

Importance of succession, harvest, and climate change in determining future composition in U.S. Central Hardwood Forests

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Abstract. Most temperate forests in U.S. are recovering from heavy exploitation and are in intermediate successional stages where partial tree harvest is the primary disturbance. Changes in regional forest composition in response to climate change are often predicted for plant functional types using biophysical process models. These models usually simplify the simulation of succession and harvest and may not consider important species-specific demographic processes driving forests changes. We determined the relative importance of succession, harvest, and climate change to forest composition changes in a 125-million ha area of the Central Hardwood Forest Region of U.S. We used a forest landscape modeling approach to project changes in density and basal area of 23 tree species due to succession, harvest, and four climate scenarios from 2000 to 2300. On average, succession, harvest, and climate change explained 78, 17, and 1% of the variation in species importance values (IV) at 2050, respectively, but their contribution changed to 46, 26, and 20% by 2300. Climate change led to substantial increases in the importance of red maple and southern species (e.g., yellow-poplar) and decreases in northern species (e.g., sugar maple) and most of widely distributed species (e.g., white oak). Harvest interacted with climate change and accelerated changes in some species (e.g., increasing southern red oak and decreasing American beech) while ameliorated the changes for others (e.g., increasing red maple and decreasing white ash). Succession was the primary driver of forest composition change over the next 300 years. The effects of harvest on composition were more important than climate change in the short term but climate change became more important than harvest in the long term. Our results show that it is important to model species-specific responses when predicting changes in forest composition and structure in response to succession, harvest, and climate change.

Key words: assemblage; competition; dispersal; distribution; forest landscape model; LANDIS PRO; LINKAGES II; regional scales; site scales; species importance value.

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INTRODUCTION

Temperate deciduous forests are among the major biomes on earth and provide important ecological, economic, and social services to society. Most temperate deciduous forests in the

eastern U.S. experienced heavy exploitation in the 19th and early 20th centuries and some of these were completely deforested while others are now recovering (FAO 2012). These recovering forests are in intermediate stages of development and are undergoing rapid successional changes

as a result of growth, competition, dispersal, and establishment (Oliver and Larson 1996). As large-scale industry timber harvest moved from temperate deciduous forests to other less explored forest biomes, fine spatial scale (<10 ha) non-industrial timber harvest, mostly in the form of partial harvest of large trees of preferred species, becomes the primary anthropogenic disturbance (Shifley et al. 2012). These disturbances can change forest composition and structure and alter successional trajectories (Schuler 2004, Deluca et al. 2009). Furthermore, climate change may affect species establishment and mortality and alter forest composition in the region (Iverson et al. 2008, Morin and Thuiller 2009, Mette et al. 2013, Brandt et al. 2014).

Predictions of forest change at regional scales (>100 million ha) often rely on niche and biophysical process models (Morin and Thuiller 2009). Niche models (also called bioclimatic envelope models) relate observed species' distributions to environmental predictors using a variety of statistical methods and have been extensively used to predict the potential impacts of climate change on tree species distributions (Guisan and Thuiller 2005, Boulangeat et al. 2012). Recent advances in niche models include dispersal functions to predict species range shifts accounting for the effects of seed source, habitat fragmentation, and dispersal distance (e.g., Iverson et al. 2008, Meier et al. 2012). Biophysical process models, on the other hand, predict stock (e.g., biomass) and fluxes (e.g., aboveground net primary production) of plant functional types by incorporating leaf photosynthesis, carbohydrate allocation, and nutrient and water cycling (Sitch et al. 2003, Morin et al. 2008, Medvigy et al. 2009, Tang et al. 2010, Hickler et al. 2012). Despite the recognized importance of succession and harvest, both niche and process models usually use coarse spatial resolutions (e.g., 10–20 km) in regional scale predictions and consequently succession and disturbances (e.g., harvest and fire) are either simplified or ignored (Neilson et al. 2005, Purves and Pacala 2008, Iverson et al. 2011, McMahon et al. 2011). Therefore, we still lack an understanding of the relative importance of succession, disturbance, and climate change in determining future forest composition changes.

Forest landscape models are explicitly designed to incorporate site-scale succession and

landscape-scale disturbance to simulate forest change at landscape scales (He and Mladenoff 1999). They have been recently used to examine the relative importance of succession, disturbance, and climate change in affecting forest change (e.g., biomass) at landscape scales (e.g., 10^4 – 10^7 ha). For example, Scheller and Mladenoff (2005) used the LANDIS II forest landscape model in northern Wisconsin and found that tree harvest and wind were as important as the effects of climate change alone in influencing the magnitude of forest composition change and the direction of tree species richness change. Schumacher and Bugmann (2006) used the LANDCLIM forest landscape model in the Swiss Alps and projected that climate change would cause extensive forest cover changes beginning in the coming decades, fire was likely as important as climate, and harvest was less important compared with the direct effects of climate change. Gustafson et al. (2010) used the LANDIS II model in south-central Siberia and found that biomass was more strongly affected by timber harvest and insect outbreaks than by the direct effects of climate.

Studies investigating the relative importance of these endogenous and exogenous processes at regional scales and spanning short- to long-time frames have rarely been done. This is mainly because forest landscape models were unable to operate at sufficiently large geographic extents with a resolution fine enough to represent site- and landscape-scale processes. Maximum simulation capacity (number of pixels) of forest landscape models was in the range of 10^6 – 10^7 cells (He 2008). Recent advances in the LANDIS PRO forest landscape model have expanded the simulation capacity to 10^8 cells at 90–270 m resolution (Wang et al. 2014a). The simulation capacity of LANDIS PRO makes it possible to predict forest change for a large temperate deciduous forest region under alternative climate scenarios while mechanistically simulating site- and landscape-scale processes. The future forest composition and structure can be assessed based on projected density, basal area, importance values, and biomass of tree species down to the raster cell level.

We used the LANDIS PRO forest landscape model to project forest composition changes due to succession, harvest, and climate change over

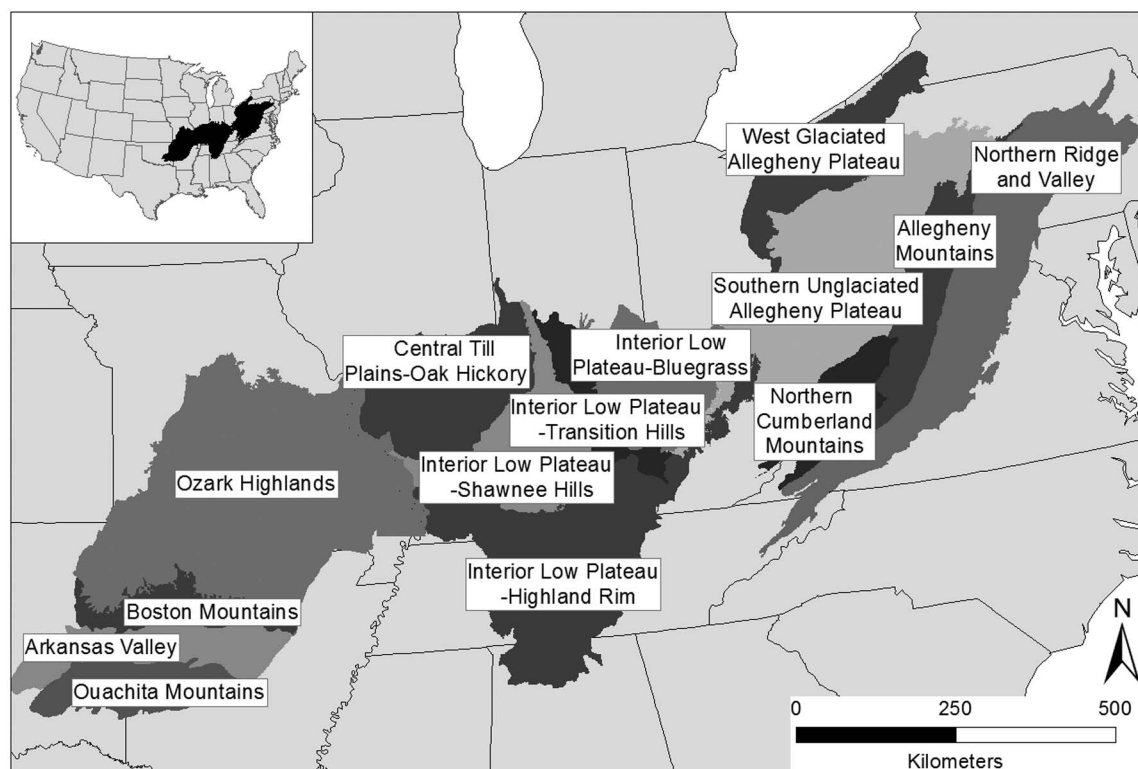


Fig. 1. The study area covered 14 ecological sections and 125 million hectares, in which we projected forest composition changes under current climate and three climate change with and without harvest scenarios in the Central Hardwood Forest Region, USA, 2000–2300.

