College of Agriculture and Life Sciences Faculty Publications

College of Agriculture and Life Sciences

1-1-2014

Potential future dynamics of carbon fluxes and pools in New England forests and their climatic sensitivities: A model-based study

Guoping Tang
Desert Research Institute Reno

Brian Beckage
University of Vermont

Benjamin Smith
Lunds Universitet

Recommended Citation

Potential future dynamics of carbon fluxes and pools in New England forests and their climatic sensitivities: A model-based study

Guoping Tang[1,2], Brian Beckage[2], and Benjamin Smith[3]

[1]Division of Earth and Ecosystem Sciences, Desert Research Institute, Reno, Nevada, USA, [2]Department of Plant Biology, University of Vermont, Burlington, Vermont, USA, [3]Geobiosphere Sciences Centre, Department of Earth and Ecosystem Sciences, Lund University, Lund, Sweden

Abstract Projections of terrestrial carbon (C) dynamics must account for interannual variation in ecosystem C exchange associated with climate change, increasing atmospheric CO_2 concentration, and species dynamics. We used a dynamic ecosystem model to (i) project the potential dynamics of C in New England forests under nine climate change scenarios (CCSs) for the 21st century and (ii) examine the sensitivity of potential C dynamics to changes in climate and atmospheric CO_2 concentration. Our results indicated that forest net primary productivity (NPP) and soil heterotrophic respiration (RH) averaged 428 and 279 $gC/m^2/yr$ and New England forests sequestered CO_2 by 149 $gC/m^2/yr$ in the baseline period (1971–2000). Under the nine future CCSs, NPP and RH were modeled to increase by an average rate of 0.85 and 0.56 $gC/m^2/yr^2$ during 1971–2099. The asymmetric increase in NPP and RH resulted in New England forests sequestering atmospheric CO_2 at a net rate of 0.29 $gC/m^2/yr^2$ with increases in vegetation and soil C. Simulations also indicated that climate warming alone decreases NPP, resulting in a net efflux of C from forests. In contrast, increasing precipitation by itself stimulates CO_2 sequestration by forests. At the individual cell level, however, changes in temperature or precipitation can either positively or negatively affect consequent C dynamics. Elevation of CO_2 levels was found to be the biggest driver for modeled future enhancement of C sequestration. Without the elevation of CO_2 levels, climate warming has the potential to change New England forests from C sinks to sources in the late 21st century.

1. Introduction

Temperate forests in North America are significant sinks of atmospheric CO_2 and play a critical role in the global carbon (C) cycle [*Heinemeyer et al.*, 2007]. Climate change and increasing atmospheric CO_2 concentration are expected to alter species distribution and composition in these forests, which in turn have implications for the terrestrial C cycle [*Wramneby et al.*, 2008]. Projecting the future dynamics of C in these forests and their climatic sensitivities is significant for assessing the importance of these forests in global C cycling [*Shibata et al.*, 2005], including whether they will remain C sinks or become sources during the 21st century [e.g., *Pepper et al.*, 2005]. For example, *Rey and Jarvis* [2006] argued that the response of soil heterotrophic respiration (RH) to increases in temperature is crucial for predicting responses of forest C budgets to climate change. Information on the spatial variability of soil C is critical to assess overall C balance in terrestrial ecosystems [*Davis et al.*, 2004].

Accurate projections of forest C dynamics and their climatic sensitivities at large spatial scales require models that include feedback between environmental variables, plant physiology, and soil organic matter (SOM) decomposition [*Kramer et al.*, 2002], while also accounting for plant population and community dynamics [*Wramneby et al.*, 2008]. The vegetation models also should simulate transient responses of forests to gradual changes in climate and atmospheric CO_2 [*Simioni et al.*, 2009] because changes in forest composition affect C cycling in terrestrial ecosystems [*Tao and Zhang*, 2010]. Dynamic vegetation models (DVMs) simulate plant physiological and biogeochemical processes as well as shifts in species distribution and composition. DVMs therefore are important tools for analyzing the dynamics of C fluxes and pools and their climatic sensitivities in terrestrial ecosystems [*Mahecha et al.*, 2010].

We have used LPJ-GUESS [*Smith et al.*, 2001], a dynamic ecosystem model, to estimate current forest net primary productivity (NPP) and biomass [*Tang et al.*, 2010] as well as project the potential transient dynamics

of species distribution and composition in the 21st century in New England [*Tang et al.*, 2012]. In these studies, we implemented LPJ-GUESS using high-resolution climate data that are at a monthly time step for the period 1901–2099 and at a 30 arc sec spatial resolution. These simulations indicated that projected future climate change has the potential to shift contemporary forests of New England northward and to higher elevations and induce more complex forest dynamics such as reversed conversion between species with similar bioclimatic ranges [*Tang et al.*, 2012]. Shifts in distribution and conversions among species as well as complex interactions among climate, vegetation, and edaphic factors are likely to complicate forest C dynamics and their climate sensitivities at fine spatial scales.

Therefore, the objectives of this study are to (i) estimate baseline (1971–2000) C fluxes and pools in New England forests and project their future potential dynamics until 2099; (ii) examine the sensitivities of C dynamics to changes in temperature, precipitation, and atmospheric CO_2 concentration alone, respectively; and (iii) test if the elevation of CO_2 concentration is mainly responsible for future potential enhancement of forest C sequestration in New England. We address these objectives by focusing on forest NPP, soil RH, net ecosystem exchange (NEE), vegetation, and soil C in New England forests and their potential transient dynamics during 1971–2099. We conducted experimental simulations to examine the sensitivities of simulated C dynamics to changes in temperature, precipitation, and increasing atmospheric CO_2 concentration alone, respectively, and the role of elevation of CO_2 concentration in controlling future forest C sequestration in New England.

2. Methods and Materials

2.1. Estimates of C Fluxes and Pools by LPJ-GUESS

LPJ-GUESS [*Smith et al.*, 2001; *Sitch et al.*, 2003] is an individual-based, dynamic ecosystem model designed for simulating species distribution and composition as well as C cycling in terrestrial ecosystems. More details of LPJ-GUESS are available in supporting information Appendix S1. Below, we briefly introduce the calculations of two C fluxes (i.e., RH and NEE) and two pools (i.e., vegetation and soil C) for reference. In LPJ-GUESS, assimilated C through plant photosynthesis is reduced at the end of a simulation year by a fixed fractional (i.e., 10%) allocation to reproduction (e.g., flowers, cones, seeds, and vegetative propagules for mature plants). Biomass from plant reproduction is added to litter. The remaining C is then allocated to living tissue compartments as new biomass, including leaf (C_l), root (C_r), sapwood (C_s), and heartwood (C_h) biomass. These four biomass compartments add up to the total vegetation C (VC) (kgC/m^2):

$$VC = C_l + C_r + C_s + C_h \tag{1}$$

Allocation in LPJ-GUESS is performed on an annual time step, satisfying a set of allometric relationships specific to each plant function type (PFT) as given by *Smith et al.* [2001]. In each year, a proportion of leaf, root, and sapwood is turned over and enters the litter pool, further augmented by biomass from tree, understory mortality, and reproduction. Part of litter (L) is decomposed by microbes and released directly as CO_2 to the atmosphere. The rest of the litter becomes soil organic C that is divided in LPJ-GUESS into fast (SC_{fast}) (kgC/m^2) and slow (SC_{slow}) (kgC/m^2) decomposition components. Part of soil organic C is further decomposed by soil microbes and released as CO_2 from the soil to the atmosphere. To sum up, soil RH in LPJ-GUESS is calculated as

$$RH = SC_{fast} \times fr_{fast} + SC_{slow} \times fr_{slow} + r * L \tag{2}$$

where r is an emprical coefficient with a value of 0.25; fr_{fast} and fr_{slow} are the decomposition rates for fast and slow soil C decomposition pools, respectively. Both fr_{fast} and fr_{slow} are adjusted by soil moisture content (SMC), soil respiration temperature response rate (ST), and converted from annual to a daily basis following *Sitch et al.* [2003]:

$$\begin{cases} fr_{fast} = k1 \times ST \times (0.25 + 0.75 \times SMC)/365.0 \\ fr_{slow} = k2 \times ST \times (0.25 + 0.75 \times SMC)/365.0 \end{cases} \tag{3}$$

where $k1$ and $k2$ are SOM decay constants (0.015 for $k1$ and 0.001 for $k2$) for fast and slow decomposition components. ST incorporates damping Q_{10} response due to temperature acclimation [*Lloyd and Taylor*, 1994]. Based on initial model calibration, we empirically assumed that about 2 parts per thousand (i.e., 2‰) of fast and slow deceomposition pools in soil are dissolved and washed away from soil, respectively, due to relatively high annual precipitation in New England. The remaining soil organic C after microbial decomposition and water

Table 1. Definition of Eight Plant Function Types for New England and Related PFT Attributes[a]

