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Abstract Projections of vegetation distribution that incorporate the transient responses of vegetation to climate change are likely to be more efficacious than those that assume an equilibrium between climate and vegetation. We examine the non-equilibrium dynamics of a temperate forest region under historic and projected future climate change using the dynamic ecosystem model LPJ-GUESS. We parameterized LPJ-GUESS for the New England region of the United Sates utilizing eight forest cover types that comprise the regionally dominant species. We developed a set of climate data at a monthly-step and a 30-arc second spatial resolution to run the model. These datasets consist of past climate observations for the period 1901–2006 and three general circulation model projections for the period 2007–2099. Our baseline (1971–2000) simulation reproduces the distribution of forest types in our study region as compared to the National Land Cover Data 2001 (Kappa statistic=0.54). Under historic and nine future climate change scenarios, maple-beech-basswood, oaks and aspen-birch were modeled to move upslope at an estimated rate of 0.2, 0.3 and 0.5 myr^{-1} from 1901 to 2006, and continued this trend at an accelerated rate of around 0.5, 0.9 and 1.7 myr^{-1} from 2007 to 2099. Spruce-fir and white pine-cedar were modeled to contract to mountain ranges and cooler regions of our study region under projected future climate change scenarios. By the end of the 21st century, 60% of New England is projected to be dominated by oaks relative to 21% at the beginning of the 21st century, while northern New England is modeled to be dominated by aspen-birch. In mid and central New England, maple-beech-basswood, yellow birch-elm and hickories co-occur and form novel species associations. In addition to warming-induced northward and upslope shifts, climate change causes more complex changes in our simulations, such as reversed conversions between forest types that currently share similar bioclimatic ranges. These results underline the importance of considering community interactions and transient dynamics in modeling studies of climate change impacts on forest ecosystems.

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1 Introduction

Climate is an important determinant of species distributions (Davis and Shaw 2001; Parmesan and Yohe 2003). Climatic change associated with the onset of the Younger Dryas (YD) cold interval at the end of the last glaciation shifted vegetation across northeastern America toward cold-tolerant species like spruce; cold-tolerant species were then replaced by temperate white pine, beech and oaks as climate warmed at the end of the YD (Oswald et al. 2009). Climate was likely a cause of the mid-Holocene decline of eastern hemlock in temperate forests of the northeastern U.S. (Foster et al. 2006). Recent climate change has been associated with upslope shifts of northern hardwood forests along montane elevation gradients over the period 1964–2004 (Beckage et al. 2008). The influence of recent and past climate on forest distribution suggests that future climate change will result in continued change in the composition and distribution of forests in the northeastern U.S. (e.g. Evans and Perschel 2009).

Predicting the ecological effects of climate change is increasingly important as the rate and magnitude of anthropogenic perturbation of the climate system increases. Projections of the responses of forests to climate change can anticipate species shifts and their ecological effects (Farnsworth and Ogurcak 2006). The composition and distribution of New England forests also has global implications because of their significance in sequestrating atmospheric CO_2 (Hooker and Compton 2003) thereby mitigating climate change (Evans and Perschel 2009). Past projections of forest response to climate change in the New England region have been based on statistical or process based models that assume vegetation is in equilibrium with climate. The climate envelope-based studies (e.g. Iverson and Prasad 2001; McKenny et al. 2007) have assumed that vegetation and climate are in equilibrium and have ignored the impacts of climate and atmospheric CO_2 concentration on the physiological and biogeochemical dynamics of vegetation. Equilibrium process model-based studies (e.g. Tang and Beckage 2010) consider the physiological and biogeochemical dynamics of vegetation but still assume vegetation and climate are in equilibrium. In addition, both climate-envelope and equilibrium vegetation models ignore not only the process of ecological succession in terrestrial vegetation but also the non-linear effects of climate change on the trajectory of vegetation change (Bachelet et al. 2001). As a result, they are unable to simulate the transient dynamics of terrestrial vegetation under climate change, such as the interannual variations of plant growth and the succession of plants through time (Prentice and Solomon 1990; Sitch et al. 2003; Tang and Bartlein 2008).

Vegetation distribution is often not in equilibrium with climate condition (Woodward and Beerling 1997). Dynamic vegetation models (DVMs) have been developed to account for the non-equilibrium nature of vegetation by including the lags and feedbacks resulting from tree life histories and their interactions at the population and community levels. Some DVMs with greater mechanistic detail may consider the differential birth, growth and death of individual trees as a function of species' response to climatic factors, light and nutrients (e.g. LPJ-GUESS, Smith et al. 2001). The resulting models are therefore able to simulate the transient changes in vegetation composition and distribution (Tang and Bartlein 2008), such as the drought-induced species mortality (Bachelet et al. 2001). In addition, DVMs simulate the physiological and biogeochemical processes of plants, such as photosynthesis and the carbon flux between different compartments (e.g. leaf, stem, root and litter). They are able to model the growth of plants over space and time, on scales ranging from days to centuries and from local to global (Woodward and Lomas 2004). DVMs often explicitly consider the differential physiological traits of plants, such as shade- and drought-tolerance and fire resistance. Depending on the study system (region) and model, this may enable researchers to differentiate major species at the
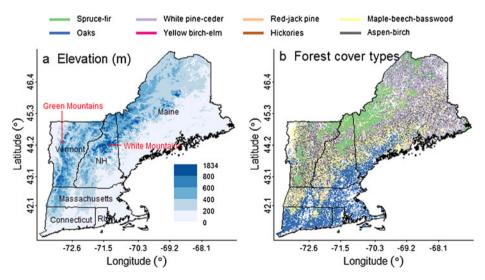
regional or local scale, which may be generalized as the same plant functional type in an equilibrium model (Koca et al. 2006).

In this study, we applied a dynamic ecosystem model, LPJ-GUESS (Smith et al. 2001), to examine the potential transient dynamics of forest composition and distribution in New England under historical (1901–2006) and future (2007–2099) projected climate change. We used relatively high-resolution climate data at 30-arc second spatial resolution to run LPJ-GUESS. Historical climate data in monthly-step were derived from PRISM (Daly et al. 2000, 2002) and CRU TS 3.0 (Mitchell and Jones 2005) data sets. We developed nine future climate change scenarios (CCS) based on three GCM runs, i.e. HadCM3 (Gordon et al. 2000; Pope et al. 2000), CGCM3.1 (Kim et al. 2002, 2003) and ECHAM5 (Jungclaus et al. 2005), driven by three IPCC (International Panel on Climate Change) SRES (Special Report on Emission Scenarios) B1, A1B and A2 storylines that bracket the range of likely future climate trajectories. We believe that our analysis provides for an improved understanding on the potential consequences of global climate change on forest composition and distribution in New England, compared with earlier studies that have relied on equilibrial assumptions.

