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RESEARCH ARTICLE

Changes in forest biomass and tree species distribution under climate change in the northeastern United States

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Abstract
Context Forests in the northeastern United States are currently in early- and mid-successional stages recovering from historical land use. Climate change will affect forest distribution and structure and have important implications for biodiversity, carbon dynamics, and human well-being.
Objective We addressed how aboveground biomass (AGB) and tree species distribution changed under multiple climate change scenarios (PCM B1, CGCM A2, and GFDL A1FI) in northeastern forests.
Methods We used the LANDIS PRO forest landscape model to simulate forest succession and tree harvest under current climate and three climate change scenarios from 2000 to 2300. We analyzed the effects of climate change on AGB and tree species distribution.
Results AGB increased from 2000 to 2120 irrespective of climate scenario, followed by slight decline, but then increased again to 2300. AGB averaged 10 % greater in the CGCM A2 and GFDL A1FI scenarios than the PCM B1 and current climate scenarios. Climate change effects on tree species distribution were not evident from 2000 to 2100 but by 2300 some northern hardwood and conifer species decreased in occurrence and some central hardwood and southern tree species increased in occurrence.
Conclusions Climate change had positive effects on forest biomass under the two climate scenarios with greatest warming but the patterns in AGB over time were similar among climate scenarios because succession was the primary driver of AGB dynamics. Our approach, which simulated stand dynamics and dispersal, demonstrated that a northward shift in tree species distributions may take 300 or more years.

Keywords Demography · Disturbance · Dispersal · Forest landscape model · LANDIS PRO · LINKAGE II · Occurrence

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Introduction

Most forests are affected by natural and anthropogenic processes operating at different scales. Climate change is projected to alter the distribution, composition, and

function of forests at regional scales (e.g., Thuiller et al. 2004). Seed dispersal and disturbances (e.g., fire, harvest) affect forest changes at landscape scales (Dale et al. 2001; Neilson et al. 2005; Weed et al. 2013; Wang et al. 2015). Biotic processes such as demography and competition interact with regional- and landscape-scale processes (Normand et al. 2014) to affect forest composition and structure at site scales. Thus, predictions of future forest changes should account for these multi-scaled processes and their interactions (McMahon et al. 2011).

The northeastern United States is the most densely forested, populated, and economically developed region in the United States and provides important services (e.g., biodiversity, biomass, timber products, and carbon storage) to society (Shifley et al. 2014). Climate change could have profound effects on productivity, mortality, and colonization in northeastern forests, which could have important implications for services these forests provide (e.g., Perschel et al. 2007; Mohan et al. 2009; Brandt et al. 2014; Duveneck et al. 2016; Iverson et al. 2016). Researchers have investigated changes in northeastern forests under climate change using empirical data from flux towers (e.g., Turner et al. 2013) and inventories (e.g., McGarvey et al. 2015), niche models (e.g., Frumhoff et al. 2007; Iverson et al. 2008), and process models (e.g., Albani et al. 2006; Vanderwel and Purves 2014; Bachelet et al. 2015). Predictions by niche models suggest that under warmer temperature and more variable precipitation regimes, habitats for spruce-fir forests and northern hardwood forests would substantially diminish and could be replaced by habitats that are more suitable for oak-hickory forests at end of this century (e.g., Iverson et al. 2008). Empirical data and process models suggest northeastern forests will continue to sequester biomass (carbon) in the coming decades as they recover from historical land use (e.g., Pan et al. 2011; Thompson et al. 2011). However, these studies usually ignore or simplify site-scale processes (e.g., demography, competition) or landscape-scale processes (e.g., dispersal, disturbance) (Neilson et al. 2005; Purves and Pacala 2008; Iverson et al. 2011). Thus, it remains highly uncertain how tree species distribution and biomass will change spatially and temporally in northeastern forests.

Northeastern forests are in early- to mid-successional stages recovering from historical land use (Thompson et al. 2013). The region has a unimodal age distribution and nearly 80 % of the forest is 40–80 years old (MacCleery 2011). Many trees will reach their life-span in the next century and mortality could potentially decrease aboveground biomass. This mortality, however, will release growing space for new seedlings and their growth will contribute to an accumulation of biomass again. These demographic processes (growth, birth, death) provide inertia in the ability of tree species to respond to climate change (Doxford and Freckleton 2012). Windthrow is a common natural disturbance in this region while mortality from fire, insects, and disease is less common. Tree harvest, primarily in the form of partial harvest on private lands, is the major anthropogenic disturbance (Canham et al. 2013). Harvest affects forest responses to climate change through altering species composition, age structure, and regeneration dynamics (Dale 2001; Vanderwel and Purves 2014; Wang et al. 2016). Harvest can have even greater effects on forest change than direct effects of climate change (Wang et al. 2015). Therefore, tree growth, aging, and regeneration will interact with succession, harvest, and climate change to affect tree species distribution and biomass in northeastern forests.

We used a forest landscape modeling approach to predict changes in forest biomass and distribution under climate change with harvest and windthrow disturbances in the northeastern United States. Forest landscape models can simulate site- and landscape-scale processes and have been used to predict forest changes under climate change at landscape and regional scales (e.g., Gustafson et al. 2010; Thompson et al. 2011; Luo et al. 2014; Liang et al. 2015; Duveneck et al. 2016; Wang et al. 2016; Xiao et al. in press). We used the LANDIS PRO forest landscape model to simulate population and community dynamics driven by current forest structure, succession, disturbances, and abiotic controls by soil, terrain, and climate at a spatial resolution of 270 m (Wang et al. 2013a, 2014a). We used millions of individual tree records in the U.S. Forest Service Forest Inventory and Analysis database (FIA data, Woudenberg et al. 2010) to explicitly parameterize the model (Wang et al. 2014b). Our objectives were to address how aboveground forest biomass and tree species distribution will spatially and temporally change under alternative climate scenarios with current harvest levels and windthrow. We hypothesized that succession would explain the most variation in AGB and species distribution but that climate would explain significant

variation in the distribution of some species by 2300. We hypothesized that some northern conifer and hardwood species would show the greatest declines in occurrence in response to climate change in the region based on their current distributions and results from niche models (Iverson et al. 2008).