the next 300 years in the Central Hardwood Forest Region of U.S. (CHFR), one of the most extensive temperate deciduous forests in the world. We addressed three questions of general interests to ecologists, conservationists, and especially land managers in the CHFR: (1) How will tree species' importance values change under alternative climate and harvest scenarios? (2) What is the relative importance of succession, harvest, and climate change in determining the future changes in species importance value? (3) How will the relative importance of succession, harvest, and climate change vary among species and over time?

METHODS

Study area

Our study area included a large portion of the CHFR and covered 125,204,336 hectares from eastern Oklahoma to western Virginia, and southern New York to Alabama (Fig. 1). The

area encompassed 14 ecological sections, 100 subsections, and a variety of vegetation, terrains, soils, and climates (Cleland et al. 2007; Fig. 1). The eastern portion of the study area is characterized by the dissected Appalachian Plateaus with sharp ridges, low mountains, and narrow valleys. The western portion of the area is highly dissected and rolling but varies from relative flat Central Till Plains to open hills and irregular plains (e.g., Interior Low Plateau), to high Ozark Highlands. The soil types are mostly alfisol, inceptisols, mollisols, and ultisols. The climate was continental with long, hot summers and cool winters. Mean annual temperatures followed an east-west gradient ranging from 4° to 18°C with the warmer temperatures in the south. Annual precipitation ranged from 50 cm in the northwest to 165 cm in the southeast and reached as much as 200 cm on some Appalachian peaks, occurring mostly in spring and fall.

The area was 70% forest land (i.e., forests,

woodlands, savannas) and the remaining area was predominated by agricultural and urban land use (Johnson et al. 2009). About 81% of forest lands were privately owned (e.g., family and corporate). Most forests were dominated by deciduous species such as oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), American beech (*Fagus grandifolia* Ehrh.), cherry (*Prunus* spp.), ash (*Fraxinus* spp.), and yellow-poplar (*Liriodendron tulipifera* L.).

Modeling approach and experimental design

We designed a factorial experiment with four climate scenarios and two levels of harvest (no-harvest and partial harvest at current volume levels). We used the same initial forest conditions for all scenarios and predicted forest change from 2000 to 2300 using 10-year time steps at 270-m resolution. We ran five replicate simulations for each scenario to capture the variability that resulted from stochastic functions in the models (Murphy and Myers 2003).

We modeled the most prominent 23 tree species which accounted for over 70% of total basal area and one pseudo species to represent growing space occupied by all remaining species (Table 1). We parameterized the pseudo species as understory tree because there were a substantial number of small understory trees in the region due to nearly a century of fire suppression and the 23 tree species we directly modeled represented most species dominating the canopy. Given that limitations exist in the number of species that can be modeled by forest landscape models, we believed we were able to more realistically simulate interspecific competition for resources among major species and understory species by accounting for the growing space occupied by the remaining tree species as a pseudo species, as opposed to ignoring it. We grouped species based on their geographic distribution as northern, southern, or widely distributed to help summarize general patterns in results (Table 1).

We used LANDIS PRO to simulate succession, windthrow, and harvest. LANDIS PRO tracks the number of trees and diameter at breast height (DBH) by species and age cohort in each raster cell. We used the Succession module in LANDIS PRO to simulate tree growth, longevity-caused mortality, competition-caused mortality (self-

thinning), resprouting, fecundity, seed dispersal, and establishment (Wang et al. 2013a). We mechanistically simulated dispersal by accounting for seed source location and abundance, dispersal distance (dispersal kernel), habitat fragmentation (e.g., forest, urban, water body, and agricultural land), and abiotic and biotic suitability for establishment, survival, and growth (Wang et al. 2013a).

We simulated partial tree harvest using the LANDIS PRO Harvest module by incorporating multiple managements units (U.S. Forest Service Inventory and Analysis [FIA] inventory units [Woodall et al. 2010]) with different diameter-limit harvest regimes (Fraser et al. 2013). We derived parameters for diameter-limit harvest for each FIA unit based on the harvest information recorded from 1995–2005 FIA data (e.g., minimum entering and residual stand basal area, proportion of private lands [average of 1% each year], and tree species preferences). The amount of basal area harvested in a stand was controlled by the entering and residual stand basal area parameters. This approach to volume-regulated harvest could actually represent thinning from above, clearcutting, or partial harvest at the pixel level (approximately 7.3 ha), which was able to capture variation in harvest regime across the region (Canham et al. 2013). We simulated windthrow as a stochastic and top-down disturbance (average of 0.14 % each year) in all eight scenarios, where old and large trees were removed first.

Climate data and climate change scenarios

We accounted for environmental heterogeneity in vegetation, topography, soil, temperature, and precipitation by stratifying the geographical region into 600 landtypes by intersecting 100 ecological subsections and 6 landforms derived from DEM (Dijak 2013). We incorporated regional climate patterns by downscaling general circulation models (GCMs) predictions to each land type. We assumed resource availability (measured as maximum growing space, MGSO) and species assemblage (measured as species establishment probability for each species, SEP) were uniform within a landtype and different among landtypes. Novel climates affected MGSO and species demography by modifying SEPs and tree mortality for each landtype. We modeled

Table 1. Species life history parameters used in the forest landscape model LANDIS PRO to project forest composition change from 2000–2300 in the Central Hardwood Forest Region, U.S.A. We grouped species based on their geographic distribution as northern (N Spp.), southern (S Spp.), or widely distributed species (W Spp.) to help summarize general patterns in results.

Common name and species	Mature/ longevity	Shade tolerance	Max dispersal distance (m/year)	Vegetative probability	Min/max sprouting age	Max DBH (cm)	Max SDI (trees/ha)	No. potential germination seeds/ mature tree
N Spp.								
Northern red oak, <i>Q. rubra</i> L.	30/200	3	270	0.7	10/120	65	570	20
Sugar maple, <i>A. saccharum</i> Marsh.	20/300	5	540	0.8	20/80	75	570	140
American beech, <i>Fagus grandifolia</i> Ehrh.	20/300	5	270	0.8	10/100	70	570	400
Eastern hemlock, <i>Tsuga Canadensis</i> Carr.	20/300	5	540	0	0/0	70	900	120
Black cherry, <i>Prunus serotina</i> Ehrh.	20/150	2	270	0.8	20/100	65	570	15
White ash, <i>Fraxinus Americana</i> L.	30/250	3	540	0.6	10/150	65	570	30
Eastern white pine, <i>P. strobus</i> L.	20/250	3	540	0	0/0	70	850	40
Red spruce, <i>Picea Rubens</i> Sarg.	20/300	4	540	0	0/0	65	990	40
S Spp								
Post oak, <i>Q. stellate</i> Wangenh.	40/250	3	270	0.6	10/100	70	570	40
Southern red oak, <i>Q. falcate</i> Michx.	20/200	3	270	0.6	10/100	65	570	15
Yellow poplar, <i>Liriodendron tulipifera</i> L.	20/250	2	540	0.5	20/150	70	700	100
SweetGum, <i>Liquidambar styraciflua</i> L.	30/200	2	270	0.6	20/200	65	570	40
Shortleaf pine, <i>Pinus echinata</i> Mill.	20/200	2	270	20	70/150	70	990	50
Loblolly pine, <i>P. taeda</i> L.	20/150	3	270	0.4	50/100	70	1100	25
Eastern redcedar, <i>Juniperus Virginian</i> L.	10/300	2	270	0	0/0	65	1100	50
W Spp.								
White oak, <i>Quercus alba</i> L.	40/300	4	270	0.6	10/100	75	570	100
Chestnut oak, <i>Q. prinus</i> L.	20/300	4	270	0.7	10/170	75	570	100
Black oak, <i>Q. velutina</i> Lam.	20/150	3	270	0.6	10/100	65	570	20
Scarlet oak, <i>Q. coccinea</i> Muenchh.	30/150	3	270	0.7	10/100	65	570	30
Red maple, <i>Acer rubrum</i> L.	10/150	4	540	0.9	10/100	65	700	13
Pignut hickory, <i>Carya glabra</i> Mill.	30/200	3	270	0.6	20/200	65	570	40
Mockernut hickory, <i>C. tomentosa</i> Nutt.	30/200	3	270	0.6	20/200	65	570	40
Shagbark hickory, <i>C. ovate</i> K. Koch	30/250	3	270	0.6	20/200	65	570	40
Pseudo species	30/200	3	540	0.5	20/120	60	1000	15

