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Critical land change information enhances understanding of carbon balance in the U.S.

(Running Title: U.S. land change and carbon balance)

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Conflict of Interest

The authors have no conflict of interest to declare.

Author contributions

JL and BMS have equal contributions to this work.

JL, QZ carried out the IBIS modeling work.

BMS, TRL, TS, TW carried out the land cover change analysis.

SMH, CHK, TJH carried out fire data analysis.

ZZ, BR involved in the whole study design with JL and BS.

LSH guided the understanding and use of the COLE database.

DZ helped with forest thinning quantification.

NBB processed the SSURGO soil data.

JS contributed to data archiving.

SL, MAC, HJ, DTP, JC, YL, BP contributed to carbon modeling and/or carbon analysis in many aspects.

All authors contributed to and approved the final manuscript.

Data Accessibility

Spatial input and output data supporting the conclusions of the study are available through the USGS ScienceBase repository. The parallel IBIS model code (pibis) and some post-processing programs are available from the corresponding authors upon request.

Abstract

Large-scale terrestrial carbon estimating studies using methods such as atmospheric inversion, biogeochemical modeling, and field inventories have produced different results. The goal of this study was to integrate fine-scale processes including land use and land cover change into a largescale ecosystem framework. We analyzed the terrestrial carbon budget of the conterminous U.S. from 1971 to 2015 at 1-km resolution using an enhanced dynamic global vegetation model (DGVM) and comprehensive land cover change data. Effects of atmospheric CO2 fertilization, nitrogen deposition, climate, wildland fire, harvest, and land use/land cover change (LUCC) were considered. We estimate annual carbon losses from cropland harvest, forest clearcut and thinning, fire, and LUCC were 436.8, 117.9, 10.5, and 10.4 TgC yr⁻¹, respectively. Carbon stored in ecosystems increased from 119,494 to 127,157 TgC between 1971 and 2015, indicating a mean annual net carbon sink of 170.3 TgC yr⁻¹. Although ecosystem net primary production increased by approximately 12.3 TgC yr⁻¹, most of it was offset by increased carbon loss from harvest and natural disturbance and increased ecosystem respiration related to forest aging. As a result, the strength of the overall ecosystem carbon sink didn't increase over time. Our modeled results indicate the conterminous U.S. carbon sink was about 30% smaller than previous modeling studies, but converged more closely with inventory data.

Keywords: carbon sequestration, ecosystem productivity, land use and land cover change, wildfire, ecosystem model, DGVM

Significance:

Differences in input data and methods cause discrepancies in large regional carbon assessment results. Carbon sequestration estimates from bottom-up ecosystem models are usually smaller than estimates from atmospheric inversion models and larger than field inventory results. Here, we quantify carbon dynamics of the conterminous U.S. at 1-km spatial resolution focusing on detailed land cover changes over recent decades, using several proven and established national data products. Our research highlights that the combined impacts of land management, human-dependent land use change, and natural disturbance on carbon are greater than those associated with climate variability, and that process modeling can converge with field inventory data when detailed land cover change information is used.

Introduction

Regionally and globally, large uncertainties exist in quantifying biological carbon (C) sequestration in terrestrial ecosystems (IPCC, 2007; Arneth et al., 2017). Atmospheric inversion models, terrestrial biogeochemical models, and field inventories typically give notably different results (King et al., 2015; Hayes et al., 2012). Grassi et al. (2018) indicate that a model—inventory discrepancy in the global anthropogenic net land-use emissions (about 1.5 GtC yr⁻¹) can be mostly explained by conceptual differences in dealing with forest related land use and environmental changes. For the conterminous U.S., estimates of the annual C sink during recent decades range from 200 to 685 TgC, varying greatly by method, period of analysis, and ecosystem type (**Table S0-1**). The recent SOCCR-2 report (Birdsey et al., 2018) indicates that estimates of the U.S. land C sink (excluding aquatic system) are converging around 275 TgC, including 201 TgC in forestland.

