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Climate change and tree harvest interact to affect future tree species distribution changes

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Abstract

1. Tree harvest and climate change can interact to have synergistic effects on tree species distribution changes. However, few studies have investigated the interactive effects of tree harvest and climate change on tree species distributions.
2. We assessed the interactive effects of tree harvest and climate change on the distribution of 29 dominant tree species at 270 m resolution in the southern United States, while accounting for species demography, competition, urban growth and natural fire. We simulated tree species distribution changes to year 2100 using a coupled forest dynamic model (LANDIS PRO), ecosystem process model (LINKAGES) and urban growth model (SLEUTH).
3. The distributions of 20 tree species contracted and nine species expanded within the region under climate change by end of 21st century. Distribution changes for all tree species were very slow and lagged behind the changes in potential distributions that were in equilibrium with new climatic conditions.
4. Tree harvest and climate change interacted to affect species occurrences and colonization but not extinction. Occurrence and colonization were mainly affected by tree harvest and its interaction with climate change while extinctions were mainly affected by tree harvest and climate change.
5. *Synthesis and applications*. Interactive effects of climate and tree harvest acted in the same direction as climate change effects on species occurrences, thereby accelerating climate change induced contraction or expansion of distributions. The overall interactive effects on species colonization were negative, specifically with positive interactive effects at leading edges of species ranges and negative interactive effects at trailing edges. Tree harvest generally did not interact with climate change to greatly facilitate or ameliorate species extinction. Our modelling results highlight the importance of considering disturbances and species demography (e.g. post-harvest regeneration dynamics) when predicting changes in tree distributions.

KEYWORDS
colonization, combined effects, competition, disturbance, extinction, forest dynamic model, seed dispersal, species range shift

1 | INTRODUCTION

Many species have shifted their distributions in response to recent anthropogenic-driven environmental changes such as climate change, habitat loss and fragmentation. These shifts are generally towards the poles or upward in elevation and are reported for a wide range of taxa (Alexander et al., 2018; Parmesan & Yohe, 2003). However, recent studies suggest that many species are not shifting fast enough to keep pace with future rapid climatic change and thus become vulnerable to range contractions and population declines (Miller & McGill, 2018). This may be particularly true for tree species, which usually have limited dispersal capacity and long regeneration time (Krapek & Buma, 2018; Renwick & Rocca, 2015; Sittaro, Paquette, Messier, & Nock, 2017).

The ability of tree species to track climate change is primarily driven by the demographic processes: growth, fecundity, dispersal, colonization and mortality (Nathan & Muller-Landau, 2000). These demographic processes are co-determined by multiscale factors such as site-scale biotic interactions, landscape-scale disturbances (e.g. fire, harvest, habitat fragmentation) and regional-scale abiotic controls (e.g. temperature, precipitation and soil) (Boulanger, Taylor, Price, Cyr, & Sainte-Marie, 2018; Normand, Zimmermann, Schurr, & Lischke, 2014). Biotic interactions determine the competitive balance on local sites and affect trees' ability to colonize and grow (Neuschulz, Merges, Bollmann, Gugerli, & Böhning-Gaese, 2018; Putnam & Reich, 2017). Disturbances usually operate at scales from hundreds of metres to a few kilometres and affect forest composition and structure through directly altering tree species abundance, age structure and competition and indirectly affecting post-disturbance regeneration dynamics (Dale, 2001). Disturbances are also believed to interact with environmental changes to have great synergistic effects on tree species distribution changes (García-Valdés et al., 2015; Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018).

Climate-distribution models such as niche models and biophysical process models at large scales generally incorporate effects of regional-scale abiotic controls on tree species distribution changes. However, niche models generally ignore underlying processes (e.g. demography, disturbances) that drive tree species distribution changes (Elith & Leathwick, 2009). Biophysical process models incorporate demography and biotic interactions and thus are better equipped for representing the interaction of disturbances and environmental changes when projecting tree species distribution changes (Scheiter, Langan, & Higgins, 2013). However, biophysical process models usually operate at relatively coarse spatial resolutions ranging from 10 to 50 km grids and are limited in their ability to spatially explicitly simulate individual tree species demography, disturbances and the interaction of these processes with environment changes (McMahon, Harrison, & Armbruster, 2011) There have been substantial efforts in recent years to improve the simulation realism of factors such as dispersal, biotic interactions and habitat fragmentation in modelling tree species distributions (e.g. Boulangeat, Damien, & Thuiller, 2014; García, Klein, & Jorsano, 2017; Liang et al., 2018). The interactive effects of disturbances and environmental changes on tree species distribution, however, remain a challenge and constitute a large uncertainty in projections of future species distribution changes (Garcia, Cabeza, Rahbek, & Araújo, 2014; Urban et al., 2016). Here, we provide a coupled process model-based assessment of the combined effects of tree harvest and climate change on tree species distributions in the southern United States covering the Ozark Highlands and Gulf Coastal Plains. Many widely distributed tree species (e.g. white oak), northern tree species (e.g. sugar maple) and southern tree species (e.g. loblolly pine) whose southern or northern range edges are currently located in the southern United States. (Little, 1971) will colonize newly suitable areas and undergo extinction in response to altered climate conditions (Vanderwel & Purves, 2014).

We singled out tree harvest from all other disturbance agents (e.g. fire, insect and disease), because tree harvest is the most prevalent disturbance agent compared to other disturbance agents, particularly in temperature forests (Anderson-Teixeira et al., 2013). For example, forests in the southern United States are predominately privately owned and are the most commercially harvested in the United States, producing ~60% of the total U.S. wood production and ~18% of the world's pulpwood for paper production (Prestemon & Abt, 2002). Tree harvest also disproportionately affects tree species distributions compared to other disturbance agents through immediately altering competition, age structure and composition by directly removing all trees or selected species or size groups. Tree harvest in the form of high-grading in oak–hickory forests and extensive commercial clear-cutting in southern United States is expected to interact with climate change to affect colonization and extinction (Vanderwel & Purves, 2014; Wang et al., 2015). Tree harvest could accelerate colonization through promoting regeneration and reducing competition intensity; concurrently, it could also accelerate extinction through increasing species turnover as seedlings may not colonize under novel climates. Accordingly, we hypothesized that tree harvest would accelerate tree species colonization at leading edges of their distributions, especially for newly favoured species and accelerate species extinction at trailing edges, especially for species that were not favoured by changing climates in this region.

We used a species-specific, forest dynamic landscape model, LANDIS PRO to project tree species realized distribution changes under climate change and tree harvest over the 21st century accounting for tree species demography, competition, natural fire and urban growth in the southern United States (Wang et al., 2014a). We used the LANDIS PRO model because it has been extensively calibrated with forest inventory and analysis (FIA) data (O'Connell et al., 2015) and applied to multiple regions in the eastern United States (e.g. Brandt et al., 2014; Janowiak et al., 2018; Wang, He, Thompson, & Fraser, 2017; Wang et al., 2014a,b, 2015, 2018). We addressed the following questions: (a) how will tree species distributions change under climate change over the 21st century with the current regime of tree harvest, urban growth and natural fire; and (b) are there interactive effects of tree harvest and climate change on tree species

