



# Plant diversity enhances productivity and soil carbon storage

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Edited by Susan E. Trumbore, Max Planck Institute for Biogeochemistry, Jena, Germany, and approved September 20, 2017 (received for review February 15, 2017)

Despite evidence from experimental grasslands that plant diversity increases biomass production and soil organic carbon (SOC) storage, it remains unclear whether this is true in natural ecosystems, especially under climatic variations and human disturbances. Based on field observations from 6,098 forest, shrubland, and grassland sites across China and predictions from an integrative model combining multiple theories, we systematically examined the direct effects of climate, soils, and human impacts on SOC storage versus the indirect effects mediated by species richness (SR), aboveground net primary productivity (ANPP), and belowground biomass (BB). We found that favorable climates (high temperature and precipitation) had a consistent negative effect on SOC storage in forests and shrublands, but not in grasslands. Climate favorability, particularly high precipitation, was associated with both higher SR and higher BB, which had consistent positive effects on SOC storage, thus offsetting the direct negative effect of favorable climate on SOC. The indirect effects of climate on SOC storage depended on the relationships of SR with ANPP and BB, which were consistently positive in all biome types. In addition, human disturbance and soil pH had both direct and indirect effects on SOC storage, with the indirect effects mediated by changes in SR, ANPP, and BB. High soil pH had a consistently negative effect on SOC storage. Our findings have important implications for improving global carbon cycling models and ecosystem management: Maintaining high levels of diversity can enhance soil carbon sequestration and help sustain the benefits of plant diversity and productivity.

soil carbon storage | species richness | aboveground net primary productivity | belowground biomass | human disturbance

Soils represent the largest carbon stocks in Earth's terrestrial ecosystems, and compelling evidence indicates that large amounts of soil carbon in natural ecosystems have been lost in recent decades because of the effects of climate change and human disturbance (1–3). Therefore, soil carbon sequestration plays an important role in mitigating the positive feedback between terrestrial carbon and climate (2, 4). A central issue to understanding the mechanisms controlling soil carbon sequestration and a much-debated subject is how plant diversity and productivity are related to soil carbon storage (5, 6). Soil organic carbon (SOC) storage, in general, represents the balance of two main processes: carbon inputs (e.g., net carbon gain by plants) and losses (e.g., microbial decomposition) (2, 5, 7). Theoretical and experimental studies suggest

that biodiversity has the potential to influence ecosystem carbon sequestration by modifying both processes (7–9). Recent experimental studies at small spatial scales have shown that high plant diversity increases SOC storage by elevating carbon inputs (particularly belowground carbon inputs) and increasing soil microbial community diversity and activity, and/or by suppressing carbon losses from decomposition (6, 10). However, many studies at large spatial scales have reported that the patterns of SOC storage are controlled by climate, vegetation, and soil conditions (11–13). Thus, it remains unclear whether plant diversity has important positive effects on

## Significance

Soil carbon sequestration plays an important role in mitigating anthropogenic increases in atmospheric CO<sub>2</sub> concentrations. Recent studies have shown that biodiversity increases soil organic carbon (SOC) storage in experimental grasslands. However, the effects of species diversity on SOC storage in natural ecosystems have rarely been studied, and the potential mechanisms are yet to be understood. The results presented here show that favorable climate conditions, particularly high precipitation, tend to increase both species richness and belowground biomass, which had a consistent positive effect on SOC storage in forests, shrublands, and grasslands. Nitrogen deposition and soil pH generally have a direct negative effect on SOC storage. Ecosystem management that maintains high levels of plant diversity can enhance SOC storage and other ecosystem services that depend on plant diversity.

Author contributions: Y.B. designed research; Y.B. served as principal investigator (PI) of the grassland ecosystem carbon project; S.C., Yang Wang, H.W., D.Z., Z.S., J.H., J.-S.H., Yanfen Wang, J.S., L.T., X.L., M.D., and Yan Wu contributed data collection for grassland ecosystems; G.Z. served as PI of the forest ecosystem carbon project, and provided data collection for forest ecosystems; Z.X. and Z.T. served as PIs of the shrubland ecosystem carbon project, and provided data collection for shrubland ecosystems; S.C., W.W., W.X., Yang Wang, H.W., D.C., Z.W., and Y.B. analyzed data; and S.C., J.W., F.S.C., and Y.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1700298114/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1700298114/-DCSupplemental).