Methods

Study area

Our study area was forests in the northeastern United States and covered 42 million ha from northern Pennsylvania and New Jersey northward to Maine (Fig. 1). The area includes 20 ecological sections and 82 subsections and represents a diversity of vegetation, geography, and climate (Cleland et al. 2007). This region is highly forested and 70 % of forests are privately owned. Spruce/fir forests dominate the most northern part of region, northern hardwood forests dominate the area from Pennsylvania to central Maine, and oak-hickory and oak-pine forests dominate the southern part of the region (Cleland et al. 2007). Most of the area is in the Appalachian Highlands physiographic division and has rolling hills to summits greater than 1500 m. The Atlantic coastal plains range from flat to moderately dissected irregular plains. The area has highly variable climates that are affected by the Atlantic Ocean in coastal areas, Great Lakes in the inland regions, and Appalachian Mountains in the southern region. There is a strong seasonal cycle with warm and humid summers and cold winters punctuated by heavy snow and ice. Average mean temperature ranges from 3 to 10 °C and average mean precipitation ranges from 79 to 255 cm (McNab et al. 2007).

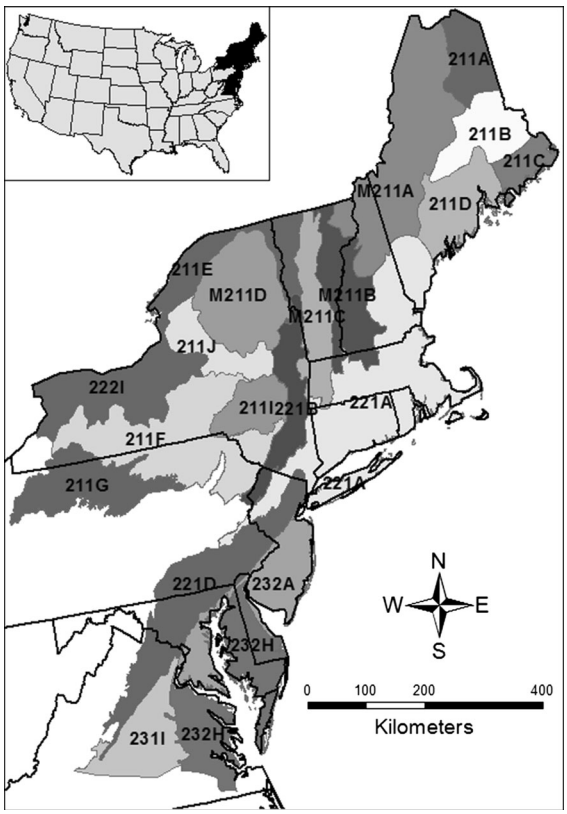

Fig. 1 The study area was located in the northeastern United States from northern Pennsylvania and New Jersey northward to Maine and covered 20 ecological sections

Climate

We considered current climate and three climate change scenarios that paired a general circulation model with an emission scenario: PCM B1, CGCM A2, and GFDL A1FI. The B1, A2, and A1FI scenarios represent the lowest, intermediate, and highest fossil fuel emissions and the PCM, CGCM, and GFDL models predict the lowest, intermediate, and highest increases in temperature in the region, respectively (IPCC 2007). Thus, by simulating these climate scenarios we were able to incorporate a range of uncertainty in future climate projections for the region. We used daily maximum and minimum temperature, precipitation, solar radiation, and day length at 1 km resolution (DAYMET, Thornton et al. 2012) for the period 1980–2009 for our current climate scenario. We obtained down-scaled climate change data for three climate change scenarios for the period 2070–2099 from the U. S. Geological Survey Center for Integrated Data Analysis Geo Data Portal (Stoner et al. 2011). We selected a point in each ecological subsection that represented the median climate values under current climate and intersected these points with the downscaled climate change projections to associate climate change projections with each subsection.

LINKAGES II and LANDIS PRO model parameterization

We used LINKAGES II (Wullschleger et al. 2003; Dijak et al. in press) to estimate species establishment

and maximum biomass under each climate scenario, which were used to derive species establishment probabilities (SEP) and maximum growing space (MGSO) parameters for LANDSI PRO. We modeled the 24 most abundant tree species based on the basal area in the FIA data for the study area (Online Appendix Table 1). We captured abiotic controls in soil, terrain, climate, and vegetation by stratifying the whole region into 656 landtypes by intersecting 82 ecological subsections and 8 landforms derived from a digital elevation model (Dijak 2013). We assumed resource availability (measured as MGSO) and species colonization (measured as SEP) were uniform within a landtype and different among landtypes. We obtained soil parameters including organic matter, nitrogen, wilting point, field moisture capacity, percent clay, sand and rock for each landtype from Natural Resources Conservation Service Soil Survey (2012). We ran LINKAGES II with the soil data for each landtype and daily climate data for current climate (1980–2009) and the three climate projections for 2100 (2070–2099) to predict individual species biomass after 30 years from bare ground and maximum biomass of mixed species plots over 300 years. We derived SEP and MGSO for LANDIS PRO from these LINKAGES II predictions (He et al. 1999; Wang et al. 2015, Online Appendix Tables 4, 5). These SEP and MGSO values reflected the overall effects of daily climate over a 30 year period for current climate or climate projections at the end of the century.

