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RESEARCH ARTICLE

Landscape- and regional-scale shifts in forest composition under climate change in the Central Hardwood Region of the United States

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Abstract
Context Tree species distribution and abundance are affected by forces operating at multiple scales. Niche and biophysical process models have been commonly used to predict climate change effects at regional scales, however, these models have limited capability to include site-scale population dynamics and landscape-scale disturbance and dispersal. We applied a landscape modeling approach that incorporated three levels of spatial hierarchy (pixel, landtype, and ecological subsection) to model regional-scale shifts in forest composition under climate change.
Objective To determine (1) how importance value of individual species will change under the PCM B1 and GFDL A1FI modeling scenarios and (2) how overall forest composition at different spatial scales will change under these climate change scenarios in the short, medium, and long term in the Central Hardwood Forest Region (CHFR).
Methods We used LANDIS PRO to predict forest composition changes from 2000 to 2300 accounting for climate change, population dynamics, dispersal, and harvest in the CHFR. We analyzed forest composition shifts under alternative climate scenarios and at multiple spatial scales.
Results Shifts in forest composition were greater under the GFDL A1FI than the PCM B1 modeling scenarios and were greatest at the scale of ecological sections followed by forest sub-regions and the whole CHFR. Forest composition shifted toward more southern and xeric species and lesser northern and mesic species.
Conclusions We suggest it is essential to include site- and landscape-scale processes in models and to evaluate changes at multiple spatial and temporal scales when evaluating changes in species composition due to climate change and disturbance.

Keywords Abundance · Harvest · Succession · Demography · LANDIS PRO · U.S. Forest Service Inventory and Analysis (FIA) data

Special issue: Macrosystems ecology: Novel methods and new understanding of multi-scale patterns and processes.

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Introduction

Tree species distribution and abundance are affected by forces operating at multiple scales. Spatial variation in climate at a regional scale is an important factor affecting tree distribution and abundance (Thuiller et al. 2004; Pederson et al. 2014). Ecological sections or subsections are ecologically defined regions in the U.S. (McNab et al. 2007) that may be useful for summarizing regional changes in forest composition. Differences in nutrient and water availability as captured by landform and soil may have a dominant effect at an intermediate landtype scale (also called ecoregions for broad-scale studies). Population dynamics and biotic interactions such as inter- and intra-species competition may play the greatest role at a site or pixel scale (Araújo and Luoto 2007; Pigot and Tobias 2013; Normand et al. 2014; Liang et al. 2015). Models can account for forces at multiple scales when predicting effects of climatic change on forests. Niche models (Guisan and Thuiller 2005; Araújo and Rahbek 2006; Iverson et al. 2008; Gritti et al. 2013) and biophysical process models (Bachelet et al. 2008; Morin et al. 2008; Medvigy et al. 2009) are common models that use a two-level hierarchy, cell and region, to model climate change effects at regional scales (Morin and Thuiller 2009). Both types of models divide the study region into grid cells (usually 20–50 km in size) at which regional climate is spatially downscaled and environmental data (e.g., soil) is aggregated (Iverson et al. 2011; McMahon et al. 2011). Process models simulate grid cell-level vegetation dynamics based on interactions between physiological drivers and plant functional types (Neilson et al. 2005). Niche models predict probabilities of species occurrence for all grid cells based on the statistical associations between the observed distributions and environmental variables (Pearson and Dawson 2003). Both types of models aggregate individual grid cells without accounting for interactions among cells to make inferences at a regional scale. From the perspective of hierarchy theory, grid cell-level simulation provides mechanisms for regional-level outcomes, whereas the region provides the spatial context for cell-level simulations (O'Neill et al. 1986).

The 20–50 km grid cell size used by niche models and biophysical process models corresponds to the size of ecological subsections and sections (McNab et al. 2007). Ecological subsections are ecologically defined but may still be too coarse to realistically simulate site-scale population dynamics and landscape-scale processes. Thus, population dynamics (e.g., tree species demography and biotic interactions in a forest stand, usually 30–500 m in size) and landscape-scale processes (e.g., dispersal and harvest, usually spanning over a few sites) are either ignored or highly simplified in niche and biophysical process models (Purves and Pacala 2008; Elith and Leathwick 2009). Population dynamics may play a greater role than climate change in affecting forest composition in temperate deciduous forests and tree harvest may accelerate shifts in composition by providing regeneration opportunities and altering the competitive balance among tree species (Thompson et al. 2011; Luo et al. 2014; Wang et al. 2015). Dispersal, occurring from hundreds of meters to a few kilometers, links site-scale population (seed abundance and distribution), dispersal capacity, and environmental constraints and is found to be a key process affecting tree species migration and composition shift (Neilson et al. 2005; Thuiller et al. 2008; Doxford and Freckleton 2012; Corlett and Westcott 2013). Site-scale population dynamics and landscape processes can be incorporated at pixel sizes of 30–500 m in landscape models to more realistically simulate regional changes in forest composition (Wang et al. 2013a, b).

We applied a landscape modeling approach that included three levels in an ecological and spatial hierarchy (pixel, landtype, and ecological subsection) to model regional-scale changes in forest composition and structure. We simulated species-level processes such as growth, mortality, and establishment and stand-level processes such as competition at a pixel scale. We simulated effects of soil nutrients and water conditions, as captured by soils and landforms, on species establishment and maximum growing space. We also simulated seed dispersal among pixels, which can result fine grain (e.g. within landtype) heterogeneity in species distributions (He and Mladenoff 1999; Wang et al. 2013a). Regional climate models can be downscaled to subsections and landtypes to affect species- and site-level processes. The simulated results under this framework are the outcome of interactions at all three scales (Wang et al. 2014a, b; Wang et al. 2015).

Forest landscape models have employed this multi-level hierarchy to simulate forest change (e.g.,

Schumacher and Bugmann 2006; He 2008), however, they have not been able to predict regional-scale (e.g., >100 million ha) forest changes because of the immense computational load. The maximum simulation capacity (number of pixels) of forest landscape models is currently in the range of 10^6–10^7 pixels (e.g., He 2008; He et al. 2011). Even at such a simulation capacity, site-scale population dynamics are simplified omitting tree density and size metrics, which are key for determining stand-scale competition for resources (e.g. light) (Bohlman and Pacala 2012). Recent advances in the LANDIS PRO forest landscape model have expanded the simulation capacity to 10^8 pixels at 30–500 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.

We used LANDIS PRO, a regional-scale forest landscape model, to simulate forest change due to succession, harvest, and climate change over the next 300 years in the Central Hardwood Forest Region of United States (CHFR). The CHFR is one of the most extensive temperate deciduous forests in the world (Johnson et al. 2009). Temperate deciduous forests are among the biomes that have been most severely influenced by global change factors such as climatic change, land use (e.g., logging, agriculture conversion), and land management (e.g., fire suppression, harvest) (Reich and Frelich 2001; Pederson et al. 2014). These factors will undoubtedly continue to alter tree species occurrence and abundance and thus lead to shifts in forest composition and structure, which will affect the ecological, economic, and social services these forests provide (Thompson et al. 2011; Anderson-Teixeira et al. 2013; Brandt et al. 2014; Vanderwel and Purves 2014). Temperate deciduous forests occupy highly populated and developed regions of the world and play an expanding role under burgeoning global populations and climate change. Understanding and anticipating their future composition shifts is critical to designing a sound management strategy for conservation, adaptation, and mitigation for change.

