

RESEARCH ARTICLE

10.1002/2014JG002818

Key Points:

- A new land use and land cover data set for the conterminous U.S. is created
- State, regional, and national land carbon sinks and sources are estimated
- Possible policies to enhance carbon sinks are discussed

Supporting Information:

- Supporting Information S1

Correspondence to:

X. Lu,
xlu@mbl.edu

Citation:

Lu, X., D. W. Kicklighter, J. M. Melillo, J. M. Reilly, and L. Xu (2015), Land carbon sequestration within the conterminous United States: Regional- and state-level analyses, *J. Geophys. Res. Biogeosci.*, 120, 379–398, doi:10.1002/2014JG002818.

Received 6 OCT 2014

Accepted 26 JAN 2015

Accepted article online 30 JAN 2015

Published online 28 FEB 2015

Land carbon sequestration within the conterminous United States: Regional- and state-level analyses

Xiaoliang Lu¹, David W. Kicklighter¹, Jerry M. Melillo¹, John M. Reilly², and Liyi Xu²

¹The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts, USA, ²Joint Program on the Science and Policy of Global Change, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA

Abstract A quantitative understanding of the rate at which land ecosystems are sequestering or losing carbon at national-, regional-, and state-level scales is needed to develop policies to mitigate climate change. In this study, a new improved historical land use and land cover change data set is developed and combined with a process-based ecosystem model to estimate carbon sources and sinks in land ecosystems of the conterminous United States for the contemporary period of 2001–2005 and over the last three centuries. We estimate that land ecosystems in the conterminous United States sequestered 323 Tg C yr⁻¹ at the beginning of the 21st century with forests accounting for 97% of this sink. This land carbon sink varied substantially across the conterminous United States, with the largest sinks occurring in the Southeast. Land sinks are large enough to completely compensate fossil fuel emissions in Maine and Mississippi, but nationally, carbon sinks compensate for only 20% of U.S. fossil fuel emissions. We find that regions that are currently large carbon sinks (e.g., Southeast) tend to have been large carbon sources over the longer historical period. Both the land use history and fate of harvested products can be important in determining a region's overall impact on the atmospheric carbon budget. While there are numerous options for reducing fossil fuels (e.g., increase efficiency and displacement by renewable resources), new land management opportunities for sequestering carbon need to be explored. Opportunities include reforestation and managing forest age structure. These opportunities will vary from state to state and over time across the United States.

1. Introduction

Land ecosystems play a major role in the global carbon budget. Carbon cycle analyses indicate that over the first decade of the 21st century, about one half of the total annual CO₂ emissions from human activities (primarily fossil fuel burning and tropical deforestation) have accumulated in the atmosphere, one quarter in the ocean, and one quarter on the land [Le Quéré *et al.*, 2014]. While it is clear that the net land sink is primarily in the Northern Hemisphere [Intergovernmental Panel on Climate Change, 2014], a more spatially detailed understanding of the sink is less certain. This has important implications for managing the global carbon budget to mitigate climate change.

In part to inform mitigation efforts, a number of studies have been done to quantify the land carbon sink at continental and national levels. For North America, King *et al.* [2012] estimate that at the beginning of the 21st century, the land sink was about 0.63 ± 0.16 Pg C yr⁻¹. For the United States, estimates of the national land sink have varied between 0.16 and 0.69 Pg C yr⁻¹ during this same time period (Table S1 in the supporting information).

While the land sink includes sequestration in a variety of ecosystems in the United States, forests play a dominant role [King *et al.*, 2007; Pacala *et al.*, 2007; Chen *et al.*, 2011; Hayes *et al.*, 2012]. The importance of U.S. forests in the nation's carbon budget is explicitly recognized in the *President's Climate Action Plan (PCAP)*, issued on June of 2013 (whitehouse.gov/president27climateactionplan). The plan also recognizes that in the face of climate change and increased risk of wildfire, drought, and pests, the capacity of U.S. forests to absorb carbon is at risk. The plan argues that "conservation and sustainable management can help to ensure that our forests continue to remove carbon from the atmosphere while improving soil and water quality, reducing wildfire risk, and otherwise managing forests to be more resilient in the face of climate change" (see PCAP, p. 11).

At the regional and state levels in the U.S., the recognition that forests deliver a host of ecosystem services including carbon sequestration has led to a number of forest management plans designed to protect the delivery of these services. In New England, a vision for the region's landscape has been developed to conserve

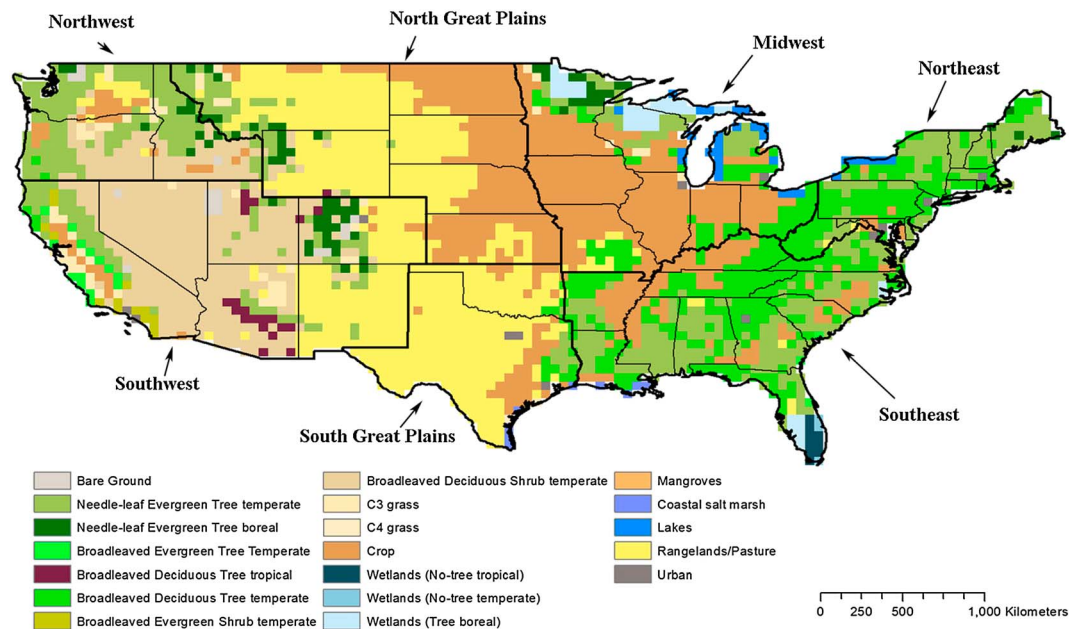


Figure 1. Dominant land cover across the conterminous United States in 2005. The resolution is 0.5° latitude × 0.5° longitude, and the bold black line represents the boundary of regions.

and enhance the capacity of the region’s millions of hectares of forest to deliver renewable energy and carbon storage (wildlandwoodlands.org). A similar but more detailed vision has been developed for the State of Massachusetts (www.wildlandsandwoodlands.org). On the West Coast of the United States, California has developed a forest management plan as part of their greenhouse gas offset program (<http://www.forestactionplans.org/states/california>). In addition, a number of states are in the process of developing similar programs.

One of the things needed to transform these visions into actions is a quantitative understanding of the rate at which land ecosystems at regional and state levels sequester carbon. State-level information is particularly important because various states have specific land management laws regulating many aspects of forest timber resources and products derived from these resources.

The large size of the conterminous U.S., which occupies a combined area of more than $8 \times 10^6 \text{ km}^2$, contains a variety of land cover types (Figure 1) that have different environmental conditions and land use histories. This variability needs to be considered in the development of effective carbon sequestration policies. In addition, the contemporary carbon dynamics in terrestrial ecosystems of the conterminous U.S. have been affected in significant ways by the legacy of centuries of land use [Houghton *et al.*, 2000b, 2012; Caspersen *et al.*, 2000; Pacala *et al.*, 2007; Kuemmerle *et al.*, 2011; Williams *et al.*, 2012]. The influence of this land use legacy also needs to be taken into account when evaluating contemporary land carbon source and sink activity. It is also important to compare land carbon sinks (or sources) to fossil fuel emissions in smaller regions such as states to better understand the total or net effect of the region on the atmospheric carbon budget.

Here we develop new estimates of land carbon sources and sinks for each of the 48 states in the conterminous United States for the period of 2001–2005 by the incorporation of recently published information on forest age structure across the United States [Pan *et al.*, 2011]. Two recent modeling studies [Williams *et al.*, 2012; Zhang *et al.*, 2012] have already used this stand age information with process-based models to estimate forest carbon sources and sinks across the conterminous United States. While Williams *et al.* [2012] also account for the influence of climate on forest carbon sequestration, Zhang *et al.* [2012] account for climate and atmospheric chemistry (atmospheric carbon dioxide concentrations and atmospheric nitrogen deposition) effects. It is not clear in these studies, however, how these forest carbon sources and sinks influence net carbon balance across the region. We extend these earlier modeling efforts by first considering the carbon dynamics of all land ecosystems in the conterminous United States and the effects of historical transitions in land use (e.g., forests to croplands, grasslands to rangelands/pastures, croplands to urban areas, and croplands to forests) on these

carbon dynamics. Similar to Zhang *et al.* [2012], we consider the influence of climate and atmospheric chemistry (atmospheric carbon dioxide concentrations, atmospheric nitrogen deposition, and ozone pollution) in addition to land use change on these dynamics. We then compare our model estimates of land carbon sources and sinks to concurrent estimates of fossil fuel emissions to examine how land carbon dynamics influence net carbon balance across the conterminous United States. Our approach couples a process-based ecosystem model and reconstruction of long-term land use and land cover change (LULCC) history, with an emphasis on accurately representing forest stand age, to assess carbon sequestration at these policy-relevant scales. This approach is an advance relative to previous simulation-based estimates because it uses a much improved database of LULCC history.

2. Materials and Methods

The Terrestrial Ecosystem Model (TEM), a process-based biogeochemistry model, is used to estimate contemporary land carbon sinks and land use legacy effects associated with the historical gains and losses of carbon in the conterminous U.S. from 1700 to 2005. These carbon fluxes are estimated at a spatial resolution of 0.5° latitude by 0.5° longitude for 3462 grid cells that comprise the conterminous U.S. The gridded carbon fluxes are then aggregated to state and regional levels. We separate the conterminous U.S. into seven regions used in the recent National Climate Assessment Report [Melillo *et al.*, 2014]: the Northeast and Southeast, which are mostly covered by forests (Figure 1); the Midwest, which is mostly covered by row crops; the Northern Great Plains and Southern Great Plains, which are mostly covered by row crops and rangelands/pastures; the Southwest, which is mostly covered by shrublands; and the Northwest, which is mostly covered by forests and shrublands. To examine the importance of the land carbon sinks relative to concurrent fossil fuel emissions, we then determine a carbon balance index (CBI) at various spatial scales. Below, we briefly describe how TEM estimates land carbon sources and sinks, how land use legacy effects are represented, how carbon estimates by TEM are evaluated, and how the CBI is determined.

2.1. Estimating Land Carbon Sources and Sinks

Land carbon sources and sinks are estimated by TEM simulation of land carbon, nitrogen, and water cycles. The TEM uses spatially referenced information on climate, elevation, soils, and vegetation to estimate monthly vegetation and soil carbon fluxes and pool sizes. The model takes into consideration how land carbon dynamics are influenced by multiple environmental factors including CO₂ fertilization, soil thermal dynamics, climate change and variability, land use change, atmospheric nitrogen deposition, and ozone pollution [McGuire *et al.*, 2010; Hayes *et al.*, 2011; Tian *et al.*, 2011; Kicklighter *et al.*, 2013; Lu *et al.*, 2013]. In this study, carbon dynamics are simulated for a mosaic of land cover cohorts contained in each 0.5° latitude by 0.5° longitude grid cell as described below. The forcing variables for TEM are time series data for land use and land cover change (LULCC), meteorology (air temperature, precipitation, and cloudiness), and atmospheric chemistry data (CO₂ concentrations, AOT40 ozone index, and nitrogen deposition). The AOT40 index is a measure of the accumulated hourly ozone levels above a threshold of 40 ppbv during a month. Static inputs are soil texture and elevation. The development of the LULCC data is described in section 2.2 and the development of the other input data sets is described in the supporting information.