SEPs and MGSO for each landtype under each climate scenario using the LINKAGES II ecosystem process model that simulated individual tree species growth and biomass as constrained by nitrogen availability, climate, and soil moisture (Wullschleger et al. 2003). We then inputted the SEPs and MGSO for each landtype under four climate scenarios into LANDIS PRO as model parameters to encapsulate the climate change effects (He et al. 1999).

We considered a current climate scenario and

three climate change scenarios that were based on combinations of different general circulation models (GCMs) and emission scenarios: PCM (B1), CGCM (T47) (A2), and GFDL (A1fi). The PCM, CGCM, and GFDL models represented a gradient from the lowest to highest predicted increases in summer temperature in the region, respectively; and B1, A2, and A1fi represented a gradient from the least to most fossil fuel intensive emission scenarios (IPCC 2007). We referred to these four scenarios from here on as

current climate, PCM, CGCM, and GFDL. The PCM scenario had an overall increase in precipitation while GFDL had the largest overall decrease for the study area. On average, mean annual maximum daily temperature increased in the region 1.06, 2.84, and 4.95°C under PCM, CGCM, and GFDL, respectively and mean total annual precipitation increased 49.8 mm under PCM and decreased 203 and 259.8 mm under CGCM and GFDL, respectively. So, by modeling forest change under these scenarios we incorporated uncertainty in climate scenarios for the region as described by IPCC (2007).

We used climate data for a 30-year period (1980–2009) for the current climate scenario including daily maximum and minimum temperature, daily precipitation, and daily wind speed at a 1/8-degree resolution (Maurer et al. 2002) and daily solar radiation and day length at 1-km resolution for 1980–2009 from DAYMET (Thornton et al. 2012) for the centroid of each ecological subsection. We obtained down-scaled climate data for PCM, CGCM, and GFDL scenarios for years 2070–2099 for each ecological subsection from the U. S. Geological Survey Center for Integrated Data Analysis (USGS CIDA) Geo Data Portal (Stoner et al. 2011). Since the downscaled climate scenarios did not project wind speed and solar radiation, we used the wind speed and solar radiation from the current climate for the three climate change scenarios.

We obtained the measures of soil organic matter, nitrogen, wilting point, field moisture capacity, percent clay, sand and rock for soil polygons from the Natural Resources Conservation Service soil survey (<http://soils.usda.gov/>). We calculated area-weighted soil properties for each landtype by intersecting landtypes with soil polygons. We used a combination of default values in LINKAGES II for species biological traits, values from other studies, or new calculated values (Wullschleger et al. 2003, Wang et al. 2013a, 2013b; Appendix A: Table A1). We used the processed climate and soil data for LINKAGES II simulations.

We simulated individual tree species to estimate SEP for current climate at year 2000 (1980–2009) and the three climate change scenarios at year 2100 (2070–2099) starting from forest floor with above soil, climate, and species data in each of the 600 landtypes. We simulated

regeneration and growth of each species for 30 years with 20 replicates and averaged replications for each landtype. The simulated biomass at simulation year 30 was used to derive SEP for each species by transforming values to a 0–1 scale (He et al. 1999; Appendix B: Table B1).

We simulated 23 tree species together starting from forest floor with the above soil, climate, and species data to estimate MGSO for each of 100 ecological subsections in each of the four climate scenarios at year 2100. We ran the LINKAGES II model for 300 years with 20 replications to capture the maximum biomass a subsection could support. We quantified the percentage change in maximum biomass for each subsection under each climate change scenario compared to the current climate scenario. We then applied the percentages to adjust MGSO values under the climate change scenarios (Appendix C: Table C1).

LANDIS PRO model parameterization

We parameterized species' longevity, maturity, shade tolerance, dispersal distance, sprouting probability, maximum stand density index (SDI), and maximum DBH from previous studies and literature (Table 1; Burns and Honkala 1990, Wang et al. 2013a, 2014a). We derived the initial forest conditions including absence/presence and number of trees by species age cohort for each raster cell for year 2000 by stochastically assigning a representative FIA plot to each cell based on landform, land cover, and size class from 1995 to 2005 FIA data (≥ 2.54 cm) using Landscape Builder (Dijak 2013). We iteratively adjusted parameters (e.g., DBH-age relationships) in Landscape Builder until the initial forest conditions in LANDIS PRO simulation results at year 0 did not differ from observed FIA data for 2000 in terms of mean basal area and density at the ecological section using a Chi-Square test (Appendices D and E: Tables D1 and E1). The model has been previously calibrated and validated at stand and landscape scale using FIA data and old-growth studies under current climate for 300 years with and without harvest; for further details on model calibration and evaluation see Wang et al. (2013a, 2014a, b, 2015). We then proceeded with simulations for the climate change scenarios. Under the three climate change scenarios, we varied values of SEPs and MGSO linearly for the first 100 years based on the point estimates for current climate

and 2100 from LINKAGES II and held values constant for the following 200 years.

Data analysis

We described the short-, medium-, and long-term changes and differences between scenarios based on simulation years 50, 100, and 300, respectively. We assessed forest composition changes in terms of importance value (IV) for each species at each raster cell ($IV = [\text{individual species density} \times 100/\text{total density} + \text{individual species basal area} \times 100/\text{total basal area}]/2$). We reported the species importance changes under three climate change scenarios with harvest compared to these under current climate scenario with harvest in the short, medium, and long term.

We determined the relative importance of succession, harvest, and climate change effects on species IVs in the short, medium, and long term using repeated-measures ANOVA in which the effects of succession were characterized using time (e.g., 0, 50, 100, 300 years) and were treated as a repeated factor. The data consisted of the values for species importance value at year 0, 50, 100, and 300 along with dummy variables indicating if the values were based on scenarios with harvest or climate change. We report the relative importance of the main and interaction effects as the proportion of the total variation explained.

RESULTS

We ran 1,112,000 replicate LINKAGES II simulations for 23 species for four climate scenarios across 600 land types and derived SEP and MGSO values for use in LANDIS PRO (Appendices B and C: Tables B1 and C1). We completed 5 replicate simulations for each of the four climate scenarios with and without harvest in LANDIS PRO.

Climate change effects

Species importance values only differed an average of 5% between the three climate change scenarios and current climate scenario in the short term (Fig. 2). In the medium and long term, however, most species had more substantial changes and the greatest changes occurred under GFDL. On average, IVs of northern species (Table

1) were 23% and 80% lower under GFDL than current climate in 2100 and 2300, respectively, and IVs of widely distributed species were 12% and 65% lower under GFDL than current climate in 2100 and 2300, respectively. Comparable differences between PCM and current climate were 3% and 10% lower for the northern species and 12% and 65% lower for widely distributed species in 2100 and 2300, respectively. Species IVs under CGCM fell between PCM and GFDL. In contrast, IVs of southern species averaged 5%, 36%, and 50% greater than current climate under PCM, CGCM, and GFDL in 2300, respectively.