We investigated the effects of two different climate change modeling scenarios on forest composition at multiple scales within the CHFR. The PCM B1 modeling scenario predicts a moderate temperature increase (+1.8 °C) and higher growing season precipitation (+4.2 cm) and the GFDL A1FI modeling scenario predicts a large temperature increase (+5.2 °C) and large precipitation decrease (−20 cm) compared to current climate. Together, they bracket the best-case and worst-case scenarios of future climate changes, under which the strongest deviations in forest composition are expected across our study region. Our objectives were to determine (1) how importance value of individual species will change under the PCM B1 and GFDL A1FI scenarios compared to current climate modeling scenario in the CHFR and (2) how overall forest composition at different spatial scales will change under these climate change modeling scenarios in the short, medium, and long term.

Methods

Study area

The study area was in the CHFR in the eastern United States, which covered 125 million hectares from eastern Oklahoma to West Virginia, and southern New York to Alabama (Fig. 1). This area encompassed 14 ecological sections and 100 ecological subsection and covered variable vegetation, terrains, soils, and climates (Cleland et al. 2007). About 70 % of this area is forested (i.e. forests, woodlands, savannas) and the remaining area is agricultural and urban land uses (Johnson et al. 2009). The region is divided into three sub-regions that reflect three climax associations (Braun 1950). The oak-hickory forest sub-region is four ecological sections in the western portion of the study area and is composed of mixtures of white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam), post oak (*Q. stellata* Wangenh.), northern red oak (*Q. rubra* L.), scarlet oak (*Q. coccinea* Muenchh.), mockernut hickory (*Carya. tomentosa* Nutt.), pignut hickory (*C.glabra* Sweet), and shagbark hickory (*C.ovata* K.Koch); The western mesophytic forest sub-region is five ecological sections in the mid-western portion of the study area and is composed of oaks, hickories, red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), American beech (*Fagus grandifolia*), yellow-poplar (*Liriodendron tulipifera*), white ash (*Fraxinus Americana* L.), and black cherry (*Prunus serotina* Ehrh.); The mixed mesophytic forest sub-region is five ecological sections in the eastern portion of the study

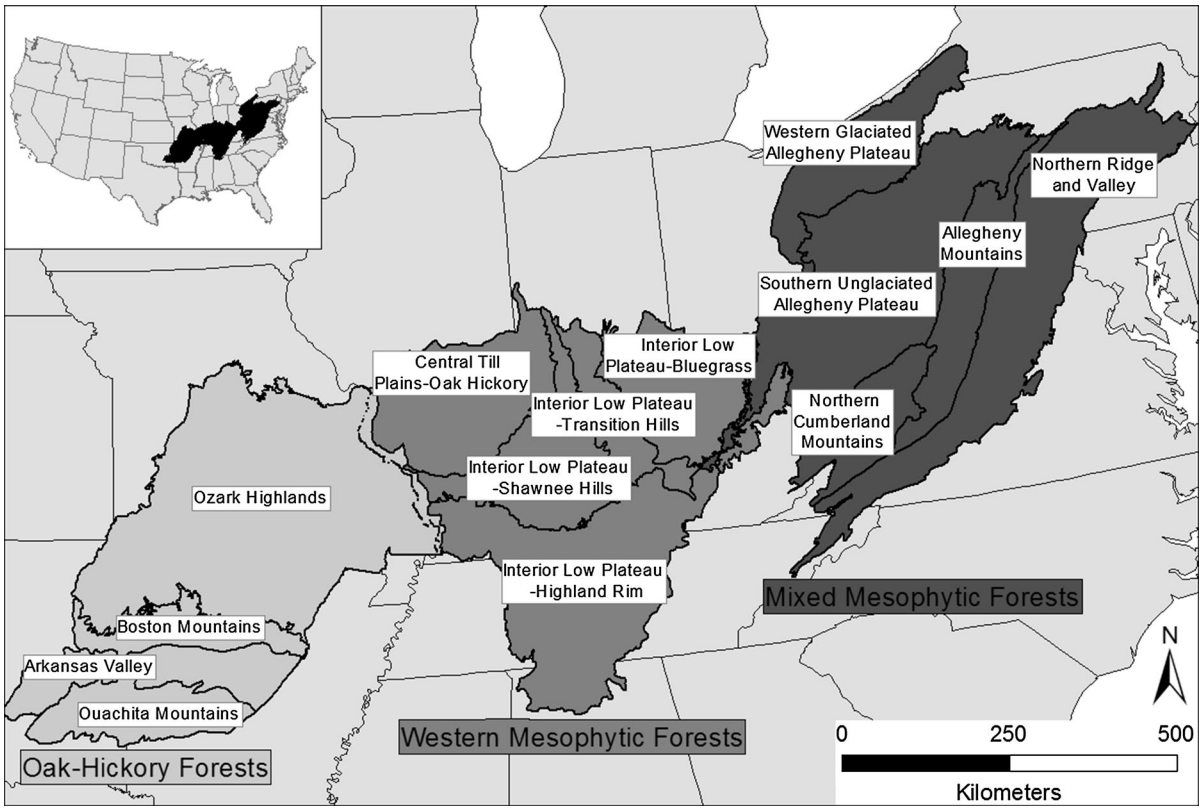

Fig. 1 The study area was located in Central Hardwood Forest Region (CHFR) in eastern U.S.A. It covered 125 million hectares and 14 ecological sections, which were grouped into three forest type sub-regions ranging from west to east: oak-hickory forest sub-region, west mesophytic forest sub-region, and mixed mesophytic forest sub-region

area and is composed of white oak, chestnut oak (*Q. prinus* L.), northern red oak, red maple, sugar maple, yellow-poplar, American beech, eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*) (Braun 1950). The soil types are mostly Alfisol, Inceptisols, Mollisols, and Ultisols (McNab et al. 2007). The current climate of the CHFR is generally characterized as a humid continental climate with cool winters and long, hot summers. Average annual temperatures follow an east–west gradient and range from 4 to 18 °C. Average annual precipitation ranges from 50 cm in the northwest to 165 cm in the southeast, occurring mostly in spring and fall (Johnson et al. 2009).

Climate scenarios

We captured the environmental heterogeneity in terrain, soil, and climate by stratifying the CHFR into 600 landtypes by intersecting 100 ecological subsections and 6 landforms derived from a digital elevation model (DEM) (Dijak 2013). We assumed resource availability (measured as maximum growing space, MGSO) and species establishment probabilitie (SEP) were uniform within a landtype. Climate change affected species demography by modifying MGSO and SEP values for each landtype. We modeled MGSO and SEPs under each climate modeling scenario using LINKAGES II, an ecosystem model that simulates individual tree species growth and mortality accounting for nitrogen availability, climates, and soil moisture (Wullschleger et al. 2003). We input SEP and MGSO values for each landtype under each climate modeling scenario into LANDIS PRO as model parameters to capture climate change effects (He et al. 1999).

We incorporated regional climate in our modeling approach by intersecting landtypes with downscaled general circulation model (GCMs) predictions. We included a current climate modeling scenario and PCM B1 and GFDL A1FI modeling scenarios, which

represented the extremes from the lowest to highest increases in summer temperatures in the region, respectively. The B1 and A1FI represented the extremes from the least to most fossil fuel intensive emission scenarios (IPCC 2007); the PCM GCM had an overall increase in precipitation while GFDL GCM had the largest overall decrease for the region (Brandt et al. 2014; Butler et al. 2015). Thus, by simulating these scenarios, we were able to generate the best- to worst- predictions of forest composition shifts to climate change and incorporated uncertainty in future climate change projections for the region as described by IPCC (2007).

