



Carbon pools in China's terrestrial ecosystems: New estimates based on an intensive field survey

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China's terrestrial ecosystems have functioned as important carbon sinks. However, previous estimates of carbon budgets have included large uncertainties owing to the limitations of sample size, multiple data sources, and inconsistent methodologies. In this study, we conducted an intensive field campaign involving 14,371 field plots to investigate all sectors of carbon stocks in China's forests, shrublands, grasslands, and croplands to better estimate the regional and national carbon pools and to explore the biogeographical patterns and potential drivers of these pools. The total carbon pool in these four ecosystems was 79.24 ± 2.42 Pg C, of which 82.9% was stored in soil (to a depth of 1 m), 16.5% in biomass, and 0.60% in litter. Forests, shrublands, grasslands, and croplands contained 30.83 ± 1.57 Pg C, 6.69 ± 0.32 Pg C, 25.40 ± 1.49 Pg C, and 16.32 ± 0.41 Pg C, respectively. When all terrestrial ecosystems are taken into account, the country's total carbon pool is 89.27 ± 1.05 Pg C. The carbon density of the forests, shrublands, and grasslands exhibited a strong correlation with climate: it decreased with increasing temperature but increased with increasing precipitation. Our analysis also suggests a significant sequestration potential of 1.9–3.4 Pg C in forest biomass in the next 10–20 years assuming no removals, mainly because of forest growth. Our results update the estimates of carbon pools in China's terrestrial ecosystems based on direct field measurements, and these estimates are essential to the validation and parameterization of carbon models in China and globally.

carbon stock | climatic influences | human influences | spatial variations | terrestrial ecosystems

Terrestrial ecosystems are a significant carbon sink on Earth, accounting for ~20–30% of the total anthropogenic carbon dioxide (CO₂) emissions to the atmosphere. Compared with oceans, terrestrial ecosystems can be readily managed to either increase or decrease carbon sequestration by restoring or degrading vegetation (1). China is a good example of this interaction between human-driven vegetation change and terrestrial carbon exchange (2, 3). For example, China's forest coverage decreased from 30 to 40% in the early 1950s to ~14% in the early 1980s because of excessive exploitation of forest resources. However, since then, nationwide vegetation restoration practices, including several key ecological restoration programs, have been implemented (4), resulting in a significant increase in forest coverage—from 13.9% in the early 1990s to 21% in the 2010s (5, 6). Corresponding to the changes in forest area and the growth of established forests, the carbon pools of China's forest ecosystems have significantly increased during these decades (7–9). Compared with forests, biomass production of grasslands and croplands is quite low, varying from 0.01 to 0.02 Pg C per year, and thus limited

change of carbon pools has occurred in China's croplands and grasslands over the past three decades (8, 9).

Although there have been several studies of the carbon pools of China's terrestrial ecosystems, the estimates of these pools have varied by more than 100 Pg C (*SI Appendix, Table S1*), suggesting an inconsistency among these estimates. This inconsistency is likely due to the limitation of sample size and data representativeness, multiplicity of data sources, and inconsistency of methodologies. In addition, previous estimates at both regional and national scales were primarily obtained based on summarized data of the regional or national censuses (e.g., China's forest inventory and China's grassland resource survey) (7, 10, 11) and not from original observations (2). Our knowledge of the driving forces causing the changes in terrestrial ecosystem carbon pools is also very limited and has impeded the application of management measures.

To fill this knowledge gap, we conducted a nationwide field campaign between 2011 and 2015 to investigate the carbon stocks of terrestrial ecosystems in China. A reviewable, consistent inventory system, independent of the routine surveys

Significance

Previous estimations of carbon budgets in China's terrestrial ecosystems varied greatly because of the multiplicity of data sources and the inconsistency of methodologies. By conducting a methodologically consistent field campaign across the country, we estimated that the total carbon pool in China's forests, shrublands, grasslands, and croplands was 79.24 ± 2.42 Pg C. The carbon density exhibited a strong dependence on climate regime: it decreased with temperature but increased with precipitation. The country's forests have a large potential of biomass carbon sequestration of 1.9–3.4 Pg C in the next 10 to 20 years assuming no removals. Our findings provide a benchmark to identify the effectiveness of the government's natural protection policies.

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conducted for forests and shrublands by the Chinese Ministry of Forestry (6) and for grasslands by the Chinese Ministry of Agriculture (12) was developed based on the spatial distributions of China's terrestrial ecosystems (*SI Appendix, Texts S1–S3*). In total, 13,030 field plots were investigated across forests, shrublands, and grasslands in mainland China using consistent methodology (*Materials and Methods* and *SI Appendix, Fig. S1*). We also conducted a systematic field investigation for croplands, with 1,341 field plots from 58 counties that represent typical cropping systems used in China (*SI Appendix, Text S4*, and *Fig. S1*). Here we defined “forest” as the land with an area of ≥ 0.067 ha dominated by trees and with a tree crown coverage of $\geq 20\%$; “shrubland” as the land dominated by shrubs with a canopy height of < 5 m and canopy coverage of $> 30\text{--}40\%$; “grassland” as the land dominated by herbaceous plants; and “cropland” as the land surface covered by crops with a minimum area of $5,400 \text{ m}^2$ that is seeded at least once per year (*SI Appendix, Texts S1–S4*).