Specifically, climate change led to substantial increases in the IVs of six southern species (e.g., yellow poplar, southern red oak, shortleaf pine, loblolly pine, eastern redcedar, and sweetgum), two widely distributed species red maple and post oak, and one northern species northern red oak. The greatest increases for most species occurred under the GFDL scenario followed by CGCM and PCM scenarios (Figs. 2 and 3) except southern red oak whose IV increased under PCM and CGCM but decreased under GFDL. For example, the IVs of yellow-poplar generally increased in the long term under PCM (13%), CGCM (97%), and GFDL (84%) scenarios with no harvest compared to those under the current climate scenario; however they decreased in the high elevations in the Appalachian Mountains (Figs. 2 and 3). Climate change resulted in decreases in the IVs of seven northern species (e.g., sugar maple, American beech, black cherry, white ash, eastern white pine, eastern hemlock, and red spruce) and most of the widely distributed species (e.g., white oak, chestnut oak, black oak, scarlet oak, pignut hickory, mockernut hickory, and shagbark hickory). Especially in the south, many species such as white oak, sugar maple, and white ash were predicted to be nearly eliminated under CGCM and GFDL scenarios (Figs. 2 and 3). For example, white oak decreased in IV in the long term by 4%, 17%, and 19% under PCM, CGCM, and GFDL scenarios, respectively. However, white oak increased in IVs in the high elevations in the Appalachian Mountains in the eastern part of the CHFR (Figs. 2 and 3).

Harvest effects

Harvest accelerated increases in IVs for yellow-

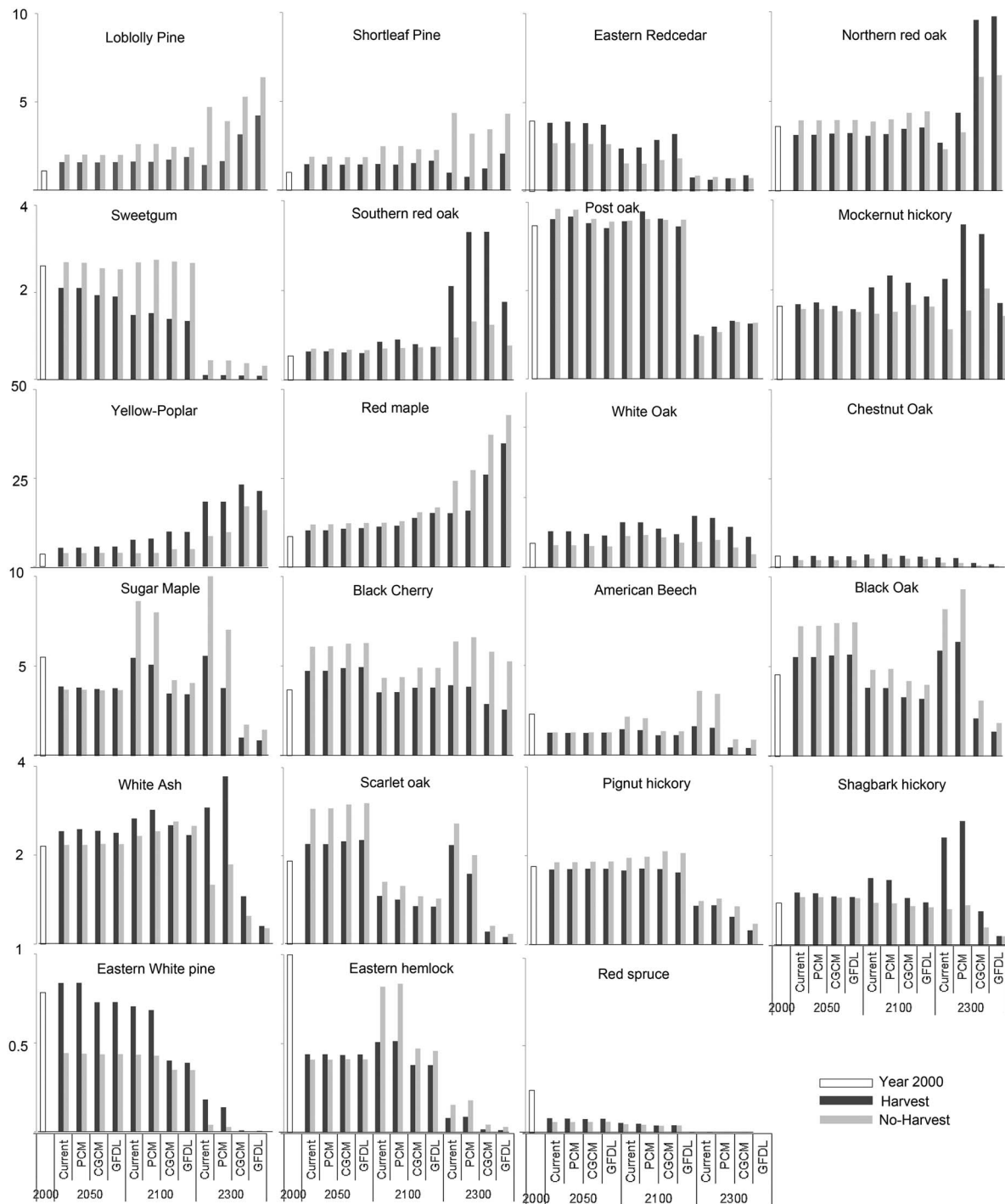


Fig. 2. Model projections of importance values for 23 tree species under current climate and three climate change with and without harvest scenarios at year 2000, 2050, 2100, and 2300 in the Central Hardwood Forest Region, USA, 2000–2300.

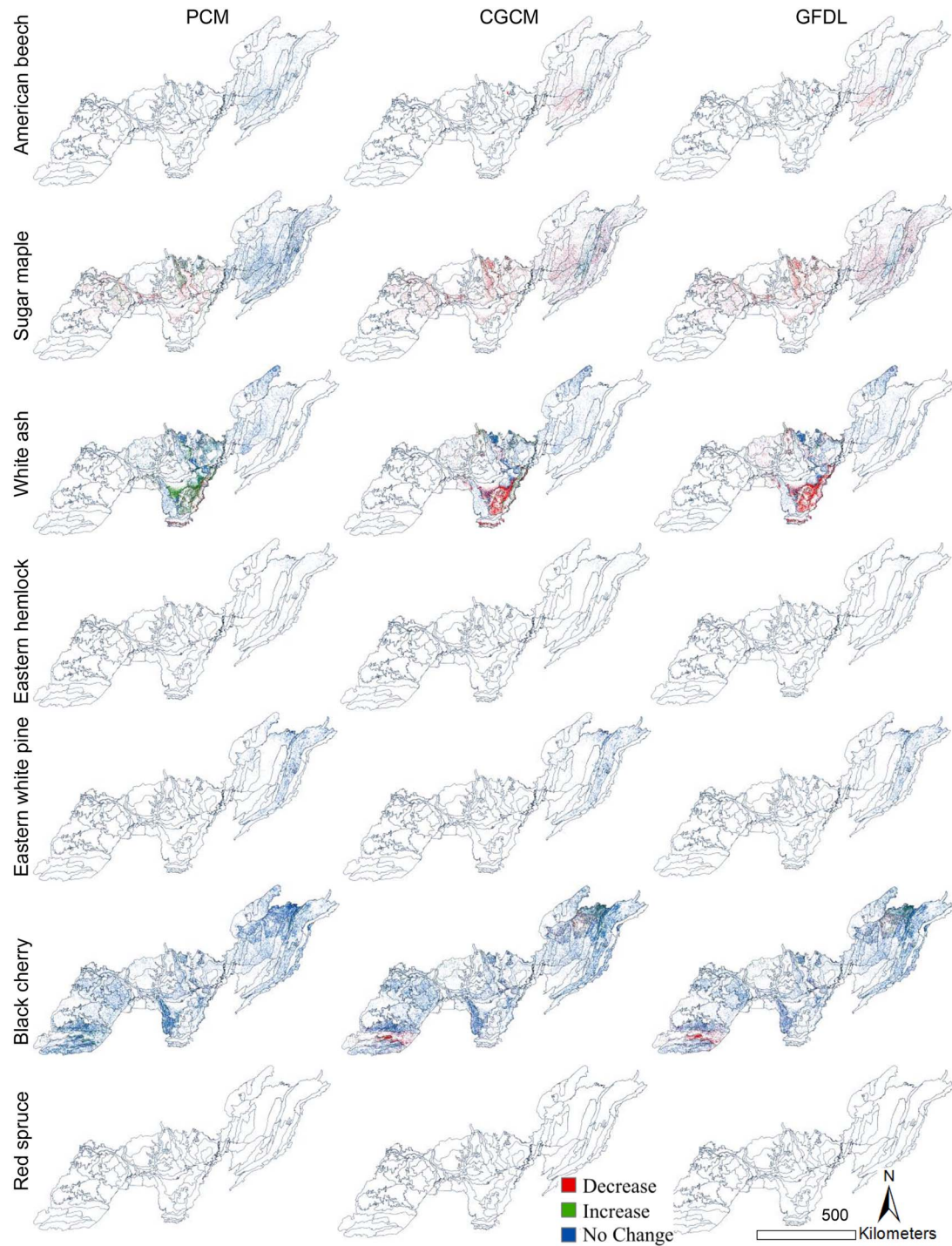


Fig. 3. Maps of projected changes in importance values for all 23 tree species at year 2300 under three climate change scenarios with harvest compared to current climate at year 2300 in the Central Hardwood Forest Region, USA.