PFT Definition	Examples of Dominant Species	LM[1]	LP[2]	ShT[3]	DrT[4]	FiR[5]
1. Spruce-fir	*Balsam fir, Black and Red spruce*	NL[6]	Evergreen	Tol[8]	0.23	0.08
2. White pine-cedar	*White pine, White ceder*	NL	Evergreen	ImT[9]	0.10	0.05
3. Red-jack pine	*Jack pine, Red pine*	NL	Evergreen	InT[10]	0.20	0.09
4. Maple-beech-basswood	*Sugar maple, American beech*	BL[7]	Deciduous	Tol	0.30	0.14
5. Oaks	*White oak, chestnut oak, black oak*	BL	Deciduous	ImT	0.28	0.14
6. Yellow birch-elm	*Yellow birch, American elm*	BL	Deciduous	ImT	0.30	0.05
7. Hickories	*Pignut hickory, shagbark hickory*	BL	Deciduous	InT	0.37	0.13
8. Aspen-birch	*Quaking aspen, Paper birch*	BL	Deciduous	InT	0.20	0.16

[a]LM[1]–leaf morphology; LP[2]–leaf phenology; ShT[3]–Shade tolerance; DrT[4]–drought tolerance used to calculate plant's water uptake from soil, which in turn limits sapling establishment; FiR[5]–fire resistance used to calculate tree mortality associated with fire probability and biomass destroyed by fire; NL[6]–needleleaf; BL[7]–broadleaf; Tol[8]–Tolerant; ImT[9]–Intermediate tolerant; InT[10]–Intolerant. Data source: *Tang et al.* [2012] and http://plants.usda.gov/characteristics.html.

removal is accumulated in soil. The net ecosystem exchange (kgC/m^2) of CO_2 between forest and the atmosphere is defined as follows:

$$NEE = RH - NPP + C_{fire} \qquad (4)$$

where NPP (gC/m^2) is the difference between plant gross primary productivity and respiration, and C_{fire} (kgC/m^2) is the biomass burned by fire and a function of fire probability and PFT-specific fire resistance [*Smith et al.*, 2001]. Because fire occurrence in our simulation is rather low due to high precipitation, the resultant biomass burnt by fire is insignificant. We adopted the "negative sign convention" for NEE: a negative value representing an overall flux from the atmosphere to ecosystems and a positive value representing an overall flux from ecosystems to the atmosphere.

In LPJ-GUESS, the elevation of CO_2 levels can increase plant water use efficiency, which can be expressed through the following equation:

$$gp = \frac{1.6 \times g}{D_s \times ca \times (1 - \gamma)} + CaC \qquad (5)$$

where gp is the daily canopy conductance of water vapor from leaf stomata ($mm\,s^{-1}$), ca is the mole fraction of atmospheric CO_2 concentration, λ is the optimal ratio of intercellular to ambient CO_2 concentration, D_s is the length of daylight in seconds (s), g is the leaf-level net daytime photosynthesis expressed as CO_2 diffusion (mm/m^2), and CaC (mms^{-1}) is the PFT-specific canopy conductance component. Elevated CO_2 levels also can enhance C-fixation efficiency of plants during photosynthesis. For example, the response (JE) of C3 plant photosynthesis to absorbed photosynthetically active radiation (APAR) is formulated as follows in LPJ-GUESS:

$$\begin{cases} JE = c1 \times APAR \times C_m \times cf/D_l \\ c1 = T_s \times \alpha_{c3} \times (ca \times p - p_o)/(ca \times p - 2.0 \times p_o) \end{cases} \qquad (6)$$

where cf is the conversion factor for solar radiation, D_l is day length (day), T_s is the temperature stress inhibition coefficient, α_{c3} is the intrinsic quantum efficiency of CO_2 uptake in C3 plants, p is atmospheric pressure (Pa), and p_o is the CO_2 compensation point (Pa). Details of CO_2 effects on C fixation and water use efficiency of plants are available in *Haxeltine and Prentice* [1996].

2.2. PFT Definitions and Climate Forcing Data

Given that human activities can greatly affect forest C dynamics, our simulations for New England excluded residential and urban areas, agricultural lands, lakes, and wetlands. As in our previous work [*Tang et al.*, 2012], we defined the vegetation in New England as local mixtures of eight PFTs based on species morphological, phenological, shade-tolerant, and drought-tolerant traits (Table 1). These PFTs encompass most, although not all, widespread species currently distributed in New England. Climate data required to run LPJ-GUESS include monthly temperature (°C), precipitation (mm), percent sunshine (%), and wet day frequency (days). Historical temperature and precipitation data for the period 1901–2006 were derived from Parameter-Elevation Regressions on Independent Slopes Model (PRISM) [*Daly et al.*, 2000], while percent sunshine and wet day frequency were derived from CRU TS 3.1 [*Mitchell et al.*, 2004] data sets, because they are not available from PRISM data. Future climate change data for the period 2007–2099 were based on three general circulation
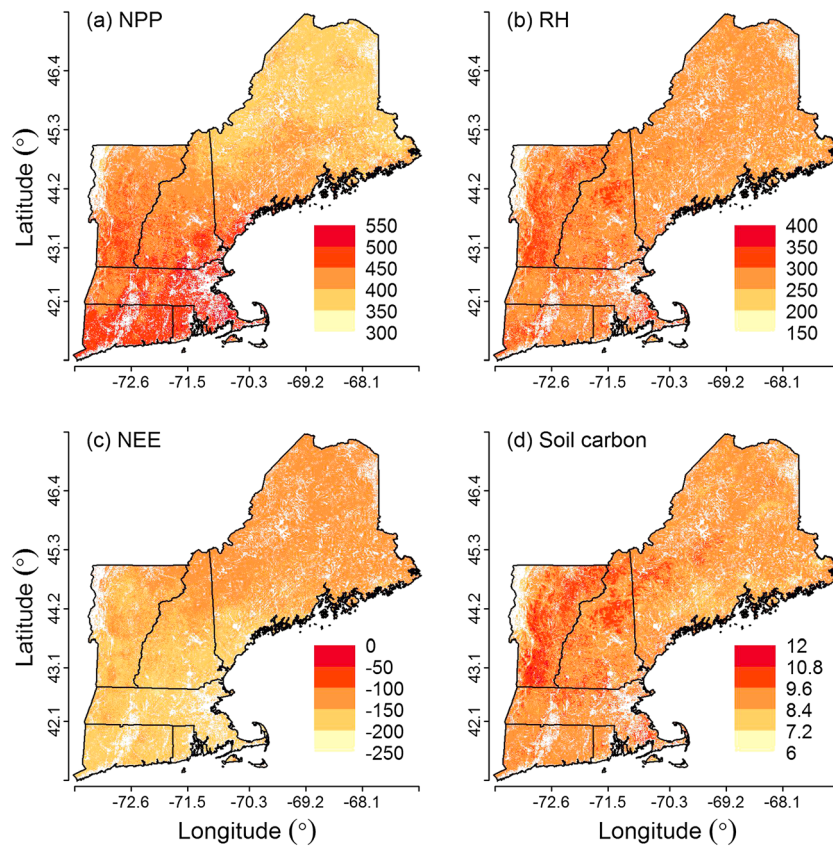
Figure 1. (a–d) The modeled baseline patterns of C fluxes and pools in New England forests. NPP source: *Tang et al.* [2010].

model (GCM) outputs, each of which was driven by three Intergovernmental Panel on Climate Change Special Report on Emission Scenarios' (SRES), respectively. The GCMs are Hadley Centre Coupled Model version 3 (HadCM3) [*Gordon et al.*, 2000], Canadian Global Coupled Model version 3.1 [*Kim et al.*, 2003], and European Centre/Hamburg version 5 (ECHAM5) [*Jungclaus et al.*, 2005]; the three SRES are B1, A1B, and A2 storylines. Data from the nine climate scenarios are considered to bracket the main range of likely future climate trajectories (Figure S1) and interpolated onto 30 arc sec resolution points using the approach described by *Tang and Beckage* [2010]. The running of LPJ-GUESS for New England followed the general modeling protocol adopted by most DVMs [e.g., *Morales et al.*, 2007] (see supporting information Appendix S1).

2.3. Sensitivity Simulations

We performed four experimental simulations based on the HadCM3 A1B climate scenario to examine (i) the sensitivity of C fluxes and pools to changes in temperature, precipitation, or atmospheric CO_2 concentration alone, respectively, and (ii) how climate change without atmospheric CO_2 enrichment affects future C dynamics in New England forests. For the first three experimental simulations, we allowed one model input variable (e.g., temperature) to vary during 1901–2099, while others (e.g., precipitation and CO_2 concentration) were fixed at their baseline mean levels. For the last experimental simulation, we allowed temperature and precipitation to vary while atmospheric CO_2 concentration was fixed at the 347.6 ppm baseline mean level throughout the study period.