Carbon cycle simulation by TEM is initiated by first estimating the uptake of atmospheric carbon dioxide by vegetation, known as gross primary productivity (GPP). For natural terrestrial ecosystems, carbon is lost from land ecosystems to the atmosphere by autotrophic respiration (R_A) and heterotrophic respiration (R_H). Net primary production (NPP) represents the creation of vegetation biomass and is estimated by subtracting R_A from GPP. The ecosystem-level carbon increment in natural ecosystems, known as net ecosystem production (NEP), is the difference between NPP and R_H .

Carbon is also lost from ecosystems due to human-related activities: livestock respiration associated with the consumption of rangelands/pasture grasses (E_L), carbon emissions associated with burning slash from timber harvest or from converting land to agriculture or urban areas (E_C), and carbon emissions associated with the decay of agricultural and woody products (E_P). The human-induced carbon pools such as food and woody products differ in the rate of decomposition. Carbon in food products is assumed to be consumed and released back to the atmosphere within 1 year by human (and livestock) respiration and decomposition of wastes. Wood and its products, on the other hand, are separated into two pools: paper and paper products and longer-lasting

wood products, which are assumed to decompose within 10 and 100 years, respectively. Currently, food and wood products are assumed to be used where they are created (i.e., no export and import of products). Thus, the net carbon exchange (NCE) between the atmosphere and terrestrial ecosystems is estimated as

$$\text{NCE} = \text{NEP} - E_L - E_C - E_P$$

A positive value of NCE represents a land carbon sink, whereas a negative value of NCE represents a land carbon source. Our NCE does not explicitly include carbon emissions associated with wildfires, insect infestations, or extreme weather events such as floods, hurricanes, or ice storms.

To examine the influence of land use legacies on contemporary carbon budgets, we summed the annual NCE in each grid cell from 1700 to 2000. A positive sum indicates a carbon surplus where the ecosystem has more carbon in 2000 than in 1700, whereas a negative sum indicates a carbon deficit where the ecosystem has less carbon in 2000 than in 1700.

2.2. Land Use/Land Cover History Reconstruction

The legacy of past land use change is considered in our study by using a disturbance cohort approach [Reilly *et al.*, 2012; Lu *et al.*, 2013] to track the effects of land use change and climate on terrestrial carbon stocks and fluxes from 1500 to 2005. Before 1500, the conterminous U.S. is assumed to have been covered by minimally disturbed natural vegetation or potential vegetation [Melillo *et al.*, 1993]. Starting from the potential vegetation map, cohorts within each 0.5° grid cell are created or modified (divided) from 1500 to 2005 according to the timing and location of land conversions as derived from the annual land use transition data of Hurtt *et al.* [2011]. These transition data describe land use changes among primary vegetation (i.e., undisturbed natural vegetation), secondary vegetation (i.e., human-disturbed natural vegetation), croplands, rangelands/pastures, and urban areas including abandonment of agricultural lands. With disturbance, the age of a new cohort (e.g., a forest stand) is initially set to zero but then increases annually until the next disturbance when its age is reset to zero. Because Hurtt *et al.*'s [2011] data indicate that little land use change occurred in the conterminous United States before 1700, we focus our analyses of land use legacies on the period between 1700 and 2000.

When forest stand ages in our LULCC data set, derived from Hurtt *et al.*'s [2011] transition data, are compared to a recent, high-resolution (1 km²) forest stand age data set (hereafter referred to as the Forest Inventory and Analysis (FIA) stand age) for North America (Figure S1 in the supporting information) developed by using forest inventory data, large fire polygons, and remotely sensed data [Pan *et al.*, 2011], a large fraction of the Hurtt-derived forest cohorts are found to be older than that indicated in the FIA stand age map. For example, most forests in the Northeast are estimated to be older than 70 in our LULCC data set, whereas the FIA data indicate forests that are younger than 70 (Figure S2 in the supporting information). Because Hurtt *et al.*'s [2011] transition data sets may have incorrectly estimated disturbances, we use the FIA stand age data set to correct the timing and locations of disturbances to forests to create a more realistic forest stand age structure across the conterminous United States that is consistent with current forest inventories. Specifically, the stand ages of forest cohorts within each 0.5° grid cell of our LULCC data set are adjusted to match the distribution of the FIA stand ages for the year 2005. Then, the newly adjusted stand ages are used to modify the timing of the last disturbance of the cohorts in our LULCC data set, which also influences the stand ages of the cohorts between the last disturbance and the previous disturbance. The details of the FIA stand age correction protocol are provided in the supporting information. The correction influences the timing of the last timber harvest of a forested cohort and when an agricultural or urban cohort is converted to forests upon abandonment. After the correction, our new LULCC data indicate a younger stand age distribution for secondary forests in the eastern part of the United States (Northeast, Southeast, Midwest, and Southern Great Plains) after 1850, but more complex changes in historical stand ages occur in the western part of the country (Figure 2).

The corrected LULCC data set is used with TEM to estimate contemporary land carbon sources and sinks and land use legacy effects in this study. To examine how the improved representation of land use history has influenced estimates of contemporary land carbon sinks, we also drive TEM with the uncorrected LULCC data set and compare the results to those derived using the FIA-corrected LULCC data set.

2.3. Simulation Protocol

To develop regional estimates of NCE, the corrected and uncorrected LULCC data sets described above are used with spatially explicit data sets of climate and atmospheric chemistry to drive TEM. In the TEM simulation, carbon, nitrogen, and water dynamics are first initialized to equilibrium conditions for the initial potential

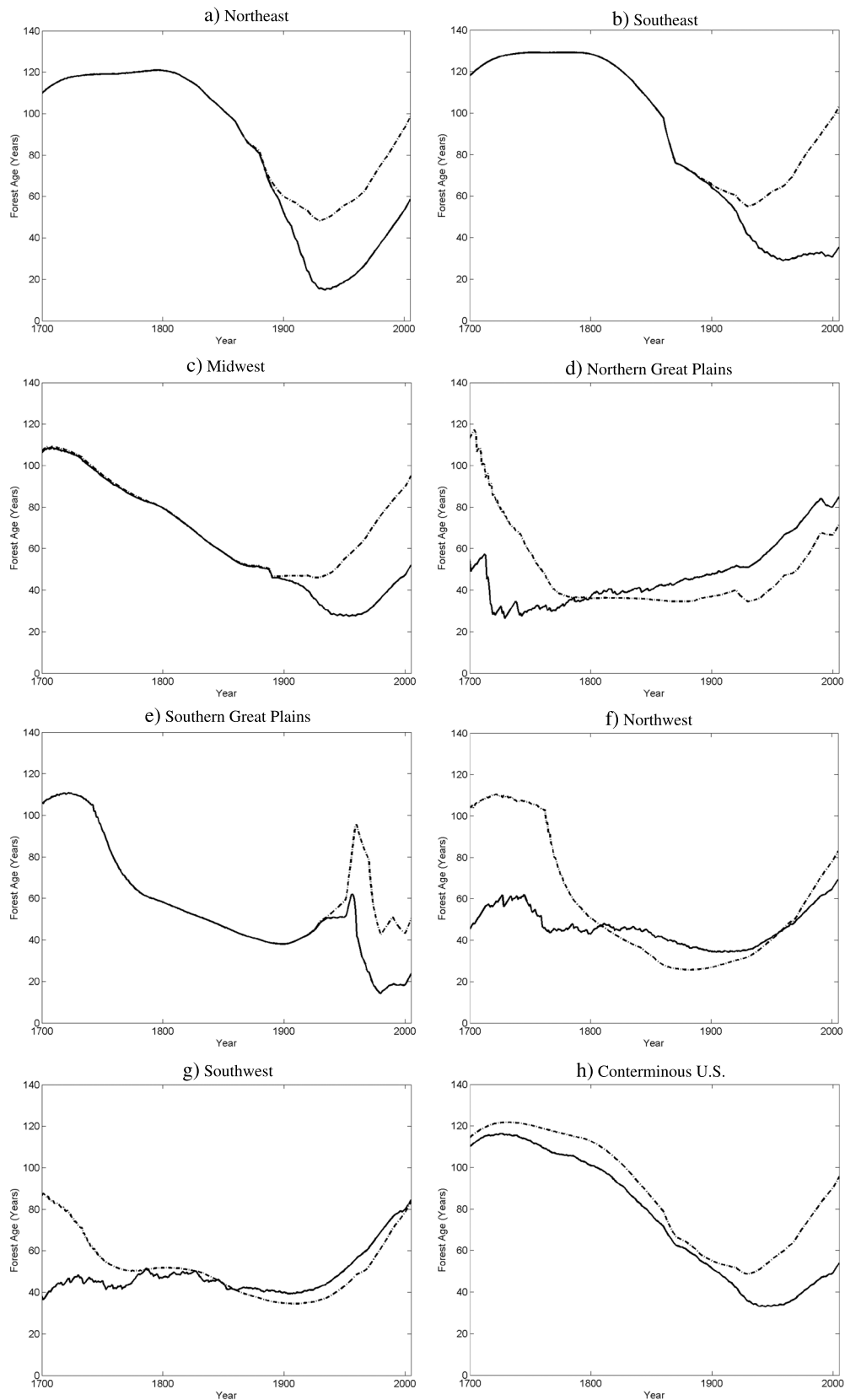


Figure 2. Regional time series of historical (1700 to 2005) stand ages of secondary forests represented by uncorrected (dash-dotted line) and FIA-corrected land cover land use data sets (solid line).

natural vegetation cohorts in a grid cell. Then, after a disturbance associated with creating the land use distribution in 1500 is introduced, a spin-up period of 450 years occurs to allow the carbon, nitrogen, and water dynamics of the newly created cohorts to come back into equilibrium with a simulated environment that includes variable climate conditions but constant atmospheric chemistry and no additional disturbances. After the spin-up period, transient carbon, nitrogen, and water dynamics are simulated for a growing number of cohorts from the year 1501 to 2005, as prescribed in the LULCC data sets, under a simulated environment that include variable climate and variable atmospheric chemistry conditions. Details of this simulation protocol are given in the supporting information.

2.4. Model Validation

We evaluate TEM by comparing model results to other types of estimates at two spatial scales. First, we compare the average annual simulated NEP with the net ecosystem exchange (NEE) of carbon dioxide (CO₂) between land ecosystems and the atmosphere measured by the eddy covariance technique at eight flux sites. By convention, a negative value of NEE means that land ecosystems are sequestering CO₂ from the atmosphere and thus, for natural ecosystems, is equivalent to a positive value of NEP if no disturbance occurs during eddy covariance measurements. Many of the sites had been disturbed prior to eddy covariance measurements (see the supporting information). To make the TEM results more comparable to the eddy covariance measurements, we use the data collected at the eddy covariance site. The disturbance history at each site is collected and translated into building the LULCC histories for the site-level simulations used for evaluation. As the climate data from a site covers a limited time period, the site data are compared to data in our gridded climate data sets for the grid cell containing the site using linear regressions. The resulting linear equations are then used to correct the gridded data to site conditions for the time periods when site data are not available for our site-level simulations.

At the state level, we compare the biomass increments in forests estimated by the TEM with the forest inventory-based estimates. Because TEM has only a single carbon pool for vegetation, we combine estimates for aboveground and belowground carbon in live seedlings, shrubs, and live trees from the inventory data for the evaluation. Biomass increment is determined by subtracting the vegetation carbon density during the last year of the forest inventory study period from that during the first year and then normalized to an annual rate by dividing by the number of years between the two survey years. Because the timing of the survey years (2000 to 2005) varied among the states (Table S2 in the supporting information), we use the longest period available from the forest inventory within this timeframe (1–6 years) from each state for comparison to the TEM estimates. Biomass increment estimates by TEM are then calculated for the same time period as the forest inventory data for each state.

