

Projecting the distribution of forests in New England in response to climate change

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ABSTRACT

Aim To project the distribution of three major forest types in the northeastern USA in response to expected climate change.

Location The New England region of the United States.

Methods We modelled the potential distribution of boreal conifer, northern deciduous hardwood and mixed oak–hickory forests using the process-based BIOME4 vegetation model parameterized for regional forests under historic and projected future climate conditions. Projections of future climate were derived from three general circulation models forced by three global warming scenarios that span the range of likely anthropogenic greenhouse gas emissions.

Results Annual temperature in New England is projected to increase by 2.2–3.3 °C by 2041–70 and by 3.0–5.2 °C by 2071–99 with corresponding increases in precipitation of 4.7–9.5% and 6.4–11.4%, respectively. We project that regional warming will result in the loss of 71–100% of boreal conifer forest in New England by the late 21st century. The range of mixed oak–hickory forests will shift northward by 1.0–2.1 latitudinal degrees (*c.* 100–200 km) and will increase in area by 149–431% by the end of the 21st century. Northern deciduous hardwoods are expected to decrease in area by 26% and move upslope by 76 m on average. The upslope movement of the northern deciduous hardwoods and the increase in oak–hickory forests coincide with an approximate 556 m upslope retreat of the boreal conifer forest by 2071–99. In our simulations, rising atmospheric CO₂ concentrations reduce the losses of boreal conifer forest in New England from expected losses based on climatic change alone.

Main conclusion Projected climate warming in the 21st century is likely to cause the extensive loss of boreal conifer forests, reduce the extent of northern hardwood deciduous forests, and result in large increases of mixed oak–hickory forest in New England.

Keywords

BIOME4, climate change, global circulation model, species shifts, tree distribution, vegetation model.

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INTRODUCTION

Global climate is projected to warm by 1.8–6.4 °C this century relative to the 1980–99 mean global temperature in response to continued anthropogenic emissions of greenhouse gases (IPCC 2007; Bates *et al.*, 2008). While terrestrial vegetation is expected to shift poleward and to higher elevations in response to projected warming (Parmesan & Yohe, 2003; IPCC, 2007), more precise projections are necessary for planning for the

conservation of biological diversity and increasing the resilience of forest ecosystems (e.g. Farnsworth & Ogurcak, 2006). Projections of forest response to global warming have been largely based on statistical models that map observed species distributions with respect to climate and then re-project these distributions under future climatic conditions (e.g. Iverson & Prasad, 2001; McKenny *et al.*, 2007). This modelling approach assumes a constant relationship between forest distribution and climate and does not account for the direct effects of CO₂

on plant performance. An alternative approach is to simulate plant distributions using process-based models (PBMs) (e.g. Kaplan *et al.*, 2003; Sitch *et al.*, 2003). PBMs simulate fundamental physiological processes that determine vegetation growth, e.g. plant photosynthesis and respiration, as mediated by climate and other environmental conditions, providing an alternative process-based method for projecting vegetation distribution in response to climate change. PBMs have been used to model the distribution of vegetation at the global scale (e.g. Sitch *et al.*, 2003), but this coarse resolution introduces substantial uncertainties in regional projections related to both the lack of detailed parameterization of regional plant functional types (PFTs) and the coarseness of the environmental data employed (e.g. Tang & Bartlein, 2008; Willis & Bhagwat, 2009). Studies that utilize PFTs parameterized for regional vegetation and that downscale general circulation model (GCM) projections to regional geographical scales can improve model projections of future vegetation distribution relative to global model runs.

In this study, we modelled the future distribution of forests across New England in response to projected climate change. Forests in New England are broadly characterized by boreal, northern hardwood and mixed oak–hickory forest types with distributions that have historically corresponded to climate gradients in addition to edaphic conditions and disturbance (e.g. Foster *et al.*, 1998, 2002; Parshall *et al.*, 2003). We used a process-based vegetation model BIOME4 (Kaplan *et al.*, 2003) to simulate the future distribution of these primary forest types under nine future climate change scenarios (CCS). Each CCS is 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) storylines, i.e. B1, A1B and A2, that bracket the range of likely climate trajectories. Our objective was to determine the potential magnitude of spatial displacement of the three widespread forest types of New England by mid- and late 21st century. Our analysis provides the public and policy makers with additional information on potential future changes in vegetation distribution in New England.

METHODS

Vegetation

We modelled the distribution of three dominant forest types in the New England landscape: boreal conifers (e.g. *Abies balsamea*, *Picea mariana* and *Picea rubens*), northern deciduous hardwoods (e.g. *Acer saccharum*, *Fagus grandifolia* and *Betula alleghaniensis*) and mixed oak–hickory forests (e.g. *Quercus alba*, *Quercus velutina*, *Carya glabra* and *Carya ovata*) (Fuller *et al.*, 1998). The distribution of these forest types reflects climatic conditions, in addition to landscape disturbance, historical land use and soil condition (e.g. Foster *et al.*, 1998, 2002; Parshall *et al.*, 2003): Boreal conifer forests are

currently widespread at higher elevations and in northern regions of New England, northern deciduous hardwoods are mainly distributed in the cooler central uplands, and mixed oak–hickory forests are found at lower elevations and more southerly regions. These forest types are generally associated with late successional stages in forest development (McLachlan *et al.*, 2000; Woods, 2000). While earlier successional stages may be present in some regions recovering from natural or anthropogenic disturbance (Fuller *et al.*, 1998), we do not evaluate the effects of historic land use in this study, and removed from this analysis all land-cover types that are currently subject to substantial human use. Although the current relationship between climate and vegetation distribution in New England is partly obscured by human activities and ecological succession following land abandonment (Hall *et al.*, 2002; Parshall *et al.*, 2003), historical evidence points to a strong relationship between climate and vegetation distribution: Rising temperatures in 14,600 yr BP coincided with increases in spruce populations following deglaciation, and subsequent warm and dry conditions after 11,600 yr BP corresponded to the replacement of spruce by pine populations (Shuman *et al.*, 2004). Climate was also a likely driver of the mid-Holocene decline of eastern hemlock as well as in changes in abundance of oaks and chestnut in New England (Shuman *et al.*, 2004; Foster *et al.*, 2006). Recent shifts of northern hardwoods to higher elevations formerly occupied by boreal forests have also been attributed to regional warming over the last century (Beckage *et al.*, 2008). Climate-driven PBMs thus provide a sound basis for projecting vegetation responses to future climate change.

Model

We modelled the distribution of boreal conifers, northern deciduous hardwoods and mixed oak–hickory forests in New England using BIOME4 (version 2b1) (Kaplan *et al.*, 2003). BIOME4 is a physiological, process-based vegetation model that simulates the equilibrium distribution of terrestrial vegetation in response to climate, soils and atmospheric CO₂ concentration. BIOME4, in its unmodified form, simulates global vegetation as mixtures of 13 PFTs. A PFT is defined as a group of plants with similar traits and environmental requirements as defined by physiological and environmental parameters within BIOME4. Biomes are then defined by mixtures of PFTs. Although BIOME4 was designed as a global vegetation model, it has also been successfully modified to simulate the response of regional vegetation to climate change in a number of studies (e.g. Diffenbaugh *et al.*, 2003; Song *et al.*, 2005; Kaplan & New, 2006; Ravindranath *et al.*, 2006) in a similar manner to our study. We have defined three PFTs that correspond to vegetation types – boreal conifer, northern deciduous hardwood and mixed oak–hickory forests – rather than to individual species, because our objective was to project general shifts in forest types and the species within these forest types have somewhat similar physiological and bioclimatic attributes.

Abies balsamea, *Picea mariana* and *Picea rubens*, for example, are all shade-tolerant species with low to medium drought tolerance (Burns & Honkala, 1990). PFT-related parameters were based on previously published literature and were further defined by analysing the climatic features of major species' distribution of each PFT using tree range maps (available at <http://esp.cr.usgs.gov/data/atlas/little/>) in combination with climate data from our baseline period, described below. Our main PFT parameters are given in Table S1.

We used BIOME4 to model the current (i.e. for the baseline period of 1961–90) and future (i.e. 2041–70 and 2071–99) distributions of forest types across New England under several emission scenarios. In addition, we tested the sensitivity of vegetation predictions for the 2041–70 period to changes in either precipitation or atmospheric CO₂ concentration: We alternatively held precipitation or atmospheric CO₂ concentration to baseline levels while allowing other climatic metrics to vary with climate projections. For the fixed-precipitation experiment, we kept monthly precipitation in the 2041–70 period the same as in the baseline simulation while allowing other input data to reach projected levels. For the fixed-CO₂ experiment, we held atmospheric CO₂ concentrations at the baseline simulation level (333 p.p.m.) while allowing other input data to reach levels projected for 2041–70. Simulations from these two experiments were then compared to simulations that used all projected data for the 2041–70 period, respectively.

Model data

We created climatologies for running BIOME4 using both PRISM (Daly *et al.*, 2000, 2002) and CRU CL 2.0 (New *et al.*, 2002) data sets with a 1961–90 baseline period (hereafter referred to as the 1976 period) for calculation of 'current' climatology. We chose this baseline period because (1) mean-monthly sunshine data required for BIOME4 are not available for other periods (e.g. 1971–2000), and (2) the 30 years of climate record for 1961–90 is immediately prior to the time of vegetation observations (1992–93) used to test our model. A 30-year climate window has been shown to be effective for simulating vegetation response to climate (Tang *et al.*, 2009). Annual atmospheric CO₂ concentration for the baseline period simulation was set at 333 p.p.m. (Schlesinger & Malyshev, 2001). The CRU CL 2.0 data set is on a 10 arc-minute global land grid while the PRISM data set used in this study is at a 2.5 arc-minute scale. We extracted the monthly percentage sunshine (%) from the CRU CL 2.0 data set but derived mean-monthly temperature and precipitation from the PRISM data set. We interpolated all climate metrics to a 30 arc-second resolution using the Shuttle Radar Topography Mission (SRTM) 30 arc-second near-globe digital elevation data (Farr & Kobrick, 2000; Rosen *et al.*, 2000). Soil data were derived from soil survey data for New England, obtained from the United States Department of Agriculture, NRCS Natural Resources Conservation Service

(<http://soildatamart.nrcs.usda.gov>). We detail our method of downscaling below.

