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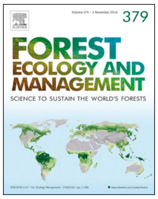

Effects of diversity, climate and litter on soil organic carbon storage in subtropical forests

Yin Li[a,b], Xiaojuan Liu[b], Wubing Xu[b,c], Franca J. Bongers[b], Weikai Bao[d], Bin Chen[e], Guoke Chen[b], Ke Guo[b], Jiangshan Lai[b], Dunmei Lin[f], Xiangcheng Mi[b], Xingjun Tian[g], Xihua Wang[h], Junhua Yan[i], Bo Yang[j], Yuanrun Zheng[b], Keping Ma[b,*]

[a] *Fujian Provincial Key Laboratory of Resources and Environmental Monitoring and Sustainable Management and Utilization, Sanming University, Sanming, Fujian 365004, China*
[b] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China*
[c] *Center for Biodiversity Dynamics in a Changing World (BIOCHANGE) & Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark*
[d] *Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization, and Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China*
[e] *Shanghai Chenshan Botanical Garden, Shanghai 200062, China*
[f] *Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing 400045, China*
[g] *School of Life Sciences, Nanjing University, Nanjing 210093, China*
[h] *Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai 200241, China*
[i] *South China Botanic Garden, Chinese Academy of Sciences, Guangzhou 510650, China*
[j] *Key Laboratory of Plant Resources and Biodiversity of Jiangxi Province, Jingdezhen University, 838 Cidu Avenue, Jingdezhen, Jiangxi 333000, China*

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ABSTRACT

Tropical and subtropical forest ecosystems play an important role in the global carbon regulation. Although positive relationships between biodiversity and soil organic carbon (SOC) storage have been found in experimental grasslands, biodiversity effects on SOC storage in natural forests remain debated. Based on a large dataset from 523 forest inventory plots across subtropical forests in China, we tested the relationship between biodiversity and SOC storage and examined whether environmental conditions (temperature, precipitation, soil properties) and litter quantity (leaf litter and root biomass) and quality (leaf litter carbon to nitrogen ratio [leaf litter C/N]) had effects on SOC storage. Furthermore, we used linear mixed-effects models to test the relative effects of biodiversity, environmental conditions, and litter quantity and quality on SOC storage. We used structural equation models to test how these variables directly or indirectly affected SOC storage. We found that species diversity, together with climatic factors (mean annual temperature and mean annual precipitation), leaf litter C/N and root biomass determined SOC storage in subtropical forests at a large spatial scale. SOC storage was most strongly affected by climatic factors, followed by leaf litter C/N. Species diversity had both direct and indirect (through root biomass and leaf litter C/N) effects on SOC storage after accounting for environmental conditions. We also found that the positive diversity–SOC storage relationships were stronger in low and medium mean annual precipitation. Our findings highlight that higher species diversity can lead to higher SOC storage and therefore the conservation of biodiversity could play an important role in climate change mitigation.

1. Introduction

Forests cover about 30% of the total land area on Earth, accounting for 75% of terrestrial gross primary production and approximately 45% of terrestrial carbon (Beer et al., 2010; Pan et al., 2013). They therefore play an important role in global carbon sequestration (Bonan, 2008). About half of carbon storage is contained in soils in the global forests (Pan et al., 2011). Preserving and promoting soil organic carbon (SOC) storage in forests has been considered as a potentially effective strategy to mitigate global climate change (Lal, 2005). A series of drivers,

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* Corresponding author at: State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China.
E-mail address: kpma@ibcas.ac.cn (K. Ma).

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involving climatic factors, soil properties and vegetation, have been proposed to explain SOC storage (Lal, 2005; De Deyn et al., 2008; Chen et al., 2018; Wiesmeier et al., 2019; Zhou et al., 2019). However, it is still poorly understood how these multiple drivers simultaneously affect SOC storage (O'Rourke et al., 2015; Wiesmeier et al., 2019). More studies, therefore, are needed to improve our understanding about the patterns and drivers of SOC storage in forest ecosystems at large spatial scales (O'Rourke et al., 2015; Wiesmeier et al., 2019; Zhou et al., 2019).

