Attributing carbon changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to 2010

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[1]   Recent climate variability (increasing temperature, droughts) and atmospheric composition changes (nitrogen deposition, rising CO_2 concentration) along with harvesting, wildfires, and insect infestations have had significant effects on U.S. forest carbon (C) uptake. In this study, we attribute C changes in the conterminous U.S. forests to disturbance and non-disturbance factors with the help of forest inventory data, a continental stand age map, and an updated Integrated Terrestrial Ecosystem Carbon Cycle model (InTEC). We grouped factors into disturbances (harvesting, fire, insect infestation) and non-disturbances (CO_2 concentration, N deposition, and climate variability) and estimated their subsequent impacts on forest regrowth patterns. Results showed that on average, the C sink in the conterminous U.S. forests from 1950 to 2010 was 206 Tg C yr^{-1} with 87% (180 Tg C yr^{-1}) of the sink in living biomass. Compared with the simulation of all factors combined, the estimated C sink would be reduced by 95 Tg C yr^{-1} if disturbance factors were omitted, and reduced by 50 Tg C yr^{-1} if non-disturbance factors were omitted. Our study also showed diverse regional patterns of C sinks related to the importance of driving factors. During 1980–2010, disturbance effects dominated the C changes in the South and Rocky Mountain regions, were almost equal to non-disturbance effects in the North region, and had minor effects compared with non-disturbance effects in the West Coast region.

1. Introduction

[2]   Forest ecosystems, major contributors to the sink of atmospheric carbon (C) in recent decades, play a vital role in the global C cycle [*Pan et al.*, 2011a]. Forests cover about 740 million acres in the United States [*Smith et al.*, 2009] and sequester about 10%–13% of U.S. industrial greenhouse gas emissions annually [*Birdsey et al.*, 2006; *U.S. Environmental Protection Agency* (*EPA*), 2009]. The forest growth rate was higher in the late twentieth century than during earlier decades because of the regrowth from past disturbances in the nineteenth century [*Birdsey and Lewis*, 2003]. However, the capacity of forest C sequestration is thought to be declining as forests age [*Birdsey et al.*, 2006].

[3]   Two sets of mechanisms are thought to be responsible for forest C sinks, including (1) forest regrowth due to age effects after disturbances and land use change, and (2) growth enhancement due to climate change, CO_2 fertilization and nitrogen (N) deposition. Long-term net C uptake by forests of the conterminous U.S. is primarily attributed to forest regrowth after disturbances (harvest, fire, insect attacks) and from abandoned agriculture [*Birdsey et al.*, 2006]. However, recent climate changes (increasing temperature, droughts) and atmospheric composition changes (nitrogen (N) deposition, rising CO_2 concentration) along with increasing wildfires and insect attacks have had significant effects on the U.S. forest C cycle [*Pregitzer and Euskirchen*, 2004; *Nunery and Keeton*, 2010]. A number of studies have shown how C dynamics respond to changing climate and atmospheric composition in an equilibrium state without consideration of disturbances and forest recovery [*Kindermann et al.*, 1996; *Kicklighter et al.*, 1999; *Tian et al.*, 2009]. Disturbances in forests and their subsequent recovery, however, have been recognized as critical drivers of C dynamics, and this information is needed to

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support monitoring, reporting, and verification requirements of global treaties [*Harden et al.*, 2000; *Birdsey and Lewis*, 2003; *Litvak et al.*, 2003; *Campbell et al.*, 2004; *Masek and Collatz*, 2006; *Hicke et al.*, 2007; *Balshi et al.*, 2009; *Johnstone et al.*, 2010]. Understanding the influence of the terrestrial biosphere on future atmospheric CO_2 growth is necessary before we can project climate in the near future [*Canadell et al.*, 2007a], and this issue has been brought to the forefront of global climate research [*Running*, 2008].

[4] Disturbances cause direct C emissions and dramatically change C, energy, and water balances and forest age structure within a forest ecosystem [*Running*, 2008]. It is estimated that about 152 million ha of forests in the U.S. are affected each decade by various disturbances such as land-use change, fire, harvesting and insect attacks [*Pan et al.*, 2011b]. Forests regenerated from disturbances tend to sequester C in the long run, although they often experience a transient C release after disturbances [*Goulden et al.*, 2011]. For example, it has been found that forest recovery after fire resulted in a ~15% increase in C sequestration at higher latitudes since the 1960s [*Harden et al.*, 2000].

[5] Stand-level studies suggested that the change of net C uptake after disturbances may exceed that from the effects of a changing climate [*Thornton et al.*, 2002], although such studies are unlikely to be representative of an entire region [*Litvak et al.*, 2003]. One study found that the variability in landscape-level C uptake due to disturbances in Oregon was equivalent to that attributable to a changing climate [*Campbell et al.*, 2004], indicating that C dynamics on a landscape comprised of stands with different ages may not directly reveal how much of the variability is caused by disturbance factors or the sensitivity of a landscape to changes in non-disturbance factors. To better understanding the terrestrial C cycle, studies of broad regions such as the conterminous U.S. need to consider disturbance history, the pulse of C emission at the time of disturbances, and subsequent regrowth after disturbances [*Pregitzer and Euskirchen*, 2004; *Running*, 2008].

[6] Analyses of conterminous U.S. forests estimate a C sink ranging from 79 Tg C yr^{-1} to more than 300 Tg C yr^{-1} since the 1980s [*Birdsey and Heath*, 1995; *Turner et al.*, 1995; *Houghton et al.*, 1999; *Caspersen et al.*, 2000; *Schimel et al.*, 2000; *Pacala et al.*, 2001; *Hurtt et al.*, 2002; *Birdsey et al.*, 2006; *Hicke et al.*, 2007; *King et al.*, 2007; *Peters et al.*, 2007; *Woodbury et al.*, 2007; *EPA*, 2009; *Pan et al.*, 2011a; *Xiao et al.*, 2011; *Zheng et al.*, 2011; *Williams et al.*, 2012]. However, the dominant causes and their relative contributions to the overall C sink of the conterminous U.S. forests remain uncertain and controversial. Some studies emphasized factors influencing growth enhancement, especially CO_2 fertilization, as the primary mechanism responsible for the U.S. forest C sink [e.g., *Houghton et al.*, 1999; *McGuire et al.*, 2001; *Joos et al.*, 2002]. Conversely, some studies emphasized the role of forest regrowth [e.g., *Caspersen et al.*, 2000; *Hurtt et al.*, 2002; *Albani et al.*, 2006; *Birdsey et al.*, 2006].

[7] Quantifying the contributions of these different mechanisms to the C uptake of the conterminous U.S. forests over recent decades is prerequisite to its projection into the near future. When combined with national inventories, process-based ecosystem models can isolate the individual factors affecting C dynamics of forests to provide insights for understanding complex interacting effects. In this study, factors are grouped into disturbance effects (C losses from disturbance events, and subsequent forest recovery following disturbance events) and non-disturbance effects (climate variability, changing atmospheric CO_2 concentration and N deposition). We quantify the disturbance and non-disturbance effects on net C changes in the conterminous U.S. forests using Forest Inventory and Analysis (FIA) data and a process-based model driven by forest stand age, climate and atmospheric composition data. Our main objective is to evaluate the effects of disturbance and non-disturbance factors on the net C changes in the conterminous U.S. forests from 1901 to 2010. Our approach provides a new perspective on net C changes and their underlying drivers to reduce current uncertainties in the terrestrial C cycle processes and improve bottom-up C modeling strategies. We use the conventional definitions of gross primary productivity (GPP) as ecosystem-level photosynthetic gain of CO_2; net primary productivity (NPP) as the difference between GPP and the respiration of plants; and net ecosystem productivity (NEP) as NPP minus heterotrophic respiration. We also define net biome productivity (NBP) as NEP minus disturbance losses. Thus, NBP describes net C changes of a forest region. Negative NBP represents a C source to the atmosphere and positive NBP a C sink from the atmosphere.

2. Material and Methods

2.1. Model Description

[8] The Integrated Terrestrial Ecosystem Carbon Cycle (InTEC) model is process-based but also closely calibrated with the FIA and other observational data. It is designed for the purpose of investigating the effects of changing climate, atmospheric composition, disturbances, and forest recovery on the long-term C and N cycles in forest ecosystems (Figure 1).

[9] The C balance of a forest ecosystem is the sum of changes in vegetation (living biomass) and soil C pools, which in turn result from NPP over a specified period of time [*Chen et al.*, 2000a, 2000b, 2000c]. Since NPP changes with climate, atmospheric composition, soil conditions and disturbances, the C balance of a forest region is a function of these external forcing factors [*Chen et al.*, 2000b]. In the InTEC model, we use two separate functions to integrate effects of non-disturbance and disturbance factors since the pre-industrial time. Historical C exchanges between forests and the atmosphere are calculated progressively from 1901 to 2010 through a mechanistic aggregation of disturbance and non-disturbance factors. As the modeling strategy is quite different from traditional ecosystem process models, some important steps involved in the model are briefly described here and more details are presented in section A of the auxiliary materials.[1]

[10] The model includes five core processes: (1) Simulation of GPP using a two-leaf canopy photosynthesis model based on Farquhar's leaf-level biochemical model [*Chen et al.*, 1999, 2000a], and spatial distributions of GPP as well as NPP in a recent reference year (NPP_{ref}) are modeled using spatial data sets of leaf area index (LAI), clumping index, land cover, soil texture, and hourly meteorology; (2) Based on the NPP