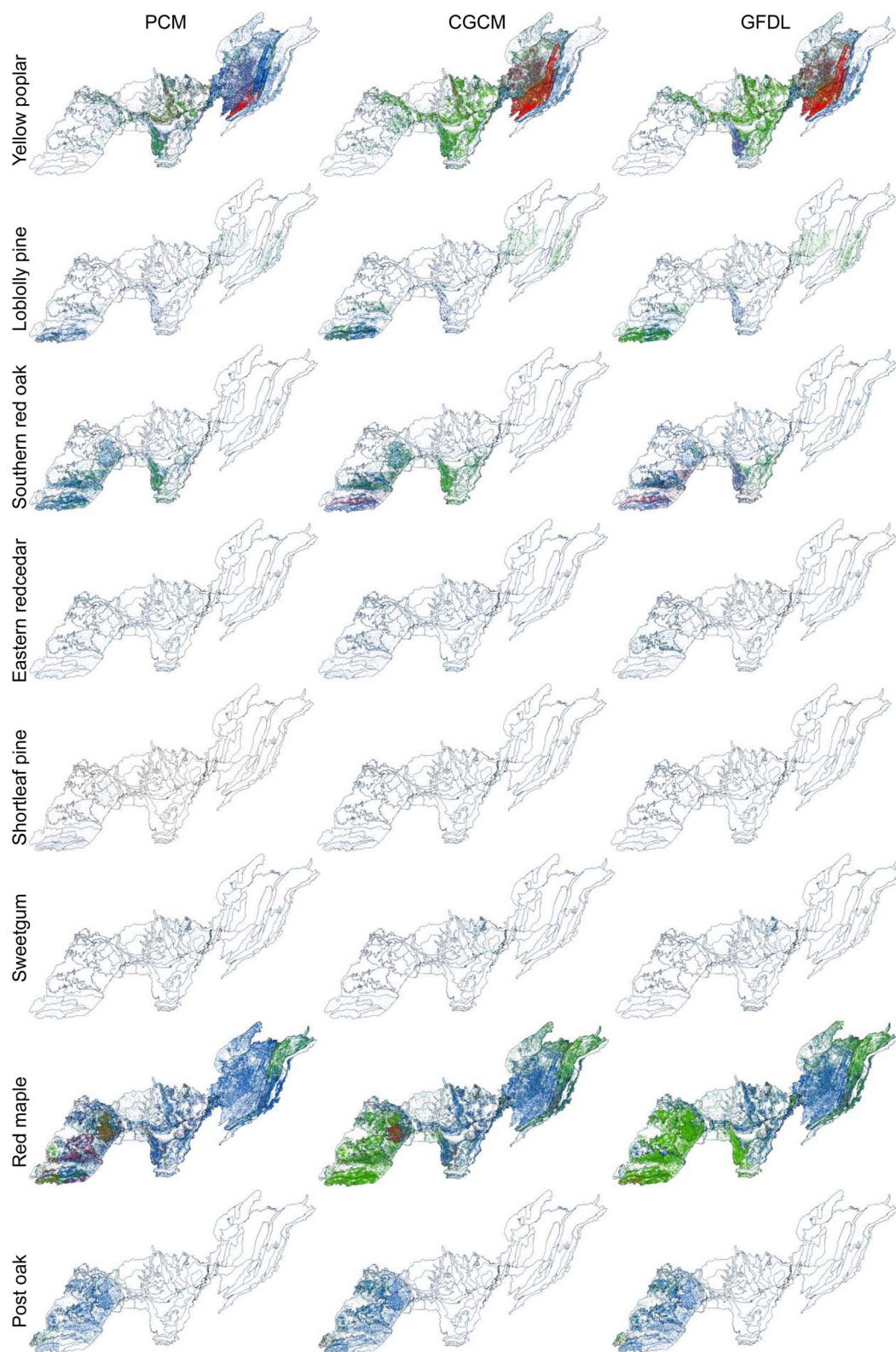


Fig. 3. Continued.

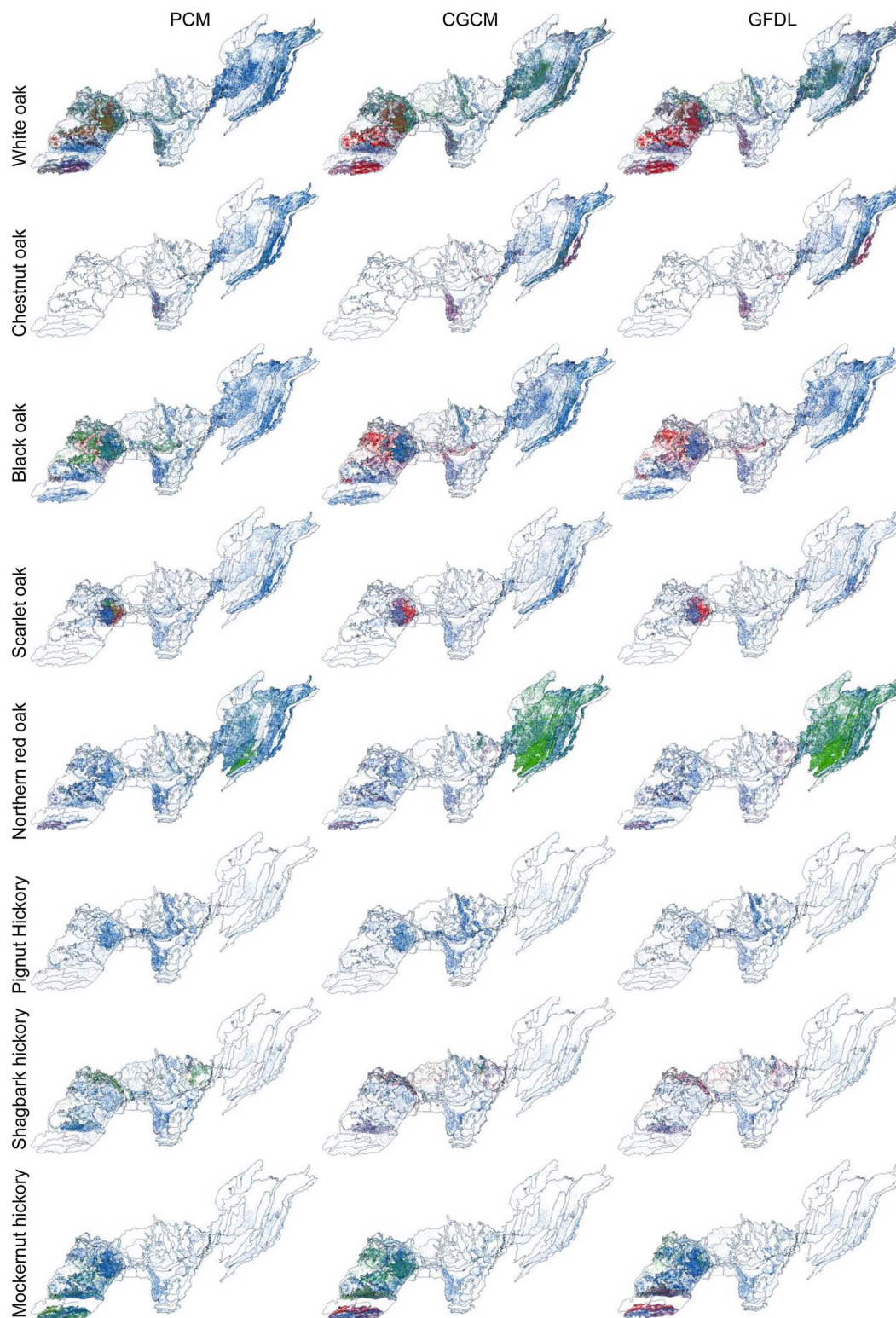


Fig. 3. Continued.