For the current climate modeling scenario, we downloaded daily climate data for maximum and minimum temperature, daily precipitation, daily solar radiation, and day length at 1 km resolution for 1990–2009 from DAYMET (Thornton et al. 2012) for each ecological subsection. We obtained the downscaled climate change projections for the two GCM-based scenarios for the period 2080–2099 for each ecological subsection from the U. S. Geological Survey Center for Integrated Data Analysis (USGS CIDA) Geo Data Portal (Stoner et al. 2011). We obtained wind speed data for current climate and climate change modeling scenarios from the National Oceanic and Atmospheric Administration-National Climatic Data Center (NOAA-NCDC 2011) for each ecological subsection.

We obtained measures of soil organic matter, nitrogen, wilting point, field moisture capacity, percent clay, sand and rock for each landtype from Natural Resources Conservation Service soil survey (Soil Survey Staff 2013, http://soils.usda.gov/). Species biological traits were compiled from the previous studies and literature (Wullschleger et al. 2003; Woudenberg et al. 2010; Appendix Table 2). In LINKAGES II, we simulated individual tree species to estimate SEP under each climate modeling scenario for each landtype using climate and soil data. The simulated biomass at simulation year 30 was used to derive SEP for each species at landtype level by transforming values to a 0 to 1 scale (He et al. 1999, Wang et al. 2015). We simulated 23 tree species together for 300 years to estimate MGSO under each climate modeling scenario using climate and soil data for each ecological subsection (Wang et al. 2015). We varied values of SEP and MGSO for the two climate change modeling scenarios linearly for the first 100 simulation years based on the point estimates for current climate and 2100 from LINKAGES II and held values constant for the following 200 years. Therefore, our predictions represented linear changes in climate change for the first 100 years but no change for years 100–200.

LANDIS PRO simulations

We used the LANDIS PRO Succession module to simulate tree growth, mortality, fecundity, dispersal, establishment, and competition (Wang et al. 2013a, 2014a). LANDIS PRO represented forests as number of trees and diameter at breast height (DBH) by species and age cohort within each pixel. We modeled the 23 most abundant tree species as determined by basal area in the U.S. Forest Service Inventory and Analysis (FIA) data (Woudenberg et al. 2010). We compiled the biological traits for each tree species including longevity, maturity, shade tolerance, dispersal distance, sprouting probability, maximum stand density index, 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 tree by age cohort for 23 tree species at year 2000 by stochastically assigning a representative FIA plot to each pixel based on landform, land cover, FIA unit, and size class from 1995 to 2005 FIA data including all trees whose DBH was equal or above 2.54 cm using Landscape Builder (Dijak 2013). The initial forest conditions, model parameters, and predictions have been previously evaluated 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, b, 2014a, b).

We simulated partial tree harvest using the LANDIS PRO Harvest module and incorporated different partial harvest regimes for each FIA unit (Fraser et al. 2013). The basal area harvested within a selected stand was determined by the initial and residual stand basal area. Depending on the basal area harvested per pixel, this approach represented thinning from above, partial harvest, or clearcutting at the raster cell level and captured the variation in harvest regimes across the region. We derived the parameters for the harvest regimes (minimum entering basal area, residual basal area, proportion of private lands, tree species

Table 1 Percent changes in tree species importance value between a current climate scenario in year 2300 and PCM B1 (upper) and GFDL A1FI (lower) modeling scenarios in year 2300 for 14 ecological sections and Central Hardwood Forest Region

	CHFR	Oak-hickory forest sub-region				Western mesophytic forest sub-region					Mixed mesophytic forest sub-region				
		OzarkH	BostM	ArkaV	OuchM	CTP-OakH	ILP-ShaH	ILP-Blueg	ILP-TraH	ILP-HRim	SUGAP	WGAP	NRV	AllegM	NCM
White Oak	−3.9	−8.9	4.7	−37.2	−37.3	1.1	7.3	4.7	33.3	1.1	13.7	1.0	−33.3	−21.5	−31.8
	−36.7	−78.1	−92.7	−89.6	−97.6	98.2	−22.0	−1.1	−32.5	−80.5	11.4	−24.8	−44.2	−35.8	−48.6
Chestnut Oak	−5.5	30.8	−38.0	–	–	1.8	−24.3	−25.4	−11.8	−47.6	−87.2	−58.9	−27.8	−75.9	−76.6
	−61.1	−99.3	−95.0	–	–	−92.9	−90.5	−90.2	−74.7	−94.9	−98.3	−76.9	−59.7	−68.8	−81.8
Post Oak	18.4	16.5	19.3	22.7	28.1	−2.0	−20.7	−26.2	−16.6	−1.7	–	–	–	–	–
	6.8	64.1	−6.0	−3.7	43.4	28.4	−7.2	29.1	80.1	82.5	–	–	–	–	–
Northern Red Oak	62.3	−35.5	−55.6	−59.7	−94.8	7.0	−19.8	9.1	41.7	−15.0	192.6	62.7	91.3	−45.3	−44.0
	199.4	−93.2	−91.5	−47.9	−97.9	−79.4	−61.7	−84.4	−88.0	−96.0	545.2	980.0	400.1	352.1	33.7
Black Oak	8.3	13.7	−46.4	−59.1	−93.9	6.9	−31.9	17.4	47.7	−21.2	−71.7	−80.5	−79.0	−83.7	−77.8
	−85.1	−94.9	−95.6	−41.9	−96.5	−91.4	−81.0	−85.6	−96.2	−96.5	−85.7	−69.9	−65.8	−79.1	−88.3
Scarlet Oak	−29.1	−43.2	−93.1	–	0.0	−23.8	−50.2	−49.6	−37.6	−70.6	−86.9	−90.2	−88.6	−89.1	−90.4
	−63.7	−98.1	−93.4	–	0.0	−96.9	−92.9	−94.8	−97.1	−94.9	−99.6	−95.1	−98.2	−87.5	−99.8
Southern Red Oak	57.4	92.1	53.9	20.6	64.1	13.3	−12.8	−9.2	−21.1	53.9	–	–	–	–	–
	−74.2	−31.1	−18.6	−84.3	−98.5	277.5	−17.8	25.8	14.2	53.0	–	–	–	–	–
Red Maple	4.6	−7.0	−29.1	10.0	8.2	5.0	−23.9	−20.0	1.1	−14.8	−16.7	−56.1	186.3	−17.6	−62.4
	123.9	259.0	151.9	113.5	99.3	135.9	52.2	41.4	76.4	239.4	33.0	−29.0	292.8	0.9	−27.2
Sugar Maple	−32.3	−80.9	−86.7	1.1	−8.9	−36.5	−58.0	−27.8	−56.2	−37.0	89.8	135.5	305.5	180.3	164.0
	−52.4	−91.0	−86.4	57.2	2.2	−75.7	−87.0	−83.9	−85.6	−68.7	−85.1	−81.5	−85.4	55.7	−80.9
Yellow Poplar	−0.2	92.7	188.2	65.9	–	−9.8	60.1	−1.6	1.4	59.5	662.2	164.3	707.0	52.1	114.5
	16.6	198.3	−5.7	−99.7	–	282.0	147.2	178.5	83.3	248.8	676.2	247.2	1122.2	14.8	60.5
American Beech	−5.3	−67.8	−85.6	7.2	2.9	−17.7	−27.0	−4.8	−31.7	−20.5	−29.1	11.7	−34.6	−23.5	−36.1
	−70.1	−69.6	−86.2	54.5	31.9	−61.8	−32.3	−61.6	−48.2	−40.9	−91.4	−92.9	−95.5	−42.0	−94.1
Eastern Hemlock	8.4	–	–	–	–	–	–	–	–	–	−15.2	49.3	−34.5	−46.9	−62.2
	−92.6	–	–	–	–	–	–	–	–	–	−90.3	−78.7	−97.3	−38.2	−72.6
Red Spruce	−26.5	–	–	–	–	–	–	–	–	–	0.0	−100.0	0.0	−99.5	0.0
	−62.3	–	–	–	–	–	–	–	–	–	0.0	−100.0	0.0	−99.7	0.0
Eastern White Pine	−24.2	–	–	–	–	–	–	–	–	–	72.1	2.7	804.6	336.2	48.6
	−73.3	–	–	–	–	–	–	–	–	–	−98.2	−99.7	−94.8	21.8	−94.9