Land use and land cover change (LUCC) is an important perturbation of the regional and global carbon cycle. Synthesis of bookkeeping models, remote sensing, and process modeling studies indicate that global LUCC-induced C emission during 1990–2009 was estimated around 1.1 PgC yr⁻¹, with an overall uncertainty of ±0.5 PgC yr⁻¹ (Houghton et al., 2012). Several long-term global and continental scale C assessments have used process-based dynamic global vegetation models (DGVMs). Although DGVMs can reflect much greater spatial and temporal variability in carbon density and response to environmental conditions than bookkeeping models, their modeled carbon stocks may differ markedly from observations (Houghton et al., 2012). One reason is that most carbon cycle processes related to LUCC were simplified in large-scale C modeling assessments (Arneth et al. 2017) because DGVMs typically operate at coarse spatial resolutions with limited representation of LUCC. For example, the Community Land Model (CLM) (Lindsay et al., 2014) and the Ecosystem Demography (ED) model (Hurtt et al., 2002) have spatial resolutions of 0.5-1.0 degree for global simulations although the MC2 model has been used at 4-km resolution for western U.S. (Bachelet et al., 2016). In some cases, other sources of LUCC C effects are adopted/combined in DGVM simulations (Schimel et al., 2016; Sitch et al., 2015) in order to reflect LUCC effects. In general, LUCC is represented in DGVMs at spatial resolutions which are relatively coarse compared to the spatial scales at which land cover change and land management occur (e.g., forest stands and municipal planning districts).

The conterminous U.S. (CONUS) has a diverse geography, comprising many ecoregions with unique biophysical and land use characteristics. The unpredictable occurrence of large wildland fires, intensive land use in forestry and agriculture, and land use change complicate attempts to assess changes in ecosystem C balance. This study integrates existing scientific knowledge, robust modeling, and the best currently available data to quantify the effects of major controlling environmental processes (atmospheric chemistry, climate variability, fire disturbance, and LUCC) on ecosystem C dynamics. The goal of this study was to include smaller scale processes such as land use and land cover in a large-scale regional ecosystem framework. Our approach evaluates C sequestration in dominant vegetation types (forests, shrublands, grasslands, croplands) in CONUS from 1971 to 2015 at 1-km resolution by reconciling a modeling approach with county-scale observations. The study focuses on changes in ecosystem productivity, C storage, and biomass C losses from disturbances. Our modeling tool and various model input data are described in the Methods and Supporting Information.

Methods

Model description

The Integrated Biosphere Simulator (IBIS) (Foley et al., 1996) is a DGVM that links mesoscale atmospheric drivers and vegetation ecophysiology in a physically consistent representation of canopy photosynthesis and stomatal conductance, while accounting for vegetation phenology and soil biogeochemistry to simulate long-term vegetation dynamics and ecosystem productivity. IBIS allows multiple plant functional types (PFT, see Table S0-3 in Supporting Information) to coexist in a single land pixel. Existence of a PFT depends on local-scale environmental conditions and is constrained by human land use. IBIS doesn't directly use forest age to calculate forest growth. Each forest PFT within a grid cell contains a single biomass carbon density. The biomass density together with the climate and disturbance variables determine the PFT's growth and mortality rates.

In this study, our modified version of IBIS introduces detailed effects of land cover change, wildland fire, forest thinning, and cropland grain/straw harvest (Liu et al., 2016). The model This article is protected by copyright. All rights reserved

was enhanced to use comprehensive gridded LUCC data. The model handles eight major land transitions/disturbances (fire, forest clearcut, forest thinning, deforestation to other vegetation, reforestation from other vegetation, agricultural expansion from grassland, agricultural contraction to grassland, and urban/infrastructure development). Carbon transfer following LUCC and fire events includes direct C harvest/combustion and additional vegetation mortality.

The modified IBIS model incorporates fractional land cover changes. Each 1-km grid cell contains multiple land cover types. Each land cover type (e.g. forest, grass and agriculture) can have multiple PFTs (see Table S0-3 in Supporting Information). Each PFT has a single set of biomass pools and fluxes. The IBIS model does not consider forest age directly. It uses biomass C density to adjust new biomass growth and mortality.

Forest thinning in a grid cell is determined by an external thinning ratio derived from the USDA Forest Service Forest Inventory and Analysis (FIA) and literature, which applies to entire forest PFTs annually. All live biomass from forest PFTs will be reduced following the thinning ratio. More details are presented in the Supporting Information.

Key input data

In this study, IBIS was enhanced to use comprehensive LUCC data: (a) 30-m vegetation height and cover type information from the USDA-USGS LANDFIRE Program; (b) five dates (1973, 1979, 1986, 1992, 2000) of 60-m resolution land cover change information from the USGS Land Cover Trends Project; (c) 30-m resolution annual wildland fire scar and burn severity information (1984-2015) from the USGS-USDA Monitoring Trends in Burn Severity (MTBS) Project; and (d) freshwater and saline wetland area fractions derived from 30-m National Land Cover Database (NLCD) and NOAA Coastal Change Analysis Program (C-CAP) data. These publicly available datasets for CONUS are the largest and most comprehensive of their kind. In addition, state/county level forest thinning rates were derived from previous studies (Zhou et al., 2013; Law et al., 2013).

