

Recovery dynamics and climate change effects to future New England forests

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Abstract

Context Forests throughout eastern North America continue to recover from broad-scale intensive land use that peaked in the nineteenth century. These forests provide essential goods and services at local to global scales. It is uncertain how recovery dynamics, the processes by which forests respond to past forest land use, will continue to influence future forest conditions. Climate change compounds this uncertainty.

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Objectives We explored how continued forest recovery dynamics affect forest biomass and species composition and how climate change may alter this trajectory.

Methods Using a spatially explicit landscape simulation model incorporating an ecophysiological model, we simulated forest processes in New England from 2010 to 2110. We compared forest biomass and composition from simulations that used a continuation of the current climate to those from four separate global circulation models forced by a high emission scenario (RCP 8.5).

Results Simulated forest change in New England was driven by continued recovery dynamics; without the influence of climate change forests accumulated 34 % more biomass and succeed to more shade tolerant species; Climate change resulted in 82 % more biomass but just nominal shifts in community composition. Most tree species increased AGB under climate change.

Conclusions Continued recovery dynamics will have larger impacts than climate change on forest composition in New England. The large increases in biomass simulated under all climate scenarios suggest that climate regulation provided by the eastern forest carbon sink has potential to continue for at least a century.

Keywords New England · Recovery dynamics · Climate change · LANDIS-II · Forests

Introduction

Northeastern United States' forests are part of one of the largest forested biomes in North America. These forests provide critical goods and services at local to global scales, including timber, tourism, water filtration, and carbon sequestration (Schwenk et al. 2012; Blumstein and Thompson 2015), and are representative of aggrading mesic temperate forests worldwide. Northeastern forests continue to recover from a long period of intensive agricultural clearing and lumbering that peaked in the late nineteenth century (Thompson et al. 2013). Despite the pervasive influence of many novel agents of global change, recovery dynamics, the processes by which forests respond to past disturbance including accrual of aboveground biomass (AGB) and turnover toward long-lived shade tolerant tree species, continue to be the dominant process driving forest change in the region (Thompson et al. 2013; Eisen and Plotkin 2015; Wang et al. in press). Whether future patterns of forest change will continue to be driven by the legacy of historical land-use under changing climate is not well understood.

Climate change has the potential to alter the current recovery trajectory. Global circulation models (GCMs) agree that climate of the Northeastern US will become increasingly warmer, but future patterns of precipitation are less clear (Ning et al. 2015). Possible direct effects of future climate change include increased growth due to longer growing seasons (IPCC 2013; Keenan et al. 2014), decreased growth in the warmest months due to greater respiration and evapotranspiration (Buermann et al. 2013), and shifts in tree species ranges as they respond to shifts in the isotherms to which they are adapted (Farnsworth and Ogurcak 2015). Indirect effects of climate change, such as changing disturbance regimes and CO₂ fertilization (Ollinger et al. 2008) will also impact forest composition and function.

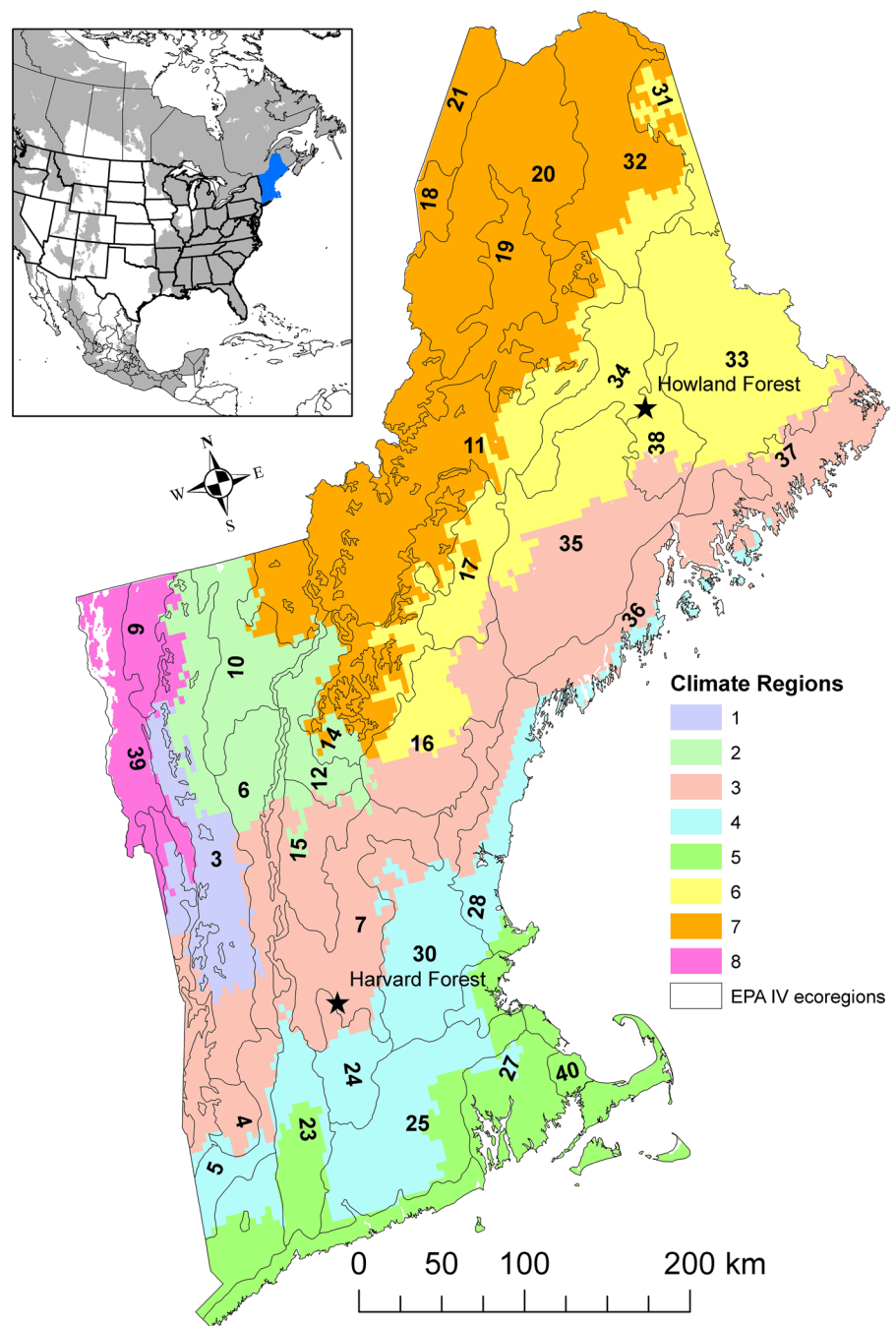
We also expect regional variation in the response of recovery dynamics to climate change, associated with forest composition, age, latitude and topographical position. Northeastern forests are characterized by large spatial heterogeneity in the occurrence of forest types, largely corresponding to climate and disturbance gradients (Cogbill et al. 2002; Foster et al. 2006). Individual tree species