2 Methods and materials

2.1 The study region

New England is located in the northeastern corner of the United States and consists of six states, i.e., Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut (Fig. 1a). The landforms in New England are relatively flat in coastal areas where elevation is in general less than 200 m. In contrast, the interior areas are dominated by mountains with varying elevation from 200 to 1,834 m. Climate patterns in New England also vary throughout the region. Northern New England is characterized by a humid continental short

Fig. 1 a The topography and geographic regions in New England. 'NH' and 'RI' correspond to New Hampshire and Rhode Island. **b** The modeled spatial distribution of eight forest cover types in New England for the baseline period 1971–2000, respectively

summer climate, with mild summers and cold winters. Southern New England and the coastal areas have a humid continental long summer climate, with warm summers and cold winters. Historically, New England forests were strongly impacted by human-related activities (Foster et al. 2002; Parshall et al. 2003). Nevertheless, the current distribution of forest trees in New England reflects, to a large degree, climatic gradients across the region: Balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and red spruce (*Picea rubens*), for example, currently predominate in regions associated with cooler climates such as at higher elevations and in northern New England, while white oak (*Quercus alba*), black oak (*Quercus velutina*) and pignut hickory (*Carya glabra*) are associated with warmer conditions found at lower elevations and in southern New England.

2.2 Model, PFT definition and parameterization

We used LPJ-GUESS (Smith et al. 2001; Sitch et al. 2003; Hickler et al. 2004), a generalized regional dynamic ecosystem model, to predict the potential transient dynamics of forest in New England under historical and future projected climate change. LPJ-GUESS combines mechanistic representations of plant physiological and biogeochemical processes with demographic gap models, such as sapling establishment, species competition and mortality. LPJ-GUESS does not simulate seed dispersal, but does simulate the succession and the growth of individual trees on a number of replicate patches, with each patch approximating in size the area of influence of a large, mature tree on its neighbors. In LPJ-GUESS, individual tree height and diameter growth are regulated by carbon allocation, conversion of sapwood to heartwood and a set of prescribed allometric relationships (Smith et al. 2001; Sitch et al. 2003). Individual trees with negative increments of carbon in different compartments (e.g. leaves) are removed from the simulation.

LPJ-GUESS accounts for multiple driving factors that affect plant phenological, physiological and biogeochemical processes, such as the effects of temperature on the kinetics of plant's photosynthesis and respiration, and atmospheric CO_2 concentration on vegetation growth, biomass and soil carbon (Smith et al. 2001; Hickler et al. 2004). In addition, it considers the effects of climate-mediated environmental disturbances like fires and drought on species composition and dynamics (e.g. mortality). In general, LPJ-GUESS simulates vegetation at a location as a mixture of plant functional types (PFT), which can represent either individual species or groups of species, determined jointly by their bioclimatic limits, their competition for below-ground resources and light, the climate-related dynamics (e.g. drought-induced damage), and the state of carbon allocation. The model simulates the leaf area index (LAI) of each PFT as well as the carbon flux between the soil, vegetation and atmosphere. LPJ-GUESS has been applied in and validated by a number of studies at both regional and local scales (e.g. Smith et al. 2001; Hickler et al. 2004; Morales et al. 2005; Koca et al. 2006). Details of the LPJ-GUESS model are available in Smith et al. (2001).

We classified dominant forest tree species in New England into eight PFTs on the basis of morphological, phenological, shade- and drought-tolerance traits (Table 1). These PFTs encompass most though not all widespread species that are currently found in New England and form eight forest cover types that are commonly considered in studies of forests in this region (e.g. Iverson and Prasad 2001). We considered the current geographic ranges of species when defining multispecies PFTs so that included species in each category have similar distributions. Given the coexistence of multiple PFTs in a grid cell, we defined the dominant PFT in a modeled grid cell as the PFT that has the highest LAI value. In addition, we excluded the areas in our simulations that are currently dominated by human land-use activities (e.g. urban areas and agriculture lands).

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Table 1 Tree species that were included in the eight plant functional types (PFT) used for simulating forests in New England

Plant functional types	Forest cover types	Species composition	
		Scientific name	Common name
1. Boreal shade tolerant needleleaf evergreen tree	Spruce-fir	*Abies balsamea*	Balsam fir
		Picea mariana	Black spruce
		Picea rubens	Red spruce
2. Northern intermediate shade tolerant needleleaf evergreen tree	Pine-spruce-cedar	*Pinus strobus*	White pine
		Picea abies	Norway spruce
		Thuja occidentalis	White cedar
3. Boreal shade intolerant needleleaf evergreen tree	Red-jack pine	*Pinus banksiana*	Jack pine
		Pinus resinosa	Red pine
4. Northern shade tolerant broadleaf deciduous tree	Maple-beech-basswood	*Acer saccharum*	Sugar maple
		Fagus grandifolia	American beech
		Tilia americana	American basswood
5. Temperate intermediate shade tolerant broadleaf deciduous tree	Oaks	*Quercus alba*	White oak
		Quercus prinus	Chestnut oak
		Quercus velutina	Black oak
6. Northern intermediate shade tolerant broadleaf deciduous tree	Birch-elm	*Betula alleghaniensis*	Yellow birch
		Ulmus americana	American elm
7. Temperate shade intolerant broadleaf deciduous tree	Hickories	*Carya glabra*	Pignut hickory
		Carya cordiformis	Bitternut hickory
		Carya tomentosa	Mockernut hickory
		Carya ovata	Shagbark hickory
8. Boreal shade intolerant broadleaf deciduous tree	Aspen-birch	*Populus tremuloides*	Quaking aspen
		Betula papyrifera	Paper birch

Some abundant or important (of economic value) species, such as eastern hemlock and black cherry, are not considered in simulation because their ranges are distinct from those of other species belonging to the same PFT

Estimates of parameters for each PFT were based on published literature (e.g. Hickler et al. 2004; Withington et al. 2006). Parameters that describe shade-tolerance, drought-tolerance and fire resistance were derived from the USDA (United States Department of Agriculture) Conservation Plant Characteristic (CPC) database (http://plants.usda.gov/about_characteristics.html). The USDA CPC database ranks the relative tolerance of plant species to drought on a four-point scale along with the relative ability of the plants to resprout, regrow or re-establish from seed after a fire. We quantified these scales (e.g. high, medium, low and none for drought tolerance) referring to published literature (e.g. Hickler et al. 2004) (Table 2). Details of quantification are available in Appendix S1 in Supplementary Material. We combined CRU TS 3.0 long-term mean climatology of temperature and Little's vector format of species distribution data for North America (http://esp.cr.usgs.gov/data/atlas/little/) to define the potential bioclimatic limits of the eight PFTs under study. We specifically used 2% and 98% percentiles of temperature and growing degree days from CRU TS 3.0 to define the lower and upper bioclimatic limits of the PFTs (Table 2).