SOC storage in natural ecosystems (e.g., forests, shrublands, and grasslands) in which environmental factors, human disturbance, and plant-soil feedbacks affect diversity-soil carbon relationships. Further studies are needed to better understand species effects on SOC storage and predict the ecological consequences of global biodiversity loss and climate change on the biological sequestration of carbon.

Ecological theories suggest that the broad-scale patterns of SOC storage, plant diversity, and productivity are controlled predominantly by favorable climates (i.e., high temperature and precipitation), although a variety of mechanisms have been proposed to explain these patterns (11, 14). Specifically, SOC storage generally increases with increasing precipitation, and for a given level of precipitation, SOC storage decreases with increasing temperature due primarily to increased respiration (5, 11). Species richness and primary productivity increase with increasing climate favorability along ecological gradients (14–16). In addition, high SOC storage can impose a positive feedback on species richness and productivity by increasing soil water-holding capacity and sustaining soil fertility (17). There is abundant evidence that human disturbance (e.g., N deposition, road density) has substantially altered biodiversity and ecosystem functions across all terrestrial biomes (18, 19). N enrichment generally increases productivity, but reduces species richness (18, 20) and enhances SOC storage (21, 22). Soil pH also regulates the capacity for SOC storage and nutrient supplies and, thereby, regulates primary productivity (23). Recent studies have proposed that high soil acidity can inhibit soil microbial activities and increase SOC accumulation (24). Together,

these studies suggest that SOC storage and the diversity-soil carbon relationship are controlled by multiple interrelated processes and complex plant-soil feedbacks.

Here, we examined the influences of environmental factors and human disturbance on SOC storage, plant diversity, productivity, and the interrelationships among these factors based on data from 6,098 field sites in China obtained using standardized sampling methods (*SI Appendix, Fig. S1*). Recognizing the multitude of factors and the effect of spatial scale on variables, we classified these field sites into 28 vegetation types that were grouped into three biome types: forests, shrublands, and grasslands. To facilitate our analysis, we also collected data on climate (temperature, precipitation, and photosynthetically active radiation), soil properties (soil pH), and human disturbance (N deposition rate and road density) for all sites. Specifically, our study was designed to address the following two questions: First, how do climate, soil properties, and human disturbance affect SOC storage via direct effects and indirect effects mediated by community properties, such as species richness (SR), aboveground net primary productivity (ANPP), and belowground biomass (BB)? Second, what role does plant diversity play in the plant-soil feedbacks among SOC storage, ANPP, and BB? To address the first question, we used structural equation models (SEMs) (25) to tease apart the direct effects of environmental and human factors on SOC storage and the indirect effects mediated by the community properties and test the predictions and hypotheses from multiple theories based on an integrative multivariate causal network in each biome type (Table 1 and *SI Appendix, Fig. S2*). To address the second question, we used general linear mixed-effects models

**Table 1. Pathways and standardized partial effect size across three biomes and proposed interpretations based on structural equation models (SEMs)**

Pathway	Forest	Shrubland	Grassland	Hypothesized mechanism
Climate → SOC	−0.512	−0.233	0.157	Climate favorability regulates soil C balance by stimulating C decomposition and increasing C losses from soils (1, 11, 12).
Human → SOC	−0.135	0.203	−0.198	N deposition inhibits decomposition of plant litter and SOC (21), while high road density leads to ecosystem degradation, diversity loss, and decreases SOC (45).
Soil pH → SOC	−0.184	−0.381	−0.164	High soil acidity inhibits soil microbial activities and increases SOC accumulation (24).
SR → SOC	0.157	0.116	0.167	High plant species richness increases SOC by increasing soil microbial diversity and activity and suppressing carbon losses (6).
ANPP → SOC	−0.097	−0.200	0.145	ANPP either increases or decreases SOC depending on the net result of plant-C inputs and C decomposition (11, 46).
BB → SOC	0.114	0.411	0.395	SOC increases with C inputs from root residues (6).
Climate → Soil pH	−0.764	−0.366	−0.500	Soil pH is controlled by climatic forcing, particularly water balance (23).
Human → Soil pH	0.166	−0.302	−0.139	High N deposition increases soil acidity (47).
Climate → SR	−0.404	0.562	−0.363	Water, energy, and their interaction control large-scale patterns of plant diversity (14).
Human → SR	0.612	−0.098	0.151	N deposition decreases plant diversity (18, 20). High road density increases both exotic species invasion and disturbance to native species (19).
Soil pH → SR	−0.492	−0.179	−0.299	High soil acidity affects plant diversity, but the underlying mechanisms are unclear (48).
Climate → ANPP	NS	0.248	0.092	Climate favorability regulates large-scale patterns of ANPP (49).
Human → ANPP	NS	0.124	0.441	N deposition generally increases ANPP (18, 20). High road density triggers ecosystem degradation and declines in productivity (45).
Soil pH → ANPP	−0.155	NS	NS	Soil pH affects primary productivity by regulating soil nutrient supply and uptake by plants (23).
SR → ANPP	0.314	0.243	0.221	High diversity increases primary productivity by complementary resource use (16, 30).
Climate → BB	−0.143	−0.776	−0.141	Climate regulates root growth and belowground biomass allocation (50).
Human → BB	−0.135	0.325	−0.164	N deposition alters belowground biomass allocation (21).
Soil pH → BB	−0.123	−0.266	−0.133	Soil acidity regulates root growth and belowground C allocation (51).
SR → BB	0.123	0.050	0.348	High species diversity increases rooting depth and belowground biomass (52).
ANPP → BB	0.552	0.724	0.346	Higher plant productivity provides more carbohydrate for roots (53).
Feedbacks*				
ANPP → SR	0.210	0.186	0.160	More productive ecosystems host more diverse plant species (54).
SOC → SR	0.130	0.111	0.326	High resource availability increases species diversity (55).
SOC → ANPP	NS	0.139	0.288	High water-holding capacity and nutrient supply increases plant productivity (49).
SOC → BB	0.098	0.271	0.376	Higher soil fertility enhances belowground biomass (56).