within forest types are expected to respond differently to forest recovery dynamics and climate change given their life history traits (e.g. shade and thermal tolerance). Uncertainty remains about the fate of regionally critical tree species, especially those predicted to be vulnerable to future conditions (e.g. sugar maple, *Acer saccharum*) (Gavin et al. 2008; Iverson et al. 2008).

Temperate forest trees are long lived and resilient and their response to climate change can be delayed by centuries (Davis and Botkin 1985). Forecasting changes in northeastern forests requires an approach that can incorporate multiple processes operating at different scales. Unlike niche models (Iverson et al. 2008) that do not incorporate physiological, succession and dispersal processes, physiologically-based, spatially-explicit mechanistic models are well designed to evaluate forest response interactions with climate (de Bruijn et al. 2014; Gustafson et al. 2014). By increasing the use of mechanistic links between tree physiology and climate drivers, such models have increased robustness for study of the response of forested landscapes to the novel climate conditions of the future (Gustafson 2013). To date, most physiologically based spatial models aggregate tree species into functional groups and may therefore miss important species-level responses to climate change, which are often important determinates of ecosystem function and services (Chandler et al. 2012).

In this study we simulated forest recovery dynamics as they are affected by projected climate change throughout New England (Fig. 1). There is concern that northeastern forests will be unable to sustain current ecosystem services under climate change (Dukes et al. 2009; Mohan et al. 2009; Tang and Beckage 2010). Our regional-scale, species-level simulations provide an understanding of future critical ecosystem services. This research will inform for example, the potential future ability of northeastern forests to sequester carbon. New England is an ideal model system to examine these interactions because the land-use history and initial patterns of recovery are well known (Thompson et al. 2013). We addressed the question: How will continued regional forest recovery dynamics affect forest biomass and species composition and how might climate change alter this trajectory?

Fig. 1 EPA level-IV (numbered) ecoregions and climate regions (colored) within the New England study area. Stars indicate net ecosystem exchange calibration sites with both the Hemlock and EMS sites represented by the *Harvard Forest* star. Inset indicates study area (blue) within North American forests (grey)



Methods

Study area

We simulated biomass and compositional change throughout the 13 million hectares of forest within the

six New England states (Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut; Fig. 1). Forests cover approximately 80 % of land area and span a gradient of boreal forests in northern Maine to oak-maple forests in southern New England (Duveneck et al. 2015). Mean annual temperatures

range from 3 to 10 °C across a north to south gradient. Mean annual precipitation ranges from 79 to 255 cm with more precipitation at higher elevations (Daly and Gibson 2002). The region was completely forested until the seventeenth century, when two centuries of logging and agricultural clearing removed more than half of the forest cover and cut over most of the rest (Thompson et al. 2013). Forest cover reached its nadir in the mid-nineteenth century, after which widespread farm abandonment and a reduction in the intensity of harvesting initiated a century of natural reforestation and forest growth. Although New England is a well-documented example of a great forest transition, New England's land-use history is paralleled in many regions of the world (Mather 1992).

Simulation model

We simulated forest change using the LANDIS-II v6.0 forest landscape model (Scheller et al. 2007) and a mechanistic growth and succession extension (PnET-succession) (de Bruijn et al. 2014) based on the PnET-II ecophysiology model (Aber et al. 1995). LANDIS-II is a spatially-interactive forest process model that has been widely used to study northern temperate-boreal forests. The PnET-Succession extension v1.0 (de Bruijn et al. 2014; Gustafson et al. 2014) simulates the competition of tree cohorts for light and water for photosynthesis using ecophysiology algorithms upscaled to a grid cell by integrating incoming radiation and water consumption within stacked layers of the canopy. Cohort biomass is used as a surrogate for tree height to simulate canopy layers, which are added when the variation in biomass among cohorts exceeds a user-defined amount. Competition for light is modeled by allocating incoming radiation through each layer with a standard Lambert–Beer formula. Varying climate scenarios are incorporated with monthly precipitation, light, maximum and minimum temperature at a monthly timestep. Growth is simulated as a competition for light and water for photosynthesis among all the cohorts on each grid cell by integrating incoming radiation and water within stacked layers of the canopy. Water balance is calculated by tracking soil water within cells based on precipitation, transpiration by cohorts, evaporation, runoff, and percolation out of the rooting zone. Within cells, cohorts compete for light and water where older