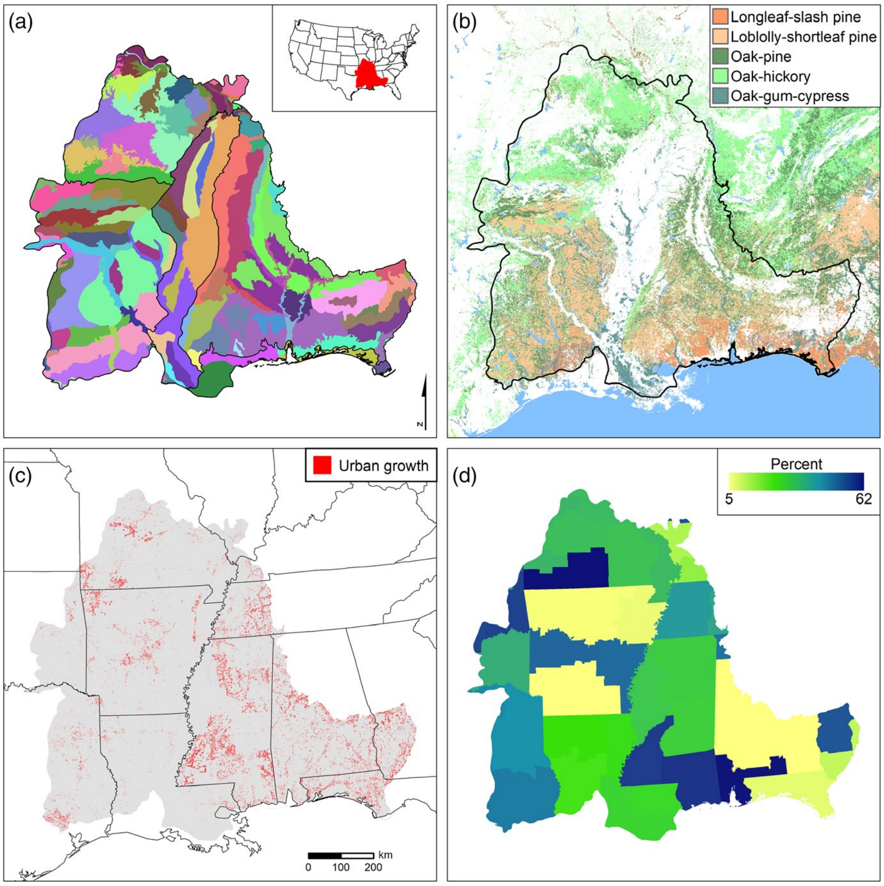

FIGURE 1 The study area included geographic location (a), subsections (a), forest types (b), urban growth (c) and harvest intensity (percent area harvested per decade) (d) [Colour figure can be viewed at wileyonlinelibrary.com]

distribution changes? If yes, what is the relative contribution of tree harvest, climate change and the interaction of tree harvest and climate change on tree species distribution changes? And, how do tree harvest and climate change act in synergy to affect tree species distribution changes?

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was located in the southern United States and covered 73 million hectares and 12 states from Missouri to Texas and Oklahoma to Florida (Figure 1). The area has diverse climates, terrains, soils and vegetation types and is characterized by 24 ecological sections and 108 ecological subsections (second and third level of the Ecological Classification System of U.S. Department of Agriculture Forest Service, respectively; Figure 1a, Cleland et al., 2007). The area consists of five major subregions: the Interior Highlands, the West Gulf Coastal Plain, the East Gulf Coastal Plain, the Mississippi Alluvial Valley and the Gulf Coast (Figure 1a).

The Interior Highlands include the Ozark Highlands and Boston Mountains (Figure 1a,b). The dominant forest types currently are oak–hickory (*Quercus* spp., *Carya* spp.) and oak–shortleaf pine (*Pinus echinata*) forests. The subregion is highly dissected and ranges from low rolling hills, steep hills, to high plateau with summits greater than 750 m in Boston Mountains. The climate is continental with long, hot summers and cool winters with most of precipitation occurring in spring and fall.

The West and East Gulf Coastal Plains span southeastern Arkansas to eastern Texas, southwestern Oklahoma to Georgia (Figure 1a,b). The terrain varies from flat plains, moderately dissected irregular plains, to mountainous landscape. The major forest types currently consist of mixed deciduous hardwoods and conifers including loblolly (*Pinus taeda*)–shortleaf pine, longleaf–slash pine (*Pinus palustris*, *Pinus elliottii*), oak–pine, oak–hickory and oak–gum–cypress forests. The climate is humid maritime with hot summers and mild winters. The precipitation is evenly distributed across the seasons with periodical mid- to late-summer droughts occurring in most years. The West and East Gulf Coastal Plains are one of the true hotspots of biodiversity and endemism with ecosystems endangered due to intensive human disturbances and climate change.

The Mississippi Alluvial Valley includes the Lower Mississippi Riverine Forest Province and is one of the most productive forested wetland ecosystems in North America (Figure 1a,b). This area has highly diverse terrain with a mosaic of ridges, swales, meander belts and back swamps. The climate is modified continental in the north

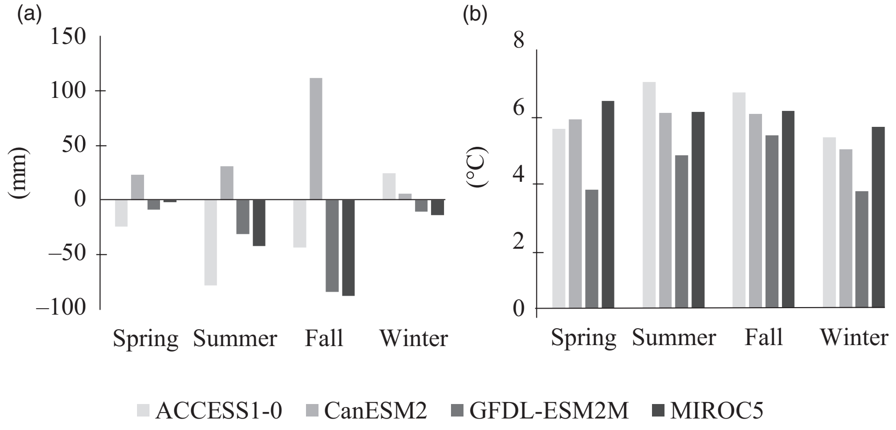

FIGURE 2 Changes in average seasonal precipitation (mm) and temperature (°C) of future climates (2007–2099) from four GCMs (ACCESS1-0, CanESM2, GFDL-ESM2M, MIROC5) under RCP 8.5 emission scenario compared to the current climates (1980–2009)

and maritime in the south. The land cover currently is largely agricultural and the major forest types include loblolly–shortleaf pine, longleaf–slash pine, oak–hickory and oak–gum–cypress.

The Gulf Coast includes marshlands in Louisiana and the entire coastline of Mississippi, Alabama and the panhandle of Florida (Figure 1a,b). This area is characterized by flat, weakly dissected alluvial plains with poorly drained soils. The dominant forest types currently are longleaf–slash pine and oak–gum–cypress.

Tree harvest in our study area consisted of two forms: high-grading in non-commercial private lands and clear-cutting in commercial forests. Other disturbance agents such as fire and urban growth largely at the expense of forests also have important impacts on forest changes in this region (Huggett, Wear, Li, Coulston, & Liu, 2013).

2.2 | Climate data and climate change scenarios

We included current climate as a baseline climate scenario and four climate change scenarios based on the ACCESS1-0, CanESM2, GFDL-ESM2M, MIROC5 general circulation models (GCMs) under the representative concentration pathway (RCP) 8.5 (Riahi, Gruebler, & Nakicenovic, 2007) (Figure 2). The RCP 8.5 emission scenario is close to current emission trajectories and is the highest emission scenario used in IPCC Fifth Assessment Report. We selected these four GCMs because they credibly simulated historical climates but predicted somewhat different future seasonal temperature and precipitation patterns, which enabled us to generate ensemble projections that integrated the uncertainties of climate change (Figure 2, Appendix S1, Rupp, Abatzoglou, Hegewisch, & Mote, 2013).

We used daily minimum and maximum temperature and precipitation, mean surface wind speed and incident solar radiation for each ecological subsection under each climate scenario. We obtained the daily climate data for the current climate scenario (1980–2009) from (Maurer, Wood, Adam, Lettenmaier, & Nijssen, 2002) and DAYMET (Thornton et al., 2014). We downloaded the daily climate data for future climate change scenarios for three time periods: 2010–2039, 2040–2069, 2070–2099, for each ecological subsection from the Coupled Model Intercomparison Project phase 5 (CMIP5, https://cmip.llnl.gov/cmip5/data_portal.html). Compared with the baseline climate scenario, the four GCMs projected the mean annual daily maximum temperature to increase 4–6°C in 2070–2099 under the RCP 8.5 emission scenario (Figure 2). Annual precipitation decreased 30–80 mm under ACCESS 1-0, GFDL-ESM2M and MIROC5 and increased 30 mm under CANESM2 (Figure 2, Appendix S1). ACESS1-0 was the warmest and driest GCM and CANESM2 the mildest and wettest GCM under the RCP 8.5 emission scenario.