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[1]Auxiliary materials are available in the HTML. doi:10.1029/2011JG001930.
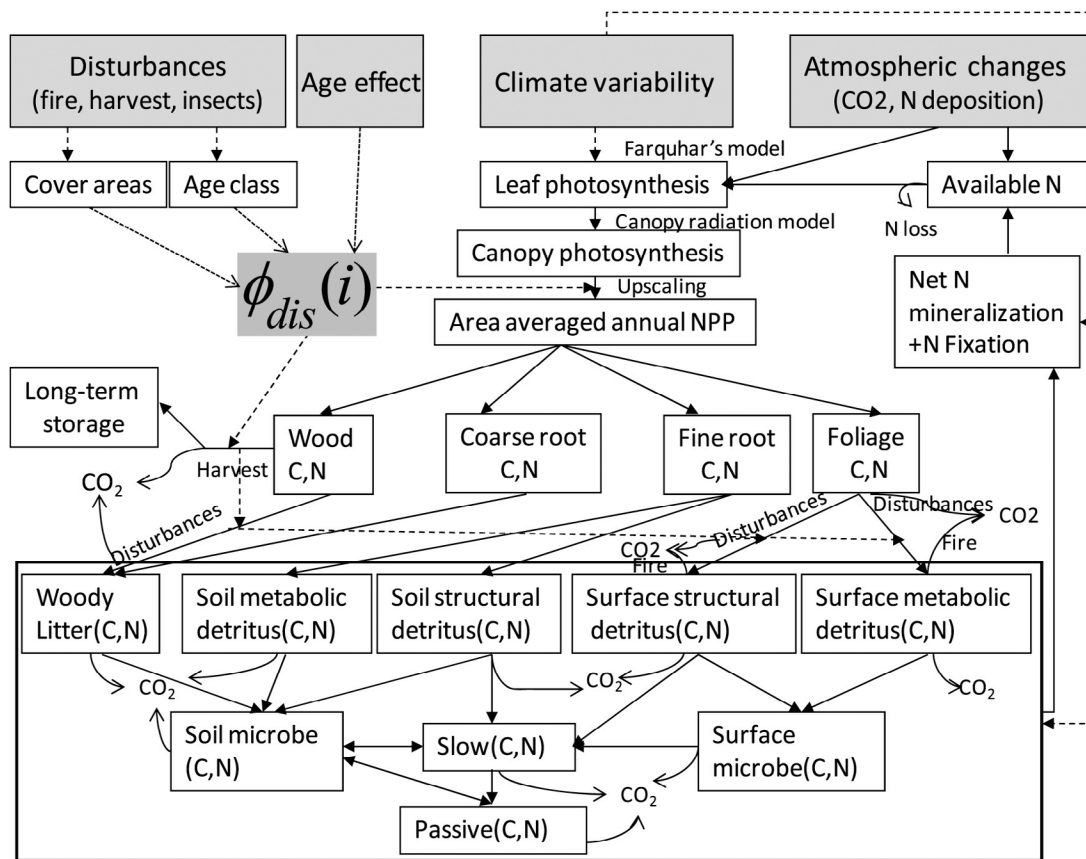
Figure 1. Detailed carbon (C)-nitrogen (N) cycle structure in the Integrated Terrestrial Carbon Cycle Model (InTEC). Solid arrows indicate C-N flow and dashed arrows indicate influences. The symbol $\phi_{dis}(i)$ indicates the disturbance function.

distribution in NPP_{ref}, annual historical NPP is reconstructed retrospectively based on past climate data (see section A.1 in the auxiliary materials); (3) Normalized NPP-age relationships derived from the FIA data are used to determine patterns of forest regrowth after disturbances (see section 2.3 and L. He et al., Relationships between net primary productivity and forest stand age derived from Forest Inventory and Analysis data and remote sensing imagery, submitted to *Global Biogeochemical Cycles*, 2011); (4) A three-dimensional distributed hydrological model is used to simulate soil moisture and temperature [*Ju and Chen*, 2005]; and (5) A modified CENTURY model [*Parton et al.*, 1987] and the net N mineralization model of *Townsend et al.* [1996] are employed to simulate soil C and N cycles.

[11] The model assumes that forest stands at initiation of the simulation in 1900 are in a dynamic equilibrium state, i.e., NPP equals heterotrophic respiration under climate and atmospheric conditions in 1900. This assumption is made in order to spin-up C pools to an initial equilibrium state at the beginning of our simulation period. NPP estimated from field data in a recent reference year (NPP_{ref}) is used as a benchmark to reconstruct historical NPP values back to 1900 according to variations of non-disturbance and disturbance factors, and the reconstructed NPP in 1900 is in turn used to adjust the initialized C pools. This methodology ensures that the C balance estimated for subsequent years is

the accumulated effects of all factors that affect the C cycle since the pre-industrial year [*Chen et al.*, 2003]. All initializations for each spatial grid cell (1 km × 1 km) are based on the initial average climate and atmospheric conditions during 1901–1910.

[12] Since stand age and disturbance information used in this study are derived from forest inventories and remote sensing products that are insensitive to partial disturbances [*He et al.*, 2011; *Pan et al.*, 2011b; *Williams et al.*, 2012], we assumed that disturbed forest areas are affected only by stand-replacing disturbances. Disturbances are explicitly considered in this model as processes that release C into the atmosphere, modify terrestrial C stocks, and initiate regrowth and subsequent changes in C pools (see section A in the auxiliary materials).

2.2. Input Data

[13] All spatial data sets were co-registered to the lat/long projection and resampled to 1 km spatial resolution (Table 1).

2.2.1. Reference NPP

[14] NPP in 2006 was estimated from MODIS products [*Zhao et al.*, 2005] and used as a benchmark to tune the initial NPP values in 1900 by numerically running the model over the study period until NPP simulated by InTEC for 2006 was agreeable within 1% to MODIS NPP in each grid cell (see section A in the auxiliary materials).

Table 1. Descriptions of Input Data Used in this Study

Input Data Sets	Description	Original Resolution	References
CRU3.0 Climate Data	Temperature, precipitation, vapor pressure	0.5°	*New et al.* [2000]
NCAR Climate Data	Temperature, precipitation, vapor pressure during 2007–2010; radiation during 1948–2010	Gauss grid	NCAR
Reference NPP	MODIS product in 2006	1 km	*Zhao et al.* [2005]
Nitrogen Deposition	Measured data during 1978–2010	Site level	*Pan et al.* [2009]
Atmospheric CO_2 Concentration	Measured data during 1958–2010	Site level	*Keeling et al.* [2008]
Forest Species	Produced using 250 m Terra MODIS imagery and forest inventory data	1 km	*Ruefenacht et al.* [2008]
GLC2000 Land Cover	Developed from SPOT4 VEGETATION data	1 km	GLC2000
Leaf Area Index	Developed from SPOT4 VEGETATION data	1 km	*Pisek and Chen* [2007]
DEM	Digital Elevation Model	1 km	GLCF
Soil Data	Wilt point and field capacity of soil water; soil depth; fraction of clay, silt and sand	0.0833°	IGBP-DIS
Forest Disturbance Maps	Developed from monitoring trend in burn severity from 1984–2008 and MODIS burned-area products during 2000–2010	1 km	*He et al.* [2011]
Historical Disturbance Data	Fire and harvest data	Regional level	*Ince* [2000]; *Adam et al.* [2006]; *Smith et al.* [2006, 2009]

2.2.2. Stand Age Structure

[15] *Pan et al.* [2011b] produced a forest age map in 2006 for the conterminous U.S. and Canada by combining FIA data, which reflects historical disturbances, and forest disturbance data from remote sensing since 1990 [*He et al.*, 2011]. The forest age map for the U.S. was recently updated to 2010 (Figure 2a) by introducing disturbance maps produced by MTBS data from 1984 to 2008 [*Eidenshink et al.*, 2007] and MODIS burned area product from 2000 to 2010 [*Roy et al.*, 2008]. Forest stands are assumed to begin regrowth immediately after disturbances, so stand ages of a disturbed area equal the time since disturbances were detected by remote sensing. Disturbance polygons from the remote sensing products were then used to replace the gridded age data from FIA [*Pan et al.*, 2011b]. The resulting forest age map implicitly reflects the legacy of past disturbances, and is a surrogate for the time since last disturbances for the conterminous U.S. forests. Combined with a forest type group map and relationships between NPP and stand ages (He et al., submitted manuscript, 2011), these age maps are also used for setting the initial year to simulate forest growth after disturbances for each 1 km grid cell.

[16] Over the last 10 years, young regrowing forests following disturbances were mainly found in the northwestern West Coast and South regions (region divisions in Figure 2a). Older, less disturbed forests were mainly found in the West Coast and Rocky Mountain regions, although regenerating young forest stands after disturbances were also scattered in these regions. Forests in the North region were of relatively mature ages and showed less effects of recent disturbances.

2.2.3. Disturbance Legacy

[17] Since stand age maps do not distinguish among different types of disturbances, we used remote sensing products and disturbance statistics to identify the causes of main disturbances in each region. To estimate fire and harvest areas, we used national fire areas from the National Interagency Fire Center (NIFC), MTBS (1984–2010) and MODIS (2000–2010), and regional harvesting data [*Ince*, 2000; *Adam et al.*, 2006; *Smith et al.*, 2006, 2009]. Areas of insect disturbance were assumed to be the difference between all disturbances combined and our estimated areas of fire and harvest disturbances.

[18] The FIA data used to construct the stand age map do not represent partial harvest practices very well, which remove only part of the biomass without resetting the FIA-recorded stand age; therefore, harvest areas used in this study only include clear-cuts and areas where most of the live biomass is removed. We estimated regional harvest areas from 1960 to 2010 [*Adam et al.*, 2006; *Smith et al.*, 2006, 2009] and national harvest areas from 1900 to 1998 [*Ince*, 2000] for specific dates over periods of 5 or 10 years. Estimates for non-survey years were derived by linear interpolation between two known points in time. The harvest areas for the period of 2007–2010 used the average values in 2006 estimated by *Smith et al.* [2009].

[19] We identified spatial distributions of fires over the period of 1984–2010 based on the MTBS (1984–2010) and MODIS (2000–2010) burned areas. We used the national NIFC fire data for the period of 1960–1983. Assuming that a forest stand is established in the year immediately after the disturbance year, a stand age map can reflect the total disturbed areas each year since the last disturbance [*Pan et al.*, 2011b]. Within a region, older forests are assumed to be more vulnerable to fire until all existing cohorts are burned [*Balshi et al.*, 2009], and then harvests occur in the remaining older forests. The insect-mortality areas for the period of 1960–2003 were then calculated by deducting the burned and harvest areas from the total disturbed area depicted by the stand age map in 2006. The disturbed areas by each disturbance types are therefore assigned to different grid cells. Our estimated pre-1960 fire areas are smaller than estimates of *Houghton et al.* [1999] and *Birdsey et al.* [2006] because the stand age map only reflect the most recent disturbance even though an area might experience several disturbances over a century [*Pan et al.*, 2011b].

[20] The estimated disturbed areas of the conterminous U.S. forests varied greatly over recent decades (Figure 3), with a maximum estimate of 5.5 million ha in the 1990s due to the increased insect mortality. Disturbed areas by fire decreased at a rate of 3.6 thousand ha per decade from the 1940s to the 1970s and then increased to 2.3 million ha in the 2000s. Harvest areas increased by a rate of 0.8 thousand ha per decade prior to 2000 and then decreased after 2000.