and larger (more biomass) cohorts receive higher priority for resources. Growth increases with available light, foliar N, and atmospheric CO₂ concentration; and decreases with age and departure from optimal temperature. Production from net photosynthesis is partitioned to biomass pools of wood, root, foliage, and reserves (nonstructural carbon). Soil water and subcanopy light also regulate monthly species establishment probabilities which stochastically determine where new cohorts will regenerate.

We calibrated the model using data from six sites by comparing simulated biomass dynamics on individual 1 ha cells to long-term observations of annual biomass from Howland Forest in Maine (Hollinger et al. 2004), Black Rock Forest in New York (Schuster et al. 2008), Hubbard Brook Forest in New Hampshire (Battles et al. 2014), and the Hemlock tower (Hadley and Schedlbauer 2002), EMS tower (Urbanski et al. 2007), and Lyford plots (Eisen and Plotkin 2015) at the Harvard Forest in Massachusetts. At sites with eddy covariance flux tower instruments (Howland, Hemlock, and EMS), we also calibrated simulated monthly net ecosystem exchange (NEE) to flux measurements of NEE. NEE is a measurement of total carbon flux from the atmosphere to the forest, but our simulations of NEE do not include soil respiration. To account for this discrepancy, we added seasonally observed soil respiration as a proportion of ecosystem respiration to simulated NEE based on observations at the Harvard (Giasson et al. 2013) and Howland Forest (Davidson et al. 2006) flux towers. For our simulations of AGB at the landscape scale, we compared observed AGB from US Forest Service Forest Inventory Analysis (FIA) plots (Bechtold and Patterson 2005) to simulated AGB of pixels representing FIA plots. Duveneck et al. (2015) described an extensive validation of species composition used in initial conditions across New England. As an addition, we simulated 4118 1 ha cells where each cell's initial forest composition was a representation of a single FIA plot using the same methods to develop landscape initial communities (Appendix I in supplementary material). We then compared observed AGB to simulated AGB at model year zero (spin-up values) using Pearson's correlation coefficient (*r*) and root mean squared error (RMSE). Finally, we compared published estimates of total forest AGB within each New England state

(Bechtold and Patterson 2005) to modeled AGB, aggregated for each New England state at year zero.

Experimental design

We simulated 100 years of forest dynamics (2010–2110) and evaluated modeled live AGB and compositional changes at 5 year time steps. We used a 250 m cell resolution resulting in >2 million active forested cells. Because our goal was to better understand the relative effect of continued recovery dynamics and anticipated climate change on future forests, we simulated natural gap-scale disturbances, but excluded all other biological and anthropogenic disturbance regimes (see Appendix I in supplementary material).

We compared simulations that assume a continuation of the current climate to simulations that depict future climate change. Simulations that continued the current climate used monthly 4 km gridded temperature and precipitation data provided by the parameter-elevation relationships on independent slopes model (PRISM; Daly and Gibson 2002) based on the period spanning 1981–2013. PRISM uses a large network of climate observations using additional spatial variation such as elevation to calculate gridded climate variables. Simulations of future climate change used downscaled climate grids developed based on a high-emission representative concentration pathway (RCP 8.5) provided by the International Panel on Climate Change (IPCC). There is considerable variation in GCM projections of the RCP 8.5. We compared four GCMs shown to most accurately simulate historical climate in the region (Sillmann et al. 2013): community climate system model v4.0 (CCSM4), community earth system model v1—community atmosphere model v5 (CESM1), Hadley global environment model v2—earth system (HADGE), and the Max Planck Institute earth system model—low resolution (MPIMLR). For each climate scenario, we used 12 km monthly downscaled projections of maximum temperature, minimum temperature, and precipitation obtained from the USGS Geo Data Portal (Stoner et al. 2013) (see Appendix I in supplementary material) as LANDIS-II inputs. For the current climate scenario, we kept CO₂ constant at 390 ppm. Under the climate change scenarios, we used the RCP 8.5 projections of increasing CO₂. We replicated each of the five scenarios (current climate + 4 GCM

projections) five times; however because simulated disturbance were rare (see Appendix I in supplementary material), model outputs were virtually deterministic, so variability among replicates was extremely low, only one replicate was used for the analysis (Thompson et al. 2011; Duveneck et al. 2014).