3. Results

3.1. Modeled Baseline Condition of C Fluxes and Pools

Our modeled forest NPP averaged 428 gC/m^2/yr and ranged from 333 to 541 gC/m^2/yr among the grid cells in the baseline condition. Higher NPP was simulated in southern New England dominated by temperate deciduous forest types (e.g., oak-hickory), compared with northern New England dominated by evergreen forest types (e.g., spruce-fir and white pine) (Figure 1a and Figure S2a in the supporting information).
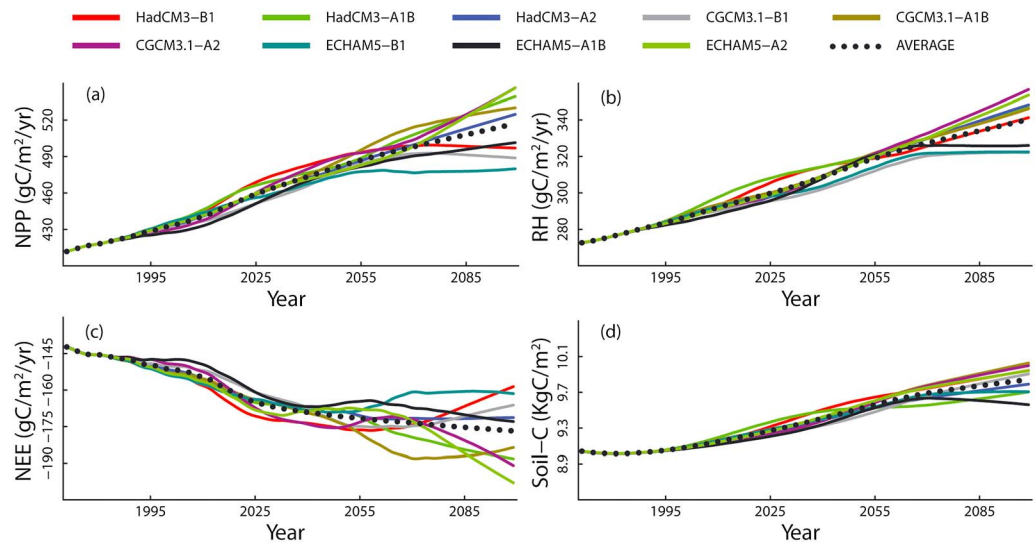
Figure 2. (a–d) The modeled trends in C fluxes and pools in New England forests during 1971–2099 under nine climate change scenarios.

Modeled soil RH averaged 279 gC/m^2/yr and ranged from 198 to 367 gC/m^2/yr among grid cells. RH was simulated to be lower in northeastern New England and generally higher in the midwestern portions of New England, especially the Green and White Mountains (Figure 1b and Figure S2b in the supporting information). Modeled NEE averaged −149 gC/m^2/yr and ranged from −231 to −15 gC/m^2/yr among grid cells. The modeled uptake of CO_2 by forests was greater in southern New England compared to northern New England (Figure 1c), indicating that the deciduous forests in New England sequester more atmospheric CO_2 than the evergreen forests in the baseline condition. Modeled C present in vegetation is greater in southern relative to northern New England (Figure S3a in the supporting information). Soil C averaged 9.0 kgC/m^2 and ranged from 6.6 to 11.5 kgC/m^2 in the baseline simulation. It was modeled to be lower at low elevations and higher at high elevations, such as the Green and White Mountains (Figure 1d).

3.2. Modeled Temporal Dynamics of C Fluxes and Pools

Averaged across the nine CCSs, forest NPP and soil RH were modeled to increase at a rate of 0.85 ($p < 0.01$) and 0.56 gC/m^2/yr^2 ($p < 0.01$) during 1971–2099 (Figures 2a and 2b). The asymmetric increase in modeled NPP and RH resulted in New England forests sequestering CO_2 from the atmosphere at a significantly increasing trend of 0.29 gC/m^2/yr^2 during the study period (Figure 2c). The overall decreasing trend in NEE (i.e., increased ecosystem uptake) however varied at different intervals and across CCSs. For example, the negative trend in NEE diverged across CCSs after 2070, with a continued strengthening of C sinks under most CCSs (e.g., ECHAM5-A2 and HadCM3-A1B) when precipitation continued to increase, while the sinks declined under some CCSs (e.g., HadCM3-B1 and ECHAM5-B1) when precipitation started to decline (Figure 2c and Figure S1b in the supporting information). The overall decreasing trend in NEE resulted in vegetation and soil C increasing at an average rate of 0.01 kgC/m^2/yr^2 across CCSs during the study period (e.g., Figure 2d). By the end of the 21st century, we project that vegetation C will increase, on average, by 18.8% and soil C by 8.9% relative to baseline conditions (Table 2).

3.3. Modeled Spatial Patterns of Change in C Fluxes and Pools

Averaged across the nine CCSs, the magnitude of changes in NPP and RH during 2071–2099 relative to the baseline period varied spatially across New England (Figures 3a and 3b). We projected that NPP will increase more than 80 gC/m^2/yr in midcentral New England but less than 80 gC/m^2/yr in northern New England and southeastern Massachusetts (Figure 3a). The increase in RH is less than 80 gC/m^2/yr in most parts of middle and northern New England but can be greater than this amount in parts of southern New England (Figure 3b). As a result, the annual uptake of CO_2 by forests was modeled to increase (more negative values) by 0–40 gC/m^2/yr in most areas of New England (Figure 3c). In parts of southern New England, however, the annual uptake of CO_2 was modeled to decrease (more positive values) by up to 80 gC/m^2/yr (Figure 3c).

**Table 2.** The Modeled Baseline (1971–2000) and Future (2071–2099) C Status[a]

	Unit	Baseline (1971–2000)			Future (2071–2099)			Change(%) in 2071–2099
		Min	Max	Mean	Min	Max	Mean	
NPP	gC/m^2/yr	333	541	428	404	628	508	20.3
RH	gC/m^2/yr	198	367	279	252	429	334	19.8
NEE	gC/m^2/yr	−231	−15	−149	−263	−105	−175	18.2
VC[†]	kgC/m^2	3.9	10.4	6.4	5.1	11.6	7.6	18.8
SC[‡]	kgC/m^2	6.6	11.5	9.0	7.9	12.2	9.8	8.9

[a]VC[†]–vegetation C and SC[‡]–soil C. The soil is 1.5 m in depth. Min and max refer to the minimum and maximum values among cells; the value of each is the 30 year (for the baseline) or 29 year (for the future) average. "Mean" refers to the average among all cells.

Modeled spatial patterns of changes in vegetation and soil C were relatively simple, showing increases in most areas of New England and that the increases were generally higher in the predominately deciduous forests of southern New England compared to the evergreen-dominated forests of northern New England (Figure 3d and Figure S3b in the supporting information). Nevertheless, projected future climate change and atmospheric CO_2 enrichment can decrease C pools in some areas of central or northern New England (e.g., Figure 3d).