2.2.4. N Deposition Data

[21] Spatially explicit N deposition data at 1 km resolution from 1979 to 2010 were interpolated by a kriging method of
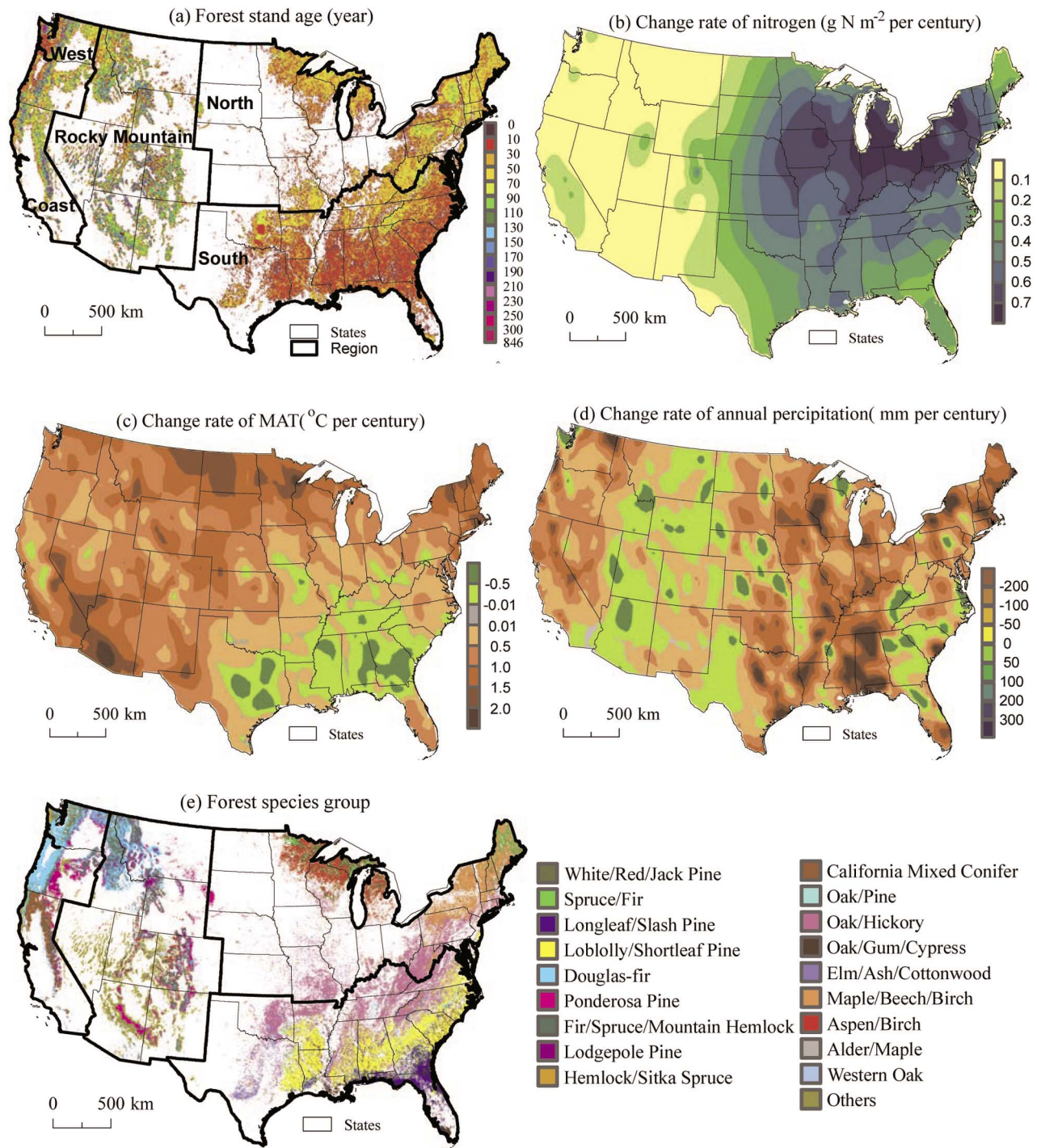
Figure 2. Distributions of forest stand age and species group, and changes in climate and atmospheric composition from 1901 to 2010. (a) Forest stand age map in 2006 (year); (b) change rate of nitrogen deposition (g N m^{-2} per century); (c) change rate of annual mean temperature (°C per century); (d) change rate of annual percipitation (mm per century); (e) forest species group map.

the dry and wet N deposition data collected at National Atmospheric Deposition Project/National Trends Network monitoring sites [*Pan et al.*, 2009]. The 1-km estimates for each grid cell from 1978 back to 1901 were proportionally extrapolated based on historical greenhouse gas emissions and the average N deposition data from 1990 to 2000 using equation (1) [*Chen et al.*, 2003]:

$$N_{dep}(i) = N_{dep_0} + \frac{(G(i) - G_0)\left(N_{dep}(i)_{ref} - N_{dep_0}\right)}{G(i)_{ref} - G_0}, \quad (1)$$
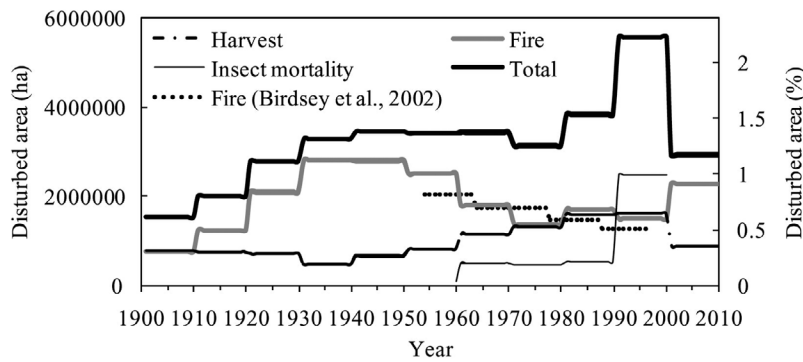
Figure 3. Forest areas disturbed by disturbance type, 1900–2010. Since remote sensing data are insensitive to partial disturbances, the disturbed areas accounted only for stand-replacing disturbances. We considered insect mortality only from 1960 to 2003.

where N_{dep} is the N deposition rate; G is the greenhouse gas emission rate; the subscripts *0, ref*, and *i* represent the initial, the reference, and the simulated year, respectively.

[22] The national mean N deposition rate across the conterminous U.S. was 3.2 kg ha^{-1} from 1901 to 2010. Regional N deposition decreased from the North region (mean value of $\sim$5.5 kg N ha^{-1}) to the West Coast region (mean value of $\sim$1.1 kg N ha^{-1}). In the past 110 years, the largest increment of N deposition on average was 0.5 g N m^{-2} yr^{-1} in the North region and the smallest increment was 0.03 g N m^{-2} yr^{-1} in the West Coast region (Figure 2b).

2.2.5. Meteorological Data

[23] Monthly mean air temperature and total precipitation for the period 1901–2006 were obtained from the 0.5° global data set at UK Climate Research Unit (CRU3.0) [*New et al.*, 2000]. The corresponding temperature and precipitation data from 2007 to 2010 were from the T62 Gaussian reanalysis data by the U.S. National Center for Atmospheric Research (NCAR). In order to adjust the bias between the two data sources, the departures for temperature and precipitation derived from comparing the mean values from 2000 to 2006 between the NCAR and CRU3.0 data sets were applied to produce new 2007–2010 data. Monthly solar irradiance data from 1948 to 2010 were from the T62 Gaussian reanalysis data of NCAR. The monthly solar irradiance before 1948 was produced using the method of *Thornton and Running* [1999]. For data coherency, radiation data before 1948 were adjusted by the additive departures of the 1901–1947 and 1948–1957 data sets. All coarse meteorological data were bi-linearly interpolated to 1 km resolution. In the past 110 years, the Rocky Mountain region experienced a dry period with rising temperature and decreased precipitation; the northern areas of $\sim$45° experienced a relatively significant warming period with longer growing seasons; but the South experienced a relatively cooler period. There was also a large increase of precipitation in the South Central region but a decrease in some areas of the southeastern region (Figures 2c–2d).

[24] Monthly atmospheric CO_2 concentration data from 1958 to 2010 were measured at Mauna Loa Observatory (MLO), Hawaii (20°N, 156°W) [*Keeling et al.*, 2008]. The CO_2 data from 1957 back to 1901 were linearly extrapolated based on CGCM2 [*Flato and Boer*, 2001]. The atmospheric CO_2 concentration increased from 280 ppmv in 1901 to 390 ppmv in 2010. We assumed that there was no spatial variation in the atmospheric CO_2 concentration for the study region.

2.2.6. Land Cover and Forest Species Data

[25] The Global Land Cover Map 2000 (GLC2000; http://www.eogeo.org/GLC2000), developed using SPOT4 VEGETATION data, was used to distinguish forest and non-forest grids in this study. Forest type classifications (Figure 2e) for the conterminous U.S. were based on 250 m Terra MODIS imagery and FIA plot data [*Ruefenacht et al.*, 2008].

2.2.7. Soil Data

[26] The soil properties for each $\sim$0.083° $\times$ 0.083° grid including field capacity, wilt point, water-holding capacity, depth of soil layer, and silt and clay fraction were derived from the International Geosphere-Biosphere Program, Data and Information System (IGBP-DIS; http://www.daac.ornl.gov).

2.3. NPP-Age Relationship

[27] A semi-empirical mathematical function was used to describe the relationships between NPP and age [*Chen et al.*, 2003]:

$$\text{NPP}(\text{age}) = a\left(1 + \frac{b\left(\frac{\text{age}}{c}\right)^d - 1}{\exp\left(\frac{\text{age}}{c}\right)}\right), \quad (2)$$

where a, b, c and d are parameters which are dependent on forest species and climate, and are determined by fitting this equation to site-specific observations (He et al., submitted manuscript, 2011). The four regression coefficients in equation (2) for the 18 forest type groups in the conterminous U.S. and a couple of major NPP-age relationships are shown in section B in the auxiliary materials.

[28] To derive NPP-age relationships for U.S. forests, we used four terms to calculate annual NPP: annual accumulation of living biomass, annual mortality of aboveground and belowground biomass, foliage turnover to soil, and fine root turnover in soil. The first two terms can be reliably estimated from the FIA data. Although the last two terms make up more than 50% of total NPP, direct estimates of these fluxes are highly uncertain due to limited availability of empirical relationships between aboveground biomass and foliage or fine root biomass. To resolve this problem, we developed a new approach using maps of LAI and forest stand age at 1 km resolution to derive LAI-age relationships for 18 major

Table 2. Designs for Six Simulations[a]

Number	Scenario	Climate	CO$_2$	Nitrogen Deposition	Forest Age
S$_{Disturb}$	Disturbance effect	Constant	Constant	Constant	Historical
S$_{NonDisturb}$	Non-disturbance effect	Historical	Historical	Historical	n/a
S$_{AllFactors}$	All effects	Historical	Historical	Historical	Historical
S$_{CO2}$	CO$_2$	Constant	Historical	Constant	Historical
S$_{NDep}$	Nitrogen	Constant	Constant	Historical	Historical
S$_{Climate}$	Climate variability	Historical	Constant	Constant	Historical

[a]"Climate" refers to the combination of precipitation and temperature in this study; "Constant" means data were held at the averaged level of 1901–1910 and kept unchanged during the simulation period; "Historical" means long-term monthly historical changes; and "n/a" indicates forest stand age was not included.

forest species groups in the U.S. (He et al., submitted manuscript, 2011). These relationships were then used to derive foliage turnover rates using species-specific trait data for leaf longevity. These turnover rates were also used to estimate fine root turnover based on reliable relationships between fine root and foliage turnover. This combination of FIA data, remote sensing, and plant trait information allowed us to derive the first regionally representative NPP-age relationships for different forest types in the U.S.