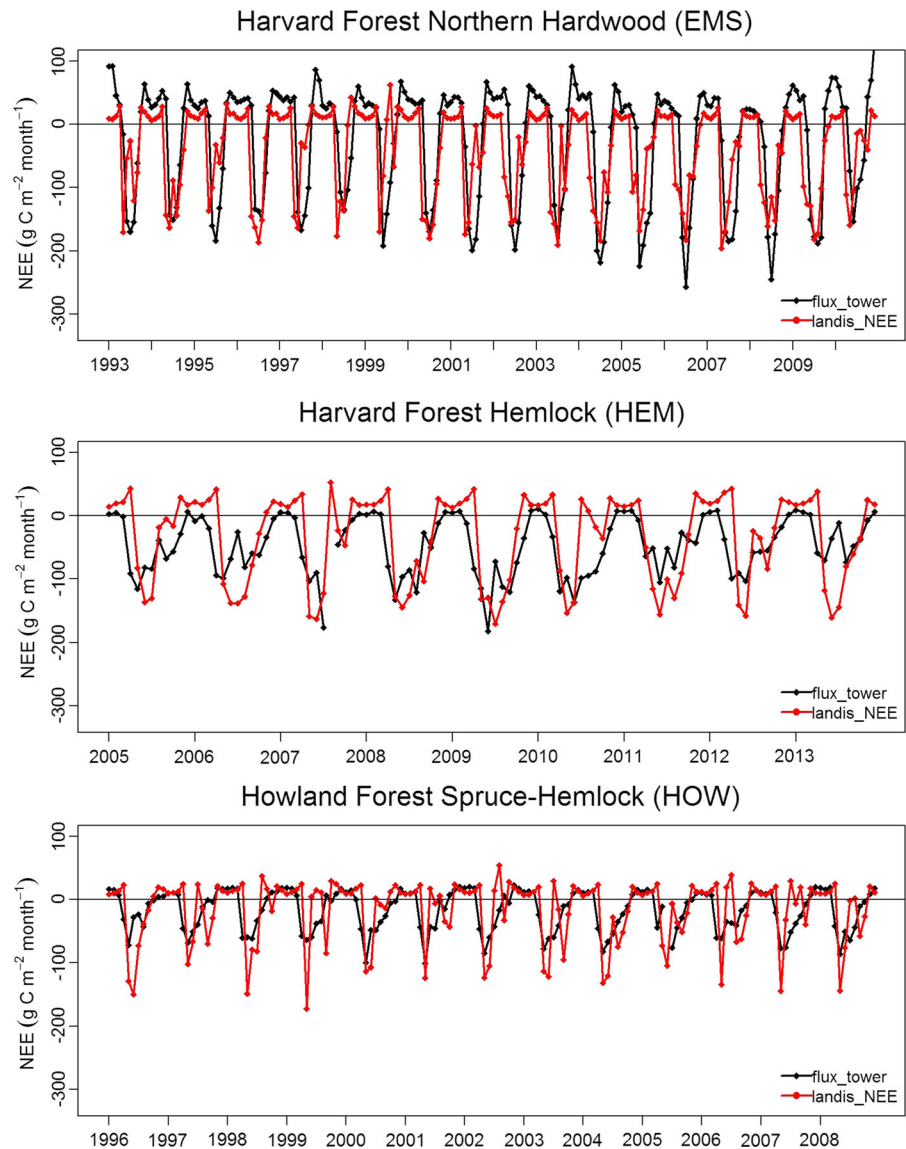
To evaluate the effect of recovery dynamics and climate change on biomass, we compared average percent change in biomass of the current climate and climate change scenarios from 2010 to 2110 within Environmental Protection Agency (EPA) level-IV ecoregions (Environmental Protection Agency 2012) (Fig. 1). We compared changes in average AGB for each of the 33 tree species and six forest types throughout the 100 year time horizon. We also mapped and compared changes in the proportion of aggregated spruce-fir, northern hardwood, and pine species to assess the spatial distribution and persistence of forest types. We plotted these forest types as red, green, blue (RGB) composite maps at year 2010 and 2110 with the current and as an example, the HADGE climate change scenario. For all analyses we used the R statistical software (R Core Team 2013) and the Raster package for R (Hijmans 2014).

Results

Calibration

Calibration simulations showed high agreement in the magnitude and timing of observed AGB and monthly NEE at multiple scales (Fig. 2). At the Harvard Forest hardwood flux tower, simulated NEE largely reproduced growing season dynamics, but underestimated respiration during winter months (positive NEE) (RMSE = 71.07 g m⁻², $r = 0.66$). At the Harvard Forest hemlock flux tower, simulated NEE largely represented observed monthly NEE (RMSE = 54.92, $r = 0.63$), however growing season growth (negative NEE) was overestimated after 2010 when photosynthetic activity began to decline due to an insect infestation that is not incorporated in our simulations. At the Howland Forest spruce flux tower, simulated NEE largely captured monthly observed NEE, but overestimated growing season NEE during a number of years (RMSR = 40.88 g m⁻², $r = 0.57$). Spin-up AGB had moderate agreement with observed AGB across 4118 FIA plots (RMSE = 6.71 kg m⁻²,

Fig. 2 Simulated monthly net ecosystem exchange (NEE) in three New England sites with eddy-covariance observations. *Negative NEE values indicate when more carbon uptake is sequestered into the forest than is released to the atmosphere*



$r = 0.29$). No validation bias was observed across forest types. For individual New England states, total simulated AGB was largely consistent with published estimates of state total forest AGB ($\pm 30\%$), but overestimated biomass in Maine where greater forested area was present.

Aboveground biomass response

Simulated forest growth under all climate scenarios resulted in increases in AGB (Fig. 3). Under current climate the average simulated AGB across New

England increased from 11.5 to 15.4 kg m⁻² (34 % increase). Under the high emission GCMs, the average simulated AGB increased to 21.0 kg m⁻² (82 % increase). Overall, biomass gains were larger in the eastern portion of the study region, especially gains attributable to climate change. At the ecoregion scale, the greatest increases in biomass from 2010 to 2110 were found in forests with the lowest initial biomass (Fig. 3), which were also typically the youngest (Appendix II in supplementary material).