Table 2 Parameters used to define the eight PFTs used in our LPJ-GUESS simulations

Forest cover types	ShT[1]	DrT[2]	FiR[3]	SLA[4] (m^2 kgC^{-1})	Lon[5] (years)	LeL[6] (years)	Tmin[7] (°C)	Tmax[8] (°C)	gdd5[9] (>5°C)
1. Spruce-fir	Tolerant	0.23	0.08	13.1	300	5	−23.0	−5.6	607
2. White pine-cedar	Intermediate	0.10	0.05	12.0	250	3	−18.7	1.7	1,092
3. Red-jack pine	Intolerant	0.20	0.09	11.0	180	2.5	−18.5	−7.1	840
4. Maple-beech-basswood	Tolerant	0.30	0.14	43.4	350	0.6	−14.2	6.1	1,375
5. Oaks	Intermediate	0.28	0.14	33.0	400	0.6	−9.3	8.1	1,890
6. Yellow birch-elm	Intermediate	0.30	0.05	41.3	250	0.6	−16.7	0.4	1,075
7. Hickories	Intolerant	0.37	0.13	32.0	250	0.6	−7.9	10.6	1,950
8. Aspen-birch	Intolerant	0.20	0.16	30.3	200	0.6	−24.8	−5.4	480

ShT[1] – Shade tolerance; DrT[2] – drought tolerance used to calculate plant's water uptake from soil, which in turn limits sapling establishment; FiR[3] – Fire resistance used to calculate tree mortality associated with fire probability and biomass destroyed by fire; SLA[4] – specific leaf area; Lon[5] – Longevity; LeL[6] – Leaf longevity; Tmin[7] – minimum temperature in coldest month for sapling establishment; Tmax[8] – maximum temperature in warmest month for sapling establishment; gdd5[9] – growing degree days above 5°C for sapling establishment. The quantification of drought tolerance, fire resistance, specific leaf area, tree longevity and leaf longevity for each PFT approximates the mean of these parameters for all species that consists of this PFT (see Appendix S1 for details)

2.3 Climate, soil and CO_2 data

We used temperature (°C), precipitation (mm), percent sunshine (%) and wet day frequency (days) all in monthly time-steps for the period 1901–2099 to run LPJ-GUESS. Monthly temperature and precipitation for the period 1901–2006 were derived from PRISM 2.5-arc second data sets (Daly et al. 2000, 2002) while monthly percent sunshine and wet day frequency for this period were downscaled from the CRU TS 3.0 data sets at 0.5° (Mitchell and Jones 2005). Our future data for the four climate variables for the period 2007–2099 were derived from HadCM3, CGCM3.1 and ECHAM5 model runs driven by each of three IPCC SRES B1, A1B and A2 storylines. These nine scenarios describe future potential economic and societal trajectories that result in different levels of greenhouse gas emissions and resultant climate change (IPCC 2007). We interpolated all monthly climate data into 30-arc second spatial resolution by targeting the SRTM 30-arc second elevation data (Farr and Kobrick 2000; Rosen et al. 2000) (Appendix S2) using the approach described in Tang and Beckage (2010). Compared to the baseline (1971–2000) condition, New England is projected to be warmer and wetter under most scenarios in the end of the 21st century (Appendix S3).

Our soil texture data (Appendix S2) for running LPJ-GUESS were derived from the USDA Soil Survey Geographic (SSURGO) Database, available from http://soils.usda.gov/survey/geography/ssurgo/. The SSURGO data provide information about the proportionate content of particles (sand, silt and clay) in a soil. We defined soil texture in New England into coarse (clay <18% and sand >65%), medium (clay <35% and sand <65% or sand<=82 and clay >18%) and fine (clay>35%) classes following the FAO rules (FAO 1991). Annual atmospheric CO_2 concentration data for the historic period 1901–2006 and for the future period 2007–2009 under SRES-B1, -A1B and -A2 storylines were taken from Schlesinger and Malyshev (2001). Projected future atmospheric CO_2 concentration in a given year is the highest for the A2 storyline while the lowest for the B1 storyline.

2.4 Modeling protocol and validation

The LPJ-GUESS simulations for New England start from "bare ground" with 10 replicate patches per grid cell for 1199 simulation years (1000 spin-up period plus 199 simulation years). The 1,000 years for 'spin up' were required for the vegetation and soil and litter pools to reach equilibrium with the long-term climate (e.g. Koca et al. 2006), or for vegetation biomass to reach a steady state in the existence of disturbances (e.g. fire), at the initial point of the simulation. The monthly climate data for the period 1901–1930 was detrended using a locally weighted scatter-plot smoothing algorithm (Cleveland 1979) prior to being used for the model spin-up; this insured there was no temporal trend in the climate data used for model spin up. After this equilibrium was reached in the 'spin up' period, the model was allowed to advance in a non-equilibrial manner, simulating the potential transient dynamics of vegetation under historical climate data (for 1901–2006) and future GCM projections (for 2007–2099), respectively.

We used the 2001 National Land Cover Data (NLCD 2001) (Kelly and White 1993; Vogelmann et al. 1998a, b) to validate modeled vegetation for New England. NLCD 2001 distinguishes three forest cover types, i.e. evergreen, deciduous and mixed forests for the United States based on foliar vegetative cover characteristics. We reclassified our modeled PFTs into categories that correspond to the three forest cover types in NLCD 2001 for evaluation of model performance. Specifically, we averaged the 30-year (1971–2000) mean of LAI at each grid cell for each PFT and then calculated the sum of average LAI for evergreen trees and deciduous trees. For comparison to the three forest classes in NLCD 2001, we defined (i) areas where the summed LAI of evergreen trees accounted for 75% or more of the total LAI as evergreen forest, (ii) areas where the summed LAI of deciduous trees accounted for 75% or more of the total LAI as deciduous forest, and (iii) areas where the summed LAI of neither evergreen nor deciduous trees accounted for as much as 75% of the total LAI as mixed forest. These reclassified forest types were compared to the three forest types in NLCD 2001 for model validation.

We used the Kappa statistic (Cohen 1960) and Fuzzy Kappa (Hagen-Zanker et al., 2005) to measure the goodness of fit between the three reclassified forest types from the model simulations and the corresponding classes in NLCD 2001. Details of how Kappa and Fuzzy Kappa statistics were calculated are described in Tang et al. (2009). Both Kappa and Fuzzy Kappa followed the same rating system: values greater than 0.75 indicate very good-to-excellent agreement, values between 0.40 and 0.75 indicate fair-to-good agreement, and values of 0.40 or less indicate poor agreement (Monserud and Leemans 1992; Landis and Koch 1977). In addition, simulations in which one input (e.g. temperature or precipitation) climate variable was allowed to vary while others were held at the baseline (1971–2000) mean conditions and simulations using the same HadCM3 A1B climate scenario but with SRES-B1 (lower) and -A1B (higher) CO_2 atmospheric concentrations were performed respectively to examine the respective effects of temperature, precipitation and elevated CO_2 on potential forest dynamics in New England.

