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Complex forest dynamics indicate potential for slowing carbon accumulation in the southeastern United States

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Over the past century forest regrowth in Europe and North America expanded forest carbon (C) sinks and offset C emissions but future C accumulation is uncertain. Policy makers need insights into forest C dynamics as they anticipate emissions futures and goals. We used land use and forest inventory data to estimate how forest C dynamics have changed in the southeastern United States and attribute changes to land use, management, and disturbance causes. From 2007-2012, forests yielded a net sink of C because of net land use change ($+6.48$ Tg C yr^{-1}) and net biomass accumulation ($+75.4$ Tg C yr^{-1}). Forests disturbed by weather, insect/disease, and fire show dampened yet positive forest C changes ($+1.56$, $+1.4$, $+5.48$ Tg C yr^{-1}, respectively). Forest cutting caused net decreases in C (-76.7 Tg C yr^{-1}) but was offset by forest growth ($+143.77$ Tg C yr^{-1}). Forest growth rates depend on age or stage of development and projected C stock changes indicate a gradual slowing of carbon accumulation with anticipated forest aging (a reduction of 9.5% over the next five years). Additionally, small shifts in land use transitions consistent with economic futures resulted in a 40.6% decrease in C accumulation.

F orests represent the largest sink of terrestrial carbon (C) and continued storage, forest growth, and removals for long life-span products may help reduce greenhouse gases in the future[1]. Over the past century, "forest transitions"[2] from a period of deforestation to reforestation and regrowth in Europe and North America, for example, have greatly expanded forest biomass and forest C sinks[3–5]. In the U.S., the net C accumulation from land use, land use change, and forestry was equivalent to 15 percent of all emissions from the energy and transportation sectors in 2013[6]. The potential for future C accumulation in forests is uncertain due in part to the combined effects of changes in forest growth rates, land use choices[7], forest management, mortality-inducing events such as insect epidemics, other disturbances such as wildfires and hurricanes, and the direct and indirect effects of climate change[8–10]. Over broad spatial scales C accumulation rates are driven by multiple co-occurring vectors of change. Understanding the relative influence of these vectors of change on overall forest C dynamics represents a considerable challenge because they rarely occur in isolation and may have compounding effects.

Several studies have examined C accumulation rates in relation to climate, atmospheric, disturbance, and land use histories using process/simulation models. Tian and colleagues[11] simulated the effects of climate, land cover change, nitrogen deposition, atmospheric CO_2 concentration, and tropospheric ozone on C sequestration and found that elevated CO_2 was the largest contributor to C sequestration and land cover change was the largest contributor to C losses in the southeastern U.S. Pan and colleagues[12] found that nitrogen deposition was the largest contributor to C accumulation in the mid-Atlantic U.S and that forest regrowth following disturbance had a greater capacity for C accumulation than did growth in old forests. Forest disturbance results in C emissions but then enhances net C uptake over the long run as forests revert to a more productive age-class but net effects depend on several factors including forest species, forest management, and environmental conditions[13,14]. In Canada, Kurz and colleagues[15] suggest that managed forests may become a source of atmospheric C due to wide-spread insect outbreaks.

At landscape and regional scales, the age-class distribution of the forest population in a region and forest aging strongly influence potential C accumulation. Forest aging, as used in this essay, addresses the temporal progression of forests (growth, normal mortality levels) as modified by disturbance (mortality and removals). Both newly

established forests and old forests have limited capacity to sequester carbon as compared to juvenile to middle-aged forests[13]. As forests across the landscape age, C accumulation rates eventually decline. For example, Nabuurs and colleagues[16] found strong indicators that forest C accumulation rates are declining in Europe. Disturbances and land use transitions influences the overall forest age structure across the landscape by either removing forests or resetting the forest to a younger age. The combined effects of forest aging, disturbance, and land use change will determine the overall rate of C accumulation in the U.S.[17] Quantifying concurrent influences of disturbances, land use change, growth, and forest cutting on forest C stock change requires a consistently measured and comprehensive data source and is fundamental to understanding C dynamics and improving projections of forest C to support policy making.

The present study uses recently remeasured forest inventory plots for the entire southeastern U.S. to identify the relative influences of forest growth, land use changes that expand or reduce forest area, and various causes of forest mortality. Because the forest inventory starts with a sampling of all land uses across a gridded landscape and includes remeasurement of permanent plots, it provides estimates of all land use transitions among forest, agricultural, developed, and other land uses. The effects of weather (e.g. hurricanes, ice storms, and tornados), fire, and insect/disease outbreaks are isolated along with the effects of forest harvesting/management and land use changes.