Simulated species response to recovery dynamics included increases in many moderately to highly

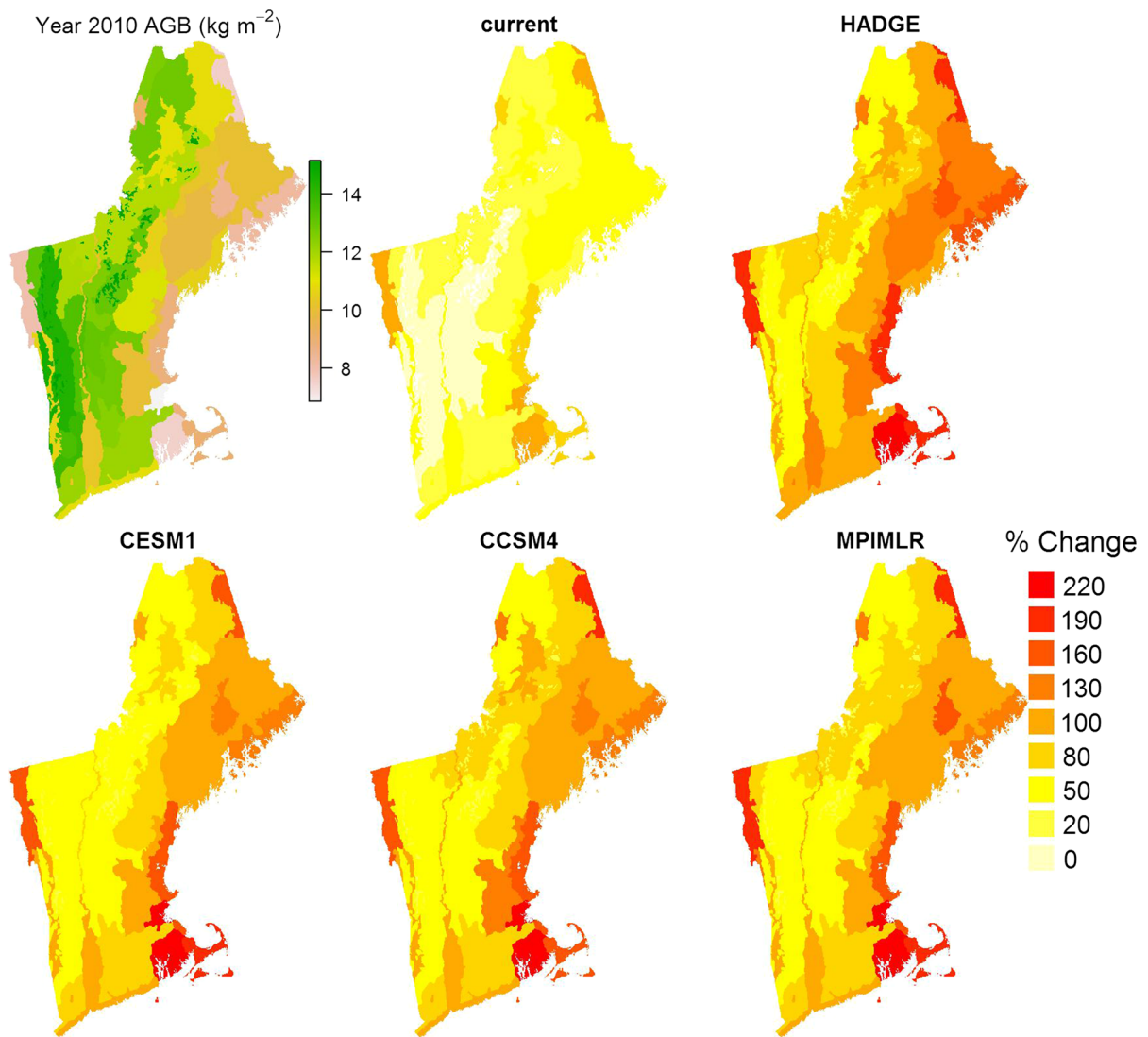


Fig. 3 Average simulated aboveground biomass (AGB) kg m⁻² at year 2010 (*upper left panel*) and percent change in (AGB) from year 2010 to 2110 within ecoregions under different climate scenarios

shade-tolerant species such as American beech (*Fagus grandifolia*), red spruce (*Picea rubens*), and Eastern hemlock (*Tsuga canadensis*) (Fig. 4). Under climate change, enhanced growth of Eastern white pine (*Pinus strobus*), sugar maple, and red maple resulted in additional increases in simulated AGB. Spruce-fir species [e.g., balsam fir (*Abies balsamea*), and red spruce] with lower optimal temperatures for growth (Appendix I in supplementary material), also resulted in greater AGB under climate change scenarios. Responses of other species are found in Appendix III in supplementary material. Within forest types,

climate change resulted in a greater proportion of pine abundance and less proportion of spruce-fir (Fig. 5a). However, both pine and spruce-fir forest types resulted in increases in AGB under climate change (Fig. 5b). In addition, large increases in northern hardwood AGB were simulated under climate change compared to current climate (Fig. 5b), although the proportion of northern hardwood AGB under climate change was very similar to current climate (Fig. 5a). Across scenarios, less dominant forest types experienced less biomass change under climate change than more dominant species.