Our field campaign investigated all carbon components of an entire ecosystem in these four vegetation groups, including above- and belowground biomass, understory plants, litter, and soils. The major purposes of this study are to estimate the carbon pools of these ecosystems and to elucidate the possible climatic and anthropogenic drivers of the spatial distributions of these carbon pools by using direct field measurements collected in this study. Note that we did not investigate the carbon pools in Taiwan, Hong Kong, Macao, and the South China Sea Islands because of the unavailability of fieldwork and the small land areas in these islands. Our study focused on forests, shrublands, and grasslands when exploring the drivers shaping the distribution of carbon stocks because croplands are intensively human managed.

Results

Carbon Stocks and Their Spatial Variations. Ecosystem carbon density (carbon stock per hectare) of forests, shrublands, and grasslands exhibited large spatial variations at the national scale (Fig. 1). Both biomass and litter carbon densities decreased from the northeastern, southern, southeastern, and southwestern regions to the northern and northwestern regions and to the Tibetan

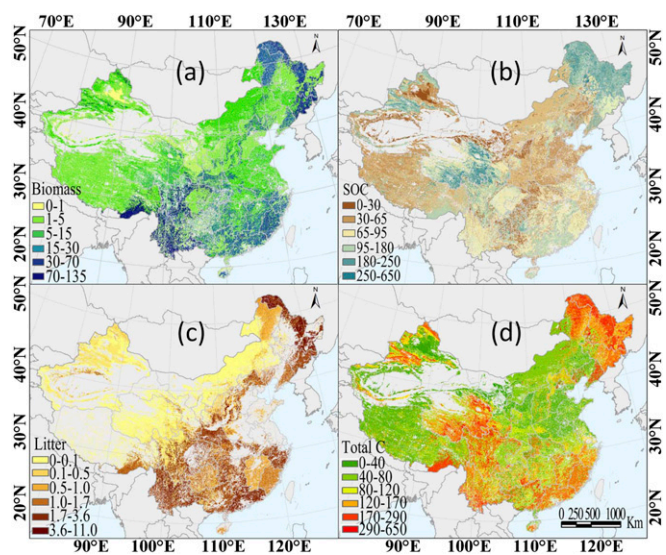


Fig. 1. Spatial distribution of ecosystem carbon density (Mg C ha^{-1}) in forests, shrublands, grasslands, and croplands in China. (A) biomass carbon. (B) Soil organic carbon (up to 1 m in depth, where applicable). (C) Litter carbon. (D) Total ecosystem carbon. The site-averaged carbon density of each biome in each province was assigned to the corresponding polygons of the ChinaCover map. (For details on the ChinaCover map and associated vegetation biomes, see ref. 5. Please note that we did not investigate the carbon pools in Taiwan, Hong Kong, Macao, and the South China Sea Islands.)

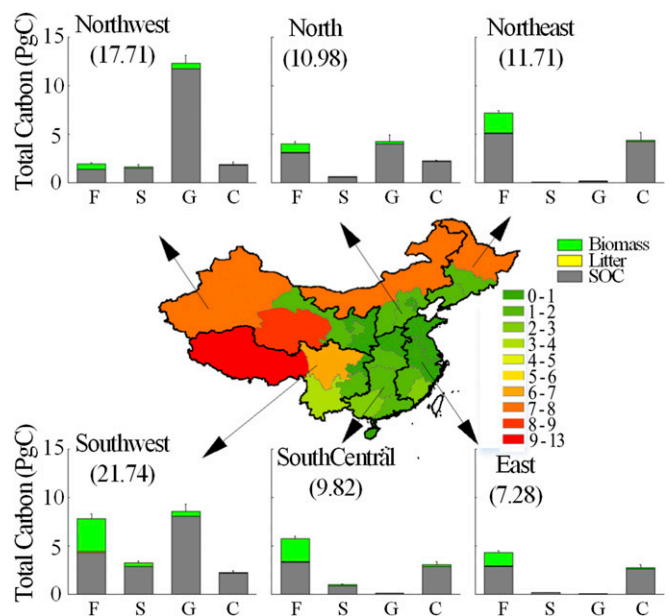


Fig. 2. Distribution of provincial-level total ecosystem carbon pools (Pg C) in China's forests, shrublands, grasslands, and croplands and their histograms by region. In each histogram, the carbon pools of biomass, litterfall, and soil in forests (F), shrublands (S), grasslands (G), and croplands (C) are shown for the six regions (Northeast, North, Northwest, East, South Central, and Southwest).

