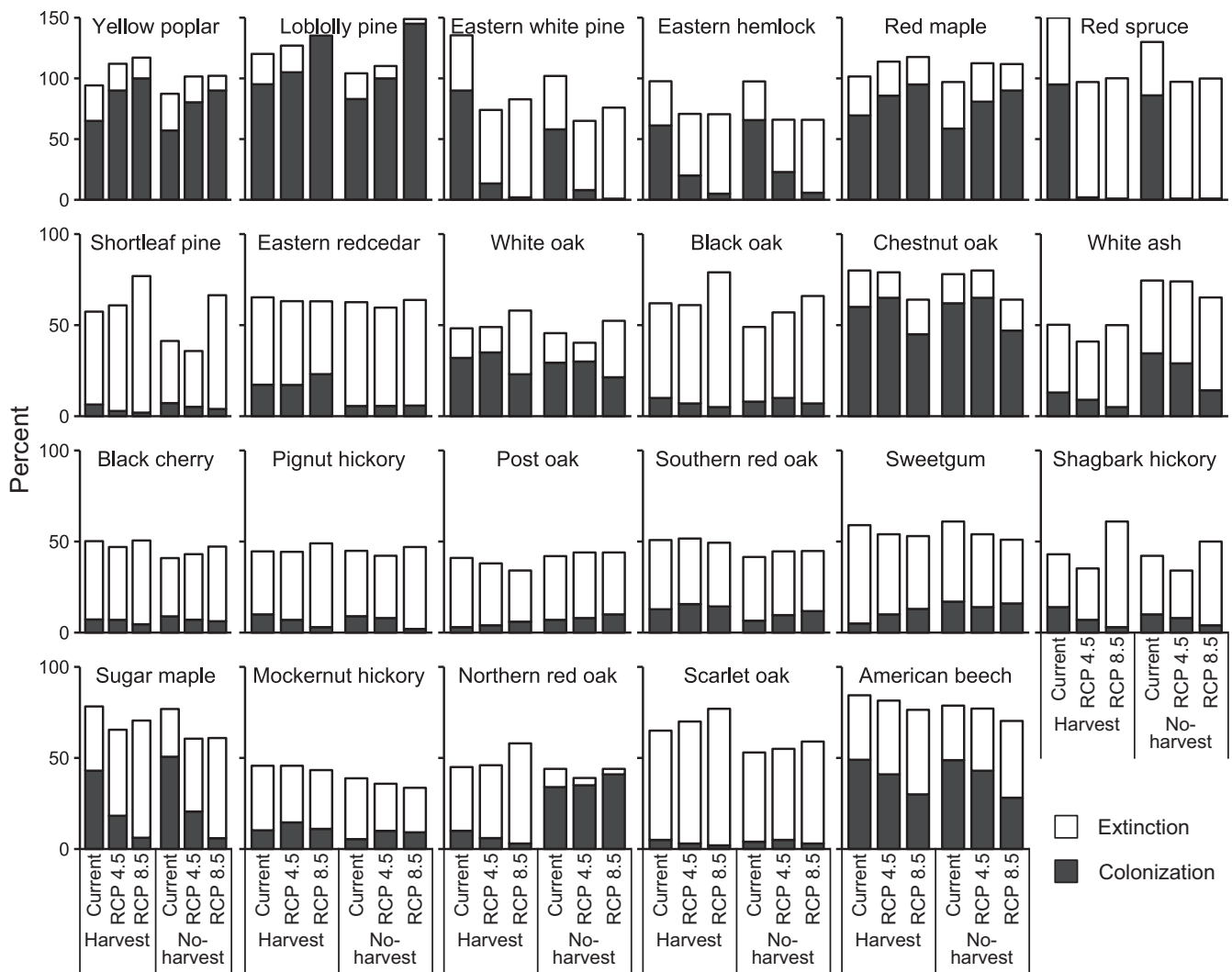


FIGURE 3 Predicted extinction and colonization rates (%) for all 23 tree species under three climate change scenarios with and without harvest at year 2300 in the Central Hardwood Forest Region, U.S.A