To better constrain the model's prognostic representation of the C cycle at regional scales, we used region-specific C densities as calibration references for each county in CONUS. MODIS-derived annual net primary productivity (NPP) from 2001 to 2005 (Zhao et al., 2005), forest live biomass and dead wood standing stock at 100 years from the Carbon On Line Estimator (COLE) tool (Van Deusen and Heath, 2016), and USDA NASS county-level crop harvest data (https://www.quickstats.nass.usda.gov/) were used to calibrate the model. The COLE tool is based on USDA Forest Service FIA data (USDA Forest Service, 2016) (http://fia.fed.us), which is also used in development of LANDFIRE and some NLCD mapped products. Details are provided in Methods and Supporting Materials.

Details of LUCC-related data are provided in Supporting Materials S1, S2, S3, and S4. **Table S0-2** provides key data links. Dynamic monthly precipitation and temperature data from 1971 to 2015, interpolated to 4-km resolution using PRISM (Daly et al., 2008), were used as the main climatic drivers. Other variables like monthly mean cloud cover fraction, wet days per month, relative humidity, and wind speed were adopted from monthly normals for 1961–1990 obtained from the UK Climate Research Unit (CRU, http://www.cru.uea.ac.uk/). The soil texture and C content were obtained from SSURGO (2015) polygon data and reprocessed/interpolated to 1-km resolution. The modeled soil profiles contain up to six layers (0 to 7, 7 to 15, 15 to 25, 25 to 50, 50 to 100, 100 to 200 cm). Sand, silt, and clay fractions of each layer are used by IBIS to calculate soil water holding capacity and permeability. Additionally, 0.5-degree spatially explicit seasonal surface CO₂ concentration (2003-2009) and annual nitrogen deposition (1970-2009) were derived from satellite-based column density measurements (Zhang et al., 2014; Lu et al., 2016). The 1-km land ownership map was derived from the Protected Areas Database of the United States, version 1.4 (USGS, 2016).

Consideration of fractional land cover

IBIS tracks annual changes in the area fractions of each land cover type within each land pixel. The original IBIS model simulated the existence of each PFT using climatic constraints only, which could give very different upper and lower canopy fractions from reality in regions

where human activities have a major influence and in regions where physical limitations on vegetation exist (such as rock, desert, or open water). In our modified version, observed fractional land cover data are used to constrain the extent of changes in LAI and the proportions of different PFTs. Land cover fractions, including the unvegetated fraction, are not allowed to change unless a relevant LUCC event happens.

Vegetation regrowth occurs following any disturbance or human-caused land use change. Disturbance applies to an entire PFT and land cover type in the model. When wildfire and forest harvest events occur (which are not permanent land cover conversions), the forest fraction will remain unchanged, with only biomass density (kgC m⁻²) being reduced; however, when deforestation occurs, all of the forest fraction will be converted to the target land cover (e.g., agricultural land, grassland, shrubland, etc.) except that we intentionally allow a small fraction of forest during urbanization. (5%)to exist Conversely, when reforestation/afforestation occurs, either natural or human induced, other land covers convert to forest, causing the forestland fraction to increase, although the forest biomass density of the entire grid cell may not immediately increase. Following LUCC events, different proportions of ecosystem C will transfer to the atmosphere, harvest products, and on-site dead wood.

Forest biomass and soil carbon initialization

We used a county-level scalar and retrospective cold-start simulations (i.e., forest biomass starts from zero) to obtain county-level average forest standing stocks at 100 years that matched with FIA-COLE observations (per hectare biomass densities). For individual forest pixels in a county, we assumed that the pixel-level forest growth rates varied around the county mean forest growth rate. The variability is driven by local environmental factors specific to its soil, climate, tree cover fraction, and PFTs. When forest area fraction changes, pixel-level ecosystem production and biomass values will change based on the new forest area fraction. Based on those pixel-level biomass-over-age growth curves, we used the "observed" 1-km forest biomass map generated from LANDFIRE data (Supporting Material S1) to determine the approximate forest age in 2000 and reconstructed the age and biomass for 1971. For a pixel

where biomass derived from LANDFIRE was larger than that simulated by IBIS at 100 years, we assumed the forest was mature and used the LANDFIRE estimate as its biomass in 1971. For a pixel where forest age backtracking indicated a stand-replacing disturbance occurred between 1971 and 2000, we assumed the previously disturbed forest was mature and set the biomass in 1971 to that of a forest with an age selected at random between 30 and 100 years. This assumption could lead to slightly lower estimates of wood harvest for the western old-growth forest and slightly higher estimates of harvest for the southeastern plantations.

