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Effects of Climate Change and Shifts in Forest Composition on Forest Net Primary Production

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Abstract

Forests are dynamic in both structure and species composition, and these dynamics are strongly influenced by climate. However, the net effects of future tree species composition on net primary production (NPP) are not well understood. The objective of this work was to model the potential range shifts of tree species (DISTRIB Model) and predict their impacts on NPP (PnET-II Model) that will be associated with alterations in species composition. We selected four 200 × 200 km areas in Wisconsin, Maine, Arkansas, and the Ohio-West Virginia area, representing focal areas of potential species range shifts. PnET-II model simulations were carried out assuming that all forests achieved steady state, of which the species compositions were predicted by DISTRIB model with no migration limitation. The total NPP under the current climate ranged from 552 to 908 g C/m^2 per year. The effects of potential species redistributions on NPP were moderate (−12% to +8%) compared with the influence of future climatic changes (−60% to +25%). The direction and magnitude of climate change effects on NPP were largely dependent on the degree of warming and water balance. Thus, the magnitude of future climate change can affect the feedback system between the atmosphere and biosphere.

Key words: carbon sequestration; climate change; leaf traits; net primary production; tree species range shifts.

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Perhaps the largest scale and most dramatic disruption of global carbon cycling due to human activity is the accelerated consumption of fossil fuels since the beginning of the industrial revolution. The current accumulation rate of atmospheric CO$_2$ as a result of fossil fuel combustion is unprecedented in the past 20 000 years (Houghton et al. 2001) and will likely double the global atmospheric CO$_2$ concentration in the next 100 years (Keeling and Whorf 2005). Due to the positive radiative forcing of the elevated atmospheric CO$_2$ concentration, predictions of global temperature increases by the end of the twenty-first century have ranged from 1 to 6 °C depending on different projection scenarios (Houghton et al 2001; IPCC 2007).

Forested ecosystems contain the largest organic carbon pools in terrestrial ecosystems (Houghton 1999; Houghton et al. 2001). Their direct involvement in gas exchange with the atmosphere through photosynthesis and autotrophic respiration are measured as the largest fluxes of carbon in the interface between land and atmosphere on earth (Field et al. 1998; Houghton et al. 2001). Thus, disturbance to forested ecosystems through either natural or anthropogenic processes can result in large perturbations in global carbon cycling. In the past several decades, numerous studies have focused on the interplay between future climatic conditions and vegetation responses (Curtis and Wang 1998; Norby et al. 2005; Körner 2006; Matthews 2006; Moore et al. 2006; Schlesinger 2006). Three major components of future climatic change include the doubling of atmospheric CO$_2$ concentration, increase in air

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temperature, and changes in spatial distributions of precipitation. The vegetation responses to climate change, which range from the ecophysiological responses to ecosystem carbon balance, can lead to net changes in net primary production (NPP). Net increase of NPP as a result of vegetation responses to climatic changes will increase the uptake of the atmospheric CO_2, creating a negative feedback within the system. Conversely, a reduction of NPP may reduce the capacity of forests to sequester carbon and thus cause a positive feedback, accelerating climate change. The direction of the feedback can have large impacts on global carbon balance and subsequently the climatic change (Woodwell et al. 1998; Norby et al. 2005).

Studies addressing the interactions between the global change (primarily elevated CO_2) and vegetation responses have been mainly focused on ecophysiological and ecosystem level responses (Curtis and Wang 1998). The effects of structural changes such as shifts in species composition and succession are not well understood (Norby et al. 2001). Different species possess a wide variety of characteristics that are relevant to NPP, such as tree architecture and carbon allocation, leaf phenology, temperature and drought tolerance, and leaf characteristics. Among these species-specific characteristics, leaf traits such as specific leaf weight (*SLW*; g/m^2) and foliar nitrogen content (N_{mass}) are directly related to the NPP potential because the combination of both factors determine the potential rate of carbon assimilation (Ellsworth and Reich 1993; Kull and Niinemets 1993; Niinemets 1995, 1996; Liu et al. 1997; Niinemets et al. 2006). Therefore, interspecific differences in potential NPP could largely be accounted for by the variation of both leaf traits among species (Bassow and Bazzaz 1997). With the projected warming in the future, tree species are predicted to undergo generally latitudinal range-shifts (Davis and Zabinski 1992; Dyer 1995; Iverson and Prasad 1998; Iverson et al. 2004). Few studies have addressed how changes in species composition will impact the carbon balance of the ecosystem although such community level changes can lead to substantial alterations of ecosystem functions such as NPP (Bolker et al. 1995). At regional to global scales, dynamic global vegetation models (DGVMs) have incorporated the changes in the distribution of plant functional types (PFTs) as a result of the projected future climate conditions (Bachelet et al. 2001; Cramer et al. 2001). Since different PFTs were assigned different parameterizations, their effects on ecosystem carbon exchange were included in the modeling procedure. However, the changes in PFTs do not reflect the patterns of community dynamics where, as evidenced by the species migrations following the last glacial retreat in North America, species compositions shifted independently of each other (Davis 1969; Delcourt and Delcourt 1987; Webb and Bartlein 1992). Simulations of carbon balance that incorporated the dynamics of individual species exhibited enhanced CO_2 sequestration as the shifting of species composition allowing certain well-adapted species to either thrive or better cope with stresses (Bolker et al. 1995). Perhaps due to the lack of extensive predictions in the individual species dynamics, similar studies at large-area spatial scales are limited.

To our knowledge, the first extensive (80 tree species) prediction of potential individual species habitat shifts under several future climatic scenarios was carried out by Iverson and Prasad (1998). Under the five future climatic scenarios predicted by general circulation models, the potential habitats of each of the 80 tree species were modeled east of the 100th meridian in the USA. These studies have been extended since then to encompass 134 tree species (Prasad et al. 2007; Iverson et al. 2008). The overarching objective of the current study was to extend this community-level prediction of species importance and understand the sign and magnitude of impacts on NPP that is attributable to the predicted future species composition. Four 200 × 200 km focal areas were selected to represent areas where considerable redistributions of species suitable habitat were predicted to occur under future climatic scenarios. By constructing a simplified model that coupled the community dynamics (DISTRIB Model, Iverson and Prasad 1998; Prasad and Iverson 1999) with the PnET-II forest carbon balance model (Aber et al. 1995), we compared the relative importance of community level changes, climate changes (temperature and precipitation), and their combined effects on NPP. In addition, the inherent variations in temperature and precipitation among geographical locations provided natural variability of both factors for sensitivity analysis. Based on the sensitivity analysis, we sought to provide general patterns of NPP changes and their linkages to environmental drivers.

Results

Effects of shifts in future species composition on NPP

The total NPP from the PnET-II simulations ranged from 552 to 908 g C/m^2 per year (Figure 1). Although distinct spatial patterns of NPP were not apparent among the four focal areas, we found two areas of high NPP in central Wisconsin (WI) and southeastern Arkansas (AR). Areas of low NPP can be found in northern Maine (ME), north-east–south-west diagonal region of AR, and mid-eastern Ohio (OH) (Figure 1).