The continuing species losses and accelerating rates of climate change are considered to have potential influences on ecosystem functioning including SOC storage (Cardinale et al., 2012; Oliver et al., 2015). Experimental studies conducted in grasslands and forests have reported positive effects of biodiversity on SOC storage (Lange et al., 2015; Li et al., 2019; Yang et al., 2019). However, biodiversity effects on SOC storage in naturally assembled communities, in particular natural forests, still remain debated (van der Plas, 2019). Some studies have found positive relationships between biodiversity and SOC storage (Gamfeldt et al., 2013; Liu et al., 2018), while others found neutral, or even negative relationships (Conti and Díaz, 2013; Adair et al., 2018), perhaps because of some abiotic factors (e.g. climatic factors and soil properties) which were more important in controlling SOC storage (van der Plas, 2019). Climate and environment variation may not only directly influence species diversity, but may also modify the strength and direction of biodiversity-ecosystem functioning (BEF) relationship (Paquette and Messier, 2011; Ammer, 2019). Empirical studies have reported that positive BEF relationship in forest and shrub ecosystems would become weaker in more favorable environments (Paquette and Messier, 2011; Chen and Chen, 2019; Guo et al., 2019). Therefore, it is crucial to understand whether species-rich forest ecosystems have higher SOC storage across large spatial scales and varying environmental conditions.

SOC storage is mainly determined by the balance between carbon input (e.g. leaf and root litter inputs) and output (e.g. microbial decomposition of litter and existing SOC) (Jastrow et al., 2007). Biodiversity may have the potential to influence SOC storage by modifying both processes. Many studies have shown that biodiversity would promote leaf and root litter production (Huang et al., 2017; Sun et al., 2017). Increased litter biomass in species-rich communities, on the one hand, would promote SOC storage directly through increased recalcitrant plant residue inputs (Chen et al., 2020), or indirectly through increased soil microbial biomass and thus microbial necromass accumulation over time (Liang et al., 2017). On the other hand, increased plant litter inputs may reduce SOC storage through accelerating decomposition of existing SOC (positive priming effect) (Sayer et al., 2011). Biodiversity may also alter quality of litter inputs and therefore impact SOC storage (Huang et al., 2017; Zhou et al., 2019). Recent studies have reported that higher quality plant litter (e.g. low litter C/N) leads to faster and more efficient accumulation of SOC than low quality plant litter (Zhou et al., 2019; Gao et al., 2020).

Climatic factors, such as temperature and precipitation, are generally regarded as important factors influencing SOC storage and often explain a large part of variation in SOC storage at regional and global scales (Jobbágy and Jackson, 2000; Jackson et al., 2017; Wiesmeier et al., 2019). In many terrestrial ecosystems, precipitation controls net primary productivity and inputs of litter carbon into soils (Jobbágy and Jackson, 2000), and thus influences SOC storage (Wiesmeier et al., 2013). Temperature is closely related to microbial decomposition of soil organic matter and thus loss of SOC (Jackson et al., 2017; Wiesmeier et al., 2019). Numerous studies have shown that SOC storage generally decreased with increased temperature when controlling for precipitation (Jobbágy and Jackson, 2000; Koven et al., 2017), mainly due to stimulated SOC decomposition. Soil properties (e.g. clay and silt content) also play an important role in SOC storage (Wiesmeier et al., 2019). Clay and silt content are related to SOC storage primarily due to their strong stabilizing capacity for SOC (Wiesmeier et al., 2019). The cation-exchange capacity (CEC) of soil has also been reported to be correlated with SOC storage (Tashi et al., 2016).

Although multiple drivers affect SOC storage (Doetterl et al., 2015; Jackson et al., 2017; Wiesmeier et al., 2019), few studies have simultaneously tested the effects of biodiversity, environmental conditions (climatic factors and soil properties) and litter quantity and quality on SOC storage in species-rich subtropical forests. Clarifying direct and indirect effects of these factors on SOC storage could improve our understanding of subtropical forests to regulate SOC storage during global change. The objective of this study is to test how SOC storage is affected by biodiversity, environmental conditions and litter quantity and quality across species-rich subtropical forests in China. Specifically, we address two questions: First, is there a significant relationship between biodiversity and SOC storage in subtropical forests? Second, how important are biodiversity, environmental conditions and litter quantity and quality as predictors of SOC storage in subtropical forests at a large spatial scale? To answer these questions, we use 523 subtropical forest plots in China to examine the correlations between biodiversity and SOC storage, and further to quantify the relative importance of biodiversity, environmental conditions and litter quantity and quality in determining SOC storage. We hypothesize that: (1) biodiversity is positively related to SOC storage after controlling for environmental conditions; (2) both litter quality (leaf litter C/N) and climatic factors (MAT and MAP) have strong effects on SOC storage in addition to biodiversity.