The southeastern U.S. (Figure 1) provides an especially useful laboratory for exploring forest dynamics: it has more forest land than 96% of the countries reported by Food and Agriculture Organization of the United Nations[18], produces >15% of global wood products from largely (89%) private forests, contains intensively managed forests (18%, as indicated by forest planting activity), and is subject to multiple extreme weather and biotic disturbances[19] (e.g., hurricanes and wildfires).

Results

From 2007–2012, total forest C increased by 81.95 Tg yr^{-1} in the region. Land use changes resulted in forest area gains and a net increase of 6.48 Tg yr^{-1} while forest dynamics (growth, mortality, cutting, forest floor accumulation) accounted for a net increase of 75.47 Tg yr^{-1}. Forest dominates land use (55% of period 2 inventory) followed by agriculture (23%) and developed (12%) uses. Approximately 95% of the area remained in the same land use between measurements. The largest transitions involved transitions of agricultural land, with 2 701 km^2 yr^{-1} shifting from agricultural to forest land uses and 2 385 km^2 yr^{-1} shifting from agricultural to developed land uses (Table 1). Forest C increased 23.36 Tg yr^{-1} as a result of agriculture to forest transitions (Figure 2) but was partially offset by a forest C decrease of 13.13 Tg yr^{-1} associated with forest to agriculture transitions. Forest to developed conversion (1 676 km^2 yr^{-1}) resulted in a decrease in forest C of 20.73 Tg yr^{-1}. Shifts from forest use to non-forest use do not mean complete depletion of the C stock; rather a portion of the forest C (largely soil carbon) is transferred to the non-forest land use.

Among disturbances that occurred between measurements, only forest cutting reduced net forest C stock (−76.7 Tg C yr^{-1}). Forests with weather, insect/disease, and fire disturbances showed net increases in forest C of +1.56, +1.4, and +5.48 Tg C yr^{-1}, respectively after accounting for salvage cutting following the initial disturbance (Figure 2). Forest disturbances result in some tree mortality, but they did not lead to net reductions in total forest C stocks over the remeasurement period due to the growth of residual trees, regeneration to fill gaps, the stability of soil organic C, and changes in residual dead material. The largest gain in forest C came from those areas without a disturbance event reflecting forest growth (including C increases in above ground, below ground, and forest floor pools) that resulted in a C accumulation of 143.77 Tg C yr^{-1} (Figure 2). This exceeds losses from forest cutting by 87%. Rather than emitted to the atmosphere, a large share of C losses from forest cutting is stored in durable wood products[20].

The net gain of forest C represents the combined effects of disturbance mortality, forest growth (above and below ground), forest floor accumulation, and the gradual decay of dead forest material. Of the 754 150 km^2 of retained forest land use, 32 388 km^2 yr^{-1} (4.3% yr^{-1}) was disturbed. The extent of forest cutting was 21 968 km^2 yr^{-1} (2.9% yr^{-1}). Insects and diseases, fire, and weather disturbances impacted 1 694 km^2 yr^{-1} (0.2% yr^{-1}), 4 411 km^2 yr^{-1} (0.6% yr^{-1}), and 4 297 km^2 yr^{-1} (0.6% yr^{-1}), respectively. Disturbance and forest cutting occurred on 2.4 times as much area as experienced a land use change.