Initialization of soil C pools was based on soil survey data. Soil C has four pools: fast, unprotected slow, protected slow, and passive. These pools are not further divided by soil layers. IBIS soil layers are mainly used for water balance calculation. Our soil C calculation in the first 10 years was similar to the fast soil spin-up method of Xia et al. (2012), which compared input and output fluxes of total soil C. When input and output fluxes became very close, the soil C pool was close to a theoretical balanced state. To maintain the overall soil C pool size close to observations, we used a set of internal scalars in the first 20 simulation years that dynamically adjust the slow soil C pool size and then deducted the slow C from the total observed soil C to obtain the size of the initial passive soil C pool. To avoid drastic declines of soil C in the simulation, we used an approach similar to the LPJ-WHy model (Wania et al., 2009) in modeling peatland soil accumulation: A maximum amount of the passive soil C (reactive, 5 kg C/m²) is allowed to participate in the soil decomposition process. The extra passive soil C (beyond 5 kg C/m²) is assumed inactive within a given year. IBIS has ground litter C and dead wood C pools in addition to the four soil C pools. Dead wood calibration was done using FIA-COLE county-level 100-year dead wood data (same as live biomass calibration). Ground fine litter was calculated with IBIS default litter decomposition parameters.

Model Calibration

Model calibrations were performed by comparing simulated county-level NPP, live biomass, dead wood, and crop yield with county-level observations of MODIS-derived NPP, FIA-derived forest live biomass, dead wood, and USDA statistics of crop yields (Figure S5-1).

The COLE tool provides 100-year forest growth curves (live and dead wood) based on FIA data for each FIA survey unit (**Table S5-1** and **Figure S5-1**). It was assumed that a 100-year-old forest did not undergo any stand-replacing disturbances, although effects of thinning, non–stand-killing fires or other disturbances are implicitly included in the FIA data. Repeated IBIS simulations were performed with disturbance events turned off and compared with the COLE-based FIA data. Scaling coefficients for each county were then calculated and applied to adjust IBIS' simulations of forest live growth and dead wood. County-level live biomass scaling coefficient was calculated as a ratio of simulated county-level 100-year forest biomass over FIA-derived county-level 100-year forest biomass. The ratio was constrained between 0.1 and 10.0 and applied to tree mortality calculation in the next simulation. Repeated adjustments helped to make the simulation and observation converge. Dead wood scaling coefficient was calculated the same way using dead wood data.

We summarized county-level annual agricultural harvest data (comprising 26 crop species) since 1960. The yield data were aggregated based on their area fractions (**Table S5-2**). The 2000-2009 averages were used to calibrate IBIS agricultural harvest amounts over the same period. The 1960-2009 grain yield trend was used to adjust grain production increase in addition to simulated effects of CO_2 fertilization.

The MODIS-derived NPP product provided full spatial and temporal coverage, which was used to calibrate IBIS NPP at the ecoregion level. IBIS does not consider individual tree/crop species and other local management factors that would be captured by remote sensing. We avoided overfitting because IBIS has its own NPP algorithm. Although this was not a pixel-level calibration, simulated NPP would still respond to spatial variability driven by climate, soil, and disturbance on the 960-m grid.

Four uncertainty statistics methods were used to evaluate model performance, including Pearson correlation coefficient (COR), root mean square error (RMSE), modeling efficiency (MEF), and mean relative difference (BIAS). Details are provided in Supporting Materials S5.

Results

Land cover transition and related carbon gains and removals

Over the study period, wildland fire and forest clearcut disturbed the most land area, followed by agricultural contraction and expansion, development, and forest to/from agricultural land (**Table 1**).

Table 1. Land cover change and fire effects on ecosystem carbon fluxes in CONUS (1971-2015 average NPP and NBP). The areas are the sum of the land pixels that had undergone the same LUCC events during 1971-2015. A positive NBP value refers to a net carbon sink on land. Fire disturbance locations overlap with the No-LUCC locations. The land area and carbon numbers on the No_LUCC row already include the numbers from the Fire row. Therefore, the numbers on the Sum/Avg row do not include the numbers from the Fire row. The fire area included 14,000+ fires from 1984 to 2015. No fire data were available from 1971-1983. Forest thinning was assumed to occur across all forested areas annually.