Table 1 continued

	CHFR	Oak-hickory forest sub-region				Western mesophytic forest sub-region					Mixed mesophytic forest sub-region				
		OzarkH	BostM	ArkaV	OuchM	CTP-OakH	ILP-ShaH	ILP-Blueg	ILP-TraH	ILP-HRim	SUGAP	WGAP	NRV	AllegM	NCM
Black Cherry	−2.1	18.3	20.7	3.1	−6.4	−8.7	−28.5	−5.9	−34.5	−1.8	165.6	−7.3	110.7	39.1	−41.8
	−32.5	−34.0	−98.2	−98.7	−98.3	28.3	−55.5	−17.9	−65.8	−73.9	61.4	−25.5	115.7	6.9	−71.3
White Ash	23.0	4.9	6.9	−30.4	−59.1	15.8	77.5	54.2	−18.9	17.9	76.3	209.0	−52.9	24.5	41.2
	−109.8	−33.4	−31.4	−5.7	−66.6	−83.5	−83.5	−54.9	−63.1	−97.1	−65.8	26.3	−53.8	0.4	−38.3
Pignut Hickory	1.1	44.4	25.2	−66.5	−58.8	−0.9	−29.2	−55.8	12.1	−13.1	40.9	−6.5	265.2	−19.3	1.4
	−64.5	−73.9	−94.3	−98.7	−97.3	8.8	−46.3	−43.7	−61.6	−78.4	−7.6	−13.1	248.9	−26.0	−52.0
Mockernut Hickory	54.3	86.4	39.1	6.6	65.3	−6.6	−44.5	−67.0	−32.5	−9.5	–	–	–	–	–
	−78.3	47.7	−50.0	38.9	−98.6	310.4	27.0	70.4	37.1	20.0	–	–	–	–	–
Shagbark Hickory	15.3	28.4	5.2	−96.9	−91.6	−2.5	−2.0	43.6	42.9	−30.4	–	–	–	–	–
	−106.7	−93.0	−97.7	−97.5	−95.9	−89.2	−75.0	−90.4	−90.9	−86.2	–	–	–	–	–
Shortleaf Pine	−23.5	−9.7	−3.4	1.6	7.3	−1.0	−30.3	18.2	−22.0	−7.0	–	–	–	–	–
	131.4	−1.3	1.9	16.4	−32.1	0.8	−39.8	−1.9	−14.6	9.3	–	–	–	–	–
Loblolly Pine	15.4	14.4	−40.1	−22.6	−34.0	4.5	−32.9	−37.1	−23.6	−34.0	39.4	−82.3	−18.1	−92.0	−76.5
	182.2	73.1	−37.1	226.0	280.6	146.4	−16.4	−76.2	42.9	−28.0	263.9	205.0	109.8	376.6	−5.2
Eastern Redcedar	−16.9	−24.2	−7.4	9.1	5.1	−4.1	−23.5	−27.5	−19.3	−8.5	−87.9		15.0	−63.9	−90.0
	32.1	44.3	5.7	25.4	−7.6	1.1	−29.9	−31.4	−25.9	3.0	9.2		6.7	−54.4	−45.7
SweetGum	−3.2	−4.6	4.2	24.5	32.1	−1.8	−19.8	43.6	−19.2	−0.3	–	–	–	–	–
	−12.4	2.5	16.3	56.6	32.2	10.4	−2.2	106.2	−10.0	26.6	–	–	–	–	–

Section names: *OzarkH* Ozark Highlands, *BostM* Boston Mountains, *ArkaV* Arkansas Valley, *OuchM* Ouchita Mountains, *CTP-OakH* CTP-Oak-hickory, *ILP-ShaH* Interior Low Plateau-Shawnee Hills, *ILP-Blueg* ILP-Bluegrass, *ILP-TraH* ILP-Transition Hills, *ILP-HighRim* Hignland Rim, *SUGAP* Southern Unglaciated Allegheny Plateau, *WGAP* Western Glaciated Allegheny Plateau, *NRV* Northern Ridge and Valley, *AlleghM* Allegheny Mountains, *NCumbM* Northern Cumberland Mountains

harvest preferences) from FIA data based on harvest records from 1995 to 2005.

We simulated succession (including tree growth, mortality, fecundity, dispersal, establishment, and competition) under current climate, PCM B1, and GFDL A1FI modeling scenarios and simulated the same tree harvest in all scenarios. We used the same initial forest conditions for all three modeling scenarios and predicted forest composition shift from 2000 to 2300 using 10-year time steps at 270 m resolution. We ran five replicates for each modeling scenario to capture the variability resulting from stochastic components in the model.

Analysis of simulation results

We calculated importance value (IV) for each tree species as IV = ([individual species density × 100/total species density] + [individual species basal area × 100/total basal area]/2). We calculated IVs for three spatial scales (ecological sections [N = 14], forest sub-region [N = 3], and the CHFR [N = 1]) for all climate modeling scenarios and simulation years 50, 100, and 300 (actual year 2050, 2100, and 2300) to represent the short-, medium-, and long-term changes in forest composition. We summarized change in species IVs under each climate modeling scenario by averaging IVs from the five replicate simulations for each scenario and calculating percent change under PCM B1 and GFDL A1FI modeling scenarios compared to current climate modeling scenario at year 300 for each ecological section and the CHFR.

We determined overall compositional shifts in the forest community by calculating the Bray-Curtis (BC) dissimilarity index (Faith et al. 1987) based on species-level IVs at the three spatial scales (ecological subsection, forest sub-region, and the CHFR) and comparing PCM B1 and GFDL FI modeling scenarios to current climate modeling scenario in the short, medium, and long term. We converted the dissimilarity index to a similarity index by subtracting it from 1. We tested if there was a significant forest compositional shift among the current climate, PCM B1, and GFDL A1FI modeling scenarios at the forest sub-region and the CHFR in the short, medium, and long term using nonparametric multivariate analysis of variance (PerMANOVA). We used the PerMANOVA procedure in the Vegan Community Ecology Package (Oksanen et al. 2009) in the R statistical language and the "adonis" function and a BC distance matrix (R Development Core Team 2006). To further visualize the forest composition shift relative to initial composition, as well as relative to the composition of two future climate modeling scenarios among ecological sections across time, we conducted nonmetric dimensional scaling (NMDS) using BC dissimilarity values for the 14 ecological sections and three time periods. We conducted the ordination using MetaMDs in the Vegan Community Ecology Package (Oksanen et al. 2009) in the R statistical language with two axes determined by a scree plot of stress values.