Table 2. The importance of succession (S), harvest (H), climate (C), and their interactions (H*C) in explaining simulated variation in species importance values in the Central Hardwood Forest Region, U.S.A., 2000–2300, based on repeated-measures ANOVA.

Common name	Short-term variation explained (%)				Medium-term variation explained (%)				Long-term variation explained (%)			
	S	C	H	H × C	S	C	H	H × C	S	C	H	H × C
Sugar maple	95	0.1	0.2	0.1	21.4	43.7	24.4	9.8	15.8	65.3	11.6	7.1
American beech	96.7	0.1	0.1	0.1	35.9	38.6	16.1	5.5	26.1	47.3	18.6	7.4
White ash	80.2	0.6	15.1	0.4	59.8	14.8	12.2	8.1	24.3	40.7	24.4	9.1
Eastern white pine	48.9	1.3	47.4	1.2	53.7	22.8	14.8	5.1	65.2	15.3	10.3	6.2
Eastern hemlock	95.4	0.1	0.1	0.1	54.0	25.8	13.9	5.3	66.6	20.2	4.1	5.1
Black cherry	66.7	0.2	32.4	0.1	61.7	17.8	14.7	4.4	45.9	19.3	25.7	5.2
Red spruce	99.2	0.1	0.3	0.1	99.4	0.1	0.1	0.1	99.5	0.1	0.1	0.1
Yellow-poplar	75.5	0.4	22.5	1.1	52.4	14.3	26.6	3.1	53.1	19.2	20.2	5.4
Loblolly pine	77.3	0.1	17.9	0.1	67.4	8.4	20.1	1.6	40.8	21.9	30.7	6.5
Shortleaf pine	75.6	0.1	18.9	0.1	62.9	9.1	22.4	2.7	45.3	12.9	32.4	6.2
Eastern redcedar	71.5	0.2	25.3	0.1	75.5	9.5	10.4	0.3	89.8	7.1	0.1	0.5
Post oak	79.8	2.5	10.1	1.4	82.6	5.7	5.2	1.7	82.2	8.3	2.1	2.1
Southern red oak	87.5	1.1	3.4	0.1	75.1	6.7	10.7	3.1	40.7	28.1	23.4	8.4
Red maple	91.2	0.5	7.9	0.1	72.5	9.7	11.6	3.6	55.4	20.1	18.4	8.9
White oak	48.5	2.0	44.1	1.0	65.8	9.4	17.7	3.5	28.2	20.6	42.1	8.5
Chestnut oak	54.3	0.1	43.1	0.1	62.9	8.4	17.1	3.1	22.1	26.8	41.4	7.2
Black oak	80.7	0.1	17.6	0.1	70.3	9.3	13.8	3.4	17.5	52.4	20.5	7.3
Scarlet oak	77.2	0.2	19.6	0.1	71.6	7.4	15.5	4.1	26.5	45.4	19.3	7.7
Northern red oak	71.2	0.3	23.8	0.2	66.7	10.6	16.7	4.5	15.1	50.6	25.4	7.5
Pignut hickory	78.3	0.4	16.4	0.5	57.3	5.2	31.8	3.5	65.7	10.1	18.5	5.1
Mockernut hickory	82.4	0.1	10.7	4.6	45.2	7.1	37.2	4.7	20.4	27.1	42.7	9.5
Shagbark hickory	86.5	3.8	1.8	2.5	60.2	6.1	26.2	2.1	31.4	34.6	25.4	7.9
Sweetgum	80.8	2.2	13.4	0.7	51.1	0.3	45.1	0.1	90.4	0.1	6.4	0.1
Average	78.3	0.7	17.0	0.6	62.0	12.6	18.4	3.6	46.4	25.8	20.2	6.0

poplar and southern red oak and decreases in IVs for sugar maple and American beech under climate change (Fig. 2). In the long term, the IVs of yellow-poplar under the climate change with harvest scenarios (e.g., 22 under GFDL-harvest) were higher than those under the climate change without harvest scenarios (e.g., 16 under GFDL-no harvest); the IVs of sugar maple under the climate change with harvest scenarios (e.g., 0.9 under GFDL-harvest) were lower than those under the climate change without harvest scenarios (e.g., 1.5 under GFDL-no harvest).

Harvest ameliorated the increases of IVs for red maple and the decreases of IVs for white oak, chestnut oak, and white ash under the climate change scenarios (Fig. 2). In the long term, the IVs of white oak under the climate change with harvest scenarios (e.g., 9 under GFDL-harvest) were lower than that those under the climate change without harvest scenarios (e.g., 4 under GFDL-no harvest). By contrast, some species such as eastern redcedar, post oak, and sweetgum were less sensitive to the additive effects of harvest under climate change in affecting impor-

tance values (Fig. 2).

Relative importance of succession, harvest, and climate change

The relative importance of succession, harvest, and climate change to variation in IVs varied among species and changed over time (Table 2). On average, succession explained 78.3, 62.0, and 46.4%; and harvest explained 17.0, 18.4, and 20.2 %; of variation in species IVs in the short, medium, and long term, respectively (Table 2). The amount of variation in IVs explained by climate change increased from 0.7% in the short term to 25.8% in the long term (Table 2). The variation explained by the interaction between climate and harvest was minor in the short term and increased to 6% in the long term (Table 2). Therefore, succession was the most important process over the next 300 years; harvest was more important than climate change in the short and medium term; and climate change was more important than harvest in the long term.

Climate change generally had greater effects for six northern species sugar maple, American beech, eastern hemlock, black cherry, white ash,

and northern red oak, four southern species yellow-poplar, shortleaf pine, loblolly pine, and southern red oak, and five widely distributed species white oak, black oak, scarlet oak, mockernut hickory, and shagbark hickory (Table 2). Harvest had larger effects for species targeted by harvest, such as white oak, chestnut oak, northern red oak, and black cherry, shade-intolerant species yellow-poplar, shortleaf pine, loblolly pine, and hickory species (Table 2).

DISCUSSION

We predicted changes in species IVs from 2000 to 2300 in a temperate deciduous forest taking into account succession, disturbance, and climate change and quantified their relative importance to these changes. Succession had large effects on importance values for a wide range of species over time. Our results suggest that succession is the primary process in temperate deciduous forests where catastrophic disturbances (e.g., clear-cutting, stand-replacing fire) are rare (Shifley et al. 2012). However, the average percent of variation in species importance values explained by climate increased from 2% to 27% in the short to long term, and for some species was as great as 87%. The delayed effects of climate change suggest that species may take decades to centuries to respond to changing climates, which is consistent with previous studies (Murphy et al. 2010, Bertrand et al. 2011, Thompson et al. 2011). 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 (Reich and Frelich 2001). Although abiotic controls may exert important roles in determining forest changes, our results suggest that succession should be accounted for when predicting forest changes under climate change in mid-successional temperate deciduous forests.

We expected to see an increase in the importance of climate change over time because climate changed gradually and mostly affected seedling establishment and juvenile mortality (Dietze and Moorcroft 2011). Our results differ from some landscape-scale studies that suggested climate change effects would be prominent in coming decades (e.g., Schumacher and Bugmann 2006). However, the difference is perhaps unsur-

prising because we presented averaged estimates of species importance values for the region in which some subsections may have greater or lesser climate effects than the region as a whole. For example, the oak-hickory forests in the westernmost Ozark Highlands may be more vulnerable to climate change than those mesophytic forests in the eastern part of the region (Brandt et al. 2014). Future climates may place biophysical constraints on the number and size of trees that can persist in different landscapes (Anderson-Teixeira et al. 2013). For example, maximum biomass was reduced 30% ~ 50% under the GFDL climate change scenario for many western and southern subsections in the CHFR (Appendix D: Table D1), which could lead to conversion of some forests to woodland and savanna (Frelich and Reich 2010).