We downscaled the 2.5 arc-minute elevation PRISM data to a 30 arc-second resolution using bilinear interpolation. We first fitted a regression model to the PRISM 2.5 arc-minute data that treats climatic value at each grid cell as a function of its latitude, longitude and elevation to estimate the local lapse rates of temperature and precipitation. The calculated local lapse rates were then used to interpolate the PRISM data to a finer 30 arc-second resolution by considering the elevation differences between PRISM points and targets from the SRTM 30 arc-second elevation data. These adjusted climatic values for PRISM points were bilinearly interpolated to obtain the value of a climate variable at a target point. The CRU sunshine data were downscaled by bilinear interpolation using the same approach.

We derived nine future CCSs for New England from HadCM3, CGCM3.1 and ECHAM5 model runs driven by SRES storylines B1, A1B and A2 for the 21st century (Nakicenovic *et al.*, 2000). These scenarios describe future potential economic and societal trajectories that result in different levels of greenhouse gas emissions and associated climate change (IPCC, 2007). The B1 scenario is characterized by environmental and social consciousness, sustainable development, and low energy use. Global population rises to 9 billion by 2050 before declining to 7 billion by 2100. The same population growth trends not only characterize the A1B storyline but also include rapid economic development, which reduces differences between industrialized and developing regions, and very high energy use that comes from both carbon and non-carbon emitting sources. The A2 scenario reflects large population growth (i.e. 15 billion people by 2100), slow technological change, continued disparity between industrialized and developing portions of the world, and high energy use. The A1B results in medium levels of GHG emissions compared to relatively higher levels in the A2 and relatively lower levels in the B1 storylines.

Future climate normals of mean-monthly temperature and precipitation were calculated using each of three GCMs and storylines relative to simulated climate normals for 1961–90. These simulated normals for 1961–90 were subtracted from future simulated climates, resulting in projected change (anomalies) in climatic conditions. These monthly series of anomalies (for temperature) or ratios (for precipitation) were bilinearly interpolated onto the SRTM 30 arc-second grid (from $\geq 1.875^\circ$ by 1.875°), then added to the downscaled baseline mean-monthly climatologies of climate variables derived from the PRISM data set. We calculated projected 30-year mean-monthly climatologies for two periods: 2041–70 (referred to as 2055 hereafter) and 2071–99 (referred to as 2085 hereafter). The climatologies for these two periods were used to project the future distribution of forests in New England using BIOME4. Future climate normals of mean-monthly percentage sunshine data were derived from GCM simulations of monthly percentage cloud-cover (%) based on historical regression coefficients between two climate variables. The

atmospheric CO₂ concentrations under the B1, A1B and A2 storyline were set at 487, 544 and 549 p.p.m. for the 2055, and 568, 657 and 724 p.p.m. for the 2085 periods, respectively (Nakicenovic *et al.*, 2000).

Model tests

We tested our BIOME4 simulations by comparing the projected baseline vegetation to the 1992 National Land Cover Data (NLCD 1992, http://landcover.usgs.gov/us_map.php). The NLCD 1992 data were derived from Landsat Thematic Mapper satellite data at 30-m spatial resolution and classified into 21 land-cover types for the United States (Kelly & White, 1993; Vogelmann *et al.*, 1998a,b). We adjusted the scale of the 30-m NLCD 1992 for New England to coincide with our model grid cells at a 30-arc-second spatial resolution. The land-cover type in each regridded cell was defined as the modal land-cover type in a 30 × 30 grid cell window. We did not use other satellite-based data such as the 1-km global land-cover characteristic data (Loveland *et al.*, 2000) or the 1-km global land-cover classification data (Hansen *et al.*, 2000) because the land-cover classifications and finer resolution of the NLCD 1992 data were more suitable for validating modelled vegetation for New England.

We excluded land-cover types either dominated by human activities such as pasture, crops, residential and urban, or having low spatial coverage, including areas dominated by wetlands, shrubs and grasslands. We also did not use mixed forest, e.g. areas dominated by trees where neither deciduous nor evergreen species represent more than 75% of the cover present, to test model results because each grid cell in our simulation was assigned a single PFT, corresponding to the PFT with the highest net primary production (NPP) for that cell. We used a simplified set of two vegetative cover classifications, i.e. deciduous forest and evergreen forest, to test model results. Deciduous forest was classified as an area where 75% or more of the tree species shed foliage simultaneously in response to seasonal change, while the evergreen forest type was where 75% or more of the tree species maintain their leaves all year. The mismatch between simulated vegetation classes and the simplified two tree-cover classifications from NLCD 1992 forced us to combine two of our modelled categories, i.e. mixed oak–hickory and northern deciduous hardwoods into one category of ‘deciduous forest’ for comparison. In summary, our boreal conifer PFT corresponds to the evergreen classification, and our combination of mixed oak–hickory and northern deciduous hardwoods correspond to the deciduous classification. The use of these broader forest classifications could result in an overestimation of our model accuracy.

We assessed the efficacy of the model predictions by evaluating (1) the model’s accuracy or probability of assignment to correct forest type, μ_f , i.e. the probability that predicted vegetation corresponds to the classification in the NLCD 1992 data set, (2) the producer’s accuracy or the probability of assignment to incorrect forest type, ϕ_f , that

refers to the probability that the NLCD 1992 data will be correctly simulated by BIOME4, and (3) the Kappa statistic, a scalar that summarizes the goodness-of-fit while accounting for chance agreement. We evaluated these metrics of model fit by first constructing a two dimensional error matrix **F** corresponding to the observed and predicted coverages for the boreal and deciduous forest cover types. For each forest type f in **F**, the model’s accuracy and the producer’s accuracy are given by:

$$\begin{cases} \mu_f = (n_{\text{pred}}^f \cap n_{\text{obs}}^f) / n_{\text{pred}}^f \\ \phi_f = (n_{\text{pred}}^f \cap n_{\text{obs}}^f) / n_{\text{obs}}^f \end{cases}$$

where n_{pred}^f and n_{obs}^f are the number of predicted and observed cells of vegetation type f , respectively. The overall accuracy (μ) of model prediction across forest types is expressed as:

$$\mu = \sum_{\mathbf{F}} (n_{\text{pred}}^f \cap n_{\text{obs}}^f) / \sum_{\mathbf{F}} (n_{\text{obs}}^f).$$

The overall Kappa statistic (κ) between two compared maps is given by:

$$\kappa = (\mu - \sum_{\mathbf{F}} \mu_f \phi_f) / (1 - \sum_{\mathbf{F}} \mu_f \phi_f).$$

Values of the Kappa statistic > 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 (Landis & Koch, 1977; Monserud & Leemans, 1992).

BIOME4 simulates potential natural vegetation whereas vegetation across much of New England has been directly influenced by human activities. We therefore also used comparatively undisturbed subregions of New England to test the performance of our model. The three subregions used for model tests were White Mountain National Forest in New Hampshire (bounding box: 71.812° to 71.041° W and from 43.894° to 44.347° N), Acadia National Park in Maine (bounding box: 69.159° to 68.01° W and from 44.007° to 44.498° N), and north-west Maine (bounding box: 70.308° to 68.592° W and from 45.950° to 47.484° N). The geographical delineation of the subregions above was based on two considerations: (1) a region was large enough to contain a significant area of at least two simulated PFTs, and (2) the region was relatively unpopulated and thus comparatively free of recent anthropogenic disturbance.

In addition to validating our model projections against NLCD 1992, we compared simulated leaf area index (LAI) and simulated annual NPP in each of our PFTs with measured or reported data for similar forests. We calculated the mean, minimum and maximum of simulated LAI and annual NPP in each PFT and compared these values to corresponding field measurements as an additional test of the model’s ability to simulate vegetation for New England. Such comparisons offer an additional avenue for assessing the goodness-of-fit of modelled vegetation when other forest cover data are not available.

RESULTS

Projected climate change

Temperature is projected to increase in the 21st century under all of our CCSs (Fig. 1). Annual mean temperature in New England is projected to increase by 2.2 to 3.3 °C by 2055 and from 3.0 to 5.2 °C by 2085, relative to the 1961–90 baseline annual mean temperature (5.9 °C) across emission scenarios for all three GCMs (Fig. 1a–c). Average increases in annual mean temperature by 2055 across all three GCMs were 2.4 °C for the B1, 3.2 °C for the A1B, and 2.9 °C for the A2 storylines (Fig. 2a,e,f). For 2085, the average increases were 3.2 °C for the B1, 4.4 °C for the A1B and 4.8 °C for the A2 storylines (Fig. 2b,f,j). The annual rates of temperature increase were 0.02, 0.03 and 0.03 °C year⁻¹ under emission storylines B1, A1B and A2 respectively for the HadCM3 GCM. Projected warming ranged from 2.2 °C under the ECHAM5 B1 scenario to 5.2 °C under the CGCM3.1 A2 scenario and was relatively uniform across New England (Fig. 2a–j).

Annual precipitation in New England is expected to increase by 4.7–9.5% by 2055 and by 6.4–11.4% by 2085 (Table 1), but trajectories of precipitation change are more variable across years and scenarios than for temperature (Fig. 1). Annual

precipitation increases consistently over the years 2003–99 for the A1B and, to a lesser degree, the A2 storylines, but tends to decrease after 2060 for the B1 storyline (Fig. 1e,f). The most consistent increases in precipitation occurred in the ECHAM5 GCM, with estimated annual precipitation increases of 1.0, 1.0 and 0.95 mm per year for the B1, A1B and A2 scenarios, respectively (Fig. 1e). Changes in annual precipitation are also spatially more variable across New England than for temperature (Fig. 2). For example, the magnitude of increase in 2055 is lower (< 6.2%) in southern New England and higher (> 6.2%) in middle and northern New England under the B1 scenario (Fig. 2c). The greatest increase in annual precipitation occurs in northern New England (> 10.6%) under most scenarios (e.g. Fig. 2g,h,k,l).