In contrast, the effect of changes in future species composition on NPP exhibited clear geographical patterns (Figure 2). Under both HAD2CM and CCC climatic scenarios, potential changes in species composition were predicted to result in a 12% decrease in NPP in western ME and 6% decreases in NPP in northern AR (Figure 2). Areas of positive effects from the potential species changes were found at the southwestern corner of the WI block under CCC scenario. The species effects were generally minimal in the OH block under both HAD2CM and CCC scenarios.

To identify which species contributed to the changes in NPP under the CCC scenario, we selected three areas exhibiting

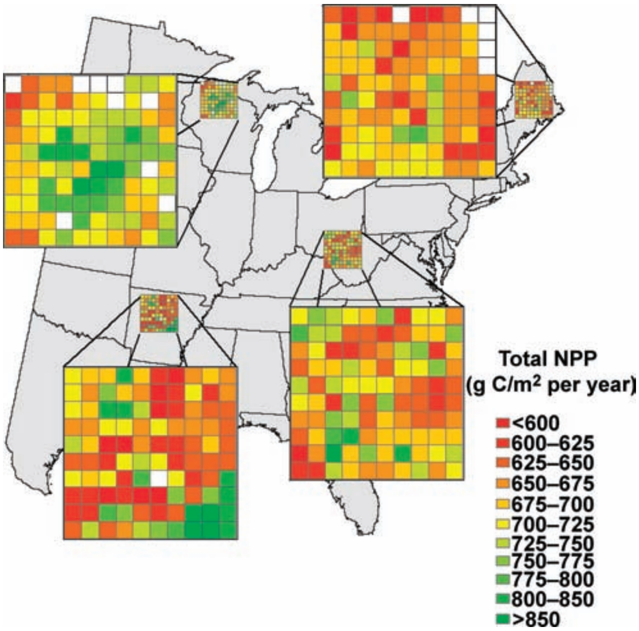

Figure 1. Net primary productivity (NPP) of forested area in each 20 × 20 km cell under the current climate. Sixteen cells (blank color fill) were excluded for the simulation due to the lack of data (e.g. outside the US boarder) or the coverage of water bodies.

substantial net increase or decrease of NPP as a result of potential changes in future species composition (Figure 3). Greater contributions to NPP from *Ulmus americana*, *Juniperus virginiana*, *Quercus alba*, *Quercus velutina*, *Prunus serotina* and *Fraxinus americana* and reduced contributions to NPP from *Populus tremuloides*, *Betula papyrifera*, and *Fraxinus nigra* resulted in a net increase of 4%–8% of NPP in southwestern WI (Figure 3). In western ME, although increases in NPP were identified from *P. serotina*, *Acer rubrum*, *Quercus rubra*, *F. americana*, *Tsuga canadensis*, *Q. alba*, and *Pinus strobus*, they did not compensate for the greater reduction in NPP from *Abies balsamea*, *Picea rubens*, *Betula papyrifera*, *Picea mariana*, and *Betula alleghaniensis* (Figure 3). These changes in species compositions resulted in a net 12% decrease of NPP in western ME. The reduction of NPP in northern AR was a result of the transition of species composition by the reductions of *Q. alba*, *Q. velutina*, *Q. rubra*, *Cornus florida*, *J. virginiana* and *Carya texana* and increases of *Pinus taeda, inus. elliottii*, and *Quercus nigra* (Figure 3). The net changes as a result of this transition of species composition ranged from −2% to −6%.

Effect of climatic changes on NPP

Future climatic changes produced more dramatic and direct influences on modeled NPP as compared with the effects of potential changes in future species composition. The net effect of future climatic changes, while keeping the current species composition unchanged on NPP, ranged from −60% in southern AR under the CCC scenario to +25% in some patches of WI, ME, and OH under the HAD2CM scenario (Figure 2). The patterns of NPP changes as a result of future climatic changes exhibited clear geographic patterns that were different between the HAD2CM and CCC scenarios. The mild increase in temperature accompanied by a large increase in precipitation under HAD2CM (Table 1) had positive effects on NPP in most of the four focal areas. Under the CCC scenario, the much warmer temperature with only slight increases in precipitation (Table 1) had negative effects on NPP in mid- to western WI (−2% to −20%), most of AR (−2% to −60%; more negative in south), and southern OH (−2% to −20%) (Figure 2). In contrast, most of the ME area exhibited increased NPP (+2% to +25%) under the CCC scenario (Figure 2).

Combined effects of changes in species composition and climate

The combined effects of changes in species composition and climate on NPP exhibited similar geographical patterns to those under climatic changes only (Figure 2). Under the HAD2CM scenario, with the species composition unchanged, the effects were positive in most of the WI and OH areas. Combined with the negative effects of potential changes in species composition, the number of cells exhibiting increased NPP under the HAD2CM scenario was reduced in ME and AR (Figure 2). Under the CCC scenario, the additive effects of species and climatic changes were shown in northern AR and most of the ME area. The former exhibited a more dramatic decrease of NPP under combined effects due to the negative effects of both species and climate changes. The latter exhibited more neutral effects under the combined effects due to the opposite effects of species and climate change.

Sensitivity analysis of environmental factors on NPP

The variations of NPP among cells can partly be explained by environmental factors such as annual mean temperature, annual total precipitation and soil water-holding capacity, depending on the different focal areas and climatic scenarios (Figure 4). NPP was generally positively correlated with annual mean temperature below certain temperature thresholds. This pattern was primarily driven by variations between climatic scenarios because the relationship of NPP and temperature within each scenario was weak (Table 2). In WI, OH, and AR, annual NPP increased with a mild increase in annual mean temperature and a substantial increase in annual precipitation from the current to HAD2CM climatic scenarios (Figure 4). At the much increased temperature and only slightly increased precipitation under the CCC scenario, NPP decreased significantly with increasing temperature ($P < 0.001$; Table 2). These patterns