Results

Climate change effects on the species importance values

Tree species IVs varied greatly among ecological sections under the current climate, PCM B1, and GFDL A1FI modeling scenarios by year 2300 (Table 1). The greatest changes in species IVs were in the Boston Mountains ecological section on the southwest border of the CHFR and adjacent to prairie to the south and west. There was a large increase in red maple (+151.9 %) and decreases in oaks (e.g., white oak, −92.7 %), hickories (e.g., shagbark hickory, −97.7 %), and sugar maple (−84.4 %). The greatest increases in IVs were in the Northern Ridge and Valley ecological section in the mixed mesophytic forest sub-region. Yellow-poplar (+1122.2 %), northern red oak (+400.1 %), red maple (+292.8 %), and pignut hickory (+248.9 %) showed great increases, whereas eastern white pine (−94.8 %), scarlet oak (−98.2 %), and black oak (−65.8 %) showed large decreases. Differences in importance values between current climate modeling scenario and PCM B1 and GFDL A1FI modeling scenarios varied among ecological sections. For example, the IV for white oak was −78.1 % smaller under GFDL A1FI scenario than current climate modeling scenario but 98.2 % greater in the Ozark Highlands and Central Till Plains-Oak Hickory ecological section (Table 1).

Climate change effects on the forest composition shifts at multiple scales

There were no significant changes in overall species composition among current climate, PCM B1, and

GFDL A1FI modeling scenarios based on perMANOVA tests for the region and subregion in the short term ($P > 0.4$) but changes were significant ($P < 0.05$) for the CHFR and all but one sub-region in the medium and long term (Table 2). Forest composition at the regional scale was similar to current climate modeling scenario under PCM B1 scenario in the short medium and long term with similarity values >0.9 (Fig. 2a); however, under GFDL A1FI scenario similarity was reduced to 0.65 by the long term (Fig. 3a). There was less similarity of forest composition of both PCM B1 and GFDL A1FI scenarios with current climate at the sub-regional scale but similarity was generally less for GFDL A1FI scenario (Fig. 2b–d). The greatest species composition shift occurred in the oak-hickory forest sub-region under the GFDL A1FI scenario (Fig. 3b, similarity value = 0.45), followed by the western mesophytic forest sub-region (Fig. 3c, similarity value = 0.50), and the mixed mesophytic forest sub-region (Fig. 2d, similarity value = 0.6). At the ecological subsection scale, forest composition under the PCM B1 scenario was generally similar to that under current climate modeling scenario (Fig. 3a). Subsections with lower similarity under PCM B1 scenario were mostly in the southern portion of the CHFR including the East Central Ouachita Mountains, White River Hills, and Outer Bluegrass subsections and subsections at higher (or lower) elevations such as northern Ridge and Valley (Fig. 3a). However, similarities were substantially lower under GFDL A1FI scenario. Similarities were generally lower in most subsections in the oak-hickory forest and western mesophytic forest sub-region than in subsections in the mixed mesophytic forest sub-region (Fig. 3b).

The NMDS analysis provided additional insight into variation in forest composition as represented by tree species IVs among ecological sections, forest sub-regions, and climate modeling scenarios. The first axis in the ordination primarily reflected a precipitation gradient. Ecological sections within their respective forest sub-regions were ordinated along a gradient of increasing precipitation from oak-hickory forests to mixed-mesophytic forests, which also mimicked their geographic distribution (Fig. 4a). Also within subsections and within the region scenarios tended to be ordinated from the driest (GFDL A1FI in 2300) to wettest (Current climate in 2000 or 2300). The change of tree species IVs among scenarios for the region as a whole was much less than the change within individual subsections within a sub region as indicted by the spread of points on both axes (Fig. 4a). The comparison of PCM B1 and GFDL A1FI scenarios in 2300 to current climate modeling scenarios revealed that forest composition shifted toward being more xeric; this was especially evident for ecological sections within oak-hickory forest sub-regions as shown by their wide spread across axis one (Fig. 4a). The distribution of tree species in ordination space provided insight into what the changes in subsections and the region meant in terms of changes in the importance of individual species (Fig. 4b). Mesic tree species including red spruce, eastern hemlock, eastern white pine, sugar maple, and American beech had higher scores on axis one whereas xeric tree species including post oak, southern red oak, shortleaf pine, loblolly pine, eastern redcedar, sweetgum, and shagbark hickory had lower scores (Fig. 4b).

The second axis in the ordination was primarily associated with temperature; ordination scores under PCM B1 and GFDL A1FI modeling scenarios were higher than those under the current climate modeling scenario (Fig. 4a). Tree species IVs shifted towards southern species under PCM B1 and GFDL A1FI

Table 2 Nonparametric MANOVA permutation tests for the hypothesis of no change in species composition among current climate, PCM B1, and GFDL A1FI climate modeling scenarios for the Central Harwood Forest Region and three forest sub-regions at year 2050, 2100, and 2300

	Year 2050		Year 2100		Year 2300	
	F. model	p	F. model	p	F. model	p
Central Hardwood Forest Region	0.005	0.511	0.154	0.041	3.232	0.015
Oak-hickory forest sub-region	0.009	0.441	0.256	0.031	5.715	0.033
Western mesophytic forest sub-region	0.001	0.676	0.133	0.047	3.429	0.011
Mixed mesophytic forest sub-region	0.091	0.583	0.176	0.231	0.718	0.044

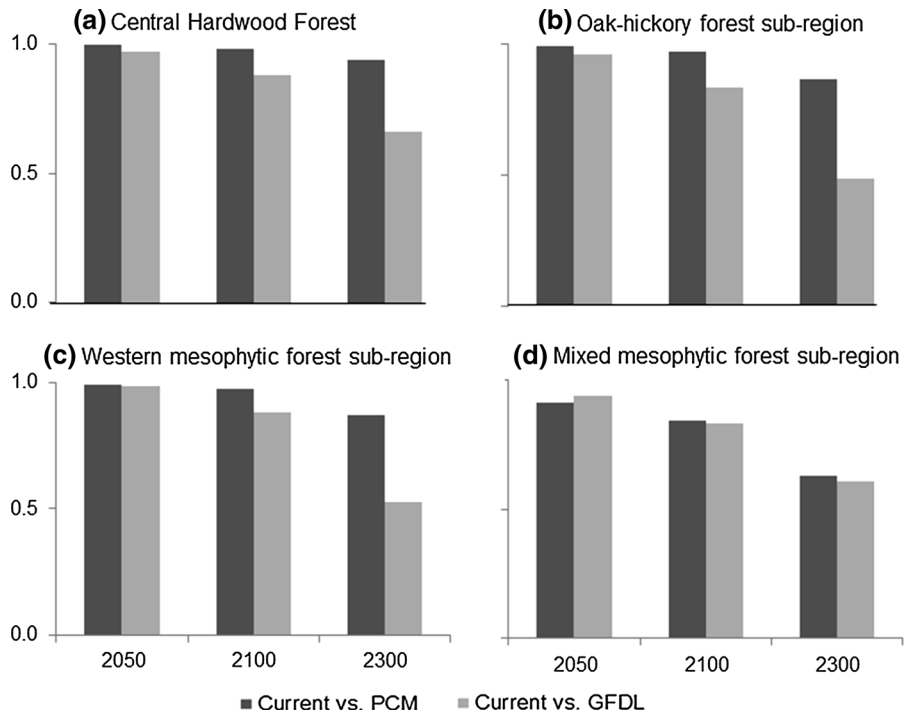

Fig. 2 The similarity (1-Bray–Curtis dissimilarity) between the forest composition from current climate modeling scenario versus PCM B1 (**a**) and GFDL A1FI (**b**) for Central Hardwood Forest Region (CHFR) (**a**), oak-hickory forest sub-region (**b**), west mesophytic forest sub-region (**c**), and mixed mesophytic forest sub-region (**d**) at year 2050, 2100, and 2300

warming scenarios. Thus, southern tree species including loblolly pine, southern red oak, mockernut hickory, post oak, and yellow-poplar had relatively higher scores on the second-axis whereas northern tree species including sugar maple, pignut hickory, black cherry, American beech, and white ash had lower scores on the second axis (Fig. 4b). Furthermore, the second axis also reflected forest succession and harvest, because the ordination under current climate modeling scenario at year 2300 generally had higher scores than those at the initial year 2000 (Fig. 4a). This represented the increases in IVs for species that could benefit from both late-succession and forest harvest such as northern red oak, white oak, black oak, black cherry, yellow poplar, red maple, and loblolly pine (Fig. 4b).