Model tests

The overall vegetation patterns simulated by BIOME4 agree well with those in the NLCD 1992 data (Fig. 3a vs. b). The model's overall accuracy (μ) in predicting vegetation across New England was 0.77 with an overall Kappa statistic (κ) of 0.49 (Table 2), indicating that the BIOME4 is 'fair to good' at simulating vegetation for New England (Monserud & Leemans, 1992). For example, both the simulated vegetation and the

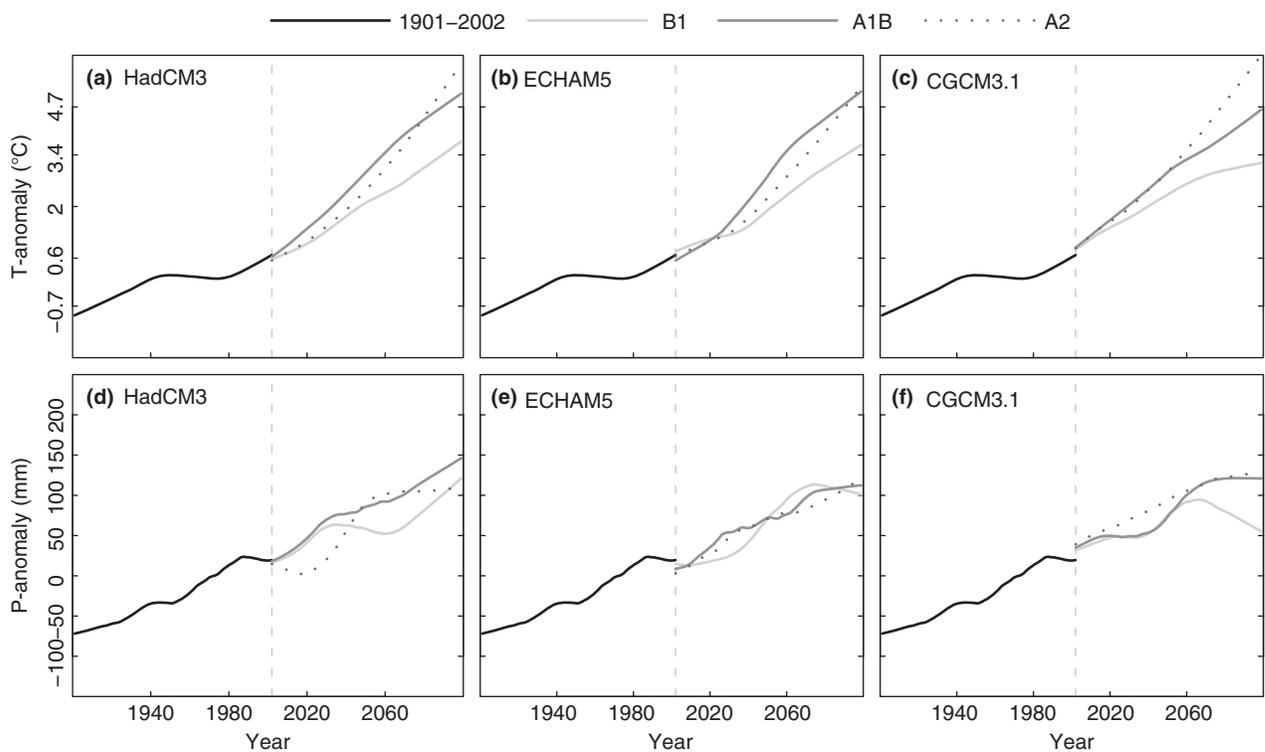


Figure 1 Projected annual mean temperature and precipitation over the years 2003–99 based on three GCMs: HadCM3 (a,d), ECHAM5 (b,e) and CGCM3.1 (c,f). Observed annual mean temperature and precipitation based on PRISM data are to the left of the dashed vertical line (the year 2002) in each panel, and to the right are the model projections under the B1, A1B and A2 storylines, respectively. The discontinuities between observed and simulated trajectories for some panels result because (1) the projected future changes are relative to 30-year mean climatologies for 1961–90 rather than that of the closest period (e.g. 1971–2000 or 1973–2002), and (2) a bias of the given GCM projections relative to actual observations.

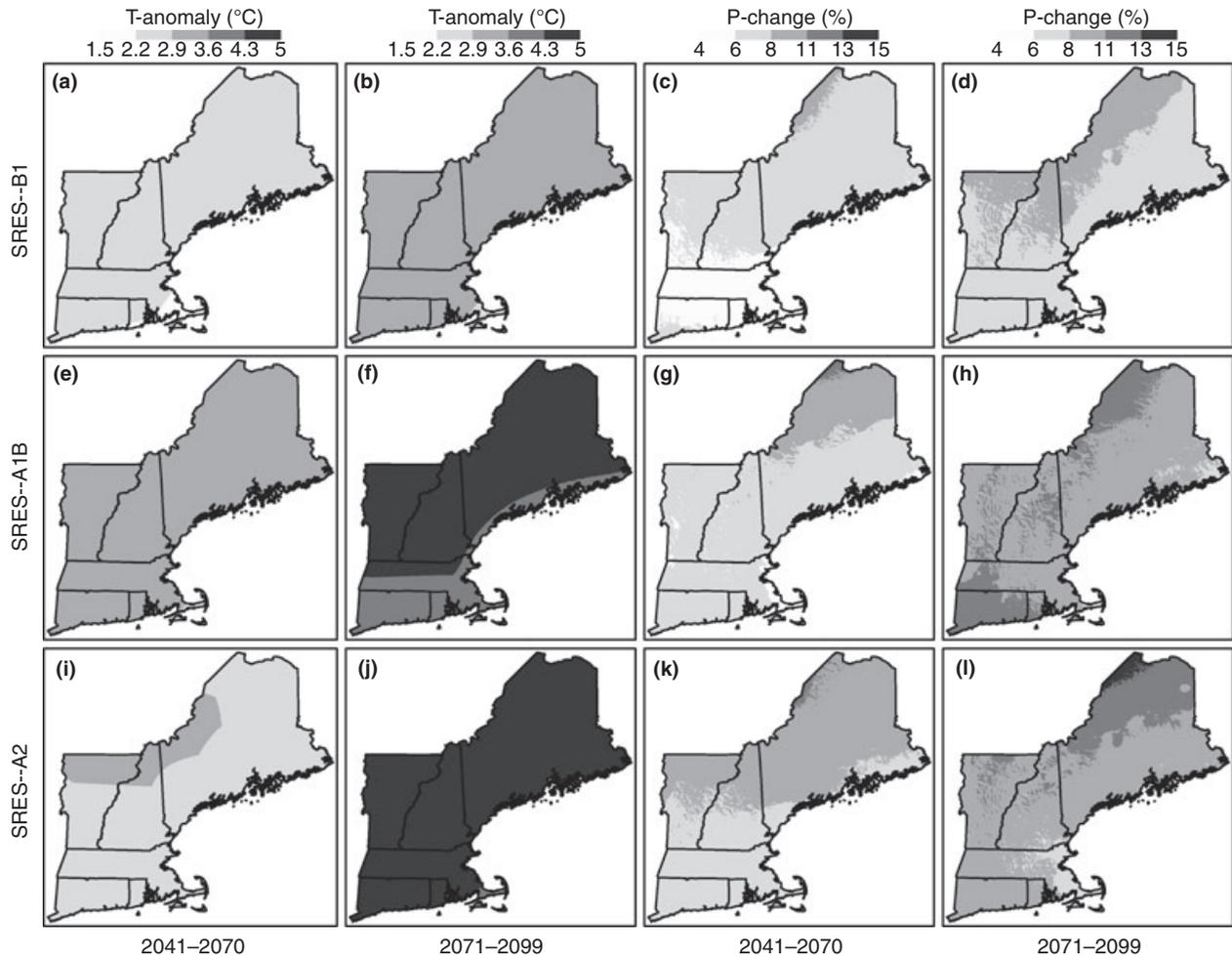


Figure 2 The spatial patterns of projected change in annual mean temperature and precipitation for the periods 2041–70 and 2071–99 with reference to the baseline (1961–90) climatology under the SRES B1, A1B and A2 storylines. The data shown here for each storyline are means over all three GCMs forced by the given storyline.

NLCD 1992 data show that southeastern and northwestern Maine (Fig. 3) are dominated by boreal forest. The model's ability to simulate both the boreal conifer forest (as 'evergreen' for model test) and the northern deciduous hardwoods (as 'deciduous' for model test) in Maine is reflected by the model's high accuracy ($\mu_f > 0.74$) and the high overall accuracy ($\mu = 0.80$) and the 'fair to good' overall Kappa statistic ($\kappa = 0.60$) for this region (Table 2). In addition, the simulated mixed oak–hickory forest (as 'deciduous' for model test) in Connecticut and southern Massachusetts coincides with the deciduous forest type in the NLCD 1992 data, resulting in the high model's accuracy ($\mu_f = 0.85$) in simulating the deciduous forest for New England (Table 2). The BIOME4-simulated boreal conifer forest in Vermont and New Hampshire is mainly distributed in mountainous areas such as in Green Mountain National Forest and the White Mountain National Forest, agreeing well with the NLCD 1992 data (Fig. 3).