Tree harvest was more important than climate change in affecting species IVs in the short and medium term. Harvest directly removed large, economically preferred tree species and thus had species specific effects that led to immediate and substantial changes in forest composition and successional trajectories, which is consistent with observed effects of these practices (Schuler 2004, Deluca et al. 2009, Vanderwel and Purves 2014). Tree harvest accelerated or ameliorated forest changes by providing establishment opportunities and tilting the competitive balance to favor or not favor certain species. Niche models usually ignore disturbance such as harvest and most process models approximate harvest by deterministically removing a percentage of aboveground forest biomass (Medvigy et al. 2009), a fraction of plant functional types (e.g., Sitch et al. 2003), or some age classes of plant functional types (e.g., Zaehle et al. 2006). These models may not realistically simulate the remaining forest composition and structure because they do not explicitly take into account harvest preferences for certain species, size classes, post-harvest establishment, and interspecific competition. Therefore, we believe our mechanistic approach to simulating harvest and succession provides a more realistic simulation of how forest composition and structure may actually change compared to niche and simpler process models.

Forest responses to succession, harvest, and climate change were species specific. For exam-

ple, “super-generalist” species like red maple experienced dramatic increases in importance value under climate change because of its ability to thrive in a wide variety of ecological conditions, while shade-intolerant yellow-poplar gradually increased in importance value under climate change and harvest because of its ability to establish and grow fast in canopy gaps. These results highlight that climate change and harvest alter the forest composition through gaining or losing species, rather than losing plant functional types. Such species-specific responses are difficult to capture using plant functional types (McMahon et al. 2011). Capturing changes at the tree species level are important, because changes in dominant species from oaks to red maple and yellow-poplar, could have important impacts on biodiversity and a wide range of services such as carbon storage, wildlife habitat, and forest products. Niche models usually predict response of one species at a time (e.g., presence/absence; Guisan and Thuiller 2005, Iverson et al. 2008) whereas process models usually predict changes of plant functional types (but see Morin et al., 2008). Although niche and process models are efficient in capturing the general responses of forest composition to climate change, we believe our species-specific predictions more realistically simulate interactions among species and between species and the environment.

We used a landscape modeling approach that projected the responses of tree species abundance for the entire CHFR under climate change while mechanistically simulating site-scale succession and landscape-scale disturbance at a relatively fine spatial resolution of 270 m. However, there are always tradeoffs between simplicity and complexity versus spatial extent in large-scale modeling. We assumed that all individuals of a given tree species shared the same species life attributes (e.g., longevity, shade tolerance class, maximum DBH) and demography (e.g., fecundity) across the region when, in fact, variation likely occurred in these attributes. However, we did address spatial variation in several key species and site attributes by varying maximum growing space, species seedling establishment probabilities, and species DBH-age relationships with landtype, which ultimately affected tree growth, mortality, and establishment (Wang et

al. 2013a). We also only simulated 23 dominant tree species and lumped all remaining tree species as one pseudo species group so that the total growing space in a stand was occupied. This represents a tradeoff between process-based forest landscape models such as ours, which can only simulate a modest number of tree species, and niche models that can fit models for many species (e.g., 184 species in Tree Atlas; Iverson et al. 2008). We only considered a simplified climate change scenario that represents a gradual change in the first 100 years and unchanging conditions for 200 years thereafter. Thus, our predictions represented forest responses over a 300 year period, but only based on climate change for the first 100 years as predicted by GCM models.

Other factors not included in our study may have contributed to uncertainty in our projections. We assumed the extent of forest in the region did not change while in reality urban growth may further fragment forest and result in less forested area (Kuemmerle et al. 2012). Insect and disease outbreaks and fire may increase with climate warming and affect tree species composition (Weed et al. 2013). For example, the emerald ash borer (*Agrilus planipennis*) has killed millions of native ash trees (*Fraxinus* spp.) throughout Midwestern North America (Prasad et al. 2010) and climate warming will likely accelerate its spread (DeSantis et al. 2013). Our approach modeled the primary effects of climate as temperature, precipitation, growing season length, and drought effects on maximum growing capacity, tree mortality, and tree establishment. We did not directly simulate nitrogen deposition and CO₂ fertilization effects on tree growth (Lenz et al. 2014), which can have significant impacts on aboveground biomass (Griepentrog et al. 2015).

Despite the limitations associated with forest landscape modeling, there are good reasons why our modeling approach is well suited for understanding and projecting how forest composition may change across a large region. First, LANDIS PRO has been extensively tested and applied in previous studies (Wang et al. 2013a, 2014b, 2015, Brandt et al. 2014, Luo et al. 2014, Liang et al. 2015). Second, the initial forest compositions and harvest parameters were derived from millions of FIA tree records. Third, the projected forest

composition and structure under current succession and harvest matched the reported old-growth studies in the CHFR. Fourth, we mechanistically accounted for many detailed processes such as growth, competition, dispersal, establishment, and harvest, which are not similarly addressed in previous modeling approaches.

Our results have important implications for forest adaption and resilience management strategies. The lagged effects of climate change and the overwhelming importance of succession in driving forest change suggest that stand dynamics cannot be ignored when planning management for resilience or adaptation and that other management related issues may be more pressing. For example, oak decline is a wide-spread problem and potentially more urgent concern in the CHFR that can be addressed by management to reduce stand density and change species composition (Shifley et al. 2012, Wang et al. 2013b). Forest management that favors species that are expected to be better adapted to future climate conditions may promote resilience and adaptation to climate change (Buma and Wessman 2011); for example, planting southern species such as loblolly pine, whose seed sources are currently limited in the CHFR, might facilitate its adaptation to a warming climate (Brandt et al. 2014).

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LITERATURE CITED

- Anderson-Teixeira, K. J., A. D. Miller, J. E. Mohan, T. W. Hudiburg, B. D. Duval, and E. H. Deluca. 2013. Altered dynamics of forest recovery under a changing climate. *Global Change Biology* 19:2001–2021.
- Bertrand, R., J. Lenoir, C. Piedallu, G. Riofrío-Dillon, P. Ruffray, C. Vidal, J. Pierrat, and J. Gégout. 2011. Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479:517–520.
- Boulangeat, I., D. Gravel, and W. Thuiller. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15:584–593.
- Brandt, L., et al. 2014. Central hardwoods ecosystem vulnerability assessment and synthesis: a report from the central hardwoods climate change response framework project. General Technical Report NRS-124. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Buma, B., and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2(5):64.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture handbook 654. USDA Forest Service, Washington, D.C., USA.
- Canham, C. D., N. Rogers, and T. Buchholz. 2013. Regional variation in forest harvest regimes in the northeastern United States. *Ecological Applications* 23(3):515–522.
- Cleland, D. T., J. A. Freeouf, J. E. Keys, G. J. Nowacki, C. Carpenter, and W. H. McNab. 2007. Ecological subregions: sections and subsections of the conterminous United States [1:3,500,000]. General Technical Report WO-76. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Deluca, T., M. A. Fajvan, and G. Miller. 2009. Diameter-limit harvesting: effects of residual trees on regeneration dynamics in Appalachian hardwoods. *Northern Journal of Applied Forestry* 26(2):52–60.
- Desantis, R. D., W. K. Moser, D. D. Gormanson, M. G. Bartlett, and B. Vermunt. 2013. Effects of climate on emerald ash borer mortality and the potential for ash survival in North America. *Agricultural and Forest Meteorology* 178–179:120–128.
- Dietze, M. C., and P. R. Moorcroft. 2011. Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology* 17(11):3312–3326.
- Dijak, W. 2013. Landscape Builder: software for the creation of initial landscapes for LANDIS from FIA data. *Computational Ecology and Software* 3(2):17–25.
- FAO. 2012. State of the world's forests 2012. Food and Agriculture Organization of the United Nations, Rome, Italy.