2. Materials and methods

2.1. Study area and forest inventory data

We sampled 523 plots from China's subtropical forests, which were measured during the period of 2011–2012, and located at least 100 m from the nearest edge or road, to reduce edge effects. The main forest types include broad-leaved forest, coniferous forest and mixed coniferous broad-leaved forest. Plots varied in size, 0.06 (n = 272) and 0.1 ha (n = 251). These plots were set up in western and eastern China, and spanned a geographic range from 24.92° to 34.73° N in latitude, and from 99.46° to 121.09° E in longitude (Fig. 1). Across studied plots, mean annual temperature ranged from 1.2 to 19.7 °C, mean annual precipitation from 573 to 1,926 mm, and elevation from 3 to 4,269 m a.s.l.. In the field surveys, all stems ≥ 3 cm in DBH (diameter at breast height = 1.3 m) in each plot were individually recorded, measured, and identified to species-level. For species that could not be identified in the field, specimens were collected and identified by relevant experts in the lab. Taxonomic names were verified against *Catalogue of Life China* (Checklist 2015, http://www.sp2000.org.cn/) and *Flora of China* (http://www.efloras.org/).

2.2. Soil sampling and measurements

Stratified soil samples were collected in 2011–2012 by depth increments of 0–10, 10–20 and 20–30 cm. At each sampling plot, at least five independent samples per plot were taken using a split tube sampler after surface litter was removed. We pooled all samples of the same soil depth per plot into one sample, resulting in three composite samples per plot. The soil samples were air-dried, sieved with a 2-mm mesh sieve, handpicked to remove fine roots and other coarse debris, and then ground in a ball mill for subsequent measurements of SOC content. We measured SOC content using a CN-element analyzer (PE-2400 II, Perkin Elmer, Waltham, Massachusetts, USA).

We determined soil bulk density from intact soil cores at depths of 0–10, 10–20 and 20–30 cm for each plot. Specifically, soil samples were collected with a soil auger equipped with stainless-steel cylinder, then oven-dried (105 °C for 48 h) to constant weight and weighed. Soil bulk density was calculated as the ratio of oven-dry soil mass and container volume. The SOC storage per plot in the 30 cm of the soil was calculated as:

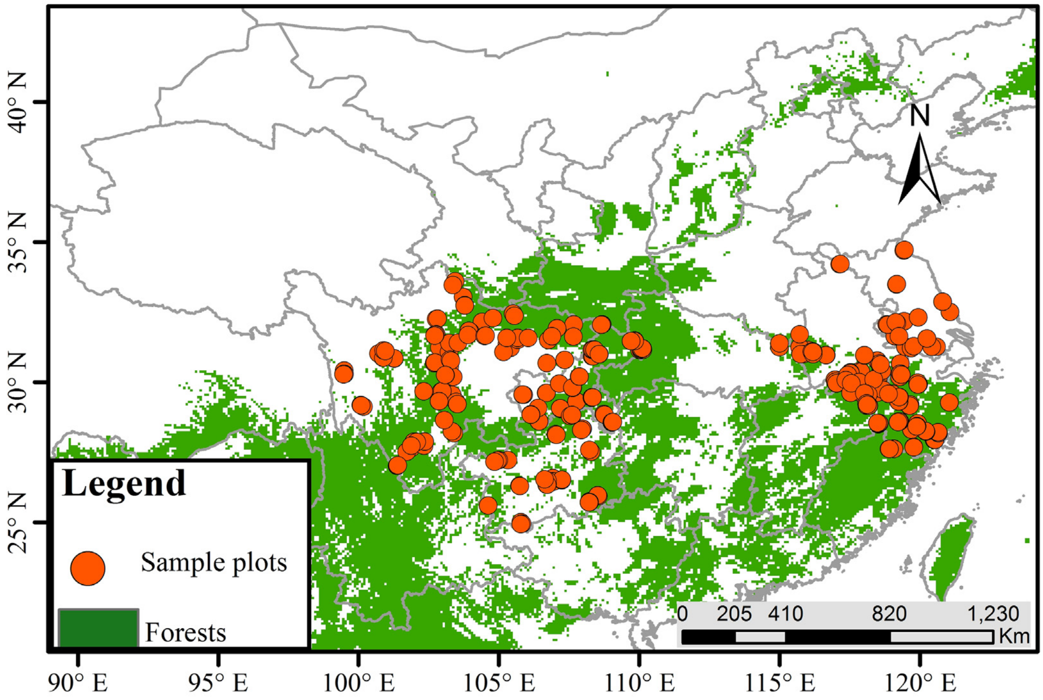

Fig. 1. Locations of the 523 plots across subtropical forests in China. The base vegetation map is modified from the 2012 MODIS global land cover map (www.landcover.org/data/lc/) with IGBP Land Cover Type Classification.

$$\mathrm{SOC}_{\mathrm{storage}} = \sum_{i=1}^{n} BD_i \times SOC_i \times H_i \times (1 - \mathrm{C}_i)/10$$

in which $SOC_{storage}$ is SOC storage (0–30 cm) (Mg ha^{-1}), i represents each soil depth, BD_i is the soil bulk density (g cm^{-3}), SOC_i is the SOC content (g kg^{-1}), C_i is percentage of rock fraction $>$ 2 mm and H_i is the thickness (cm) of each depth.

2.3. *The quantity and quality of litter estimation*

We estimated root biomass and leaf litter biomass to represent quantity of litter. Leaf litter C/N was used to represent the quality of litter. Root biomass of each plot was estimated using relevant allometric equations with diameter at breast height and tree height as predictors (Ecosystem Carbon Sequestration Project, 2015) (Table S1).

In each plot, we collected forest floor litter samples using a 25 × 25 cm wooden frame. At lease five forest litter samples were taken. We weighed each of the five samples, and then pooled the five samples into one sample, resulting in one composite sample per plot. The leaf litter samples were dried to constant weight at 70 °C and weighed. The dried leaf litter samples were ground in a ball mill, and were analyzed for C and N content using a CN-element analyzer (PE-2400 II, Perkin Elmer, Waltham, Massachusetts, USA). The leaf litter C/N ratios were directly measured and calculated as the ratio of carbon content (g kg^{-1}) to nitrogen content (g kg^{-1}) per litter sample.

2.4. *Biodiversity metrics*

In this study, we calculated species diversity and functional diversity to test their effects on SOC storage. We used the Shannon's index as a proxy of species diversity to account for species richness and evenness (Li et al., 2019; Zhang et al., 2012). The Shannon's index was calculated as:

$$H_S = \sum\nolimits_{i}^{S} p_i \times \ln(p_i)$$

where p_i is the proportion of individuals of species i in the plot, while S is the number of tree species.

We calculated functional diversity using wood density, maximum stem diameter, leaf area and specific leaf area, as these traits are shown to influence carbon storage and are commonly used in BEF studies (Conti and Díaz, 2013; Lin et al., 2016). The maximum stem diameter of each species was determined from our dataset, with values assigned equal to the largest diameter value in the data set for a given species (Li et al., 2019a). Wood density for major tree species, which composed over 95% of the basal area (> 3 cm DBH) across all the plots, were determined using the density of the nearest branch attached to the main trunk (following Liu et al., 2016). The branch wood density was calculated as oven-dried mass (80 °C, 48 h) divided by water-displaced volume of three to five segments cutting from three separate branches for each tree (Liu et al., 2016). For a few species, we extracted the wood density from literature (Zhang et al., 2011) and the global wood density data base (Chave et al., 2009). We measued leaf area and specific leaf area for each species following the protocol of Liu et al. (2016). Specifically, we sampled 5–10 healthy, sun-exposed and intact leaves for each tree, scanned for leaf area, and dried 48 ha at 60 °C to determine dry mass weight. For functional diversity, we used functional dispersion (FDis) which sums weighted distances from the centroid of all species in a community (Laliberté and Legendre, 2010).