2.3 | Coupled modelling approach

We modelled the most abundant 29 tree species that were determined based on their basal area in FIA data, which accounted for 80%–95% of total basal area for each ecological section (Table 1). We used a coupled modelling approach that included the ecosystem process model LINKAGES 3.0 (Dijak et al., 2017), the urban growth model SLEUTH (Belyea & Terando, 2015) and the forest dynamic landscape model LANDIS PRO (Wang et al., 2014a) to spatially explicit simulate tree species distribution changes considering the initial tree species distribution and abundance, species biological traits, demography, competition, disturbances, environmental changes and their interaction (Figure 3).

We used urban growth projections from SLEUTH to reduce the forested lands each decade in which species and community dynamics were simulated in LANDIS PRO. We used LINKAGES 3.0 to simulate the physiological effects of temperature, precipitation, terrain and soil on tree species potential distributions by simulating establishment and growth under each climate scenario; tree species potential distributions from LINKAGES 3.0 were represented using species potential colonization probability (measured as tree species establishment probability, SEP) and maximum growing space or carrying capacity (MGSO). SEP and MGSO were then inputted into LANDIS PRO to regulate species demography (e.g. growth, establishment, mortality) and link climate change to disturbances (Wang et al., 2015). We used LANDIS PRO to project changes in

TABLE 1 Species biological traits used in the LANDIS PRO forest dynamic landscape model

Scientific name	Common name	Maturity/ longevity (years)	Shade tolerance	Max. dispersal distance (m/year)	Vegetative probability	Min/Max. sprouting age (years)	Max. DBH (cm)	Max. SDI (trees/ha)	No. Potential germination seeds/ mature tree
Acer saccharum Marsh.	Sugar maple	20/300	5	2,160	0.8	20/80	75	570	300
Liriodendron tulipifera L	Yellow poplar	20/200	2	2,160	0.5	20/150	70	700	30
Fraxinus americana L.	White ash	30/250	3	1,620	0.6	10/150	65	570	30
Quercus rubra L.	Northern red oak	30/200	3	1,080	0.7	10/120	65	570	20
Ulmus americana	American elm	40/200	3	1,620	0.7	10/60	60	900	50
Quercus alba L.	White oak	40/300	4	1,080	0.7	10/100	75	570	40
Quercus falcate Michx.	Southern red oak	30/200	3	1,080	0.7	10/100	65	570	20
Ulmus alata	Winged elm	40/200	4	1,620	0.7	10/60	60	900	50
Nyssa sylvatica	Blackgum	30/250	4	810	0.6	10/60	70	570	40
Prunus serotine Ehrh.	Black cherry	20/150	2	1,080	0.8	20/100	65	570	30
Fraxinus pennsylvanica	Green ash	30/250	3	1,620	10/80	10/80	65	570	30
Quercus lyrata	Overcup oak	30/300	3	1,080	0.5	10/100	75	570	20
Pinus echinata Mill.	Shortleaf pine	20/200	2	1,350	0.8	10/30	70	990	50
Nyssa aquatica	Water tupelo	30/300	2	810	0.7	10/100	75	570	40
Quercus lyratapagoda	Cherrybark oak	30/200	2	1,080	0.7	10/100	65	570	20
Carya tomentosa Nutt.	Mockernut hickory	30/200	3	1,080	0.6	10/200	65	570	30
Quercus lyrataphellos	Willow oak	20/300	2	1,080	0.7	10/100	75	570	20
Celtis laevigata	Sugarberry	30/150	4	1,080	0.6	10/50	60	1,000	20
Quercus lyratastellate Wangenh.	Post oak	40/250	3	1,080	0.6	10/100	70	570	40
Quercus lyrataveltutina Lam.	Black oak	20/150	3	1,080	0.6	10/100	65	570	20
Quercus lyratanigra	Water oak	20/150	2	1,080	0.5	10/80	65	570	20
Nyssa biflora	Swamp tupelo	20/250	2	810	0.7	10/100	70	570	40

(Continues)

TABLE 1 (Continued)

Scientific name	Common name	Maturity/ longevity (years)	Shade tolerance	Max. dispersal distance (m/year)	Vegetative probability	Min/Max. sprouting age (years)	Max. DBH (cm)	Max. SDI (trees/ha)	No. Potential germination seeds/ mature tree
Liquidambar styraciflua L.	Sweetgum	30/200	2	1,620	0.6	10/200	65	570	40
Acer rubrum L.	Red maple	10/150	4	2,160	0.9	10/100	65	700	7
Quercus lyratalaurifolia	Laurel oak	20/150	4	1,080	0.6	10/60	65	570	20
Taxodium distichum	Baldcypress	20/300	4	1,080	0.5	10/30	75	1,200	50
Pinus elliottii	Slash pine	20/150	2	1,350	0.2	10/50	70	1,100	50
Pinus taeda L.	Loblolly pine	20/200	3	1,350	0.8	10/30	70	1,100	30
Pinus palustris	Longleaf pine	20/200	2	1,350	0.5	10/50	70	990	50

tree species realized distributions forward in time by simulating species growth, fecundity, dispersal, colonization, mortality, competition, natural fire and tree harvest. We conducted LANDIS PRO simulations at 270 m resolution, which was a reasonable compromise between realistically simulating demography, disturbances and environmental changes and the needed computer resources for simulations.

2.3.1 | Urban growth projections – SLUETH model

We used urban growth projections for each decade from 2020 to 2100 at 60 m resolution from the urban growth model SLEUTH, which were available from North Carolina State University (Belyea & Terando, 2015). We resampled the 60-m resolution maps to 270-m resolution using the "nearest" function in ArcGIS 10.3. We removed raster cells from forest lands that were simulated by LANDIS PRO each decade if SLEUTH predicted the probability of converting from forest to urban was greater than 50%. About 10% of the forested lands in the West Gulf Coastal Plain and the Gulf Coast subregions in Alabama, Georgia, and Florida, and about 3%–4% of the other three subregions were converted to urban from 2020 to 2100 (Figure 1c).

2.3.2 | Species potential distributions – LINKAGES 3.0 model

We projected potential distribution changes and estimated the SEP and MGSO for each species under each climate scenario on 1,080 land types. We created land types by intersecting 108 ecological subsections and the 10 most abundant soil types (series) based on area in the Soil Survey Geographic Database (SSURGO; Soil Survey Staff 2015). We obtained soil data for each land type including thickness, soil organic matter, nitrogen, water content at field capacity, water content at saturation, wilting point, percent clay, sand and rock, hydraulic conductivity at field capacity and an exponent for estimating hydraulic conductivity from SSURGO (http://soils.usda.gov/). We compiled species biological traits required by LINKAGES 3.0 including maximum growth rates, drought tolerance, shade tolerance, nitrogen tolerance and growing degree-day requirements from previous studies, which calibrated the biological traits for 62 eastern U.S. tree species in LINKAGES 3.0 (Dijak et al., 2017; Wang et al., 2015).