We compared the simulated future changes in forest distribution between the period 2071–2099 and the period 1961–1990 with those simulated using an equilibrium vegetation model in a previous study (Tang and Beckage 2010). For comparison, we combined our modeled eight forest cover types into three categories, i.e., boreal conifer forest, northern deciduous hardwoods and mixed oak-hickory forest, to match those from the equilibrium simulation. We calculated the mean of latitude, elevation and area from all cells for a given forest type in the two periods being compared. The differences in latitude or elevation or ratios in areal extent between the baseline and future periods are compared with their counterparts from the equilibrium simulation.

3 Results

3.1 Model validation

Our modeled distributions of eight PFTs (e.g., eight forest types) are broadly consistent with general climate-determinant vegetation distribution in New England (e.g. Fuller et al. 1998) (Fig. 1b). For example, the spruce-fir is modeled to predominate in northern New England and at high elevations, such as in the Green Mountains of Vermont and the White Mountains of New Hampshire (Fig. 1a, b). In these areas, monthly mean temperature is comparatively lower than in other regions across New England (Appendix S2). The modeled deciduous forests, like maple-beech-basswood, yellow birch-elm and aspen-birch, which are major components of northern deciduous hardwoods in New England, are mainly distributed in mid or central cooler uplands (Fig. 1a,b). The oaks, the dominant species in mixed oak and hickories forest, are modeled to dominate in southern New England and at low elevations such as in southern Maine (Fig. 1a, b).

The modeled overall distributions of the three aggregated forest types (i.e., the eight PFTs combined into evergreen, deciduous and mixed forest) agree well with the NLCD 2001 data (Fig. 2a, b). The model's overall Kappa and Fuzzy Kappa statistics of 0.54 indicate that LPJ-GUESS does well in simulating these three forests in New England. For example, both model simulations and NLCD 2001 show that southeastern and northwestern Maine are dominated by evergreen and mixed forests, resulting in the individual Kappa statistics 0.56 for evergreen forest and 0.50 for mixed forest (Table 3). The simulated evergreen forest (consisting of spruce-fir and white pine) in Vermont and New Hampshire is mainly distributed in mountain areas such as in the Green Mountains and the White Mountains, consistent with NLCD 2001 (Fig. 2). In southwestern New Hampshire, the model simulates some evergreen forests like white pine-cedar, also corresponding well to evergreen forest classified in the NLCD 2001.

Our model is also able to accurately simulate deciduous forests for New England. For example, the NLCD 2001 shows that Connecticut and Rhode Island are dominated by deciduous forests, coinciding well with modeled oaks in these two states (Fig. 2). Visually, the modeled evergreen, deciduous and mixed forests in eastern, mid and western Massachusetts
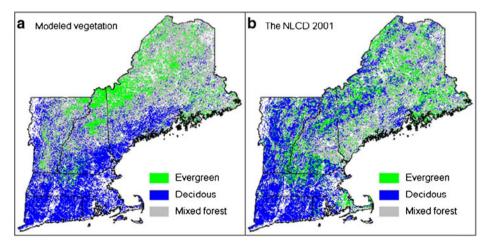

Fig. 2 Comparison of three forest types derived from model simulations and aggregated into deciduous, evergreen, or mixed forest types classifications for comparison with NLCD 2001

Table 3 Statistics used in the accuracy assessment of modeled vegetation for New England

Statistics	Forest cover types		
	Evergreen	Deciduous	Mixed
Model's accuracy[a]	76%	75%	64%
Producer's accuracy[b]	56%	70%	79%
Overall accuracy	70%		
Individual Kappa	0.56	0.55	0.50
Overall Kappa	0.54		
Individual Fuzzy Kappa	0.56	0.52	0.50
Overall Fuzzy Kappa	0.54		

[a] The model's accuracy is the probability that predicted vegetation corresponds to the classification in the NLCD 2001 data set

[b] The producer's accuracy is the probability that the number of grid cells classified as a forest cover type in the NLCD 2001 data will be correctly simulated by the model
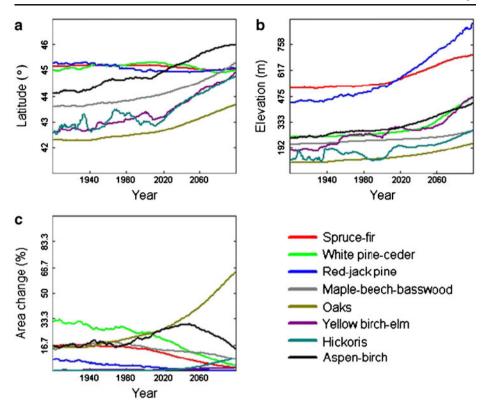
are similar to their counterparts in the NLCD 2001 except for southeastern Massachusetts, where the model simulates deciduous forest while the NLCD 2001 classified vegetation mainly as evergreen (Fig. 2a,b). In actuality, southeastern Massachusetts is dominated by a mixture of pitch pine and oaks. For regions to the west of the Green Mountains of Vermont, the modeled deciduous forest, which consists of oaks, maple-beech-basswood and aspen-birch (Fig. 1b), is consistent with the deciduous forest classified in the NLCD 2001. The relatively high individual kappa (0.55) and fuzzy kappa (0.52) justify the model's performance in simulating deciduous forest for New England (Table 3). Other evaluations based on modeled LAI (Appendix S4), forest NPP and biomass (Tang et al. 2010) also justified the model's performance in simulating vegetation for New England.