In addition to capturing general vegetation patterns across New England, the model was also able to accurately simulate vegetation with low human land use. The model's accuracy (μ_f)

in simulating boreal conifer forest and northern deciduous hardwoods in White Mountain National Forest (area A in Fig. 3) was as high as 0.86 (Table 2), suggesting concordance of the modelled spatial patterns with that specified in the NLCD 1992 data (Fig. 3a vs. b) and consistent with the high overall accuracy ($\mu = 0.79$) and the 'fair to good' overall Kappa statistic ($\kappa = 0.58$) (Table 2) for this region. Similarly, the BIOME4-simulated vegetation distribution for the Acadia National Park (area B in Fig. 3) agrees well with that classified in the NLCD 1992 data as illustrated by the high overall accuracy ($\mu = 0.74$). Although the model's accuracy is relatively low ($\mu_f = 0.20$) in simulating the deciduous hardwoods in Acadia National Park, the number of grid cells dominated by this forest type accounts for only 15% of the total number of grid cells (1946).

We do note, however, that at finer scales the modelled vegetation may not reproduce the spatial patterns and texture apparent in the NLCD 1992 data. For example, the modelled boreal conifer forest in southeastern Maine and the northern New Hampshire is broader and more continuous than that

Table 1 Projected changes in annual mean temperature and total annual precipitation in New England for 2041–70 and 2071–99 compared to the baseline period 1961–90.

Change in annual	Scenario	HadCM3		ECHAM5		CGCM3.1	
		2055*	2085†	2055*	2085†	2055*	2085†
Temperature (°C)	B1	2.3	3.2	2.2	3.2	2.6	3.0
	A1B	3.2	4.6	3.2	4.6	3.2	4.0
	A2	2.7	4.8	2.6	4.3	3.3	5.2
Precipitation (%)	B1	4.7	8.0	7.9	9.9	8.0	6.4
	A1B	8.0	10.5	6.9	8.6	7.8	11.2
	A2	9.2	9.6	7.5	8.8	9.5	11.4

The 30-year (1961–90) mean annual temperature and precipitation in New England is 5.9 °C and 1109 mm.

*Refers to the period 2041–70.

†Refers to the period 2071–99.

classified in the NLCD 1992 data (Fig. 3a vs. b). This difference results, in part, from the fragmented nature of vegetation in New England due to human activities but which BIOME4 does not explicitly consider, so that the modelled vegetation tends to be more continuous than that classified in the NLCD 1992 data. In addition, the climate data used to run BIOME4 were derived from the 2.5 arc-minute PRISM and the 10 arc-minute CRU CL 2.0 data, and these data might not capture enough climatic variation at 30 arc-second spatial resolution across New England to simulate fine-scale vegetation patterns. In

Table 2 The accuracy assessment of our model simulations of forests in New England.

Region	Vegetation*	Model's accuracy (μ_f)	Producer's accuracy (ϕ_f)	Overall accuracy (μ)	Overall Kappa statistic (κ)
North-western Maine	Evergreen	0.87	0.74	0.80	0.60
	Deciduous	0.74	0.86		
White Mountain NF	Evergreen	0.86	0.70	0.79	0.58
	Deciduous	0.74	0.88		
Acadia NP	Evergreen	0.86	0.82	0.74	0.06
	Deciduous	0.20	0.25		
New England	Evergreen	0.62	0.72	0.77	0.49
	Deciduous	0.85	0.80		

NF, national forest; NP, national park.

*For comparison with NLCD 1992 data, we considered both the northern deciduous hardwoods and the mixed oak–hickory forest as deciduous forest cover type, and the boreal conifer forest as evergreen forest cover type.

contrast, the NLCD 1992 data were derived from satellite images at 30-m spatial resolution, which should better capture the spatial variation of vegetation at a finer scale than our model simulations. Finally, because we combined northern

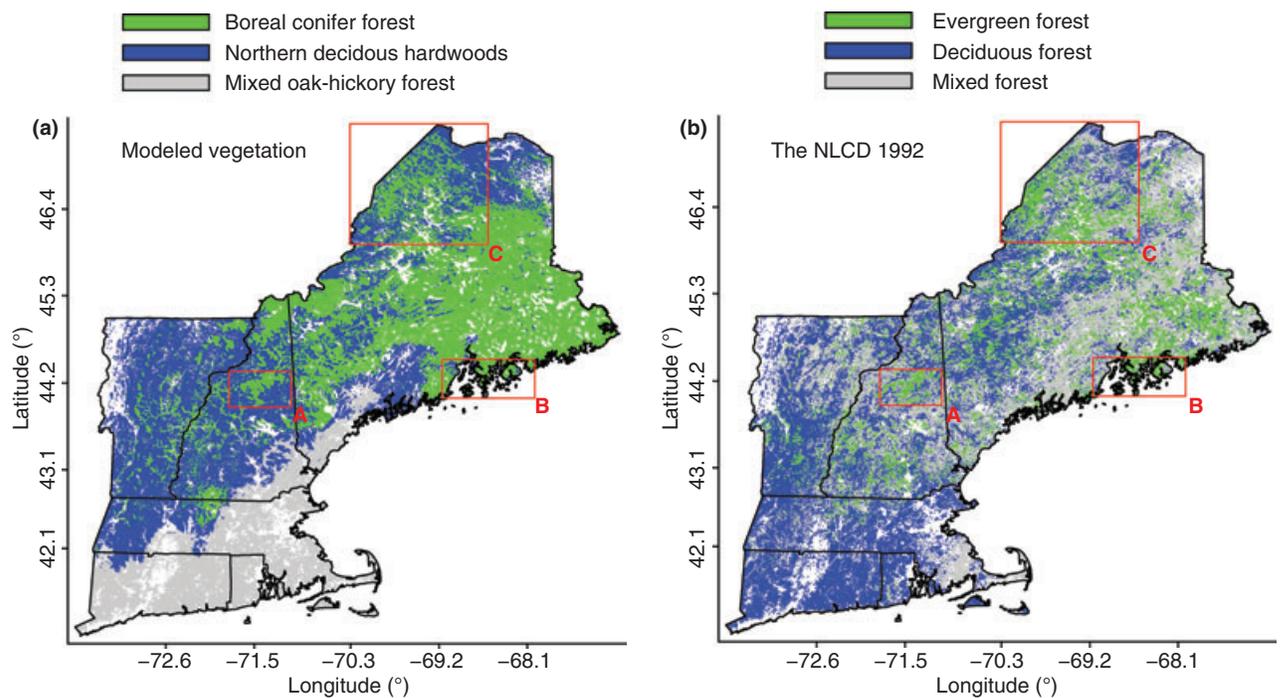


Figure 3 Comparison between (a) the modelled vegetation for the period 1961–90 and (b) the land-cover classification in the 1992 National Land Cover Data. Areas A, B and C are three subregions, i.e. the White Mountain National Forest, the Acadia National Park and north-western Maine, used to test the model simulation. White areas in (a) and (b) are lakes, land cover of limited extent and human use land covers that are excluded from model tests.

Table 3 Test of BIOME4-simulated LAI and NPP for forests in New England.

		Mixed oak–hickory forest		Northern deciduous hardwoods		Boreal conifer forest	
		Model	Observed	Model	Observed	Model	Observed
LAI (m ² m ⁻²)	Mean	3.34	3.84	4.04	3.38	3.09	2.99
	Min.	2.76	2.90	3.26	0.36	2.51	0.48
	Max.	4.07	4.50	4.51	7.30	3.48	7.40
NPP (g m ⁻² year ⁻¹)	Mean	835	810	678	695	633	644
	Min.	696	660	542	199	322	440
	Max.	930	1010	819	999	816	914

Observed leaf area index (LAI) and net primary production (NPP) data are from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. (<http://www.daac.ornl.gov>). We used measured LAI in similar forests (see Table S2) to test modelled LAI for New England. Gridded NPP (Zheng et al., 2003) for forests dominated by boreal conifers was used to test modelled NPP in boreal conifer forest, and NPP for temperate deciduous broadleaf forest dominated by upland oaks was used to compare modelled NPP in mixed oak–hickory forests. Because of the lack of observed NPP data for northern deciduous hardwoods, we used NPP for forests dominated by aspen in Superior National Forest of Minnesota (USA) to test modelled NPP for northern deciduous hardwoods.

deciduous hardwoods and mixed oak–hickory forest together as deciduous forest in the model test, simulations of their specific distributions were not tested by the NLCD 1992.

The modelled optimum LAI for our three PFTs agree well with field observations in similar forests in other regions of the USA. Our modelled LAI averaged 3.34 in mixed oak–hickory

forest, 4.04 in northern deciduous hardwoods, and 3.09 in boreal conifer forest, close (difference < 20%) to average observations of 3.84, 3.38 and 2.99 in similar forests respectively (Table 3). The magnitudes of modelled LAI in each grid cell (Fig. S1a) are within the ranges of LAI observations, as illustrated by the minimum and maximum LAI in each PFT from both simulation and observations (Table 3). Burrows *et al.* (2002), for example, reported a mean LAI of 3.45 in northern hardwoods in Park Falls, Wisconsin (USA) in July of 1999 based on eddy flux measurements.

BIOME4's ability to simulate vegetation for New England was also supported by the consistency of modelled optimum annual NPP with field measurements. The modelled mean annual NPP is 835 g m⁻² year⁻¹ in oak–hickory forest, 678 g m⁻² year⁻¹ in northern deciduous hardwoods, and 633 g m⁻² year⁻¹ in boreal conifer forests, closely approximating (within 3%) average NPP of 810, 695 and 644 g m⁻² year⁻¹ measured in similar forests, respectively (Table 3). The magnitudes of modelled NPP at a grid cell level (Fig. S1b) are also within the ranges of observed values (Table 3). Our simulated values are also supported by specific studies of forest NPP in the eastern USA: Brown & Schroeder (1999), for example, reported that annual NPP in eastern hardwoods ranged from 750 to 1150 g m⁻² year⁻¹, with an area-weighted average of 970 g m⁻² year⁻¹. In contrast, annual NPP in softwoods ranged from 580 to 980 g m⁻² year⁻¹, with an area-weighted average of 870 g m⁻² year⁻¹.