Shannon's index was calculated using the 'vegan' package and functional dispersion using the 'FD' package in R 3.6.0 (R Core and Team, 2019).

2.5. *Environmental conditions*

Environmental conditions included climatic factors, elevation and soil properties. Climatic factors included mean annual precipitation (MAP) and mean annual temperature (MAT) which are often thought to be closely related to species diversity (Gaston, 2000) and SOC storage (Wiesmeier et al., 2019). The data for MAP and MAT were downloaded from the WorldClim database with a resolution of 30 arc seconds (Hijmans et al., 2005). Elevations of the sampled plots were recorded by a portable global positioning system (GPS). Soil properties (CEC, clay and silt content) for each plot were retrieved from a 30 arc-second

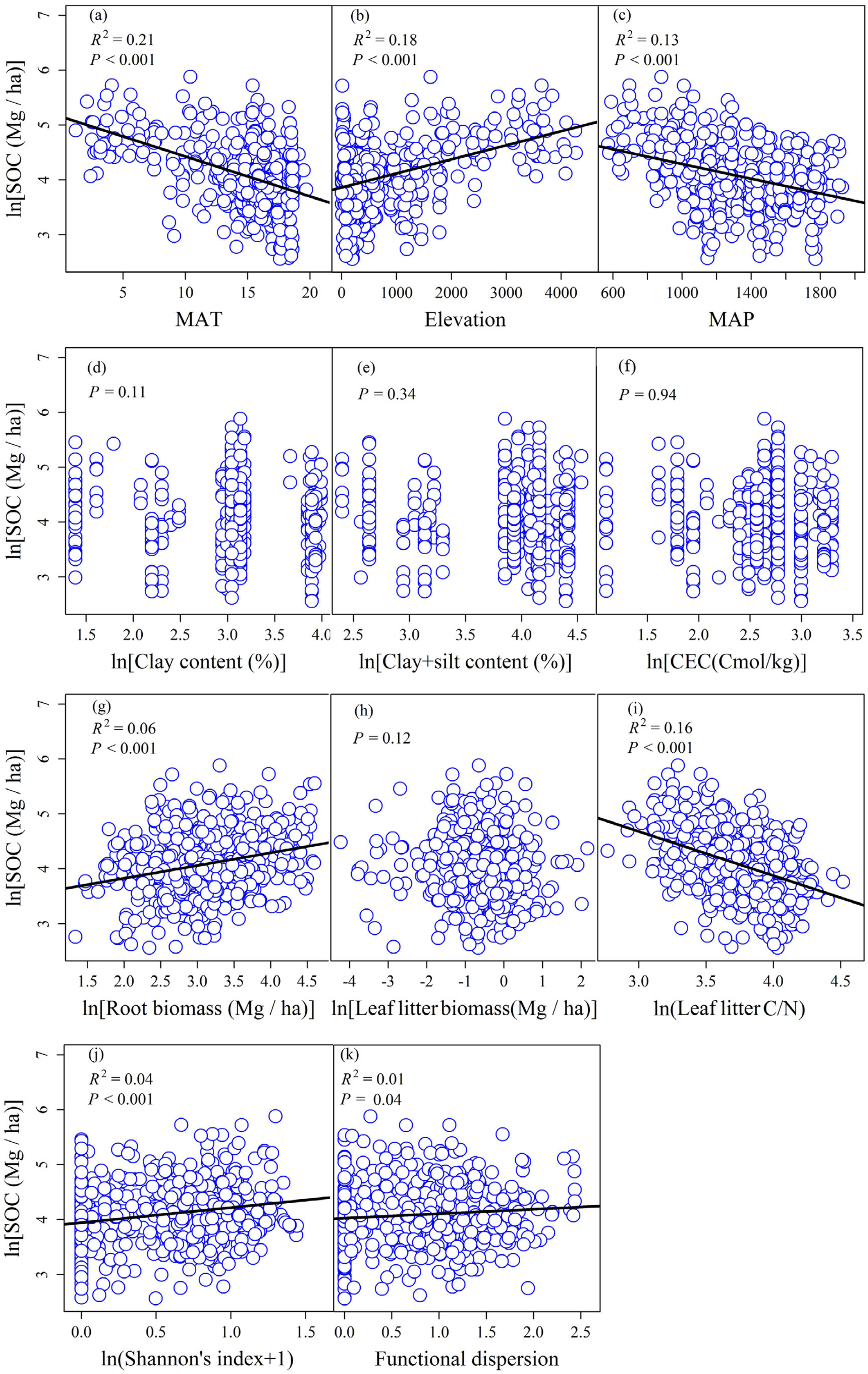

Fig. 2. Bivariate relationships between SOC storage and MAT, MAP, elevation, clay content, clay + silt content, CEC, root biomass, leaf litter biomass, leaf litter C/N, Shannon's index and functional dispersion (N = 523).

resolution Harmonized World Soil Database 1.2 (HWSD v1.2) [FAO/IIASA/ISRIC/ISSCAS/JRC 2012].

2.6. Statistical analyses

We first used Pearson correlation coefficients to test the pair-wise relationships between SOC storage and each predictor of biodiversity (Shannon's index and functional dispersion), root biomass, leaf litter biomass, leaf litter C/N and environmental conditions (MAP, MAT, elevation and soil properties). To improve normality and linearity, SOC storage, Shannon's index, root biomass, leaf litter biomass, leaf litter C/N, CEC, clay content and clay + silt content (sum of clay and silt content) were natural log-transformed prior to all analyses.

A multiple linear regression was used to test whether the diversity–SOC storage relationship changed with MAP. The terms in the model were fitted in this sequence: SOC storage ~ diversity + MAP + diversity × MAP, where diversity refers to log-transformed Shannon's index.