	AREA	NPP	NPP_SUM	NEP	NEP_SUM	NBP	NBP_SUM
Change Type	(km²)	$(kgC m^{-2} yr^{-1})$	(TgC yr ⁻¹)	$(kgC m^{-2} yr^{-1})$	(TgC yr ⁻¹)	$(kgC m^{-2} yr^{-1})$	(TgC yr ⁻¹)
No_LUCC	6835273	0.36	2480.7	0.10	665.5	0.027	182.9
Fire	547034	0.33	181.5	0.04	23.4	0.010	5.5
Forest Clearcut Harvest	316501	0.55	175.2	0.09	28.5	-0.044	-14.0
Deforestation to Ag.	39515	0.43	16.9	0.16	6.1	-0.030	-1.2
Reforestation from Ag.	38512	0.61	23.5	0.15	5.8	0.065	2.5
Forest to Development	38735	0.38	14.8	0.09	3.4	-0.023	-0.9
Grass to Development	15702	0.18	2.8	0.04	0.7	-0.019	-0.3
Ag. to Development	50164	0.27	13.8	0.09	4.5	-0.021	-1.1
Ag. expansion from Grass	123993	0.30	37.3	0.16	20.2	-0.004	-0.5
Ag. contraction to Grass	183977	0.28	51.0	0.04	8.1	0.015	2.8
Sum/Avg (excluding fire row)	7642373	0.368	2816	0.097	743	0.022	170

The mean annual C loss was 572.6 TgC yr⁻¹, including grain harvest (284.5), straw harvest (152.3), forest clearcut harvest (31.9), forest thinning (86.0), direct emissions from fires (10.5), and C losses related to other land transitions (10.4). These C losses were partly compensated by vegetation regrowth. For example, over the 45 years, average total net biome productivity (NBP; negative values denote C loss) of all clearcut harvest sites was -14.0 TgC yr⁻¹, whereas the average annual C removal on clearcut sites was 31.9 TgC yr⁻¹. Similarly, all wildfire sites together sequestered 5.5 TgC yr⁻¹, while their average annual C loss in combustion was 10.5 TgC yr⁻¹. Fire emission was not available before 1984 due to lack This article is protected by copyright. All rights reserved

of wildfire data. This would cause underestimation of C loss in those years. The underestimation might be close to the average annual fire emissions during 1984–1990 (6 TgC yr $^{-1}$), which was lower than the fire emissions during 2011–2015 (25 TgC yr $^{-1}$). Urban development areas on average lost 2.3 TgC yr $^{-1}$. Areas with unchanged land cover sequestered 182.9 TgC yr $^{-1}$.

Carbon trends and spatial distribution

Figure 1 shows the simulated trends in key ecosystem C fluxes and stocks from 1971 to 2015. Due to the combined contributions of CO₂ fertilization, plant phenology, climate change, and land change impacts, average NPP increased by about 23% during 1971–2015 (18.5% in forests, 7% in shrubland, 27.9% in grassland, and 31.7% in agricultural systems), calculated using the linear trendline of the 45-year NPP values. NPP of agricultural land had the highest increase partly due to farming and biotechnology advances, which were represented in the model empirically, based on 1960-2010 crop yield data. Average total NBP was 170 TgC yr⁻¹, ranging from a loss of 104 TgC yr⁻¹ in 1988 to a maximum uptake of 366 TgC yr⁻¹ in 2004. Clearcut harvest removals averaged 32 TgC yr⁻¹ and were lowest in the 1970s (21 TgC yr⁻¹) and highest in the late 1980s (36 TgC yr⁻¹), whereas forest thinning removed approximately 86 TgC yr⁻¹ in 2000s, and reached 25 TgC yr⁻¹ during 2001–2015, with large interannual variation. C losses in agricultural harvests (grain + straw) increased steadily from 374 TgC yr⁻¹ to 505 TgC yr⁻¹ over the simulation period. Total C increases in live biomass, dead wood, other plant litter, and soil were 4.19, 1.16, 0.57, and 1.75 PgC, respectively. More than half of the C stock increase was in live biomass (55%), followed by soil (23%), dead wood (15%), and litter (7%).