Plateau (Fig. 1 *A* and *C*). However, the soil carbon density displayed complex variations: the maximum density occurred on Mount Xing'an in the northeastern region, Mounts Qilian and Bayan Har in Qinghai, and Mounts Tianshan and Alta in northern Xinjiang, followed by the southern and southeastern regions. The lowest soil carbon densities were in the lower basins in Xinjiang, the Hexi Corridor in Gansu, and on part of the Loess Plateau (Fig. 1*B*). The mean ecosystem carbon density showed the highest value in forest ecosystems ($163.8 \pm 8.4 \text{ Mg C ha}^{-1}$), which is ~ 1.8 times higher than that in shrublands ($89.9 \pm 4.4 \text{ Mg C ha}^{-1}$) and grasslands ($90.3 \pm 5.3 \text{ Mg C ha}^{-1}$) (see *SI Appendix, Table S2* for details). Overall, the area-weighted average ecosystem carbon density of all three vegetation groups was $115.7 \pm 6.2 \text{ Mg C ha}^{-1}$, with 23.1 ± 5.7 , 0.8 ± 0.9 , and $91.8 \pm 9.2 \text{ Mg C ha}^{-1}$ stored in biomass, litter, and soil.

The total carbon pool of these three ecosystems was $62.93 \pm 3.39 \text{ Pg C}$, of which biomass, litter, and soil organic carbon [(SOC) at a 1-m depth, where applicable] were 12.55 ± 3.07 (20%), 0.46 ± 0.48 (0.7%), and $49.92 \pm 4.98 \text{ Pg C}$ (79.3%), respectively (*SI Appendix, Table S3*). The largest carbon pool was in forests ($30.83 \pm 1.57 \text{ Pg C}$, 49%), followed by grasslands ($25.40 \pm 1.49 \text{ Pg C}$, 40.4%), and shrublands ($6.69 \pm 0.32 \text{ Pg C}$, 10.6%). Geographically, $19.53 \pm 0.54 \text{ Pg C}$ (31%) was stored in southwestern China (Fig. 2) because of its large area and high carbon densities in vegetation biomass and soils. By contrast, only $4.55 \pm 0.11 \text{ Pg C}$ (7%) was stored in eastern China (Fig. 2), where carbon densities were quite low (Fig. 1*D*).

In addition, we used the Random Forest simulation (a machine-learning approach) to elucidate the detailed spatial patterns of carbon density and then estimated the national total carbon pools (for details, see *SI Appendix, Text S2*). The biome-scale mean carbon densities based on the Random Forest simulation showed a good coincidence with those based on the area-weighted average approach (*SI Appendix, Fig. S2*). The overall carbon stock of forests, shrublands, and grasslands totaled $64.17 \pm 1.92 \text{ Pg C}$, which is highly consistent with our estimate using the area-weighted average approach ($62.93 \pm 3.39 \text{ Pg C}$) (*SI Appendix, Table S3*).

Compared with these three ecosystems, the cropland ecosystem had lower biomass carbon density ($3.06 \pm 0.87 \text{ Mg C ha}^{-1}$),

but similar soil carbon density ($92.04 \pm 4.06 \text{ Mg C ha}^{-1}$) (*SI Appendix, Table S2*). Higher values occurred in the northeastern regions, followed by the southwestern regions, while lower values were found in the dry areas in northern China. Overall, the total carbon pool of China's croplands was estimated as $16.32 \pm 0.41 \text{ Pg C}$ (*SI Appendix, Table S3*).

Carbon Allocation Between Below- and Aboveground Biomass and Between Soil and Vegetation. Both above- and belowground biomass carbon densities varied among forests, shrublands, and grasslands (Fig. 3). The site-averaged aboveground biomass carbon densities were 42.5 ± 4.6 (mean \pm 1 SD) Mg C ha^{-1} in forests, $3.3 \pm 4.6 \text{ Mg C ha}^{-1}$ in shrublands, and $0.4 \pm 0.6 \text{ Mg C ha}^{-1}$ in grasslands, respectively. Their site-averaged belowground biomass carbon densities were 10.7 ± 7.1 , 3.1 ± 4.6 , and $3.5 \pm 4.8 \text{ Mg C ha}^{-1}$, respectively. The allocation of below- to aboveground biomass carbon (root to shoot ratio, or RS ratio) differed markedly among forests and shrublands (*SI Appendix, Fig. S4*), and the biomes in each vegetation group (*SI Appendix, Fig. S5A*).

The site-averaged soil carbon densities showed greater variations than did biomass carbon densities (Fig. 3). The mean SOC densities were $126 \pm 98.1 \text{ Mg C ha}^{-1}$ in forests, $60.2 \pm 83.2 \text{ Mg C ha}^{-1}$ in shrublands, and $58.4 \pm 69.3 \text{ Mg C ha}^{-1}$ in grasslands. The ratio of soil to biomass carbon density showed large variation across sites within vegetation groups (*SI Appendix, Fig. S4*). Compared with forests, shrublands showed much larger ratios of soil carbon to vegetation biomass carbon because of the relatively smaller vegetation biomass densities in shrublands (*SI Appendix, Figs. S4 and S5B*).