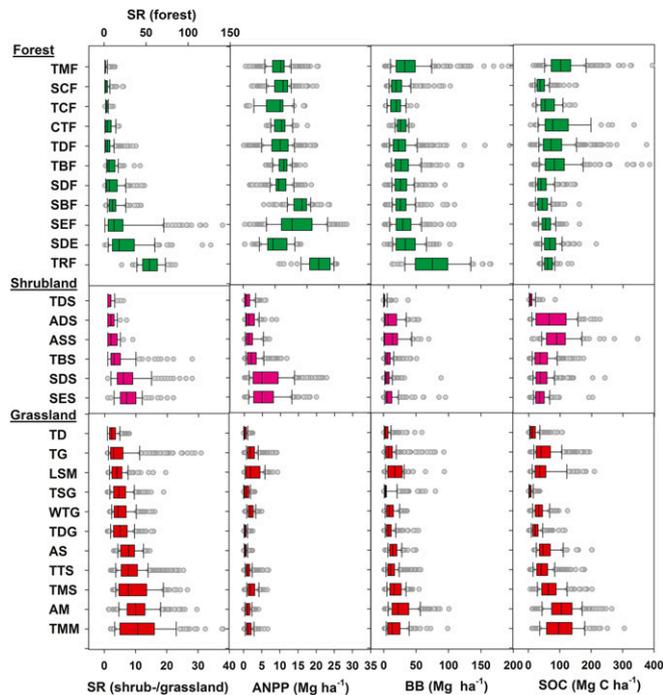
Magnitude of pathway is presented by standardized partial effect size fitted by the SEM shown in *SI Appendix, Fig. S2*. All significant pathways are shown ( $P < 0.10$ ). NS means no significant effect ( $P > 0.10$ ).

\*Feedbacks are fitted separately based on the SEM shown in *SI Appendix, Fig. S2B*.

to determine the relationships of SR with ANPP, BB, and SOC storage. We also used SEMs to explore the feedbacks between SOC storage, SR, ANPP, and BB in each biome type.

## Results

**Patterns of SR, ANPP, BB, and SOC Storage Across Different Vegetation Types in China.** Our study sites are distributed broadly across geographical and climate gradients in China, covering three biome types and 28 vegetation types (*SI Appendix, Table S1 and Fig. S1*). Plant SR, ANPP, BB, and SOC storage in the 0- to 30-cm soil layers varied substantially among the different vegetation types within each biome type and across different biome types in Chinese terrestrial ecosystems (Fig. 1). On average, SR was 10.2 tree species in the forests (plot size = 1,000 m<sup>2</sup>), 5.0 shrub species in the shrublands (plot size = 100 m<sup>2</sup>), and 6.7 herbaceous species in the grasslands (plot size = 1 m<sup>2</sup>). ANPP averaged 12.8 Mg·ha<sup>-1</sup> in forests, 3.7 Mg·ha<sup>-1</sup> in shrublands, and only 1.3 Mg·ha<sup>-1</sup> in grasslands. BB was 32.3 Mg·ha<sup>-1</sup> in forests, 8.5 Mg·ha<sup>-1</sup> in shrublands, and 12.5 Mg·ha<sup>-1</sup> in grasslands. SOC storage averaged 73.8 Mg C·ha<sup>-1</sup> in forests, 47.1 Mg C·ha<sup>-1</sup> in shrublands, and 47.3 Mg C·ha<sup>-1</sup> in grasslands (Fig. 1 and *SI Appendix, Table S1*). At the biome type level, SR, ANPP, BB, and SOC were strongly correlated with climate factors, including the mean annual temperature (MAT) and mean annual precipitation