Discussion

Forest composition shifts under climate change

There was a hierarchy of spatial scales in forest responses to climate change. The forest composition shifts were greatest among ecological sections followed by forest sub-regions and whole CHFR, because variations were decreased when scaling up from 14 ecological sections, to three forest sub-regions, and one whole CHFR. The western forest sub-regions (oak-hickory forest and western mesophytic forest) generally experienced greater forest composition shifts than the eastern sub-region (mixed mesophytic forests) under the GFDL A1FI warming scenario. There were greater shifts in forest composition under the GFDL A1FI than PCM B1 scenarios in the western sub-regions, whereas shifts in forest composition were similar between the climate scenarios in the mixed mesophytic forest sub-region. We suggest that western oak-hickory sub-region was more vulnerable to climate change than the eastern mixed mesophytic forest sub-region.

While the shift in forest composition could be low for a sub-region, composition shift could still be high for some subsections within the sub-region that effectively acted as refugia (e.g., Muscatatuch flats and valleys and Crawford uplands in western mesophytic forest region). This was because besides climatic controls at the regional and sub-region scale, nutrient and water conditions encapsulated by soil and landform at intermediate landtype scale within a subsection were unique and could lead to different species responses from those under similar climate but

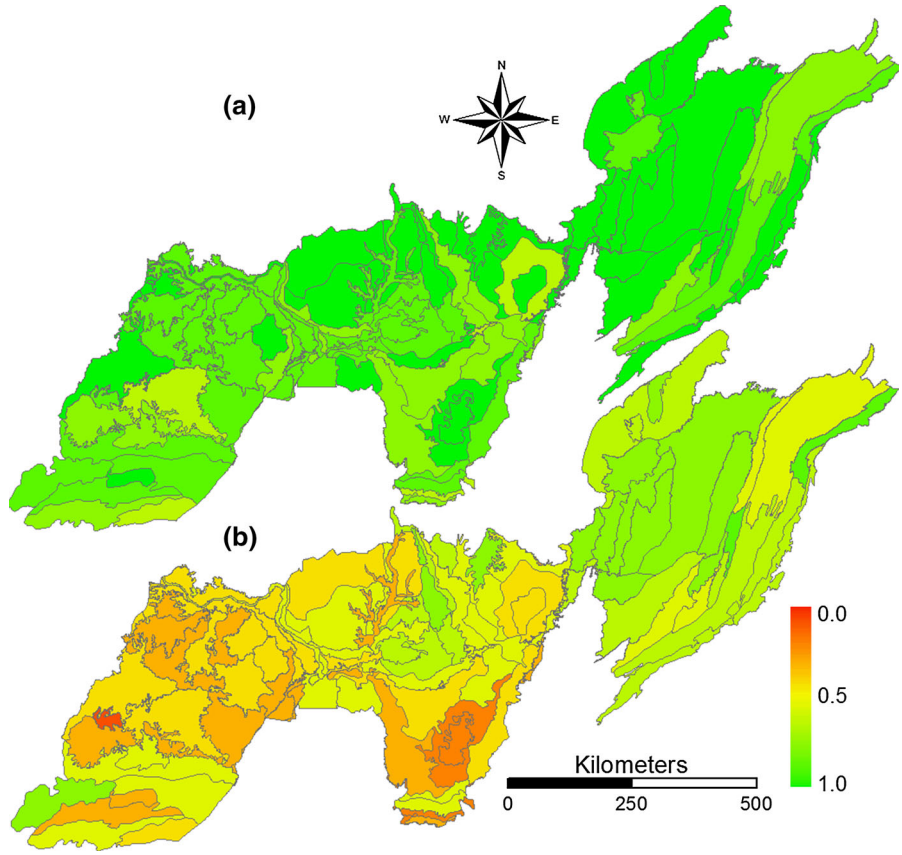

Fig. 3 The similarity (1-Bray–Curtis dissimilarity) between the forest composition from current climate modeling scenario versus PCM B1 (**a**) and GFDL A1FI (**b**) for each ecological subsection at year 2300 in the Central Hardwood Forest Region (CHFR), U.S.A

with different soils and landforms. We suggest this is important to include the intermediate-scale factors and controls in regional scale modeling.

We showed that it will take a long time (i.e. 300 years) for substantial shifts in forest composition to occur in response to climate change. The long time frame for effects of climate change and the overwhelming importance of population dynamics 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 (Churchill et al. 2013; Kerhoulas et al. 2013). For example, oak decline is a wide-spread problem and potentially more an 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; for example, planting southern species such as loblolly pine, whose seed sources are currently limited in the CHFR, might facilitate forest adaptation to a warming climate (Brandt et al. 2014).

Tree species importance value under climate change

We showed that forest composition shifts at section level may be similar (toward the same direction) under PCMB1 and GFDL A1FI modeling scenarios. However, the responses of individual tree species varied greatly resulting from complex interactions between climate, soil, species biological traits, competition, and harvest. For example, the general reduction of oak species' IVs in many ecological sections may be related to harvest as harvest was simulated in all scenarios and oaks were the most harvested species in the region according to FIA (Woudenberg et al. 2010). Harvest may facilitate response to climate change by accelerating species turnover. We showed that the changes in tree species