Effects of Climatic Factors on Carbon Stocks. To illustrate relationships between ecosystem carbon stocks and climatic variables, we divided all of the field data into two groups according to a mean annual precipitation (MAP) of 400 mm (i.e., the threshold of an arid climate) and a mean annual temperature (MAT) of 10°C (i.e., the threshold of a warm temperate climate) to detect how ecosystem carbon sectors (total, biomass, litter,

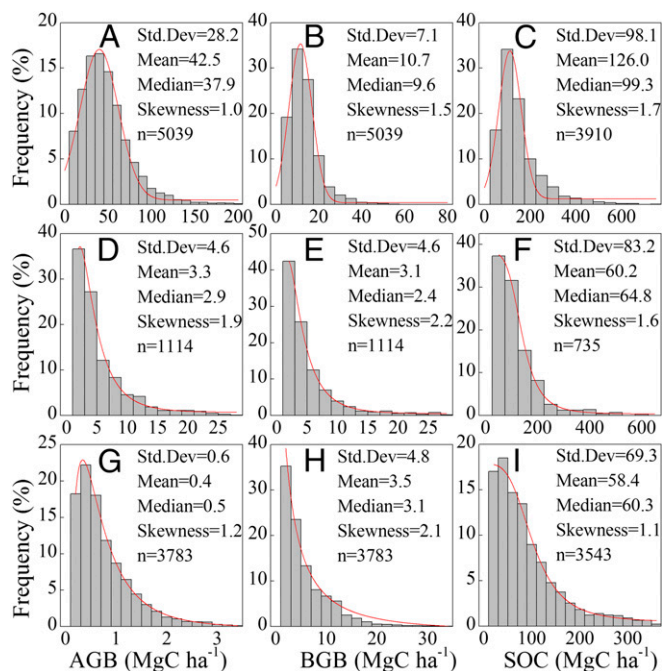


Fig. 3. Frequency distribution of carbon densities of different carbon sectors in China's forests, shrublands, and grasslands. (A, D, and G) Aboveground biomass (AGB). (B, E, and H) Belowground biomass (BGB). (C, F, and I) Soil organic carbon (SOC). Line in A–C: forests; line in D–F: shrublands; line in G–I: grasslands.

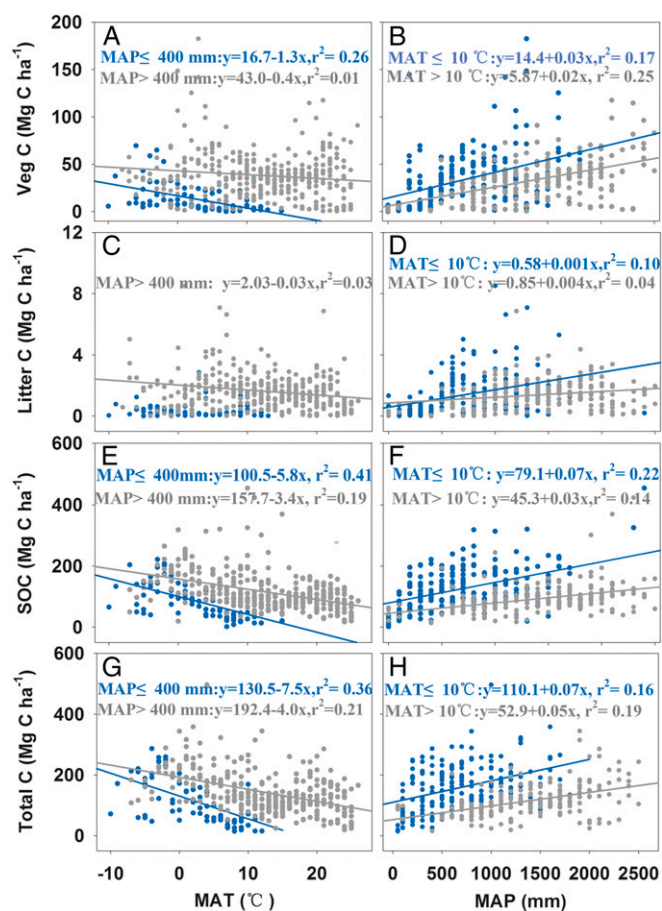


Fig. 4. Relationships between carbon density and MAT and MAP in forests, shrublands, and grasslands in China for two MAT groups ($\leq 10^\circ\text{C}$ and $> 10^\circ\text{C}$) and two MAP groups ($\leq 400 \text{ mm}$ and $> 400 \text{ mm}$). (A and B) Vegetation biomass carbon. (C and D) Litter carbon. (E and F) Soil organic carbon. (G and H) Whole-ecosystem carbon. Each dot shows the average carbon density within each 1°C MAT and 100 mm MAP.

and soil carbon) respond to climatic regimes under different climatic conditions, as these two climatic thresholds are important in China's climatic classification (13). As a result, the spatial pattern of the carbon density showed a strong correlation with the climate variables (Fig. 4 and *SI Appendix, Fig. S6*). In general, the total carbon density and all carbon sectors (biomass, litter, and soil) decreased with increasing MAT but had a lower decreasing rate in the regions where the MAP exceeded 400 mm. By contrast, they increased with increasing MAP and showed a higher increasing rate in the regions in which $\text{MAT} < 10^\circ\text{C}$ (Fig. 4).