**Fig. 1.** Median and interquartile range of plant SR, ANPP, BB, and SOC storage in 0–30 cm soil depth across different vegetation and biome types. The boundary of the box indicates the 25th and 75th percentile. Error bars denote the 90th and 10th percentiles. Abbreviations of vegetation types: ADS, subalpine deciduous broadleaved shrubland; AM, alpine meadow; AS, alpine steppe; ASS, subalpine sclerophyllous evergreen broadleaved shrubland; CTF, cold temperate coniferous forest; LSM, lowland and saline meadow; SBF, subtropical coniferous-broadleaved forest; SCF, subtropical coniferous forest; SDE, subtropical deciduous-evergreen broadleaved forest; SDF, subtropical deciduous broadleaved forest; SDS, subtropical deciduous broadleaved shrubland; SEF, subtropical evergreen broadleaved forest; SES, subtropical evergreen broadleaved shrubland; TBF, temperate coniferous-broadleaved forest; TBS, temperate deciduous broadleaved shrubland; TCF, temperate coniferous forest; TD, temperate desert; TDF, temperate deciduous broadleaved forest; TDG, temperate desert steppe; TDS, temperate desert shrubland; TG, tropical grassland; TMF, temperate montane coniferous forest; TMM, temperate mountain meadow; TMS, temperate meadow steppe; TRF, tropical rainforest and monsoon forest; TSG, temperate sandy grassland; TTS, temperate typical steppe; WTG, warm temperate grassland.

(MAP) (*SI Appendix, Fig. S3*). Generally, SR and ANPP were positively correlated with MAT and MAP in all biome types. BB and SOC were negatively correlated with MAT but positively correlated with MAP except in forests (*SI Appendix, Fig. S3 and Table S2*).

**Effects of Climate, Soil, and Human Disturbance on SOC Storage.** Considering only the direct effects of drivers on SOC storage, climate favorability (high temperature and precipitation) showed a consistent negative relationship with SOC storage in all biome types except in grasslands, which mostly occurred in less climatically favorable sites (Fig. 2). With decreasing climate favorability, the magnitude of the negative partial effect ( $r_{\beta}$ ) of climate on SOC storage declined from forests ( $r_{\beta} = -0.51$ ) to shrublands ( $r_{\beta} = -0.23$ ) and shifted to positive in grasslands ( $r_{\beta} = 0.16$ ; Table 1) because of the increasing relative importance of precipitation as a limiting factor (*SI Appendix, Table S2*). We further split the dataset of each biome type into two regions based on MAP of each sampling site. For forests and shrublands, sampling sites were classified into arid and subhumid region (MAP < 800 mm) and humid region (MAP > 800 mm). For grasslands, sampling sites were classified into arid and semiarid region (MAP < 400 mm) and subhumid and humid region (MAP > 400 mm). Again, the negative effects of climate favorability (e.g., high temperature) on SOC storage were consistently observed in each region, except in subhumid and humid grasslands (*SI Appendix, Fig. S4*). In addition, the effects of climate favorability on SOC storage were also mediated by SR and BB, both of which exhibited consistently positive effects on SOC storage in all biome types (Fig. 2). In forests, the indirect climate effects mediated by SR and BB were negative, reinforcing the direct climate effect on SOC storage. In shrublands, the strongest indirect effect was negative (through BB—reinforcing the direct effect of climate), and there was a positive indirect effect of climate acting through SR. In grasslands, the indirect effects through SR and BB were negative in contrast to the weak positive effects through climate (Fig. 2). Although the direct effect of ANPP on SOC storage was negative in forests and shrublands, the indirect effect of ANPP on SOC storage was consistently positive in all biome types, mediated by SR (through feedbacks) and BB (Table 1 and *SI Appendix, Fig. S5*). The SEMs further revealed that feedbacks of high SOC storage to SR, ANPP, and BB as well as high ANPP to SR were consistently positive in all biome types (Table 1 and *SI Appendix, Fig. S5*).