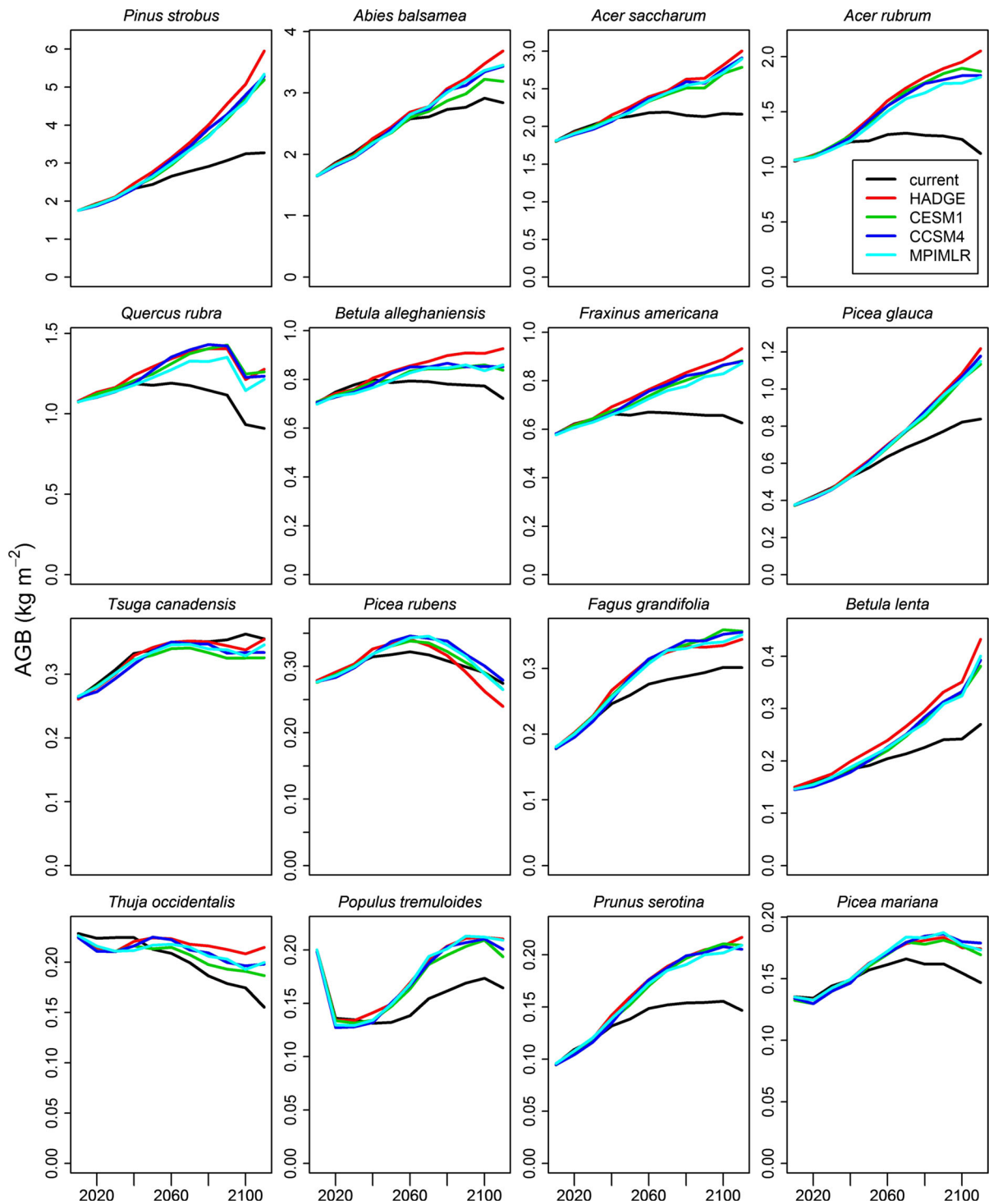
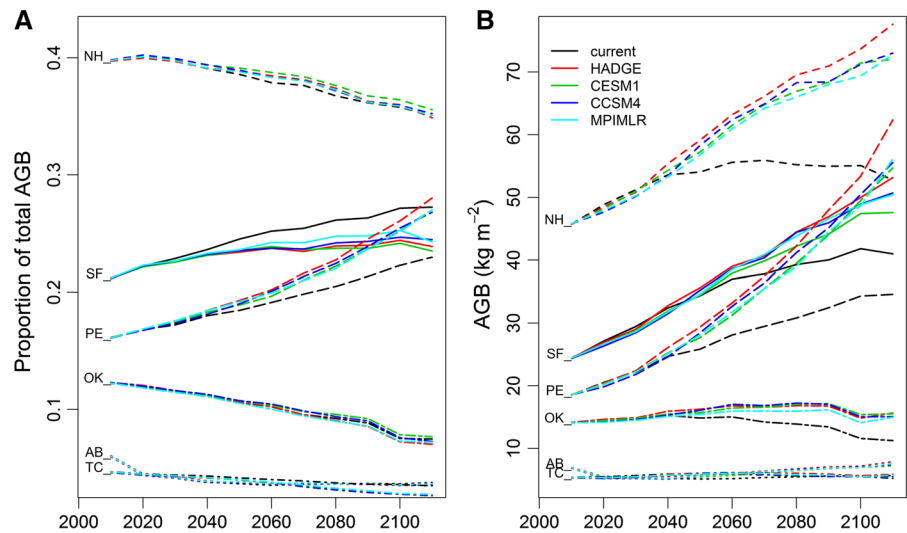


Fig. 4 Mean aboveground biomass of dominant species simulated through time under five climate scenarios. Other species are found in Appendix II in supplementary material

Fig. 5 Proportional (a) and average (b) changes in aboveground biomass by forest type. *NH* Northern hardwood, *SF* spruce-fir, *PE* pine, *AB* aspen-birch, *OK* oak, *TC* tamarack-cedar-hemlock



Spatially, northern hardwood, pine, and spruce-fir species changed similarly in proportional abundance compared to current abundance (Fig. 6a) under both current (Fig. 6b) and a future climate scenario (Fig. 6c). Comparing current climate to climate change at 2110 showed few differences in the spatial dominance of forest types. For example, in both current and climate change, spruce-fir persisted in areas such as the high elevation White Mountains (near the center of the New England landscape). Likewise, species composition in areas originally dominated by northern hardwood forest types in southern New England stayed relatively constant across a climate change scenario (Fig. 6).