We used the LANDIS PRO succession module to simulate tree growth, aging, fecundity, dispersal, resprouting, establishment, and competition (He et al. 2012; Wang et al. 2013a, 2014a). We derived the biological traits for each species from previous studies and literature (Online Appendix Table 1, Burns and Honkala 1990; Wang et al. 2013a, b, 2014b, 2015). We derived the initial forest conditions including absence/presence, number of trees, and diameter at breast height (DBH) by age cohort for 24 tree species on each raster cell for year 2000 from 1995 to 2005 FIA data including trees $\geq$2.54 cm using Landscape Builder, which stochastically assigned a representative FIA plot to each cell based on FIA unit, landform, land cover, and stand size class (Dijak 2013; Wang et al. 2014b). By incorporating decadal values for SEP and MGSO derived from daily simulation of climate in LINKAGES II, we captured the average responses of species to changing climate in terms of establishment and early growth and MGSO or carrying capacity on a landtype. As a result, warmer or drier climates could reduce species establishment and result in higher mortality due to greater competition resulting from a lower MGSO; however, LANDIS PRO did not directly simulate climate effects such as direct morality from drought.

Calibration and evaluation

We insured that the initial forest conditions in LANDIS PRO were similar to the observed conditions by adjusting dbh-age relationships by site quality in Landscape Builder until the initial conditions matched the observed FIA data in terms of age structure, basal area, and density for ecological sections (Online Appendix Tables 2, 3). We calibrated model parameters (e.g., growth rates, number of potential germination seeds) and evaluated simulation results for species composition, stand development, and successional trajectories at stand and regional scales under current climate conditions using FIA data and old-growth studies from the region using the approach described by Wang et al. (2014b).

Harvest and windthrow

We included harvest and wind disturbances in all scenarios at levels that approximated the current level of these events in the region. We parameterized harvest by management units in the LANDIS PRO Harvest module (Fraser et al. 2013). Management units represented private industrial, non-industrial forest lands, and public forest lands by FIA units and thus captured the regional-scale variation in harvest regimes (Canham et al. 2013). We simulated two levels of partial harvest in each management unit using thinning from above that left 35 or 85 m^2/ha residual basal area. We varied the percent of the unit harvested and the preferred species for harvest to result in removals similar to those reported in the harvest information in 1995–2005 FIA data. Harvest in any unit was equally split between the two levels of partial harvest and the percent area treated per decade varied from 10 % in some FIA Units in Maine, 8 % in Maryland, 7 % in Vermont and New York, 6 % in Pennsylvania and Maryland, to a low of 0.4 % in Rhode Island. Stands within a management unit were selected for harvest based on a basal area ranking algorithm. We stochastically simulated a background

level of windthrow disturbance that removed the oldest age cohort on 2–4 % of pixels per decade. We acknowledge that our harvest and windthrow parameters were simplified approximations of actual events but they did capture the volume of timber removed in the region and our goal was to include these disturbances to the best of our ability with available data to make model results more useful than models that do not include these events.

Experimental design and data analysis

We designed a one-factor simulation experiment with four levels of climate (current, PCM B1, CGCM A2, and GFDL A1FI). We predicted forest changes from 2000 to 2300 using a 10 year time step with three replicates for each climate scenario to capture stochastic variation (Murphy and Myors 2003). The values of SEP and MGSO changed each decade for the three climate change scenarios from 2000 to 2100 but were held constant from 2100 to 2300 because the climate projections only extended to 2100. We recognize the high degree of uncertainty around 300 year projections. However, we thought it was important to demonstrate the effects of an additional 200 years of stand dynamics in response to the climate change that occurred through 2100 because species turnover can take a long time (Wang et al. 2015).

We summarized the differences in AGB and tree species distribution among scenarios at year 2050, 2100, and 2300 to represent short-, medium-, and long-term responses, respectively. We reported results from one replicate simulation for each scenario because of extremely small variation among replicates (Thompson et al. 2011; Wang et al. 2015). We reported the region-wide average AGB under each climate scenario over 300 simulation years. We calculated species occurrence as the percentage of the total forested cells in which a species was present. We summarized the percent changes in species occurrences for the entire region between the initial occurrence in year 2000 and year 2050, 2100, and 2300. We characterized changes as expansion or contraction if species occurrences increased or decreased, respectively, at year 2050, 2100, and 2300. To capture the spatial variation in AGB and species distribution, we calculated and mapped the percent changes in AGB for each ecological section under three climate change scenarios compared to current climate scenario at year 2050, 2100, and 2300. We also mapped extinction, colonization, and persistence rates as the percentage of cells in which a species changed from present to absent, absent to present, or remained present, respectively, under a climate change scenario compared to current climate scenario at year 2050, 2100, and 2300.

We assessed the relative influence of climate scenario, year (e.g. succession), and the interaction climate $\times$ year on AGB and tree species distributions using a repeated measures Analysis of Variance. The response variable was the region-wide average AGB (Mg/ha) or the percent occurrence of each of the 24 tree species for the region from three replicates at year 2050, 2100, and 2300 under each of the four climate scenarios. We treated the responses at 2050, 2100, and 2300 as repeated measures, which resulted in a total 12 subjects (4 scenarios $\times$ 3 replicates) and a total sample size of 36 observations (12 subjects $\times$ 3 repeated measures). We estimated the relative influence of each factor as the percent of the total variation attributed to each effect based on Type III sums of squares and reported P values for the significance of each factor while accounting for the repeated measures design.

Results

AGB changes

AGB dynamics had a similar pattern for the four climate scenarios. AGB increased rapidly from 2000 to 2120, then decreased slightly until 2180, and then gradually increased to 2300 (Fig. 2). The first period of increase resulted from continued tree growth and self-thinning in these early to mid-successional forests. The decrease in AGB occurred because many short-lived tree species, such as red maple and black oak, which established in the early- to mid-1900s reached longevity and were replaced by young trees. The growth of newly established young trees then offset the longevity-caused mortality of long-lived tree species (e.g., white oak, sugar maple, and American beech) and resulted in the following increase in AGB to 2300.