We estimated SEP for each species on each land type by simulating species establishment and growth from bare ground over 30 years. We calculated SEPs from the maximum biomass reached by a species on each land type by converting biomass to a relative scale of 0–1 across species (He, Mladenoff, & Crow, 1999; Wang et al., 2015). We estimated MSGO as the maximum total biomass reached on each subsection by simulating the establishment and growth of plots composed of the 29 mixed-tree species over 300 years. We calculated mean SEP and MSGO from 20 replicate simulations in LINKAGES 3.0 of the current climate scenario (1980–2009) and the four climate change scenarios for three time periods (2010–2039, 2040–2069, 2070–2099). Since LINKAGES 3.0 used daily climate data, it captured the individual tree species' responses to the effects

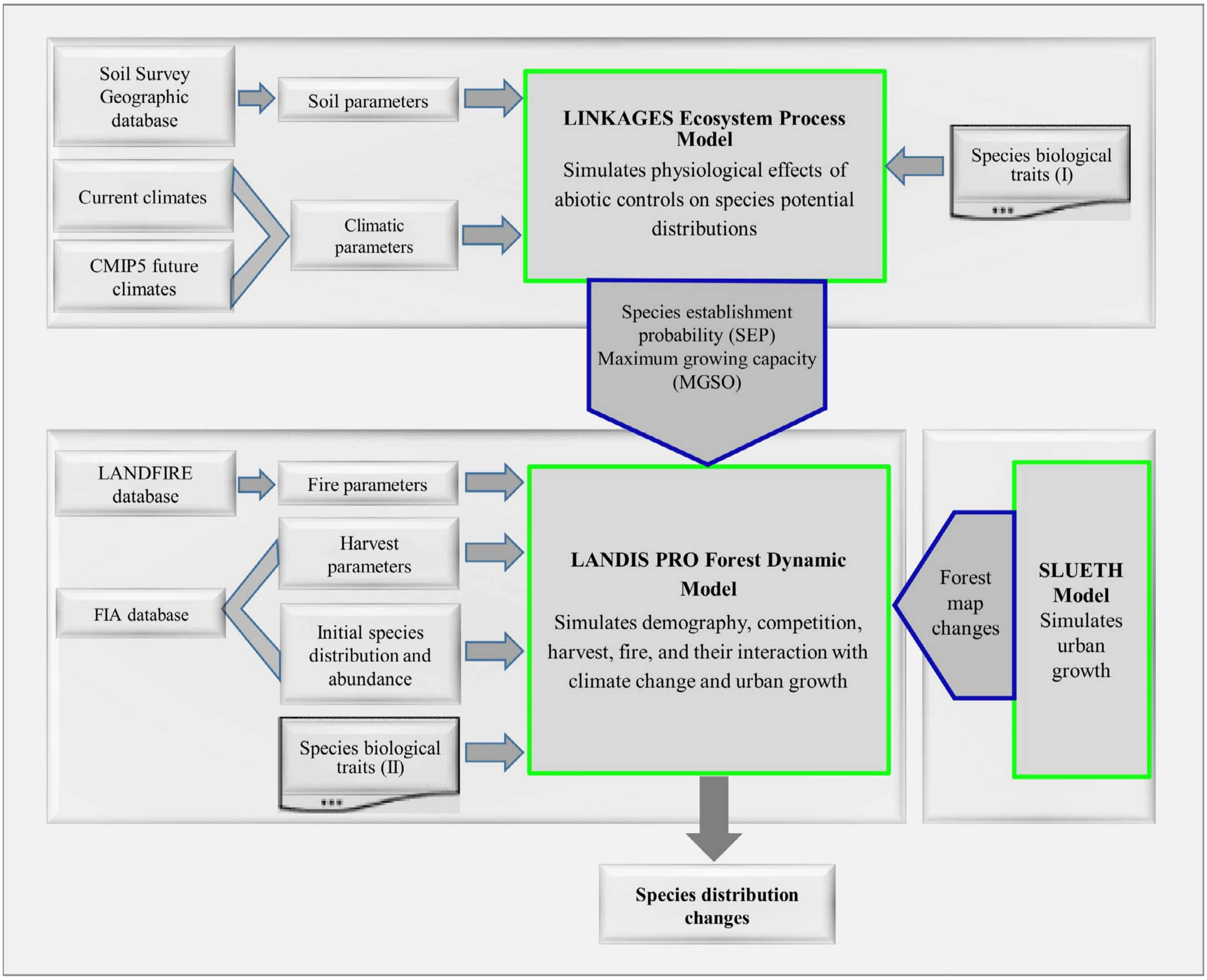

FIGURE 3 A coupled modelling approach that included the ecosystem process model LINKAGES 3.0, the urban growth model SLEUTH and the forest dynamic landscape model LANDIS PRO was used to spatially explicit simulate tree species distribution changes [Colour figure can be viewed at wileyonlinelibrary.com]

of changed climate and climate extremes. For example, drought reduced establishment (SEP) and growth (MGSO), which resulted in greater stem mortality in LANDIS PRO through competition for growing space. Further details of the LINKAGES 3.0 model and our application of it for estimating SEP and MGSO were described in Wang et al. (2017) and Dijak et al. (2017) (See Appendix S2 for selected results of SEP and MGSO).

2.3.3 | Species realized distributions – LANDIS PRO model

LANDIS PRO represents individual tree species as age cohorts and tracks distribution (absence/presence) and abundance (number of trees and diameter at breast height (DBH)) by age cohort for individual tree species in each raster cell (Wang et al., 2014a). We used Landscape Builder (Dijak, 2013) to derive the initial forest conditions including distribution and abundance by age cohort for 29 tree species on each 270 m-raster cell at year 2010 based on 2000–2015 FIA data for trees ≥2.54 cm (O'Connell et al., 2015). We verified the initial forest conditions for LANDIS PRO simulations in terms of age structure, density and basal area at year 0 with FIA data for 2000–2015 (O'Connell et al., 2015) for each ecological section to insure the initial forest conditions realistically presented the observed forests (Appendix S3).

Tree species demography (including growth, fecundity, dispersal, colonization and mortality) in LANDIS PRO is mainly driven by species biological traits including longevity, maturation age, shade tolerance, fire tolerance, dispersal shape parameter, minimum sprouting age, maximum sprouting age, sprouting probability, maximum stand density index and maximum DBH. We parameterized species biological traits from previous studies and literature (Table 1; Brandt et al., 2014; Burns & Honkala, 1990; Wang et al., 2014a,b, 2015, 2018). Tree growth is simulated using individual polynomial age–DBH relationships, which we estimated using FIA data and varied among ecological sections to capture environmental heterogeneity. Tree age cohorts generate seeds once reaching maturation age. Seed abundance is determined by age cohort density and species reproductive rates. Seed dispersal is determined by dispersal capacity and habitat connectivity. Dispersal is simulated using a fat-tailed dispersal kernel to capture the long-distance dispersal (Clark, Poulsen, Bolker, Connor, & Parker, 2005). Seedlings colonization is determined by abiotic suitability (SEP, MGSO) and biotic suitability (competitive capacity). Competition-caused stem mortality is initiated once MGSO is reached in stand exclusion, understorey re-initiation and old growth stages and simulated using Yoda's self-thinning theory, where mortality decreases with increasing average tree size (Wang et al., 2014a; Yoda, Kira, Ogawa, & Hozumi, 1963); for further detailed description of LANDIS PRO, see Wang et al. (2014a).

We simulated the current tree harvest regime using the LANDIS PRO Harvest Module (Fraser, Wang, He, & Thompson, 2019). We used FIA units as management units and simulated different harvest strategies for each unit (e.g. harvest type, percent harvested, species preference) to capture the variation in harvest practices across the region. We parameterized the percent area harvested per decade and residual basal area for each management unit using remotely sensed disturbance records (LANDFIRE 2012) and the area harvested by landownership reported in FIA data (O'Connell et al., 2015). We simulated two types of harvest in each management unit consisting of high-grading and clear-cutting. We varied the percentage of the unit harvested and the preferred species for harvest to capture similar removals to those reported since 1995–2015 (O'Connell et al., 2015). The percent area harvested per decade varied from 2.5% to 45% with a greater percentage in southern pine commercial forests (Figure 1d).

We simulated current natural fire regime using the LANDIS PRO Fire Module (Fraser et al., 2019). Wildfire size and frequency were parameterized based on fire records from 1980 to 2014 using data from LANDFIRE (2012) and Monitoring Trends in Burn Severity (Eidenshink et al., 2007).

We validated the LANDIS PRO model under current and future climates by comparing simulation results against empirical data and other modelling results (e.g. niche models; Wang et al., 2014b; Fraser, He, Shifley, Wang, & Thompson, 2013; Iverson et al., 2017). We followed the framework developed by Wang et al. (2014b) to validate short-term predictions against FIA data and validate long-term predictions against old-growth forest data and consistency with forest succession and stand dynamic theories. We also validated harvest effects on stand dynamics (basal area, stem density) against published harvest studies (Fraser et al., 2013). Overall, the validation results showed that the model predictions were consistent with observed patterns under current climates. We also compared the predicted responses of individual tree species under climate change from the LANDIS PRO model with the SHIFT-DISTRIB niche model predictions in the eastern United States (Iverson et al., 2017). The comparisons indicated high agreement for most tree species at year 2300 because tree species responses reached equilibrium with novel climates in both models. However, the niche model predicted greater increases for favourable tree species and greater decreases for unfavourable tree species than LANDIS PRO at year 2100. The niche model was not able to simulate species demography and assumed unlimited seed dispersal, whereas LANDIS PRO captured extinction lags and colonization lags through simulating demographic inertia and more realistic seed dispersal. Thus, the discrepancies revealed different mechanisms underlying the two modelling approaches (see Appendix S3 for details about model initialization, calibration and validation).