Human activity also had both direct and indirect effects on SOC storage, with the direct effects being negative in forests and grasslands and positive in shrublands (Fig. 2). The indirect effects of human activity on SOC storage were mediated by SR, ANPP, and BB. In forests and grasslands, intensified human activity, presumably N deposition, generally had positive effects on ANPP (grassland only) and SR, which were counterbalanced by decreased BB, leading to a relatively weak negative effect on SOC storage (Table 1 and *SI Appendix, Table S2*). However, intensified human activity was positively correlated with SOC storage in shrublands, and this relationship was further strengthened by the significant positive effect of SOC on BB (Fig. 2). High soil pH exhibited a negative effect on SOC storage in all biome types through its direct effects and the indirect effects mediated by SR and BB (Fig. 2). Both climate favorability and intensified human activity (e.g., N deposition) showed a consistent negative correlation with soil pH, and the reduced soil pH partly buffered the negative effects of climate favorability and/or intensified human activity on SOC storage through its effects on SR and BB. The indirect effects of climate on SOC were also mediated by soil pH, which declined with increasing climate favorability (Fig. 2 and Table 1). In addition, the negative effects of human activity on SOC storage were stronger in wet regions than in dry regions for all biome types, especially in grasslands (*SI Appendix, Fig. S4*). Collectively, the indirect pathways of climate, soil pH, and human activity resulted in consistently positive effects of SR and BB on SOC storage across different biome types (Table 1).

We further conducted partial regression analysis to assess the independent effect of each significant predictor variable (i.e., climate, human activity, soil pH) on SOC storage when the effects of other independent variables involved in the fitted SEM models were controlled. For each biome type, the partial regression coefficients

were extremely similar to those of the standardized effect sizes (path coefficients) from the SEM analysis (*SI Appendix, Fig. S6*).

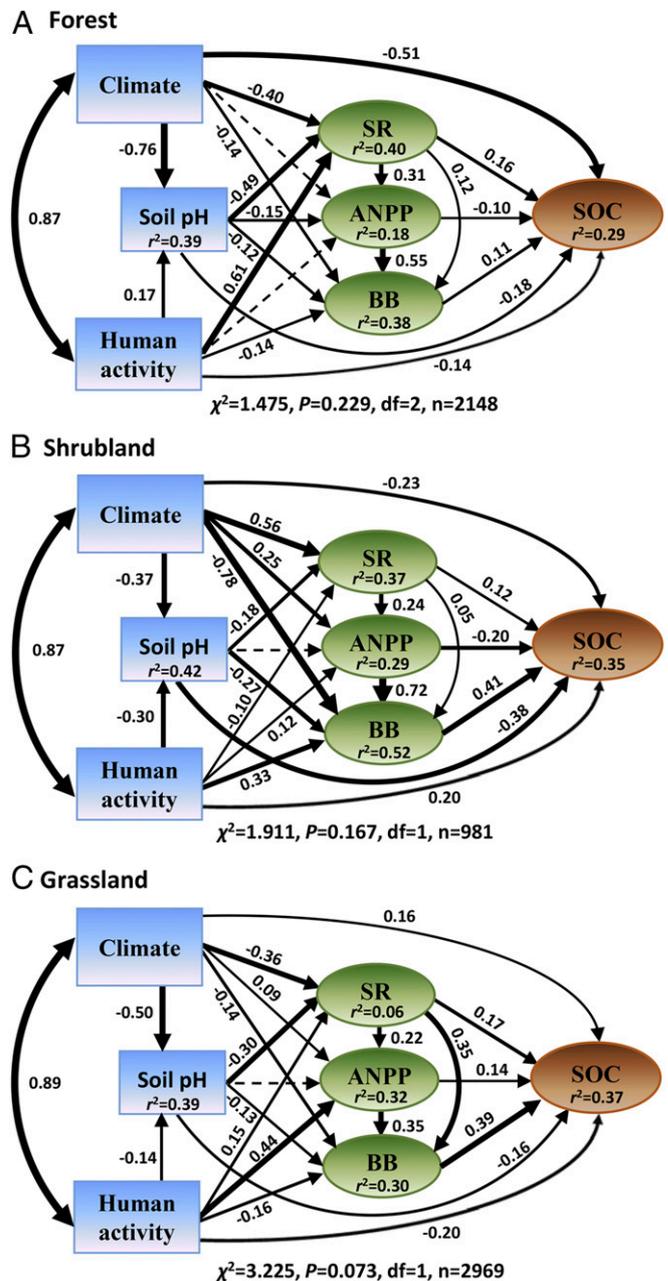
**Relationships of SR, ANPP, and BB to SOC Storage at Different Organizational Levels.** At the vegetation-type level, significant positive-linear relationships of SR with ANPP, BB, and SOC storage were found for most of the vegetation types (Fig. 3). However, substantial variations in the slope and intercept of SR–ANPP, SR–BB, and SR–SOC relationships were observed among different vegetation types within each biome type, especially in shrublands and grasslands (Fig. 3). At the biome-type level, results of linear mixed-effects model (LMM) analysis showed that vegetation types generally had a significant random effect on both the intercept and slope of the SR–ANPP, SR–BB, and SR–SOC relationships in all biome types (*SI Appendix, Tables S5 and S6*). When the effect of vegetation types was considered as a random-effect factor, the relationships of SR–ANPP, SR–BB, and SR–SOC were predominantly positive linear across all sites in each biome type, except the SR–SOC relationship in forests (Fig. 3).