[29] To apply these relationships to the conterminous U.S., they were extrapolated to the actual ages available from forest age maps (section 2.2.2), and divided by their maximum NPPs in their forest life cycles to produce curves of normalized productivity (F$_{npp}$) with values ranging from 0 to 1.0. These relationships were used to simulate forest regrowth after disturbances and changes in the different C components.

2.4. Simulation Designs

[30] A series of scenarios was designed to examine the relative individual and combined effects of non-disturbance and disturbance factors on the conterminous U.S. forest C cycle (Table 2) (Table 3). The InTEC model was run for scenarios of only disturbance factors (S$_{Disturb}$), only non-disturbance factors (S$_{NonDisturb}$), and a full scenario of disturbance and non-disturbance factors (S$_{AllFactors}$). The two simulations (S$_{Disturb}$ and S$_{NonDisturb}$) against the simulation of the full scenario (S$_{AllFactors}$) were used to examine what the effect would be if excluding non-disturbance factors or disturbance factors. To identify the effects of changing atmospheric composition and climate variability, another three scenarios (S$_{CO2}$, S$_{NDep}$, and S$_{Climate}$) of only atmospheric CO$_2$ concentration, only N deposition, and only climate variability were also run with inclusion of disturbance factors. The latter three simulations compared with the simulation of the disturbance scenario (S$_{Disturb}$) were used to examine the individual effect of each non-disturbance factor.

2.5. Model Validation and Comparison

[31] Given the spatial and temporal scales of our analysis, it is difficult to conduct a direct validation. Estimates of U.S. forest C from forest inventory-based methods directly reflect the dynamics of forest C affected by both disturbance and non-disturbance factors. We used these inventory-based estimates for comparing and validating the InTEC model results. The C stock in living biomass was estimated and aggregated from state-by-state annual volume data surveyed periodically from 1970 to 2003 [Birdsey, 1992; Birdsey and Lewis, 2003; Heath et al., 2003]. The C stock in soil was estimated by empirical models based on temperature, precipitation, forest age and land-use history [Birdsey and

Heath, 1995; Birdsey and Lewis, 2003; Heath et al., 2003]. Annual C changes were estimated by linearly interpolating changes of C stock for the interval years between two consecutive inventories. The total C stock is the sum of the C in living biomass and soil (the residue of total forest ecosystem and living biomass, broadly defined to include woody debris). We summarized the FIA data and the corresponding modeled results at the state level for comparisons.

3. Results

3.1. Model Validation Using Forest Inventory Data

[32] Our estimated C stocks and changes for recent years were within the range of inventory-based reports (Tables 3–4). State-by-state comparisons between the model estimates of C stock and the FIA estimates (Figure 4) suggested that the model generally captures the magnitude of C stock in the conterminous 48 states ($R^2 = 0.85$, $RMSE = 0.3$ Pg C, $MBE = 0.007$ Pg C), with a slight overestimation in living biomass C stock ($R^2 = 0.83$, $RMSE = 0.13$ Pg C, $MBE = -0.071$ Pg C) and underestimation in soil C stock ($R^2 = 0.78$, $RMSE = 0.27$ Pg C, $MBE = 0.09$ Pg C). Comparisons of C changes between our study and the FIA estimates also indicated that the model predicts decadal C changes reasonably well (Table 4) although we slightly overestimated C changes in the 1990s.

Table 3. Comparison of Carbon Stocks (Pg C) From Previous Forest Inventory and Analysis Published Data With Estimates in This Study, 1950s–2000s

C Pools	1950s	1960s	1970s	1980s	1990s	2000s	Sources
Total	n/a	n/a	n/a	n/a	51	52	Woodbury et al. [2007]
	n/a	n/a	n/a	~38	n/a	n/a	Birdsey [1992]
	26	29	35	37	38	39	Birdsey and Heath [1995]
	n/a	n/a	n/a	n/a	~37	n/a	Turner et al. [1995]
	45	47	49	50	52	n/a	Heath et al. [2003]
	n/a	n/a	n/a	38	40	n/a	Birdsey and Lewis [2003]
	n/a	n/a	n/a	n/a	45	47	EPA [2009]
	44	45	47.5	48	50	51	This study
Biomass	n/a	n/a	n/a	12	n/a	n/a	Birdsey [1992]
	10	11	12	13	13	14	Birdsey and Heath [1995]
	19	20	23	24	26	n/a	Heath et al. [2003]
	n/a	n/a	n/a	11	12	n/a	Birdsey and Lewis [2003]
	n/a	n/a	n/a	n/a	20	21	EPA [2009]
	14	15	17	19	20	21	This study

Table 4. Estimates of Carbon Sinks (Tg C yr^{-1}) in the Conterminous U.S. With Positive Values Indicating Sinks of C and Negative Values Indicating Sources of C to the Atmosphere

Value in This Study	Estimate	Method	Period	Source
179	162[a]	PnET-CN model	1991–2000	*Pan et al.* [2009]
233	79[b]	Forest inventory	1980–1989	*Turner et al.* [1995]
233	202	Forest inventory	1980–1989	*Birdsey and Heath* [1995]
209	164	Forest inventory	1963–1997	*Heath et al.* [2003]
207	173[c]	Forest inventory	1953–2001	*Birdsey et al.* [2006]
218	162	Forest inventory	1990–2005	*Woodbury et al.* [2007]
214	179	Forest inventory	1990–1999	*EPA* [2009]
222	238	Forest inventory	2000–2006	*EPA* [2009]
210	180	Forest inventory	1992–2001	*Zheng et al.* [2011]
263	47	Forest inventory +CASA	2005	*Williams et al.* [2012]
233	214	Forest inventory +FORCARB model +ED model	1980–1989	*Pacala et al.* [2001]
233	37[d]	Book-keeping	1980–1989	*Houghton et al.* [1999]
228	80[e]	VEMAP	1980–1993	*Schimel et al.* [2000]
214	230	ED + Miami-LU model	1990–1999	*Hurtt et al.* [2002]

[a]The value is estimated for Mid-Atlantic region (35°N –47.5°N, 71°W –85.5°W).
[b]The value is only for Timberland.
[c]The C sink excludes soil component.
[d]The C sink is due only to land use change.
[e]The C sink is due only to climate variability and CO_2 fertilization.

3.2. C Emission Estimates

[33] Long-term trends of C emissions from disturbances estimated by InTEC indicate that from 1960 to 2010 the total C emissions for the conterminous U.S. forests did not change significantly although disturbed areas increased greatly and inter-annual variability was very large (Figure 5e). The average total C emission was 80 Tg C yr^{-1} with a slight decrease in the last 5 years. The corresponding C emission due to harvest and insect-attack was 45 Tg C yr^{-1}, and the corresponding C emission due to fire was 36 Tg C yr^{-1}. These results indicate that the C emission due to disturbance events was not simply correlated with disturbed areas because of time lags in decomposition processes and changes of C stocks over landscapes following various disturbances. From the 1980s to 2000s, disturbances mainly occurred in the Rocky Mountain, northwestern West Coast and South regions. The C emission per unit area was largest in old forests of the Rocky Mountain region due to the large C stocks

in those forests and high natural disturbance rates, whereas the largest total C loss was in the South region with ~21 Tg C yr^{-1} in the 1990s due to extensive harvesting. Thus, forest C dynamics in a region would be greatly affected by asymmetric effects of disturbances aggregated over years and landscapes.

3.3. Responses of NPP to Disturbance and Non-Disturbance Effects

[34] Disturbance and non-disturbance effects changed NPP of the conterminous U.S. forests in different ways. The results of a full effect simulation ($S_{AllFactors}$) showed an increase of NPP from 1780 Tg C yr^{-1} in the 1950s to 1974 Tg C yr^{-1} in the 2000s (Figure 5a). In the simulation with only disturbance factors ($S_{Disturb}$), NPP increased from 1697 Tg C yr^{-1} in the 1950s to 1721 Tg C yr^{-1} in the 2000s with the highest value of 1750 Tg C yr^{-1} occurring in the 1980s. In the simulation considering only historical changes of non-
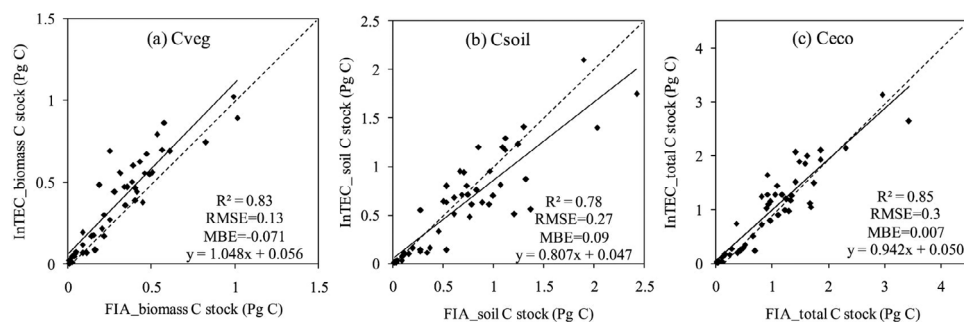