The age structure of the forest is fundamental to understanding potential future C accumulation. When considering non-harvested areas, the C accumulation rate (Mg C ha^{-1} yr^{-1}) for the region peaks at age classes 10–15 years and 15–20 years and then declines with age (ages based on first period measurements, Figure 3a). C accumulation rate drops by >50% by age class 35–40 and by >75% by age class 65–70. Over 50% of the area harvested occurred between ages 10–35,
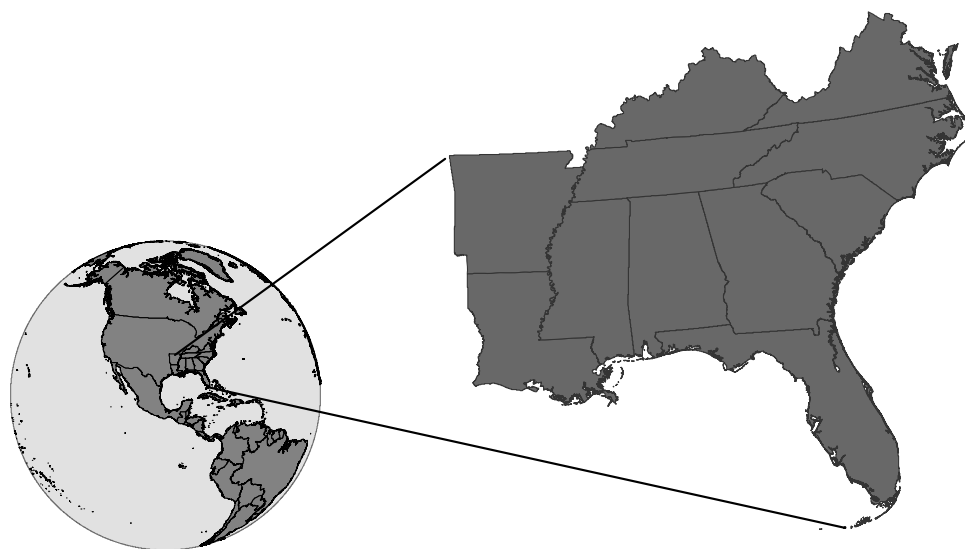

Figure 1 | Eleven state study region in the southeastern United States. Maps were generated using ArcGIS 10.0 (www.esri.com/software/arcgis).

Table 1 | Land use transition matrix for the southeastern United States (circa 2007–2012). The 2007 estimates for each land use are presented in the column heading. Entries on the diagonal are the total areal extent (km²) of land that remained in the same land use category and entries on the off-diagonal are annual change (km² yr⁻¹). Standard errors are available in Table S2

		Beginning Land Use				
		agriculture	developed	forest	other	water
		(328,335 km²)	(158,985 km²)	(771,691 km²)	(35,014 km²)	(111,568 km²)
Ending Land Use	agriculture	298,051	1,257	1,390	151	93
	developed	2,385	145,972	1,676	95	104
	forest	2,701	933	754,150	444	277
	other	225	145	153	29,236	542
	water	138	75	157	252	105,810

likely reflecting the management of planted forests in the region (Figure 3b). As a result of rapid regrowth, forest cutting was not associated with a net C loss in forests less than 25 years old.

A projection model was developed based on observed transitions to simultaneously consider the influence of land use change, forest aging, and forest disturbance (cutting, weather, fire, insects and diseases) on forest C accumulation rates for the next inventory period (2012–2017). We applied four scenarios to our projection model. For scenario 1 we posited that the observed aging and disturbance patterns would continue to affect forest development for the next ~5 years, but held forest area constant. C accumulation slowed under this scenario: the area that was forest from 2007–2012 would accumulate 9.5% less C per year (from 75.47 Tg C yr⁻¹ to 68.32 Tg C yr⁻¹) from 2012–2017 because of the disturbance/aging processes alone (Figure 4). For scenario 2, we further assume that the observed 2007–2012 land use transitions would continue from 2012–2017 and this resulted in total forest C accumulation falling from 81.95 Tg C yr⁻¹ to 78.56 Tg C yr⁻¹, a reduction of 4.1%.

There is substantial uncertainty regarding future land use transitions but as Wear and Gries[21] suggest, C stock transfers into forests from land use transitions will be especially sensitive to development pressures and the interface between agriculture and forest land uses.

For example, if the agriculture to forest transition decreased by 10%, the forest to developed transition increased by 10%, and forest aging and disturbance continued as observed (scenario 3) the total forest C stock change decreased from 81.95 Tg C yr⁻¹ (2007–2012) to 74.84 Tg C yr⁻¹ (2012–2017), a reduction of 9.5%. Long term projections indicate as much as 1 862 km² yr⁻¹ of net forest land losses in this region through 2060[17]. For scenario 4 we simulate changes in C with a reversal of observed agriculture-forest net land use changes (i.e., assume a net shift of 1 311 km² yr⁻¹ from forest to agriculture rather than the opposite), continue other land use changes, forest disturbances, and forest aging as observed. Under scenario 4, net C change would be reduced from 81.95 Tg C yr⁻¹ (2007–2012) to 48.63 Tg C yr⁻¹ (2012–2017). The scenario's total forest area reduction of 1 643 km² yr⁻¹ or 0.2% yr⁻¹ would therefore result in a 40.6% decrease in forest C stock change.