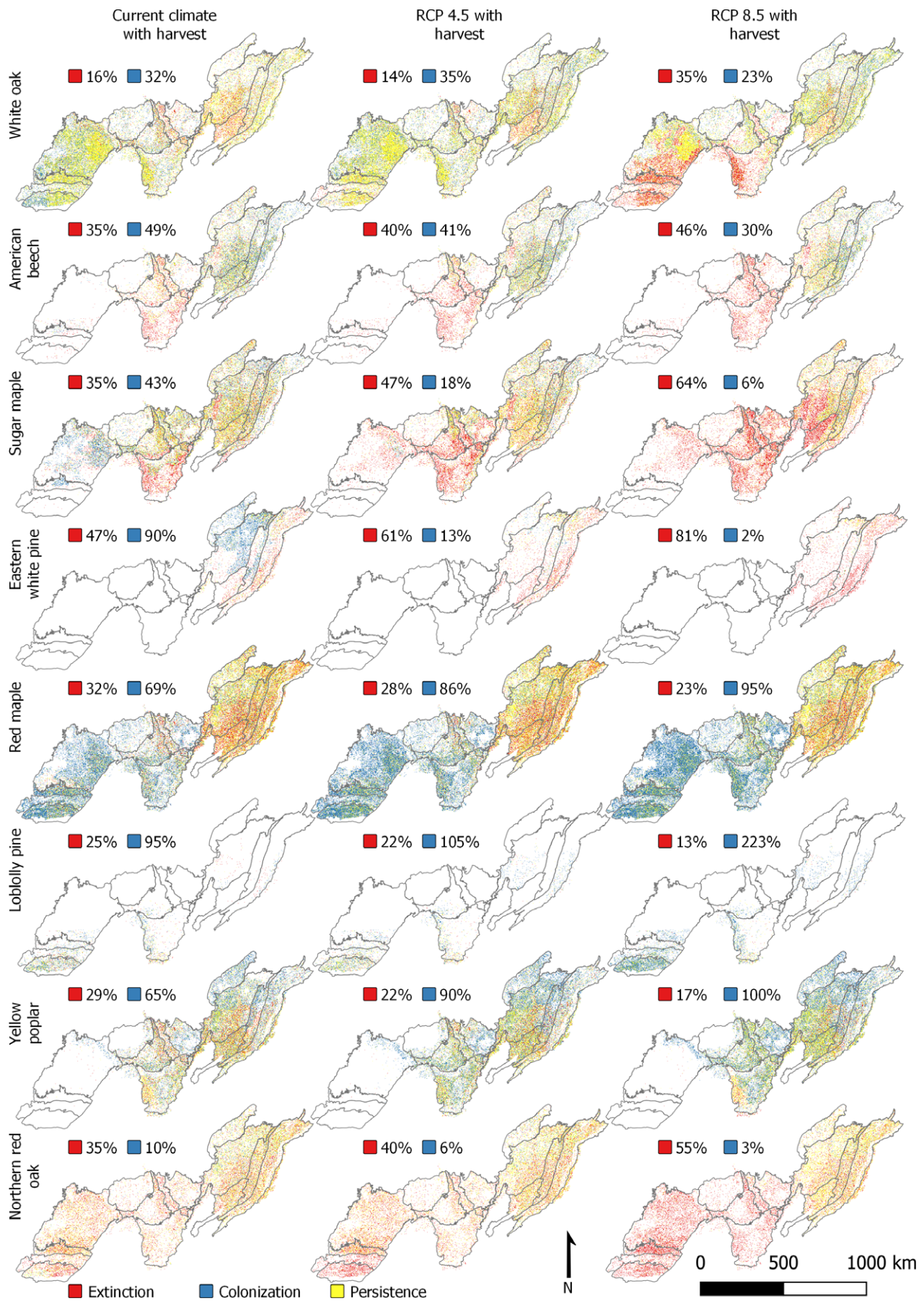
harvest) were higher than those under the climate change without harvest scenarios (e.g., 45% under RCP 8.5-no harvest) (Figure 3).