2.5. Carbon Balance Index (CBI)

To better understand the importance of the land carbon sinks in national, regional, and state carbon budgets, we also compared NCE estimates to the corresponding fossil fuel emissions for the 2001–2005 period. We define the carbon balance index (CBI) as the percentage of fossil fuel emissions compensated for by the land carbon sink (i.e., $100 \text{ NCE}/E_{\text{ff}}$).

For the fossil fuel emissions, the Department of Energy's Energy Information Administration (DOE-EIA) has already developed state-level estimates of fossil fuel emissions in the United States for the period of 2000–2010 [*Energy Information Administration (EIA)*, 2013]. We aggregate the gridded TEM estimates of NCE to the regional and state levels and divide the resulting value by the appropriate DOE-EIA fossil fuel estimates to determine regional and state CBIs.

3. Results

3.1. Contemporary Carbon Sequestration

3.1.1. National Level

The amount of net carbon stored by terrestrial ecosystems (NCE) is $323 \pm 191 \text{ Tg C yr}^{-1}$ from the atmosphere during the period of 2001–2005 (the mean ± 1 standard deviation of the 5 year period) when using the corrected LULCC data set. Forests represent the largest sink of atmospheric CO₂ in the conterminous U.S. (Table 1), accounting for $313 \pm 40 \text{ Tg C yr}^{-1}$ or about 97% of the U.S. land carbon sink. The forest sink is a net estimate that is discounted for the release of carbon from forest product pools (Table 2). For this time interval,

Table 1. Regional NCE (Tg C yr⁻¹, Mean ± Their Stand Deviation) for Land Covers of the Conterminous U.S. Over the Period of 2001 to 2005

Region	Croplands	Rangelands/Pasture	Urban	Forests	Shrublands	Grasslands	Other ^a	Total
Southeast	-9 ± 12	-2 ± 2	-1 ± 0	176 ± 26	0 ± 0	0 ± 1	-7 ± 1	156 ± 33
Midwest	-6 ± 17	-1 ± 3	0 ± 0	59 ± 11	0 ± 0	1 ± 4	12 ± 3	66 ± 35
Northeast	-2 ± 3	0 ± 0	-3 ± 1	43 ± 10	0 ± 0	0 ± 0	0 ± 1	39 ± 11
Northern Great Plains	13 ± 42	3 ± 25	0 ± 0	4 ± 2	0 ± 0	0 ± 1	0 ± 0	20 ± 65
Southwest	2 ± 11	0 ± 16	1 ± 1	7 ± 11	5 ± 22	1 ± 2	0 ± 1	15 ± 57
Northwest	3 ± 6	0 ± 1	0 ± 0	11 ± 5	0 ± 2	0 ± 0	0 ± 0	14 ± 12
Southern Great Plains	2 ± 29	-2 ± 32	0 ± 0	14 ± 4	0 ± 0	0 ± 1	0 ± 0	13 ± 65
Total	4 ± 80	-3 ± 60	-3 ± 2	313 ± 40	6 ± 22	1 ± 7	5 ± 3	323 ± 191

^aIncludes wetlands, mangrove, and bare lands.

shrublands, wetlands, grasslands, and croplands also function as small carbon sinks, while rangelands/pastures and urban areas represent small carbon sources (Table 1).

3.1.2. Regional Level

Forests are the dominant carbon sinks in all but one region (Table 1) when using the corrected LULCC data set. The Northern Great Plains is the exception, where extensive cropland soils are a major carbon sink (65%). Forests occupy a relatively small area (8% of land area and 20% of NCE; Table 3) in this region. In the Southeast, Northeast, and Southern Great Plains, the forest carbon sinks are larger than the corresponding regional carbon sinks because the forest sinks are partially offset by carbon losses from other land cover types in these regions.

Although other factors may affect NCE, we found that the rate of carbon sequestration per unit forest area is inversely correlated ($r = -0.97, p < 0.0003$; based on the seven regional data in the Table 3) with mean stand age among the regions. Relatively younger forests occur in the Southern Great Plains and the Southeast, and relatively older forests occur in the Northern Great Plains and the Southwest (Table 3). The younger forests of the Southeast account for more than half of the carbon sequestered by all U.S. forests. Conversely, the relatively older forests in the Northern Great Plains and the Southwest are less effective sinks, only taking up 4 and 7 Tg C yr⁻¹, and accounting for 1% and 2% of the total carbon absorbed by nation's forests, respectively.

3.1.3. State Level

The NCE estimates developed with the corrected LULCC data indicate that land ecosystems are sequestering carbon in 45 of the 48 states of the conterminous United States. The state-level NCE estimates range from 0 Tg C yr⁻¹ in Iowa to 25 Tg C yr⁻¹ in Alabama (Table S3 in the supporting information). Forests are the largest land sink in 38 of these states. The largest forest carbon sinks occur in three states of the Southeast (Alabama, Mississippi, and Georgia) and account for 23% of the total national forest carbon sink. Besides forests, wetlands are relatively important carbon sinks in some northern states (Michigan, Wisconsin, and Minnesota), where they account for 23–36% of a state's land sink (Table S3 in the supporting information). Wetlands in these three states sequestered 12 ± 2 Tg C yr⁻¹. In states where forests are largely absent, such as Kansas, South Dakota, and Nevada, croplands, rangelands/pastures, and shrublands often function as the dominant carbon sinks (Table S3 in the supporting information), but these sinks are generally small and highly variable

Table 2. Source of Carbon Fluxes (Mean ± Their Standard Deviation, Tg C yr⁻¹) From Disturbances Among Land Covers in the United States Over the Period of 2001 to 2005

Land Cover	Net Ecosystem Production	Resource Management and Consumption					NCE
		Livestock Respiration	Conversion Flux	Consumption of Agricultural Products	Decomposition of 10 Year Woody Products	Decomposition of 100 Year Woody Products	
Croplands	236 ± 73	0 ± 0	-1 ± 0	-227 ± 16	-2 ± 0	-2 ± 0	4 ± 80
Rangelands/pasture	230 ± 67	-230 ± 11	-2 ± 0	0 ± 0	0 ± 0	-1 ± 0	-3 ± 60
Urban	3 ± 1	0 ± 0	-5 ± 1	0 ± 0	-1 ± 0	0 ± 0	-3 ± 2
Forests	390 ± 44	0 ± 0	-16 ± 6	0 ± 0	-43 ± 9	-18 ± 0	313 ± 40
Shrublands	6 ± 22	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	6 ± 22
Grasslands	1 ± 7	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 7
Others	21 ± 4	0 ± 0	-6 ± 2	0 ± 0	-8 ± 1	-2 ± 0	5 ± 3
Total	887 ± 197	-230 ± 11	-30 ± 8	-227 ± 16	-54 ± 11	-23 ± 0	323 ± 191

Table 3. Characteristics of Regional Forests (Area, Percent Cover, Area-Weighted Mean Stand Age, Area-Weighted Mean NCE, Total NCE, and Mean ± Their Stand Deviation) During 2001–2005 Using Uncorrected (U) and FIA-Corrected (C) Land Cover and Land Use Change Data Sets^a

Region	Forest Area (km ²)	Forest Cover (%)	Mean Stand Age (Years)		Mean Forest NCE (Mg C km ⁻² yr ⁻¹)		Forest NCE (Tg C yr ⁻¹)	
			U	C	U	C	U	C
Southeast	805,167	58	103	37	87 ± 63	219 ± 32	70 ± 51	176 ± 26
Midwest	323,695	24	95	52	100 ± 28	185 ± 34	32 ± 9	59 ± 11
Northeast	408,240	74	98	58	52 ± 24	107 ± 24	21 ± 10	43 ± 10
Southern Great Plains	46,799	5	50	25	278 ± 107	299 ± 85	13 ± 5	14 ± 4
Northwest	280,324	43	83	69	15 ± 11	40 ± 18	4 ± 3	11 ± 5
Southwest	267,728	15	83	84	32 ± 34	25 ± 41	9 ± 9	7 ± 11
Northern Great Plains	120,124	8	71	85	31 ± 17	31 ± 17	4 ± 2	4 ± 2
Conterminous U.S.	2,252,077	28	95	54	68 ± 30	140 ± 18	153 ± 67	313 ± 40

^aThe table is sorted by decreasing values of forest NCE estimated with the FIA-corrected data set.

from year to year. In two states, forests sink are matched by either cropland (Idaho) or shrubland (Utah) sinks. The eight states in which forests are neither the primary nor codominant carbon sinks sequestered $16 \pm 49 \text{ Tg C yr}^{-1}$ in 2001–2005.

3.2. Validation of Contemporary Results

We have evaluated TEM by comparing model results to other types of contemporary estimates at two spatial scales. At the site level, the simulated NEP is generally within a standard deviation of the observed interannual variability in NEP (Table 4). However, the TEM estimates do not account for carbon sequestration in some ecosystem components such as woody debris [Lu et al., 2013], the loss of carbonate and organic carbon to neighboring river networks, or the gaseous loss of methane and volatile organic carbon [Chapin et al., 2006]. At the state level, the TEM estimates of biomass increment are also generally within the error range of the FIA estimates (Figure S3 in the supporting information). The TEM estimates are based on the biomass increment estimates of all the simulated forest cohorts within a state, whereas the FIA estimates are based on a sampling of permanent plots within a state.

3.3. Historical Carbon Sequestration

Land cover and land use have changed dramatically across the conterminous U.S. from 1700 to 2000 (Figure 3). Overall, disturbances associated with historical land use change have led to a net loss of 13 Pg C from 1700 to 2000, which is equivalent to 11% of the standing carbon stock in the conterminous U.S. in 1700. Most of these carbon losses occurred as a consequence of forests and grasslands being converted to croplands and rangelands/pastures (Table 5). Wetland disturbances, including drainage to establish croplands, also contributed to the loss of carbon from the U.S. over this time period. About 37% of the historical carbon loss from croplands, rangelands/pastures, and wetlands has been compensated by carbon gains in forests. Another 2% of this carbon loss has been compensated by the combined gain of carbon in shrublands, grasslands, and urban areas.

Table 4. Characteristics (Location, Land Cover Type, Measurement Period, NEP Observed by Eddy Covariance Measurements, and TEM NEP Estimates) of Selected Eddy Covariance Flux Sites

Site	Location		Land Cover type ^a	Period	Average Observation, NEP (g C m ⁻² yr ⁻¹) ^b	Average TEM NEP (g C m ⁻² yr ⁻¹) ^b	Reference
	Latitude	Longitude					
Audubon Ranch, AZ	31.5907	−110.5092	GRA	2000–2006	67.3 ± 40.1	26.8 ± 70.8	Xiao et al. [2010]
Blodgett Forest, CA	38.8952	−120.6327	ENF	1999–2002	117.6 ± 83.0	136.8 ± 225.1	Misson et al. [2005]
Duke Forest, NC	35.9782	−79.0942	ENF	1998–2004	463.0 ± 166.1	508.4 ± 223.7	Oren et al. [2006]
Harvard Forest, MA	42.5378	−72.1715	DBF	1992–2000	200.0 ± 40.0	130.0 ± 140.0	Lu et al. [2013]
Metolius, OR	44.5794	−121.5000	ENF	2001	118.0	189.7	Law et al. [2003]
Loblolly Pine, NC	35.8031	−76.6679	ENF	2005–2007	640.0 ± 247.9	787.3 ± 43.8	Noormets et al. [2010]
Mize, FL	29.7648	−82.2448	ENF	2001–2004	227.4 ± 421.1	139.9 ± 337.5	Bracho et al. [2012]
WrcWind River, WA	45.8205	−121.9519	ENF	1998–2008	49.0 ± 40.0	26.1 ± 82.9	Wharton et al. [2012]

^aENF: evergreen needle forest, DBF: deciduous broadleaf forest, and GRA: grassland.