Discussion

Understanding relative contributions of disturbance vectors, land use change, and harvesting is crucial for developing improved projections of forest C and for focusing policy. Socioeconomic and biophysical processes will interact to determine forest area and forest conditions. Future disturbance rates and patterns also depend on
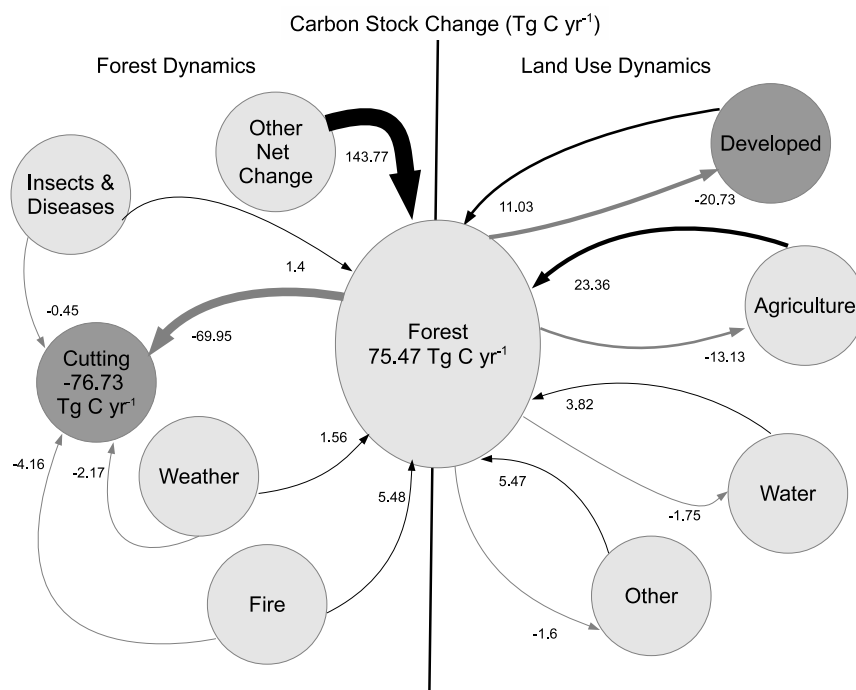

Figure 2 | Forest carbon stock changes (Tg C yr⁻¹) resulting from land use dynamics (right side) and forest dynamics within forest land uses (left side). Line thickness is proportional to the flow. Standard errors are available in Tables S3 and S4.
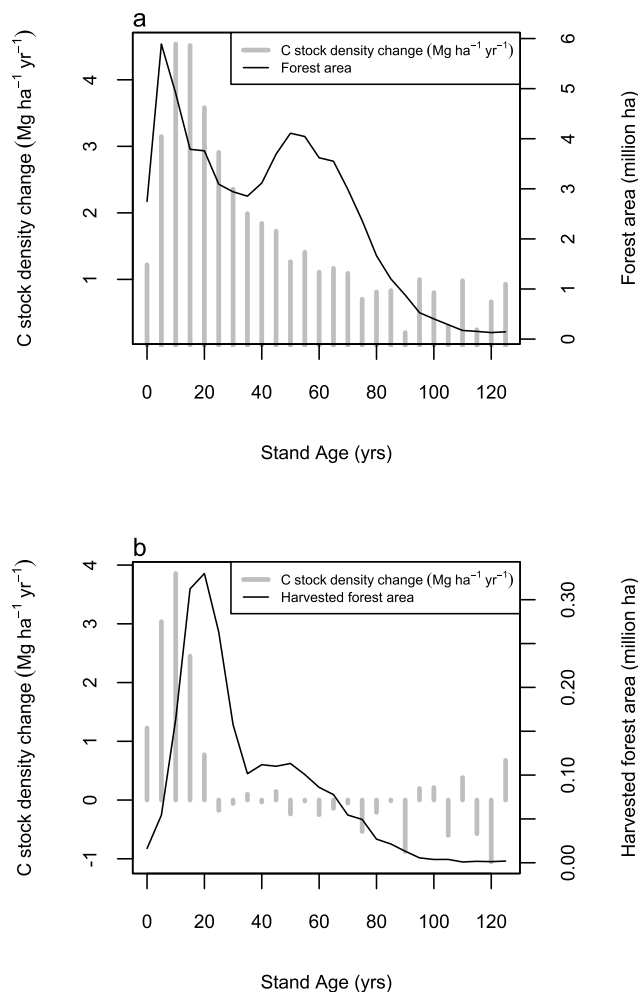
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Figure 3 | (a) C stock density change (Mg ha^{-1} yr^{-1}) by 5-year stand age class (left y, based on initial plot measurements) for forest stands that were not cut between measurements. Forest area in each time 1 age class (right y). (b) C stock density change (Mg ha^{-1} yr^{-1}) by 5-year stand age class (left y) for all forest stands. Harvested forest area in each age class (right y).