Climate, succession, and the interaction between climate and succession explained 29, 64, and 4 % of the variation in AGB, respectively ($P < 0.001$ for all effects). AGB was greatest under GFDL A1FI scenario followed by CGCM A2, current climate, and PCM B1 scenarios (Fig. 2). AGB was nearly identical under

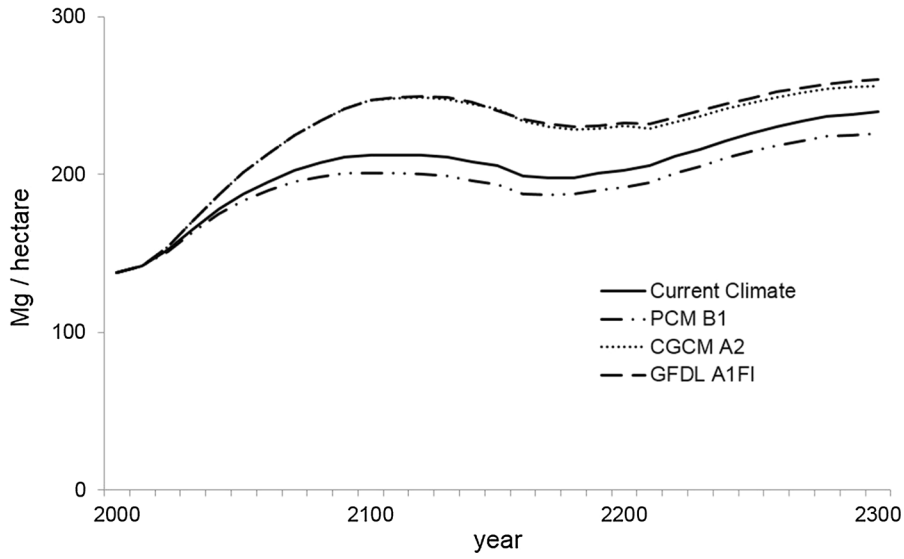

Fig. 2 Predicted region-wide aboveground biomass (AGB, Mg/ha) under four climate modeling scenarios from 2000 to 2300 in the northeastern United States

GFDL A1FI and CGCM A2 scenarios and was 13.4 Mg/ha (7.2 %), 17.8 Mg/ha (9.1 %), and 22.3 Mg/ha (11 %) greater than the current climate scenario at year 2050, 2100, and 2300, respectively (Fig. 2). AGB was similar under PCM B1 and current climate scenarios (Fig. 2).

The effects of climate change on AGB varied spatially across the region. The greatest increases in AGB under the climate change scenarios were in the most northern subsections in Maine (e.g., International Boundary Plateau, St. John Upland, Aroostook Hills, and Aroostook Lowlands subsections) and hilly and upland subsections in the middle Atlantic coastal plains (e.g., Atlantic Southern Loam Hills and Delmarva Upland subsections) (Fig. 3). The greatest decreases in AGB under climate change scenarios were in some east-coast subsections in Maine (e.g., Central Maine Embayment and Main Eastern Interior subsections) and some high-elevation mountain subsections in Adirondack-New England Mixed-Conifer Forests (e.g., White Mountains, Taconic Mountains, and Southern Piedmont Subsections), and some upland subsections in Northern Atlantic Coastal Plain (e.g., Western Chesapeake Uplands Subsection) (Fig. 3).

Tree species distribution

The region-wide occurrences of 24 tree species were significantly affected by climate, succession, and the interaction between climate and succession (Table 1). Climate and succession explained 1–30 and 40–95 % of variation in species occurrences, respectively (Table 1). The interaction effects between climate and succession increased over time and explained 5–40 % of variation in species occurrences (Fig. 4).

Climate change had minimal effects on the occurrences of tree species from 2000 to 2100 (Fig. 4). Extinction rates averaged 5–10 % at 2050 and increased to 10–20 % at 2100 and colonization rates averaged 5–15 % at 2050 and increased to 10–25 % at 2100 (Online Appendix Figs. 1, 2). However, by 2300, climate change had substantial effects on occurrences for many tree species. Changes in species occurrences at 2300 generally fell into three groups. The first group significantly contracted their range in the region and decreased in occurrence under the three climate change scenarios; it included mostly cold-climate coniferous species and northern hardwood species (eastern hemlock, balsam fir, black spruce, red spruce, northern white cedar, eastern white pine, pitch pine, Virginia pine, quaking aspen, and yellow birch), and some central hardwood species (scarlet oak, black oak, and pignut hickory) (Fig. 4). Extinction rates averaged 40–90 % at 2300, mostly occurring near the southern boundaries of their distributions (Fig. 5). The second group significantly expanded their occurrences under the three climate change scenarios and included mostly southern species (yellow-poplar and loblolly pine) and some central hardwood species (white oak and chestnut oak) (Fig. 4). Colonization rates averaged