## Discussion

Our study used extensive field sampling of forests, shrublands, and grasslands across China and combined the predictions from multiple theories into an integrative model to compare the direct effects of climate, soil, and human impacts on SOC storage and the indirect effects mediated by SR, ANPP, and BB in natural ecosystems. The findings from this study suggest three broad generalizations.

First, our results support the general theoretical predictions and empirical findings that broadscale patterns of SOC storage are regulated predominantly by climate favorability (1, 5, 11, 13). The strong negative effect of climate favorability (high temperature and precipitation) on forest SOC storage and the strong negative effect of high temperature on shrubland SOC storage indicate that carbon losses through heterotrophic respiration may play a predominant role in controlling the spatial patterns of soil carbon sequestration in these two biome types. This finding is consistent with regional-scale carbon flux observations (26). However, we found that climate favorability, particularly high precipitation, was associated with both higher SR and higher BB, which had consistent positive effects on SOC storage in all biome types, thus offsetting the direct negative effect of favorable climate on SOC. More importantly, our results suggest that the positive effects of SR and BB on SOC are likely reinforced by the positive feedbacks of high SOC storage to SR and BB. Findings from long-term experiments indicate that the feedbacks of high SOC to SR and BB can play important roles in governing the relationships between biodiversity and carbon and nutrient cycles in natural ecosystems (27). The consistent positive effects of SR and BB on SOC storage found in the current study are corroborated by recent experimental studies showing that high plant diversity increases belowground carbon inputs, enhances diversity and activity of soil microbial communities, and suppresses carbon losses from microbial decomposition, thereby increasing SOC storage (6, 10, 28). This study represents a test of the plant diversity-soil carbon storage hypothesis in natural ecosystems at broad spatial scales.

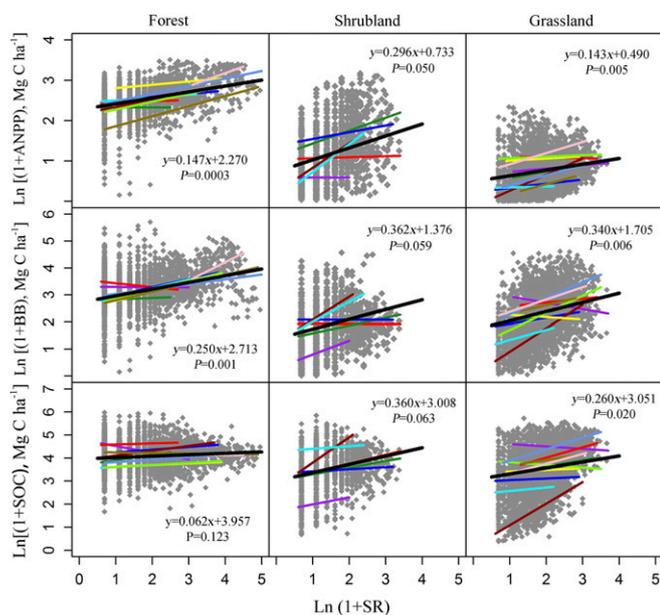
Second, our results indicate that the indirect effects of climate on SOC storage depend on the shape of the diversity-productivity relationships. At the biome-type level, the relationships of SR–ANPP and SR–BB were consistently positive in all biome types although the slope and intercept of SR–ANPP and SR–BB relationships differed substantially among different vegetation types within each biome type. This finding suggests that higher plant diversity leads to greater ANPP and BB, which enhances belowground carbon inputs and, thereby, SOC storage (29). Positive diversity-productivity relationships have also been reported by recent broad-scale studies in forests (16) and grasslands (15, 30). In addition, many experimental studies have proposed that high plant diversity increases ANPP and BB as well as the resistance of productivity to climate extremes (9, 31, 32). However, higher ANPP does not necessarily lead to greater carbon sequestration in soils, especially in warm and mesic ecosystems where carbon turnover and release processes may be major determinants of soil