Figure 4 | **Forest C stock change (Tg C yr^{-1}) from 2012 to 2017 based on integrated land use – forest age structure model.** Scenario 1: forest remaining as forest from 2007-2012 projected to 2017. Scenario 2: Forest remaining as forest from 2012–2017 plus additions to forest land from other land uses. Land use transitions to forest were assumed to occur at the 2007–2012 rates. Scenario 3: Forest remaining as forest from 2012–2017 plus additions to forest land from other land uses. The 2007–2012 land use transition rates for agriculture to forest were decreased by 10% and the transitions from forest to developed were increased by 10%. All other rates remained at observed levels. Scenario 4: Forest remaining as forest from 2012–2017 plus additions to forest land from other land uses. The 2007–2012 land use transition rates for agriculture to forest were reversed.

climate futures. Drought, for example, provides simultaneous influences on wildfire extent and severity, insect dynamics, and tree mortality. Future forest C dynamics will depend on the interaction and relative contributions of all these change vectors and modeling frameworks that account for these interactions are crucial.

Several recent studies used process models to examine the effects of atmospheric chemistry (CO_2 and N fertilization) and disturbances on C sequestration rates[11–13]. These remote sensing/ecosystem modeling efforts typically relied on spatially modeled data (e.g. land cover, deposition, climate, soils) with little or no overlap of actual observations across variables[22]. Our estimates of plot-level C used C models for each pool with inputs from repeated measures of tree and plot-level variables (e.g. tree diameters, forest type, etc.) to estimate each C pool and observed disturbance and land use categories to summarize the data. These models of C pools are the basis for estimating forest components of the U.S. National Greenhouse Gas Inventories and represent best approximations for each pool[6].

Our results regarding the importance of disturbance align with Zhang and colleague's[13] finding that disturbance plays a major role in overall C dynamics in the southeastern U.S. Forest cutting was substantially more important than fire, insects and diseases, and weather disturbance over the time frame of our study and our results show the potential for double counting if 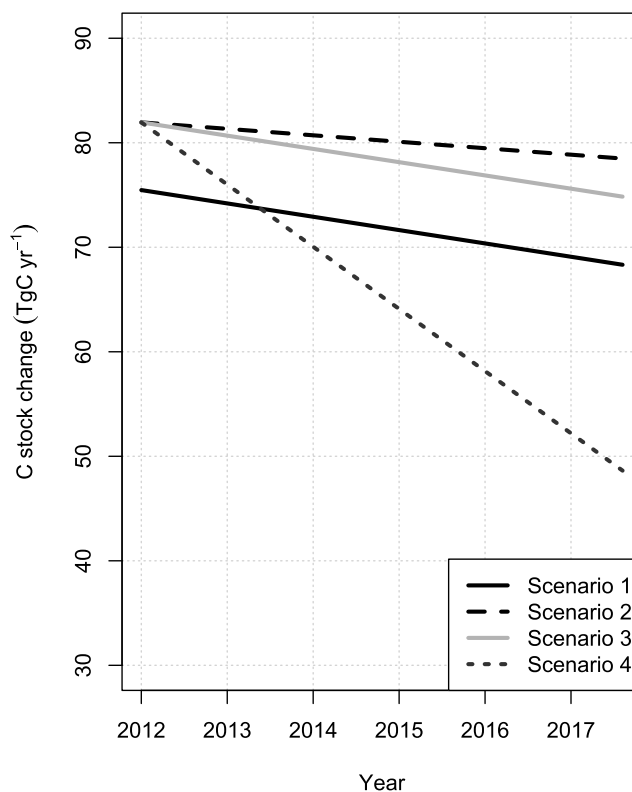the interaction of disturbance events is not considered (Figure 2, supplemental material: Double counting results). We did not include atmospheric chemistry effects in our analysis except that the observed growth rates from the remeasured inventory data reflect any actual atmospheric chemistry effects on growth. A recent study[23] suggests a growth enhancement effect of 8.4–21.6% over a 26 year period based on inventory data from Japan. However, there is disagreement on the magnitude of these effects[4,24] and we did not include potential future atmospheric chemistry effects in our short-term projections.