2.4 | Experimental design

We designed a two-factor simulation experiment with two harvest regimes (no harvest regime, current harvest regime) and five levels of climate (current climate and four climate change scenarios), resulting in total of 10 simulation scenarios. We used LANDIS PRO with the same initial forest conditions for the 10 simulation scenarios to project tree species distribution changes (realized distributions) from 2010 to 2100 with a 10-year time step. We conducted five replicate simulations of each scenario in LANDIS PRO to incorporate stochasticity, but variation was minimal among replicates. Urban growth and natural fire were included as background disturbances in all 10 simulation scenarios. We treated the current climate scenario without tree harvest as the baseline scenario.

We mapped the projected changes in species potential distributions by each ecological subsection as the ratio of predicted species biomass under given climate change scenario at year 2100 to current climate scenario at year 2010 using LINKAGES 3.0 simulation results. The changes in species potential distribution were characterized into seven categories: extirpated (0/>0), large decrease (0–0.4), small decrease (0.4–0.8), no change (0.8–1.2), small increase (1.2–2.0), large increase (>2.0) and colonization (>0/0).

We analysed effects of tree harvest and climate change on changes in tree species realized distributions in terms of occurrences, relative extinction rates and relative colonization rates using LANDIS PRO simulation results at year 2100. We defined species presence in a raster cell as a minimum of 108 stems, which corresponded to at least one tree (>2.54 cm) in a FIA plot based on FIA's expansion factor in this region. We calculated average species occurrences at year 2100 from the five replicates for each of 10 simulation scenarios as the percentage of the forested raster cells in the study area. We calculated and mapped species relative extinction and colonization rates as the percentage of raster cells where a species was present under the baseline scenario at year 2100 that changed from present to absent or absent to present in the scenario being considered respectively. We then averaged species occurrences, relative colonization rates and relative extinction rates for the four climate change scenarios to represent an ensemble prediction, which were referred to as the mean RCP 8.5 results. We characterized 29 tree species into declining or increasing species if species occurrences decreased or increased under mean RCP8.5 without tree harvest compared with the baseline scenario at year 2100.

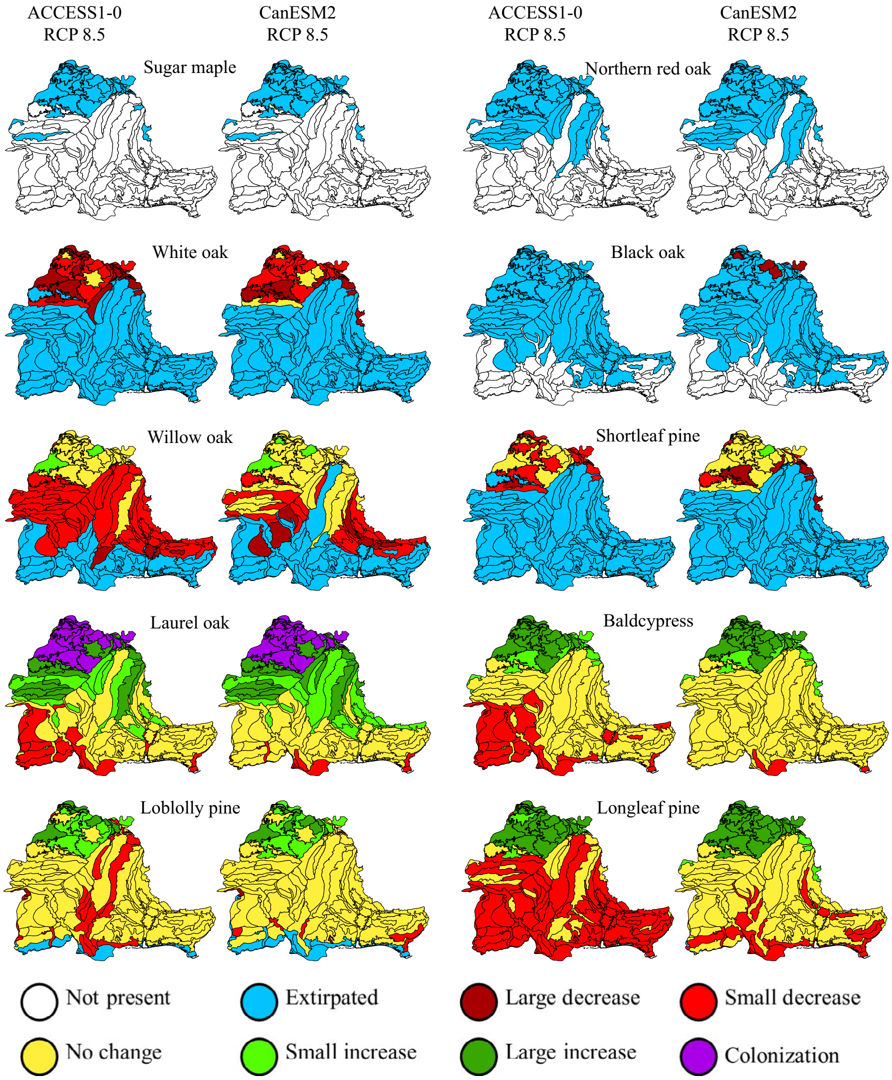

FIGURE 4 Potential distribution changes by ecological subsection for selected 10 tree species under two selected GCMs under RCP8.5 emission scenario by end of 21st century compared to current climates. Note that ACESS1-0 was the warmest and driest GCM while CANESM2 was the mildest and wettest GCM among our four included GCMs under RCP8.5 emission scenario [Colour figure can be viewed at wileyonlinelibrary.com]

We estimated effect sizes for climate change, tree harvest and the combination and interaction of climate change and tree harvest on tree species occurrences, relative extinction rates and relative colonization rates by calculating the relative differences in each response variable between the scenarios of interest for each species at year 2100 as: (Scenario$_1$ − Scenario$_2$)/Scenario$_2$ (García-Valdés et al., 2015). We calculated tree harvest effects as the relative differences between the tree harvest scenario and non-tree harvest scenario under current climate conditions; climate change effects as the relative differences between the current climate scenario and climate change scenario, both without tree harvest; and combined effects as the relative differences between the climate change scenario with tree harvest and current climate without tree harvest. We calculated additive effects for tree harvest and climate change as the sum of tree harvest and climate change effects and interactive effects for tree harvest and climate change as the difference between the combined and additive effects. We calculated average effect sizes for tree harvest, climate change and their interaction for declining and increasing species groups respectively. Note that our analyses focused on an average response among four climate change scenarios and effect sizes rather than statistical significance because of standard errors of estimates are very small when based on millions of raster cells.

3 | RESULTS

3.1 | Tree species potential distributions

Tree species' potential distributions generally shifted northward (Figure 4, Appendix S4). Northern hardwood (e.g. sugar maple and northern red oak) and central hardwood (e.g. white oak and black oak) tree species experienced substantial losses of potential distribution and some tree species were nearly extirpated from the region (Figure 4, Appendix S4). Most southern tree species (e.g. willow oak and shortleaf pine) had great decreases in potential distribution in the southern part of the region and slightly increased in the northern part of the region (Figure 4, Appendix S4). Some southern tree species (e.g. laurel oak, baldcypress, loblolly pine and longleaf pine) persisted in most of their current ranges but experienced small decreases in the southern part of their ranges and large increases near the northern edge of their ranges (e.g. the Interior Highlands) (Figure 4, Appendix S4).