3.4. Sensitivities of C Fluxes and Pools to Climate Change

Averaged across New England, simulations exploring climatic sensitivity indicated that climate warming alone will decrease forest NPP throughout the study period and increase soil RH until approximately 2020 (Figure 4a). After 2020, RH was negatively correlated with temperature increases. In contrast, NEE showed a consistently upward trend (reduced C uptake) with warming alone throughout the study period (Figure 4a). The trend in NEE was 9.4 gC/m^2/yr^2 ($p < 0.01$) as temperature increased by 1°C, suggesting that climate
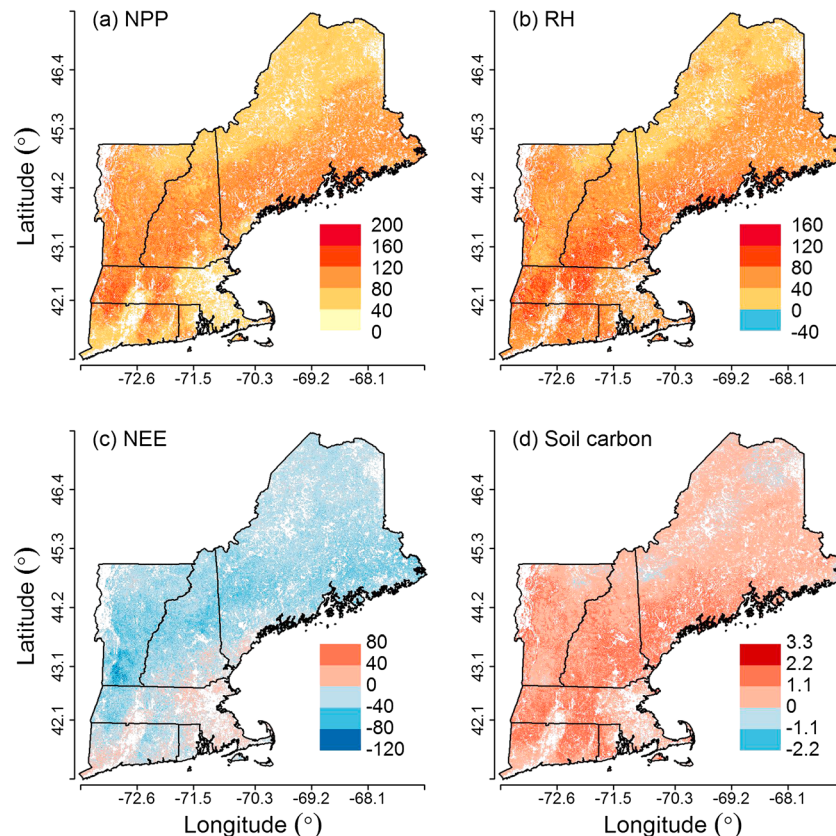
Figure 3. (a–d) The modeled changes in C fluxes and pools in New England forests during 2071–2099 relative to baseline (1971–2000) conditions.
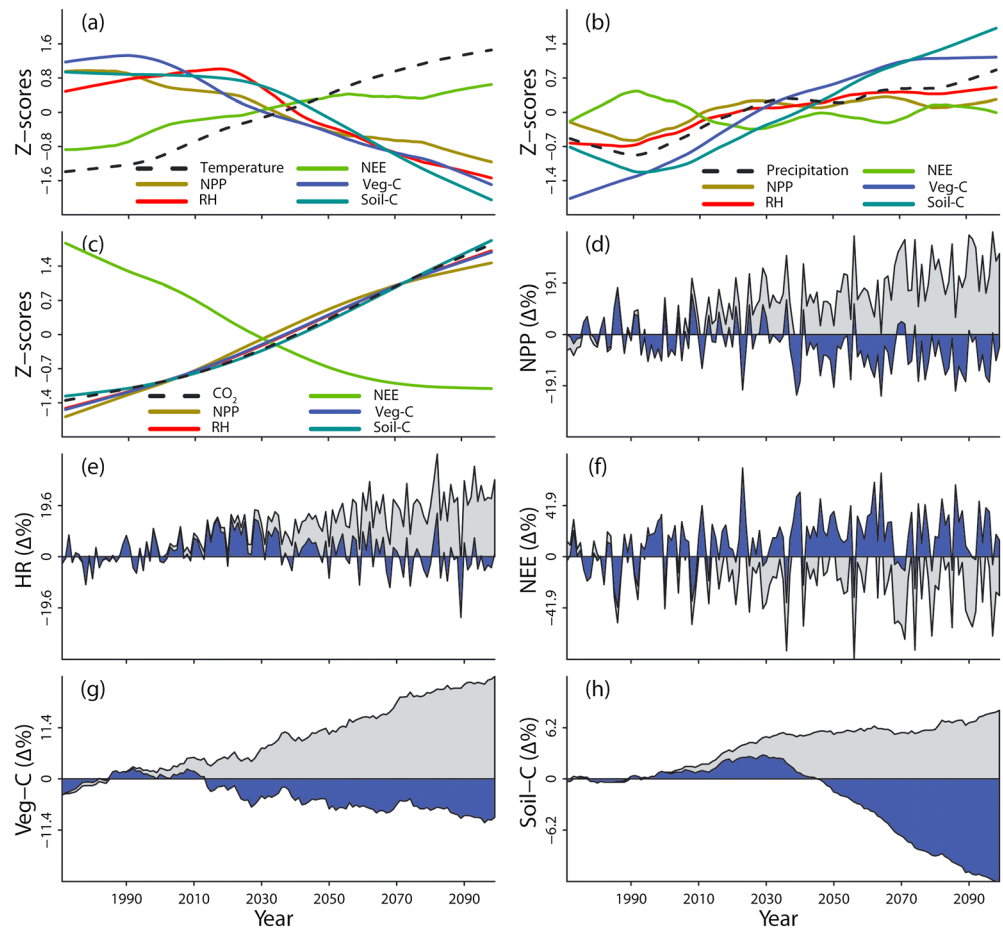
Figure 4. Effects of variation in (a) annual mean temperature, (b) total precipitation, and (c) atmospheric CO_2 concentration alone on C dynamics during 1971–2099. (d–h) Comparisons of simulated C dynamics between scenario with (gray) and without (blue) considering elevation of CO_2 levels under the HadCM3 A1B scenario. Data shown in Figures 4d–4h are percent changes relative to the baseline conditions.

warming alone has the potential to cause New England forests to become C sources within this century. As a result, vegetation and soil C were projected to decrease consistently in response to warming alone (Figure 4a).

In contrast to temperature sensitivity, forest NPP and soil RH were modeled to increase with increasing precipitation alone (Figure 4b and Figure S4 in the supporting information). Averaged across New England, the increasing rate was 0.08 gC/m^2/yr^2 ($p < 0.01$) for NPP and 0.10 gC/m^2/yr^2 ($p < 0.01$) for RH. The resultant NEE exhibited an overall negative trend, although not significant ($p = 0.56$), with precipitation (Figure 4b), indicating that increased precipitation alone has the potential to cause New England forests to sequester more atmospheric CO_2. As a result, vegetation and soil C increased at a rate of 0.005 ($p < 0.01$) and 0.001 gC/m^2/yr^2 ($p < 0.01$), respectively, under wetter conditions (Figure 4b). Elevated concentrations of atmospheric CO_2, uncoupled to temperature and precipitation change, enhanced NPP and RH at a rate of 0.38 ($p < 0.01$) and 0.17 gC/m^2/yr^2 ($p < 0.01$), respectively, in our experimental simulation. The associated NEE trended downslope at a rate of 0.22 gC/m^2/yr^2 ($p < 0.01$) (Figure 4c), indicating that New England forests will tend to assimilate more C in response to rising CO_2 concentrations. Vegetation and soil C were thus modeled to increase under the experimental simulation of CO_2 increase alone (Figure 4c).

Simulation based on climate change alone indicated that NPP and RH will decrease in the middle-to-late 21st century compared to baseline conditions, which are the opposite results from the simulation considering future CO_2 enrichment (Figures 4d and 4e). Without the elevation of CO_2 levels, the decrease in NPP was significant ($p < 0.01$), while it was not significant ($p = 0.16$) for RH. The asymmetric changes in modeled NPP and RH caused NEE to increase significantly ($p < 0.01$) during the study period (Figure 4f). As a result,
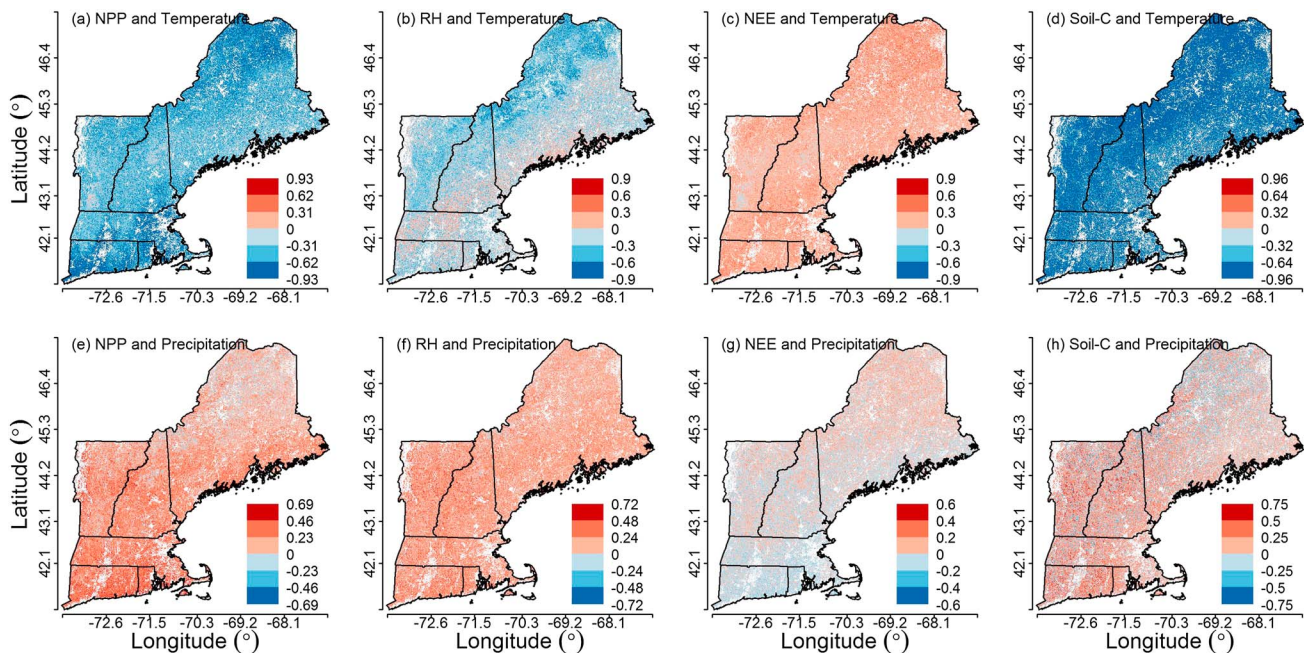
Figure 5. (a–h) The spatial heterogeneity of climatic sensitivities of simulated C fluxes and pools as illustrated by the correlation coefficients calculated for each grid cell.

vegetation and soil C were modeled to decrease in the future, contrasting with their significant increases under the simulation considering CO_2 enrichment (Figures 4g and 4h). Based on the HadCM3 A1B scenario, we estimated that NPP, RH, vegetation, and soil C during 2071–2199 will be 8%, 2%, 7%, and 10% lower, respectively, with NEE 19% higher than under baseline conditions when future elevation of CO_2 levels were not considered in the model simulation.