We used linear mixed-effects models to examine the effects of biodiversity, environmental conditions and litter quantity and quality on SOC storage. MAP, MAT, elevation, CEC, clay content and clay + silt content, Shannon's index, functional dispersion, root biomass, leaf litter biomass, leaf litter C/N were used as fixed-effects. Forest type ($n = 3$) and site identity ($n = 2$, western and eastern China) were used as random-effects in the mixed-effects models. We used the variance inflation factor (VIF) to identify any multicollinear variables in the linear mixed-effects models. The criterion VIF < 3 was used to select suitable fixed-effects variables in the mixed-effects models to remove strongly multicollinear variables (Ouyang et al., 2019). Consequently, the full model contained Shannon's index, functional dispersion, MAP, MAT, clay + silt content, leaf litter C/N, leaf litter biomass and root biomass. We also fitted and compared all subsets of the full model according to corrected Akaike information criterion (AIC_c) (see Table S2), and selected the best model with the lowest AIC_c (Burnham and Anderson, 2002). Linear mixed-effects models and model selection were conducted using the packages 'lme4′ (Bates et al., 2014) and 'lmerTest' (Kuznetsova et al., 2014) and 'MuMln' (Bartoń, 2016) in R 3.6.0, respectively.

Structural equation models (SEMs) were used to tease apart the potential direct and indirect effects of biodiversity, environmental conditions and litter quantity and quality on SOC storage. Based on expected relationships between SOC storage and potential driving factors, we established a base model that linked environmental conditions, biodiversity and litter quantity and quality to SOC storage. We considered the following potential paths in the base model (Fig. S1). First, we hypothesized that biodiversity, environmental conditions and litter quantity and quality have direct effects on SOC storage. Second, environmental conditions may also have indirect effects on SOC storage via biodiversity and litter quantity and quality. Third, biodiversity may indirectly affect SOC storage through its effect on litter quantity and quality. The chi-square (χ^2) statistic and P value of the whole model were used to assess the overall goodness of fit of a SEM (Grace, 2006). To examine whether the diversity effect on SOC storage changed with soil depth, we also performed seperate SEM analyses for each soil depth. Path coefficients represent the direction and strength of direct effects between two variables. SEMs were performed using the package 'lavaan' in R 3.6.0 (R Core and Team, 2019).