^bMean ± standard deviation of the interannual variation during the measurement periods.

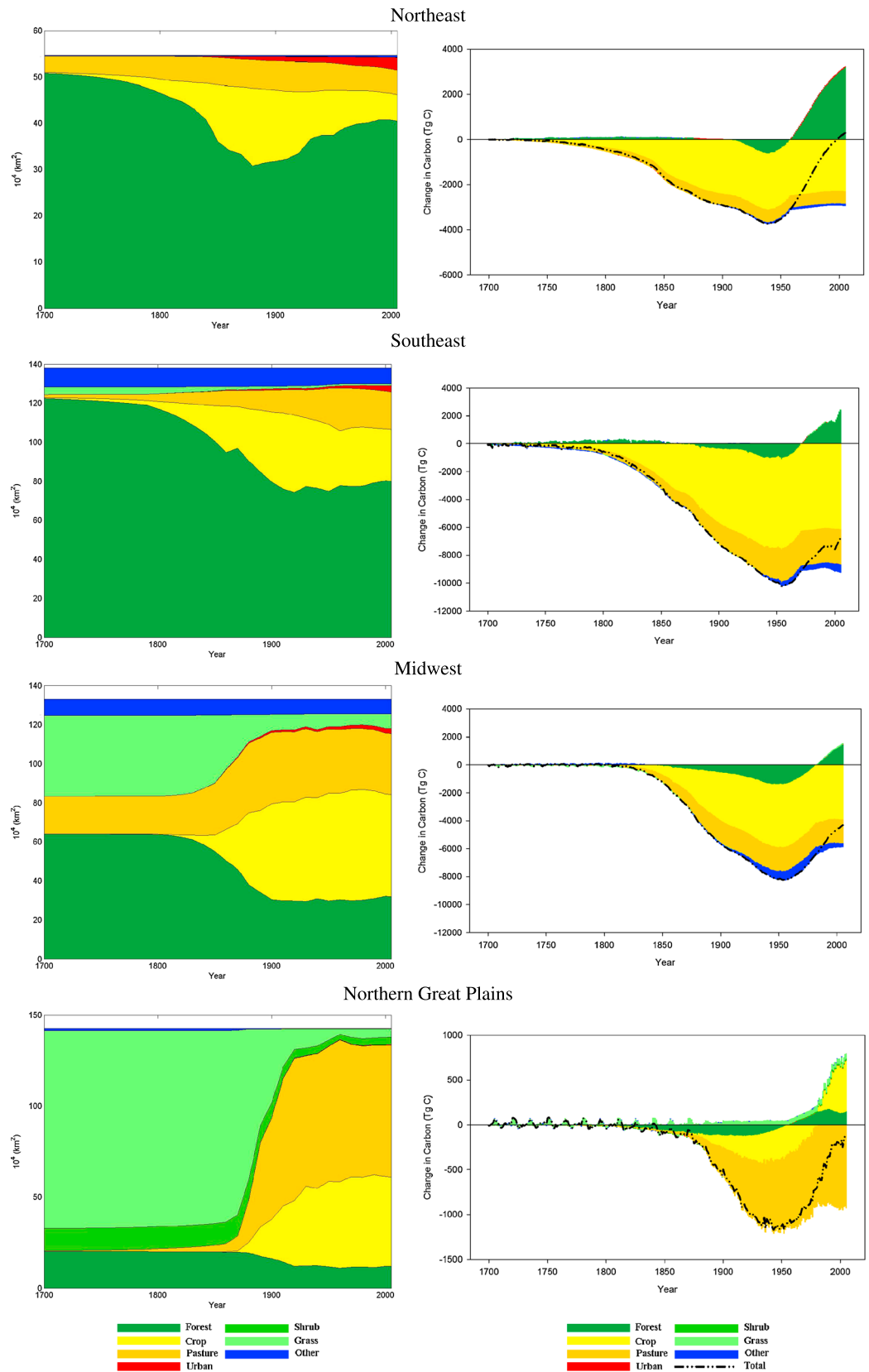


Figure 3. Regional changes in historical (1700 to 2005) (left) land cover and (right) associated carbon storage. The black dash lines at the right represent net change in carbon storage since 1700.

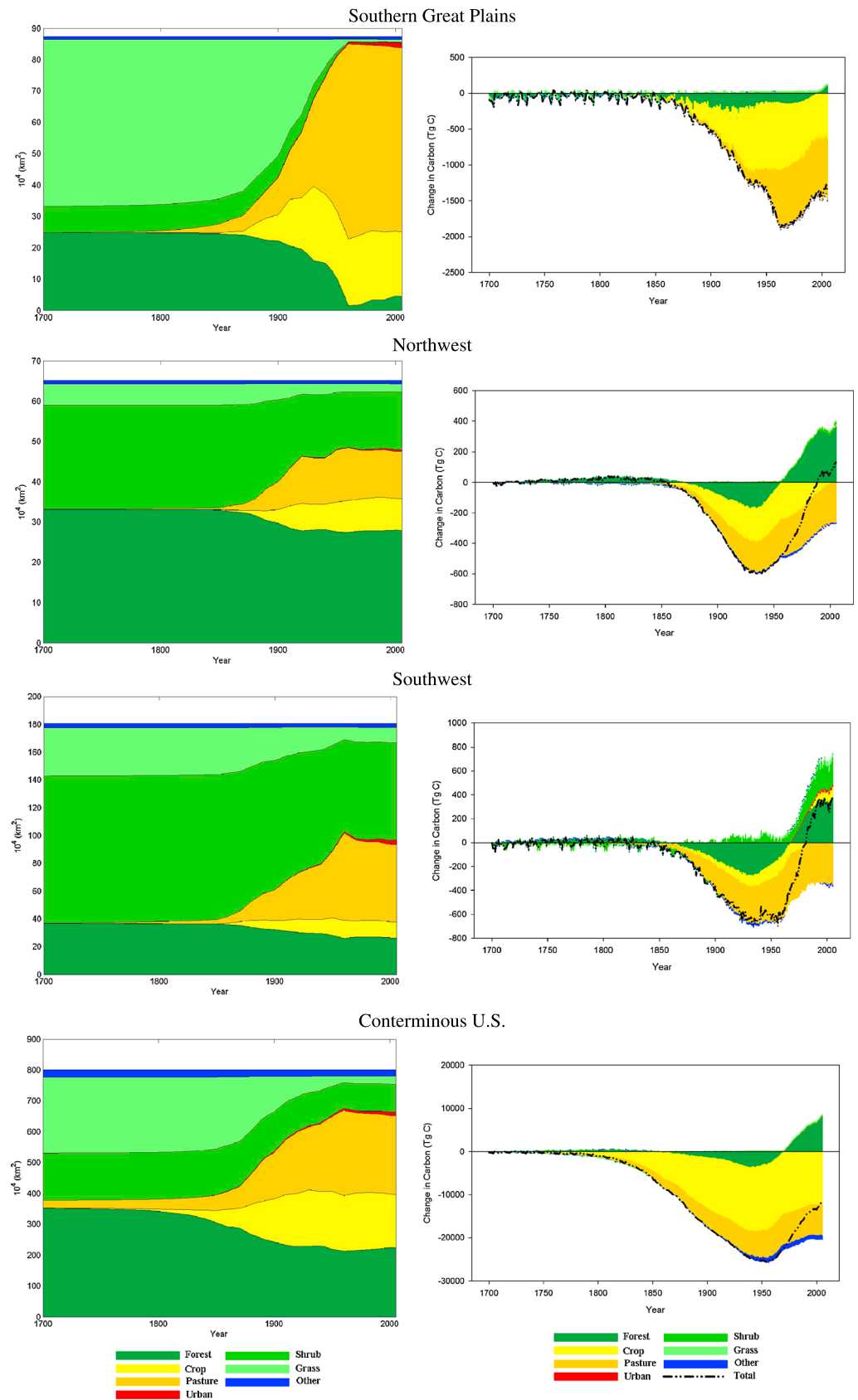


Figure 3. (continued)

Table 5. Regional Changes in Carbon Storage (Tg C) for Land Covers of the Conterminous U.S. Over the Period of 1700 to 2000^a

Region	Croplands	Rangelands/Pastures	Urban	Forests	Shrublands	Grasslands	Other ^b	Total
Southwest	75	-355	21	349	197	32	-8	310
Northeast	-2,301	-538	16	2,997	0	0	-80	93
Northwest	-5	-265	-1	315	19	1	-4	60
Northern Great Plains	505	-944	2	135	18	52	0	-232
Southern Great Plains	-649	-848	3	31	11	20	-3	-1,434
Midwest	-3,902	-1,697	5	1,204	0	42	-298	-4,645
Southeast	-6,134	-2,476	-5	1,571	0	5	-534	-7,573
Total	-12,411	-7,123	41	6,602	245	152	-927	-13,421

^aThe table is sorted by the total changes in carbon storage.

^bIncludes wetlands, mangrove, and bare lands.

The influence of land use legacies on historical terrestrial carbon dynamics varies across the United States. In the Southwest, Northeast and Northwest, ecosystems have actually gained a small amount of carbon when carbon stocks in 2000 are compared to those in 1700 (Table 5). In contrast, the Southeast, Midwest, and Southern Great Plains have had large carbon losses over this same period. These losses have been large enough to more than counterbalance the gains in the other regions of the conterminous U.S., which explains the net carbon loss at the national level. Although the largest carbon gains in forests occur in the Northeast, Southeast, and Midwest, concurrent large carbon losses in cropland and rangelands/pasture have overwhelmed the forest carbon gains in the Southeast and Midwest (Table 5).

At the state level, 14 states have gained carbon and 34 states have lost carbon over the historical period (Table S5 in the supporting information). Forests account for most of the carbon gains in 10 states, and forest carbon gains compensated for up to 99% of the carbon losses in all the states that have lost carbon. The largest carbon gains have occurred in California and North Dakota, whereas the largest carbon losses have occurred in Missouri and Arkansas. Most of the carbon gains in California and Missouri occur in forests, but carbon losses from croplands and rangelands/pastures have overwhelmed the forest carbon gains in Missouri. In North Dakota, croplands account for most of the historical carbon gain. In Arkansas, forests have contributed to the loss of carbon by the state's ecosystems over the historical period.

3.4. Effect of Land Cover and Land Use Change on Net Carbon Exchange

Our NCE estimates depend on the ability of land ecosystems to take up atmospheric carbon dioxide as represented by net ecosystem production (NEP) and the loss of land carbon back to the atmosphere from human activities as represented by livestock respiration (E_L); conversion losses (E_C); and the decomposition of agricultural products, 10 year woody products, and 100 year woody products (summed as E_p). At the national scale, NCE is only 36% of NEP, which is $887 \pm 196 \text{ Tg C yr}^{-1}$, during the period of 2001 to 2005 (Table 2). The rest of the NEP carbon gains are compensated by livestock respiration (26%), consumption/decomposition of agricultural products (26%), conversion losses (3%), decomposition of 10 year woody products (6%), and decomposition of 100 year woody products (3%). Thus, the relationship between NEP and land carbon sinks varies among land uses and land covers. Although rangelands/pastures and croplands account for 26 and 27% of the national NEP, most of this carbon is lost by livestock respiration, consumption/decomposition of agricultural products, and conversion losses, so very little carbon is sequestered in these ecosystems (Table 2). In contrast, conversion losses and decomposition of 10 year and 100 year woody products compensate relatively little of the forest NEP, so that most of this carbon (80%) is sequestered in forest ecosystems. As a result of these ecosystem differences, the relationship between NEP and NCE varies among regions (Table 6) and states (Table S6 in the supporting information) with relatively less NEP being compensated by carbon losses from human activities (i.e., larger land carbon sinks) in regions and states covered by large areas of forests and relatively more NEP being compensated by carbon losses from human activities (i.e., smaller land carbon sinks) in regions and states covered by large areas of rangelands/pastures and croplands.