3.5. Complexity of Climatic Sensitivities of C Fluxes at the Individual Cell Level

At the individual cell level, our results indicate that climate warming alone can either increase or decrease C fluxes, although increase in NPP and RH and decrease in NEE occurred only in a few simulated cells (Figures 5a–5c). The positive and negative effects of climate warming also are applicable to vegetation and soil C at the level of individual cells. For example, among the 224,588 simulated cells, the number of cells where a negative relationship with climate warming occurred accounted for 92.5% for NPP (Figure 5a), 82.2% for RH (Figure 5b), 0.8% for NEE (Figure 5c), 76.6% for vegetation C (Figure S3c in the supporting information), and 97.8% for soil C (Figure 5d). Likewise, we found that increases in annual precipitation alone can either enhance or diminish C fluxes and pools as illustrated in Figure 5 and Figure S3d in the supporting information. Compared to temperature sensitivity, the effects of precipitation on C fluxes and pools were spatially more heterogeneous (Figure 5).

4. Discussion

4.1. Accuracy of Modeled Dynamics of C Fluxes and Pools

We tested the model's ability to simulate baseline forest NPP and biomass against forest inventory assessment (FIA)-based NPP and biomass estimates for similar forests [*Brown et al.*, 1999; *Jenkins et al.*, 2001; *Tang et al.*, 2010] as well as the distribution of dominant plant species in New England forests [*Tang et al.*, 2012] under the baseline condition. For example, our modeled vegetation biomass among grid cells ranged from 3.9 to 10.4 kgC/m^2 (Table 2), which is within the vegetation biomass range of 6.0 to 13.0 kgC/m^2 that has been observed in temperate forests [*Lal*, 2005]. The comparison of the modeled spatial patterns of the eight forest cover types with the National Land Cover Database 2001 [*Kelly and White*, 1993; *Vogelmann et al.*, 1998] yielded an overall Kappa statistics of 0.54, indicating that LPJ-GUESS can accurately simulate the current forest distribution in New England. These comparisons justified the model's use in New England.

Our modeled soil RH for New England forests agrees well with the data from some field-based studies. *Savage and Davidson* [2001] observed that annual ecosystem respiration (autotrophic + heterotrophic respiration) ranged from 640 to 870 gC/m^2/yr at Harvard upland sites in Massachusetts and from 660 to 800 gC/m^2/yr at Howland upland sites in Maine during 1995–1999. *Goulden et al.* [1996] found that the annual ecosystem respiration in Harvard forest ranged from 930 to 1140 gC/m^2/yr during 1991–1995. Our modeled soil RH ranged from 212 to 341 gC/m^2/yr in Harvard forest (approximately 72.2°W and 42.5°N) and from 274 to 300 gC/m^2/yr in Howland forest (approximately 68.7°W and 45.2°N). According to *Arevalo et al.* [2010], soil RH accounts for approximately 33% of ecosystem respiration during the growing season. Therefore, we inferred that the simulated ecosystem respiration varied from 642 to 1033 gC/m^2/yr in Harvard forest and from 830 to 909 gC/m^2/yr in Howland forest, comparable with our simulated ecosystem respiration.

Our modeled RH however seems much lower than other reported data. *Melillo et al.* [2002, 2011] found that the total soil respiration averaged 640 gC/m^2/yr and RH accounted for 74% to 80% of the total soil respiration in Harvard forest. The derived soil RH is about 182 to 220 gC/m^2/yr greater than our simulated value (average 292 gC/m^2/yr) for this forest. Furthermore, *Hanson et al.* [2000] indicated that the ratio of root to the total soil respiration generally vary from 45.8% to 60.4% for forest ecosystems. According to these ratios, our modeled RH in Harvard forest can be up to 95 gC/m^2/yr less than or equal to the observed values under an assumption that total soil respiration averaged 640 gC/m^2/yr [*Melillo et al.*, 2011]. These discrepancies indicate that additional field-based and modeling studies are necessary to accurately quantify the total soil respiration and partition soil autotrophic and heterotrophic respiration. For example, *Hanson et al.* [2000] also suggested that the ratio of root respiration to the total soil respiration could vary from 5% to 100%, depending on forest type, experimental setting, and analytical approaches.

New England forests likely have been C sinks since the abandonment of human-related agricultural activities in the 1800s. *Williams et al.* [2012] indicated that New England forests are currently sequestering atmospheric CO$_2$ at about 78 to 111 gC/m^2/yr, a narrower range than our simulated sequestration rate of 15 to 231 gC/m^2/yr. *Urbanski et al.* [2007] found that the annual net flux of CO$_2$ in a mixed deciduous forest in central Massachusetts averaged −250 gC/m^2/yr and ranged from −470 to −100 gC/m^2/yr. The annual forest NEE averaged −180 gC/m^2/yr in Howland forest in Maine [*Scott et al.*, 2004] and ranged from −280 to −140 gC/m^2/yr in Harvard forest in Massachusetts during 1991–1995 [*Goulden et al.*, 1996]. Our modeled forest NEE averages (−158 gC/m^2/yr in Harvard forest and −151 gC/m^2/yr in Howland forest during 1991–1995) are 92 gC/m^2/yr greater than the observed data in Harvard forest and 29 gC/m^2/yr greater than that in Howland forest. Nevertheless, they still fall within the ranges of above field observations. Discrepancies in average NEE estimates also suggest the necessity of a more accurate field-based and modeling studies on C exchanges among soil, vegetation, and the atmosphere. For example, assuming that forest NEE averages −140 to −280 gC/m^2/yr while soil RH accounts for 74% to 80% of the total soil respiration (640 gC/m^2/yr) in Harvard forest [*Melillo et al.*, 2002, 2011], the resultant NPP ranges from 613 to 962 gC/m^2/yr, which is much greater than the FIA-based NPP estimates for similar forests, averaging 446 gC/m^2/yr for maple-beech-birch and 466 gC/m^2/yr for oak-hickories in New England [*Pan et al.*, 2006].

Our modeled soil C is broadly consistent with other reported data. *Huntington et al.* [1988] reported that soil C in New Hampshire forests averaged 7.2 kgC/m^2 (originally 160 MgC/ha in dry mass converted to C flux using a factor of 0.45), close to our modeled annual mean of 9.0 kgC/m^2 for New England forests. *Davis et al.* [2004] reported that soil C in the upper 1 m of soil in southern New England hardwood forests ranged from 4.95 kgC/m^2 in the excessively drained Psamments to 26.37 kgC/m^2 in the very poorly drained Saprists, a range containing our modeled values that varied from 6.6 to 11.5 kgC/m^2 among grid cells (Table 2). In boreal forests of west Alberta, Canada, *Banfield et al.* [2002] reported that soil C ranged from 8.3 to 15.6 kgC/m^2, still encompassing our modeled range of 8.6 to 11.5 kgC/m^2 for spruce-fir and red-jack pine.

Although modeled C fluxes and pools in the baseline condition were generally comparable with results from earlier studies, our simulation excluded the effects of human activities on forest C dynamics. Forest disturbance history—such as forest regrowth following agricultural abandonment and harvesting—has been viewed however as a major mechanism responsible for the present C uptake in New England [e.g., *Albani et al.*, 2006; *Williams et al.*, 2012]. Therefore, our simulations may overestimate the role of climate warming and elevated CO$_2$ levels in the present C sinks in New England forests. Nevertheless, studies in areas with

known forest disturbance history [e.g., *McMahon et al.*, 2010] indicated that forest growth enhancement is strongly correlated with trends in temperature and atmospheric CO_2 concentrations. For example, the enhancement of growth (53%) in quaking aspen during the past five decades—a dominant species widely distributed in New England forests and considered in this study—was mainly attributed to elevated CO_2 levels [*Cole et al.*, 2010], especially under the condition of high-moisture availability. These studies justify that our simulated baseline and future C dynamics are reasonable, especially from the perspective of exploring how changes in climate and CO_2 concentration may affect the C dynamics in New England forests.