The short-term effects of forest aging on C accumulation are substantial. Based on our scenario 1 (stable forest land base, no land use change), forest aging decreased C accumulation by 9.5% over 5.7 years but forest aging does not result in C accumulation approaching zero in the long run. Rather the C accumulation decreases at a decreasing rate until the steady state solution of $\sim$ 48 Tg C yr^{-1}. Different future disturbance severities and rates influence both the age transition matrix and C accumulation rates used in the projection model and therefore can change the steady state solution (see supplemental material: Steady state solutions and cautions). Currently we parameterize our projection model based on observed forest data and create various land use change scenarios to provide an empirically driven approach to forecasting C accumulation. Improvements to our projection model could be made by allowing for modification of C accumulations rates to

account for atmospheric chemistry effects and shifts in disturbance amounts and severities.

Elucidating forest C dynamics over broad spatial scales requires the use of models because forest C is not observed directly. In this research, live and dead tree biomass is linked to tree measurements while soil organic carbon is based on coefficients applied to broad soil categories. Down dead wood, understory vegetation, and forest floor C, were modeled as a function of live tree C and other stand-level attributes[6]. There is substantial uncertainty in estimates of down dead wood[25], understory vegetation, and forest floor C. But these pools are relatively small components of total C stock[6]. Soil organic C is a substantial component of total C stock but is relatively stable compared to live tree C[26]. Improvements to these C models would reduce uncertainty in the analysis presented here. See Supplemental Material: Uncertainty for further discussion.

The predominately privately owned forests of the southeastern U.S. are among the most widely managed and utilized forests in the world as indicated by its production of >15% of global fiber products from 1% of the world's forest area. Despite the high level of harvest required to provide fiber products, the forest C reservoir expanded over the remeasurement period. The C inventory is highly dynamic as land use changes shifted substantial C stocks into and out of the forest pool. Land transitions to forest remain important and our results indicate that the southeastern U.S. continues to accumulate C through reforestation and regrowth, but there is potential for a slowing of C accumulation in the near future.

Forest cutting in the humid subtropical southeastern U.S. is generally associated with rapid regrowth of forests by natural regeneration or planting, followed by forest management practices (e.g., thinning, fertilization, etc.) that optimize forest productivity in intensively managed stands[27]. A share (17–25%) of harvested forest C augments harvested wood product (HWP) C pools in the US[20] after accounting for age and product specific decay rates. Skog[20] suggests that the net result of new storage and emissions from historical stocks shows the HWP C pool expanding by > 30 Tg C yr^{-1} in the US between 2000 and 2005. Precise projections of HWP dynamics requires a detailed accounting of historical wood products stocks, but applying the recent transfer ratio to our removals estimates (assuming the midpoint or 21%), would increase baseline forest C change from 81.95 Tg yr^{-1} to 98.05 yr^{-1}. Our analysis of change in forest C dynamics assumes removals and therefore the transfer of forest C to harvested wood products remains constant across time periods (consistent with observed slow change in the national HWP C accounts) and would therefore not bias the inter-temporal comparisons. Our findings indicate that forest C accumulation from growth is substantially higher than C emissions from forest cutting. For unharvested forests, site-level growth following disturbance more than compensates for C losses, as disturbed forests showed a net gain in C. Whether this growth response will continue to compensate for disturbances depends on the extent, severity, and frequency of future disturbance; however, our results clearly show that evaluating disturbance related emissions without considering post-disturbance growth responses would bias results and potentially skew policies.

Our results show southeastern U.S. forests as resilient to disturbance related mortality, with no net loss of C indicated for forest plots with disturbances exclusive of forest cutting. This result may not hold in other regions where environmental conditions may be less conducive to rapid forest regeneration and growth—i.e., in regions with shorter growing seasons and higher aridity—but indicates a strong resilience of forest C to disturbance in a humid subtropical setting. Aging of forests will reduce forest C accumulation and reduce the capacity to offset losses from future land use changes. Comparing across the various changes in forests in this region, forest cutting, forest aging, and land use changes clearly dominate forest C dynamics and highlight the need for careful assessment of policies and program that affect forest management and land use transitions in rural areas.