Furthermore, we found a close relationship between ecosystem carbon density and the wetness index (P/PET , a surrogate of the moisture index that indicates the ratio of precipitation to potential evapotranspiration) ($r^2 = 0.92$, $P < 0.0001$) (*SI Appendix, Fig. S7*) (14). Interestingly, an annual P/PET value of 1.0 strongly corresponded to the ecosystem carbon density value of 100 Mg C ha^{-1} and to the threshold to segment the linear relationship between carbon density and the wetness index. Specifically, the carbon density showed a strong correlation with P/PET when the density was ≤ 1.0 ($r^2 = 0.96$, $P < 0.0001$); otherwise, the correlation was poor when the density was > 1 ($r^2 = 0.16$, $P = 0.154$). These results suggest that carbon density exhibits various feedbacks to climate under different moisture conditions.

Effects of Human Activities on Carbon Stocks. To examine the effects of human activities on different carbon sectors in forests, shrublands, and grasslands, we divided all field sites into two

groups based on the degree of human disturbance: sites with intensive human influences, which included forest plantations and intensively grazed grasslands, and other sites with fewer human influences, which included natural forests, primary shrublands, and natural or less-grazed grasslands (*SI Appendix, Text S5*). Our results indicate that intensive human activities have reduced both the above- and belowground biomass of most vegetation types (*SI Appendix, Fig. S5A*) with overall reductions of 21% ($r^2 = 0.96$, $P < 0.001$) for aboveground biomass and 24% ($r^2 = 0.61$, $P < 0.01$) for belowground biomass (*SI Appendix, Fig. S8*). Interestingly, the reduction in belowground biomass was almost proportional to the reduction in aboveground biomass, thus resulting in insignificant changes in the RS ratio. In contrast to forests and shrublands, human activities have significantly reduced aboveground biomass in two of the four grassland types, but they have not consistently decreased the belowground biomass, leading to an elevated RS ratio in heavily influenced grassland sites. However, human disturbance did not exert significant effects on soil carbon stocks for all biome types; the overall SOC density of 14 vegetation types with intensive disturbances was approximately equivalent to that with fewer intensive effects (slope of linear regression = 0.97, $r^2 = 0.61$, $P < 0.01$) (*SI Appendix, Fig. S8D*).

Discussion

Comparison of Carbon Pools with Previous Estimates. The extensive field survey in the present study has provided a full picture of the ecosystem carbon stocks in the forests, shrublands, grasslands, and croplands of China. Our estimate of China's forest biomass carbon density was higher than that in previous studies (55.7 vs. 41.3 Mg C ha⁻¹) (*SI Appendix, Table S1*) (10). This difference probably resulted from the changes in forest areas and age structures as well as the inconsistency in methodology. As shown in *SI Appendix, Table S1*, both forest area and biomass carbon density has significantly increased in recent decades. For example, China's forest area and mean biomass density increased from 132 × 10⁶ ha and 37.9 Mg C ha⁻¹ in the period of 1994–1998 to 149 × 10⁶ ha and 41.2 Mg C ha⁻¹ in the period of 2004–2008, respectively (9, 15). Studies have also shown that areal expansion and forest growth have nearly equally contributed to the increase in forest biomass carbon pools in China (15, 16). This suggests that the differences between our estimates and the previous estimates are largely attributed to changes in forest area and forest growth. In addition, our estimates of the carbon density of shrublands and grasslands were similar to most previous estimates (*SI Appendix, Table S1*). The higher value for grassland biomass (10.2 Mg C ha⁻¹) reported by Ni (17) may be because the global averages of carbon densities were used. The previous soil carbon density estimates were 1.6–1.8 times higher than our measurements (*SI Appendix, Table S1*). This difference is likely because most of the previous studies were based on data

from the national soil survey and ignored gravel in soils and spatial discrepancies of soil depths (*SI Appendix, Table S1*).

We estimated that the total carbon pools of both the biomass and the soils of forest, shrubland, grassland, and cropland ecosystems in China were 13.1 ± 2.2 Pg C and 65.7 ± 3.5 Pg C, respectively (*SI Appendix, Table S1*; also see *SI Appendix, Table S3*, for details). To evaluate the total carbon pool of all terrestrial ecosystems in the country, we incorporated the carbon stock data from wetlands (18), built-up lands (19), and other land ecosystems (i.e., tree orchards, tree gardens, shrub orchards, shrub gardens, and lawns) (20–22) into our estimation. We therefore estimated the total terrestrial carbon pool in mainland China to be 89.3 ± 1.1 Pg C (Table 1). Note that our estimates did not include deep soil carbon (>1 m in depth), although deep soil carbon may be substantial, especially in forests (23), grasslands (23), wetlands (18), and loess ecosystems (24).