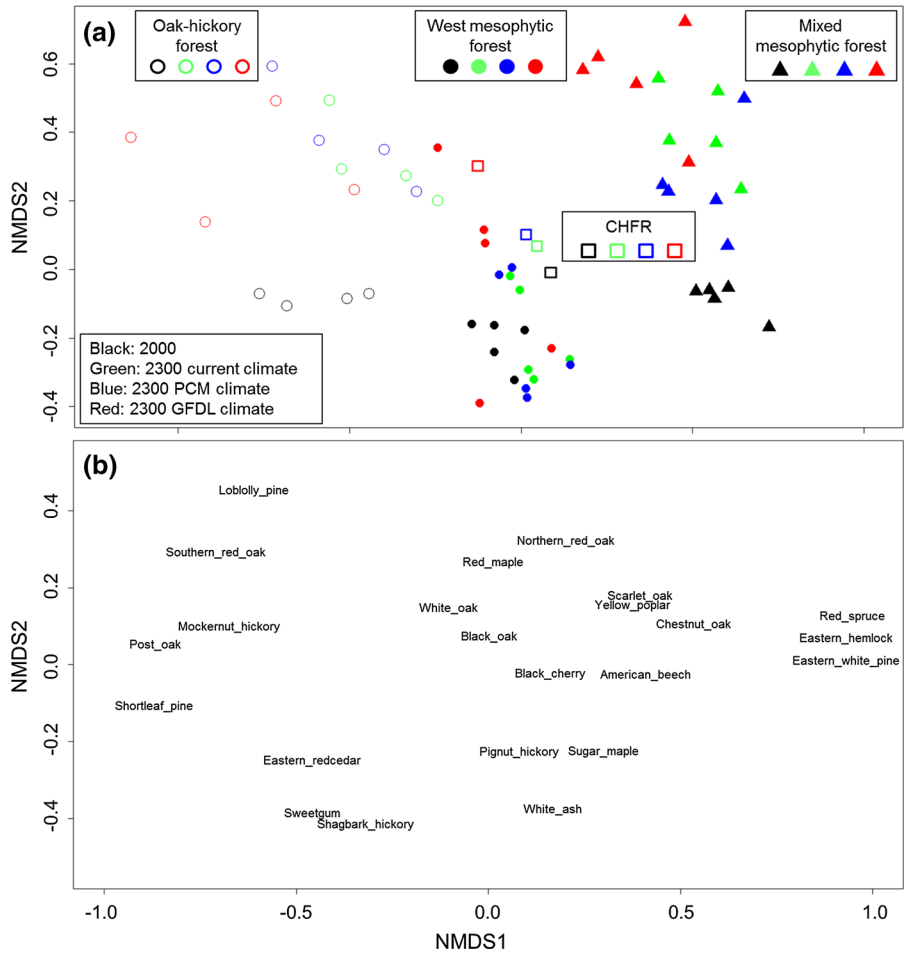

Fig. 4 Nonmetric multidimensional scaling ordination showing **a** ecological sections and **b** 23 tree species in ordination space indicating forest composition shifts among three climate modeling scenarios through time (2000–2300). Final ordination included two axes; stress = 0.107. Each point in the ordination represents one ecological section at one date; data for each section include tree species importance value

IVs in many ecological sections had similar trends under both PCM B1 and GFDL A1FI modeling scenarios, but the degree of changes in IVs varied greatly. For example, in the Northern Ridge and Valley ecological section, the increase of IVs for yellow-poplar was from 707.0 % under PCM B1 scenario to 1122.2 % under GFDL A1FI scenario. Northern red oak was the only oak species gaining IV whereas other oak species lost IV under both climate warming scenarios in this ecological section. Northern red oak is a northern species compared to other oak species (Little 1971). Because the novel warming climate was close to optimum growth temperature for northern red oak, thus its growth rate was maximized under climate change. Northern red oak was also a stronger competitor than other oak species that were outcompeted by warming climate-favored species such as yellow-poplar and red maple in the novel habitats. This result reinforced that biotic interactions occurring at pixel-scale affected forest compositions at broad spatial scales (revealed here at the ecological section scale) (Araújo and Luoto 2007; Pigot and Tobias 2013).

In many cases, tree species showed opposite responses under PCM B1 and GFDL A1FI scenarios. For example, sugar maple was generally a declining species under warming climate. However, with moderate temperature increase in PCM B1 scenario and increase in precipitation, it showed an increase in IV in some ecological sections. However, sugar maple had substantial decreases in IV under warmer and dryer conditions in the GFDL A1FI scenario. We suggest that consideration of seasonal temperature and precipitation patterns along with species' biological traits in assessing forest composition shift under warming climate was important (Webb et al. 2010).

Caveats and limitations

Several factors not included in our study may contribute to uncertainty in our predictions. We assumed that forest area in the region would not change. However, land use change, primarily urban growth in the CHFR may result in less forested area, fragmented forest, and barriers to dispersal (Kubisch et al. 2011). Fire, insect, and disease outbreaks may increase under climate change and significantly affect forest composition (Weed et al. 2013). We assumed that the primary effects of climate change could be represented by daily temperature and precipitation effects on growing season length, drought, and tree species establishment and early growth. We did not consider nitrogen deposition and CO_2 fertilization.

Conclusions

We presented a landscape modeling approach to project forest composition for the CHFR at multiple levels of a spatial and ecological hierarchy. Changes in tree species density, basal area, and IV at each pixel resulted from the interactions of population dynamics at pixel level, dispersal and harvest at landscape scale, soil water and nutrient variation at the intermediate landtype scale, and regional climate patterns downscaled to a subsection scale. Our approach allowed us to account for population and landscape level processes at the level of a pixel (270 m) that are not usually accounted for in regional simulations of species distributions by niche and biophysical process models. We believe our approach resulted in more realistic projections of changes in species IV at the scale of subsections, sections, sub-regions, and regions.

The magnitude of shifts in forest composition were greatest under the most extreme climate warming scenario. Shifts in forest composition were greatest at the scale of ecological sections followed by forest subregions and the whole CHFR. Forest composition shift under climate change was small in the short term but large in the medium and long term. We suggest it is essential to include site- and landscape-scale processes in models and to evaluate changes at multiple spatial and temporal scales when evaluating changes in species composition due to climate change and disturbance.

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References

Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, Delucia EH (2013) Altered dynamics of forest recovery under a changing climate. Glob Chang Biol 19:2001–2021

Araújo MB, Luoto M (2007) The importance of biotic interactions for modeling species distributions under climate change. Glob Ecol Biogeogr 16:743–753

Araújo MB, Rahbek C (2006) How does climate change affect biodiversity. Science 313(5792):1396–1397

Bachelet D, Lenihan J, Drapek R, Neilson RP (2008) VEMAP versus VINCERA: a DGVM sensitivity to differences in climate scenarios. Glob Planet Chang 64:38–48

Bohlman S, Pacala S (2012) A forest structure model that determines crown layers and partitions growth and mortality rates for landscape-scale applications of tropical forests. J Ecol 100:508–518

Brandt L, He HS, Iverson LR, Thompson FR, Butler P, Handler S, Janowiak M, Shannon DP, Swanston C, Tirpak J, Walk J, Wang W, Watts L, Weigel D, Westin S (2014) Central hardwoods ecosystem vulnerability assessment and synthesis: a report from the central hardwoods climate change response framework project. General Technical. Reports. NRS-124. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, p 254

Braun EL (1950) Deciduous forests of Eastern North America. Philadelphia: Blakiston

Burns RM, Honkala BH (tech. Coords.) (1990) Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654, USDA Forest Service, Washington, D.C., USA

Butler PR, Iverson L, Thompson FR, Brandt L, Handler S, Janowiak M, Shannon PD, Swanston C, Karriker K, Bartig J, Connolly S, Dijak W, Bearer S, Blatt S, Brandon A, Byers E, Coon C, Culbreth T, Daly J, Dorsey W, Ede D, Euler C, Gillies N, Hix DM, Johnson C, Lyte L, Matthews S, McCarthy D, Minney D, Murphy D, O'Dea C, Orwan R, Peters M, Prasad A, Randall C, Reed J, Sandeno C, Schuler T, Sneddon L, Stanley B, Steele A, Stout S, Swaty R, Teets J, Tomon T, Vanderhorst J, Whatley J, Zegre N (2015) Central Appalachians forest ecosystem vulnerability assessment and synthesis: a report from the central Appalachians climate change response framework project. General Technical. Reports. NRS-146. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, p 310

Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter C, McNab WH (2007) Ecological subregions: sections and subsections of the conterminous United States [1:3,500,000] [CD-ROM]. In: Sloan AM (ed), Cartography General Technical Report WO-76. Washington, DC: U.S. Department of Agriculture, Forest Service

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends Ecol Evol 28:482–488

Dijak W (2013) Landscape builder: software for the creation of initial landscapes for LANDIS from FIA data. Comput Ecol Softw 3(2):17–25