### 4.2. Climate Sensitivities of C Fluxes and C Pools

In mesic, temperate ecosystems like the forests of New England, climate warming enhances forest NPP through an expansion of the growing season and more rapid recovery of the winter-damaged photosynthetic apparatus [*Bergh et al.*, 2003]. Numerous studies confirmed that the growing season length strongly correlates with NPP [e.g., *Piao et al.*, 2007]. Earlier spring onset results in higher productivity in spring in New England [*Richardson et al.*, 2009]. In our study, however, increasing temperature alone caused the amplitude of NPP decrease in summer and early fall resulting from soil moisture deterioration to be greater than that of an increase in spring and late fall in response to lengthening of the growing season (Figure S5a in the supporting information). Changes in the seasonality and intensity of precipitation however are likely to alter such modeled relationships [*Adair and Burke*, 2010].

Increases in precipitation can ameliorate soil moisture stress and thus promote an increase in NPP. In our simulations, forest NPP was indeed strongly and linearly correlated with soil moisture content (Figure S5b in the supporting information). Such a relationship however is not spatially uniform. In central and southern New England, where annual temperature is comparatively higher (Figure S4a in the supporting information) and deciduous forests dominate, forest productivity benefits greatly from an increase in precipitation (Figure 5e). In northern New England and at high elevations, where annual temperature is generally lower (Figure S4a in the supporting information) and evergreen forests dominate, the influence of precipitation on NPP is more-or-less neutral or can be negative (Figure 5e), because water is not limiting in these areas under current climate conditions (also see supporting information Appendix S2).

Soil microbes decompose SOM and release CO_2 into the atmosphere. Averaged across New England, our modeled soil RH before 2020 was positively correlated with temperature because warming increases microbial decomposition of organic matter (Figure 4a). This result is consistent with field experiments where soil RH is overall strongly and positively related to temperature [*Bradford et al.*, 2008], and increases in temperature speed up decomposition [*Grant et al.*, 2003]. In New England, *Savage et al.* [2009] found that the seasonal variation in the soil respiration in Harvard forest was strongly correlated with soil temperature, partially because warming accelerates the microbial decomposition of soil organic C [*Koarashi et al.*, 2009]. In the long term, however, acclimation of soil respiration to the warming trend may occur [*Luo et al.*, 2001], and forest NPP tends to decrease under warming condition (Figure 4a). Modeled RH under continuous warming condition tended to decrease after 2020 because of both the acclimation of soil respiration and the lower production of litter for decomposition resulting from NPP decrease (Figure 4a).

Net sequestration of CO_2 by forests only will be realized when the enhancement of NPP is greater than the simultaneous enhancement of RH [*Kurz et al.*, 2008]. The overall positive relationship between NEE and temperature in our simulations may be attributed to the fact that warming alone increased evapotranspiration and lowered soil moisture content, which in turn decreased NPP due to soil moisture limitations (Figure 4a). *Chen et al.* [2009] found that annual C uptake by a Douglas fir forest in Canada significantly decreased due to water deficiency in summer and autumn resulting from increased annual mean temperature from 1997 to 2006. Due to a decrease in NPP and an increase in NEE, vegetation and soil C were modeled to decrease under warmer condition alone (Figure 4a). *Koarashi et al.* [2009] suggested that climate warming could accelerate microbial decomposition of soil C, enhance release of CO_2 from soil to the atmosphere, and eventually reduce soil C.

Soil RH was overall positively correlated with increases in annual precipitation because NPP tended to increase under wetter conditions (Figure 4b), and thus, more litter was available for decomposition. This finding was in accordance with field measurements conducted in Massachusetts, where RH was found to increase gradually as volumetric soil moisture increased from a lower threshold of 15% [*Suseela et al.*, 2012]. In addition, a model-based study [*Luo et al.*, 2008] on seven sites with forests including conifers and oaks
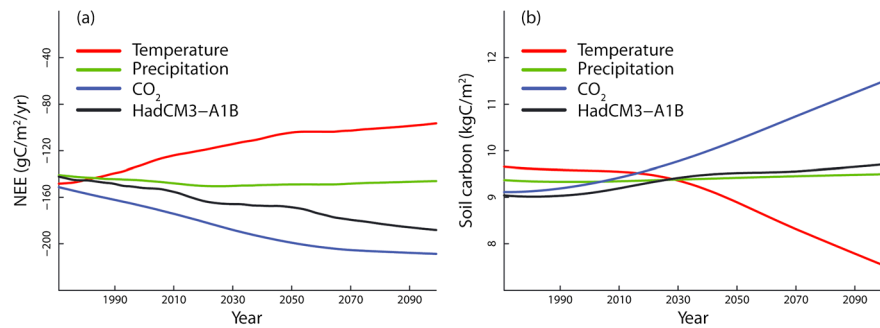
Figure 6. (a and b) Increasing atmospheric CO_2 concentration is mainly responsible for projected future increases in C sequestration by New England forests. The plotted data are based on three experimental simulations forced by the HadCM3 A1B scenario.

indicated that RH increased consistently under doubled precipitation treatments in relation to the control simulation. NEE was not significantly correlated with increases in precipitation alone (Figure 4b) largely because NPP and RH were modeled to increase at an approximate rate (0.08 gC/m^2/yr for NPP and 0.10 gC/m^2/yr for RH) as soils became moister. Although NEE did not show a significant trend with more precipitation, additional precipitation did lead to larger pools of vegetation and soil C associated with greater NPP under wetter conditions (Figure 4b). Our finding of an increase in soil C under wetter conditions is consistent with *Post et al.* [1982], arguing that soil C storage increases as the ratio of potential evapotranspiration to precipitation decreases.

4.3. Effects of Changes in CO_2 Concentration on C Fluxes and Pools

Elevation of CO_2 concentration has the potential to enhance C-fixation efficiency of plants directly (equation (6)) and improve their water use efficiency indirectly (equation (5)), which may explain the simulated increase in NPP and decrease in NEE with increasing CO_2 concentration alone (Figure 4c). A meta-analysis of 15 years of free-air CO_2 enrichment (FACE) experiments confirmed that forest C uptake and aboveground production increased under high atmospheric CO_2 concentration [*Ainsworth and Long*, 2005]. This observed response in FACE experiments was reproduced by LPJ-GUESS [*Hickler et al.*, 2011]. CO_2 fertilization tends to enhance RH via enhanced litter production. The increased rate of NPP (1.23 gC/m^2/yr^2) however was more than that of RH (0.80 gC/m^2/yr^2), suggesting that the elevated CO_2 concentrations will contribute positively to C sequestration by New England forests.

Modeled future NPP and forest C sequestration are lower in the absence of elevation of CO_2 levels, in accordance with *Albani et al.* [2006], who found that predicted C uptake rates under a similar forcing scenario are 14% lower than observed in the eastern U.S. This finding helps explain that the two C pools were modeled to decrease in the future under the scenario ignoring atmospheric CO_2 enrichment (Figures 4g and 4h). Compared to the effects of changes in temperature or precipitation alone, CO_2 fertilization was simulated to be the strongest driver for net uptake of CO_2 (Figure 6a) and increases of C storage in New England forests (Figure 6b). Likewise, *Ju and Chen* [2008] suggested that CO_2 fertilization was mainly responsible for increasing soil C in Canadian forests from 1981 to 2000, compared to climatic factors and fire. Nevertheless, other studies [e.g., *Pepper et al.*, 2005] suggested that C-nitrogen interaction plays an important role in forest C sequestration and production.

4.4. Complexity and Implication of Climatic Sensitivities of C Fluxes and Pools

Shifts in vegetation distribution and species conversions can affect C dynamics in terrestrial ecosystems [*Tao and Zhang*, 2010]. *Tang et al.* [2012] indicated that climate change could cause a more complex vegetation dynamics such as reversed conversion between species that share similar bioclimatic limits. Other studies [e.g., *Luo et al.*, 2008; *Suseela et al.*, 2012] have found that ecological drivers—such as changes in temperature and precipitation, species conversion, and edaphic factors—interplay and jointly control ecosystem C dynamics. We found that, for example, where NPP and RH showed the greatest increases from 1971 to 2099, the dominant species were modeled to be converted mainly from maple-beech-basswood or white pine to oaks in the future (Figures 3a and 3b), a result of warming-induced northward and upslope movement of

Table 3. The Complexity of Precipitation Sensitivity of C Fluxes and Pools as Indicated by Modeled Soil Moisture Content (SMC) and Species Dynamics Between the Baseline (1971–2000) and Future (2070–2099) Condition[a]

Variables	SMC (mm)	Dominant Species Remain Identical			Dominant Species Changed		
		(%)	Increase (%)	Decrease (%)	(%)	Increase (%)	Decrease (%)
NPP		61.2	72.9	27.1	38.8	29.0	71.0
RH		61.2	66.9	33.1	38.8	66.7	33.3
NEE	Increase[±]	61.2	46.2	53.8	38.8	49.4	50.6
VC[†]	(98.5%)	61.2	65.9	34.1	38.8	42.1	57.9
SC[‡]		61.2	57.8	42.2	38.8	45.1	54.9
NPP		43.3	53.8	46.2	56.7	41.8	58.2
RH		43.3	58.0	42.0	56.7	60.7	39.3
NEE	Decrease[±]	43.3	51.3	48.7	56.7	47.3	52.7
VC[†]	(1.5%)	43.3	60.7	39.3	56.7	51.2	48.8
SC[‡]		43.3	50.5	49.5	56.7	43.5	56.5

[a]VC[†]–vegetation C and SC[‡]–soil C. Plus minus sign represents the calculated percentage of increase or decrease in soil water moisture relative to the baseline condition for all 224,588 simulated cells.

oaks [*Tang et al.*, 2012, Figure 3]. The spatial heterogeneity of climatic sensitivities of C fluxes and pools indicated that species shifts and conversions as well as interactions among climate, soil, and vegetation can complicate consequent forest C dynamics at the individual cell level (see supporting information Appendix S2).