There were minimal differences in the potential distribution changes among the four climate change scenarios for northern hardwood (e.g. sugar maple and northern red oak) and central hardwood (e.g. white oak and black oak) tree species, whereas there were greater differences for southern tree species (e.g. willow oak, laurel oak, longleaf pine) (Figure 4, Appendix S4). This was in part because many northern and hardwood species experienced complete or near extirpation from the study area under any of the climate change scenarios. Southern tree species generally suffered greater decreases in the southern part of the region under the mildest climate change scenario compared with the most severe climate change scenario; for example, laurel oak, baldcypress and longleaf pine experienced small decreases in the southern part of their ranges under ACESS1-0 RCP8.5 scenario while they generally experienced no evident changes under CANESM2 RCP8.5 scenario in these area; loblolly pine experienced no evident changes in the southern part of its range (e.g. the West and East Gulf Coastal Plains, the Mississippi Alluvial Valley) under CANESM2 RCP8.5 scenario while it would suffer small decreases in the Mississippi Alluvial Valley under ACESS1-0 RCP8.5 scenario.

3.2 | Tree species realized distributions

Species occurrences, on average, were less under the mean RCP 8.5 than current climate scenarios and greater with tree harvest than without harvest scenarios (Appendix S5); however, there were important species-specific differences. Species occurrences under current climate versus the mean RCP 8.5 scenario averaged 17.1% and 16.8% without tree harvest and 28.8% and 25.7% with tree harvest scenario respectively (Appendix S5, Table 2).

Occurrences of 20 tree species (hereafter called declining tree species) were an average of 0.57% lower under the mean RCP 8.5 than current climate scenarios and 0.32% greater for nine tree species (hereafter called increasing tree species) at year 2100 (Figure 5, Table 2). Declining tree species included all northern species (sugar maple, northern red oak, white ash and black cherry), all central hardwood species (white oak, black oak, mockernut hickory, yellow-poplar and American elm) and most southern species (shortleaf pine, southern red oak, post oak, willow oak, overcup oak, cherrybark oak, water tupelo, winged elm, sugarberry, blackgum and green ash). Increasing tree species included most of southern pine species (loblolly pine, longleaf pine and slash pine), the widely distributed species red maple and some southern hardwood species (laurel oak, water oak, swamp tupelo, sweetgum and bald cypress) (Figure 5, Table 2).

Tree species relative extinction rates at 2100 (i.e. relative to the baseline scenario at 2100) under the mean RCP 8.5 averaged 5.4% and 11.8% without and with tree harvest respectively. Tree species relative colonization rates under the mean RCP 8.5 were 2.1% and 68.1% without and with tree harvest respectively (Table 2). Colonization for most tree species occurred in the northern part of the region, suggesting northward shifts in their realized distributions, for example, loblolly pine and sweetgum in the southern Interior Highlands; green ash, water oak and baldcypress in the upper West and East Gulf Coastal Plains; longleaf pine, willow oak, swamp tupelo and laurel oak in the mid-West and East Gulf Coastal Plains; and slash pine in the lower West and East Gulf Coastal Plains (Figure 6, Appendix S6). In addition, loblolly pine, sweetgum and some other southern species also colonized new areas along in the southern part of their current ranges. Extinction generally occurred for most of northern hardwood and central hardwood tree species and some southern tree species in the southern part of their ranges. For example, sugar maple and northern red oak had extinctions in the southern Interior Highlands; white ash in the upper West and East Gulf Coastal Plains; white oak, black cherry, southern red oak and shortleaf pine in the mid-West and East Gulf Coastal Plains; and winged elm in the lower West and East Gulf Coastal Plains (Figure 6, Appendix S6).

3.3 | Interactive effects of climate change and harvest

Effect sizes for climate change on species occurrences were −4.7% for the declining tree species and 1.9% for the increasing tree species. Effect sizes for tree harvest on species occurrences were 81.5% and 80.4% for the declining and the increasing tree species respectively. Size of the combined effects of climate change and tree harvest on species occurrences was 46% and 84.3% for the declining and the increasing tree species respectively (Figure 7). These combined effects were much smaller than the additive effects for the declining tree species (76.8%) and similar (82.3%) for the increasing tree species, resulting in interactive effects of −30.8% and 2.0% for the declining and the increasing species respectively (Figure 7). Thus, on average, the changes in tree species occurrences were predominantly attributed to tree harvest followed by its synergistic effects with climate change and climate change alone.

Effect sizes for tree harvest were 9.3% and 90.8% on relative extinction and colonization rates for the declining tree species, while effect sizes for climate change were 6.6% and 1.9% on relative extinction and colonization rates respectively (Figure 6). Effect sizes for combined effects of climate change and tree harvest were 13.9% and 59.9% on relative extinction and colonization rates, respectively, for the declining tree species. Combined effects were slightly less than the additive effects (15.9%) for relative extinction rates but much less than the additive effects (92.7%) for relative colonization rates, resulting in small interactive effects (−2.0%) for relative extinction rates and large interactive effects (−32.8%) for relative colonization rates for the declining tree species (Figure 7). Effect sizes for tree harvest on relative extinction and colonization rates for the increasing tree species were 6.2% and 87.5%, respectively, and effect sizes for climate change were 2.4% and 2.1% respectively. The combined effects on relative extinction and colonization rates were 6.6% and 86.2%, respectively, and additive effects were 8.6%

TABLE 2 Predicted tree species distribution changes in occurrences, relative extinction rates and relative colonization rates under alternative climate and tree harvest scenarios

	Species occurrences (%)				Relative extinction rates (%)			Relative colonization rates (%)		
	Non-harvest		Harvest		Non-harvest	Harvest		Non-harvest	Harvest	
	Current climate	RCP8.5	Current climate	RCP8.5	RCP8.5	Current climate	RCP8.5	RCP8.5	Current climate	RCP8.5
Sugar maple	2.6	2.0	3.9	2.5	24.2	16.4	27.5	2.0	67.6	22.8
Yellow poplar	12.6	11.5	31.4	22.6	9.6	3.7	12.2	1.5	154.2	92.1
White ash	6.4	6.0	13.9	9.5	9.2	8.5	13.1	2.4	125.2	61.4
Northern red oak	10.5	9.9	14.7	10.6	6.1	9.3	16.7	0.7	49.2	17.1
American elm	13.0	12.4	21.5	15.4	7.4	17.1	26.1	2.2	82.1	44.4
White oak	33.4	31.8	57.5	46.5	5.7	3.3	6.9	0.9	75.8	46.3
Southern red oak	17.8	17.0	34.1	26.4	6.6	9.5	14.8	1.9	101.0	63.1
Winged elm	22.3	21.3	42.3	36.8	7.7	8.6	12.1	3.5	98.4	77.4
Blackgum	20.8	20.0	37.9	32.7	6.7	6.6	9.0	2.8	89.1	66.1
Black cherry	20.1	19.3	36.2	28.0	6.2	10.4	15.7	2.3	90.7	55.4
Green ash	14.1	13.7	33.2	28.2	6.1	5.8	8.6	3.0	140.6	108.0
Overcup oak	5.3	5.2	8.8	7.2	4.7	9.2	12.9	1.6	74.3	47.6
Shortleaf pine	20.1	19.5	35.0	24.7	4.2	16.9	28.3	1.3	90.8	51.2
Water tupelo	3.2	3.1	5.6	4.6	4.0	3.3	5.0	1.1	78.8	50.0
Cherrybark oak	9.2	8.9	17.6	15.8	5.6	14.2	16.2	2.8	106.4	88.0
Mockernut hickory	19.3	18.8	29.5	26.3	4.6	9.6	10.9	1.8	62.1	46.9
Willow oak	6.1	6.0	16.5	14.3	4.8	9.4	11.4	2.4	178.8	146.0
Sugarberry	9.7	9.5	13.3	12.4	4.1	12.3	14.7	2.1	49.6	42.5
Post oak	29.0	28.5	44.8	41.5	2.9	5.5	6.7	1.1	59.9	49.5
Black oak	18.3	18.1	24.7	20.7	1.9	6.0	8.8	0.7	41.2	22.3
Average	*14.7*	*14.1*	*26.1*	*21.3*	*6.6*	*9.3*	*13.9*	*1.9*	*90.8*	*59.9*
Water oak	34.4	34.5	50.5	51.0	1.7	8.4	8.1	1.5	55.2	54.1
Swamp tupelo	3.3	3.4	6.8	6.9	2.6	3.6	3.5	2.6	108.5	110.4
Sweetgum	46.0	46.3	65.8	66.2	1.4	2.6	2.6	1.0	45.5	44.3
Red maple	48.1	48.4	78.8	79.2	2.5	3.1	3.2	1.8	67.0	65.9
Laurel oak	9.9	10.1	17.3	17.3	4.9	10.4	10.4	4.0	85.6	85.8
Baldcypress	5.5	5.6	10.6	10.9	3.1	10.0	9.7	2.6	103.6	102.4
Slash pine	6.5	6.7	12.5	12.6	2.4	12.2	11.4	2.9	104.5	105.0
Loblolly pine	42.8	44.2	59.0	59.7	1.2	4.0	3.9	1.0	41.7	41.0
Longleaf pine	4.8	5.0	12.7	13.3	4.3	10.0	10.5	3.6	176.3	166.8
Average	*22.4*	*22.7*	*34.9*	*35.2*	*2.7*	*7.1*	*7.0*	*2.3*	*87.5*	*86.2*
Total average	*17.1*	*16.8*	*28.8*	*25.7*	*5.4*	*8.6*	*11.8*	*2.1*	*89.8*	*68.1*