Doxford SW, Freckleton RP (2012) Changes in the large-scale distribution of plants: extinction, colonization and the effects of climate. J Ecol 100:519–529

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Plant Ecol 69:57–68

Fraser JS, He HS, Shifley SR, Wang WJ, Thompson FR (2013) Simulating stand-level harvest prescriptions across landscapes: LANDIS PRO harvest module design. Can J Forest Res 43:972–978

Gritti ES, Duputié A, Massol F, Chuine I (2013) Estimating consensus and associated uncertainty between inherently different species distribution models. Methods Ecol Evol 4:442–452

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

He HS (2008) Forest landscape models, definition, characterization, and classification. For Ecol Manag 254:484–498

He HS, Mladenoff DJ (1999) Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. Ecology 80:81–99

He HS, Mladenoff DJ, Crow TR (1999) Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol Model 114:213–233

He HS, Yang J, Shifley SR, Thompson FR (2011) Challenges of forest landscape modeling—simulating large landscapes and validating results. Landsc Urban Plan 100(4):400–402

IPCC (2007) The Physical Science Basis. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL). Cambridge University

Iverson LR, Prasad AM, Matthews SN, Peters M (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For Ecol Manag 254:390–406

Iverson LR, Prasad AM, Matthews SN, Peters MP (2011) Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. Ecosystems 14:1005–1020

Johnson PS, Shifley SR, Rogers R (2009) The ecology and silviculture of Oaks, 2nd edn. CAB International, Oxfordshire

Kerhoulas LP, Kolb TE, Hurteau MD, Koch GW (2013) Managing climate change adaptation in forests: a case study from the U.S. Southwest. J Appl Ecol 50:1311–1320

Kubisch A, Poethke HJ, Hovestadt T (2011) Density-dependent dispersal and the formation of range borders. Ecography 34:1002–1008

Liang Y, He HS, Wang WJ, Fraser JS, Wu Z, Xu J (2015) The site-scale processes affect species distribution predictions of forest landscape models. Ecol Model 300:89–101

Little EL Jr (1971) Atlas of United States trees, volume 1, conifers and important hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1146, p 9, 200 maps

Luo X, He HS, Liang Y, Wang WJ, Wu Z, Fraser JS (2014) Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China. Landscape Ecol 29:1187–1200

McMahon SM, Harrison SP, Armbruster WS (2011) Improving assessment and modeling of climate change impacts on global terrestrial biodiversity. Trends Ecol Evol 26(5): 249–259

McNab WH, Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA (2007). Description of "ecological subregions: section of the conterminous United States". USDA Forest Service General Technical Report WO-76B, pp 1–57

Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2. J Geophys Res 114:G01002. doi:10.1029/2008JG000812

Missouri Climate Center (2010) College of Agriculture, Food and Natural Resources, University of Missouri. http://climate.missouri.edu/news/arc/sep2009.php, http://climate.missouri.edu/news/arc/apr2010.php. Accessed 10 Jun 2010

Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90(5):1301–1313

Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. J Ecol 96(4):784–794

National Oceanic and Atmospheric Administration-National Climatic Data Center (NOAA-NCDC) (2011). http://www7.ncdc.noaa.gov/. Accessed 1 July 2011

Neilson RP, Pitelka LF, Solomon AM, Nathan R, Midgley GF, Fragoso JMV, Lischke H, Thompson K (2005) Forecasting regional to global plant migration in response to climate change. Bioscience 55(9):749–759

Normand S, Zimmermann NE, Schur FM, Lischke H (2014) Demography as the basis for understanding and predicting range dynamics. Ecography 37:1149–1154

Oksanen JR, Kindt P, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2009) Vegan: community ecology package. R package version 1.15-4. http://CRAN.R-project.org/package=vegan

O'Neill RV, DeAngelis D, Waide J, Allen TFH (1986) A hierarchical concept of ecosystems. Princeton University Press, Princeton

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Pederson N, D'Amato AW, Dyer JM, Foster DR, Goldblum D, Hart JL, Hessl AE, Iverson LR, Jackson ST, Martin-Benito D, McCarthy BC, McEwan RW, Mladenoff DJ, Parker AJ, Shuman B, Williams JW (2014) Climate remains an important driver of post-European vegetation change in the eastern United States. Glob Chang Biol 21:2105–2110

Pigot AL, Tobias AT (2013) Species interactions constrain geographic range expansion over evolutionary time. Ecol Lett 16:330–338

Purves D, Pacala S (2008) Predictive models of forest dynamics. Science 320:1452–1453

R Development Core Team (2006) R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Reich RB, Frelich L (2001) Temperate deciduous forests. Encyclopaedia of global environmental change, vol 2. Wiley, Chichester, pp 565–569

Schumacher S, Bugmann H (2006) The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Glob Chang Biol 12:1435–1450

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Database for Missouri. http://soils.usda.gov/. Accessed 1 Jun 2013

Stoner AMK, Hayhoe K, Yang X (2011) Downscaled climate projections by Katharine Hayhoe. http://cida.usgs.gov/climate/hayhoe_projections.jsp. Accessed 1 Nov 2011

Thompson JR, Foster DR, Scheller RM, Kittredge D (2011) The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. Ecol Appl 21(7):2425–2444

Thornton PE, Thornton MM, Mayer BW, Wilhelmi N, Wei Y, Cook RB (2012) Daymet: Daily surface weather on a 1 km grid for North America, 1980–2012. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A. http://daymet.ornl.gov/. Accessed 1 July 2011

Thuiller W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental range of data to project current and future species distributions. Ecography 27:165–172

Thuiller W, Albert CH, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE (2008) Predicting global change impacts on plant species distributions: future challenges. Perspect Plant Ecol Evol Syst 9:137–152

Vanderwel MC, Purves DW (2014) How do disturbances and environmental heterogeneity affect the pace of forest distribution shifts under climate change? Ecography 37:10–20

Wang WJ, He HS, Spetich MA, Shifley SR, Thompson FR III, Fraser JS (2013a) Modeling the effects of harvest alternatives on mitigating oak decline in a Central Hardwood Forest landscape. PLoS One 8(6):e66713. doi:10.1371/journal.pone.0066713

Wang WJ, He HS, Spetich MA, Shifley SR, Thompson FR III, Larsen DR, Fraser JS, Yang J (2013b) A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. Ecosphere 4(9):106. doi:10.1890/ES13-00040.1

Wang WJ, He HS, Fraser JS, Thompson FR III, Shifley SR, Spetich MA (2014a) LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. Ecography 37:225–229

Wang WJ, He HS, Spetich MA, Shifley SR, Thompson FR (2014b) Evaluating forest landscape model predictions using empirical data and knowledge. Environ Model Softw 62:230–239

Wang WJ, He HS, Thompson III FR, Fraser JS, BB Hanberry, WD Dijak (2015) The importance of succession, harvest, and climate change in determining future forest composition changes in U.S. Central Hardwood Forests. Ecosphere (in press)

Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL 2010. The Forest Inventory and Analysis Database: Database Description and Users Manual Version 4.0 for Phase 2. General Technical Reports RMRS-GTR-245. Fort Collins, CO: United States Department of Agriculture Forest Service, Rocky Mountain Research Station. 336 p

Wullschleger SD, Gunderson CA, Tharp ML, West DC, Post WM (2003) Simulated patterns of forest succession and productivity as a consequence of altered precipitation. In: Hanson PJ, Wullschleger SD (eds) North American temperate deciduous forest responses to changing precipitation regimes. Springer, New York, pp 433–446