Model projections

Our model simulations of future forest distribution indicate a general shift from boreal conifers and northern deciduous

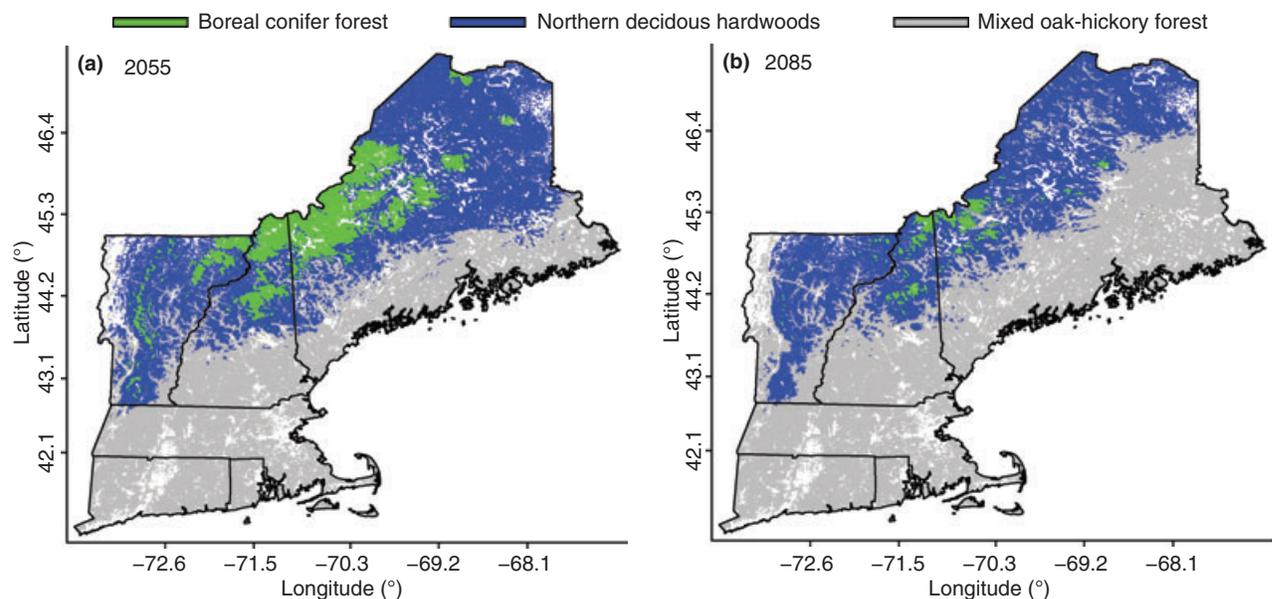


Figure 4 The distribution of mixed oak–hickory, northern deciduous hardwood and boreal conifer forests in two future periods 2041–70 (referred to as 2055) and 2071–99 (referred to as 2085) in New England. The vegetation type in each grid cell is based on the modal value of each grid cell across all nine climate changes scenarios.

hardwoods to mixed oak–hickory forest (Fig. 4). The mixed oak–hickory forest in southern New England is expected to move northward and increase in area through the mid and late 21st century under all CCS (Fig. 3a vs. Fig. 4; Table 4). We estimate, for example, that the northern boundary of the mixed oak–hickory forest will migrate northward by 0.7 latitudinal degrees (*c.* 75 km) by 2055 (Fig. 3a vs. Fig. 4a) and 1 latitudinal degrees (*c.* 101 km) by 2085 (Fig. 3a vs. Fig. 4b; HadCM3 B1 in Table 4). The corresponding southern boundary of the northern deciduous hardwoods is expected to shift northward, e.g. the latitudinal distribution of northern deciduous hardwoods is projected to increase by 0.6 latitudinal degrees (*c.* 67 km) by 2055 and by 0.8 latitudinal degrees (*c.* 90 km) by 2085 (Fig. 3a vs. Fig. 4h) under the ECHAM5 A2 scenario (Table 4). Under all scenarios, boreal conifer forest (e.g. Fig. 4d,j,p) is projected to contract to mountain ranges and to the region centred on the corner of northern New Hampshire and north-western Maine by 2085, because annual temperature in these areas tends to be the lowest across New England (Fig. S2a). The contraction of boreal conifer forest to higher elevations in mountain ranges can result in an apparent southerly shift in latitudinal range under most scenarios in 2085 (Table 4), i.e. when northern lowlands lose their boreal conifer forest.

Projected climate change is estimated to shift both the northern deciduous hardwoods and the mixed oak–hickory forest to higher elevations (Table 5). The average elevation of northern deciduous hardwoods is 279 m a.s.l. in the baseline simulation under current conditions, but increases by 52 m

Table 4 Projected latitudinal shifts of simulated forest types in New England.

GCM	Scenario	Mixed oak–hickory forest		Northern deciduous hardwoods		Boreal conifer forest							
		2055	2085	2055	2085	2055	2085						
		°	km	°	km	°	km						
H3	B1	0.7	75	1.0	101	0.5	55	0.8	85	0.3	32	-0.1	-12
	A1B	0.9	95	1.4	147	0.8	86	0.9	98	-0.1	-13	-0.2	-16
	A2	0.7	77	1.6	165	0.7	74	1.0	104	0	3	-0.3	-30
E5	B1	0.7	79	1.4	145	0.2	26	0.9	99	0.5	53	0	0
	A1B	1.3	135	1.8	196	0.9	97	0.8	85	0	2	-0.1	-12
	A2	1.0	111	1.6	170	0.6	67	0.8	90	0.4	44	-0.1	-12
CG	B1	1.2	130	1.6	167	0.5	53	1.0	102	0.5	55	0	2
	A1B	1.5	160	1.8	192	1.1	118	0.8	86	0.1	10	-0.1	-15
	A2	1.4	148	2.1	219	1.0	105	0.6	60	0	2	0	1
Average shift		1.0	112	1.6	167	0.7	76	0.8	90	0.2	21	-0.1	-10

H3, HadCM3; E5, ECHAM5; CG, CGCM3.1.

Contraction of ranges upslope can cause some negative latitudinal shifts to occur (i.e. vegetation moves southward). This is the case for boreal conifers in high latitudes of New England, for example, where this forest type is expected to contract upslope into mountain ranges that can be at lower latitudes than northern New England. The projected latitudinal shifts are based on the average position of the PFTs in two future periods relative to the baseline period (1961–90).

Table 5 Projected altitudinal shifts of simulated forest types in New England.

GCM	Scenarios	Mixed oak–hickory forest		Northern deciduous hardwoods		Boreal conifer forest	
		2055	2085	2055	2085	2055	2085
		(m)	(m)	(m)	(m)	(m)	(m)
HadCM3	B1	40	45	-75	-20	253	433
	A1B	47	56	-27	67	430	723
	A2	42	73	-51	93	364	874
ECHAM5	B1	47	54	-106	10	184	346
	A1B	53	98	-3	117	355	608
	A2	50	70	-58	67	219	539
CGCM3.1	B1	54	66	-34	31	194	321
	A1B	73	92	26	84	309	483
	A2	61	130	9	238	347	677
Average shift		52	76	-35	76	295	556

Changes in precipitation, temperature, and CO₂ can cause the expansion of northern deciduous hardwoods to lower elevations in some scenarios.

and 76 m by 2055 and 2085, respectively, averaged across all GCMs and scenarios. The average elevation is also projected to increase for the boreal conifer forest by 295 m and 556 m by 2055 and 2085, respectively (Table 5). The increase in apparent elevation of boreal forest, however, was primarily driven by losses of this community at lower elevations rather than a general shift to higher elevations, as boreal forests already occupy the highest elevations in our region (> 800 m a.s.l.; NLCD 1992).

Projected climate change may cause a large portion of New England to be potentially dominated by mixed oak–hickory forest by the end of the 21st century (Fig. 4). The total number of grid cells dominated by mixed oak–hickory forest (37,261 of 215,509 of total simulated grid cells for 1976) increased under all scenarios; the magnitudes of the increases ranged from 99% under the HadCM3 B1 scenario to 276% under the CGCM3.1 A1B scenario by the 2055 period, and from 149% under the HadCM3 B1 scenario to 431% under the CGCM3.1 A2 scenario by the 2085 period (Table 6). New England is also expected to lose a large portion of the northern deciduous hardwoods and the boreal conifer forest (Fig. 3 vs. Fig. 4). Boreal conifer forests (89,634 grid cells under the baseline simulation) are expected to lose on average 61% of their areal extent in New England by 2055 and 91% by 2085 across all scenarios, while northern deciduous hardwoods (93,114 grid cells under the baseline simulations) are expected to lose 11% and 26% of their area by the 2055 and 2085 periods, respectively.

Our computational experiments, which examined the sensitivity of vegetation distribution to changes in CO₂ concentration, indicated that rising CO₂ concentration can reduce the losses of boreal conifer forests (Fig. 5). The spatial extent of the boreal conifer forest is reduced when CO₂ concentrations are held at baseline levels but with the same magnitude of climate change (Fig. 5a vs. b). When atmospheric CO₂ concentration

Table 6 Projected future changes in potential area of simulated forest types in New England.

GCM	Scenarios	Mixed oak–hickory forest		Northern deciduous hardwoods		Boreal conifer forest	
		2055	2085	2055	2085	2055	2085
		(%)	(%)	(%)	(%)	(%)	(%)
HadCM3	B1	99	149	15	24	-57	-87
	A1B	143	237	26	0	-86	-99
	A2	110	282	32	-17	-79	-100
ECHAM5	B1	116	228	-23	-19	-25	-76
	A1B	210	345	-9	-45	-77	-97
	A2	173	272	-27	-18	-44	-95
CGCM3.1	B1	208	273	-51	-41	-34	-71
	A1B	276	330	-41	-44	-72	-92
	A2	240	431	-23	-77	-76	-99
Average change		175	282	-11	-26	-61	-91

The estimate percentage change is based on the number of grid cells for each forest type in the baseline (1961–90) and future (2041–70 or 2071–99) simulations.

was held constant at 333 p.p.m. in 2055 as in the baseline simulation, for example, climate change alone under the B1 storyline decreased the boreal conifer forest by 77%, 46% and 74% in the HadCM3, ECHAM4 and CGCM3.1 runs, respectively, which are greater losses than experienced under the same climate scenarios but with atmospheric CO₂ concentration increased to 487 p.p.m., e.g. 57%, 25% and 34% (Table 6).