Summaries of carbon stocks and fluxes by land cover class and by decade from 1971-2015 are listed in **Table 2**. Overall, the estimated CONUS terrestrial ecosystem C sink of 170 TgC yr⁻¹ (not including C sink in aquatic systems and harvested wood product) offset about 11.5% of total CONUS fossil fuel emissions (1,476 TgC yr⁻¹) (3). The highest decadal NBP occurred in the 1990s (188 TgC yr⁻¹), due to favorable climate and relatively small areas disturbed. However, NBP was low in the 2000s (166 TgC yr⁻¹), when C removals in agriculture, fire disturbances, and LUCC increased. The average NBP of 2011-2015 recovered to 192 TgC/yr.

Table 2. Overall carbon fluxes and stocks in CONUS by land cover type and by decade. Flux values by land cover are the 1971-2015 averages. Stock values by land cover are for 2015. The "Other" lands This article is protected by copyright. All rights reserved

include all lands in CONUS with non-vegetation cover of greater than 85%, mostly barren, and urban areas. Area unit is km²; C stock unit is TgC; C flux (NPP, NEP, NBP) unit is TgC/yr

	Area (1971)	Area (2015)	NPP	NEP	NBP	Live Biom C	Dead Biom C	Litter C	Soil C	Total C
Forest	2737374	2709645	1448	280	129	15407	2374	3454	40461	61695
Crop	2018467	1958302	747	395	21	1875	208	696	28429	31209
Shrub	1670473	1651758	282	28	14	1051	428	723	11004	13206
Grass	1174161	1185146	325	35	14	624	104	638	14727	16094
WdCrop	10066	10066	7.6	5.1	0.1	22	0	6	104	132
Other	31833	127456	7.8	0.9	-7.6	63	8.0	16.4	947	1034
Sum	7642374	7642374	2817	744	170	19043	3123	5533	95672	123371
1970s			2607	653	171	17488	2676	5277	95041	120482
1980s			2698	686	145	18559	2948	5378	95265	122150
1990s			2868	776	188	19354	3174	5605	95671	123804
2000s			2947	796	166	19984	3430	5701	96227	125342
2010s			3105	866	192	20543	3630	5865	96645	126683
AVG 71-15			2816	743	170	19035	3121	5532	95673	123360

Figure 2 shows the spatial patterns of ecosystem NPP, NEP, NBP, and C removals from fire and harvest averaged over the 45-year simulation period. The U.S. west coast and the eastern U.S. had generally high NPP and NBP, mostly in forested regions. Agricultural land had the highest NEP and medium high NPP, but its NBP was low due to grain and straw removals.

Discussion

Implications for LUCC-based C modeling

Our study provides a number of important insights on the quantification of LUCC and fire effects on CONUS C cycling. First, the interannual variations in NPP and NEP were driven mainly by climate variability without counting LUCC and fire effects. In our study, LUCC and fire disturbance caused C loss of approximately 573 TgC (STD=68 TgC) per year on average (including 437 TgC yr⁻¹ loss from agricultural land), which offset 77% of total NEP (743 TgC yr⁻¹). This huge C loss greatly exceeded year-to-year variability (STD) in NPP (199 TgC yr⁻¹), NEP (121 TgC yr⁻¹), and NBP (96 TgC yr⁻¹). If we look at forestlands only, C losses caused by clearcut and thinning (104 TgC yr⁻¹, STD=13.2 TgC yr⁻¹) also exceeded the variations of forest NPP (93 TgC yr⁻¹), NEP (53 TgC yr⁻¹), and NBP (47 TgC yr⁻¹). This demonstrates that human land use and natural disturbance are key factors in the C balances of the CONUS ecosystems, with larger magnitude and smaller variation than climate variability effects.

Second, most terrestrial C sinks occur in areas unaffected by LUCC, primarily on forestlands, with about 55% of the C sink allocated to living biomass. Although forest NPP and NEP increased by 18.5% and 33.4%, respectively, forest NBP basically remained the same during the study period. This leveled NBP of forest was attributable to a combination of increased C gain from NPP and increased C loss from heterotrophic respiration, LUCC, and fire disturbances.