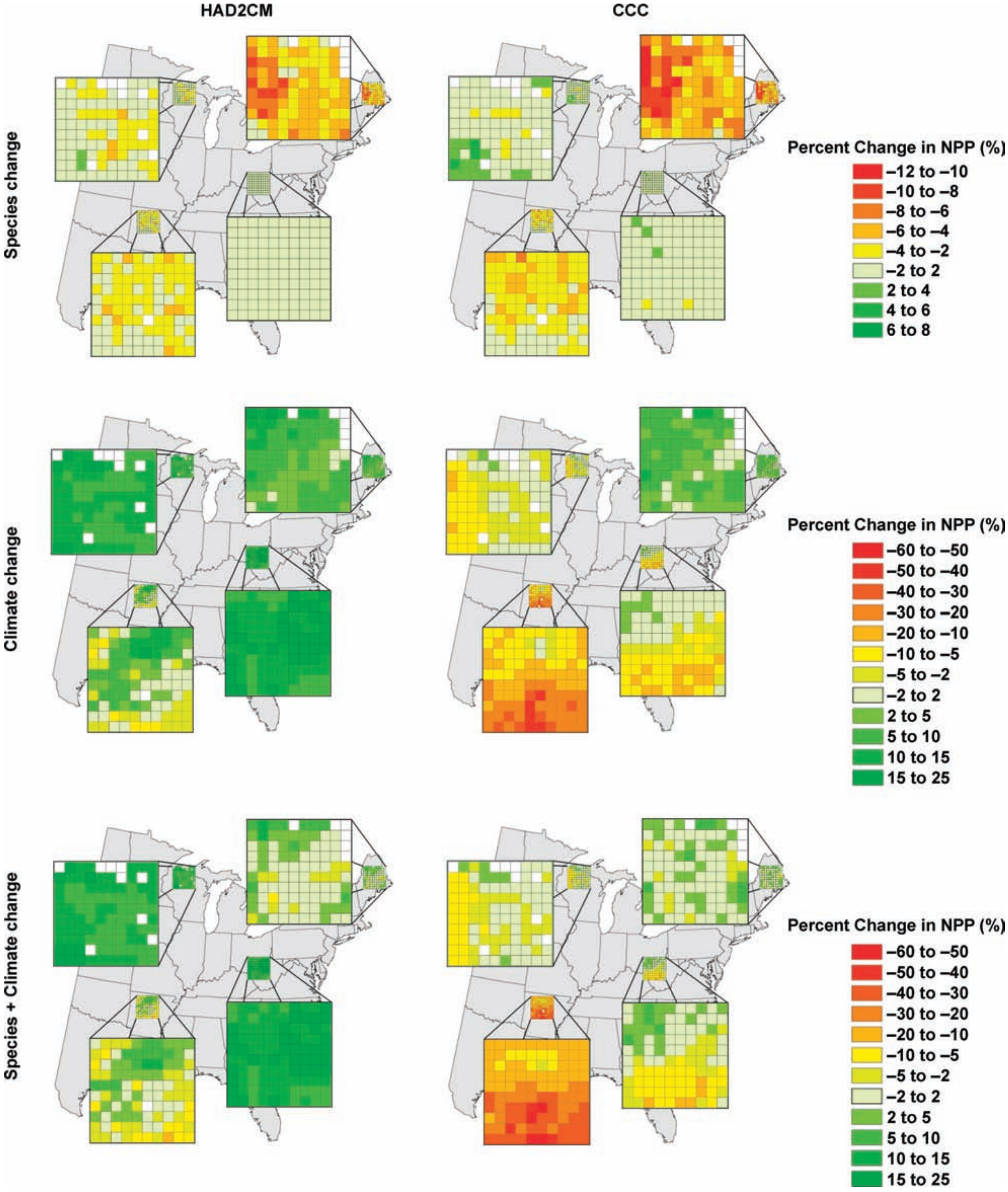

Figure 2. Percent changes of annual net primary productivity (NPP) due to the effects of species range shift, climate change and the combination of both. HAD2CM and CCC are climatic scenarios, under which the effects of resulting species range shifts, climate change, and the combination of both on NPP were simulated. Due to the much narrower range of variations, the color ramp for species change effects was different from the other two effects.

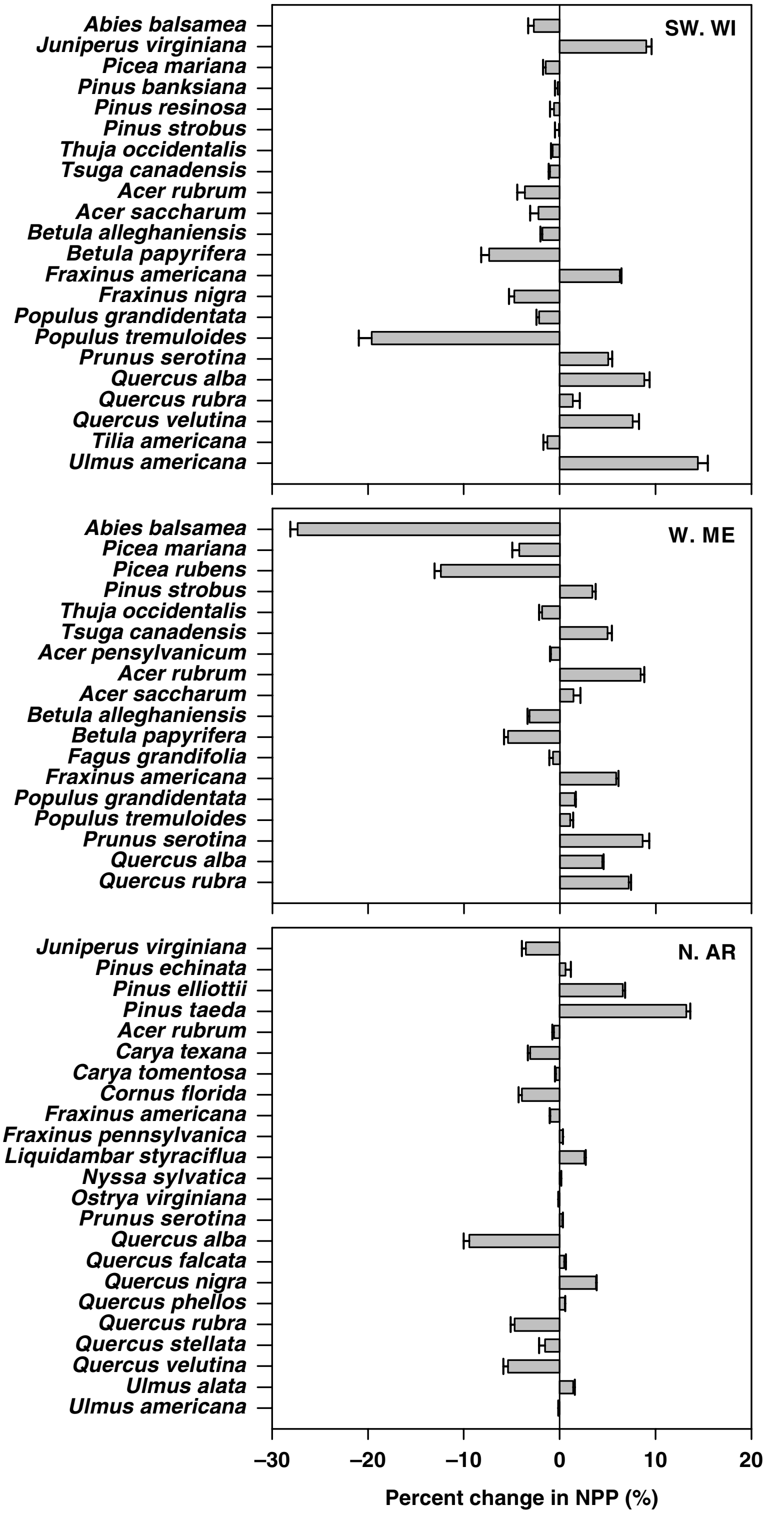

Figure 3. The net effect of species-specific changes in the abundance on net primary productivity (NPP) of areas where substantial species effects on NPP were predicted under CCC climatic scenario. The areas include northern Arkansas (49 cells; $<$ 2% NPP change), southwestern Wisconsin (13 cells; $>$ 2% NPP change), and western Maine (24 cells; $<$ 6% NPP change).