Driving Forces of Carbon Pools. Our results indicate that the biogeographical patterns of each carbon pool in forests, shrublands, and grasslands coincide with temperature and precipitation distribution patterns (Fig. 4 and *SI Appendix, Fig. S6*), suggesting a critical role of climate in shaping the distribution of carbon stocks. Furthermore, we found a nonlinear relationship between ecosystem carbon density and climatic moisture (P/PET), with a threshold change at $P/PET = 1$. Carbon density was much more closely correlated with climatic moisture in dry areas ($P/PET < 1$; $r^2 = 0.96$, $P < 0.0001$) than in humid areas ($P/PET > 1$; $r^2 = 0.16$, $P = 0.154$) (*SI Appendix, Fig. S7*), revealing that the ecosystem carbon stock is more constrained by water availability in the dry areas than in the humid areas. This is not surprising, because precipitation is generally the determinant factor for plant production and microbial respiration in arid areas (25), while temperature and nutrient availability are more important for plant production, microbial decomposition, and carbon stocks in humid regions (26), as previously demonstrated (27).

Our results also suggest that carbon stocks are sensitive to human activities, particularly for shrublands and grasslands (*SI Appendix, Fig. S5*). The substantial effects of human activities on ecosystem carbon density provide guidance for land-based carbon management strategies. Conservation practices in China, such as the Grain for Green program and the Natural Forest Protection projects, have significantly stimulated carbon uptake into forest and shrubland biomass and have promoted soil carbon sequestration in those ecosystems (28). However, in some intensively managed ecosystems, such as bamboo forests and meadow grasslands, human activities have also increased soil carbon stocks (*SI Appendix, Fig. S5B*), but persistent carbon increase in the soils depends on management strategies and the extent of human activities (29).

Table 1. Carbon pools in the terrestrial ecosystems of mainland China

Ecosystem	Area, ×10 ⁶ ha	Vegetation, Pg C	Soil, Pg C	Source
Forest	188.2	10.48 ± 2.02	19.98 ± 2.41	This study
Shrubland	74.3	0.71 ± 0.23	5.91 ± 0.43	This study
Grassland	281.3	1.35 ± 0.47	24.03 ± 2.52	This study
Cropland	171.3	0.55 ± 0.02	15.77 ± 0.57	This study
Wetlands	35.6	0.27	6.18	18
Built-up land	25.3	0.17	1.78	19
Other land	9.5	0.76	1.34	20–22
Nonvegetated land	160.9	NA	NA	
Total	946.4	14.29 ± 0.74	74.98 ± 1.28	

Vegetation and soil carbon pools in forests, shrublands, grasslands, and croplands were estimated using field campaign data from this study and corresponding areas from the ChinaCover map (5). Carbon pools in wetlands, built-up land, and other land were estimated by ground-based data from previous studies and the corresponding area from the ChinaCover map. Other land includes tree orchards, tree gardens, shrub orchards, shrub gardens, lawns, etc. Nonvegetated land includes bare rock, Gobi desert, salina, and permanent ice/snow. NA, not applicable.

Potential of Carbon Sequestration in China's Terrestrial Ecosystems.

We found that the carbon stock in the soils of China's forests, shrublands, and grasslands was 3.9 times higher than that in the biomass (*SI Appendix, Table S1*), which is a higher ratio than the estimates for the continental United States (3.0) and Europe (3.5) (30). The large proportion of soil to ecosystem carbon pool may be attributed to the low biomass carbon densities in China (8). Indeed, the area-weighted mean biomass carbon densities of the forests (55.7 Mg C ha⁻¹), shrublands (8.9 Mg C ha⁻¹), and grasslands (4.8 Mg C ha⁻¹) in China (*SI Appendix, Table S2*) were substantially lower than the global means [94.2 Mg C ha⁻¹ for forests (31) and 7.2 Mg C ha⁻¹ for grasslands (32)]. Large areas of young forests and widespread grazing are likely responsible for the low biomass carbon density of forests and grasslands in China (9, 15). For example, nearly 90% of forests are less than 60 y old, with a biomass of less than 60 Mg C ha⁻¹ (Fig. 5), which is significantly lower than the biomass (104.7 ± 30.3 Mg C ha⁻¹) of China's old forests (≥100 y) and the mean of global forests.