3.2 The potential transient dynamics of forest distributional change

Our simulations indicate that deciduous forests have already shifted northward in response to historical climate change and the trend in atmospheric CO_2 concentration (Fig. 3a). Maple-beech-basswood, oaks and aspen-birch were simulated to shift northward at a rate of 401 myr^{-1} (R^2=0.93) (averaged over all scenarios and hereafter), 333 myr^{-1} (R^2=0.90) and 784 myr^{-1} (R^2=0.90) over the years 1901–2006, with continuing northward shifts at an increased rate of 1567 myr^{-1} (R^2=0.99), 1,392 myr^{-1} (R^2=0.99) and 1,612 myr^{-1} (R^2=0.99) over the years 2007–2099. For evergreen forest, the distribution of spruce-fir was relatively stable before 2006 but shifted southward to regions of higher elevation in our study area at a rate of 228 myr^{-1} (R^2=0.84) after 2007. In contrast, the distribution of red-jack pine shifted southward at a rate of 356 myr^{-1} (R^2=0.82) over the years 1901–2006 while white pine-cedar shifted northward at a rate of 301 myr^{-1} (R^2=0.86) in this period (Fig. 3a). As of 2007, the latitudinal distribution of these two evergreen forests reversed: the white pine-cedar shifted southward at a rate of 535 myr^{-1} (R^2=0.90) but red-jack pine shifted northward at a rate of 129 myr^{-1} (R^2=0.52). The contraction of spruce-fir and white pine-cedar to higher elevations such as Green Mountain in Vermont and to the cooler region centered on the corner of northern New Hampshire and northwestern Maine resulted in the southward shift of these forests (Fig. 4).
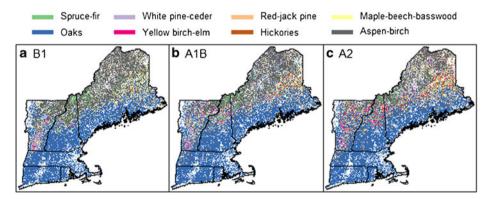
Our simulations suggest that historical climate change has shifted all forests to higher elevations and that projected future climate change will continue this trend (Fig. 3b). Maple-beech-basswood, oaks and aspen-birch were simulated to move upslope at a rate of around

Fig. 3 Projected historic (1901–2006) and future (2007–2099) dynamics of eight forest cover types in New England. The values in all panels for each forest cover type (or dominant PFT) are averaged values based on all grid cells for each specified cover type and across nine climate change scenarios, including simulations based on historical climatic conditions

0.2 myr^{-1} (R^2=0.94), 0.3 myr^{-1} (R^2=0.95) and 0.5 myr^{-1} (R^2=0.93) over the years 1901–2006, and this trend continued at an increased rate of around 0.5 myr^{-1} (R^2=0.91), 0.9 myr^{-1} (R^2=0.97) and 1.6 myr^{-1} (R^2=0.99) over the years 2007–2099, respectively. However, the

Fig. 4 The modeled spatial distribution of eight forest cover types for New England in 2071–2099 under SRES B1, A1B and A2 scenarios. The forest cover type in a grid cell was defined as the mode of forest cover types based on the highest leaf area index under three GCM runs

elevational increases in evergreen forests, especially for spruce-fir and white pine-cedar, resulted mainly from losses of these communities at low elevations rather than general shifts to high elevations, as was the case for deciduous forests, which are usually found at lower elevations in our study region. Evergreen forests mostly occupy the highest elevations in our region and so are unable to migrate to higher elevations, but rather are lost at lower elevations (Fig. 3b).

Our model indicated that historical climate change has reduced the areal extent of evergreen forests in New England and future projected climate change is expected to result in further losses of evergreen forests (Fig. 3c). The simulated extent of spruce-fir, white pine-cedar and red-jack pine decreased at an annual rate of around 0.2% (R^2=0.74), 0.3% (R^2= 0.84) and 1.6% (R^2=0.93) over the years 1901–2006 and continued to decrease at an annual rate of 0.9% (R^2=0.99), 0.9% (R^2=0.99) and 0.7% (R^2=0.88) over the years 2007–2099. We estimate that oaks increased in area by 0.4% per year (R^2=0.92) before 2006 but will increase by 2.1% per year (R^2=0.98) after 2006. Compared to other forests, aspen-birch was modeled to increase at an annual rate of 0.5% (R^2=0.79) before 2050 but decrease at an annual rate of 1.7% (R^2=0.98) after 2051. Maple-beech-basswood were simulated to increase at an annual rate of 0.4% (R^2=0.88) before 1970 but to decrease at an annual rate of 0.4% (R^2=0.97) after 1970.

3.3 The projected forests distribution in the end of this century

Projected future climate change will continue to result in compositional and range shifts. Compared to the baseline simulation, our model indicated that maple-beech-basswood, spruce-fir, white pine-cedar, red pine-jack pine will decrease by 82%, 80%, 98% and 44% by 2085 respectively while oaks are projected to increase by 166% (Table 4). Two less common forest types in New England, namely yellow-birch (597 out of 224 588 grid cells in baseline simulation) and hickories (22 cells in baseline simulation) are projected to increase the most in percentage terms due to their small size in the baseline period (Table 4). Overall, 60% of New England is projected to be dominated by oaks while northern New England is modeled to be dominated by aspen-birch by the end of the 21st century (Fig. 4). Yellow-birch, hickories and maple-beech-basswood will co-occur in a transition zone between southerly oaks and northerly aspen-birch and evergreen forests, especially in mid or central uplands of New England (Fig. 4).

3.4 Conversions between forest types

Our simulations indicated that two types of replacements or conversions might occur in New England. First, the southerly-distributed species (e.g. oaks) tend to always replace northerly distributed species (e.g. white pine and aspen-birch) under regional warming and elevated CO_2 concentration (Tables 4 and 5). Second, species with similar bioclimatic ranges might exhibit complex climate change-induced conversion patterns. For example, white pine-cedar was modeled to decrease by 80%, of which 20% was converted to aspen-birch (Table 4). In fact, however, about 3938 grid cells dominated by aspen-birch in 1985 were replaced by white-pine cedar in 2085. At the same time, about 15875 cells originally dominated by white pine-cedar in 1985 were converted to aspen-birch in 2085 (Table 5). A similar phenomenon governed the simulated shift between aspen-birch and maple-beech-basswood (Table 5).

3.5 Effects of climate change and CO_2 enrichment on LAI

When averaged across all cells, temperature increases alone tended to decrease LAI in forests (Fig. 5a–h). Precipitation increases alone tended to enhance LAI in most forests

Table 4 Internal conversions for eight forest cover types from 1985 to 2085

Forest cover types	1985 Cells	2085 Δ (%)[a]	Forest cover type internal conversion contribution (%)							
			SF[1]	PC[2]	JP[3]	MBB[4]	Oaks	BE[5]	Hick[6]	AB[7]
1. Spruce-fir	33319	−82		−10	1	−4	−10	−3	−3	−53
2. White pine-cedar	58910	−80	5		2	−17	−40	−2	−8	−20
3. Red-jack pine	6111	−98	−4	−14		−3	−11	−2	−4	−60
4. Maple-beech-basswood	37321	−44	3	27			−80		−5	11
5. Oaks	47803	166	7	49	2	63		1		44
6. Yellow birch-elm	597	454	163	169	25	16	−94		−3	179
7. Hickories	22	53473	3735	20883	984	9034	347	86		18404
8. Aspen-birch	40505	7	43	30	9	−10	−52	−3	−10	

Data shown here are averaged values based on simulations for the period 1971–2000 (refer to as 1985) and for the period 2071–2099 (refer to as 2085)