Table 1. The climate drivers used for the PnET-II simulations included photosynthetically active radiation (PAR; μmol/m^2 per s), annual mean temperature (°C), and total precipitation (cm). Data reported are the mean (± *SE*) of 100 cells within each focal area. Simulations were carried out under current, HAD2CM, and CCC climatic scenarios (see text) which varied in temperature and precipitation. PAR did not vary between climatic scenarios

		Annual mean temperature (°C)			Annual total precipitation (cm)		
Focal area	PAR (μmol/m^2 per s)	Current	HAD2CM	CCC	Current	HAD2CM	CCC
WI	535.88 ± 1.59	4.64 ± 0.06	7.36 ± 0.06	9.61 ± 0.05	82.20 ± 0.29	94.62 ± 0.16	90.25 ± 0.20
ME	551.31 ± 1.00	4.59 ± 0.10	6.39 ± 0.10	8.94 ± 0.09	106.33 ± 0.70	130.65 ± 0.75	110.33 ± 0.49
AR	728.95 ± 1.02	15.06 ± 0.10	17.39 ± 0.10	20.74 ± 0.08	124.67 ± 0.82	154.61 ± 0.46	138.32 ± 0.58
OH	650.41 ± 1.81	11.46 ± 0.07	13.31 ± 0.04	17.08 ± 0.06	105.86 ± 0.55	135.94 ± 0.67	113.36 ± 0.38

AR, Arkansas; ME, Maine; OH, Ohio; WI, Wisconsin.

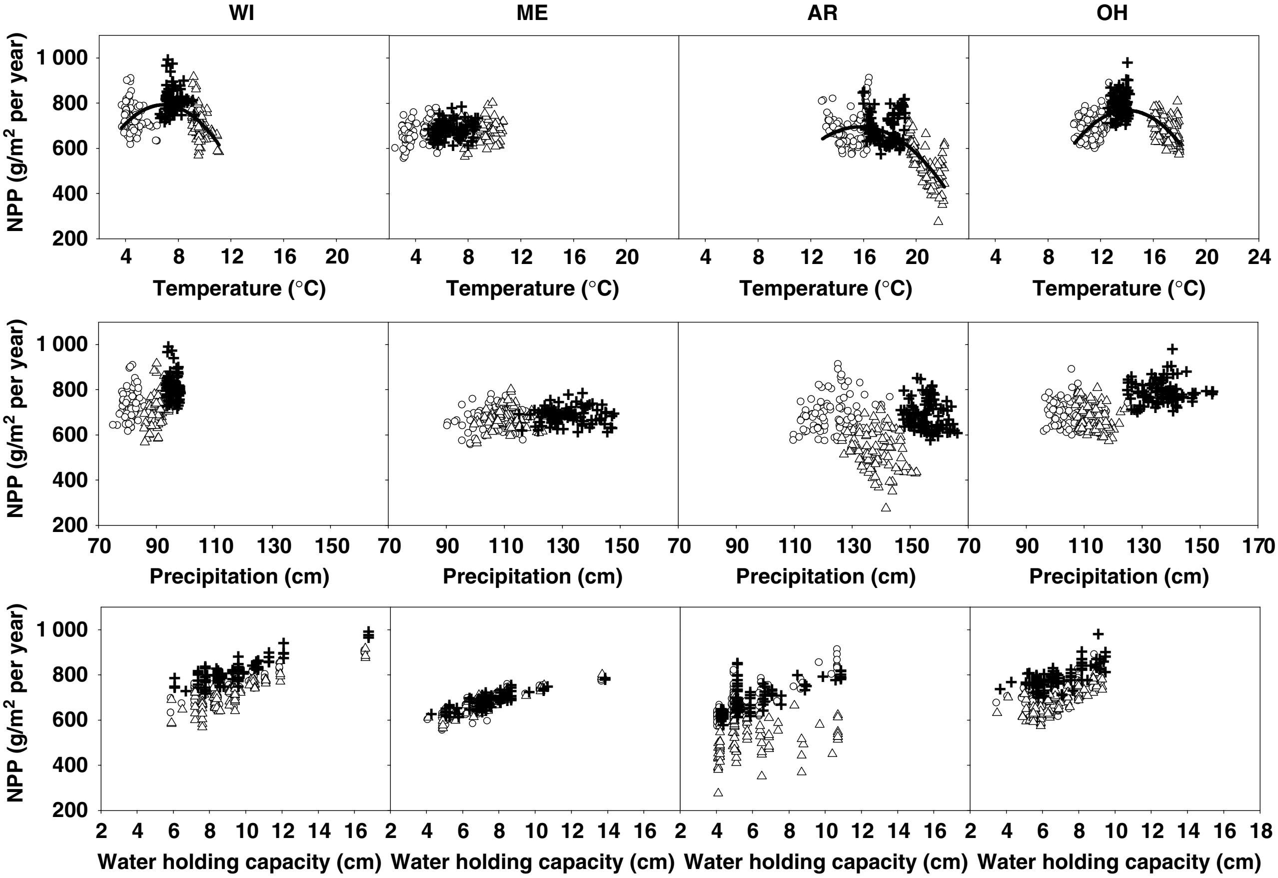

Figure 4. Sensitivity analysis of annual mean temperature, precipitation, and water-holding capacity on the responses of annual net primary productivity (NPP). Under current (○), HAD2CM (△), and CCC (+) climatic scenarios, NPP of combined species and climatic change effects were used for the analysis. Annual mean temperature and precipitation of each 20 × 20 km cell varied with climatic scenarios while water-holding capacity was kept constant for each individual cell. See Table 2 for the statistical results and the polynomial curve fitting of the relationships between NPP and temperature in Wisconsin (WI), Arkansas (AR) and Ohio (OH).

of NPP changes in response to temperature in WI, OH, and AR were well accounted for by quadratic polynomial regression functions with R^2 ranging from 0.26 in WI and 0.55 in AR (Table 2). In ME, NPP was positively and linearly correlated with temperature without reaching a temperature threshold (Figure 4 and Table 2).

The relationships between NPP and precipitation were mostly not significant within each climatic scenario with the exception

Table 2. Pearson correlation coefficients of the relationships between net primary productivity (NPP) and environmental variables. Under HAD2CM and CCC climatic scenarios, NPP of combined species and climatic change effects were used for the analysis. Annual mean temperature and precipitation of each 20 × 20 km cell varied with climatic scenarios, while water-holding capacity was kept constant for each individual cell. Cells located outside the US border or at water bodies were not included; therefore, less than 100 cells were included in this analysis.