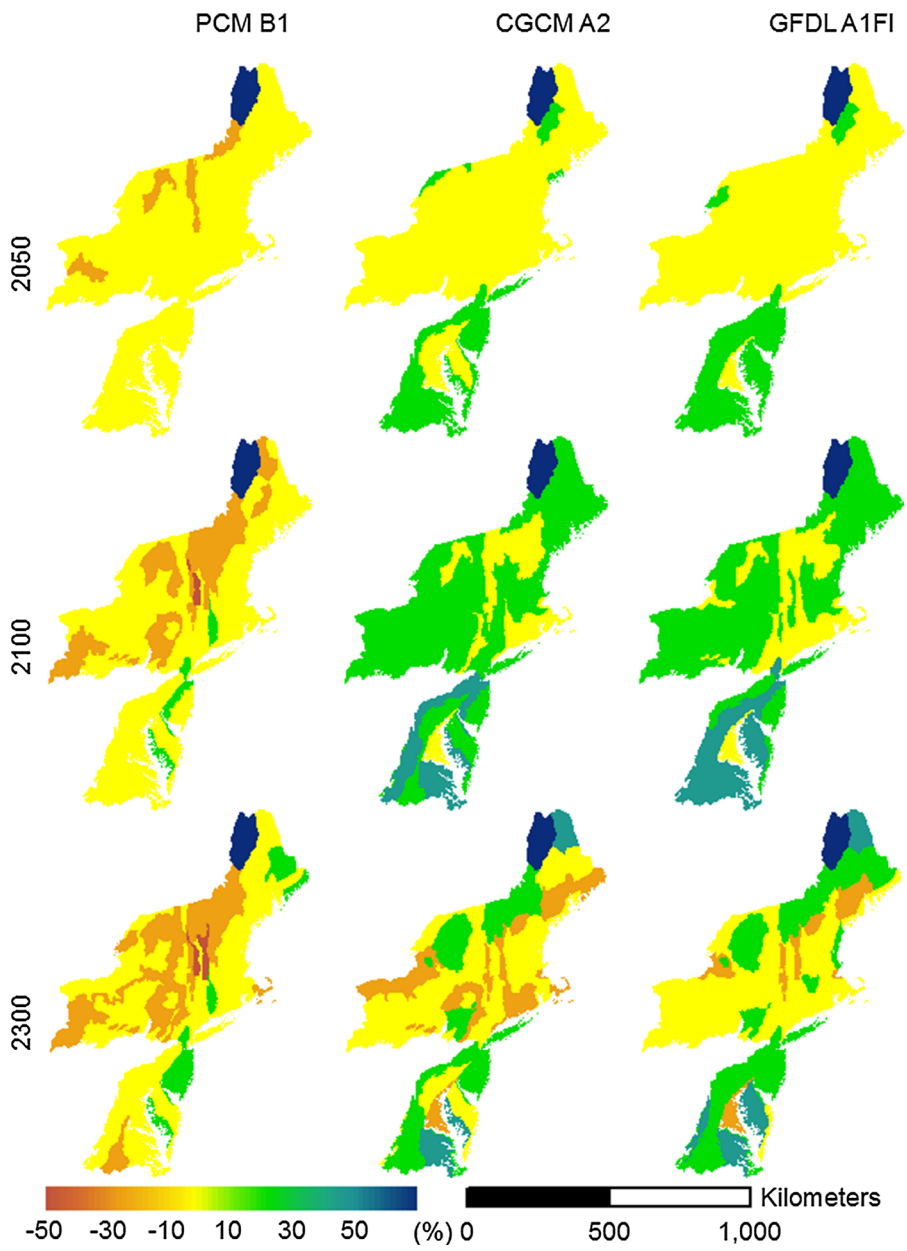

Fig. 3 The percentage changes in aboveground biomass (AGB) for each ecological subsection between the climate change modeling scenario and current climate modeling scenario at year 2050, 2100, and 2300 in the northeastern United States. (Color figure online)

30–60 % at 2300 and colonization mostly occurred along the northern boundaries of their distributions (Fig. 5). The third group of species persisted at similar levels of occurrence across the region with colonization generally balancing extinction under three climate change scenarios; it included some northern hardwood species (American beech, sugar maple, black cherry, white ash, northern red oak, and red maple) and central hardwood species (shagbark hickory) (Fig. 4). Extinction and colonization rates averaged 20–35 % at 2300 (Fig. 5).

Discussion

Temporal changes in AGB were similar under all climate scenarios and the most severe climate warming scenarios resulted in <11 % increases in AGB.

Table 1 Variation explained and significance of the effects of climate change, year, and the interaction of climate change × year in percent occurrence of 24 tree species in the northeastern United States based on forest landscape model simulations from 2000 to 2300

	Climate change		Year		Climate change × year	
	Variation explained (%)	*P*	Variation explained (%)	*P*	Variation explained (%)	*P*
Eastern hemlock	3.33	<0.001	88.36	<0.001	7.60	<0.001
Balsam fir	13.89	<0.001	60.94	<0.001	24.93	<0.001
Black spruce	18.50	<0.001	43.97	<0.001	37.48	<0.001
Red spruce	12.90	<0.001	59.76	<0.001	27.00	<0.001
Northern white cedar	10.70	<0.001	62.77	<0.001	26.03	<0.001
Eastern white pine	3.27	0.003	83.53	<0.001	11.02	<0.001
Pitch pine	4.30	<0.001	83.66	<0.001	11.50	<0.001
Virginia pine	16.86	<0.001	55.37	<0.001	27.71	<0.001
Quaking aspen	19.85	<0.001	36.80	<0.001	42.71	<0.001
Yellow birch	11.18	<0.001	62.42	<0.001	25.10	<0.001
Scarlet oak	12.62	<0.001	57.84	<0.001	28.76	<0.001
Black oak	3.32	0.008	78.06	<0.001	15.97	<0.001
Pignut hickory	3.25	0.022	80.47	<0.001	11.72	<0.001
Yellow-poplar	31.26	<0.001	42.56	<0.001	26.18	<0.001
Loblolly pine	25.61	0.003	27.89	<0.001	28.91	<0.001
White oak	24.17	<0.001	44.35	<0.001	26.98	<0.001
Chestnut oak	21.17	0.001	50.75	<0.001	17.30	<0.001
American beech	1.60	0.085	93.80	<0.001	0.56	0.757
Sugar maple	2.73	0.058	90.92	<0.001	0.61	0.853
Black cherry	1.35	0.371	86.29	<0.001	3.31	0.252
White ash	3.34	0.646	45.98	<0.001	4.40	0.881
Northern red oak	6.29	0.025	81.20	<0.001	3.15	0.293
Shagbark hickory	4.83	0.017	82.06	<0.001	7.02	0.007
Red maple	0.96	0.506	81.5	<0.001	0.96	0.956