[a] Positive value means "gain from" and negative value means "loss to". SF[1] – Spruce-fir; PC[2] – White pine-cedar; JP[3] – Red-jack pine; MBB[4] – Maple-beech-basswood; BE[5] – Yellow birch-elm; Hicks[6] – Hickories; AB[7] – Aspen-birch
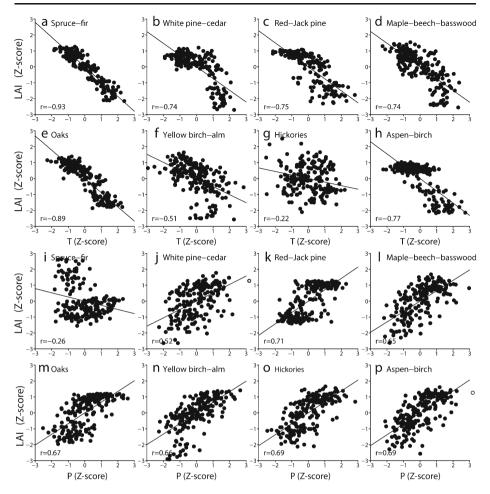
(Fig. 5j–p), except for spruce-fir that dominate at highest elevations where annual precipitation is high (Fig. 5i). Our simulation also indicated that increase in CO_2 concentration alone appeared to enhance LAI in all forests. The simulated LAI increase in spruce-fir, white pine-cedar and red-jack pine under high CO_2 concentration is greater than that in maple-beech-basswood (Fig. 6a). In addition, compared to forests of similar bioclimatic limits like spruce-fir and maple-beech-basswood, aspen-birch appears to benefit more from regional warming and elevated-CO_2 condition (Fig. 6a). Among all forests, LAI increases in oaks and hickories are the greatest as temperature rises (Fig. 6a).

Table 5 Transition matrix of modeled cells of each forest cover type between 1985 and 2085

Forest cover types in 2085	Forest cover types under the baseline condition (1985)							
	SF[1]	PC[2]	JP[3]	MBB[4]	Oaks	BE[5]	Hickories	AB[6]
1. Spruce-fir	5674	71	359					27
2. White pine-cedar	3238	4028	862	31	3			3938
3. Red-jack pine	116		21					
4. Maple-beech-basswood	1247	9949	158	4849	13	16		4520
5. Oaks	3454	23406	697	30045	47687	560	21	21238
6. Yellow birch-elm	970	1008	147	114				1067
7. Hickories	817	4571	215	1977	97	18		4028
8. Aspen-birch	17799	15875	3649	303				5683

Data shown here are averaged values based on simulations for the period 1971–2000 (refer to as 1985) and for the period 2071–2099 (refer to as 2085). SF[1] – Spruce-fir; PC[2] – White pine-cedar; JP[3] – Red-jack pine; MBB[4] – Maple-beech-basswood; BE[5] – Yellow birch-elm; AB[6] – Aspen-birch. The values in each column indicate the number of cells occupied by a forest cover type under the baseline (1985) simulation were either converted to a different type or kept same (diagonal numbers) under the future (2085) simulation as listed in each row
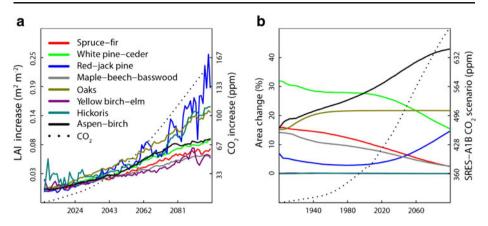
Fig. 5 Temperature increases alone **a–h** decrease annual mean LAI in all forests while precipitation increases alone **j–p** enhance annual mean LAI in most forests, except for spruce-fir **i** that dominates at highest elevations where annual precipitation is high. For plotting, all variables were normalized as Z-score that is derived by subtracting the population mean from an individual and then dividing the difference by the population standard deviation

3.6 Comparison of dynamically and statically modeled future changes

Our modeled future changes in forest distribution between the period 2071–2099 and the period 1961–1990 under nine CCSs are generally consistent with those modeled using an equilibrium model (Tang and Beckage 2010) (Table 6). For example, northern deciduous hardwoods are projected to shift northward by 1.1 latitudinal degrees and to be reduced in area by 17% and 19% relative to their baseline simulations under the dynamic and static simulations, respectively. Nevertheless, the upslope movement of boreal conifer forest (150 m) under the dynamic simulation is 410 m lower than that under the equilibrium simulation (560 m). Similarly, the northward shift of mixed oak-hickory forest (1.4 latitudinal degree) under the dynamic simulation is 0.6° less than that (2.0 latitudinal degree) under the static simulation (Table 6).

Fig. 6 **a** Increase in atmospheric CO_2 concentration from SERS B1 (*lower*) to A1B (*higher*) storyline enhances annual mean LAI in eight forest cover types, as illustrated by the differences in annual mean LAI between two simulations under the same climate driving scenario (i.e., HadCM3 A1B) but with different CO_2 concentrations scenarios (SERS B1 vs. SERS A1B). **b** Our simulation with CO_2 increases with other climatic variables kept constant at 30-year' (1971–2000) mean conditions indicated that increases in atmospheric CO_2 concentration is responsible for projected dominance of northern New England by aspen-birch in the late 21st century

4 Discussion

4.1 The difference between modeled and the NLCD forest distribution

Although LPJ-GUESS is able to simulate the current vegetation distribution in New England, major differences between our modeled forests and those classified in the NLCD 2001 still occur in northeastern Vermont, northern New Hampshire and northwestern corner of Maine (Fig. 2). Our modeled evergreen forest is broader and spatially more continuous than is indicated by NLCD 2001. Disregarding limitations in the accuracy of the NCLD 2001 in representing the distribution of forest types in these regions, the differences may result from: (i) the simple classification of our soil texture data used to run our model (Appendix S2) (e.g., soil texture determines soil water holding capacity and thus affects the

Table 6 Comparison of LPJ-GUESS (dynamic) to BIOME4 (equilibrium) projected future changes in forest distribution between the time periods 2071–2099 and 1961–1990

Average changes in	Boreal conifer forest		Northern deciduous hardwoods		Mixed oak-hickory forest	
	LPJ-GUESS	BIOME4	LPJ-GUESS	BIOME4	LPJ-GUESS	BIOME4
Latitude (°)[a]	0.8	1.0	1.1	1.1	1.4	2.0
Altitude (m)[b]	149	556	125	85	80	76
Area extent (%)	−82	−91	−17	−19	209	282

[a] For boreal conifer forest and northern deciduous hardwoods, the latitude refers to their southern boundary. For mixed oak hickory forest, it refers to the northern boundary