3.5. Carbon Balance Index

From 2001 to 2005, the net annual flux from fossil fuel emissions is $1585 \pm 26 \text{ Tg C yr}^{-1}$ [EIA, 2013]. As land ecosystems of the conterminous U.S. sequestered $323 \pm 191 \text{ Tg C yr}^{-1}$ from the atmosphere during this

Table 6. Source of Carbon Fluxes (Mean ± Standard Deviation of 5 Year Period, Tg C yr⁻¹) From Disturbances Among the Regions in the United States Over the Period of 2001 to 2005^a

Region	Net Ecosystem Production	Resource Management and Consumption					NCE
		Livestock Respiration	Conversion Flux	Consumption of Agricultural Products	Decomposition of 10 Year Woody Products	Decomposition of 100 Year Woody Products	
Southeast	277 ± 39	-10 ± 0	-19 ± 6	-42 ± 4	-38 ± 8	-12 ± 0	156 ± 33
Midwest	152 ± 36	-12 ± 0	-3 ± 1	-62 ± 3	-5 ± 1	-4 ± 0	66 ± 35
Northeast	56 ± 12	-1 ± 0	-4 ± 0	-6 ± 1	-3 ± 1	-3 ± 1	39 ± 11
Northern Great Plains	153 ± 68	-79 ± 5	-1 ± 0	-51 ± 8	-1 ± 0	-1 ± 0	20 ± 65
Southwest	80 ± 60	-48 ± 6	-1 ± 1	-12 ± 1	-3 ± 1	-1 ± 0	15 ± 56
Northwest	33 ± 13	-7 ± 0	-1 ± 1	-7 ± 1	-3 ± 1	-1 ± 0	14 ± 12
Southern Great Plains	136 ± 67	-73 ± 5	-1 ± 0	-47 ± 6	-1 ± 0	-1 ± 0	13 ± 65
Total	887 ± 196	-230 ± 11	-30 ± 8	-227 ± 16	-54 ± 11	-23 ± 0	323 ± 190

^aPositive values represent carbon gains by land ecosystems and negative values represent carbon losses.

period, we estimate a national mean CBI equal to 20, which indicates that the national land carbon sinks can only compensate for 20% of the nation's fossil fuel emissions.

Although all regions and most states are net carbon sources (CBI < 100), the importance of these land carbon sinks on net carbon balance varies among the regions and states (Figure 4). Land carbon sinks are least important, in a relative sense, in the Southern Great Plains (CBI=6) and the Southwest (CBI=7), where the vegetation is dominated by low-stature plants such as crops, rangelands/pasture grasses, and shrubs with low carbon sequestration potential. These sinks are relatively more effective in the Northwest (CBI=40) and the Southeast (CBI=38), where forests are more prevalent. In the Northwest, the land carbon sinks are relatively small (14 ± 12 Tg C yr⁻¹), but the fossil fuel emissions in this region are also relatively small (36 ± 1 Tg C yr⁻¹) because hydroelectric dams are used to generate most of the electricity in the region [EIA, 2012] and the land carbon sinks compensate 40% of the fossil fuel emissions mostly from transportation. In contrast, the large land

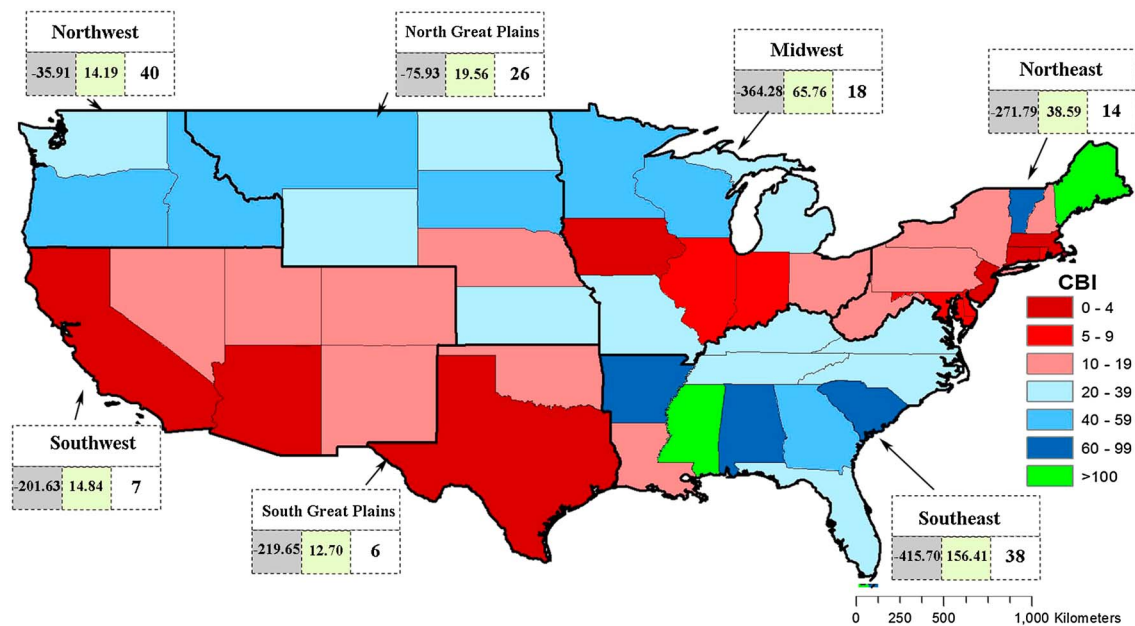


Figure 4. Regional and state carbon balance index (CBI) in the conterminous U.S. during 2001–2005. The lowest offset percentages are in the states colored reddish brown. The states colored green indicate that they are net carbon sinks, with land carbon sequestration more than offsetting fossil fuel carbon emissions. The states colored in various shades of blue and green are at or above the national mean CBI, which is 20. The regional summaries represent averaged rates of fossil fuel emissions (Tg C yr⁻¹, values are highlighted in grey), TEM-estimated net carbon exchange between land ecosystems and the atmosphere (Tg C yr⁻¹, values are highlighted in green), and the CBIs over 5 years (2001–2005). The negative values in the regional summaries indicate sources of carbon to the atmosphere, while the positive values indicate land carbon sinks.

carbon sinks in the Southeast ($156 \pm 33 \text{ Tg C yr}^{-1}$) compensate for 38% of the large fossil fuel emissions in this region ($416 \pm 11 \text{ Tg C yr}^{-1}$), mostly from transportation and the burning of coal to generate electricity.

Within a region, there can be large differences in CBI among states (Table S7 in the supporting information), particularly in the eastern part of the United States: CBI ranges from 2 in Massachusetts and New Jersey to 134 in Maine in the Northeast, CBI ranges from 19 in Louisiana to 123 in Mississippi in the Southeast, and CBI ranges from 0 in Iowa to 49 in Minnesota in the Midwest. Thus, no fossil fuel emissions in Iowa are compensated by land sinks. In contrast, the land sinks in Maine (CBI = 134) and Mississippi (CBI = 123) are more than able to compensate for the states' fossil fuel emissions, so that these states act as net carbon sinks.

3.6. Effect of Stand Age Corrections on Net Carbon Exchange Estimates

The use of the corrected LULCC data set has had a large influence on our NCE estimates across the conterminous United States as compared to the uncorrected LULCC data set. Overall, we estimate that the amount of carbon stored by terrestrial ecosystems during 2001 to 2005 is $173 \pm 211 \text{ Tg C yr}^{-1}$ from the atmosphere using the uncorrected LULCC data set, which is only about 53% of the national land carbon sink estimated with our FIA-corrected LULCC data set. The national forest carbon sink ($153 \pm 67 \text{ Tg C yr}^{-1}$) using the uncorrected LULCC data is 49% of the sink estimated with the FIA-corrected data set. The smaller national forest carbon sink (i.e., NCE) when using the uncorrected data set relative to the corrected data set is caused by a 59% decrease in NEP. The effect of this reduced NEP on the national forest carbon sink, however, is partially compensated by concurrent decreases in the carbon emissions associated with land conversion and the decay of woody products (Table S8 in the supporting information). With the uncorrected LULCC data set, the forest carbon sink is more equally distributed among the regions with the Southeast accounting for 46% of the national forest carbon sink and the Northwest and the Northern Great Plains, each accounting for about 3% of the national forest carbon sink (Table S9 in the supporting information).

The reductions in NCE are generally related to the difference in stand age between the two LULCC data sets, with older forests prescribed by the uncorrected data set for most regions (Table 3) and states (Table S4 in the supporting information) of the conterminous United States. In the Northern Great Plains and the Southwest, however, this general relationship between stand age and NCE does not hold for some states. In Colorado, a reduction in mean stand age by 5 years using the corrected LULCC data set causes a 43% decrease in the NCE estimate. In contrast, a reduction in mean stand age of 3 to 7 years in Idaho and California, respectively, associated with using the corrected LULCC data set causes almost no change in NCE estimates. In other states in these western regions, the FIA correction causes mean stand age to increase: Wyoming (79 to 84 years old), Montana (70 to 76 years old), New Mexico (37 to 98 years old), Utah (75 to 79 years old), Arizona (35 to 104 years old), Nevada (26 to 77 years old), and South Dakota (77 to 86 years old). These increases in stand ages cause NCE estimates to decrease in Montana, Utah, and Arizona but to increase in Wyoming, New Mexico, and South Dakota. The change in mean stand age has no effect on the NCE estimates in Nevada.

4. Discussion

Our analyses indicate that land carbon sinks and the spatial variations of those sinks are influenced by a combination of vegetation type, climate, and current as well as past land management practices. Forests generally act as larger sinks than other land cover types. The largest forest sinks currently occur in the Southeast.

Although many natural abiotic and biotic factors, such as wildfire and insect damage, can reduce forest carbon sinks, a large forest area in a region normally leads to a strong regional carbon sink. The Northeast and Southeast together contain more than 54% of all forests in the conterminous U.S., with a combined forest area of $1,200,000 \text{ km}^2$. The forests of these two regions account for 68% of the total land carbon sink (Table 2).