Changes in summer precipitation are projected to either slow down (when summer precipitation increases) (Fig. 6b) or speed up (when summer precipitation decreases) the replacement of northern deciduous hardwoods by mixed oak–hickory forest (Fig. 6c). For example, the simulated extent of the northern deciduous hardwoods increased by 10% and 6% in 2055 under the HadCM3 and ECHAM5 B1 scenarios, where projected summer precipitation increased by 2–9% compared to the baseline precipitation (Fig. 6d,e). In contrast, the extent of the northern deciduous hardwoods decreased by 21% by 2055 under the CGCM3.1 B1 scenario, where projected summer precipitation decreased by 4–14% compared to the baseline precipitation (Fig. 6f). Changes in summer precipitation within a range of -10% to 10% relative to baseline precipitation, however, had minimal effect on boreal conifer forest.

DISCUSSION

We project that New England will lose the majority of its boreal conifer forest (91% averaged over scenarios) as well as some northern deciduous hardwoods (26% averaged over scenarios) in response to a projected 3.0–5.2 °C warming and 6.4–11.4% increase in annual precipitation by 2085. Mixed oak–hickory forest, in contrast, is projected to nearly triple in area (282% averaged over scenarios) in New England by the end of this century. We estimate that the northern deciduous hardwoods will shift northward by 0.8° latitude (*c.* 90 km) and by 76 m to higher elevations, while mixed oak–hickory forests will shift northward by 1.6° latitude (*c.* 167 km) and by 76 m to higher elevations (Tables 4 and 5). The corresponding

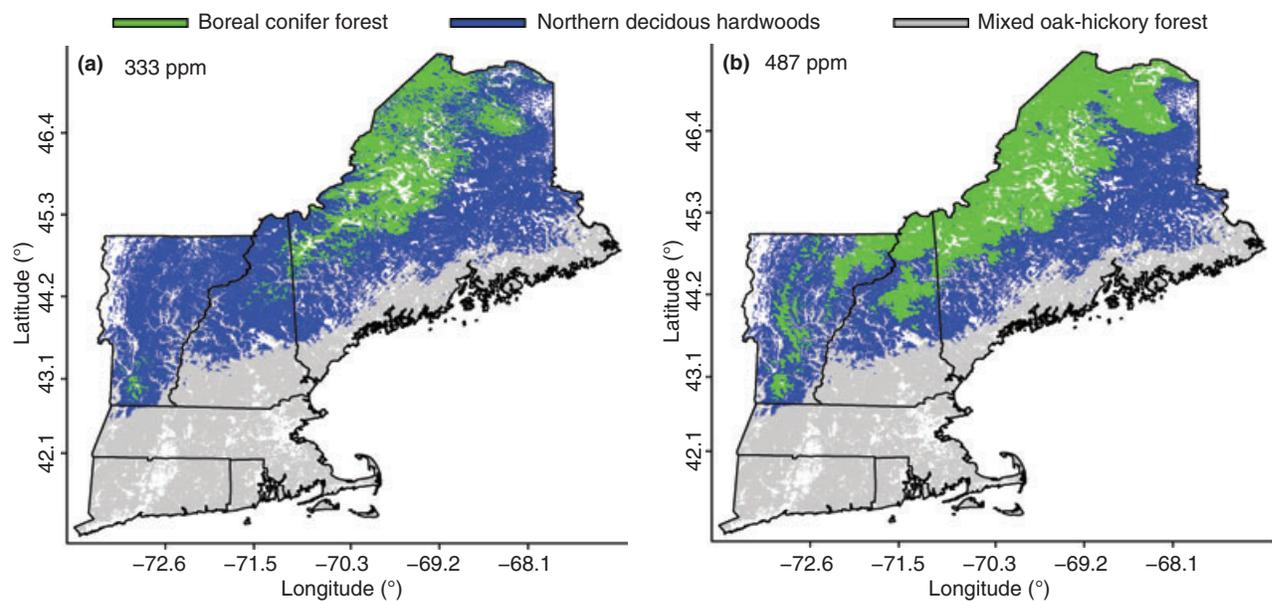


Figure 5 Increases in atmospheric CO₂ concentration promote the persistence of boreal conifer forest under projected climate warming scenarios. Panel (a) is modelled vegetation in 2055 under the B1 storyline with CO₂ concentration set at 333 p.p.m. Panel (b) is modelled vegetation in 2055 under the same storyline but with CO₂ concentration set at 487 p.p.m. The vegetation type in each grid cell is based on the modal value of each grid cell across all three GCMs.

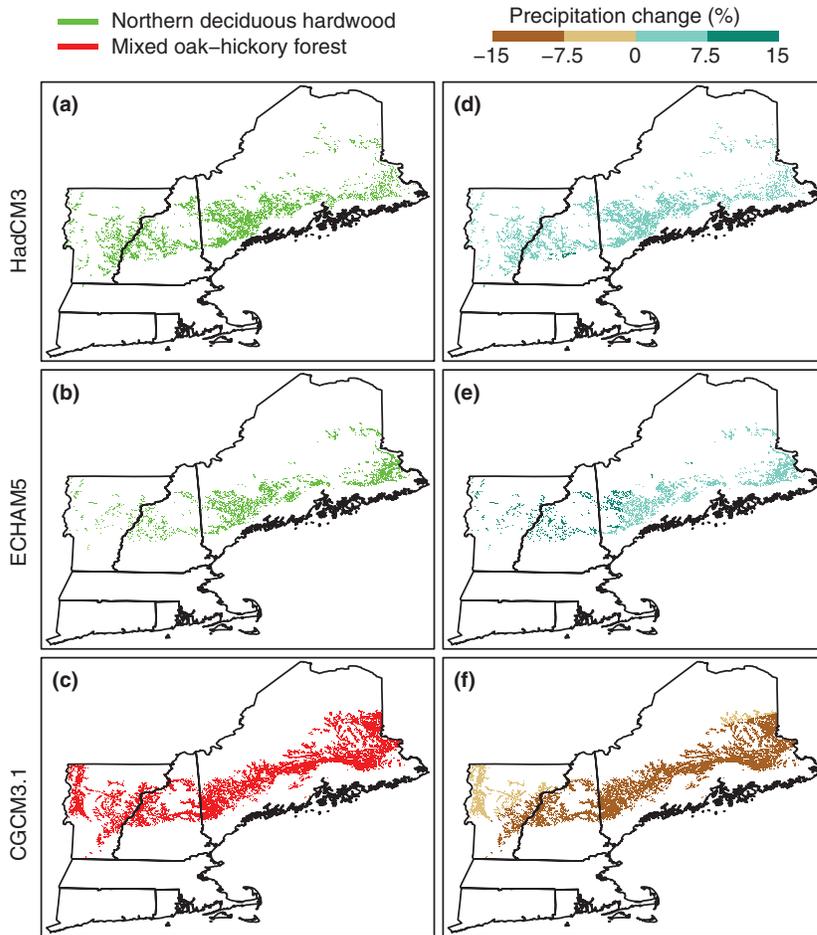


Figure 6 Sensitivity of simulated vegetation to changes in precipitation. An increase in summer precipitation of 5% and 7% results in northern deciduous forest rather than oak-hickory forest in areas of green for the HadCM3 (a) and ECHAM5 (b) GCMs. These changes in coverage represent a 6% and 10% increase in northern deciduous forest, respectively. A decrease in summer precipitation of 10%, in contrast, results in oak-hickory forest rather than the northern deciduous hardwoods in areas represented by red (c). This change represents a 40% increase in oak-hickory forest. Panels (d–f) show the changes in summer precipitation corresponding to the panels on the left. The data shown here are based on comparisons between simulations using projected precipitation for 2055 under the B1 storyline and simulations using the baseline precipitation. Temperature and CO₂ concentration in each pair of compared simulations are as same as those projected under the B1 storyline.

potential migration rates of 0.8–1.5 km per year are similar to rates calculated for biome shifts in other modelling studies (e.g. Malcolm *et al.*, 2002). Past migration rates of similar forests have been estimated to range from $< 100 \text{ m year}^{-1}$ (McLachlan *et al.*, 2005) to 250 m year^{-1} (Davis, 1989), suggesting that these forests may not be able to shift as rapidly as climate. Recent studies have already confirmed that climate warming in the 20th century has been associated with shifts of vegetation to both higher latitudes and elevations (e.g. Parmesan & Yohe, 2003; Beckage *et al.*, 2008), and increasing impacts are expected in the future (e.g. Thuiller *et al.*, 2005). These projections of vegetation shifts in New England are driven by projected regional climate change, and assume that climate is the major factor controlling the bioclimatic range limits of vegetation at regional scales (e.g. Dirnbock *et al.*, 2003) as the effects of land-use change, disturbance, etc. are not considered.

Although our model results project that the boreal conifer forest will move northward and contract to the northern New Hampshire and the northwestern Maine, climate change may not completely extirpate this forest type from New England this century. Previous studies based on regression tree analysis (e.g. Iverson & Prasad, 2001) projected the extirpation of spruce-fir forest types from New England under five CCS and doubled CO₂ concentrations. Our simulations based on

BIOME4 and new GCM data driven by different storylines indicate that the boreal conifer forest may still persist in New England in the late 21st century under some scenarios but its distribution will contract to the ranges of mountains (see Fig. 4). The continued presence of boreal conifers in our simulations is likely because (1) the temperature in these scenarios does not increase enough ($< 4.6 \text{ }^\circ\text{C}$) to exceed the bioclimatic range limits of the boreal conifer species, and (2) the inclusion of the physiological effects of CO₂ on plant growth in BIOME4 offsets the negative effects of climate change on the boreal conifer forest (e.g. VEMAP Members., 1995; Lapola *et al.*, 2009). The greatest risks to the boreal conifer forest occur under the HadCM3 A1B (Fig. S3d) and A2 (Fig. S3f), the ECHAM5 A1B (Fig. S3j) and the CGCM3.1 A2 (Fig. S3r) scenarios, under which annual temperature is projected to increase by at least $4.6 \text{ }^\circ\text{C}$.