In our simulations, changes in temperature or precipitation alone either positively or negatively affected simulated C dynamics whether or not the simulated dominant species retained or changed compared to the baseline period (1971–2000). For example, soil moisture content (SMC) under the experimental simulation of varying precipitation increased in 98.5% of all simulated cells during 2071–2099 compared to the baseline period. Among cells where SMC increased, 61.2% maintained dominant species and 38.8% experienced species shifts. For cells where dominant species remained identical, 72.9% showed an increase in NPP, 66.9% in RH, 46.2% in NEE, 65.9% in vegetation C, and 57.8% in soil C. In contrast, the remainder of the cells showed a decrease in NPP, RH, NEE, vegetation, and soil C, respectively (Table 3). A similar situation occurred for cells, where SMC was modeled to decrease in the future (Table 3). The complication of climatic sensitivity of simulated C dynamics suggests that studies are still necessary to examine how climate change, species conversion, and edaphic factors interact to jointly control C dynamics.

5. Summary and Conclusions

Our modeled NPP, RH, and NEE in New England forests averaged 428, 279, and -149 gC/m^2/yr, respectively, in the baseline condition, indicating that New England forests are currently acting as C sinks. The asymmetric increase in modeled NPP (0.85 gC/m^2/yr^2) and RH (0.56 gC/m^2/yr^2) resulted in New England forests sequestering CO_2 from the atmosphere at a net rate of 0.29 gC/m^2/yr^2 during the study period. By the end of the 21st century, we project that vegetation and soil C in New England forests will increase, on average, by 18.9% and 8.9%, respectively, relative to baseline conditions.

Projected future increases in NPP and RH and decreases in NEE vary spatially across New England. The absolute magnitudes of changes in NPP and RH were generally smaller in northern and parts of southern New England and larger in midcentral New England. The spatial patterns of modeled vegetation and soil C are relatively straightforward: increases in most areas of New England, with greater increases in southern New England dominated by deciduous forests than in northern New England dominated by evergreen forests.

Climate warming alone tends to decrease NPP while increasing NEE, indicating that New England forests have the potential to become a weaker C sink under warmer conditions alone. In contrast, increasing precipitation alone tends to increase NPP while decreasing NEE, indicating that New England forests are likely to assimilate more C under wetter conditions alone. At the individual cell level, however, changes in temperature or precipitation alone can either positively or negatively affect C dynamics. The elevation of CO_2 concentration is found to be the biggest driver for modeled future enhancement of forest C sequestration in New England. In the absence of atmospheric CO_2 enrichment, projected warming has the potential to change New England forests from C sinks to sources.

The discrepancies between modeled and field-based average estimates of RH and NEE illustrated in this study suggest that accurate quantification of soil respiration and C sinks as well as partition between soil autotrophic and heterotrophic respiration are essential for quantifying terrestrial C budgets. Studies also are needed to examine how climate change, species shifts and conversions, and edaphic factors interact to control forest C dynamics. In addition, projected future C dynamics in New England forests are largely determined by the climate and CO_2 conditions associated with the nine future CCSs. More realistic predictions require improvement of the model itself and consideration of forest disturbance history [e.g., *Albani et al.*, 2006], pathogens, and invasive species on terrestrial C dynamics.

References

Adair, E. C., and I. C. Burke (2010), Plant phenology and life span influence soil pool dynamics: Bromus tectorum invasion of perennial C3-C4 grass communities, *Plant Soil*, *335*, 255–269.

Ainsworth, E. A., and S. P. Long (2005), What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2, *New Phytol.*, *165*, 351–372.

Albani, M., D. Medvigy, G. C. Hurtt, and P. R. Moorcroft (2006), The contribution of land-use change, CO_2 fertilization and climate variability to the Eastern US carbon sink, *Global. Change Biol.*, *12*, 2370–2390.

Arevalo, C. B. M., J. S. Bhatti, S. X. Chang, R. S. Jassal, and D. Sidders (2010), Soil respiration in four different land use systems in north central Alberta Canada, *J. Geophys. Res.*, *115*, G01003, doi:10.1029/2009JG001006.

Banfield, G. E., J. S. Bhatti, H. Jiang, and M. J. Apps (2002), Variability in regional scale estimates of carbon stocks in boreal forest ecosystems: Results from west-central Alberta, *For. Ecol. Manage.*, *169*, 15–27.

Bergh, J., M. Freeman, B. Sigurdsson, S. Kellomäki, K. Laitinen, S. Niinistö, H. Peltola, and S. Linder (2003), Modelling the short-term effects of climate change on the productivity of selected tree species in Nordic countries, *For. Ecol. Manage.*, *183*, 327–340.

Bradford, M. A., C. A. Davies, S. D. Frey, T. R. Maddox, J. M. Melillo, J. E. Mohan, J. F. Reynolds, K. K. Treseder, and M. D. Wallenstein (2008), Thermal adaptation of soil microbial respiration to elevated temperature, *Ecol. Lett.*, *11*, 1316–1327.

Brown, S. L., P. Schroeder, and J. S. Kern (1999), Spatial distribution of biomass in forests of the eastern USA, *Forest Ecol. Manag.*, *123*, 81–90.

Chen, B. Z., T. A. Black, N. C. Coops, P. Krishnan, R. Jassal, C. Brümmer, and Z. Nesic (2009), Seasonal controls on interannual variability in carbon dioxide exchange of a near-end-of rotation Douglas-fir stand in the Pacific Northwest, 1997-2006, *Global Change Biol.*, *15*, 1962–1981.

Cole, C. T., J. E. Anderson, R. L. Lindroth, and D. M. Waller (2010), Rising concentrations of atmospheric CO_2 have increased growth in natural stands of quaking aspen, *Global Change Biol.*, *10*, 2186–2197.

Daly, C., G. H. Taylor, W. P. Gibson, T. W. Parzybok, G. L. Johnson, and P. A. Pasteris (2000), High-quality spatial climate data sets for the United States and beyond, *T. Am. Soc. Agri. Eng.*, *43*, 1957–1962.

Davis, A. A., M. H. Stolt, and J. E. Compton (2004), Spatial distribution of soil carbon in southern New England hardwood forest landscapes, *Soil Sci. Soc. Am. J.*, *68*, 895–903.

Gordon, C., C. Cooper, C. A. Senior, H. Banks, J. M. Gregory, T. C. Johns, J. F. B. Mitchell, and R. A. Wood (2000), The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments, *Clim. Dyn.*, *16*, 147–168.

Goulden, M. L., J. W. Munger, S.-M. Fan, B. C. Daube, and S. C. Wofsy (1996), Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability, *Science*, *271*, 1576–1578.

Grant, R. F., W. C. Oechel, and C.-L. Ping (2003), Modelling carbon balances of coastal arctic tundra under changing climate, *Global Change Biol.*, *9*, 16–36.

Hanson, P. J., N. T. Edwards, C. T. Garten, and J. A. Andrews (2000), Separating root and soil microbial contributions to soil respiration: A review of methods and observations, *Biogeochemistry*, *48*, 115–146.

Haxeltine, A., and I. C. Prentice (1996), BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types, *Global Biogeochem. Cycle.*, *10*(4), 693–709.

Heinemeyer, A., I. P. Hartley, S. P. Evans, J. A. Carreira de la Fuente, and P. Ineson (2007), Forest soil CO_2 flux: Uncovering the contribution and environmental responses of ectomycorrhizas, *Global Change Biol.*, *13*, 1786–1797.

Hickler, T., et al. (2011), Projecting tree species-based climate-driven changes in European potential natural vegetation with a generalized dynamic vegetation model, *Global Ecol. Biogeogr.*, *21*, 50–63, doi:10.1111/j.1466-8238.2010.00613.