Discussion

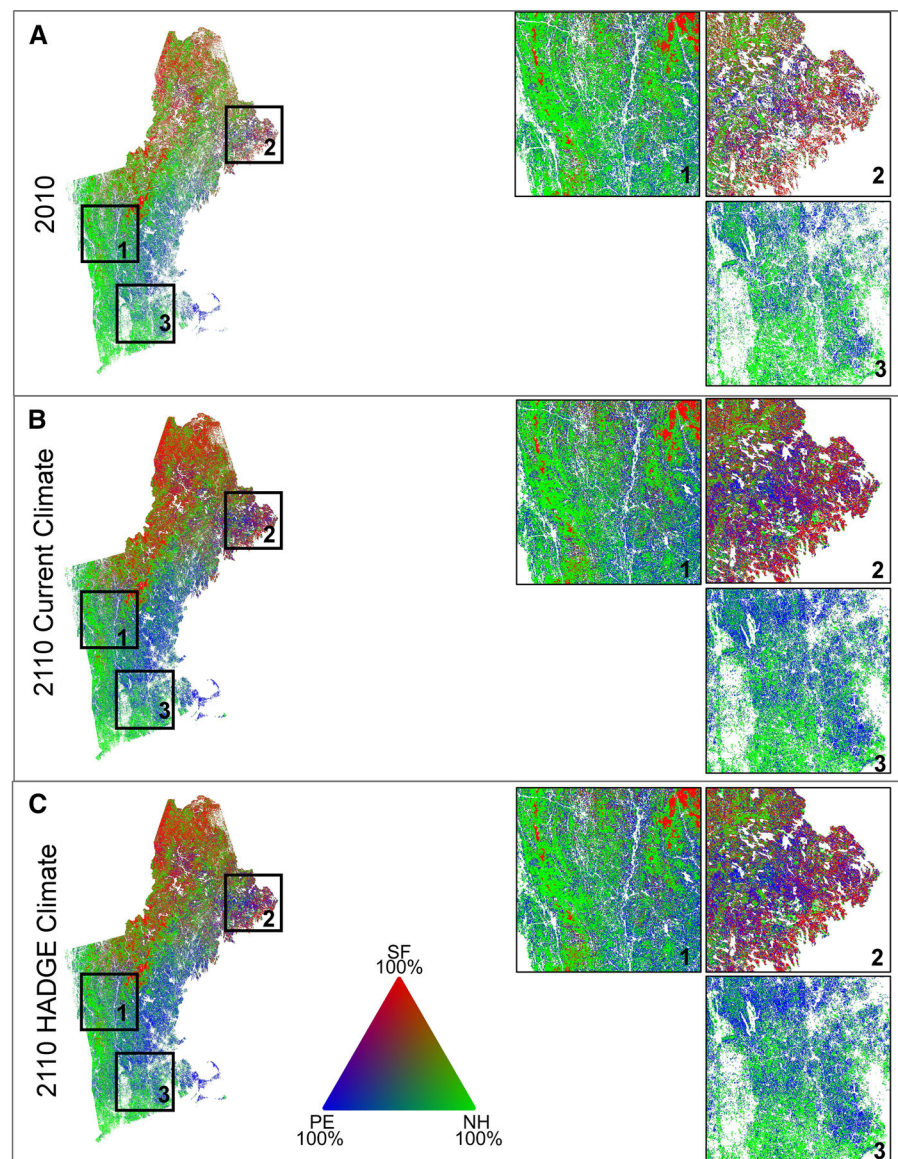
New England's forests are accruing AGB at a rapid rate and the simulations suggest that the regional ecosystem will continue to serve as an important sink for at least another century. Our results corroborate other studies that suggest that these forests are still recovering from colonial land-use and remain well below their maximum biomass capacity (Hurt et al. 2002; Thompson et al. 2011; Eisen and Plotkin 2015; Wear and Coulston 2015; Wang et al. in press). This has implications for critical local and global ecosystem services including carbon sequestration, tourism, habitat, biodiversity and the regional forest-based industries. The largest potential increases in AGB may

be in eastern New England where land use history, climate, and soil properties have otherwise limited growth. Under climate change, additional increases in biomass accrual are expected in addition to those increases expected from recovery dynamics.