Third, our estimates are generally more consistent with results from inventory-based methods, which consistently estimate a smaller land C sink than ecosystem models and atmospheric inversion methods (**Table S0-1**). Simulated forestland C sink in the 1990s was 125 TgC yr-1. If we consider an estimated 25 TgC yr⁻¹ sink in harvested wood products (HWP) (USEPA, 2014; Pan et al., 2011), our adjusted 1990s forest NBP estimate would be 150 TgC yr⁻¹. Because our forest summary included only land cells where forest cover was dominant, and because we used fractional land cover in the model, a portion of the carbon sink in shrublands, grasslands, and agricultural lands (total about 63 TgC yr⁻¹) could be attributed to additional carbon uptake by trees. Our statistics indicate that average tree biomass density on forestland, agricultural land, shrubland, and grassland during 1971–2015 was 5.60, 0.81, 0.16, and 0.20 kg C m⁻², respectively. Therefore, about 14.5% of agricultural lands, 2.9% of

shrubland, and 3.6% of grassland can be considered tree-covered land. That equals approximately 13.9% of normal forestland area. Therefore, given a forestland C sink of 125 TgC yr⁻¹ in 1990s, we can assume an additional C sink of 17 TgC yr⁻¹ for forests in non-forest dominant lands. Sparse trees on agricultural land usually have higher productivity than trees in a forest stand due to better soil N and water supply and edge effect. But sparse trees on non-agricultural lands may reside in a harsh environment (such as cold mountaintop) and have lower productivity than normal forest. Given that we have more than doubled sparse tree areas on agricultural land than on shrubland and grassland, we think the additional 17 TgC yr⁻¹ C sink is conservative and reasonable. Our new adjusted forest NBP estimate for the 1990s would be 167 TgC yr⁻¹, which is very close to some forest inventory studies, such as Pan et al (2011, 179 TgC yr⁻¹), Heath et al (2011, 162 TgC yr⁻¹), and Woodbury et al (2007, 169 TgC yr⁻¹) 1). For the 2000s, our adjusted estimate of forest NBP (with dynamic climate data used) is still 167 TgC yr⁻¹. This value is a little lower than the inventory-based forest NBP (199 TgC yr⁻¹) that usually has limited response to climate variability. However, our estimates of 2011-2015 forest C sink is 195 TgC yr ¹, which is close to inventory results. On the contrary, our adjusted average NBP on all land types for 1991-2010 was 202 TgC yr⁻¹, which is significantly lower than that obtained from other models (average of 331 TgC yr⁻¹) and the SOCCR2 NBP estimates (275 TgC yr⁻¹).

Our model's agreement with forest inventory estimates (1990s) may be partially explained by our calibration of modeled live biomass C stock and dead woody C stock against surveyed county-level 100-year old forest stands. However, our calibration was done before fire and LUCC data were used. Therefore, our LUCC-related C budget is mostly independent from an inventory-based C budget. Our regional model calibration approach is likely the big difference from the site-level calibration approach used by other DGVM models. Additionally, our model considered land ownership, by which public or protected lands (mostly in the western U.S.) have reduced thinning rates compared to private lands (mostly managed land in the eastern U.S.). Overall, our findings represent the most comprehensive C modeling exercise utilizing available LUCC data for CONUS. Results indicate that combined effects of direct management, human-caused LUCC, and natural disturbance on C budget are larger than those associated with climate variability. However, we acknowledge that natural disturbances (such as wildland fires) also vary with climate. So additional work is needed to understand the full influence of climate variability.

Using a bookkeeping modeling approach, Piao et al. (2018) found that lower land-use emissions were responsible for the global increased land carbon sink since the 2000s. From our study, overall LUCC-induced total biomass removals (beyond fire emission) gradually increased, with the 2000-2009 period being slightly lower than the 1990s and the 2010-2015 period, which is consistent with the global trend. Land conversions had relatively higher C emissions (biomass removals) during 1985-2000, and logging reached the highest level during late 1980s and early 1990s. But CONUS wildland fires significantly intensified since the 2000s.

Pugh et al. (2019) pointed out that age-related forest carbon sink is predominantly located in the middle latitudes. Although IBIS doesn't track forest age, our study seems to support that statement. From our study, IBIS showed significant increases in forest NPP and sustained NBP level even with gradually increased biomass removals and fire combustions. Our initial analysis indicated that, after excluding climate effects, forest NPP increased by 17% during 1971-2015. Considering this NPP increase, the model can generate 100-year total tree biomass that matches the 100-year biomass level derived from inventory. We believe the driving forces behind the NPP increase are the CO₂ enrichment effect and forest age effect. Currently, although the IBIS model's photosynthesis formula includes a conservative CO₂ fertilization algorithm, we cannot separate the contributions of the two factors effectively. Further work is needed to quantify the relative contributions of forest age and CO₂ fertilization.