		WI		ME		AR		OH	
Environmental variables	Climatic scenarios	*n*	*r*	*n*	*r*	*n*	*r*	*n*	*r*
Annual mean temperature (°C)	Current	91	-0.32^{**}	94	0.26^{*}	99	0.13^{ns}	100	0.18^{ns}
	HAD2CM	91	0.00^{ns}	94	0.11^{ns}	99	-0.01^{ns}	100	0.09^{ns}
	CCC	91	-0.45^{***}	94	0.18^{ns}	99	-0.69^{***}	100	-0.41^{***}
	Overall†	273	-0.12^{*}	282	0.14^{*}	297	-0.65^{***}	300	-0.22^{***}
Precipitation (cm)	Current	91	0.09^{ns}	94	0.07^{ns}	99	0.15^{ns}	100	-0.05^{ns}
	HAD2CM	91	-0.09^{ns}	94	0.00^{ns}	99	-0.13^{ns}	100	0.03^{ns}
	CCC	91	0.34^{**}	94	0.13^{ns}	99	-0.22^{*}	100	-0.42^{***}
	Overall	273	0.38^{***}	282	0.10^{ns}	297	0.01^{ns}	300	0.55^{***}
Water-holding capacity (cm)	Current	91	0.82^{***}	94	0.82^{***}	99	0.77^{***}	100	0.66^{***}
	HAD2CM	91	0.84^{***}	94	0.83^{***}	99	0.70^{***}	100	0.69^{***}
	CCC	91	0.81^{***}	94	0.86^{***}	99	0.15^{ns}	100	0.81^{***}
	Overall	273	0.67^{***}	282	0.83^{***}	297	0.37^{***}	300	0.53^{***}

ns, not significant ($P > 0.05$); $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

†The overall relationships between annual mean temperature (X) and NPP (Y) in Wisconsin (WI), Arkansas (AR), and Ohio (OH) followed polynomial regression functions: $Y = 314.22 + 138.71\,X - 10.06\,X^2$ ($F_{2,270} = 48.57$, $P < 0.0001$, $R^2 = 0.26$) in WI; $Y = -927.26 + 205.96\,X - 6.53\,X^2$ ($F_{2,294} = 176.55$, $P < 0.0001$, $R^2 = 0.55$) in AR; $Y = -1037.19 + 257.70\,X - 9.19\,X^2$ ($F_{2,297} = 98.52$, $P < 0.0001$, $R^2 = 0.40$) in OH.

of WI and OH under the CCC scenario (Table 2). Interestingly, a highly significant and negative relationship ($r = -0.42$; $P < 0.001$) between NPP and precipitation was found in OH under the CCC scenario. However, the overall relationships between NPP and precipitation were positive in WI and OH (Table 2). NPP exhibited a significant, positive, linear response to water-holding capacity (WHC; cm) with the exception of the relationship under the CCC scenario in AR (Table 2). Among these significant relationships ($P < 0.001$), the correlation coefficient (r) ranged from 0.66 to 0.86 within each climatic scenario (Table 2). The overall relationships between NPP and WHC were all significant ($P < 0.001$) with the correlation coefficient ranging from 0.37 in AR to 0.83 in ME (Table 2).

Discussion

Forests are constantly changing in stand structure and species composition (Bormann and Likens 1979; Oliver and Larson 1996). At large spatial and temporal scales, tree species in North America have undergone constant range shifts associated with the gradually warming climate over the past 18 000+ years since the last glaciation (Davis 1969; Delcourt and Delcourt 1987). With a faster rate of climate change predicted by modern general circulation models (Mitchell et al. 1995; Laprise et al. 1998; Houghton et al. 2001), the current tree species distributions are predicted to change more rapidly in the future (Davis and Zabinski 1992; Dyer 1995; Iverson and Prasad 1998; Bachelet et al. 2001; Cramer et al. 2001). The net effects of such species redistributions on NPP will depend on the future species compositions and their interaction with future climate. Preliminary to the parameterization of a more realistic model, we created a simplified model to understand the direction and magnitude of such species redistribution effects (sensitivity analysis) on NPP.

In this study, we predicted that community-level changes in species composition will have a substantial impact on NPP. Changes in NPP as a result of species redistribution ranged from −12% to +8%, depending on the geographical locations. In western ME, the transition from spruce-fir forest to deciduous forest resulted in up to a 12% decrease in NPP. This decrease in NPP was probably due to a relatively shortened growing season for trees because the forests will transition from coniferous (evergreen leaves) to deciduous (dormant in winter) forests. In southwestern WI, the greater *SLW* of *Quercus* species resulted in the increase of NPP with the transition from the deciduous species of northern locales (e.g., *Acer*, *Betula* and *Populus* species) to *Quercus*-dominated forests. In northern AR, the transition from oak-hickory-dominated forests to southern pines such as *Pinus elliottii* and *Pinus taeda* resulted in slightly decreased NPP.

It should be noted that the predictions of species redistributions were based on the potential changes in suitable habitat for each species. The DISTRIB model did not account for actual successful migration and establishment or the landscape continuity and pattern, which are necessary for the prediction of the future presence or absence of tree species. Due to the habitat fragmentation and accelerated rate of climate change,

Table 3. The targeted species and their corresponding overall importance values in each of the four focal areas (see Figure 1 for the locations of each focal area). The overall importance values were calculated as the mean of relative importance values under the current, HAD2CM, and CCC climatic scenarios and were used as the criteria for the selection of targeted species.

Targeted species	WI	ME	AR	OH
Abies balsamea	4.24	11.87		
Juniperus virginiana	1.63		3.46	1.75
Picea mariana	1.77			
Picea rubens		6.63		
Pinus banksiana	1.84			
Pinus echinata			8.96	2.82
Pinus elliottii			1.88	
Pinus resinosa	1.98			
Pinus strobus	2.23	4.37		
Pinus taeda			9.14	2.27
Pinus virginiana				2.39
Thuja occidentalis	1.64	4.74		
Tsuga canadensis	1.29	4.92		
Acer pensylvanicum		1.52		
Acer rubrum	11.09	13.31	2.51	6.05
Acer saccharum	10.36	5.88		5.20
Betula alleghaniensis	1.58	3.80		
Betula papyrifera	3.83	3.48		
Carpinus caroliniana				1.22
Carya texana			4.61	
Carya tomentosa			2.59	
Cornus florida			3.08	5.17
Fagus grandifolia		5.68		2.16
Fraxinus americana	2.62	2.99	0.93	3.58
Fraxinus nigra	2.82			
Fraxinus pennsylvanica			1.06	
Juglans nigra				1.38
Liquidambar styraciflua			4.98	
Liriodendron tulipifera				4.75
Nyssa sylvatica			3.27	2.31
Ostrya virginiana			1.33	1.26
Oxydendrum arboreum				1.31
Platanus occidentalis				1.12
Populus grandidentata	1.85	1.39		
Populus tremuloides	9.73	2.64		
Prunus serotina	4.31	2.11	1.11	2.33
Quercus alba	2.29	1.25	5.81	5.77
Quercus coccinea				1.40
Quercus falcata			2.41	
Quercus nigra			1.95	
Quercus prinus				2.66
Quercus rubra	3.97	2.73	1.86	2.37
Quercus stellata			6.84	4.75
Quercus velutina	1.90		3.18	3.36
Robinia pseudoacacia				1.51
Sassafras albidum				3.45
Tilia americana	2.62			
Ulmus alata			4.40	1.94
Ulmus americana	3.65		0.91	2.29
Ulmus rubra				1.48
Total	79.25	79.33	76.29	78.07