Since changes in AGB over time were much greater than differences among climate scenarios, we suggest that AGB dynamics were mostly driven by succession and that regional-scale predictions of future forest biomass should incorporate successional processes because of their importance. The temporal patterns in AGB that we predicted were likely because the northeastern forests were below maximum stocking or biomass capacity (Lichstein et al. 2009; Pan et al. 2011) and recovering from historical land use. The predicted increases in AGB over the 21st century were generally consistent with other model predictions (e.g., LANDIS-II, ED) that suggest forest biomass will increase at least until 2060 for the state of Massachusetts (Thompson et al. 2011) and to the end of the 21st century in the eastern United States (Albani et al. 2006). On average, climate change had positive effects on region-wide AGB, which likely resulted from overall warmer temperatures and longer growing seasons. However, changes in AGB varied spatially and excessive warming may cause growth declines (Anderegg et al. 2015). Increases in AGB could be viewed as a positive impact of climate change, however, our simulations did not account for changes in land use, such as urban growth, which may threaten the ability of the region to sequester biomass in the coming decades (e.g., Thompson et al. 2011; Bachelet et al. 2015). Thus, policy-makers may need to consider alternative land-use policies and practices that increase and prolong biomass sequestration while

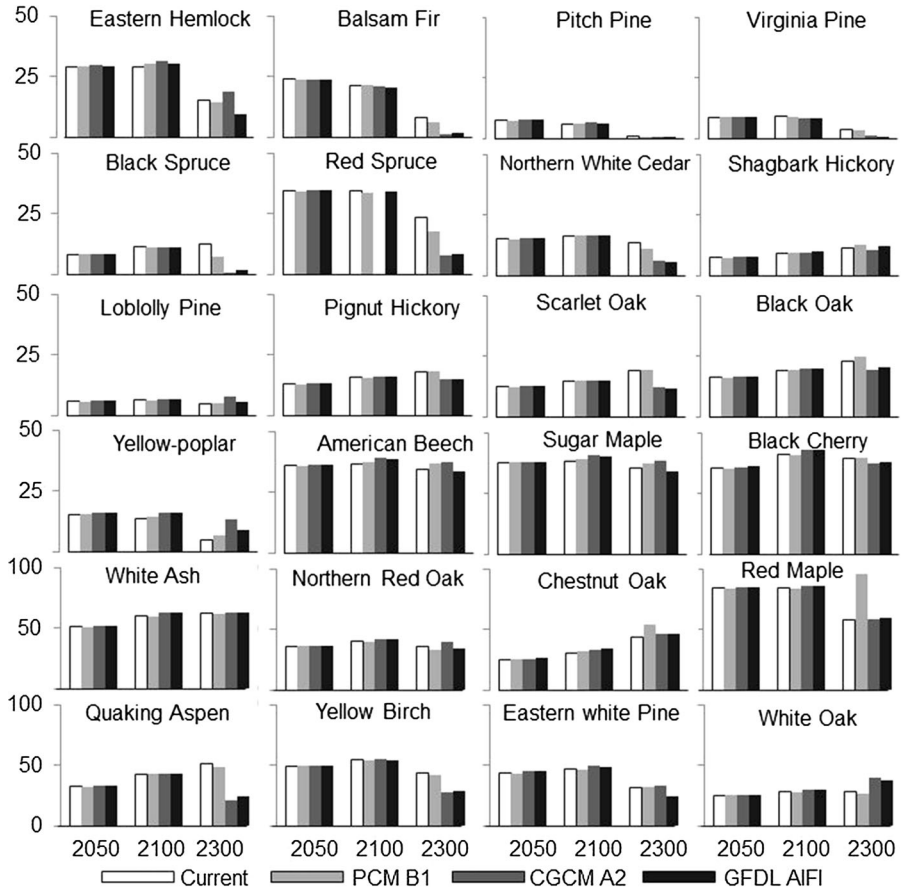

Fig. 4 Region-wide occurrences (%) for 24 tree species under current climate and PCM B1, CGCM A2, and GFDL A1FI climate scenarios at year 2050, 2100, and 2300 in the northeastern United States

fulfilling demands for economic and social services such as real estate development in suburban and rural areas (Raciti et al. 2012).

There is greater uncertainty in forest biomass dynamics in the future (2100–2300) and in the latter stages of forest succession (e.g., >200 years). Bormann and Liken (1979) predicted that AGB declined in stands 200–350 years old and remained stable in stands >350 years old. Keeton et al. (2011) found biomass only slightly declined as dominant trees exceeded 300 years old but then increased to 400 years and more. We predicted AGB declined slightly from 2120 (dominant age 160–200 years old) and reached nadir at 2180 (220–260 years old) and then increased to 2300 (340–380 years old). The initial decline may have occurred earlier than predicted by Bormann and Liken (1979) and Keeton et al. (2011) because we included harvest in our simulations and landscapes were multi-aged. The predicted increases in AGB to 340–380 years old were consistent with increases to 400 years old and more (Ziegler 2000; Keeton et al. 2011), but not consistent with stable biomass at ages >350 (Bormann and Liken 1979) or decreases after 230–260 years old (Tyrrell and Crow 1994). These differences may arise from the different approaches used or differences between our regional results and site-specific results. Although there were a range of possibilities and greater uncertainties in the latter stages of AGB dynamics, we can generalize that AGB will likely decline over the next century as forests mature and age but eventually northeastern forests may have potential to sequester biomass into very late stages of succession (e.g., 300–400 years old).