- Fraser, J. S., H. S. He, S. R. Shifley, W. J. Wang, and F. R. Thompson. 2013. Simulating stand-level harvest prescriptions across landscapes: LANDIS PRO harvest module design. *Canadian Journal of Forest Research* 43:972–978.
- Frelich, L. E., and P. B. Reich. 2010. Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Frontiers in Ecology and the Environment* 8(7):371–378.
- Griepentrog, M., T. I. Eglinton, F. Hagedorn, M. W. I. Schmidt, and G. L. B. Wiesenberger. 2015. Interactive effects of elevated CO₂ and nitrogen deposition on fatty acid molecular and isotope composition of above- and belowground tree biomass and forest soil fractions. *Global Change Biology* 21:473–486.
- Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8:993–1009.
- Gustafson, E. J., A. Z. Shvidenko, B. R. Sturtevant, and R. M. Scheller. 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecological Applications* 20(3):700–715.
- He, H. S. 2008. Forest landscape models, definition, characterization, and classification. *Forest Ecology and Management* 254:484–498.
- He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. *Ecology* 80:81–99.
- He, H. S., D. J. Mladenoff, and T. R. Crow. 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecological Modeling* 114:213–233.
- Hickler, T., et al. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography* 21:50–63.
- IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254:390–406.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. P. Peters. 2011. Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems* 14:1005–1020.
- Johnson, P. S., S. R. Shifley, and R. Rogers. 2009. The ecology and silviculture of Oaks. Second edition. CAB International, Oxfordshire, UK.
- Kuemmerle, T., T. Hickler, J. Olofsson, G. Schurgers, and V. C. Radeloff. 2012. Reconstructing range dynamics and range fragmentation of European bison for the last 8000 years. *Diversity and Distributions* 18(1):47–59.
- Lenz, A., Y. Vitasse, G. Hoch, and C. Körner. 2014. Growth and carbon relations of temperate deciduous tree species at their upper elevation range limit. *Journal of Ecology* 102:1537–1548.
- Liang, Y., H. S. He, W. J. Wang, J. S. Fraser, Z. Wu, and J. Xu. 2015. The site-scale processes affect species distribution predictions of forest landscape models. *Ecological Modelling* 300:89–101.
- Luo, X., H. S. He, Y. Liang, W. J. Wang, Z. Wu, and J. S. Fraser. 2014. Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China. *Landscape Ecology* 29(7):1–14.
- Maurer, E. P., A. W. Wood, J. C. Adam, D. P. Lettenmaier, and B. Nijssen. 2002. A long-term hydrologically-based data set of land surface fluxes and states for the conterminous United States. *Journal of Climate* 15(22):3237–3251.
- McMahon, S. M., S. P. Harrison, and W. S. Armbruster. 2011. Improving assessment and modeling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution* 26(5):249–259.
- Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research* 114:G01002.
- Meier, E. S., H. Lischke, D. R. Schmatz, and N. E. Zimmermann. 2012. Climate, competition, and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* 21:164–178.
- Mette, T., K. Dolos, C. Meinardus, A. Bräuning, B. Reineking, M. Blaschke, H. Pretzsch, C. Beierkuhnlein, A. Gohlke, and C. Wellstein. 2013. Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere* 4(12):145.
- Morin, X., and W. Thuiller. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology* 90(5):1301–1313.
- Morin, X., D. Viner, and I. Chuine. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology* 96(4):784–794.
- Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2010. Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters* 13:1233–1244.
- Murphy, K. R., and B. Myers. 2003. Statistical power analysis: a simple and general model for traditional and modern hypothesis tests. Second edition.

- Lawrence Erlbaum, Mahwah, New Jersey, USA.
- Neilson, R. P., L. F. Pitelka, A. M. Solomon, R. Nathan, G. F. Midgley, J. M. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. *BioScience* 55(9):749–759.
- Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. Update edition. Wiley, New York, New York, USA.
- Prasad, A. M., L. R. Iverson, M. P. Peters, J. M. Bossenbroek, S. N. Matthews, T. D. Sydnor, and M. W. Schwartz. 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. *Landscape Ecology* 25:353–369.
- Purves, D., and S. Pacala. 2008. Predictive models of forest dynamics. *Science* 320:1452–1453.
- Reich, R. B., and L. Frelich. 2001. Temperate deciduous forests. Pages 565–569 in *Encyclopaedia of global environmental change*. Volume 2. Wiley, Chichester, UK.
- Scheller, R. M., and D. J. Mladenoff. 2005. A spatially dynamic simulation of the effects of climate change, harvesting, wind, and tree species migration on the forest composition, and biomass in northern Wisconsin, USA. *Global Change Biology* 11:307–321.
- Schuler, T. M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. *Canadian Journal of Forest Research* 34(5):985–997.
- Schumacher, S., and H. Bugmann. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Global Change Biology* 12:1435–1450.
- Shifley, S. R., F. X. Aguilar, N. Song, S. I. Stewart, D. J. Nowak, D. D. Gormanson, W. K. Moser, S. Wormstead, and E. J. Greenfield. 2012. Forests of the northern United States. General Technical Report NRS-90. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Sitch, S., et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamics global vegetation model. *Global Change and Biology* 9:161–185.
- Stoner, A. M. K., K. Hayhoe, and X. Yang. 2011. Downscaled climate projections by Katharine Hayhoe. http://cida.usgs.gov/climate/hayhoe_projections.jsp
- Tang, G., B. Beckage, B. Smith, and P. A. Miller. 2010. Estimating potential forest NPP, biomass and their climatic sensitivity in New England using a dynamic ecosystem model. *Ecosphere* 1(6):18.
- Thompson, J. R., D. R. Foster, R. M. Scheller, and D. Kittredge. 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications* 21(7):2425–2444.
- Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelmi, Y. Wei, and R. B. Cook. 2012. Daymet: daily surface weather on a 1 km grid for North America, 1980–2012. <http://daymet.ornl.gov/>
- Vanderwel, M. C., and D. W. Purves. 2014. How do disturbances and environmental heterogeneity affect the pace of forest distribution shifts under climate change? *Ecography* 37:10–20.
- Wang, W. J., H. S. He, F. R. Thompson III, J. S. Fraser, and W. D. Dijak. 2015. Landscape- and regional-scale shifts in forest composition under climate change in the Central Hardwood Region of the United States. *Landscape Ecology*, doi: 10.1007/s10980-015-0294-1.
- Wang, W. J., H. S. He, J. S. Fraser, F. R. Thompson III, S. R. Shifley, and M. A. Spetich. 2014a. LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. *Ecography* 37:225–229.
- Wang, W. J., H. S. He, M. A. Spetich, S. R. Shifley, and F. R. Thompson. 2014b. Evaluating forest landscape model predictions using empirical data and knowledge. *Environmental Modelling and Software* 62:230–239.
- Wang, W. J., et al. 2013a. A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. *Ecosphere* 4(9):106.
- Wang, W. J., H. S. He, M. A. Spetich, S. R. Shifley, F. R. Thompson, III, and J. S. Fraser. 2013b. Modeling the effects of harvest alternatives on mitigating oak decline in a Central Hardwood Forest landscape. *PLoS ONE* 8(6):e66713.
- Weed, A. S., M. P. Ayres, and J. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs* 83(4):441–470.
- Woodall, C., B. Conkling, M. Amacher, J. Coulston, S. Jovan, C. Perry, B. Schulz, G. Smith, and S. W. Wolf. 2010. The forest inventory and analysis database. Version 4.0: database description and user's manual for Phase 3. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Wullschleger, S. D., C. A. Gunderson, M. L. Tharp, D. C. West, and W. M. Post. 2003. Simulated patterns of forest succession and productivity as a consequence of altered precipitation. Pages 433–446 in P. J. Hanson and S. D. Wullschleger, editors. *North American temperate deciduous forest responses to changing precipitation regimes*. Springer-Verlag, New York, New York, USA.
- Zaehle, S., et al. 2006. The importance of age-related decline in forest NPP for modeling regional carbon balances. *Ecological Applications* 16:1555–1574.

SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–E are available online: <http://dx.doi.org/10.1890/ES15-00238.1.sm>