Variations in local environmental conditions (climate, soil fertility, and air quality; see Figure S4 in the supporting information) also influence forest carbon sinks. Generally, forests sequester more carbon with increases in precipitation (Figure 5). If sufficient moisture is available, forests also sequester more carbon with increases in mean annual air temperature up to about 20°C (Figure 5). Less carbon sequestration may occur with warmer temperatures because (1) increases in air temperature have larger effects on the release of carbon from autotrophic and heterotrophic respiration than on the uptake of carbon by photosynthesis [Sokolov *et al.*, 2008]

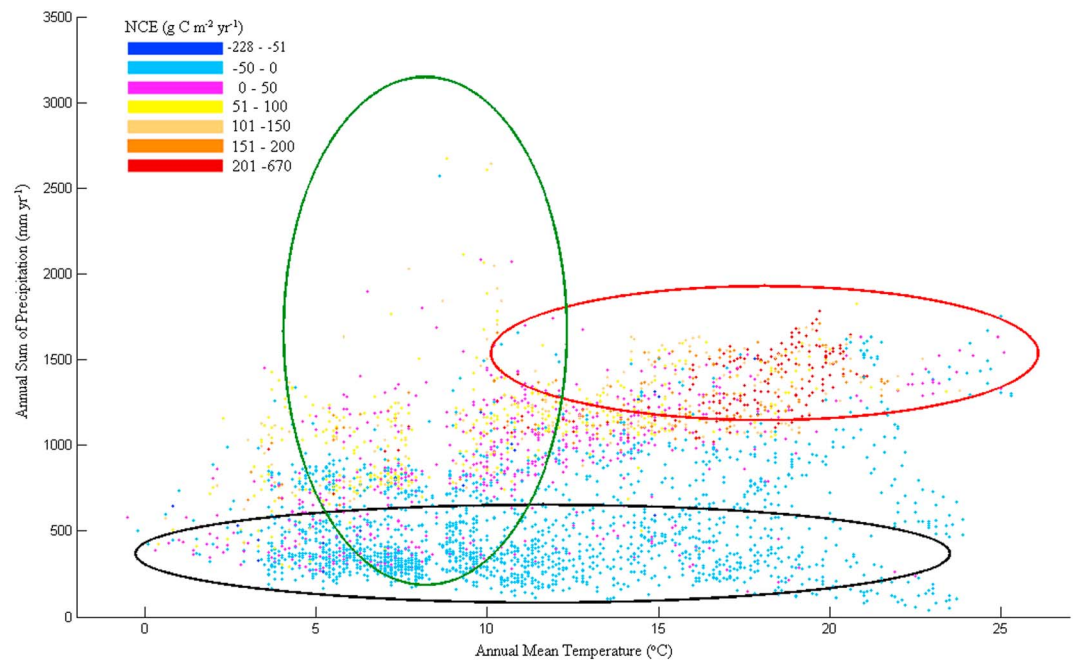


Figure 5. Annual mean forest net carbon exchange (NCE) in relation to air temperature and precipitation. Each data point represents the mean annual forest NCE for each half grid cell during 2001–2005. The red, green, and black circles stand for the major data points for the Southeast, Northwest, and Southwest regions, respectively.

and (2) increases in evapotranspiration associated with warmer temperatures may cause moisture to become less available for a given amount of precipitation, which then limits carbon uptake [Felzer *et al.*, 2011].

Our analysis shows that the relative importance of air temperature and precipitation for NCE varies among the regions. In the Southeast, NCE is more sensitive to variations in air temperature than precipitation (Figure 5). In contrast, NCE is more sensitive to variations in precipitation than air temperature in the Northwest. In the Southwest, which experiences relatively little precipitation throughout the region, the highest rates of NCE occur at lower air temperatures, when evapotranspiration and respiration rates are also low. In addition to climate, Felzer *et al.* [2004] have shown that ozone pollution decreases carbon sequestration. Felzer *et al.* [2004] and Zhang *et al.* [2012] have shown that enhancing soil fertility with additions of nitrogen either through fertilizer applications or through deposition in precipitation increases carbon sequestration in the conterminous United States.

4.1. Land Use Legacy Effects

Variations in disturbance history across the conterminous United States have led to variations in historical land carbon dynamics (Figure 3) and the forest stand ages observed today (Figure S1 in the supporting information). These land use legacies on the carbon cycle are influenced both directly by land use change decisions made in the past and indirectly by historical changes in other environmental factors interacting with historical land use change effects.

In the conterminous United States as a whole, land use change led to a loss of carbon before the early 1900s, as the nation converted natural vegetation, especially forests, to croplands and rangelands/pastures to support a growing human population. Then, land ecosystems began to sequester carbon [Houghton *et al.*, 2000a; Drummond and Loveland, 2010]. In addition, widespread applications of inorganic nitrogen fertilizers to crops began in the 1950s to enhance production. The higher productivity of fertilized croplands required less land to support continued growth of the U.S. population, so the conversion of forests to croplands slowed [Brown *et al.*, 2005]. The reduced pressure on forest resources allowed forest stands to grow older (Figure 2) and store more carbon. Fire suppression, especially in the western U.S., also reduced carbon losses and allowed forests to grow older and store more carbon [Houghton *et al.*, 1999]. In the Southwest, Northeast, and Northwest, the amount of carbon sequestered by forests toward the end of the study period was more

than enough to compensate for the earlier losses of carbon despite the fact that each region had a smaller forest area in 2005 than in 1700 (Figure 3). In other regions, the carbon sequestration in forests in the 20th century was not able to overcome earlier carbon losses.

Beyond the pan-regional temporal patterns described above, the magnitude and timing of land use change disturbances and their effects on carbon dynamics varied across the conterminous United States. With a large influx of immigrants, large areas of forests in the Northeast, Southeast, and Midwest were converted to croplands and rangelands/pastures during the 1700s and 1800s, leading to large losses of carbon during this time period (Figure 3). Beginning in the last half of the 1800s, large areas of cropland in the Northeast were abandoned [Compton and Boone, 2000] as farmers moved to better soils in other regions and forests became reestablished within the Northeast. Thus, a portion of the contemporary land carbon sink in the Northeast is related to recovery from past abandonment of croplands and pastures. In contrast, relatively little agricultural area has been abandoned to forests in the Southwest and Northwest (Figure 3). These secondary forests have older stand ages in 2005 than in 1700 (Figure 2), indicating that reduced disturbances, perhaps from fire suppression, in these regions have allowed these forests to store more carbon today than in the past. Although forests in the Northeast are also estimated to store more carbon in 2005 than in 1700, the contemporary secondary forests are younger than those estimated for 1700. The larger carbon density of these younger contemporary forests indicates that environmental conditions such as increased atmospheric carbon dioxide [Kicklighter *et al.*, 1999; Schimel *et al.*, 2000], atmospheric nitrogen deposition [McMahon *et al.*, 2010; Thomas *et al.*, 2010; Fleischer *et al.*, 2013], and climate [Sokolov *et al.*, 2008] are now more favorable for sequestering carbon in this region than in the past.

Although the largest contemporary carbon sink occurs in the Southeast (Table 1), it is also the location of the largest historical carbon deficit in the conterminous United States (Table 5). The historical reduction of standing stocks of carbon can enhance contemporary land carbon sinks by reducing the loss of carbon back to the atmosphere from plant respiration and decomposition of organic matter relative to the uptake of atmospheric carbon dioxide by regrowing vegetation. As observed in the Northeast, forest regrowth can increase carbon stocks in the region, but the increased carbon stocks would also enhance respiration losses to eventually reduce carbon sequestration. Our land use history data set indicates that unlike most other regions of the country, Southeast forests have been repeatedly disturbed to maintain a mean stand age between 33 and 37 years old since 1950. Pan *et al.* [2011] estimate that 60% of the forested area in the south is dominated by managed forests between 20 and 60 years old. Thus, most forest ecosystems across the Southeast are in various stages of recovery from current timber harvest activities, extensive timber harvest in the highlands during the early 20th century or the abandonment of croplands. The constant disturbance in managed forests tends to slow the buildup of carbon within forest ecosystems of the Southeast because carbon is constantly being removed from the ecosystem and stored in woody products. However, more favorable environmental conditions (e.g., enhanced atmospheric carbon dioxide concentrations, enhanced atmospheric nitrogen deposition, and climate) and enhanced management intensity may partially counterbalance these constant disturbance effects to enhance land carbon sinks. Therefore, it is just as important to consider the fate of carbon stored in wood products, including their half life, as it is to consider the fate of carbon stored in vegetation and soils when evaluating land carbon sinks.

Our NCE estimates do indeed attempt to account for the consumption and decomposition of wood products on these land carbon sources and sinks (Tables 2 and 6). However, we have assumed that the fractions of the harvested tree biomass that is lost to the atmosphere from conversion or fuelwood use (40%), added to soil organic matter as slash (33%), or transferred to 10 year and 100 year product pools (20% and 7%, respectively) are the same for all regions of the conterminous United States in our study. As these fractions may vary among regions, our regional-level and state-level estimates of carbon sequestration may be improved by considering these regional differences in future studies. Overall, carbon sequestration would increase if a smaller fraction of harvested tree biomass is lost during conversion or fuelwood use and a larger fraction of harvested tree biomass is allocated instead to woody product pools, particularly the 100 year woody product pool. At the national scale, the improvements in NCE estimates with these modifications may be somewhat limited as conversion losses are estimated to be 9% and the fluxes from the decomposition of the 10 year and 100 year woody product pools are estimated to be 17% and 7%, respectively, of the NCE estimate for the conterminous United States. However, these improvements in NCE estimates may be more important at the state level as the sum of these forest carbon losses is either greater than or equal to the corresponding NCE estimates for Maryland, Massachusetts, Colorado, and Iowa (Table S10 in the supporting information).

The lateral movement of woody and agricultural products can also influence regional- and state-level land carbon sinks. In our study, we assumed that agricultural and woody products are consumed or decomposed in the same grid cell where they were created. In reality, however, these products will be shipped to other parts of the country or even exported overseas. In relation to our NCE estimates, this lateral movement will enhance the land carbon sink in the region or state where the product was created and diminish the sink in the region or state where it was shipped before being consumed or decomposed [Kicklighter *et al.*, 2012]. The consequences of this lateral movement of agricultural and woody products on regional and state carbon budgets still need to be explored.

4.2. Comparison to Other Studies

Our estimate of the land carbon sink in the conterminous United States ($323 \pm 191 \text{ Tg C yr}^{-1}$) is in the middle of estimates reported in previous studies (Table S1 in the supporting information). These previous estimates vary in the time periods they represent and have been determined using a variety of approaches including inventories, atmospheric inversion models, and terrestrial biosphere models. Inventory-based approaches determine land carbon sink estimates from changes in land carbon stocks. Atmospheric inversion models estimate land carbon sinks by difference based on changes in atmospheric carbon dioxide concentrations and assumptions about the uptake of atmospheric carbon dioxide by oceans. Terrestrial biosphere models estimate land carbon sinks based on carbon fluxes from various ecosystem processes occurring on the land surface. Each approach has its strengths and weaknesses which have been discussed elsewhere [Hayes *et al.*, 2012; Williams *et al.*, 2012; Zhang *et al.*, 2012].

Our estimate of contemporary carbon sequestration in national forests ($313 \pm 40 \text{ Tg C yr}^{-1}$) is higher than comparable estimates from two recent studies that also incorporated the FIA stand age information [Williams *et al.*, 2012; Zhang *et al.*, 2012]. Although all of these studies use stand age information to track disturbance histories within forests, the estimates of land carbon sinks may vary as a result of differences in time periods considered; approaches used to account for age effects on the uptake of atmospheric carbon dioxide by vegetation; and assumptions about the importance of atmospheric chemistry, wildfires, and land use legacies on terrestrial carbon dynamics. First, while our study reported contemporary land carbon sinks based on NCE estimates between 2001 and 2005, Williams *et al.*'s [2012] study has estimated a national land carbon sink of 47 Tg C yr^{-1} for a single year 2005, and Zhang *et al.* [2012] estimated a mean national land carbon sink of 206 Tg C yr^{-1} for the time period from 1950 to 2010. When the same time period is used for model comparisons, our NCE estimate of 266 Tg C yr^{-1} for 2005 is still much higher than the estimate by Williams *et al.* [2012], but our mean NCE estimate of 201 Tg C yr^{-1} for the period of 1950 to 2005 is very close to the estimate by Zhang *et al.* [2012].

The three models use different approaches to estimate age effects on the uptake of atmospheric carbon dioxide by vegetation. Both Williams *et al.* [2012] and Zhang *et al.* [2012] use a relationship between stand age and NPP to simulate the effects of vegetation structure on net carbon uptake by vegetation, but the two studies use different algorithms to describe this relationship. In contrast, TEM uses a relationship between gross primary production (GPP) associated with photosynthesis and the standing stock of vegetation carbon to simulate the effects of vegetation structure on net carbon uptake by vegetation [Tian *et al.*, 2003]. While vegetation carbon stocks increase as a forest stand ages during regrowth, the changes in vegetation carbon stocks also depend on local environmental conditions and are not explicitly a function of stand age. Thus, a forest growing under more favorable climate and atmospheric chemistry conditions will take up more atmospheric CO_2 at a particular stand age than a forest growing under less favorable conditions. Williams *et al.* [2012] use an age-accumulation approach, which does not capture growth enhancements due to changes in climate, atmosphere CO_2 , or atmospheric nitrogen deposition and lead to lower estimates of land carbon sinks as discussed by Zhang *et al.* [2012]. Both TEM and Zhang *et al.* [2012] are able to capture growth enhancements due to changes in climate, atmosphere CO_2 , and atmospheric nitrogen deposition. The TEM also considers the effects of ozone pollution on net carbon uptake, which reduces the net carbon uptake of atmospheric carbon dioxide by vegetation [Felzer *et al.*, 2004]. Nonetheless, these differences are unlikely to account for the majority of the much lower estimate of Williams *et al.* [2012] for 2005, and further investigation of differences in methods is warranted.