There was great spatial variation in the effects of climate change on AGB across the region. Climate change increased the AGB for the cool-climate conifer forests, northern hardwood forests, and loblolly-shortleaf pine forests, because warmer and wetter climates and longer growth season increased some species

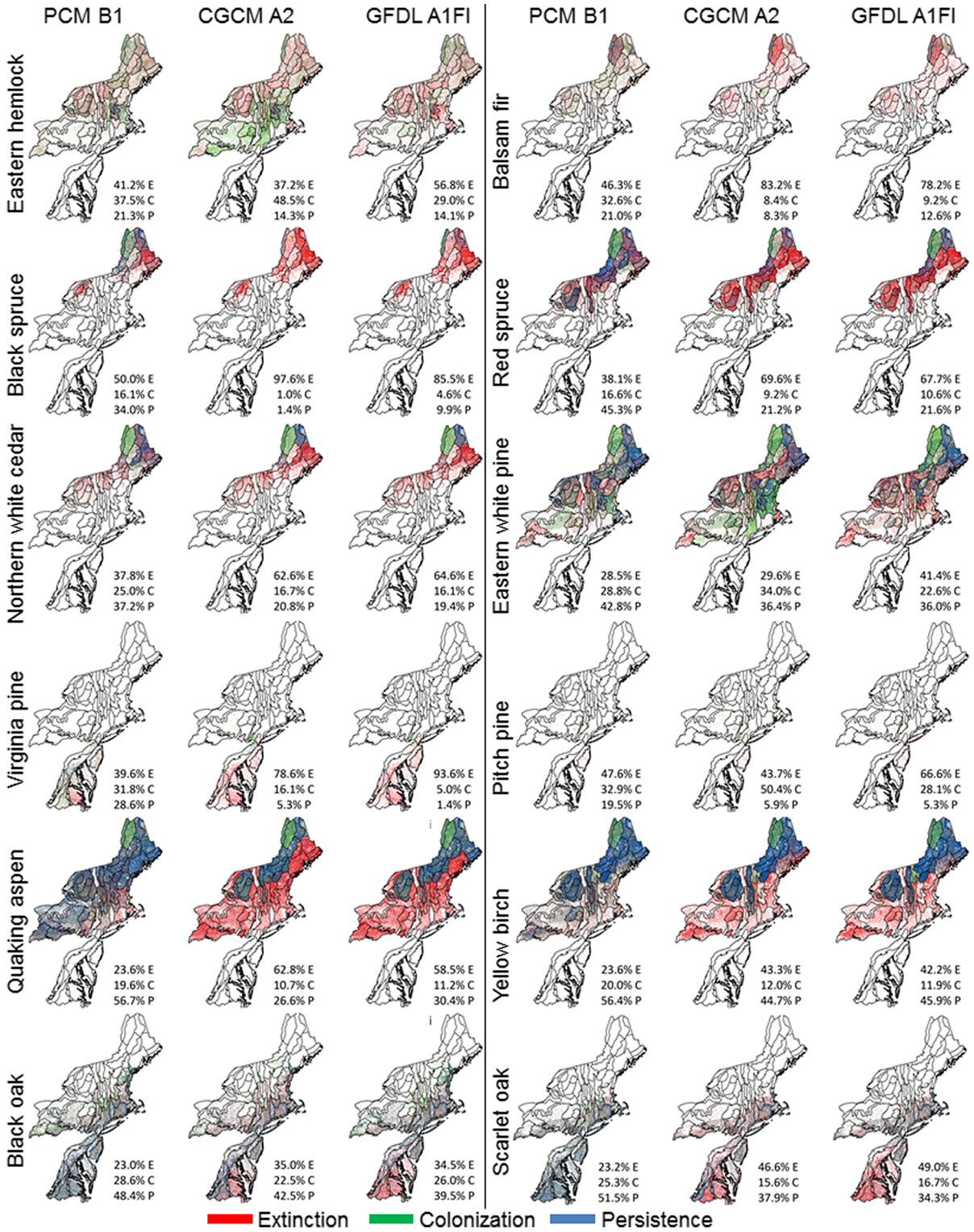

Fig. 5 Predicted extinction (*in red*), colonization (*in green*), and persistence (*in blue*) rates for 24 tree species under PCM B1, CGCM A2, and GFDL A1FI modeling scenarios at 2300 in the northeastern United States. (Color figure online)