Increasing atmospheric CO₂ concentration, which, of course, largely drives climate change, appears to reduce the negative effects of climate change on the distribution of the boreal conifer forest in New England (Fig. 5). Rising CO₂ concentrations can reduce plant transpiration by inducing the stomatal closure of plants that increases their water use efficiency (e.g. Claessens *et al.*, 2006), and thus causes higher rates of net canopy CO₂-fixation in relation to water loss

(Osborne *et al.*, 2000). Boreal conifer tree species are comparatively sensitive to drought (see USDA, NRCS 2009; The PLANTS Database, <http://plants.usda.gov>) and may gain more in NPP from elevated CO₂ than deciduous hardwoods (Tjoelker *et al.*, 1998). In our simulations, for example, annual mean NPP increased by 175 g m⁻² year⁻¹ for boreal conifers and by 164 g m⁻² year⁻¹ for deciduous hardwoods under high CO₂ (487 p.p.m.) simulations for 2055 compared to low CO₂ (333 p.p.m.) experiments. Differential responses to elevated atmospheric CO₂ could result in a relative competitive advantage of boreal conifers compared to deciduous hardwoods. This effect could result in increasing losses of boreal conifer forest in New England even if CO₂ levels were stabilized if global temperatures continued to rise in response to an accumulated thermal debt (e.g. Meehl *et al.*, 2005).

Previous studies have indicated the importance of changes in precipitation in addition to temperature in determining vegetation distribution (e.g. Dirnbock *et al.*, 2003; Rehfeldt *et al.*, 2006). Our study demonstrates that the effect of precipitation change, with a range of -10% to 10% relative to the baseline precipitation, depends on the target vegetation. For example, simulations that alternatively held precipitation at baseline or 2055 levels resulted in less than a 1% difference in the total number of grid cells projected to contain boreal conifer forest, while projected CO₂ concentrations and temperatures were allowed to change with the B1 storyline. In contrast, precipitation increases in summer reduce the replacement of northern deciduous hardwoods by mixed oak-hickory forest (Fig. 6a,b) while precipitation decreases in summer cause their further replacement (Fig. 6c). Northern deciduous hardwoods tend to be physiologically less drought-tolerant than the mixed oak-hickory forests (see USDA, NRCS 2009; The PLANTS Database, <http://plants.usda.gov>), so that changes in precipitation have the potential to shift the competitive balance between these two PFTs.

Although BIOME4 was developed to simulate equilibrium potential vegetation at global spatial scales, we were able to successfully use this model to simulate regional vegetation in a landscape that has a history of human activities and disturbance (Fuller *et al.*, 1998; Parshall *et al.*, 2003). The model's tests against both vegetation in relatively undisturbed regions and across the whole of New England demonstrate the potential of BIOME4 to simulate vegetation in New England (Table 2). Additional comparisons with two important ecological indicators (LAI and NPP) support the application of BIOME4 to forests in New England (Table 3). In contrast to niche-based, statistical models, we were able to account for the physiological effects of CO₂ on plant growth and vegetation distribution in BIOME4, showing that rising CO₂ can ameliorate increased water stress under elevated temperature thus affecting vegetation distribution (e.g. VEMAP Members, 1995).

We caution, however, that BIOME4 is an equilibrium vegetation model that assumes that vegetation is in equilibrium with climate and does not consider successional changes or transient states as the vegetation composition

shifts. The rate at which vegetation responds to climate change depends on the time (or lag) required for vegetation to reach a new equilibrium in response to climate change. Our projections should therefore be viewed as the potential distribution of these forest types in New England under a given climate condition. In addition, BIOME4 assumes that climate is a major factor in determining vegetation distribution over a broad spatial scale. However, other factors, such as seed dispersal, local-scale disturbances and human activities, can be important factors controlling vegetation distribution in a given area, influencing the time for vegetation to reach an equilibrium with climate or even inhibiting the landscape from attaining its potential forest state. Finally, the aggregation of species into PFTs ignores the spectrum of species-specific migration rates and climatic tolerances, potentially hindering the accuracy of future projections and reducing the heterogeneity and complexity of spatial patterns of modelled vegetation distribution (e.g. Neilson *et al.*, 2005).

CONCLUSION

1. Annual mean temperature in New England is projected to increase by 2.2–3.3 °C in 2055 and by 3.0–5.2 °C in 2085 across emission scenarios for all three GCMs, compared to the 1961–90 annual mean temperature of 5.9 °C. Projected warming ranged from 2.2 °C under the ECHAM5 B1 scenario to 5.2 °C under the CGCM3.1 A2 scenario and was relatively uniform across New England. Annual total precipitation in New England is also expected to increase by 4.7–9.5% by 2055 and by 6.4–11.4% by 2085 under all scenarios, but increases in precipitation are more variable across years and scenarios than for temperature. Changes in annual precipitation are also spatially more variable across New England than for temperature. Compared to the baseline annual precipitation (1109 mm), the magnitude of increase is the lowest (< 6.2%) in southern New England under the B1 scenario and the highest (> 10.6%) in northwestern Maine under the A1B scenario.

2. The BIOME4-simulated vegetation pattern agrees well with the land cover in the NLCD 1992 data. When the model was tested against observed vegetation in the whole of New England, the overall Kappa statistic ($\kappa = 0.49$ indicating 'fair to good' fit) justifies BIOME4's application to New England even though BIOME4 was originally developed to simulate potential natural vegetation at the global scale. Comparisons with observed ecological indicators (LAI and NPP) in similar forests further justify the application of BIOME4 to New England.

3. Mixed oak-hickory forest in southern New England is projected to move north by 1.6 latitudinal degrees (*c.* 167 km) due to a regional warming of 3.0–5.2 °C by the end of this century. Projected future climate change is expected to shift both northern deciduous hardwoods and mixed oak-hickory forest upslope by 76 m by the end of the 21st century. The upslope movement of the northern deciduous hardwoods and

oak–hickory forest coincides with an approximate 556 m upslope retreat, driven by losses of this forest type at lower elevations rather than colonization of higher elevations, of the boreal conifer forest by the end of the 21st century.

4. Projected climate change will result in reduced areas of the boreal conifer forest in New England this century. The magnitudes of losses of the boreal conifer forest range from 25% in 2055 under the ECHAM5 B1 scenario to 100% in 2085 under the HadCM3 A2 scenario. The extirpation of the boreal conifer forest from New England is most likely to occur in our simulations when annual mean temperature increases more than 4.6 °C. Projected climate change reduces the extent of northern deciduous hardwoods in most scenarios, but changes ranged from a 24% increase by 2055 under the HadCM3 B1 scenario to a 77% loss in 2085 under CGCM3.1 A2 scenario. Mixed oak–hickory forests, in contrast, are projected to increase by 149% in the HadCM3 B1 scenario to 431% in the CGCM3.1 A2 scenario by the end of the 21st century. Increases in atmospheric CO₂ concentration tend to reduce losses of boreal conifer forest in New England, while precipitation change influences the relative abundance of northern deciduous hardwoods and mixed oak–hickory forests.

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REFERENCES

- Bates, B.C., Kundzewicz, Z.W., Wu, S. & Palutikof, J.P. (eds) (2008) *Climate change and water*. Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, 210 pp.
- Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T. & Perkins, T. (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences USA*, **105**, 4197–4202.
- Brown, S.L. & Schroeder, P.E. (1999) Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. *Ecological Application*, **9**, 968–980.
- Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America*. Vol. 2. *Conifers*. USDA, Washington, DC.
- Burrows, S.N., Gower, S.T., Clayton, M.K., Mackay, D.S., Ahl, D.E., Norman, J.M. & Diak, G. (2002) Application of geostatistics to characterize LAI for flux towers to landscapes. *Ecosystems*, **5**, 667–679.
- Claessens, L., Hopkinson, C., Rastetter, E. & Vallino, J. (2006) Effect of historical changes in land use and climate on the water budget of an urbanizing watershed. *Water Resources Research*, **42**, W03426. doi:10.1029/2005WR004131.
- Daly, C., Taylor, G.H., Gibson, W.P., Parzybok, T.W., Johnson, G.L. & Pasteris, P. (2000) High-quality spatial climate data sets for the United States and beyond. *Transactions of the American Society of Agricultural Engineers*, **43**, 1957–1962.
- Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L. & Pasteris, P. (2002) A knowledge-based approach to the statistical mapping of climate. *Climate Research*, **22**, 99–113.
- Davis, M.B. (1989) Lags in vegetation response to greenhouse warming. *Climatic Change*, **15**, 75–82.
- Diffenbaugh, N.S., Sloan, L.C., Snyder, M.A., Bell, J.L., Kaplan, J., Shafer, S.L. & Bartlein, P.J. (2003) Vegetation sensitivity to global anthropogenic carbon dioxide emissions in a topographically complex region. *Global Biogeochemical Cycles*, **17**, 1067. doi:10.1029/2002GB001974.
- Dirnbock, T., Dullinger, S. & Grabherr, G. (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, **30**, 401–417.
- Farnsworth, E.J. & Ogurcak, D.E. (2006) Biogeography and decline of rare plants in New England: historical evidence and contemporary monitoring. *Ecological Applications*, **16**, 1327–1337.
- Farr, T.G. & Kobrick, M. (2000) Shuttle Radar Topography Mission produces a wealth of data. *American Geophysical Union Eos*, **81**, 583–585.
- Foster, D.R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems*, **1**, 96–119.
- Foster, D.R., Clayden, S., Orwig, D.A., Hall, B. & Barry, S. (2002) Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA. *Journal of Biogeography*, **29**, 1359–1379.
- Foster, D.R., Oswald, W.W., Faison, E.K., Doughty, E.D. & Hansen, B.C.S. (2006) A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. *Ecology*, **87**, 2959–2966.
- Fuller, T.L., Foster, D.R., McLachlan, J.S. & Drake, N. (1998) Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems*, **1**, 76–95.
- Gordon, C., Cooper, C., Senior, C.A., Banks, H.T., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147–168.
- Hall, B., Motzkin, G., Foster, D.R., Syfert, M. & Burk, J. (2002) Three hundred years of forest and land-use change in Massachusetts, USA. *Journal of Biogeography*, **29**, 1319–1335.
- Hansen, M., DeFries, R., Townshend, J.R.G. & Sohlberg, R. (2000) Global land cover classification at 1km resolution using a decision tree classifier. *International Journal of Remote Sensing*, **21**, 1331–1365.