Figure 4. The state-by-state comparison of simulated carbon stocks with inventory estimates for the lower 48 states in the 2003 report year. Since forest inventory survey years for each state were from 1985 to 1998, the simulated C stock in the corresponding years were averaged to compare with inventory estimates. The simulated results were run in $S_{AllFactors}$ that integrated all effects on C dynamics (Table 2). The forest ecosytem C stock is the sum of biomass and soil C (broadly defined to include litter and woody debris) stocks. The solid line is the regression line while the dashed line is the 1:1 line. RMSE is the root mean square error; MBE is the mean bias error (=average (Y−Ypredicted)). All statistics are significant at the 0.01 level.
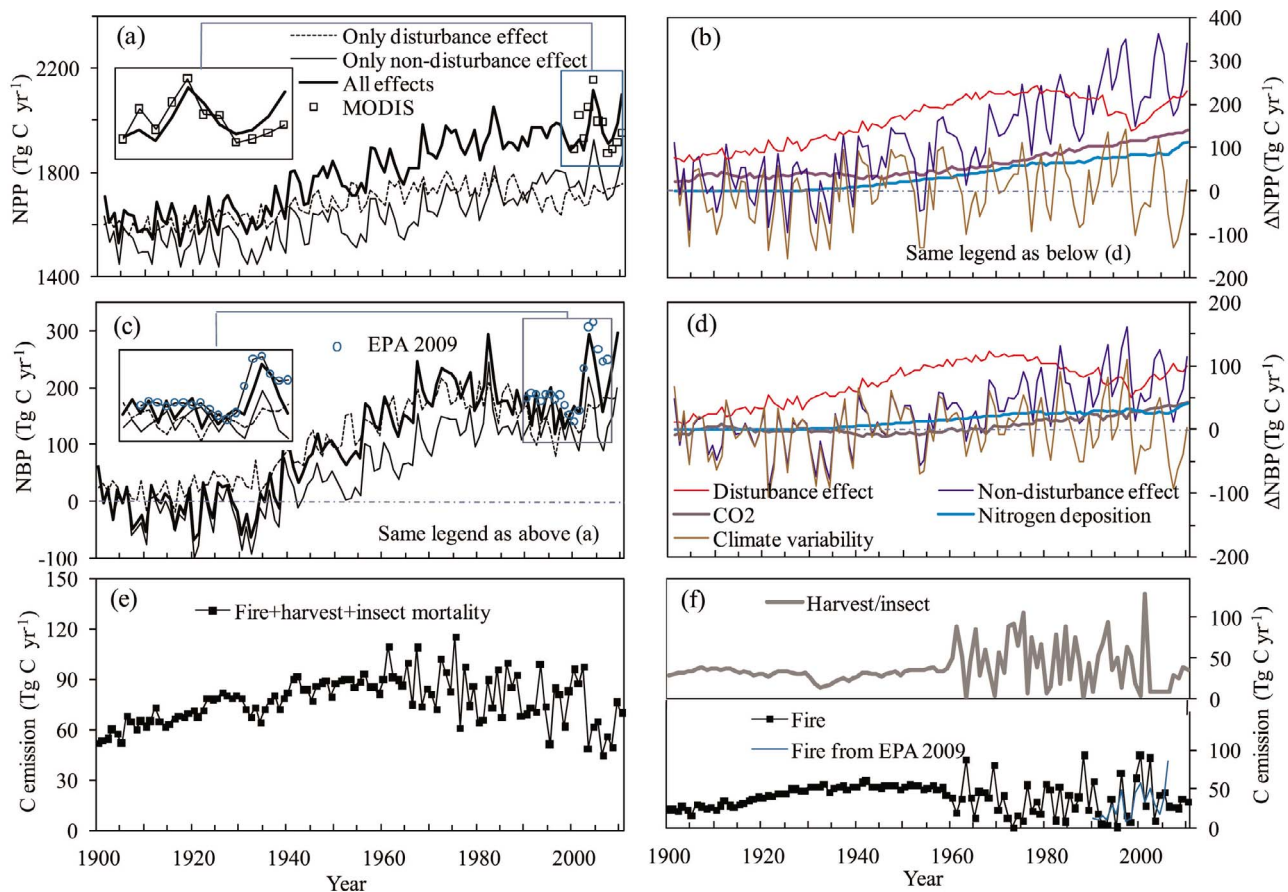
Figure 5. Carbon dynamics of forests in the conterminous U.S. from 1901 to 2010 and responses to interannual variability of disturbance and non-disturbance effects: (a) simulated net primary productivity (NPP) and its responses; (b) the relative singular effects of disturbance and non-disturbance factors on NPP; (c) simulated net biome productivity (NBP) and its responses; (d) the relative singular effects of disturbance and non-disturbance factors on NBP; (e) total carbon emissions from disturbances; (f) the corresponding C emissions from fire and harvest + insect mortality, respectively. Disturbance effects include C losses in disturbance events (harvest, fire and insect attacks), subsequent regrowth with stand age; non-disturbance effects include climate variability, atmospheric CO_2 concentration, and N deposition. Positive NBP values in Figure 5d represent sinks of C from the atmosphere, and negative NBP values represent sources of C to the atmosphere. The Δ values for the CO_2, N and climate effects are the differences between NBP from S_{CO2}, S_{NDep}, $S_{Climate}$ and NBP from $S_{Disturb}$. The Δ values for the disturbance and non-disturbance effects are the differences between NBP from $S_{AllFactors}$ and NBP from $S_{NonDisturb}$ and $S_{Disturb}$, which are used to reveal what is missing when excluded disturbance or non-disturbance effects. The postive Δ values represent enhancement effects on NPP/NBP and vice versa. Descriptions of each simulation are given in Table 2. Blue dash-dotted line in Figures 5b–5d is the zero value line. The black square in Figure 5a represents the annual NPP values from MODIS from 2000 to 2010 [*Zhao and Running*, 2010]. The blue circle in Figure 5c represents NBP estimates by the EPA from 1990 to 2007 [*EPA*, 2009]. The C emission from fire estimated by the EPA are also shown in Figure 5f. Five-year moving mean values in Figures 5e–5f are used to show the general trends because the historical record of events was not measured in successive years.

disturbance factors ($S_{NonDisturb}$), NPP increased from 1593 Tg C yr^{-1} in the 1950s to 1780 Tg C yr^{-1} in the 2000s. The simulation ($S_{Disturb}$) with only disturbance factors showed that NPP was reduced by 175 Tg C yr^{-1} (9.3%) over the 1950–2010 period if non-disturbance effects were excluded, while the simulation ($S_{NonDisturb}$) that excluded disturbance effects suggested that NPP was reduced by 204 Tg C yr^{-1} (10.8%) for the same period (Figure 5b). Further, residuals derived from these comparisons indicate that individual non-

disturbance effects of rising CO_2 concentration, N fertilization, and climate variability contributed 115 (6.4%), 82 (4.6%), and 9 (0.5%) Tg C yr^{-1} respectively to the total NPP increase during this period (Figure 5b). Although climate variability made the smallest contribution to the total NPP increase, it resulted in large inter-annual variations to the increase of total NPP.

[35] Overall, the increase of NPP was mainly attributed to forest regrowth due to disturbance factors before the 1980s,
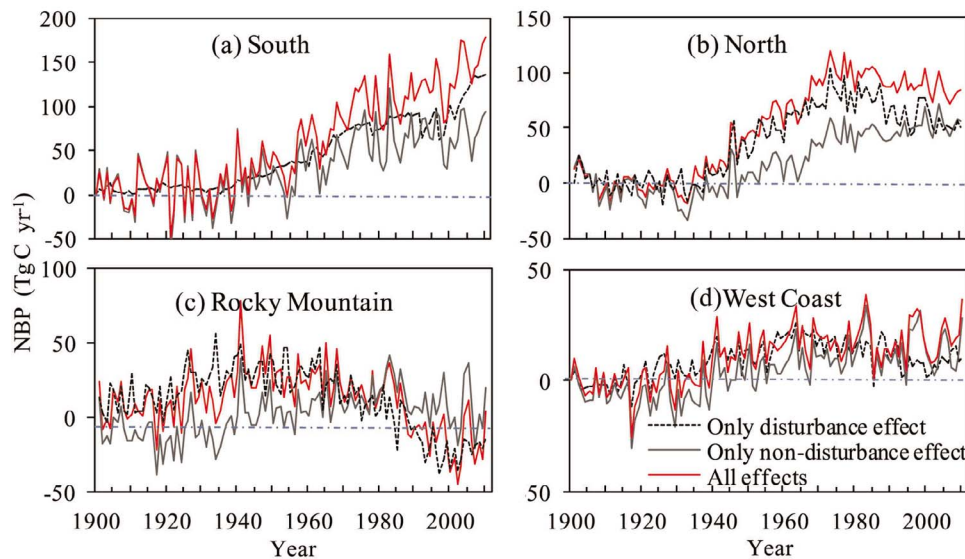
Figure 6. Changes of regional NBP and its responses to disturbance and non-disturbance factors, 1900–2010, in (a) the South, (b) the North, (c) the Rocky Mountain region, and (d) the West Coast region. Disturbance effects include carbon losses in disturbance events (harvest, fire, and insect attacks), subsequent regrowth with stand age; non-disturbance effects include climate variability, atmospheric CO_2 concentration, and N deposition. All simulations are presented in Table 2, and the four geographical regions are shown in Figure 2a. Positive values represent sinks of C, and negative values represent sources of C to the atmosphere.

but after the 1980s, to the enhancement effects of non-disturbance factors (such as increasing CO_2), which reversed the decreasing trend under disturbance factors. These results illustrate the importance of including disturbance factors in estimating continental C dynamics.

3.4. Disturbance and Non-Disturbance Effects on NBP

3.4.1. Effects on the Continental NBP

[36] The average NBP for the conterminous U.S. forests with consideration of both disturbance and non-disturbance effects ($S_{AllFactors}$) was 206 Tg C yr^{-1} with 87% (180 Tg C yr^{-1}) of the sink accumulating in living biomass and 13% (26 Tg C yr^{-1}) in soil (the residue of total forest ecosystem and living biomass) from 1950 to 2000.

[37] NBP in the conterminous U.S. forests responded differently to disturbance and non-disturbance factors (Figure 5c). NBP increased under all simulation scenarios. In the disturbance-only simulation ($S_{Disturb}$), NBP peaked in the late 1970s and early 1980s (184 Tg C yr^{-1}) due to forest regrowth. Increased disturbance events (Figure 3) and forest aging reduced the U.S. forest C sink by 32 Tg C yr^{-1} in the late 1980s and 1990s (Figure 5e). In the non-disturbance-only simulation ($S_{NonDisturb}$), the estimated NBP increased from 40 Tg C yr^{-1} to an average of 138 Tg C yr^{-1} in the 2000s (Figure 5c). The variations of NBP ($S_{AllFactors}$) followed a similar pattern to NBP under the disturbance-only simulation ($S_{Disturb}$) (Figure 5c), indicating the importance of accounting for disturbance effects during a study period, particularly as they are the summed result of C release due to disturbance events and C uptake due to forest regrowth.

[38] Relative to disturbance effects ($S_{Disturb}$), non-disturbance effects on the total NBP ($S_{NonDisturb}$) were smaller before the 1980s but became larger between the 1980s and 1990s. For the period of 1950–2010, simulated NBP with disturbance

factors alone ($S_{Disturb}$) accounted for 156 Tg C yr^{-1}, and simulated NBP with non-disturbance factors ($S_{NonDisturb}$) accounted for 111 Tg C yr^{-1}. In comparison to the full scenario ($S_{AllFactors}$), the estimated NBP of the conterminous U.S. forests was reduced by 95 Tg C yr^{-1} if disturbance effects were excluded, and reduced by 50 Tg C yr^{-1} if non-disturbance effects were excluded (Figure 5d).