4 | DISCUSSION

We predicted changes in tree species' distributions from 2000 to 2300 for a large temperate deciduous forest region considering population dynamics, disturbance, and abiotic controls, and their interaction. We demonstrated that population dynamics was generally the most important process affecting changes in species' distributions over time but climate change became the most important process

for 8 of 23 species by 2300. Tree harvest was more important than climate change in the short and medium term whereas climate change was more important than harvest in the long-term. These findings contrast with the fundamental assumptions underlying niche models that abiotic controls are the primary determinants of species distributions while demography, biotic interactions, and disturbance play relatively minor roles and thus are generally not included in these models (Elith & Leathwick, 2009). Almost all temperate deciduous forests in eastern North America, western and central Europe, and eastern Asia forests have been severely exploited and disturbed by human influences (Anderson-Teixeira et al., 2013). Although abiotic controls may exert the most important role in determining

FIGURE 4 Predicted tree species spatial distributions of extinction (red) and colonization rates (blue) for selected tree species: white oak, American beech, sugar maple, eastern white pine, red maple, loblolly pine, yellow poplar, and northern red oak under three climate scenarios with harvest at year 2300 in the Central Hardwood Forest Region, U.S.A. (Note: yellow colours showed tree species would persist under given scenario)



species potential distributions, we found that population dynamics and tree harvest can be more important than climate change in driving changes in species realized distributions in these forests. Therefore, we suggest population dynamics and tree harvest or other dominant disturbance factors should be explicitly included when predicting future species' distributions under climate change in temperate deciduous forests.

We found in the first 100 years of simulation most tree species expanded their distributions irrespective of any climate or harvest scenario. This is because, under current climate scenario, many tree species may not fill all climatically suitable areas due to nonclimatic factors, such as dispersal limitation and competition ability (Svenning & Skov, 2004). For example, Svenning and Skov (2004) found that <50% of the climatically suitable areas for many tree species were currently occupied. The expansions of tree species under climate change scenarios in the first 100 years of simulation are because tree species are long-lived organisms (e.g., up to several hundred years) and substantial extinctions may take centuries to occur due to time-lagged responses of tree species to novel climate conditions (Miller & McGill, 2018; Sittaro, Paquette, Messier, & Nock, 2017). These findings differ with many studies in this region that suggest climate change could lead to substantial contractions by end of this century (e.g., Iverson, Prasad, Matthews, & Peters, 2008). Iverson et al. (2008) used the DISTRIB-SHIFT niche model and predicted that 6 of 23 species simulated in our study would lose 20%–40% of their potential distributions; Morin and Thuiller (2009) used the BIOMOD niche model and predicted that sugar maple would lose 40%–50% of the potential distribution under alternative climate change scenarios by end of this century. Given we chose the climate scenarios as similar as possible to those used in niche models, the major differences between our predictions and those made by niche models were because we specifically simulated a gradual change in climate and incorporated species demography that enabled tree species to have inertia in response to climate change (MacLean & Beissinger, 2017). We suggest that models that do not simulate population dynamics based on species demographic traits (e.g., current age, growth, longevity) may overestimate species extinctions by end of 21st century.

We found that northern species with limited distributions such as eastern hemlock, eastern white pine, and red spruce had low colonization rates and nearly went extinction by 2300. This is likely because of dispersal limitation due to their low initial abundance and restricted distribution. We also showed that the colonization of southern species such as loblolly pine was slow and limited to their northern range boundaries. Such time-delayed dispersal is mainly because the number of dispersal events is in part determined by the time required for juveniles to mature and produce seeds, which usually takes decades (Moles, 2004). The combination of long generation time and low density near range boundaries results in slow colonization rates (Kubisch, Poethke, & Hovestadt, 2011; Sittaro et al., 2017). Dispersal has to date been one of the most prominent uncertainties in predicting future species distributions (Alexander et

al., 2018; Saltr  et al., 2015; Thuiller et al., 2008). We simulated dispersal as a site- and landscape-scale process with a single event occurring from hundred meters to a few kilometers and accounted for location and abundance of parent trees, species-specific dispersal distance, dispersal barriers, and biotic and abiotic suitability (Shifley et al., 2017; Wang et al., 2013). Thus, our model accounts for source-sink dynamics, and density- and distance-dependent dispersal. Despite the uncertainties in parameters (e.g., dispersal distance) for dispersal, our approach filled a gap in tree species distribution modelling by incorporating realistic species dispersal processes under climate change and is a step forward in addressing uncertainties in dispersal and species distribution.