Huntington, T. G., D. F. Ryan, and S. P. Hamburg (1988), Estimating soil nitrogen and carbon pools in a Northern hardwoods forest ecosystems, *Soil Sci. Soc. Am. J.*, *52*, 1162–1167.

Jenkins, J. C., R. A. Birdsey, and Y. Pan (2001), Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data, *Ecol. Appl.*, *11*, 1174–1193.

Ju, W. M., and J. M. Chen (2008), Simulating the effects of past changes in climate, atmospheric composition, and fire disturbance on soil carbon in Canada's forests and wetlands, *Global Biogeochem. Cycles*, *22*, GB3010, doi:10.1029/2007GB002935.

Jungclaus, J. H., N. Keenlyside, M. Botzet, H. Haak, J.-J. Luo, M. Latif, J. Marotzke, U. Mikolajewicz, and E. Roeckner (2005), Ocean circulation and tropical variability in the AOGCM ECHAM5/MPI-OM, *J. Clim.*, *19*, 3952–3972.

Kelly, P. M., and J. M. White (1993), Preprocessing remotely sensed data for efficient analysis and classification, Applications of Artificial Intelligence 1993: Knowledge-Based Systems in Aerospace and Industry, *PSPIE*, *1993*, 24–30.

Kim, S. J., G. M. Flato, and G. J. Boer (2003), A coupled climate model simulation of the Last Glacial Maximum, Part 2: Approach to equilibrium, *Clim. Dyn.*, *20*, 635–661.

Koarashi, J., M. Atarashi-Andoh, S. Ishizuka, S. Miura, T. Saito, and K. Hirai (2009), Quantitative aspects of heterogeneity in soil organic matter dynamics in a cool-temperate Japanese beech forest: A radiocarbon-based approach, *Global Change Biol.*, *15*, 631–642.

Kramer, K., et al. (2002), Evaluation of six process-based forest growth models using eddy-covariance measurements of CO_2 and H_2O fluxes at six forest sites in Europe, *Global Change Biol.*, *8*, 213–230.

Kurz, W. A., G. Stinson, and G. Rampley (2008), Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances?, *Philos. Trans. R. Soc. B*, *363*, 2261–2269.

Lal, R. (2005), Forest soils and carbon sequestration, *Forest Ecol. Manag.*, *220*, 242–258.

Lloyd, J., and J. A. Taylor (1994), On the temperature dependence of soil respiration, *Funct. Ecol.*, *8*, 315–323.

Luo, Y., et al. (2001), Acclimatization of soil respiration to warming in a tall grass prairie, *Nature*, *413*, 622–625.

Luo, Y., et al. (2008), Modeled interactive effects of precipitation, temperature and [CO_2] on ecosystem carbon and water dynamics in different climatic zones, *Global Change Biol.*, *14*, 1–14.

Mahecha, M. D., et al. (2010), Comparing observations and process-based simulations of biosphere-atmosphere exchanges on multiple timescales, *J. Geophys. Res.*, *115*, G02003, doi:10.1029/2009JG001016.

McMahon, S. M., G. G. Parker, and D. R. Miller (2010), Evidence for a recent increase in forest growth, *Proc. Natl. Acad. Sci. U.S.A.*, *107*(8), 3611–3615.

Melillo, J. M., P. A. Steudler, J. D. Aber, K. Newkirk, H. Lux, F. P. Bowles, C. Catricala, A. Magill, T. Ahrens, and S. Morrisseau (2002), Soil warming and carbon-cycle feedbacks to the climate system, *Science*, *298*, 2173–2176.

Melillo, J. M., et al. (2011), Soil warming, carbon nitrogen interactions, and forest carbon budgets, *Proc. Natl. Acad. Sci. U.S.A.*, *108*, 9508–9512, doi:10.1073/pnas.1018189108.

Mitchell, T. D., T. R. Carter, P. D. Jones, M. Hulme, and M. New (2004), A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: The observed record (1901–2000) and 16 scenarios (2001–2100), in *Tyndall Working Paper*, vol. 55, pp. 25, Tyndall Centre, UEA, Norwich, U. K.

Morales, P., T. Hickler, D. P. Rowell, B. Smith, and M. T. Sykes (2007), Changes in European ecosystem productivity and carbon balance driven by regional climate model output, *Global Change Biol.*, *13*, 108–122.

Pan, Y., R. Birdsey, J. Hom, K. McCullough, and K. Clark (2006), Improved estimates of net primary productivity from MODIS satellite data at regional and local scales, *Ecol. Appl.*, *16*, 125–132.

Pepper, D. A., S. J. Del Grosso, R. E. McMurtrie, and W. J. Parton (2005), Simulated carbon sink response of shortgrass steppe, tallgrass prairie and forest ecosystems to rising [CO_2], temperature and nitrogen input, *Global Biogeochem. Cycles*, *19*, GB1004, doi:10.1029/2004GB002226.

Piao, S. L., P. Friedlingstein, P. Ciais, N. Viovy, and J. Demarty (2007), Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades, *Global Biogeochem. Cycles*, *21*, doi:10.1029/2006GB002888.

Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger (1982), Soil carbon pool and world life zones, *Nature*, *298*, 156–159.

Rey, A., and P. Jarvis (2006), Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST), *Global Change Biol.*, *12*, 1894–1908.

Richardson, A. D., D. Y. Hollinger, D. B. Dail, J. T. Lee, J. W. Munger, and J. O'keefe (2009), Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests, *Tree Physiol.*, *29*, 321–331.

Savage, K. E., and E. A. Davidson (2001), Interannual variation of soil respiration in two New England forests, *Global Biogeochem. Cycles*, *15*(2), 337–350.

Savage, K., E. A. Davidson, A. D. Richardson, and D. Y. Hollinger (2009), Three scales of temporal resolution from automated soil respiration measurements, *Agric. Forest Meteorol.*, *149*, 2012–2021.

Scott, N. A., C. A. Rodrigues, H. Hughes, J. T. Lee, E. A. Davidson, D. Bryan Dail, P. Malerba, and D. Y. Hollinger (2004), Changes in carbon storage and net carbon exchange one year after an initial shelterwood harvest at Howland Forest, ME, *Environ. Manage*, *33*, S9–S22.

Shibata, H., T. Hiura, Y. Tanaka, K. Takagi, and T. Koike (2005), Carbon cycling and budget in a forested basin of southwestern Hokkaido, northern Japan, *Ecol. Res.*, *20*, 325–331.

Simioni, G., P. Ritson, M. U. Kirschbaum, J. McGrath, I. Dumbrell, and B. Copeland (2009), The carbon budget of *Pinus radiata* plantations in south-western Australia under four climate change scenarios, *Tree Physiol.*, *29*, 1081–1093.

Sitch, S., et al. (2003), Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model, *Global Change Biol.*, *9*, 161–185.

Smith, B., I. C. Prentice, and M. T. Sykes (2001), Representation of vegetation dynamics in the modeling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space, *Global Ecol. Biogeogr.*, *10*, 621–637.

Suseela, V., R. T. Conant, M. D. Wallenstein, and J. S. Dukes (2012), Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment, *Global Change Biol.*, *18*, 336–348.

Tang, G., and B. Beckage (2010), Projecting the distribution of forests in New England in response to climate change, *Divers. Distrib.*, *16*, 144–158.

Tang, G., B. Beckage, B. Smith, and P. A. Miller (2010), Estimating potential forest NPP, biomass and their climatic sensitivity in New England using a regional dynamic ecosystem model, *Ecosphere*, *1*(6), 18, doi:10.1890/ES10-00087.1.

Tang, G., B. Beckage, and B. Smith (2012), The potential transient dynamics of forests in New England under historical and projected future climate change, *Clim. Change*, *114*, 357–377.

Tao, F. L., and Z. Zhang (2010), Dynamic responses of terrestrial ecosystems structure and function to climate change in China, *J. Geophys. Res*, *115*, G03003, doi:10.1029/2009JG001062.

Urbanski, S., C. Barford, S. Wofsy, C. Kucharik, E. Pyle, J. Budney, K. McKain, D. Fitzjarrald, M. Czikowsky, and J. W. Munger (2007), Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest, *J. Geophys. Res.*, *112*, G02020, doi:10.1029/2006JG000293.

Vogelmann, J. E., T. Sohl, and S. M. Howard (1998), Regional characterization of land cover using multiple sources of data, *Photogramm. Eng. Rem. Sens.*, *64*, 45–47.

Williams, C. A., G. J. Collatz, J. Masek, and S. N. Goward (2012), Carbon consequences of forest disturbance and recovery across the conterminous United States, *Global Biogeochem. Cycles*, *26*, GB1005, doi:10.1029/2010GB003947.

Wramneby, A., B. Smith, S. Zaehle, and M. Sykes (2008), Parameter uncertainties in the modelling of vegetation dynamics–effects on tree community structure and ecosystem functioning in European forest biomes, *Ecol. Model.*, *216*, 277–290.