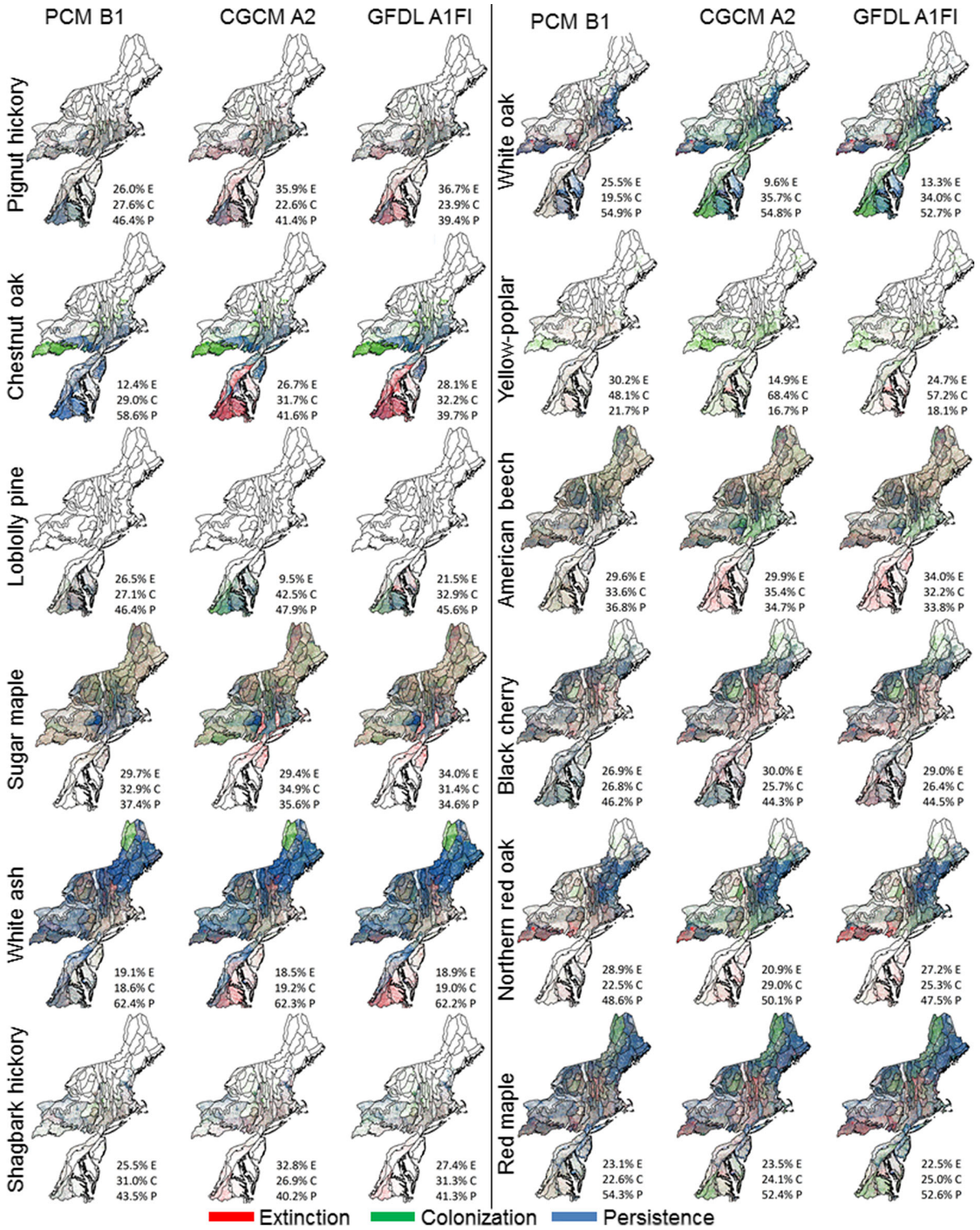

Fig. 5 continued

productivity. However, climate change decreased AGB for the mixed forests on the east coast of Maine, northern hardwood forests in the Northern Atlantic Coastal Plain, and Mixed-Conifer Forests in the high-elevation mountain areas because warmer and drier climates decreased forest productivity.

We found minimal changes in the occurrences of most tree species under climate change by 2100, suggesting a lagged response by trees to climate change. Major changes in tree species distributions will not likely occur by the end of 21st century and may take hundreds of years. In contrast, niche models predict tree habitats may change substantially by 2100 (e.g., McKenney et al. 2007; Iverson et al. 2008; Morin and Thuiller 2009). For example, under severe climate change scenarios, habitats for spruce/fir and maple/beech/birch forests are predicted to nearly disappear by end of 21st century in the northeastern United States (Iverson et al. 2008). Our approach showed lagged responses of tree species to climate because it simulated population change based on species demography (growth, birth, mortality, and dispersal). Tree species are long-lived organisms (e.g., up to several hundred years), which enables them to resist extinction during unfavorable climatic conditions. For example, even though sugar maple and American beech were not favored by future climates in the southern and central region, extinction rates were still low at 2100 because most trees had not reached their longevity yet. However, extinction of sugar maple and American beech became high by 2300 because mature trees died and the species could not regenerate under warmer climates. Therefore, we suggest it is important to consider species demography when forecasting changes in tree species distributions.

Our predictions generally agree with niche-model predictions (e.g., DISTRIB-SHIFT) on the potential for large declines of northern hardwood species (e.g. quaking aspen, yellow birch) and northern conifer species (e.g. balsam fir, black spruce, red spruce, pitch pine), especially under severe climate change scenarios in the south, and increases in oak-hickory and southern species (e.g. yellow poplar, loblolly pine) by 2300. Our approach mechanistically simulated dispersal, and we predicted trees species would shift northward. For example, northern hardwood species may migrate into the northern boreal forest region and southern species and widely distributed species (e.g., white oak) may migrate into the northern hardwood forest region. These changes would likely have significant implications for wildlife, recreation, and forest industry. The near extirpation of spruce/fir forests would reduce habitats for many wildlife species such as snowshoe hare (*Lepus americanus*), Bicknell's thrush (*Catharus bicknelli*), American marten (*Martes americana*), and the endangered Canada lynx (*Lynx canadensis*) and greatly exacerbate stresses on forested-based manufacturing industry (e.g., pulp and paper industry) and local economy (e.g., Maine) (Shifley et al. 2014).

Our findings have important implications for forest management because forecasts of forest landscape change in response to climate change needed for forest management planning. Management of forests for climate mitigation or adaptation will likely be balanced with other management objectives such as biodiversity and timber products. Land use and management may need to consider the types of spatial and temporal patterns in forest response to climate change predicted here along with human demographic and economic factors and biophysical constraints. Forest management that favors carbon-dense southern species and central hardwood species is likely to promote resilience and adaptation of forests to climate change in the region. Some species may not be able to shift quickly enough to keep pace with changing climates without assisted migration.

Our predictions are subject to a number of uncertainties. Our approach incorporated the effects of daily temperature and precipitation, growing season, and drought on decadal values for species establishment and site carrying capacities (e.g. SEP and MGSO parameters in LANDIS PRO). It's not clear to what extent these decadal values for SEP and MGSO fully captured the daily effects of climate modeled in LINKAGES II, but there were numerous examples where SEP and MGSO varied in response to differences among climate scenarios. We are pursuing additional research to determine the sensitives LINKAGES and LANDIS PRO using SEP and MGSO derived from LINKAGES to different daily and annual patterns in climate. We did not consider the effects of rising CO_2 and N fertilization on forests, which could offset some negative effects of climate change. We did not consider fire, insect, and disease outbreaks, which may increase under warming climates and increasing drought events (Weed et al. 2013). Lastly we did not consider additional climate change beyond 2100 and

acknowledged the inherent uncertainly in any landscape projections extending 300 years. Nevertheless our simulation results generally supported our hypotheses and provide support for the importance of species demographics and success on tree species occurrences over the next century but that over longer time frames (i.e. 100–300 years) climate change could result in substantial shifts in some tree species distributions.

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