The large proportion of young and middle-aged forests in China suggests a substantial potential for carbon sinks in the future. Considering the biomass-age effect (Fig. 5 and *SI Appendix, Table S4*) and assuming a stable forest area and sustainable forest management, we estimate that biomass carbon stocks in China's forests will increase by 1.19 and 2.97 Pg in 2020 and 2030, respectively (*SI Appendix, Table S5*). These projected forest biomass carbon increments are comparable to those of a similar study that used forest inventory data and biomass-age relationships (1.73 ~ 3.11 Pg C) (33), but lower than the estimates by the forest C sequestration model (5.64~9.86 Pg C) (34). Future biomass carbon density should be larger than our estimates if forest areal expansion (16), vegetation restoration and protection, and soil carbon increases are taken into account. Global change factors such as CO₂ enrichment, climate warming, and nitrogen deposition may also affect the carbon sequestration of terrestrial ecosystems in China (15, 35, 36). In addition, nationwide vegetation restoration practices, ecological improvement programs, and natural conservation policies may enable carbon gains to continually increase in the future (3, 4). However, it should be cautioned that the imbalance between timber supply and demand under the current forest management policies could increase wood and fiber importation in China. The rising demands of timber imports may result in an international concern because of increasing ecological footprints (37).

Implications. Our nationwide field campaign provides both an up-to-date estimate of the ecosystem carbon pools in China's forests, shrublands, grasslands, and croplands and a baseline for

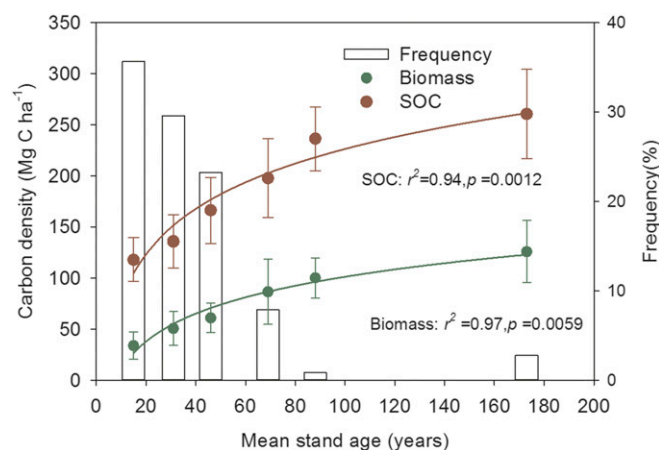


Fig. 5. Changes in average biomass and SOC density with mean forest age along with the frequency distribution of the number of sampling sites vs. mean forest age. The error bar shows 1 SD.

evaluating the effects of the afforestation and conservation practices and future use. Our results show that unsustainable management generally reduced ecosystem carbon density, with more negative impacts on soil carbon than on vegetation biomass carbon. Compared with the human impacts, the restoration and conservation practices are likely to increase carbon uptake in China's terrestrial ecosystems and compensate for the ecological footprint in the future. The large areas of young forests in China promise continued carbon sinks in both the vegetation and the soil. In addition, our field-based data, which was collected across a large biogeographic extent ranging from subarctic/alpine to tropical ecosystems and from dry to humid ecosystems, are fundamental for the validation and parameterization of other carbon-cycling studies and carbon models in China and other regions of the world.

Materials and Methods

China's four major vegetation groups—forest, shrubland, grassland, and cropland—were surveyed in this study (for details on the definition of these vegetation groups, see *SI Appendix, Texts S1 and S4*). The vegetation groups were further subdivided into 14 biomes, including 6 forest biomes, 4 shrubland biomes, and 4 grassland biomes, which is consistent with the level II vegetation classification of ChinaCover (5). Considering that bamboo forests differed from other forest biomes, we separated them from other level II forest types by overlaying the distribution map of bamboo forests on the ChinaCover map (see *SI Appendix, Text S3* for details). Ecosystem carbon stocks of forests, shrublands, grasslands, and croplands were then estimated using carbon density data derived from field investigations and areas of each level II vegetation type from ChinaCover.

Protocols for Field Surveys. A reviewable, consistent field inventory protocol and laboratory methodology were developed in this study (*SI Appendix, Texts S1–S4*). Based on the distributions of China's forests, shrublands, and grasslands and their species composition and structure, we determined sampling sites of these natural ecosystems across the country according to the representativeness of the vegetation types and the sampling method outlined by the Intergovernmental Panel on Climate Change (IPCC) (38, 39). All of the measurements were conducted between 2011 and 2015. For croplands, 1,341 field plots (>1 m) were investigated across 58 counties that have typical cropping systems as those used in China by using systematic sampling approaches (*SI Appendix, Fig. S1*). For details on the methods of field sampling and carbon stock estimation, see *SI Appendix, Text S4*.