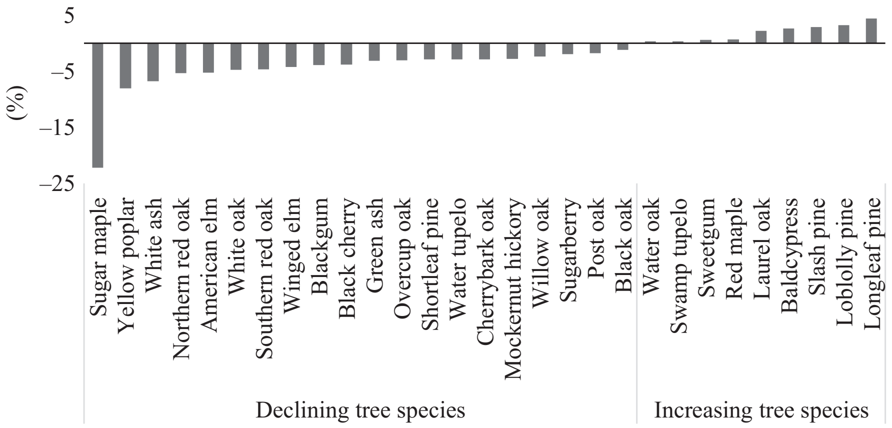

FIGURE 5 The relative difference in species occurrences between the mean RCP 8.5 results and current climate scenario both without tree harvest at year 2100, in which negative values were declining tree species and positive values were increasing tree species

and 89.6%, respectively, resulting in interactive effects of −2.0% and −3.4%, respectively, for the increasing tree species (Figure 7). Thus, on average, extinction rates were modest and mainly attributed to tree harvest and climate change while colonization rates were greater and mainly attributed to tree harvest and its synergistic effects with climate change.

4 | DISCUSSION

Although previous studies have assessed the impacts of environmental changes (e.g. climate change, land use change) on tree species distributions, this study is one of only a few to provide an assessment of the interactive effects of tree harvest and climate change on tree species distribution changes at a relatively fine resolution (270 m) over such a large region. We found tree harvest and climate change interacted to affect species occurrences and colonization but not extinction. The interactive effects were in the same direction as climate change effects on species occurrences, thereby accelerating climate change-induced distribution contraction and expansion for the decreasing and the increasing species respectively. We also found that occurrence and colonization were mainly affected by tree harvest and its interaction with climate change, in addition to climate change. Species extinctions were mainly affected by tree harvest and climate change.

Our study provides insight into the mechanisms underlying tree species range dynamics and the implications of those shifts under environmental changes. Tree harvest played the most important role in driving distribution changes followed by its interaction with climate change and climate change alone. Industrial tree harvest with a very short rotation in this region could directly modify species abundance and indirectly facilitate tree species turnover within a few decades. Such rapid, immediate strong responses to tree harvest contrasted the lagged responses of tree species to climate change. It is widely accepted that macroclimate is the most important determinant of tree species ranges (Whittaker, 1975). However, the relative importance of tree harvest over climate change effects is not surprising given that our simulation period was relatively short (100 years) compared to the longevity of trees. In addition, while the extent of our study area was large, it was relatively small compared to the ranges of the species studied, especially northern and central hardwood tree species.

Tree harvest promoted colonization for most trees species by releasing growing space for regeneration, which was particularly important for early successional tree species (e.g. yellow-poplar, white ash, longleaf pine, Table 2). However, the overall interactive effects of tree harvest and climate change on species colonization were negative, specifically with positive interactive effects at leading edges and negative interactive effects at trailing edges. At leading edges, the interactive effects acted in the same direction as the positive effects of tree harvest and climate change on colonization and thus accelerated the northward shift under climate change (Figure 6b,d). But at trailing edges of distributions, the interactive effects on colonization were negative while the effects of tree harvest and climate change were positive, and thus ameliorated colonization under climate change, especially for the declining tree species. This was because tree species continued filling their ranges under the current climates because many tree species had not filled all climatically suitable areas due to non-climatic factors such as dispersal limitation (Svenning, Normand, & Skov, 2008); however, they would not colonize these areas under climate change even if there was available growing space released by tree harvest (Figure 6). Therefore, tree harvest and post-harvest regeneration dynamics can play a significant role in accelerating tree species shifts at the leading edges of their ranges under changing climates.

Tree harvest alone resulted in some extinctions by promoting tree species turnover. However, we found that tree harvest generally did not interact with climate change to facilitate or ameliorate extinctions. This was because tree species may take centuries to respond to changing climates due to inherent demographic inertia that enables tree species resist extinction during unfavourable climatic conditions (Sittaro et al., 2017). As a result, our 100-year simulation period may not be long enough for interactive effects to manifest. However, over longer temporal scales (e.g. few centuries), tree harvest may accelerate tree species extinctions in the southern portion of their range, and thus the northward shift of the trailing edges of their ranges, through speeding up species turnover and shorting species persistence under changing climates (e.g. Vanderwel & Purves, 2014).