AR, Arkansas; ME, Maine; OH, Ohio; WI, Wisconsin.

the migration of tree species may fail to keep up with the shifts in the ranges of suitable habitats (Davis and Zabinski 1992; Iverson et al. 2004). This will likely result in further declines in NPP due to possible reductions in forested area and additional environmental stresses imposed on the surviving trees (Higgins and Harte 2006). Since tree species are parameterized primarily through variations of *SLW* and N_{mass}, the simulation of such species-specific stress responses to climate change will require more detailed parameterization of variables such as the optimum temperature of photosynthesis, and stomatal response to vapor pressure deficit. Species redistributions, when taking into account more species-specific variables and the risk of extinction due to rapid climatic change, can have larger potential impacts on NPP than we simulated.

The range of NPP change due to climatic changes was wider than that due to species redistributions alone. The sign and magnitude of changes varied depending on climatic scenarios and geographic locations. A clear latitudinal gradient corresponding to the influence of climatic change on NPP was found particularly under the much warmer CCC scenario. NPP of forests tended to have a more negative response to future climatic change at lower latitudes. Under the HAD2CM scenario, which had slightly warmer and largely increased precipitation, NPP changes exhibited mostly positive responses except for the warmest area in southern AR.

The patterns of changes in NPP as a result of climatic change can generally be depicted by the parabolic response function ("hump-shaped") between NPP and annual mean temperature (Bachelet et al. 2001; Norby et al. 2001). The annual mean temperature associated with the maximum NPP can be regarded as the threshold temperature transition point (Bachelet et al. 2001). Below the temperature threshold, NPP generally increased with increasing temperature. Conversely, NPP responded negatively to increasing annual mean temperature when it was above the temperature threshold. In addition, this temperature threshold varied between different focal areas and was closely coupled with annual precipitation. The much lower annual precipitation of the WI focal area also had a lower temperature threshold than that of OH and AR. The temperature threshold in ME was not reached because of its cooler climate at high latitude and relatively high annual precipitation. Based on the geographic patterns of NPP change under the HAD2CM and

CCC scenarios, we suggest that temperature and precipitation collectively determine the temperature threshold. This temperature threshold, which, to some extent, was associated with the water balance, determined the direction of NPP changes under the future climatic scenarios. The importance of water balance regarding its impacts on NPP was also reflected by the close relationships between NPP and water-holding capacity. The identification of the temperature threshold for NPP response is critical because it determines the direction of NPP response to future climatic change and subsequently the direction of feedbacks in the carbon cycling of the atmosphere-terrestrial ecosystem interface.

The combined effects of species redistribution and climatic change on NPP were generally additive, even though we expected to see more complex interactions between these two factors. For example, the allowance of species redistribution could ameliorate the overall environmental stress to the forests with the immigration of more suitable species. In one study, the incorporation of dynamic species composition in a gap model simulation enhanced the positive effects of CO_2 fertilization by 30% (Bolker et al. 1995). With the simple characterization of species-specific differences using *SLW* and N_{mass}, such complex interactions of species redistribution and climatic changes were not depicted in our simulations. The inclusion of more species-specific variables such as shade tolerance, optimum temperature for photosynthesis, leaf phenology, and drought tolerance will likely provide more realistic simulations.

In this paper, we compared the relative importance of, and the interactions between, climatic change and species redistribution on NPP. By targeting key species-specific features (N_{mass} and *SLW*) and climatic drivers (temperature and precipitation), we found climatic change had greater potential in its effects on NPP than species redistribution. We did not include the CO_2 fertilization effect due to the unknown persistence of such an effect in a mature forest. The effect of CO_2 fertilization, if the effect persists, may increase the temperature threshold of NPP response by increasing water-use efficiency. Based on a synthesis of four Free-Air CO_2 Enrichment (FACE) study sites in the deciduous forests of the USA, elevated CO_2 generally enhanced NPP by 23% in those young stands (Norby et al. 2005). Under the more likely and dramatic CCC climatic scenario, such enhancement of CO_2 fertilization will compensate little NPP decline imposed by climatic change. However, the evidence so far shows that the effect of CO_2 fertilization could largely become diminished within 3–5 years after growth becomes limited by another resource (Körner 2006). In addition, the extra carbon gained as a result of elevated CO_2 in a mature stand was mostly allocated to labile carbon belowground, which would likely enhance soil respiration and render minor increases of long-term carbon storage (Körner et al. 2005). Therefore, we argue that the effects of CO_2 fertilization will not fully compensate for the negative effects of future climatic changes on NPP, particularly when we take into account the potential negative effects of environmental stresses and extinction imposed by rapid climatic change and habitat fragmentation. Future moderation of climatic change will require not only the reduction of CO_2 emissions (or active atmospheric CO_2 sequestration) but also the preservation of habitat continuity. The latter would ensure less obstruction in species redistribution and likely facilitate the community level adjustments to climatic change.

Materials and methods

DISTRIB model

The DISTRIB model is a statistical model that predicts the suitable habitats of tree species in the eastern USA under future climatic scenarios (Iverson and Prasad 1998). It is based on a regression tree analysis (RTA) procedure that bridges the relationships between the current tree species distribution (represented as relative importance values based on relative basal area and relative stem density) of the forest inventory analysis (FIA) database (Hansen et al. 1992) and their environmental variables. The 33 environmental variables included climate factors, soil properties, land use/cover factors, elevation, and landscape pattern (see Iverson and Prasad 1998 for details of data sources). The current monthly temperature and precipitation were acquired in either 10 × 10 km format (US Environmental Protection Agency 1993) or 0.5 × 0.5° format from USDA Forest Service at Corvallis, OR (R. Neilson and R. Drapek, pers. comm., 1996).

Regression tree analysis is a recursive data partitioning algorithm (De'ath and Fabricius 2000) that is used by the DISTRIB model to sequentially partition the species importance values into two subsets based on the best environmental predictor at each split. The predictor at each split was chosen to maximize the difference between the two subsets while minimizing the variance within each of the two subsets. For each species, the output of the RTA procedure is a set of tree-structured decision rules for the outputs of importance values. Variables that function at larger scales generally split the datasets earlier in the model than those that function at local scales. To predict the future suitable habitat of each individual tree species, the current climatic variables were swapped with the outputs from two scenarios of the future climatic equilibriums under doubled atmospheric CO_2 concentration: (i) Hadley Centre for Climate Prediction and Research (HAD2CM) model (Mitchell et al. 1995); and (ii) Canadian Climate Centre (CCC) Model (Table 1; Laprise et al. 1998).