We showed that tree harvest interacted with climate change and played important roles in affecting species distribution changes in temperate deciduous forests. For example, harvest accelerated the colonization rates for shade-intolerant species (e.g., yellow poplar), because they were better adapted to new climates and could fully take advantage of the canopy gaps created by harvest; harvest increased colonization rates for white oak by providing colonization opportunities and ameliorated its extinction rates through reducing competition. This finding is consistent with previous studies indicating harvest can accelerate or ameliorate species colonization and extinction rates by providing establishment opportunities and providing a competitive advantage or disadvantage to species simulations (e.g., Vanderwel & Purves, 2014). The amount and type of harvest and other disturbance also affected outcomes. Shortleaf pine likely decreased in occurrences because it was not competitive without frequent fire and more even-aged harvest, even though future climates were more suitable for it in much of the region. The importance of harvest has important implications for forest management and highlights the potential benefits of tree harvest as silvicultural strategies for climate change adaptation management, e.g., through maintaining current species abundance and composition in order to promote the forest resilience, or facilitating change to accelerate species turnover to species that are better adapted to new climates.

Changes in distribution varied by individual species as a result of species-specific demographic traits such as shade tolerance, longevity, niche widths for temperature and precipitation, fecundity, dispersal capability, establishment probability, and initial distribution. Most of northern, some southern, and most of widely distributed species contracted and shifted northward and upward (e.g., Appalachian Mountains) to track novel favourable climates. Some of these species may migrate into northern hardwood or boreal forest regions and increase in occurrences there, especially under severe climate change scenarios. By contrast, most of southern species, some widely distributed species, and few northern species expanded their distributions and were migrating from the southeastern U.S. These species-specific responses are difficult to capture in models using plant functional types. For example, Vanderwel and Purves (2014) showed that northern temperate hardwoods plant functional types including maple species, northern red oak, and American beech would extinct in Ozark Highlands under climate change and harvest could prevented the colonization of the species within this functional type. We similarly found that sugar

maple would undergo extinction, but red maple generally persisted in the Ozark Highlands because red maple had wider fundamental niches and could better adapt to climate change than sugar maple (Figure 4); We also showed that harvest ameliorated the colonization for sugar maple and American beech under climate change, but harvest accelerated the colonization for northern red oak because it was an intermediate shade-tolerant species compared to sugar maple and American beech and could take advantage of growing space released by harvest.

Our predictions are subject to a number of uncertainties. Urban growth, as the primary land use change in the region, may further fragment habitats and impede the rate of tree species' northward and upward shifts (García-Valdés et al., 2015; Saltré et al., 2015). We assumed that the primary causal relationships with climate change were the effects of temperature and precipitation on maximum growing capacity, tree mortality, and seedling establishment without accounting for the effects of rising CO₂ concentration and N deposition, which will play an important role in future vegetation dynamics (Griepentrog, 2015; Scheiter et al., 2013). For example, Free Air CO₂ Enrichment experiment demonstrated that elevated CO₂ increased the net primary productivity of young temperate forests (Norby, Warren, Iversen, Medlyn, & McMurtrie, 2010); Biophysical models found that elevated CO₂ can accelerate forest regeneration and alter forest succession rates and pathways (e.g., Miller, Dietze, Delucia, & Anderson-Teixeira, 2016). Despite these potential limitations, there are good reasons why our modelling approach is well-suited for understanding and predicting how tree species distributions change as a result of endogenous and exogenous processes. First, LANDIS PRO has been extensively tested and applied in the eastern United States (e.g., Jin et al., 2017; Wang et al., 2013, 2015, 2017, 2018; Wang, He, Fraser, et al., 2014; Wang, He, Spetich, et al., 2014). Second, the majority of parameters including species demographic traits, harvest parameters, and initial tree species distribution and composition were derived from millions of tree records in FIA data. Third, we simultaneously incorporated population dynamics, tree harvest, and climate change for a large temperate deciduous forest region at a relatively fine spatial resolution of 270 m, especially compared to previous modelling approaches.

In conclusion, we demonstrated broad underlying patterns in the process of distribution changes for 23 temperate tree species. We highlighted the importance of population dynamics and harvest in projecting species distribution changes under climate change. We suggest that it is essential to include demographic processes, inter-specific competition, and harvest when predicting the future regional species distribution under climate change in temperate deciduous forests.

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BIOSKETCH

Wen J. Wang is interested in investigating the roles of climate change, land use change, disturbance, and management on biodiversity and carbon dynamics in forest ecosystems at landscape and regional scales.

Author contributions: WJW, FRT, and HSH conceived the ideas; WJW conducted the model simulations and data analyses with assistance from JSF and WDD; and WJW, FRT, and HSH led the writing.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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