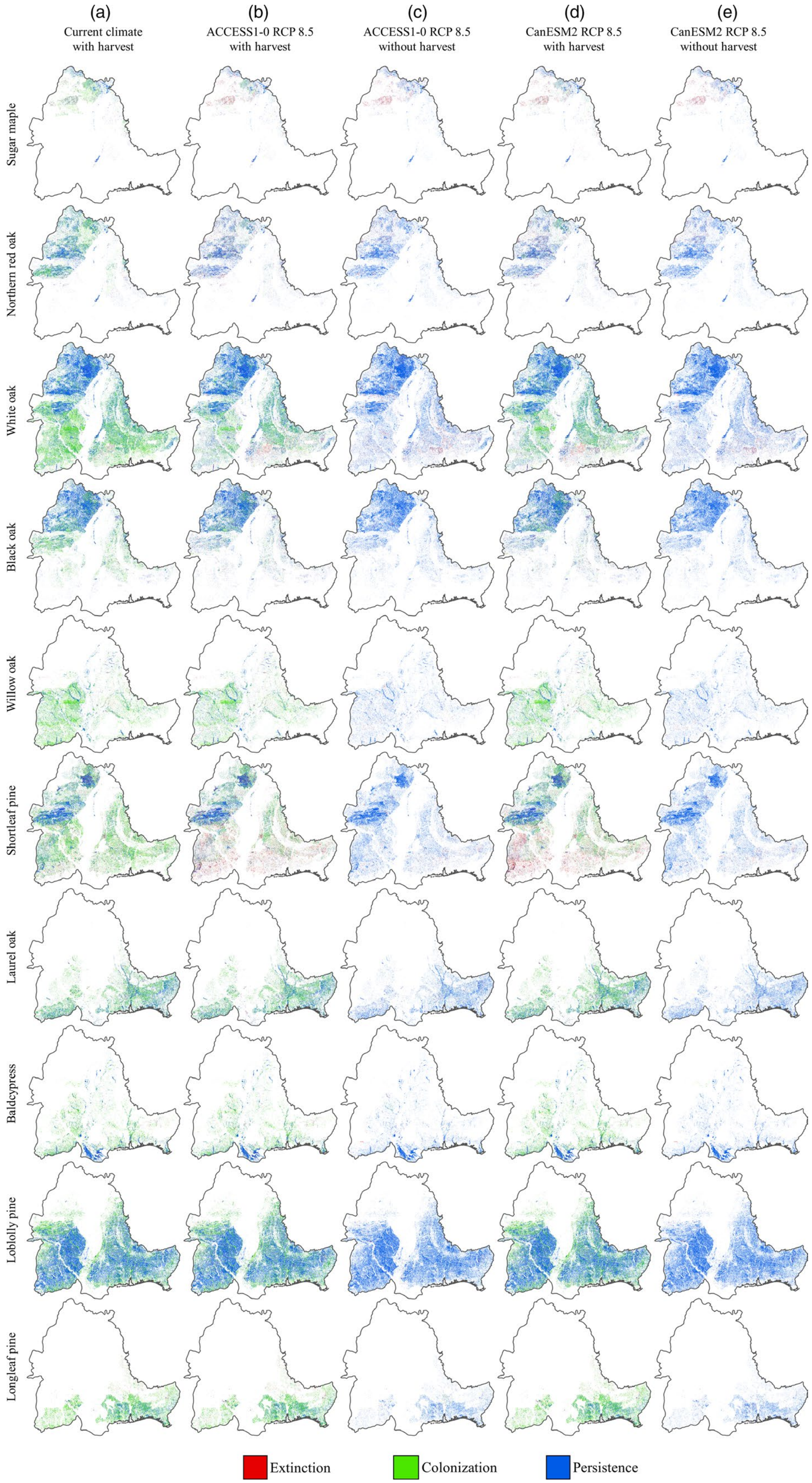

FIGURE 6 Predicted persistence (blue), extinction (red) and colonization (green) rates for selected 10 tree species under current climate with tree harvest scenario (a), ACESS1-0 RCP 8.5 (b, c) and CANESM2 RCP 8.5 (d, e) with and without tree harvest scenarios at year 2100, which were derived through comparing the species distributions under given scenario with the baseline scenario [Colour figure can be viewed at wileyonlinelibrary.com]

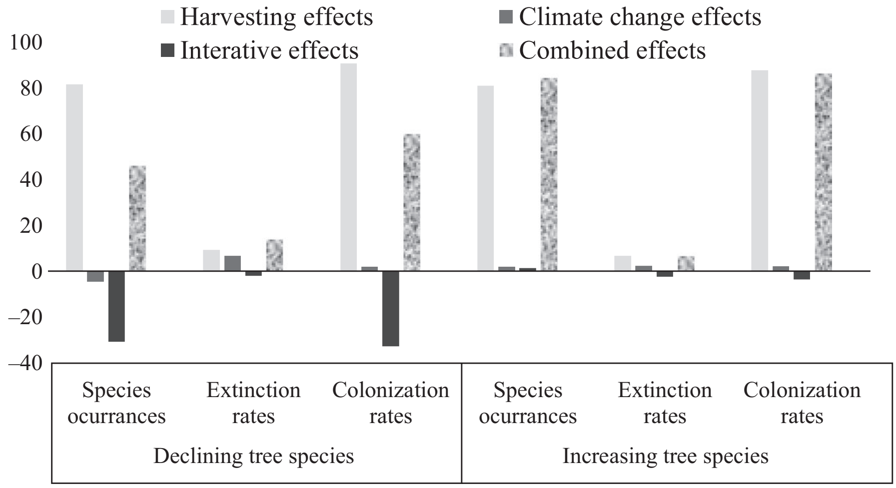

FIGURE 7 The average effect sizes of tree harvest, climate change and their interaction and combination on tree species distribution changes in terms of occurrences, extinction rates and colonization rates for the declining and the increasing species groups

We found substantial northward shifts in tree species potential ranges and a lesser shift in realized distributions. Climate change decreased occurrence of 20 of 29 tree species in the study area including all northern and central hardwood tree species and some southern tree species. However, the leading edges of realized range shifts were very slow and lagged behind changes in potential distributions that were determined by abiotic conditions and climatic conditions by end of 21st century. For example, the whole Interior Highlands became suitable for loblolly pine and longleaf pine under climate change (Figure 4). However, longleaf pine only shifted to the mid-East and West Gulf Coast Pains and loblolly pine to the upper East and West Gulf Coast Pains and colonized small areas in the very southern Interior Highlands (Figure 6). Such slow shifts were likely because of limited dispersal capacity, long maturity (e.g. decades) and dispersal barriers from habitat loss and fragmentation. Thus, our results suggest that range shifts of most tree species will not keep pace with climate change. This finding is in line with many previous studies that suggest most of tree species will not move fast enough to track and adjust to the pace and magnitude of climate change (Sittaro et al., 2017) and biotic factors (e.g. dispersal, colonization) dominate the leading edge limits (Putnam & Reich, 2017; Saltré, Duputié, Gaucherel, & Chuine, 2015). Nonetheless, failures of tree species to track with rapid changing climates will have potential negative consequences for biodiversity and ecosystem services that forests provide (Dawson, Jackson, House, Prentice, & Mace, 2011; Garcia et al., 2014).

Our findings about the importance of tree harvest and its synergistic effects with climate change on tree species distribution changes have important implications for conservation management. Tree harvest is one of the most important global change pressures worldwide, particularly in temperate forests that are severely influenced by climate change, land-use change and land management (e.g. fire suppression, harvest) (Anderson-Teixeira et al., 2013). These factors will undoubtedly continue altering tree species distributions and thus biodiversity and ecosystem services provided by these forests (Garcia et al., 2014; Reich & Frelich, 2001). Given the importance of interactive effects in this study, we suggest multiple drivers of distribution changes should be evaluated simultaneously because interactive effects cannot be determined when effects are considered independently. Most research on future tree species distribution changes focuses mainly or even exclusively on climate change and therefore may misestimate the pace or extent of ranges shifts.

Our results suggest that tree species range shifts are not likely to keep pace with climate change, and thus, some form of climate adaptation management may be needed to meet forest sustainability objectives. Silvicultural prescriptions and tree harvest can potentially be used to maintain current species abundance and composition in order to promote forest resilience, accelerate changes to novel species assemblages that are better adapted to new climates or facilitate dispersal to assist migration. Ultimately, however, adaptation strategies will need to be developed through strong collaborative engagement with stakeholders to best meet their natural resources planning and decision-making needs.

A number of factors not considered in this study may contribute to uncertainty in our projections. For example, we only simulated current fire regime as background disturbance. However, disturbances such as insect and fire are expected to increase with warming climates and affect tree species distributions (Weed, Ayres, & Hicke, 2013). We assumed the primary effects of climate change on tree species demography as temperature, precipitation, growing season length and drought without considering nitrogen deposition and CO_2 fertilization, which can have important impacts on tree species distributions (Griepentrog, Eglinton, Hagedorn, Schmidt, & Wiesenberg, 2015). Despite such limitations, there are good reasons why our approach is well suited for assessing how tree harvest and climate change interact to affect tree species distributions. Initial tree species distribution and abundance and tree harvest and fire regimes were parameterized against extensive forest inventory data. LANDIS PRO has been shown in previous studies to well capture forest distribution, composition, structure and succession trajectories and stand dynamics (Brandt et al., 2014; Janowiak et al., 2018; Jin et al. 2017; Wang et al., 2014b, 2015, 2017, 2018). With our coupled modelling approach, we were able to incorporate many details of the initial tree species distribution and composition, tree species demography, competition, disturbances, climate change and their interaction at fine resolutions that would not be possible with other kinds of models.

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DATA ACCESSIBILITY

All simulation data are available at: https://doi.org/10.5281/zenodo.2546922 (Wang et al., 2019).

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