**Fig. 2.** SEMs fitted to connections among SR, ANPP, BB, and SOC storage and the effects of climate, soil, and human activity variables on SR, ANPP, BB, and SOC in forests (A), shrublands (B), and grasslands (C). Numbers adjacent to arrows represent the standardized path coefficients. Climate is PCA component 1 of mean annual precipitation, mean annual temperature, and photosynthetically active radiation. Human activities represent a composite variable including nitrogen deposition rate and road density.  $R^2$  indicates the proportion of variance explained. Solid arrows represent significant paths ( $P < 0.10$ ), and dashed arrows represent nonsignificant paths ( $P > 0.10$ ).

carbon stocks (26). In our study, the negative effect of ANPP on SOC in forests and shrublands indicates that the carbon losses associated with microbial respiration may offset the positive effect of BB on SOC storage (33). In contrast, the positive relationships of SR–ANPP and SR–BB in grasslands may further strengthen the positive effect of SR to SOC because most grasslands in China occur in climatically less favorable sites where carbon decomposition rate is relatively low (34).

Third, we found that human disturbance and soil pH had both direct and indirect effects on SOC storage. The direct effects of



**Fig. 3.** Relationships of SR with ANPP, BB, and SOC storage at 0–30 cm soil depth in forests (Left), shrublands (Center), and grasslands (Right). Colored lines present regression plots of different vegetation types as indicated in Fig. 1. Bold black lines indicate SR–ANPP, SR–BB, and SR–SOC relationships at the biome-type level. The intercept and slope were the fixed effects of SR on response variables estimated by linear mixed-effects model (random slope model), with the effect of vegetation type as a random factor. All variables were natural logarithm transformed before regression analysis.

human disturbance on SOC storage were presumably caused by the impacts of N deposition on SOC, which were negative in forests and grasslands and positive in shrublands. The negative effects of N deposition on SOC may be caused by a reduction in microbial carbon contribution to stable soil carbon pools (35), whereas the positive effects may be attributable to the N-induced increase in root biomass (21, 22). Several studies have shown that elevated N inputs generally decrease the abundance of mycorrhizal fungi, which is an important source of recalcitrant soil carbon (36, 37). Greater N availability also decreases decomposition of SOC by regulating production and activity of microbial extracellular enzymes (38). In addition, high road density, an indicator of intense human disturbances, may cause habitat degradation and diversity loss and reduce SOC storage (19). Moreover, the consistently strong negative effects of high soil pH on SOC storage suggest that high soil pH may decrease the capacity for SOC storage and nutrient supply in all biome types (39). A recent study reported that high soil acidity increased SOC accumulation by inhibiting microbial activity and accelerating the leaching of dissolved organic carbon to subsoils (24). Finally, human disturbance and soil pH also affect SOC indirectly through changes in SR, ANPP, and BB. High levels of N deposition can also result in soil acidification and consequently lead to mobilization of heavy metals (e.g.,  $Al^{3+}$  and  $Mn^{2+}$ ) and loss of acid-intolerant species (40).

In general, by combining methods of SEM, partial regression, and linear mixed-effects model, our analysis presents strong evidence that SR, ANPP, and BB can be just as important as the direct effects of environmental drivers, although uncertainties exist because of the difficulties in disentangling the effects of MAT, MAP, and nitrogen deposition. These findings suggest that SOC storage can be substantially enhanced by fostering SR and BB. As SR only referred to tree species in forests and shrub species in shrublands, the role of plant diversity may be underestimated for these biome types. This strong positive species effect on carbon sequestration has not been well captured by global carbon-cycling models and is a potentially important mechanism that should be recognized. Our study also has important management implications

because maintaining high levels of diversity can enhance soil carbon sequestration, while maintaining the benefits of plant diversity and productivity on other ecosystem services (9, 15, 16, 31, 41).