[b] Altitude is averaged value for all simulated cells. Because BIOME4 simulates more losses of boreal conifer forest and northern deciduous hardwoods, the contraction of boreal conifers and northern hardwoods to high elevation area result in the big difference in averaged elevation changes. The LPJ-GUESS modeled eight forest cover types were reclassified as three types, i.e. boreal conifers, northern deciduous hardwoods and mixed oak-hickories, for comparison

uptake of water by plants); (ii) the exclusion of topographic effects (e.g. aspect) on vegetation distribution (e.g., shade-intolerant species adapt better in south-facing slopes of mountains); (iii) the inadequacy of climate data in capturing the spatial climatic variation at finer scales, which affects species occurrence along elevational gradients; and (iv) the uncertainties in model parameters (e.g., the drought tolerance of species affects its sapling establishment and different combination of parameters can lead to dominance of one tolerance class, especially for deciduous forests (Wramneby et al. 2008)). Nevertheless, we were able to model a transition zone (i.e. the mixed forest) between evergreen and deciduous forest that does not appear to be present in NLCD 2001 but is known to occur in some regions like in the Green Mountains (Fig. 2). This gives some indication that our simulation might better reflect the nature of forest compositional change over space than the NLCD 2001.

4.2 Modeled potential historical and future vegetation dynamics

The range limits of species in LPJ-GUESS are primarily controlled by temperature indices for sapling establishment, such as the minimum temperature in coldest month, the maximum temperature in warmest month and the growing degree days (> 5°C) (Table 2). In our simulations, deciduous forests shifted northward in response to temperature increases observed in the 20th century and projected increase for the 21st century (Appendix S3). In contrast, three evergreen forests, i.e. spruce-fir, white pine-cedar and red pine-jack pine, were projected to shift southward in the late 21st century (Fig. 3a), because of losses of these forests at lower elevations in the higher latitudes in our study region (Fig. 3a vs. Fig. 4). Overall, the modeled past (before 2006) migration rates of 330 m yr^{-1} for oaks and 400 m yr^{-1} for maple-beech-basswood exceed observed species shifts in similar forests, which range from <100 (McLachlan et al. 2005) to 250 m yr^{-1} (Davis 1989). Nevertheless, historical evidence indicates that the mean center locations of 71 rare plants in New England shifted northward by an average of 68 km between the periods 1820–1975 and 1976–2004 (Farnsworth and Ogurcak 2006), approximating a rate of 370 m yr^{-1} in the period 1820–2004. The modeled future migration rate of 1590 m yr^{-1} for northern deciduous forests and 1390 m yr^{-1} for oaks is consistent with earlier studies for New England (Tang and Beckage 2010) as well as other studies (e.g. Jay et al. 2002, migration rate in high latitude >1,000 m yr^{-1}). We caution, however, that our model simulations do not consider dispersal limitations.

   The average elevation increase under warming and elevated-CO_2 concentration is driven by two distributional shifts, alone or in combination, namely the loss of species at low elevations and the upslope shift of species. Because spruce-fir and red pine-jack pine are dominant mainly at the highest elevations and are modeled to decrease in the future (Fig. 3c), their elevation increases result primarily from their losses at low elevations. For example, compared to the baseline simulation (Appendix S5), spruce-fir is modeled to decrease by 82% by the period 2071–2099 (referred to as 2085 and hereafter) with 53% of these losses replaced by aspen-birch that occurs at lower elevations (Table 4 and Fig. 3b).

   The elevation increases in northern deciduous hardwoods result from both warming-induced upslope movement (e.g. Beckage et al. 2008) and losses of these communities at low elevations. For example, maple-beech-basswood is projected to decrease by 44% by 2085, stemming primarily from the combined effects of an 80% loss to oaks at lower elevations and 27% gain from white-pine cedar at higher elevations (Table 4 and Fig. 3b). The projected elevational increases in oaks and hickories result solely from their upslope movement, in part, because they never appear to be displaced by other forest types in our simulations (Table 4). By 2085, maple-beech-basswood and oaks were simulated to move

upslope by 85 m and 72 m, close to previous estimates of 76 m for both forests (Tang and Beckage 2010). The losses of spruce-fir at low elevations and the shift of white pine to higher elevations results in the uplands (> 450 m) being dominated by white pine (12371 cells compared to 6,000 cells for spruce-fir in 2085) in the late 21st century as observed historically under warming condition (e.g. Oswald et al. 2009).

4.3 The complexity of modeled forest cover conversions

Climate change and elevated CO_2 concentration induce forest conversion through effects on species competition for light, water and nutrients. The southerly-distributed species (e.g. oaks) tend to always replace northerly-distributed species (e.g. white pine and aspen-birch) under regional warming and elevated CO_2 concentration (Tables 4 and 5) because they have relatively larger specific leaf area and are more drought tolerant (Table 2). However, the northward and upslope shifts of forest under regional warming are not the only plausible aspects of climate change-induced vegetation dynamics. Counter-intuitive shifts in the opposing direction to isotherm migration are also possible or even likely to occur as indicated by the reversed conversions in our simulations. Such reversed conversions may be attributed to differences in (i) the physiological traits of species and (ii) the response to regional warming and elevated CO_2 concentration. For example, aspen-birch is comparatively more drought tolerant than white-pine cedar. If regional warming decreases soil moisture in a location, aspen-birch will adapt better to the new condition than white-pine cedar, and vice versa. Likewise, even though the southerly-distributed white-pine cedar tends to generally replace the northerly-distributed aspen-birch, the latter is modeled to gain more (e.g., the higher LAI increase) from elevated CO_2 concentrations and regional warming in the future (see discussion below).

4.4 Effects of climate change and CO_2 enrichment on vegetation dynamic

Historical evidence indicates that vegetation dynamics in New England are most strongly driven by climate (Hall et al. 2002; Foster et al. 2002, 2006). Although recent studies (e.g. Shuman et al. 2004) have argued that temperature trends do not explain all aspects of vegetation dynamics in New England, changes in both precipitation (or soil moisture balance) and CO_2 concentration play an important role in shifting forest growth and composition in New England (Tang and Beckage 2010). In reality, variation in temperature, precipitation, and CO_2 concentration are likely to jointly exert control on forest dynamics in New England according to our simulations and relevant studies (e.g., Tang et al. 2010). For instance, multiple regression analyses showed that the variations of annual LAI (averaged across all grid cells) in almost all forests were positively and linearly correlated with the variations of both temperature and precipitation in New England (Appendix S6). At the cell level, however, the effects of climate change on vegetation such as LAI are more complex and both positive and negative effects can occur depending on the climate change scenario (e.g., Bachelet et al. 2001).