Sampling design. We divided the country into three types of grid sizes—100 km², 400 km², and 900 km²—on the basis of vegetation distribution using a 1:1,000,000 vegetation map (40). A grid size of 100 km² was designed for tropical and subtropical regions with rich species diversity, and 400 and 900 km² were for temperate and alpine vegetation regions where species diversity is relatively poor (*SI Appendix, Fig. S1*). In total, 35,800 grids were documented across the country, and then they were overlaid on vegetation and administrative maps to obtain the numbers of the grids for each vegetation group (forests, shrublands, and grasslands) and for each of the 30 provinces. In each province, 3–5% of the grids were randomly chosen for field investigations. Based on the information on local vegetation (e.g., historical inventory data), we determined the location of the sites in each grid before our field work. The field investigations were conducted at the preset locations or near them when they were not accessible (less than 10% of total investigation sites). Overall, 7,800, 1,200, and 4,030 sites were established for the field measurements in forests, shrublands, and grasslands, respectively.

Plot size. For the forests, at each site, one 1,000-m² plot (600 m² in a few cases of plantations) was established, consisting of 10 subplots (10 × 10 m²). All stems in the tree layer were measured throughout the plot. Three quadrats (2 × 2 m²) were randomly established in the plot to investigate the understorey plants, including shrubs, seedlings, and herbaceous plants. One quadrat (1 × 1 m²) was randomly established in each subplot to measure the standing litterfall. For shrublands, at each site, three replicated 25-m² plots (100 m² in a few cases) were investigated. The distance between any two replicates was less than 50 m. The shrub layer was surveyed throughout the plot. The herb layer was investigated in the four quadrats (1 × 1 m²) located at the four corners of the plot. For grasslands, at each site, 10 quadrats (1 × 1 m²) were surveyed along a 100-m-long transect.

Items recorded. The following four item categories were recorded/measured for each site: (i) geographical information (geographical coordinates, elevation, aspect, and slope); (ii) soil properties (soil type, depth, gravel content, and bulk density); (iii) vegetation properties [origin of vegetation (natural or planted), community type, stand age, canopy coverage]; and (iv)

human disturbances (management type and degree of intensity; for details on the criteria of human influence intensity, see *SI Appendix, Text S5*).

For the forest plots, the diameter at breast height (DBH; breast height = 1.3 m) and the height of all trees with a DBH ≥ 5 cm in the entire plot were measured. The abundance, DBH, and basal diameter as well as the mean heights of both woody individuals that had a DBH < 5 cm and herbaceous plants in the three understory quadrats (2×2 m²) were measured. For shrubland plots, the basal diameter, height, and crown width of all individuals were investigated in the entire plot. For grassland plots, the height and crown width of all individuals were recorded. All plant species were identified in situ or in a herbarium.

Collection of Plant and Soil Samples and Laboratory Analyses. Stems, branches, leaves, and roots of the dominant species in forests and shrublands and the above- and belowground parts of the dominant species in grasslands were sampled and transported to the laboratory for carbon analysis. Soil samples were collected to measure soil texture, bulk density, and organic carbon at depth intervals of 0–10, 10–20, 20–30, 30–50, and 50–100 cm using a soil auger. Within each depth interval, at least five samples from forest and shrubland plots were collected along two diagonal lines. For the grassland sites, at least 10 samples were collected within each plot. The carbon contents of the plant organs, litters, and soils were measured using both a CN analyzer (PE-2400 II; Perkin-Elmer) and the Walkley-Black wet digestion method (41).

Estimation of Biomass, Soil, and Litter Carbon Stocks. The site-averaged carbon density was derived directly from field measurements. The average carbon density of each biome (*SI Appendix, Table S3*) was obtained from the provincial area-weighted average and its corresponding area. The carbon stock of each vegetation group in a given province (there are 30 provinces in mainland China) was the sum of the carbon stocks of biomes in the province. To compare our estimates with those of previous studies, we further divided the country into six administrative regions and calculated area-weighted averages and total carbon stocks for each administrative region (Fig. 2) (7).

The total carbon pool of the country was the sum of the carbon stocks in the 30 provinces (for details on the calculation of site-averaged ecosystem carbon density and regional-scale ecosystem stocks, see *SI Appendix, Text S2*).

In addition, we used the Random Forests simulation (a machine-learning approach) to elucidate the detailed spatial patterns of carbon density and to test the accuracy of our estimation. We also estimated the potential for forest biomass carbon sequestration by multiplying the projected carbon densities by 10 and 20 y using the age–biomass relationship and the corresponding vegetation area (see *SI Appendix, Text S2*, for details).

Climate Data. Long-term meteorological data, MAT, and MAP were obtained from the National Ecosystem Research Network of China (www.cnern.org.cn). Using the geographical coordinates of each study site, we extracted site-specific meteorological data from the nearest meteorological stations and corrected for elevation to represent the climatic conditions at the actual sampling sites. The wetness index (*PIPET*) of each site was calculated using the method outlined by Zhou et al. (14).

Statistical Analyses. One-way ANOVA followed by the least-significant difference test was used to test the significance of the differences in the carbon densities, RS ratios, and the ratios of soil to biomass carbon among vegetation groups, biomes, and the different intensities of human activities at $P < 0.05$. Ordinary least squares regression was performed to examine the effects of climatic variables on terrestrial carbon density. All statistical analyses were performed using SPSS 22.0.

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