## Materials and Methods

**Study Sites.** All site-level data for the forests, shrublands, and grasslands were obtained from the datasets of the “Strategic Priority Research Program—Climate Change: Carbon Budget and Relevant Issues” of the Chinese Academy of Sciences (42). In total, more than 13,000 sites were established for the field measurements (43). In this study, all artificial forest sites were excluded because most plantations are monocultures. Only sites with complete data on the SR, aboveground biomass (AGB), BB, and SOC storage were selected. In total, 6,098 sites were included in this study, including 2,148 sites for forests, 981 sites for shrublands, and 2,969 sites for grasslands. These sites represent 28 different vegetation types associated with different climate zones (i.e., cold temperate, temperate, subtropical, and tropical zones) and functional groups (e.g., coniferous vs. broadleaved, deciduous vs. evergreen) (SI Appendix, Table S1).

**Vegetation and Soil Survey.** Field inventories of all sites were conducted from 2011 to 2013. For detailed sampling protocols, please refer to Tang et al. (43). Specifically, standardized sampling and measurement protocols were applied in the vegetation and soil survey of each biome type. In forests, a plot with an area of 20 m × 50 m was investigated at each site. The number of tree species was recorded within each plot and used as the measure of SR of a particular site. The diameter at breast height (DBH) and height of each tree (DBH ≥ 5 cm) were measured to estimate the stand biomass and the aboveground and belowground proportions using allometric equations. In shrublands, three plots with areas of 5 m × 5 m (10 m × 10 m for desert shrublands) were sampled within each site. All shrub species in each plot were recorded, and the average number of shrub species over three plots was used as the measure of SR a particular site. Two different methods were used for evaluating the AGB and BB of the shrubs. For shrubs with a main stem, shrub height, diameter of basal stem, and crown were measured, and then AGB and BB of shrubs were calculated using allometric equations. For shrubs without main stems, all aboveground and belowground parts were harvested (1 m × 1 m) in each plot to evaluate the AGB and BB. In grasslands, 10 1 m × 1 m plots were sampled along a 100-m transect within each site. The aboveground and belowground parts of plants were harvested to estimate the AGB and BB of each plot. The number of herbaceous species in three to five plots was recorded as SR. The SR and the AGB and BB over all plots of each site were averaged and used as a measure of the site-level SR and the AGB and BB.

At least five soil samples were collected from each plot of forest, shrubland, and grassland sites using a soil auger. Air-dried soil samples were used to measure the gravel content (>2 mm) (GC), soil bulk density (BD), and SOC concentration. SOC storage was calculated by multiplying (1 – GC), BD, and SOC concentration in each soil layer. The sum of SOC in the 0- to 30-cm soil depth was used to represent SOC storage at a particular site.

To distinguish the role of dominant functional groups in ecosystem structure and function, only the SR, ANPP, and BB of the trees, shrubs, or herbaceous species were considered in the data analyses of forests, shrublands, and grasslands, respectively. Additional details for ANPP estimation are available in SI Appendix, SI Materials and Methods.

**Climate, Soil and Human Activity Variables.** For each site, MAT and MAP were calculated using the WorldClim data layers ([www.worldclim.org/](http://www.worldclim.org/)), and the average daily photosynthetically active radiation (PAR) was obtained from the National Earth System Science Data Sharing Infrastructure ([www.geodata.cn/](http://www.geodata.cn/)). Soil pH value for each site was obtained from SoilGrids1 km via [www.isric.org/explore/soilgrids](http://www.isric.org/explore/soilgrids). N deposition rate (ND) for each site was obtained from the gridded long-term N deposition database (44). Data on the road density (RD) were obtained from the National Earth System Science Data Sharing Infrastructure ([www.geodata.cn/](http://www.geodata.cn/)). Additional details for MAT, MAP, PAR, soil pH, ND, and RD are available in SI Appendix, SI Materials and Methods.

**Statistical Analyses.** Details for statistical methods used in this study are available in SI Appendix, SI Materials and Methods.

**ACKNOWLEDGMENTS.** We thank all participants, a group of more than 1,000 scientists, for their contributions to the field work and laboratory analysis and Jingyun Fang, Guirui Yu, David Hooper, Shuijin Hu, Huifeng Hu, and Nianpeng He for their valuable comments and suggestions on an early version of this paper. This work was financially supported by the Strategic Priority Research Program of the Chinese Academy of Sciences Grant XDA05050000 and the National Natural Science Foundation of China Grants 31630010 and 31320103916.

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