Without the incorporation of factors such as habitat fragmentation, population dynamics, and the potential migration speed of each individual species, the DISTRIB model does not predict the future species abundance; however, it predicts the suitable habitat of each tree species in the future. The DISTRIB model is a species-specific vegetation model that provides an extensive coverage of species (80 tree species) and area (east of the 100th meridian in the USA). The most recent updates of the model include data for 134 species and are available online (Prasad et al. 2007).

Study area

Four focal areas (Figure 1), including northern Wisconsin (WI), central Maine (ME), northern Arkansas (AR), and southeastern Ohio-western West Virginia (OH) were chosen to represent areas predicted to undergo large changes in the future (Prasad and Iverson 1999). In addition, these areas were also chosen to represent different forest types and ecoregions. Due to the predicted large changes of species composition in these focal areas, the overall relative importance values, which were calculated as the mean of relative importance values under the current, HAD2CM, and CCC scenarios, were used as the criteria for the selection of tree species in the simulations (Table 3). The top 18 (ME) to 28 (OH) most important species that constituted approximately 80% of the overall relative importance values were selected as the targeted species for each focal area (Table 3). The spatial coverage of each focal area was 200 × 200 km. Each focal area contained 100 cells of 20 × 20 km, which represented the spatial resolution of the modeling procedure in this study. The percent forest cover for focal areas within WI, ME, AR, and OH were 51.32 ± 3.08 (mean ± *SE*), 92.14 ± 0.79, 80.05 ± 2.08, and 90.23 ± 1.77, respectively (NLCD 2001). The annual mean photosynthetically active radiation (PAR), temperature, and total precipitation for each of the four focal areas under the current and future climatic scenarios are listed in Table 1.

Parameterization of PnET-II model

PnET-II is a monthly time-step and generalized forest carbon balance model (Aber et al. 1995). The carbon uptake in the PnET-II model is based on a photosynthesis subroutine (*Psn*), which assesses potential photosynthesis rate (A_{max}) by a linear function of leaf nitrogen content (N_{mass}; %). Basal respiration is a constant fraction (default = 0.1) of A_{max}. Potential gross photosynthesis ($1.1 \times A_{max}$) is turned down as a function of the vapor pressure deficit effect of stomatal closure (DVPD) and deviation from optimum temperature for photosynthesis (DTemp). Day and nighttime temperature is applied in a Q_{10} (default $Q_{10} = 2$) function for the calculation of realized respiration rates. Within-canopy variations of photosynthesis rates are accounted for by changes in *SLW* along the vertical profile (50 layers) of the forest stand (equations see Aber and Federer 1992). The other five subroutines include: AtmEnviron, Phenology, WaterBal, SoilResp, AllocateMo, and AllocateYr. AtmEnviron calculates vapor pressure deficit (VPD), day length, and growing degree days using monthly weather data. The phenology subroutine determines the date of leaf and wood growth by growing degree days. WaterBal calculates the water balance and the level of water stress. Canopy gross photosynthesis is further adjusted in the WaterBal subroutine depending on the level of water stress. SoilResp calculates the soil respiration rate as a linear function of mean monthly temperature. AllocateMo allocates net photosynthesis with the presence of DVPD, DTemp, and water stress to the labile carbon pool and further to plant respiration, wood and root growth. At the end of each year, AllocateYr allocates the surplus carbon either to buds for the next year's foliar production or to wood for storage.

Leaf traits such as N_{mass} and *SLW* are among the most sensitive variables in the PnET family of models (Aber et al. 1996). Variations of both N_{mass} and *SLW* are best characterized by inter-specific differences (Bassow and Bazzaz 1997; Chiang 2007). Because this study encompassed large spatial coverage and number of species, a geodatabase (Chiang and Brown 2005) of N_{mass} and *SLW* was created to understand the central tendency and spread of both variables in North America. The geodatabase merged one online database (Pardo et al. 2005), two review papers (Yin 1993; Wright et al. 2005), field data from southern Ohio (Chiang 2007), and 38 additional sources reviewed by J.-M. Chiang (605 observations). For the parameterization of PnET-II in this study, we selected leaf N_{mass} and *SLW* of the targeted species that were from mature trees and under no manipulative treatments (control) (see Supplementary Materials). Leaf and wood phenology varies among four functional vegetation types: spruce/fir, pine, ring-porous hardwood, and diffuse-porous hardwood (Aber et al. 1995). The default values were used for other canopy, photosynthesis, water balance, carbon allocation and soil respiration variables (Aber et al. 1995).

PnET-II simulations were run using the same climate dataset as the DISTRIB model. Monthly mean temperature and precipitation varies among three climatic scenarios (Current, HAD2CM, and CCC; see Table 1 for annual means). In general, HAD2CM predicted slightly warmer temperatures with substantial increases in precipitation, whereas CCC predicted large increases in air temperature with only moderate increases in precipitation (Table 1). Monthly PAR (μmol/m^2 per s) was calculated by integrating the daily global solar radiation (direct + diffuse; MJ/m^2) according to the latitude of each cell (Coops et al. 2000) and converted to photon flux density (μmol/m^2 per s) assuming 1 mol photons containing 2.17×10^5 Joules of energy (McCree 1981). PAR did not vary with the climatic scenarios in PnET-II simulations. Water-holding capacity (WHC; cm) was converted from available water capacity (% volume).

Merging of PnET-II and DISTRIB models

PnET-II simulations were run for each targeted species at each of the 400 cells for 20-year periods under the climatic equilibrium of current and future (HAD2CM and CCC) scenarios (Figure 5). Species-specific variables include *SLWMax*, N_{mass}, and phenology. Cell-specific variables include climate (temperature, precipitation, and PAR), WHC, and latitude. The outputs from the PnET-II simulations were the NPP of each targeted tree species (*j*) at each cell (*i*) under the current climate (NPPCur_{ij}) or future climatic scenarios (NPPFut_{ij}). The outputs of the DISTRIB model were the importance values of each targeted tree species at each cell under the current climate (CIV_{ij}) or future climatic scenarios (FIV_{ij}). The NPP for each cell (NPP_i) was calculated as the weighted mean of NPP from each species using the importance values from DISTRIB model outputs as weights. The combinations of using either current or future outputs for both PnET-II and DISTRIB models rendered NPP_i outputs under four circumstances: (i) current species composition and current climatic scenario; (ii) current species composition and future climatic scenarios; (iii) future species composition and current climatic scenario; and (iv) future species composition and future climatic scenarios. NPP outputs were not adjusted for potential differences in percent forest cover over time. NPP outputs were reported as g C per m^2 forested area per year.