Reducing model uncertainties

Many aspects of this study still have notable uncertainties. First, dead wood C is one of the big unknowns in C modeling. In this study, although we calibrated our model with surveyed overall forest dead wood C stock at 100 years, we still do not have good dead wood C initialization. In addition, we did not explicitly model the effects of insects, disease, and physical agents such as flooding on tree mortality. Adding greater details to the tree mortality process, including the transfer of live tree carbon to dead tree carbon and the temporal changes in decomposition rates of standing and downed dead wood pools (Landry et al., 2016a; 2016b), would improve NBP calculations in future work. Second, although total C removal from forests (including clearcut, thinning, and other deforestation events) was about 128 TgC yr⁻¹, which matched inventory-based estimates (Williams et al., 2016), thinning practices by region and by ownership across CONUS are still highly uncertain, especially in the interior western

U.S. Separation of partial thinning and clearcut can be further improved when better annual clearcut data become available. Third, estimates of annual land area burned also have considerable uncertainty. By mapping fires from 1984-2015 using Landsat data, Hawbaker et al (2017) found 31% more area burned than reported in MTBS in the western U.S., 312% more in the Great Plains, and 233% more in the eastern U.S. Therefore, the apparently low C removals due to fire may be attributed to the focus of the MTBS database on large fires (defined as 1,000 acres in the west and 500 acres in the eastern US). Finally, given that spatially explicit and comprehensive historical land change data were not available, we generated annual wall-to-wall land cover maps (1971-2015) based on land cover change sampling. The overall accuracy of land cover change sampling was reported to be 85% (USGS Land Cover Trends Project). Yet, new approaches, including annual wall-to-wall remote sensing products (e.g. USGS Land Change Monitoring, Assessment, and Projection (LCMAP) project) and robust land cover change models, will be very helpful to reconstruct more realistic land cover and biomass histories. In addition, DGVMs that can deal with fractional land cover change will be useful for large-scale, coarse resolution regional and global simulations. This feature of our model allows direct use of future land cover products such as the harmonized land use projections (Hurtt et al., 2011) developed for the IPCC's Fifth Assessment Report.

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Conflict of Interest

The authors have no conflict of interest to declare.

Author contributions

JL and BMS have equal contributions to this work.

JL, QZ carried out the IBIS modeling work.

BMS, TRL, TS, TW carried out the land cover change analysis.

SMH, CHK, TJH carried out fire data analysis.

ZZ, BR involved in the whole study design with JL and BS.

LSH guided the understanding and use of the COLE database.

DZ helped with forest thinning quantification.

NBB processed the SSURGO soil data.

JS contributed to data archiving.

SL, MAC, HJ, DTP, JC, YL, BP contributed to carbon modeling and/or carbon analysis in many aspects.

All authors contributed to and approved the final manuscript.

Data Accessibility

Spatial input and output data supporting the conclusions of the study are available through the USGS ScienceBase repository. The parallel IBIS model code, including parameter files, are available from the corresponding authors and also available on Github: https://github.com/jxliu2018/pIBIS.

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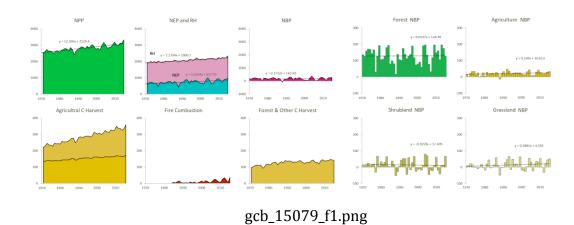
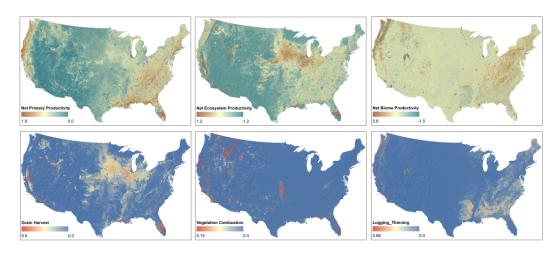


Figure 1. Temporal trends of major carbon fluxes of CONUS from 1971 to 2015. Units are TgC yr-1. RH: ecosystem heterotrophic respiration. NPP: net primary productivity; NEP: net ecosystem productivity; NBP: net biome productivity. A positive NBP value refers to a net carbon sink on land.



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Figure 2. Spatial distribution of 45-year average net primary productivity (NPP), net ecosystem productivity (NEP), net biome productivity (NBP), and carbon losses from grain harvest, tree harvest, and fire. Unit is kgC m-2 yr-1.