Methods

Data. We used the USDA Forest Service Forest Inventory and Analysis data for our analysis (http://apps.fs.fed.us/fiadb-downloads/datamart.html). The Forest Inventory and Analysis program uses a repeated measure, rotating panel design, where each panel typically constitutes 20% of the entire sample (i.e., a 5 panel design). Each panel is a quasi-systematic sample that covers all land and water in each population with a sampling intensity of one 674.5 m^2 ground plot per 2 403 ha of land and water area. Eleven States in the S.E. U.S comprise our study area (Figure 1) and include ~49 000 plots with repeated samples.

Forest age was an important component in this research. For each sample location that was classified as a forest land use, age was determined by coring three dominant or co-dominant trees that represent a plurality of non-overtopped trees. Stand age was the average height of these three trees. This same approach was used for both even and uneven-aged stands.

C models. For each measured plot, C values were estimated for eight pools (down dead wood, forest floor, live trees above ground, live trees below ground, standing dead wood, soil organic C, understory vegetation above ground, and understory vegetation below ground) using the models described by U.S. EPA[6]. Tree measurements (e.g., species, height, diameter) were used to calculate forest stand C density for the above ground and below ground components of live trees and standing dead trees. Understory C was modeled as a function of live C density and the community type of the forest stand. Carbon in down dead wood was a function of the community type of the forest stand and the live tree C density (above and below ground) plus an additional component to account for logging residue. Forest floor C was modeled as a functions of the age and community type of the forest stand. Soil organic C was based on the STATGO soil type database. Total C was the sum of the eight individual pools.

Land use classification. We used a land use classification (supplemental material Table S1) that was consistent with IPCC good practice guidelines[28]. Based on these IPCC guidelines, harvested areas that are replanted or left to naturally regenerate remain in forest land use. Forested areas that were naturally disturbed (e.g., fire) also remain in a forest land use, even though the above ground C components may be mostly removed. Others[29] have used forest cover classifications which do not follow IPCC good practice guidelines[30], resulting in different inferences.

Estimates: land use change, C stock change, and disturbances. A land use transition matrix was constructed based on measured annual rates of transitions among agriculture, developed, forest, other, and water land uses. Records for plots defined by forest land use at either time 1 or time 2 contained additional forest stand and tree level attributes used to quantify forest age structure, forest C, and forest disturbance. An annual C density change was calculated for each land use transition. For plots that contained forest at time 1 and time 2 the proportion of the plot disturbed by forest cutting, fire, insects or diseases, and weather events was calculated along with the corresponding plot-level annual C density change. We used a post-stratified estimator[31] to construct population estimates of the areal extent of land use transitions, C stock change from land use transitions, the areal extent of disturbances, and the C stock change associated with those disturbances. See supplemental material for more information.

Projections. Land use change, disturbances, and forest aging were the drivers behind the projections. We developed an integrated land use change - forest age structure projection model parameterized with observed age transitions for persistent forests (5-year age classes, after accounting for disturbances), observed land use transitions, observed forest C stock density change by age class, observed C stock transfers from forest to other land uses by age class, and observed C stock transfer from other land uses to forest by age class. Scenarios were defined by modifying one or more of these transition elements. The area transition matrix was used to project land use forward to 2017, and the age structure of forest land use in 2017 was projected using the historical forest age transition matrix. C stock change was then calculated based on the area of each forest age class and the corresponding C stock change densities. C stock transfer from other land uses to forest derived from the land use transitions and the non-forest to forest stock transfer C stock change densities by age class. The same approach was applied to stock transfers from forest land use to other land uses. The projected C stock change was the C accumulation of forest under the new age structure (which includes the influence of observed disturbance dynamics) plus C stock transfer from non-forest land uses, minus C stock transfers to other land uses. The effects of alternative land use change rates were constructed by modifying the land use transition matrix. Additional details are provided in the supplemental materials.

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Acknowledgments

Author contributions

J.W.C., D.N.W. and J.M.V. designed the study; J.W.C. and D.N.W. performed the analysis; and all authors contributed to the interpretation of the results and the writing of the paper.

Additional information