Assumptions and caveats

Under the simplified model that bridged the prediction of potential species composition changes with NPP, several assumptions were made. First, the merging of two models can potentially lead to accumulation of errors. Second, we assume that *SLW* and N_{mass} were inherent leaf traits that varied primarily among species and were constant between different geographical locations. Although *SLW* is generally affected by the light environment, N_{mass} and the maximum *SLW* measured from

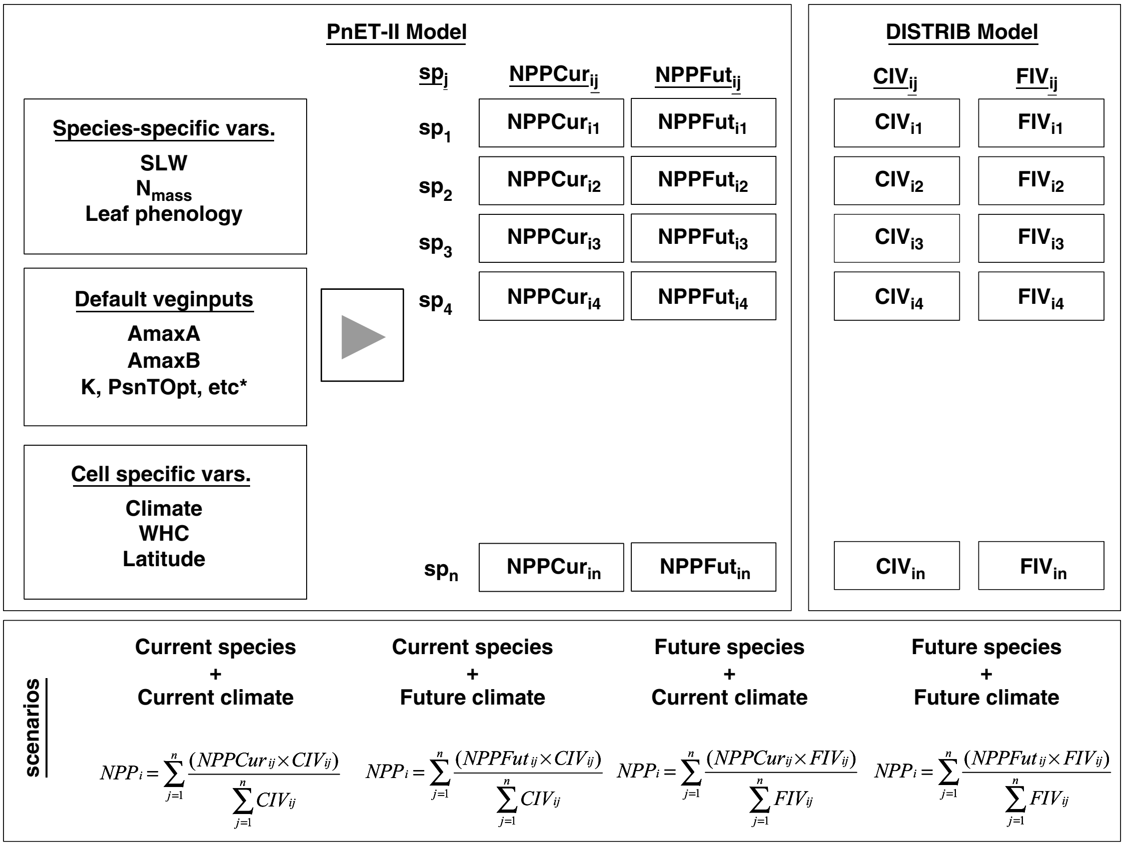

Figure 5. The merging of PnET-II (forest carbon balance model) and DISTRIB (forest species composition model) models. $A_{max}A$, intercept of the relationship between foliar nitrogen content and maximum photosynthetic rate; $A_{max}B$, slope of the relationship between foliar nitrogen content and maximum photosynthetic rate; CIV_{ij}, the relative importance value of the ith cell for the jth species under the current climate; FIV_{ij}, the relative importance value of the ith cell for the jth species under the future climatic scenarios; K, canopy light attenuation constant; N_{mass}, leaf nitrogen content (% mass); NPPCur_{ij}, net primary productivity of the ith cell (20 × 20 km cell) for jth species under the current climate; NPPFut_{ij}, net primary productivity of the ith cell for the jth species under the future climatic scenarios (HAD2CM or CCC); PsnTOpt, optimum temperature for photosynthesis (°C); SLW, specific leaf weight (g/m^2); vars., variables; WHC, water holding capacity (cm). *Other default parameter inputs are listed in Aber et al. (1995).

leaves at the top of the canopy are relatively conserved for each individual species (Bolker et al. 1995; Osone and Tateno 2005; Chiang 2007). Second, contributions of NPP from different species were proportional to their respective importance values. Thus, NPP of each 20 × 20 km cell was calculated as the weighted (weight = IV) mean of NPP from each species. Third, at the relatively large spatial scale (size of grid cell = 20 × 20 km), interactions among species, such as competition, were not considered. Species coexisted freely as long as their potential habitats overlapped.

Due to the limitations of data availability and the model itself, many factors that potentially had greater impacts on NPP were not included. For example, the effects of CO_2 fertilization as a result of elevated atmospheric CO_2 concentration in the future were not incorporated in our model. Although experimental data have exhibited consistent and positive growth response of plants to elevated CO_2 (Curtis and Wang, 1998), the positive effects were largely attenuated after 3–5 years when growth was limited by another resource (Körner 2006). In addition, studies of CO_2 fertilization effects were limited to small-scale experiments (e.g., open-top chamber for CO_2 enrichment) or young stands (e.g., Free-Air CO_2 Enrichment; FACE) due to the inherent difficulty in the experimental design. Although one recent study on a mature forest exhibited enhanced CO_2 assimilation due to elevated CO_2 (Körner et al. 2005), the treatment did not provide additional contributions to the long-term carbon storage such as the basal area increment. Instead, most extra carbon was allocated to labile carbon belowground, which would likely enhance soil respiration. The other factor that has a potentially large impact on the NPP outputs is land-use changes (Houghton and Hackler 1999). Future land-use patterns were not incorporated in our model; therefore, the common denominator for our NPP outputs was forested land (NPP per forested area). In addition, the species redistributions predicted by the DISTRIB model were based on their potential and suitable habitats. DISTRIB does not incorporate the migration speed and habitat continuity; thus, it does not predict the actual presence of each tree species at century's end. Finally, interspecific differences in NPP and their NPP response to environments were determined solely by their leaf traits (*SLW* and N_{mass}). Species-specific factors such as shade tolerance, optimum temperature for photosynthesis, drought tolerance, and leaf phenology might have been important; however, those data were either not available or hard to quantify in model simulations. Future research should incorporate those species-specific factors to provide a better manifestation of species-specific NPP responses to the environment.

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Supporting Information

The following supporting information is available for this article:

Supporting Information A1
Parameter inputs of species-specific N_{mass} and specific leaf weight (SLW) for PnET-II simulations. Source number corresponds to the references listed in appendix A2.

Supporting Information A2
References corresponding to the source number in appendix A1. Numbers 1–23 were obtained via a literature search by J-M Chiang. Numbers 24 and 25 were the unpublished data from J-M Chiang, and S Ryu and J Chen, respectively. Numbers 27–31 were obtained from Wright et al. (2002). Numbers 32–55 were obtained from a review paper by Yin (1993). Numbers 56–146 were obtained from an on-line database by Pardo et al. (2005).

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