Our study does not explicitly consider the influence of wildfires on land carbon sinks, whereas this influence is considered by both Williams *et al.* [2012] and Zhang *et al.* [2012]. Wildfires have two disturbance effects on

land carbon dynamics. First, wildfires cause a rapid release of carbon from the disturbance itself to diminish land carbon sinks in the year the fire occurred. *Williams et al.* [2012] and *Zhang et al.* [2012] have estimated these fire emissions from the conterminous United States to be 10 to 36 Tg C yr⁻¹, respectively. Second, the recovery of an ecosystem from a wildfire may enhance land carbon sinks over a longer time period as vegetation regrows on the disturbed site. While the stand age data set of *Pan et al.* [2011] may not identify a stand-replacing disturbance as a wildfire, the stand age information reflects the time and location that a disturbance did indeed occur. The difference in the historical mean stand ages between the corrected and uncorrected LULCC data sets for the Northern Great Plains, the Northwest, and the Southwest as compared to the trends in other regions of the country (Figure 2) suggests that the corrected LULCC data are capturing the effect of wildfires on stand age. In our study, we treated such disturbances as if they were timber harvests rather than wildfires, but we would have removed vegetation biomass at the time and location of the wildfires and would have simulated the enhanced land carbon sink associated with the recovery of the ecosystem from the (wildfire) disturbances. With our approach, we would also have accounted for the carbon emissions to the atmosphere associated with the wildfires, but some of the carbon associated with fire emissions would have been redirected to the 10 year and 100 year product pools to be released to the atmosphere over a longer time period with our timber harvest assumptions.

The three studies also differed in how land use legacies are treated in the respective model simulations. In both *Williams et al.* [2012] and *Zhang et al.* [2012], the area of forests did not change throughout the study period, and only forest disturbances related to wildfire and timber harvest (also insect attack in *Zhang et al.* [2012]) were considered. Thus, these two studies would not have captured the historical carbon dynamics associated with forests transitioning back and forth to agricultural activities or urban areas. For example, a cohort that had been covered by unfertilized cropland for a long period of time before being abandoned to forests would have lost a lot of soil organic matter (see Figure 3) and would have a reduced rate of heterotrophic respiration (R_H) compared to a forest cohort that was always covered by forest. The reduced R_H would allow forest NEP from abandoned croplands to be higher than the NEP of a disturbed forest unless a fire had consumed some of the soil organic matter.

4.3. Carbon Balance Index

The CBI analyses indicate that the relative effectiveness of regional land carbon sinks for mitigating climate change is dependent upon the magnitude of the corresponding fossil fuel emissions in a region. Large land carbon sinks are needed to compensate for large emissions of fossil fuels so that it is desirable to enhance land carbon sinks. Unfortunately, the land carbon sinks in many parts of the country (e.g., the Southwest and Southern Great Plains) are so small that other policies need to be developed for these regions to mitigate climate change. One approach might be the production and use of biomass for heating, electricity, and biofuels for transportation instead of fossil fuels.

State-level CBIs vary as a result of population densities, area of forest cover, forest productivity, and use of fossil fuels for transportation, industry, and electric power generation. Low CBIs usually occur in urban states with large populations, but forest cover may be very different among these states. For example, Massachusetts (CBI = 2) and Texas (CBI = 4) have 83% and 6% forest cover, respectively. We also found that the state-level CBIs are related to the interstate flow of energy such as electricity. Florida, Georgia, and Virginia have large populations but still have CBIs larger than the national average. One reason for the larger CBIs is that they avoid much fossil fuel consumption by importing electricity from other states [EIA, 2013]. In comparison, West Virginia which has a population of less than 2 million has low CBI because half of the electricity generated in the state is delivered to the grid that distributes energy to the urban/suburban coastal corridor from Boston to Washington, D. C. [EIA, 2013]. Climate is another factor affecting CBIs. For example, a drought in the Midwest during 2002 caused land ecosystems to lose carbon and lead to lower CBIs such that Iowa had a CBI equal to zero during our study period.

Our analyses have also identified a few issues that influence CBI and should be addressed in future studies. First, we have not explicitly included the effects of wildfire on land carbon sinks in our study. Wildfires will diminish land carbon sinks to lower CBI when they occur, but the recovery of ecosystems following wildfires may enhance land carbon sinks to increase CBI for some time postdisturbance. Wildfires are more likely to be an issue for the drier western states than the relatively wet eastern states. Second, the lateral movement of agricultural and woody products may also influence state CBIs. The export of food products from states like

Kansas, Iowa, Nebraska, and South Dakota will enhance the land carbon sink in these states from the perspective of the atmosphere to increase the CBIs, whereas the import and use of food products in states along the urban/suburban corridor from Boston to Washington, D. C., will diminish the land carbon sink and lower the CBIs for the associated states. Similarly, the export of wood products from Georgia, Alabama, Mississippi, and Louisiana will enhance the land carbon sink in these states from the perspective of the atmosphere to increase the CBIs, whereas the import and use of wood products in other states will diminish the land carbon sink and lower the CBIs in these states. Finally, our analysis indicates that NCE decrease as forests age. Therefore, we expect that CBIs of forested states will decrease in the future if the forests are not disturbed and fossil fuel emissions remain constant.

4.4. Implications for Global Land Carbon Sink Estimates

In addition to informing regional and local policy makers, our results also have implications for global land carbon sink estimates. Our NCE estimate based on the corrected LULCC data set indicates that the conterminous U.S. accounts for 17% of the current global terrestrial carbon sink estimated with a mass balance approach [Le Quéré *et al.*, 2014]. In this study, the improvement in the representation of forest age structure in the conterminous United States using the FIA stand age data has resulted in model estimates of land carbon sinks that are twice those derived from an uncorrected LULCC data set based on Hurtt *et al.*'s [2011] land use transition data. The increase in land carbon sinks are related to additional disturbances prescribed in the corrected LULCC data set which causes younger forests to be represented in model simulations of the conterminous United States. Some of these additional disturbances are related to natural disturbances, such as stand-replacing wildfires [Williams *et al.*, 2012; Zhang *et al.*, 2012], but other disturbances may be related to land use change not captured by Hurtt *et al.*'s [2011] data. Although natural disturbances have never been meant to be a part of Hurtt *et al.*'s [2011] land use transition data, our study indicates that the inclusion of these additional disturbances can have a large influence on model estimates of land carbon sinks. As Hurtt *et al.*'s [2011] land use transition data are now being used to represent land use change in Earth system models [e.g., Eby *et al.*, 2013; Kumar *et al.*, 2013], model estimates based on these data may be underestimating land carbon sinks associated with disturbances across the globe. If stand age information is available in other parts of the globe, it should be incorporated into analyses to improve our understanding of the role of terrestrial ecosystems on global carbon dynamics.

5. Conclusion

Land carbon sinks vary substantially across the conterminous United States. Forests generally account for most of the land carbon sink at national-, regional-, and state-level scales. The largest carbon sinks currently occur in the large area of forests in the Southeast as a result of favorable environmental conditions supporting the regrowth of forests from ongoing intensive timber management and the past abandonment of croplands and rangelands/pastures. Although land carbon sinks are large enough to completely compensate fossil fuel emissions in Maine and Mississippi, the national land carbon sinks compensate only 20% of the nation's fossil fuel emissions. These land carbon sinks might be enhanced in the future with careful management of forest age structure and the fate of the resulting woody products and/or reforestation of some nonforested areas.

Contemporary land carbon sinks depend on past land use history. By reducing standing carbon stocks, past land use modifies the relationship between the photosynthetic uptake of atmospheric carbon dioxide by regrowing vegetation and the release of carbon dioxide back to the atmosphere from plant respiration and decomposition of detritus and soil organic matter to enhance current land carbon sinks. While land carbon sinks currently occur in all regions and most states of the conterminous United States, less carbon is stored in land ecosystems of most regions today than in 1700. This suggests that U.S. land ecosystems have the capacity to store more carbon in the future. Our analyses also suggest that changes in environmental conditions may also allow U.S. land ecosystems to store even more carbon in the future than that found in 1700. However, this potential enhanced sequestration is dependent upon whether thresholds are reached in the response of land ecosystems to the relative changes in air temperature and precipitation associated with a warming climate and how atmospheric chemistry may be influenced by concurrent policies to reduce air pollution. Moreover, the future land sink may be reduced as forests age or forested area become diminished due to competing demands for land.

For process-based terrestrial biogeochemistry models, a good representation of land use history or its influence on contemporary carbon stocks is crucial for estimating current land carbon sources and sinks and how these sources and sinks may change in the future. In our study, the use of stand age information doubles our estimate of the land carbon sink in the conterminous U.S. This indicates that the use of forest stand age information in other parts of the globe may also improve estimates of land carbon sinks in areas beyond the conterminous United States.

While forest protection is essential to mitigating climate change, it is important to recognize that land resources, including forests, can also provide other ecosystem services. Forests stabilize landscapes, purify air and water, moderate microclimates, and provide fuel, building materials. In addition, forests provide essential habitat for wildlife, and recreational opportunities. Our research provides quantitative estimates of the carbon sequestration service that can inform decisions about integrated land management strategies at national, regional, and state levels. In addition, our modeling framework can be used in the future to explore the potential consequences of different land management opportunities, such as reforestation and managing forest age structure, on carbon sequestration and these other ecosystem services. These opportunities will vary from state to state and over time across the United States.

Acknowledgments

The data presented in this study can be obtained for free by request to D. W. Kicklighter at dkicklighter@mbledu. This work was supported by NSF grants 104918, 1137306, and 1237491; EPA grant XA-83600001-1; and DOE grant DE-FG02-94ER61937.