3.4.2. Effects on Regional NBP

[39] The contributions of disturbance and nondisturbance effects to NBP varied greatly between regions from 1950 to 2010 (Figure 6). In the southern region, NBP increased greatly in both $S_{Disturb}$ and $S_{NonDisturb}$ simulations. The contribution of disturbance effects to NBP was 22 Tg C yr^{-1} more than that of non-disturbance effects (53 Tg C yr^{-1}) (Figure 6a). In the North region, NBP with only disturbance effects was twice as large as that with only non-disturbance effects from the 1950s to 1980s (Figure 6b). As the contribution of non-disturbance effects increased, NBP under both scenarios ($S_{Disturb}$ and $S_{NonDisturb}$) became equivalent after the 1990s. In the Rocky Mountain region, NBP with simulations of $S_{AllFactors}$ and $S_{Disturb}$ had similar change patterns and magnitudes (Figure 6c), whereas NBP with $S_{NonDisturb}$ indicated a small C sink of 10 Tg C yr^{-1}. Because positive non-disturbance effects could not sufficiently offset increased negative disturbance effects, the overall C balance shifted from a sink to a source in the late 1980s. In the West Coast region (Figure 6d), NBP decreased with the simulation of $S_{Disturb}$ but the overall NBP ($S_{AllFactors}$) did not decrease, indicating that the contribution of non-disturbance effects played a more important role in NBP when the sink related to disturbance factors had declined as forests aged and disturbance events increased in the western U.S. For the recent decades from 1980 to 2010, as shown by the results, disturbance effects dominated the C stock changes in the South and
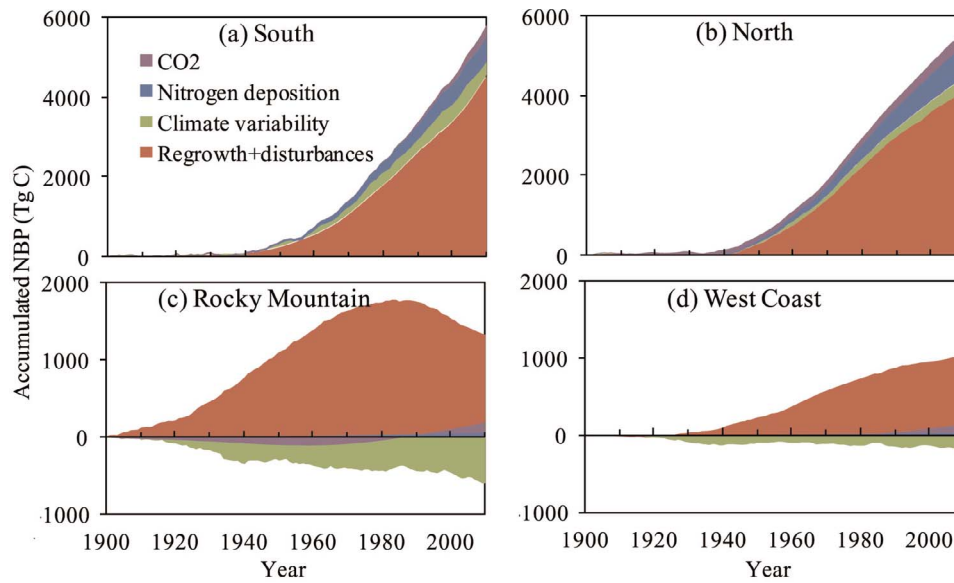
Figure 7. Contributions of elevated CO_2 concentration, N deposition, climate variability, and regrowth + disturbances to regional accumulated NBP.

Rocky Mountain regions; the effects on the C stock changes owing to disturbance and non-disturbance factors were about equal in the North region; and the non-disturbance factors had major impacts on C stock change in the West Coast region.

3.5. Attribution of Accumulated NBP to Different Effects

[40] The accumulated NBP over the past 110 years varied spatially across the conterminous U.S. forests (Figures 7–8). Total NBP accumulation in the North region was 4.64 Pg C, to which non-disturbance factors contributed 1.05 Pg C (23%) and disturbance factors contributed 3.59 Pg C (77%). The CO_2 effect alone accounted for 0.12 Pg C, N deposition for 0.69 Pg C, and climate for 0.17 Pg C of the accumulated NBP increase. Total NBP accumulation in the South region was 5.14 Pg C, to which non-disturbance factors contributed 1.25 Pg C (24%) and disturbance factors 3.89 Pg C (76%). The effect of CO_2 alone accounted for 0.15 Pg C, N deposition for 0.49 Pg C, and climate for 0.41 Pg C. Although forests in the South were subjected to rotational harvesting, the accumulated NBP still contributed the largest portion to the total NBP accumulation of the conterminous U.S. forests due to quick regrowth and high productivity. Total NBP accumulation in the western U.S. (including the West Coast and Rocky Mountain regions) was 2.44 Pg C, to which non-disturbance factors contributed −0.06 Pg C (−2%) and disturbance factors 2.49 Pg C (102%). CO_2 fertilization and N deposition accounted for 0.19 Pg C and 0.06 Pg C of the total accumulation, respectively, while climate reduced the NBP accumulation by 0.64 Pg C. Our simulation indicates that disturbance effects were primarily responsible for NBP accumulation because of high C uptake in regrowth forests, although their contribution differed among regions.

[41] The spatial distribution of accumulated NBP also shows that middle-aged forests sequestered more C than old-growth and young forests (Figure 2a and Figure 8). The largest NBP accumulation (>10 kg C m^{-2}) occurred in forests with ages of 40–70 years in the North region. In old-growth forests (>200 years old) such as those in the eastern

part of the West Coast and the northwestern and southeastern Rocky Mountain regions, NBP accumulation averaged approximately 2 kg C m^{-2}. Due to frequent droughts, fire and insect-infestation events that have increased in recent decades, NBP accumulation was reduced in some areas. For example, the mean NBP accumulation in Utah and Arizona was reduced by 1.1 kg C m^{-2}. In managed forests of the South and northwestern West Coast region, NBP accumulation averaged ~2.5 kg C m^{-2} in forests older than 15 years, while NBP accumulation was reduced by ~1.7 kg C m^{-2} in forests younger than 10 years.

[42] In general, accumulated NBP from 1901 to 2010 is the result of ecosystem responses to disturbance and non-disturbance factors that have changed over time and have geographic variability. Mean accumulated NBP was 3.96 kg C m^{-2} and total accumulation was 12.22 Pg C for the conterminous U.S. forests from 1901 to 2010. Of the total amount, disturbance factors contributed 9.97 Pg C (82%) and non-disturbance factors contributed 2.25 Pg C (18%). In this study, the effects of disturbance factors on the C budget include both the C loss caused by disturbance events and C gain from regrowing forests. Therefore, the result of the NBP accumulation from disturbance factors suggests that forests had more C uptake due to forest regrowth than C loss due to disturbance events over the century (Figure 5e). As for the contributions of individual non-disturbance factors, changes in CO_2 accounted for 0.33 Pg C (3%), changes in N deposition accounted for 1.24 Pg C (10%), changes in climate reduced accumulated NBP by 0.07 Pg C (−1%), and the interaction among these factors contributed 0.76 Pg C (6%) of the total NBP accumulation.

4. Discussion

4.1. Comparison With Existing C Estimates

[43] As an independent estimation for the conterminous U.S. forests, we compared our results with available studies
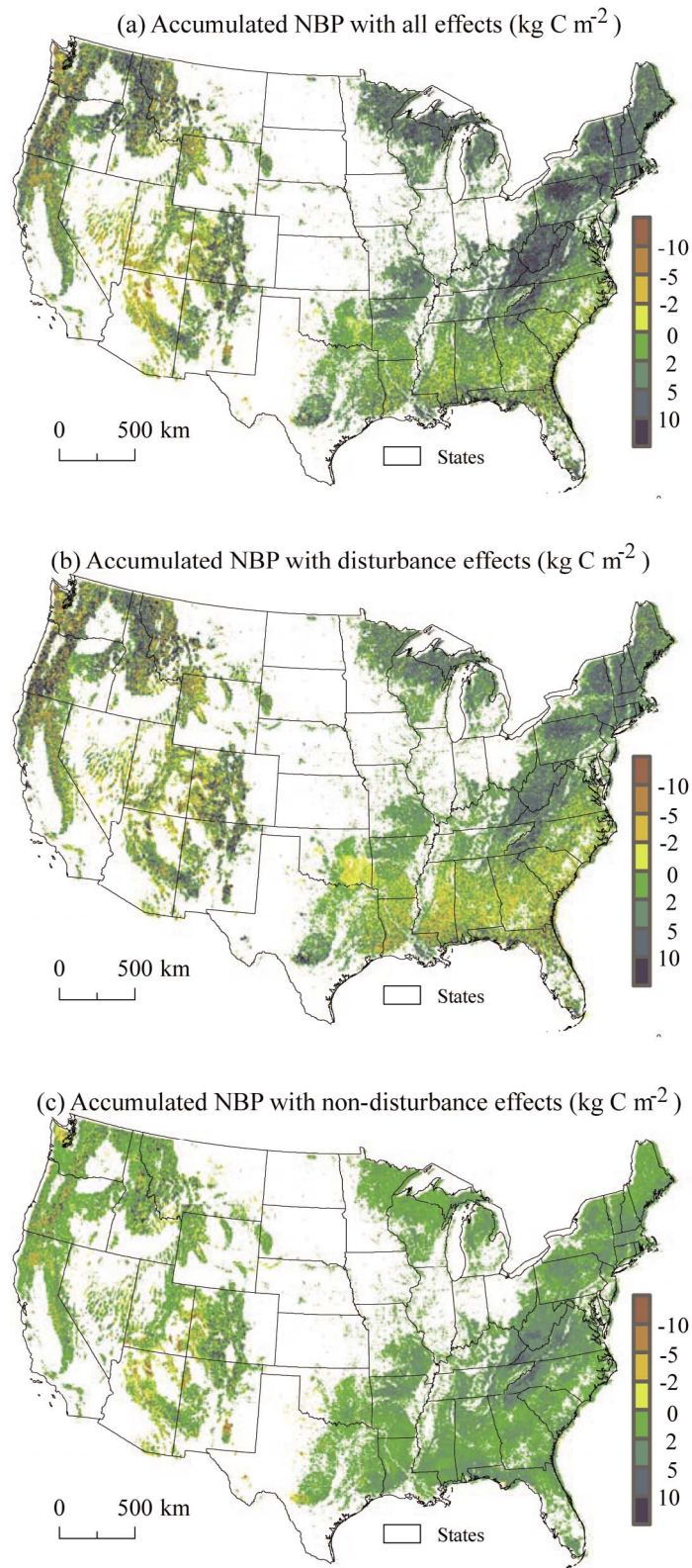
(a) Accumulated NBP with all effects (kg C m^{-2})

(b) Accumulated NBP with disturbance effects (kg C m^{-2})

(c) Accumulated NBP with non-disturbance effects (kg C m^{-2})

Figure 8. Distribution of accumulated NBP (kg C m^{-2}) in the conterminous U.S. forests in response to (a) all effects in $S_{AllFactors}$, (b) effects of disturbance in $S_{Disturb}$, and (c) effects of non-disturbance factors in $S_{NonDisturb}$ from 1900 to 2010. The simulations are presented in Table 2. Positive values represent accumulated effects that enhanced the carbon stock, and vice versa. Disturbance effects include C losses in disturbance events (harvest, fire, and insect attacks), and subsequent regrowth with stand age; non-disturbance effects include climate variability, atmospheric CO_2 concentration, and N deposition.