Elevated CO_2 concentration stimulates plant growth directly through enhancement of the carbon-fixation efficiency and indirectly through improvements in the water use efficiency, as confirmed in field studies (e.g. Ainsworth and Long 2005; Hickler et al. 2008). The difference in CO_2-induced increase in LAI and productivity has implications for future forest composition and distribution in New England. For example, the larger LAI increases in evergreen forests (Fig. 6a) imply that boreal conifers (lower drought tolerance, see Table 2) may gain more from the direct effects of elevated CO_2 concentration than does maple-beech-

basswood (higher drought tolerance, see Table 2). Tang and Beckage (2010) argued that elevated CO_2 concentration has potential to reduce the losses of boreal conifers in New England.

Our modeled continuous increase in the area of aspen-birch to 2050 (Fig. 3c) results in northern New England being dominated by aspen-birch in the late 21st century (Fig. 4). A further computational experiment using constant climate but variable CO_2 concentration indicated that CO_2 increases are responsible for the modeled areal increase of aspen-birch in northern New England (Fig. 6b). This is consistent with a recent study (Cole et al. 2010) found that quaking aspen in Wisconsin has grown much faster over the past five decades (1958–2003) than in the past due to elevated CO_2 concentration. An earlier study (Voelker et al. 2006) indicated that historical CO_2 growth enhancement declines with age in *Quercus* (e.g. oaks) and *Pinus* (e.g. pines) over the years 1850–2000. The highest LAI increases in oaks and hickories indicate that elevated-CO_2 concentration along with warming might accelerate the replacement of northern hardwoods by oaks and hickories. Such effects become more discernible after 2040 with increasing CO_2 concentration and corresponding shifts in climate (Fig. 6).

4.5 Model limitations

Although model validation against the NLCD 2001 justified the model's application to New England, the accuracy of modeled historical and future vegetation dynamics for New England is subject to at least four major sources of uncertainty. The first of these is the uncertainty in future climate change scenarios derived from runs of the three GCMs referenced in this study. The GCM data are originally coarse-grained (> 1.8˚ by 1.8˚) with respect to New England and might not capture well the spatial variation of future climatic condition across the region, which in turn affects modeled forest composition and distribution at 30-arc second resolution (Tang and Beckage 2010). The second source of uncertainty is the inclusion of only mean monthly temperature, rainfall and incoming solar radiation in driving shifts in forest composition and distribution as other climate-related factors are likely to be important. Climate change can alter the frequency and severity of forest fire, disease and pests, and the patterns of extreme weather events such as droughts and windstorms. These factors can result in severe changes in forest composition and distribution in New England (Evans and Perschel 2009). Thirdly, species dispersal limitations are not accounted for in the simulations. Dispersal limits can cause species ranges to lag behind modeled changes and thus our simulation might overestimate the rate of future shifts in forest distribution and the conversions occurring among forests. Finally, unmodeled human land use decisions, affecting land cover patterns as well as forest management, have historically greatly affected vegetation patterns and trends in New England (Foster et al. 1998; Fuller et al. 1998).

Nevertheless, we suspect that our simulated forest dynamics are likely to be a better reflection of the vegetation-climate dynamics in New England than those simulated assuming a climate-vegetation equilibrium. The overall consistency of modeled northward shifts of boreal conifer forest and northern deciduous hardwoods between this study using a dynamic vegetation model and a previous study that used an equilibrium model for the same study area (Table 6) may be due, in part, to the regional nature of the study, which limits the potential shifts of forest types. Likewise, the similarity of modeled upslope movement of mixed oak-hickory forest may be driven by both the large area of this forest type in our study region and the relatively low elevational position of this forest type. The discrepancy in modeled upslope movement of boreal conifer forest and northward shift of mixed oak-hickory forest is likely more reflective of the differences in the performance of these two

model types. Since LPJ-GUESS accounts for the temporal lags resulting from succession, the removal of PFTs with negative increments in carbon balance, and transient dynamics of vegetation under changing climate (Koca et al. 2006), the difference in projected upslope movement of boreal conifer forest, for example, is 400 to 500 m less using the dynamic model compared to the equilibrium model (Table 6), suggesting that future climate change might not shift vegetation distribution in New England as rapidly as predicted by statistical or equilibrium models.

Finally, we caution that predictions of how ecological systems are likely to respond to future climate change over decadal time scales may not be possible (Beckage et al. 2011). This is because of the great potential for unexpected interactions between species, non-linearities, and unforeseen events. Our simulation results are projections of what might happen contingent on underlying model assumptions inherent both in the model and in the environmental drivers. Nevertheless, such projections are useful for exploring the potential ecological changes that might occur in response to future climate change.

5 Conclusions

(i) Historical climate change and increases in CO_2 concentration have shifted deciduous forests northward and future projected climate change is modeled to continue to shift these forests further northward at an increasing rate. In contrast, spruce-fir and white pine-cedar are projected to contract to mountain ranges and to cooler interior areas in our study region, resulting in southward range shifts. Historical climate change likewise shifted all forests to higher elevations and future projected climate change will continue and accelerate this trend.

(ii) Historical climate change is modeled to have already reduced the extent of evergreen forests in New England and projected future climate change will cause further losses of evergreen forests, ranging from 80% for white pine-cedar to 98% for red-jack pine. For deciduous forests, our simulations indicate that oaks have increased in area at an annual rate of 0.4% before 2006 and are predicted to increase in area at an accelerated rate of 2.1% after 2006. Maple-beech-basswood increased at a rate of 0.4% before 1970 and decreased at a rate of 0.4% after 1970. By the end of 21st century, 60% of New England is projected to be dominated by oaks while northern New England is simulated to be dominated by aspen-birch. In mid and central New England, maple-beech-basswood, yellow birch-elm and hickories co-occur and form dominant forest cover types.

(iii) Precipitation increase alone enhances LAI in most forests while temperature increase alone reduces LAI in all forests in our model. Elevated concentrations of atmospheric CO_2 stimulate forest growth as suggested by the LAI increases in all forest types, but disproportionately affect forest types: Evergreen forests have a greater response to increasing CO_2 than maple-beech-basswood but a smaller response than oaks and hickories. These differential responses indicate that increase in CO_2 concentration along with rising temperatures hinders the replacement of evergreen forests by northern deciduous hardwoods but accelerates the replacement of northern deciduous hardwoods and evergreens by oaks and hickories.

(iv) Our initial comparison with an equilibrial process-based model suggests that a dynamic non-equilibrial model that accounts for the role of interactions between species, including species succession, results in different spatial and temporal dynamics of forest landscapes. The resultant simulations may better reflect the vegetation dynamics

in response to changing climate in our region. We recommend that dynamic vegetation models be used as another tool, along with equilibrial vegetation models, for understanding the potential impacts of climate change on forested ecosystems, while recognizing that the lack of explicit dispersal in these models represents an area for continued improvement in model projections.

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