Climate change effects on New England forests

Our simulations suggest that 100 years of climate change will have modest effects on forest composition. Trees are both long-lived and slow to migrate (Davis and Botkin 1985; Zhu et al. 2012); and many of the individual trees currently on the landscape will persist for the next 100 years. In addition, the dominant tree species in New England are well north of their southern range boundary and thus are resistant to local extirpations due to shifting climatic conditions. For example, recent evidence suggests that spruce-fir species are not retreating in the New England mountains, as once thought, but instead are expanding downslope as they recover from intensive harvesting at the beginning of the twentieth century (Foster and D'Amato 2015). The stability of tree species distributions in New England demonstrated through mechanistic modeling is a stark contrast from the large shifts in tree species habitat that are derived from climate niche models. This discrepancy has potentially significant consequences when niche models are driving management decisions about a future that cannot be realized given the physiological and ecological processes involved. Indeed, mechanistic simulations done

Fig. 6 Spatial distribution of northern hardwoods (NH), spruce-fir (SF), and pine (PE) forest types at year 2010 (a) and at year 2110 under current climate (b) and the HADGE climate change scenario (c). Red, green, blue color combinations represent proportional distribution of each forest type within each pixel. Numbered insets map locations are represented in corresponding black boxes



by Wang et al. (in press) were not able to reproduce the habitats portrayed in a niche model even after simulating tree migration to year 2300, a full two centuries longer than GCMs produce climate forecasts.

Our mechanistic approach to modeling climate change effects on species do suggest some species will benefit more than others. For example, throughout much of New England we projected large increases in white pine, sugar maple, and spruce-fir species under climate change. These increases are again in contrast to climate niche models, which project decreased

future suitable habitat for these species (Iverson et al. 2008). Sugar maple is an important tree species with strong economic and cultural ecosystem service value to the region. Because sugar maple is a shade tolerant species with a native range extending far to the south of New England (Little 1971), the simulation inputs of warmer temperatures, minor disturbance, and little change in precipitation resulted in large increases in biomass. Although spruce-fir species have lower optimal temperatures than other species simulated (Appendix I in supplementary material), longer growing seasons, increased CO₂, and low disturbance

frequency resulted in greater AGB under climate change. For these species, we expect that rising temperatures will increase growth rates, but only to a threshold, beyond which growth rates may decline (Sendall et al. 2015; Gustafson et al. in prep.). In addition, species are sensitive to stressors that we did not simulate (e.g., timber harvest, acid rain, insect defoliation and ice storms), which could cause decline (Gavin et al. 2008; Bishop et al. 2015). Contrarily, we did not simulate a temperature mediated response to foliar nitrogen, which may increase growth under warmer conditions (Fisichelli et al. 2015). Nevertheless, we believe that our simulations depict the major physiological and dispersal processes that will determine tree species response to climate change and therefore are more reliable than approaches based on statistical distributions of climatic conditions within species' ranges. Nonetheless, we acknowledge that climate projections under the RCP 8.5 scenario may produce unforeseen effects stemming from processes not included in this model (e.g., soil microbial activity, invasive insects or extreme weather).

Modeling strengths and limitations

Although our results do not represent the full suite of current and future processes affecting forests, we are confident in our findings, not as predictions, but as scenarios of plausible futures. By incorporating long-term measurements of NEE and a large sample of inventory plots, our calibration procedure provided confidence that successional trajectories of common New England forest types were moderately well represented. Compared to other landscape simulation modeling in the region (Scheller et al. 2011; Thompson et al. 2011), our calibration was more intensive (more data points) and our results showed similar agreement with empirical NEE and AGB. However, our calibration did not include every ecophysiological process. For example, the overestimation of summer month growth (negative NEE) for the hemlock eddy-flux tower at Harvard Forest was likely caused by damage from the hemlock woolly adelgid (*Adelges tsugae*) (Albani et al. 2010) that became established at the eddy-flux site. As PnET-Succession simulates monthly climate data, we did not include individual extreme weather events expected to be exacerbated by climate change (e.g., individual storms, or freeze events). These events have had, and will continue to

influence New England forests. Nevertheless, the anomalies that we found can generally be explained, and we have demonstrated that PnET-Succession was successful at simulating New England forests under current climate at multiple scales. PnET-Succession is particularly strong because it does include climate extremes better than most models, including other variants of LANDIS that rely on average growth and establishment rates at an annual or decadal time step. The climate extremes that have the most effect on structuring forests (e.g., droughts, heat waves, cold winters) are robustly included at a monthly time-step.

Because our focus was on recovery dynamics and the role of climate change, we did not explicitly simulate forest harvesting or land use change, which would almost certainly impact recovery dynamics (Ordonez et al. 2014; Wear and Coulston 2015). The recovery dynamics in our simulations continue patterns of recovery from agricultural abandonment and exploitive harvesting in the nineteenth century as well as the recent land-use regime. Our initial conditions represent modern forests as measured by inventory plots. These forests are a product of the contemporary land-use regime. One consequence of “turning off” the modern disturbance regime may be an overestimate of the magnitude of recovery effects and an underestimate of the climate effects. However, our results are consistent throughout the region, even in areas that are subject to little or no timber harvest or other major disturbances such as federally-owned forests in Vermont and New Hampshire and the suburban forest of southern New England. We acknowledge that land-use interactions with climate change will play an important role in structuring future New England forests and this is an important research topic. Indeed, we are exploring additional interacting drivers such as forest conversion (Ordonez et al. 2014), timber harvesting (Nunery and Keeton 2010) and insects (Albani et al. 2010) that will likely have larger impacts to New England forests than climate change alone, and may interact with climate change in unexpected ways.

We conclude that over the next century, recovery dynamics will supersede climate change effects on New England forests in terms of changes in tree species composition. Most of the dominant tree species and forest types are likely to persist, and some will thrive over the next century. However, our results do not speak to even longer-term effects when extant

trees senesce and regeneration becomes more of a driver under an altered climate.

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