using different methods and data sets spanning from the 1950s to 2000s. Estimates based on C stock changes (forest inventories) for the conterminous U.S. forests ranged from 79 Tg C yr^{-1} to more than 300 Tg C yr^{-1} (Table 4). Although the C stock change method accounts for the changes in forest C stocks consisting of C emission due to disturbances and uptake due to forest growth, this approach typically uses empirical models to estimate C stocks in litter, woody debris, slash and mineral soil C pools [*Birdsey*, 2004], and the resulting estimates have not always agreed with estimates that use different approaches [*Pacala et al.*, 2001]. Our estimates are comparable to analyses based on C stock change methods except for the estimates pertaining only to timberland [*Turner et al.*, 1995] (Table 4, Figure 5c; see also Figure C1 in the auxiliary materials), and our estimates agree well with the modeling results of *Hurtt et al.* [2002] which include the effects of both disturbances and regrowth on the historical changes of total C in the conterminous U.S. forests. However, our estimates are higher than the age-accumulation results based on FIA data constrained by the CASA model [*Williams et al.*, 2012]. Their results are also lower compared to the inventory-based estimates by *Birdsey* [2004]. The discrepancy is partially because the age-accumulation method does not consider growth enhancement and therefore underestimates NEP derived from the lower-than-normal slope of regrowth trajectories [*Williams et al.*, 2012]. Our estimates are also higher than the results by *Zheng et al.* [2011] using a remotely sensed land cover map, fire data and FIA data. In their estimate, the South region is a small net C source, which conflicts with FIA-based and our estimates. The reasons for these differences likely include (1) double accounting of C removals for overlapping events of deforestation, harvest, and fire [*Zheng et al.*, 2011]; and (2) significantly underestimating forest areas as compared to FIA data, by 2% to 70% in the forest areas for 11 states out of 13 in the South region [*Zheng et al.*, 2011]. Our estimates are lower than results based on upscaling C fluxes from the AmeriFlux network with spatial MODIS data for 2001–2006 [*Xiao et al.*, 2011]. In *Xiao et al.* [2011], regional C emissions and regrowth from disturbances were not considered. As suggested by *Desai et al.* [2005], simple upscaling methods without vegetation condition and disturbance information can lead to incomplete or erroneous C estimates.

[44] The estimated contributions of growth enhancement from climate, CO_2 fertilization, N deposition and forest regrowth to the C flux of the conterminous U.S. forests are not consistent in different studies, and we lack appropriate empirical data at ecosystem levels to validate these attributes. *Hurtt et al.* [2002] suggest that forest regrowth is primarily responsible for the conterminous U.S. C sink. The results of analysis using the PnET-CN ecosystem process model for the Mid-Atlantic region (35–47.5°N, 71–85.5°W) also indicates that long-term C uptake from the effect of forest regrowth is greater than that from the effect of growth enhancement [*Pan et al.*, 2009]. A study based on FIA data and a growth model concluded that growth enhancement only accounts for 2.0 ± 4.4% of the total C sink in the eastern U.S. [*Caspersen et al.*, 2000]. In contrast, using the same growth model of *Caspersen et al.* [2000] and FIA data, CO_2 fertilization is suggested to be the primary reason for the conterminous U.S. forest C sink [*Joos et al.*, 2002]. The disparity between these two FIA-based estimates is likely due to different calculations of growing C stock and interpretation of growth enhancement factors. However, disturbance history and forest regrowth is suggested to be the principal mechanism responsible for the sink of the eastern U.S. using independent data and a model [*Albani et al.*, 2006]. We show a similar conclusion but the effect of CO_2 fertilization is smaller than that of *Albani et al.* [2006] during the 1980s and 1990s (54 versus 190 Tg C yr^{-1}). It is possible that growth enhancement by N deposition was not included in the study of *Albani et al.* [2006]. The enhancement of the C sink by N deposition was estimated to be 70 Tg C yr^{-1} in our study. A study including only the effects of climate and CO_2 fertilization based on an ensemble of VEMAP models indicates that the effects of climate and CO_2 fertilization contributed a small portion (80 Tg C yr^{-1}) to the total C sink of the conterminous U.S. during 1980–1993, suggesting that forest regrowth had as large as or larger effects on the C sink before 1980 [*Schimel et al.*, 2000]. We agree with this point and find that climate and CO_2 fertilization enhance the conterminous U.S. forest C sink by 55 Tg C yr^{-1} and regrowth contributes 247 Tg C yr^{-1} for the same period. Given the estimated C sink due to land use change of 37 Tg C yr^{-1} during the 1980s [*Houghton et al.*, 1999], existing forests including their disturbances contributed 84% or 196 Tg C yr^{-1} to the overall C sink. For the conterminous U.S. forests, we find that contributions of these two processes varied from region to region (Figure 6, section 3.4.2). In summary, our results suggest that the effect of forest regrowth was larger than the effect of growth enhancement before the 1990s, and that the two effects were almost equivalent since the 1990s for the total C dynamic of forests in the conterminous U.S. (Figure 5d, section 3.4.1).

4.2. Roles of Disturbance Factors

[45] The importance of disturbance factors in controlling rates of C cycling in different forested ecosystems has been recognized [*Odum*, 1969; *Chen et al.*, 2004; *Campbell et al.*, 2004; *Pregitzer and Euskirchen*, 2004; *Masek and Collatz*, 2006; *Nunery and Keeton*, 2010]. Disturbance events periodically export large amounts of C to the atmosphere, and further change the stand age structure of forested ecosystems [*Campbell et al.*, 2004]. The results of this study indicate that the youngest regrowing forests (<10 years old) following disturbance events were often C sources to the atmosphere (e.g., patchy areas of the southern U.S.). Regional disturbances were diverse on the landscape and caused variations of regional net C uptake associated with forest age structure distributions. The attribution net C uptake to various factors differed between regions (Figure 6). However, beyond all these facts, our study shows that net C uptake in U.S. forests at the continental scale was controlled by disturbance factors, a conclusion that is consistent with previous studies [*Pregitzer and Euskirchen*, 2004; *Masek and Collatz*, 2006].

[46] The largest portions of net C uptake and C accumulation were credited to contributions of middle-aged regrowing forests following disturbances rather than old forests without disturbances in the conterminous U.S. (Figure 2a and Figure 8). Regrowing forests at productive ages have stronger capacity for accumulating C over decades than old-growth forests, although old-growth forests continue to sequester C at lower rates [*Pan et al.*, 2009]. Regrowing forests shortly after

disturbances are normally C sources because the initial C uptake in the early years of recovery is smaller than C release from heterotrophic respiration. It generally takes 10–30 years for regrowing forests to become net C sinks after disturbances [*Campbell et al.*, 2004; *Amiro et al.*, 2010; *Peichl et al.*, 2010; *Goulden et al.*, 2011]. During 2000–2010, the oldest forests were small C sources or sinks from −97 to 150 g C m^{-2} yr^{-1}, depending on forest types and environmental conditions [*Litvak et al.*, 2003; *Peichl et al.*, 2010]. The net C uptake of these old forests across the conterminous U.S. was 1.74 g C m^{-2} yr^{-1}. The middle-aged forests (30–80 years old) exhibited a large C sink (mean value of 186 g C m^{-2} yr^{-1}). In contrast, forests less than 10 years old were a C source (183 g C m^{-2} yr^{-1}) to the atmosphere (although 2% of these forests still exhibited net C uptake from the atmosphere).

[47] Stand-age structure of a forested ecosystem plays a critical role in determining net C uptake and C accumulation in the terrestrial ecosystem [*Campbell et al.*, 2004; *Chen et al.*, 2004; *Nunery and Keeton*, 2010]. The age structure of an ecosystem reflects its disturbance history in time and space, which greatly affects both magnitude and spatial distributions of regional C changes in the short term, and the subsequent forest regrowth after disturbances [*Chen et al.*, 2004]. Both young and old forests have small capacities to take up C, while middle-aged forests have large capacities. For example, forests have the longest life spans in the West Coast region [*Pan et al.*, 2011b], and the NBP accumulation in this region from 1901 to 2010 varied greatly (−10 to 10 kg C m^{-2}) among different age classes (Figure 8). In northwestern Washington State where forests are old on average (>400 years old), a weak C source/sink was found. In the northeastern U.S. where forests are mostly in the productive middle ages (30–80 years old), a large C sink was estimated. As a first order approximation, the stand age structure in a forested ecosystem indicates the magnitude of net C uptake.

[48] It has been suggested that disturbances could increase net C uptake in the long run as forests recover [*Campbell et al.*, 2004]. However, the time for recovery after disturbances varies, depending on forest species, forest management practices, and environmental conditions [*Litvak et al.*, 2003; *Chen et al.*, 2004; *Pan et al.*, 2009; *Peichl et al.*, 2010]. Managed forests often have higher productivity and more rapid recovery after disturbances compared with unmanaged forests. In the South region, 60% of the forested area is dominated by managed forests between 20 and 60 years old (Figure 2a) [*Pan et al.*, 2011b]; thus, this region exhibited the largest C sinks in the 2000s, and contributed a large fraction (52%) to the continental NBP accumulation. However, boreal and high-elevation forests tended to have average productivities that were lower than managed forests in the warmer South region (Figure 8). This has been demonstrated from individual chronosequences and FIA data [*Amiro et al.*, 2010]. Although 70% of areas in the North region is productive middle-aged forest between 30 to 80 years old (Figure 2a) [*Pan et al.*, 2011b], the mean C sink was smaller than that in the South, which is characterized by highly productive natural and plantation forests.

4.3. Roles of Non-Disturbance Factors

[49] There is still substantial debate about whether or not CO_2 fertilization has a significant effect on the terrestrial biosphere [*Norby et al.*, 2005; *Canadell et al.*, 2007a, 2007b;

Luo and Weng, 2011; *Pan et al.*, 2011a]. Elevated CO_2 directly stimulates photosynthesis and enhances woody biomass [*Pan et al.*, 1998]. However, the long-term effect of CO_2 fertilization is limited by N availability which regulates plant growth and net soil C accumulation [*Campbell et al.*, 2004; *Luo and Weng*, 2011]. Increased N deposition usually stimulates NPP and hence increases in woody biomass, surface litter and soil organic matter. Whether increased NPP can lead to net C sequestration is controversial [*Luo and Weng*, 2011]. Increased N input stimulates [*Knorr et al.*, 2005] or suppresses [*Janssens et al.*, 2010] soil respiration in different regions. Our results indicate that increased CO_2 and N deposition enhanced C uptake in the conterminous U.S. forests (Figure 5). N deposition had a stronger effect than CO_2 fertilization on NBP at the continental scale, but a weaker effect on the continental NPP (Figure 5). Neglecting rising CO_2 concentration and N deposition respectively would underestimate the C sink by 13 and 24 Tg C yr^{-1} respectively during the period of 1950–2010. However, the effects of their chronic changes varied markedly across different regions because the rate of N deposition is not evenly distributed across the continent (Figure 7). For example, the effect of CO_2 fertilization contributed more than N deposition to regional NPP from the South to the West Coast. In contrast, N deposition had larger effects than CO_2 fertilization on NBP in the North and South regions but smaller effects in the Rocky Mountain and West Coast regions. Because disturbances alter forest age structure, they indirectly affect the N cycling in an ecosystem through different N demands and mineralization rates, and may also conceal the enhancement effects of CO_2 and N on C accumulation due to large stochastic C emissions [*Thomas et al.*, 2010]. Comparison with the simulation of only non-disturbance factors indicates that the CO_2, N and climate effects were amplified if disturbance factors were omitted.