References

- Bracho, R., G. Starr, H. L. Gholz, T. A. Martin, W. Cropper Jr., and H. W. Loescher (2012), Controls on carbon dynamics by ecosystem structure and climate for southern U.S. pine plantations, *Ecol. Monogr.*, *82*, 101–128, doi:10.1890/11-0587.1.
- Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald (2005), Rural land use trends in the conterminous United States, 1950–2000, *Ecol. Appl.*, *15*, 1851–1863, doi:10.1890/03-5220.
- Caspersen, J. P., S. W. Pacala, J. C. Jenkins, G. C. Hurtt, P. R. Moorcroft, and R. A. Birdsey (2000), Contributions of land use history to carbon accumulation in U.S. forests, *Science*, *290*, 1148–1151, doi:10.1126/science.290.5494.1148.
- Chapin, F. S., III et al. (2006), Reconciling carbon-cycle concepts, terminology, and methods, *Ecosystems*, *9*, 1041–1050, doi:10.1007/s10021-005-0105-7.
- Chen, M., Q. Zhuang, D. R. Cook, R. Coulter, M. Pekour, R. L. Scott, J. W. Munger, and K. Bible (2011), Quantification of terrestrial ecosystem carbon dynamics in the conterminous United States combining a process-based biogeochemical model and MODIS and AmeriFlux data, *Biogeosciences*, *8*, 2665–2688, doi:10.5194/bg-8-2665-2011.
- Compton, J. E., and R. D. Boone (2000), Long-term impacts of agriculture on soil carbon and nitrogen in New England forests, *Ecology*, *81*, 2314–2330.
- Drummond, M. A., and T. R. Loveland (2010), Land-use pressure and a transition to forest-cover loss in the eastern United States, *BioScience*, *60*, 286–298, doi:10.1525/bio.2010.60.4.7.
- Eby, M., et al. (2013), Historical and idealized climate model experiments: An intercomparison of Earth system models of intermediate complexity, *Clim. Past.*, *9*, 1111–1140, doi:10.5194/cp-9-1111-2013.
- Energy Information Administration (EIA) (2012), 1990–2012 net generation by state by type of producer by energy source, Rep. EIA-906, EIA-920, and EIA-923.
- Energy Information Administration (EIA) (2013), State-level energy-related carbon dioxide emissions, 2000–2010.
- Felzer, B. S., D. K. Kicklighter, J. M. Melillo, C. Wang, Q. Zhuang, and R. Prinn (2004), Effects of ozone on net primary production and carbon sequestration in the conterminous United States using a biogeochemistry model, *Tellus Ser. B.*, *56*, 230–248, doi:10.1111/j.1600-0889.2004.00097.x.
- Felzer, B. S., T. W. Cronin, J. M. Melillo, D. W. Kicklighter, C. A. Schlosser, and S. R. S. Dangal (2011), Nitrogen effect on carbon-water coupling in forests, grasslands, and shrublands in the arid western United States, *J. Geophys. Res.*, *116*, G03023, doi:10.1029/2010JG001621.
- Fleischer, K., et al. (2013), The contribution of nitrogen deposition to the photosynthetic capacity of forests, *Global Biogeochem. Cycles*, *27*, 187–199, doi:10.1002/gbc.20026.
- Hayes, D. J., A. D. McGuire, D. W. Kicklighter, K. R. Gurney, T. J. Burnside, and J. M. Melillo (2011), Is the northern high-latitude land-based CO₂ sink weakening?, *Global Biogeochem. Cycles*, *25*, GB3018, doi:10.1029/2010GB003813.
- Hayes, D. J., et al. (2012), Reconciling estimates of the contemporary North American carbon balance among terrestrial biosphere models, atmospheric inversions, and a new approach for estimating net ecosystem exchange from inventory-based data, *Global Change Biol.*, *18*, 1282–1299, doi:10.1111/j.1365-2486.2011.02627.x.
- Houghton, R. A., J. L. Hackler, and K. T. Lawrence (1999), The U.S. carbon budget: Contributions from land use change, *Science*, *285*, 574–578, doi:10.1126/science.285.5427.574.
- Houghton, R. A., J. L. Hackler, and K. T. Lawrence (2000a), Changes in terrestrial carbon storage in the United States: 2. The role of fire and fire management, *Global Ecol. Biogeogr.*, *9*, 145–170, doi:10.1046/j.1365-2699.2000.00164.x.
- Houghton, R. A., D. Skole, C. A. Nobre, J. Hackler, K. Lawrence, and W. Chomentowski (2000b), Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon, *Nature*, *403*, 301–304, doi:10.1038/35002062.
- Houghton, R. A., J. I. House, J. Pongratz, G. R. van der Werf, R. S. De-Fries, M. C. Hansen, C. Le Quéré, and N. Ramankutty (2012), Carbon emissions from land use and land cover change, *Biogeosciences*, *9*, 5125–5142, doi:10.5194/bg-9-5125-2012.
- Hurtt, G. C., et al. (2011), Harmonization of land use scenarios for the period 1500–2100: 600 years of global gridded annual land use transitions, wood harvest, and resulting secondary lands, *Clim. Change*, *109*, 117–161, doi:10.1007/s10584-011-0153-2.
- Intergovernmental Panel on Climate Change (2014), *Climate Change Mitigation of Climate Change: Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by O. R. Edenhofer et al., Cambridge Univ. Press, Cambridge, U. K., and New York.
- Kicklighter, D. W., et al. (1999), A first-order analysis of the potential role of CO₂ fertilization to affect the global carbon budget: A comparison study of four terrestrial biosphere models, *Tellus Ser. B.*, *51*, 343–366, doi:10.1034/j.1600-0889.1999.00017.x.

- Kicklighter, D. W., A. C. Gurgel, J. M. Melillo, J. M. Reilly, and S. Paltsev (2012), Potential direct and indirect effects of global cellulosic biofuel production on greenhouse gas fluxes from future land use change, MIT Joint Program on Science and Policy of Global Change Rep. 210, Mass. Inst. of Technol., Cambridge. [Available at http://globalchange.mit.edu/files/document/MITJPSPGC_Rpt210.pdf.]
- Kicklighter, D. W., D. J. Hayes, J. McClelland, B. J. Peterson, A. D. McGuire, and J. M. Melillo (2013), Insights and issues with simulating terrestrial DOC loading of arctic river networks, *Ecol. Appl.*, *23*, 1317–1336, doi:10.1890/11-1050.1.
- King, A. W., L. Dilling, G. P. Zimmerman, D. M. Fairman, R. A. Houghton, G. H. Marland, A. Z. Rose, and T. J. Wilbanks (2007), The first state of the carbon cycle report (SOCCR): The North American carbon budget and implications for the global carbon cycle, NOAA, Natl. Clim. Data Cent., Asheville, N. C.
- King, A. W., D. J. Hayes, D. N. Huntzinger, T. O. West, and W. F. Post (2012), North American carbon dioxide sources and sinks: Magnitude, attribution, and uncertainty, *Front. Ecol. Environ.*, *10*, 512–519, doi:10.1890/120066.
- Kuemmerle, T., et al. (2011), Post-Soviet farmland abandonment, forest recovery, and carbon sequestration in western Ukraine, *Global Change Biol.*, *17*, 1335–1349, doi:10.1111/j.1365-2486.2010.02333.x.
- Kumar, S., P. A. Dirmeyer, V. Merwade, T. Del Sole, J. M. Adams, and D. Niyogi (2013), Land use/over change impacts in CMIP5 climate simulations: A new methodology and 21st century challenges, *J. Geophys. Res. Atmos.*, *118*, 6337–6353, doi:10.1002/jgrd.50463.
- Law, B. E., O. J. Sun, J. Campbell, S. Van Tuyl, and P. Thornton (2003), Changes in carbon storage and fluxes in a chronosequence of ponderosa pine, *Global Change Biol.*, *9*, 510–524, doi:10.1046/j.1365-2486.2003.00624.x.
- Le Quéré, C., et al. (2014), Global carbon budget, *Earth Syst. Sci. Data.*, *6*, 235–263, doi:10.5194/essdd-6-689-2013.
- Lu, X. L., D. W. Kicklighter, J. M. Melillo, P. Yang, B. Rosenzweig, C. J. Vörösmarty, B. Gross, and R. J. Stewart (2013), A contemporary carbon balance for the northeast region of the United States, *Environ. Sci. Technol.*, *47*, 13,230–13,238, doi:10.1021/es403097z.
- McGuire, A. D., et al. (2010), An analysis of the carbon balance of the Arctic Basin from 1997 to 2006, *Tellus Ser. B.*, *62*, 455–474, doi:10.1111/j.1600-0889.2010.00497.x.
- McMahon, S. M., G. G. Parker, and D. R. Miller (2010), Evidence for a recent increase in forest growth, *Proc. Natl. Acad. Sci. U.S.A.*, *107*, 3611–3615, doi:10.1073/pnas.0912376107.
- Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. L. Vorosmarty, and A. L. Schloss (1993), Global climate change and terrestrial net primary production, *Nature*, *363*, 234–240, doi:10.1038/363234a0.
- Melillo, J. M., T. C. Richmond, and G. W. Yohe (Eds.) (2014), Climate change impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, 841 pp., doi:10.7930/J0Z31WJ2.
- Misson, L., J. Tang, M. Xu, M. McKay, and A. Goldstein (2005), Influences of recovery from clear-cut, climate variability, and thinning on the carbon balance of a young ponderosa pine plantation, *Agric. For. Meteorol.*, *130*, 207–222, doi:10.1016/j.agrformet.2005.04.001.
- Noormets, A., M. J. Gavazzi, S. G. McNulty, J. C. Domec, G. Sun, J. S. King, and J. Chen (2010), Response of carbon fluxes to drought in a coastal plain loblolly pine forest, *Global Change Biol.*, *16*, 272–287, doi:10.1111/j.1365-2486.2009.01928.x.
- Oren, R., C. I. Hsieh, P. Stoy, J. Albertson, H. R. McCarthy, P. Harrell, and G. G. Katul (2006), Estimating the uncertainty in annual net ecosystem carbon exchange: Spatial variation in turbulent fluxes and sampling errors in eddy-covariance measurements, *Global Change Biol.*, *12*, 883–896, doi:10.1111/j.1365-2486.2006.01131.x.
- Pacala, S. W., et al. (2007), The North American carbon budget past and present, in *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle, a report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research*. Asheville, NC: National Oceanic and Atmospheric Administration, pp. 29–36, Natl. Clim. Data Cent., Asheville, N. C. [Available at <http://www.treesearch.fs.fed.us/pubs/13120>.]
- Pan, Y., J. M. Chen, R. A. Birdsey, K. McCullough, L. He, and F. Deng (2011), Age structure and disturbance legacy of North American forests, *Biogeosciences*, *8*, 715–732, doi:10.5194/bg-8-715-2011.
- Reilly, J., J. M. Melillo, Y. Cai, D. W. Kicklighter, A. Gurgel, S. Paltsev, T. Cronin, A. Sokolov, and A. Schlosser (2012), Using land to mitigate climate change: Hitting the target, recognizing the tradeoffs, *Environ. Sci. Technol.*, *40*, 5672–5679, doi:10.1021/es2034729.
- Schimel, D., et al. (2000), Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States, *Science*, *287*, 2004–2006, doi:10.1126/science.287.5460.2004.
- Sokolov, A. P., D. W. Kicklighter, J. M. Melillo, B. S. Felzer, C. A. Schlosser, and T. W. Cronin (2008), Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle, *J. Clim.*, *21*, 3776–3796, doi:10.1175/2008JCLI2038.1.
- Thomas, R. Q., C. D. Canham, K. C. Weathers, and C. L. Goodale (2010), Increased tree carbon storage in response to nitrogen deposition in the U.S., *Nat. Geosci.*, *3*, 13–17, doi:10.1038/ngeo721.
- Tian, H., J. M. Melillo, D. W. Kicklighter, S. Pan, J. Liu, A. D. McGuire, and B. Moore III (2003), Regional carbon dynamics in monsoon Asia and its implications for the global carbon cycle, *Global Planet. Change*, *37*, 201–217, doi:10.1016/S0921-8181(02)00205-9.
- Tian, H., et al. (2011), China's terrestrial carbon balance: Contributions from multiple global change factors, *Global Biogeochem. Cycles*, *25*, GB1007, doi:10.1029/2010GB003838.
- Wharton, S., M. Falk, K. Bible, M. Schroeder, and K. T. Paw U (2012), Old-growth CO₂ flux measurements reveal high sensitivity to climate anomalies across seasonal, annual, and decadal time scales, *Agric. For. Meteorol.*, *161*, 1–14, doi:10.1016/j.agrformet.2012.03.007.
- Williams, C. A., G. J. Collatz, J. Masek, and S. N. Goward (2012), Carbon consequences of forest disturbance and recovery across the conterminous United States, *Global Biogeochem. Cycles*, *26*, GB1005, doi:10.1029/2010GB003947.
- Xiao, J., et al. (2010), A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data, *Remote Sens. Environ.*, *114*, 576–591, doi:10.1016/j.rse.2009.10.013.
- Zhang, F. M., J. M. Chen, Y. D. Pan, R. A. Birdsey, S. H. Shen, W. M. Ju, and L. M. He (2012), Attributing carbon changes in conterminous U.S. forests to disturbance and nondisturbance factors from 1901 to 2010, *J. Geophys. Res.*, *117*, G02021, doi:10.1029/2011JG001930.