- IPCC (2007) Summary for policymakers. *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson), pp. 7–22. Cambridge University Press, Cambridge, UK.
- Iverson, L.R. & Prasad, A.M. (2001) Potential changes in tree species richness and forest community types following climate change. *Ecosystems*, **4**, 186–199.
- Jungclaus, J.H., Botzet, M., Haak, H., Keenlyside, N., Luo, J.-J., Latif, M., Marotzke, J., Mikolajewicz, U. & Roeckner, E. (2005) Ocean circulation and tropical variability in the AOGCM ECHAM5/MPI-OM. *Journal of Climate*, **19**, 3952–3972.
- Kaplan, J.O. & New, M. (2006) Arctic climate change with a 2 degrees C global warming: timing, climate patterns and vegetation change. *Climatic Change*, **79**, 213–241.
- Kaplan, J.O., Bigelow, N.H., Prentice, I.C., Harrison, S.P., Bartlein, P.J., Christensen, T.R., Cramer, W., Matveyeva, N.V., McGuire, A.D., Murray, D.F., Razzhivin, V.Y., Smith, B., Walker, D.A., Anderson, P.M., Andrew, A.A., Brubaker, L.B., Edwards, M.E. & Lozhkin, A.V. (2003) Climate change and Arctic ecosystems II: modeling, paleodata-model comparisons, and future projections. *Journal of Geophysical Research*, **108**, 8171. doi:10.1029/2002JD002559.
- Kelly, P.M. & White, J.M. (1993) Preprocessing remotely sensed data for efficient analysis and classification, Applications of Artificial Intelligence 1993: Knowledge-Based Systems in Aerospace and Industry. *Proceeding of SPIE*, **1993**, 24–30.
- Kim, S.-J., Flato, G.M., Boer, G.J. & McFarlane, N.A. (2002) A coupled climate model simulation of the Last Glacial Maximum, Part 1: transient multi-decadal response. *Climate Dynamics*, **19**, 515–537.
- Kim, S.-J., Flato, G.M. & Boer, G.J. (2003) A coupled climate model simulation of the Last Glacial Maximum, Part 2: approach to equilibrium. *Climate Dynamics*, **20**, 635–661.
- Landis, J.R. & Koch, G.G. (1977) Application of hierarchical Kappa-type statistics in assessment of majority agreement among multiple observers. *Biometrics*, **33**, 363–374.
- Lapola, D.M., Oyama, M.D. & Nobre, C.A. (2009) Exploring the range of climate biome projections for tropical South America: the role of CO₂ fertilization and seasonality. *Global Biogeochemical Cycles*, **23**, GB3003. doi:10.1029/2008GB003357.
- Loveland, T.R., Reed, B.C., Brown, J.F., Ohlend, D.O., Zhu, Z., Yang, L. & Merchant, J.W. (2000) Development of a global land cover characteristics database and IGBP DISCover from 1-km AVHRR data. *International Journal of Remote Sensing*, **21**, 1303–1313.
- Malcolm, J.R., Adam, M., Ronald, P.N. & Michael, G. (2002) Estimated migration rates under scenarios of global climate change. *Journal of Biogeography*, **29**, 835–849.
- McKenny, D.W., Pedlar, J.H., Lawrence, K., Campbell, K. & Hutchinson, M.F. (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience*, **57**, 939–948.
- McLachlan, J.S., Foster, D.R. & Menalled, F. (2000) Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology*, **81**, 717–733.
- McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, **86**, 2088–2098.
- Meehl, G.A., Washington, W.M., Collins, W.D., Arblaster, J.M., Hu, A.X., Buja, L.E., Strand, W.G. & Teng, H.Y. (2005) How much more global warming and sea level rise? *Science*, **307**, 1769–1772.
- Monserud, R.A. & Leemans, R. (1992) Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling*, **62**, 275–293.
- Nakicenovic, N., Alcamo, J., Davis, G., et al. 2000. *Special Report on Emissions Scenarios: A special report of Working Group III of the Intergovernmental Panel on Climate Change: Other Information: PBD: 3 Oct 2000*. Cambridge University Press, New York; Pacific Northwest National Laboratory, Richland, WA, Environmental Molecular Sciences Laboratory (US).
- Neilson, R.P., Pitelka, L.F., Louis, F., Solomon, A.M., Nathan, R., Midgley, G.F., Fragoso, J.M., Lischke, H. & Thompson, K. (2005) Forecasting regional to global plant migration in response to climate change. *BioScience*, **55**, 749–759.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Osborne, C.P., Mitchell, P.L., Sheehy, J.E. & Woodward, F.I. (2000) Modelling the recent historical impacts of atmospheric CO₂ and climate change on Mediterranean vegetation. *Global Change Biology*, **6**, 445–458.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Parshall, T., Foster, D.R., Faison, E., Macdonald, D. & Hansen, B.C.S. (2003) Long-term history of vegetation and fire in pitch pine-oak forests on Cape Cod, Massachusetts. *Ecology*, **84**, 736–748.
- Pope, V., Gallani, M.L., Rowntree, P.R. & Stratton, R.A. (2000) The impact of new physical parameterizations in the Hadley Centre climate model: HadAM3. *Climate Dynamics*, **16**, 123–146.
- Ravindranath, N.H., Joshi, N.V., Sukumar, R. & Saxena, A. (2006) Impact of climate change on forests in India. *Current Science*, **90**, 354–361.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V. & Evans, J.S. (2006) Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*, **167**, 1123–1150.
- Rosen, P.A., Hensley, S., Joughin, I.R., Li, F.K., Madsen, S.N., Rodriguez, E. & Goldstein, R.M. (2000) Synthetic aperture radar interferometry. *Proceedings of the IEEE*, **88**, 333–382.
- Schlesinger, M.E. & Malyshev, S. (2001) Changes in near-surface temperature and sea level for the Post-SRES CO₂-stabilization scenarios. *Integrated Assessment*, **2**, 95–110.

- Shuman, B., Newby, P., Huang, Y. & Thompson, W.E.B.B., III (2004) Evidence for the close climatic control of New England vegetation history. *Ecology*, **85**, 1297–1310.
- Sitch, S., Smith, B., Prentice, I.C., Arneeth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K. & Venevsky, S. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Global Change Biology*, **9**, 161–185.
- Song, M., Zhou, C. & Hua, O. (2005) Simulated distribution of vegetation types in response to climate change on the Tibetan Plateau. *Journal of Vegetation Science*, **16**, 341–350.
- Tang, G. & Bartlein, P.J. (2008) Simulating the climatic effects on vegetation: approaches, issues and challenges. *Progress in Physical Geography*, **32**, 543–556.
- Tang, G., Shafer, S.L., Bartlein, P.J. & Holman, J.L. (2009) Effects of experimental protocol on global vegetation model accuracy: a comparison of simulated and observed vegetation patterns for Asia. *Ecological Modelling*, **220**, 1481–1491. doi:10.1016/j.ecolmodel.2009.03.021.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, **102**, 8245–8250.
- Tjoelker, M.G., Oleksyn, J. & Reich, P.B. (1998) Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO₂ and temperature. *Tree Physiology*, **18**, 715–726.
- VEMAP Members (1995) Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles*, **9**, 407–437.
- Vogelmann, J.E., Sohl, T. & Howard, S.M. (1998a) Regional characterization of land cover using multiple sources of data. *Photogrammetric Engineering & Remote Sensing*, **64**, 45–47.
- Vogelmann, J.E., Sohl, T., Campbell, P.V. & Shaw, D.M. (1998b) Regional land cover characterization using Landsat Thematic Mapper data and ancillary data sources. *Environmental Monitoring and Assessment*, **51**, 415–428.
- Willis, K.J. & Bhagwat, S.A. (2009) Biodiversity and climate change. *Science*, **326**, 806–807.
- Woods, K.D. (2000) Dynamics in late-successional hemlock-hardwoods forests over three decades. *Ecology*, **81**, 11–126.
- Zheng, D.L., Prince, S.D. & Wright, R. (2003) *NPP Multi-Biome: gridded estimates for selected regions worldwide, 1989–2001i, R1. Data set*. Oak Ridge National Laboratory Dis-

tributed Active Archive Center, Oak Ridge, TN, USA. Available at: <http://www.daac.ornl.gov>.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 The simulated baseline (1961–90) (a) optimum leaf area index and (b) annual net primary productivity (NPP) in New England.

Figure S2 (a) The baseline (1961–90) annual mean temperature and (b) annual total precipitation in New England downscaled from the PRISM 2.5 arc-minute data.

Figure S3 The distribution of mixed oak–hickory forests, northern deciduous hardwood, and boreal conifer forests in two future periods 2041–70 (referred to as 2055) and 2071–99 (referred to as 2085) in New England under nine climate changes scenarios.

Table S1 Parameters used to define three plant functional types used in our simulations for New England.

Table S2 List of observed LAI data for comparisons with modelled LAI.

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