[50] In response to warming, surface litter and soil organic matter are likely to decompose at faster rates [*Ju et al.*, 2007]. Warming could increase biomass due to the increase of available soil N, leading to overall higher C accumulation [*McMurtrie et al.*, 2001]. Hence, any changes in temperature and precipitation would affect decomposition rates and available soil N for plants. Our results demonstrated that the combined direct and indirect impacts of historical changes in climate had great effects on the inter-annual variation estimates and on the U.S. forest C stock change, but averaged over time, induced only a minor increase in the rate of C stock change (Figure 5). Climate variability exhibited a positive contribution to the increase of the U.S. forest C sink in the 1950s, 1960s and 1970s, but was negative in the 1980s and 2000s. When neglecting climate variability, the estimated C sink was reduced by only 3 Tg C yr^{-1} over the period of 1950–2010 (Figure 5d). The effect of changing climate could become more significant in the future if climate variability becomes more dramatic [*Pan et al.*, 2009].

4.4. Uncertainties, Limitations, and Future Work

[51] We attempted to factor out the contributions of two different processes (regrowth due to disturbance factors and growth enhancement due to non-disturbance factors) to the C dynamics of the conterminous U.S. forests. Several limitations have not yet been overcome in using the historical disturbance data to simulate C dynamics.

[52] The validation using inventory-based data showed that InTEC could diagnose large-scale C dynamics of the U.S. forests. Nonetheless, there are still many uncertainties in our estimates for soils and at smaller scales. For example, the differences between estimates of C changes in the 1990s by different approaches can be attributed to the substantial differences in estimates of C changes in soil. Compared with FIA data, overestimation of living biomass occurs in New Mexico, Kansas, Oklahoma, Nevada, Florida, and West Virginia, which might be partially a result of coarse-scale stand age information from limited survey plots [*Pan et al.*, 2011b] and a result of reference estimates of NPP from MODIS since MODIS has biases for overestimating NPP/GPP for regions with low water holding capacity [*Pan et al.*, 2006]. Compared with MODIS NPP for the conterminous U.S. forests from 2000 to 2010, we show that InTEC estimates the magnitudes of annual total NPP with mean bias error (MBE) of -6 Tg C yr^{-1} and RMSE of 70 Tg C yr^{-1} (section C in the auxiliary materials). However, about 5%–10% of total pixels cannot agree within 1% with MODIS NPP. Sensitivity analyses of input data and model parameters to examine their impacts on estimates of C variables (F. Zhang et al., Carbon balance in conterminous U.S. forests based on historic changes in climate, atmospheric composition, and disturbances, submitted to *Global Biogeochemical Cycles*, 2012) showed that the error in NPP (-10% to 25% on average) will transmit -12% to 31% error in the amplitude of NBP during 1980–2006. However, it is important to note that significant uncertainty still exists in the FIA data [*Birdsey*, 2004; *Pan et al.*, 2009] although they reflect a wide range of impacts resulting from long-term climate change and sudden disturbance events on C dynamics.

[53] Accurate estimates of forest C stock changes require spatially explicit disturbance and stand age data over the study period. Insufficiency of these data backward through time probably caused underestimation of disturbance effects on C emissions in the beginning of the twentieth century. Compared with estimates from *Birdsey et al.* [2006] and *Houghton et al.* [1999], our pre-1940s NBP was overestimated by 50–150 Tg C yr^{-1} due to an underestimation in C emissions because current stand age maps cannot reflect disturbance history for sites that had repeated disturbances over time [*Pan et al.*, 2011b]. Comparison with the C emissions due to fire estimated by *EPA* [2009] shows that our estimates are slightly higher than EPA's (38 versus 31 Tg C yr^{-1}) on average with large inter-annual variability during the period of 1990–2006 (Figure 5f). The magnitudes of fire emissions mainly depend on the sizes of pre-disturbance C pools and the burn severity. Severity influences the amount of total C emissions at the time of fire as well as long-term C accumulation after fire [*Johnstone et al.*, 2010]. However, we did not consider fire severity in our study and assumed that 100% litter and foliage were burned and released to the atmosphere. Similarly, forests disturbed by insect infestations were treated as harvested forests when in fact impacts of insect epidemics on biomass range from moderate to severe. The simplified treatments for fire and insect disturbances in our model would cause it to underestimate C transferred to soil because stand-replacing disturbances often produce a deadwood C pool. As an approximation, if forests disturbed by insects accounted for $\sim$0.25% of the conterminous U.S. forest area, and if half of

NPP is allocated to the woody component, NBP would be underestimated by 0.16 Tg C (0.11% of the overall NBP) in our estimates. Compared with the USFS Aerial Detection Survey database, we overestimated total forest mortality from insects by about 11%, which decreased the estimate of NBP. The accuracy of the stand age distribution also influences our estimates. The standard deviation of stand age was suggested to range from 10 years in the eastern U.S. to 50 years in the western U.S. and British Columbia [*Pan et al.*, 2011b]. Sensitivity analysis showed that the U.S. forest C sink decreased by 89 Tg C yr^{-1} from decreasing 5 years of stand age and increased by 18 Tg C yr^{-1} from increasing 5 years of stand age, exhibiting opposite but asymmetric effects (Zhang et al., submitted manuscript, 2012). Reducing uncertainties in the InTEC model truly relies on improving relevant input data quality. We urge the development of these historical data sets of spatially explicit disturbances and stand age maps.

[54] Other episodic events that were not specified in this study such as storms, drought, and insect epidemics can also reduce C accumulation although they occur less extensively than fires and harvest. Storms cause tree mortality and damage, influencing the short-term C stock and long-term forest recovery [*Kurz et al.*, 2008]. Hurricane Katrina in 2005 produced C emission of $\sim$105 Tg C yr^{-1}, equivalent to 40% of our U.S. C sink (262 Tg C yr^{-1}) [*Zeng et al.*, 2009]. A pine beetle epidemic that occurred in western North American forests killed trees and transferred C to litter pools, releasing C over tens of years [*Kurz et al.*, 2008]. Drought also has increased tree mortality in the western U.S. [*van Mantgem et al.*, 2009].

[55] Interactions between disturbance and non-disturbance factors in forests are complex and important, but no patterns have been identified to help understand and simulate them in models, particularly at the regional scale [*Law et al.*, 2003; *Masek and Collatz*, 2006]. Literature reviews are often mixed, indicating that results may be site-specific and dynamic [*Amiro et al.*, 2010; *Nunery and Keeton*, 2010]. For instance, forest regrowth was suggested to have larger impacts than CO_2 and climate on C changes [*Schimel et al.*, 2000], but climate was also claimed to be a key driver changing disturbance regimes and also affecting the rate of forest recovery [*Hicke et al.*, 2007]. Experiments for age-based C processes (photosynthesis, respiration) showed that increasing CO_2 had only small or no effects [*Asshoff et al.*, 2006] although experiments in young forest stands showed an increase in NPP [*Norby et al.*, 2005]. The responses of forests to changing climate, elevated CO_2 and N deposition are suggested to be age-related [*Masek and Collatz*, 2006] and species-related [*Law et al.*, 2003]. The best mechanisms built into ecosystem process models are based on experimental results [*Pan et al.*, 2009]. However, C dynamics in forests related to climate, disturbance, management and other factors have not been broadly investigated [*Running*, 2008]. Given that, the simulated results of responses to interactive non-disturbance and disturbance factors remain uncertain to some extent.

[56] There are also some uncertainties introduced from the model itself. The model excludes C fluxes of understory vegetation (e.g., grass and short shrub), which may play a role to compensate the C loss in the early stage of forest regrowth, and cause an underestimates of C uptake. It is also important to account for negative impacts of tropospheric

ozone on forest C [*Pan et al.*, 2009]. However, this effect is not yet included in InTEC. This study, to a broad extent, is complementary to current C studies and provides an opportunity to expand our insights about the causes of historical C changes of U.S. forests. Given the importance of forest age structure for determining NBP and its variability, the paucity of knowledge on the age structure of forests and disturbance legacy remains a roadblock for C studies [*Masek and Collatz*, 2006]. Thus, the complex effects of changing climate, elevated CO_2 and N, disturbance events and successive regrowth patterns on the C cycle of the conterminous U.S. forests should be further investigated. Multiple-aged, species-diverse experiments or controlled observational studies are also needed in the future to verify these processes described in our model.

5. Conclusion

[57] Our study quantified C changes in the conterminous U.S. forests in response to changes in atmospheric composition, climate variability, and disturbance events. The factors included in this analysis were grouped into disturbance factors (disturbance events and the successive regrowth) and non-disturbance factors (atmospheric CO_2 concentration, N deposition and climate variability). Our analysis indicated that disturbance effects generally outweighed or were equivalent to non-disturbance effects on decadal C changes of the conterminous U.S. forests. As a first approximation, disturbance factors were the dominant drivers of C changes from 1980 to 2010 at the continental scale. However, the effects of disturbance and non-disturbance factors had distinct regional patterns. Disturbance effects dominated C changes in the South and Rocky Mountain regions. In the West Coast region, non-disturbance effects overweighed disturbance effects on C changes. In the North region, because forests that have recovered from harvests and agricultural activities in the early twentieth century have reached their mature ages, the effect of regrowth on increasing C gains diminished over the period of 1980–2010 to become almost equal to the non-disturbance effects which had increased gradually.

[58] The current results of the quantitative analysis to separate disturbance and non-disturbance factors for the C budget of the conterminous U.S. forests still have great uncertainties. These uncertainties are caused by the lack of spatially explicit disturbance data, poor understanding of the spatiotemporal impacts of disturbance events on C dynamics, complex interactions among disturbance and non-disturbance factors, and uncertainties in the process-based model. This study provides an opportunity to expand our insights on the primary causes of the contemporary C sink in the U.S. forests and thus by implication, the future of U.S. net emissions. In the future, new technologies for disturbance tracking, improved forest inventories for C studies, as well as more intensive field studies of interactions between disturbance and non-disturbance factors should be included in the research agenda to improve current estimates of C dynamics and future projections.

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