We noted that our plots are differential in areas with two sizes of 0.06 and 0.1 ha, which could affect estimated species diversity as the number of species increases with plot size (Rosenzweig, 1995). We examined the Spearman's rho correlation between Shannon's index and plot size and found a positive correlation ($P = 0.01$). We then calculated a boosted regression tree (BRT) to quantify the relative influence of controlling factors (MAP, MAT and soil properties) as well as plot size on Shannon's index. Plot size only accounted for < 5% of the relative influence on Shannon's index (Fig. S2), suggesting that plot size may have negligible effect on species diversity. In addition, we put the interactions between plot size and Shannon's index, functional dispersion, leaf litter biomass, root biomass and leaf litter C/N in the full mixed-effects model. We found that these interactions have no significant effects on SOC storage (Table S3). These results indicate that plot size heterogeneity may have little influence on the results of our analyses. The BRT model was implemented using the 'gbm' package in R 3.6.0 (R Core and Team, 2019).

3. Results

3.1. Bivariate relationships between SOC storage and individual predictor variables

SOC storage in the top 0–30 cm soil depth varied by an order of magnitude across subtropical forests in China, ranging from 13.0 Mg C ha^{-1} to 358.6 Mg C ha^{-1}. MAT explained the largest variation in SOC storage among all the individual predictor variables (slope = − 0.073, $F_{1,521} = 139.20$, $R^2 = 0.21$, $P < 0.001$; Fig. 2a, Table S4), followed by elevation (slope = 0.0003, $F_{1,521} = 118.2$, $R^2 = 0.18$, $P < 0.001$; Fig. 2b, Table S4). MAP had a relatively strong negative correlation (slope = − 0.0007, $F_{1,521} = 75.55$, $R^2 = 0.13$, $P < 0.001$; Fig. 2c, Table S4), while soil properties (clay content, clay + silt content and CEC) had no significant correlations with SOC storage (Fig. 2d - f, Table S4). Root biomass had a relatively weak positive relationship with SOC storage (slope = 0.232, $F_{1,521} = 37.11$, $R^2 = 0.06$, $P < 0.001$; Fig. 2g, Table S4), while leaf litter biomass had no significant effect on SOC storage ($P > 0.05$; Fig. 2h, Table S4). Leaf litter C/N significantly affected SOC storage (slope = − 0.805, $F_{1,521} = 103.80$, $R^2 = 0.16$, $P < 0.001$; Fig. 2i, Table S4), with a negative correlation. For biodiversity variables, both Shannon's index (slope = 0.274, $F_{1,521} = 22.36$, $R^2 = 0.04$, $P < 0.001$; Fig. 2j, Table S4) and functional dispersion (slope = 0.082, $F_{1,521} = 4.23$, $R^2 = 0.01$, $P = 0.04$; Fig. 2k, Table S4) had positive correlations with SOC storage.

The effects of species diversity (Shannon's index) on SOC storage changed along MAP gradients (Fig. 3, Table 1; $P = 0.008$ for diversity × MAP). The slopes of SOC storage–diversity relationships decreased with increasing MAP values, ranging from strongly positive in low MAP to weakly positive in high MAP levels (Fig. 3).

3.2. The relative importance of predictor variables on SOC storage

In the best mixed-effects model, the marginal R^2 for the fixed effects was 0.31, the conditional R^2 for the fixed and random effects was 0.33. This means that forest type and site only explained 2% of the overall variation of SOC storage as random effects (Table 2). MAT had the strongest effect on SOC storage, followed by leaf litter C/N and MAP (Table 2). There was still a significantly positive relationship between species diversity (Shannon's index) and SOC storage when environmental conditions were considered (Table2). Leaf litter C/N had a strong negative effect and root biomass had a positive effect on SOC storage, while clay + silt content and leaf litter biomass did not show in the best model (Table 2, Table S3).

3.3. Direct and indirect effects of predictor variables on SOC storage

The most parsimonious SEM indicated that all predictor variables together accounted for 32% of variations in SOC storage for the 0–30 cm depth ($R^2 = 0.32$, Fig. 4). Shannon's index and root biomass had significant positive direct effects on SOC storage, whereas MAT, MAP and leaf litter C/N had significant negative direct effects (Fig. 4, Table 3). MAT also had a strong indirect effect via root biomass. MAP had positive indirect effect via Shannon's index and root biomass, whereas it had a negative indirect effect via leaf litter C/N. Shannon's index also had strong positive indirect effects via root biomass and leaf litter C/N, strengthening the direct effect of Shannon's index on SOC

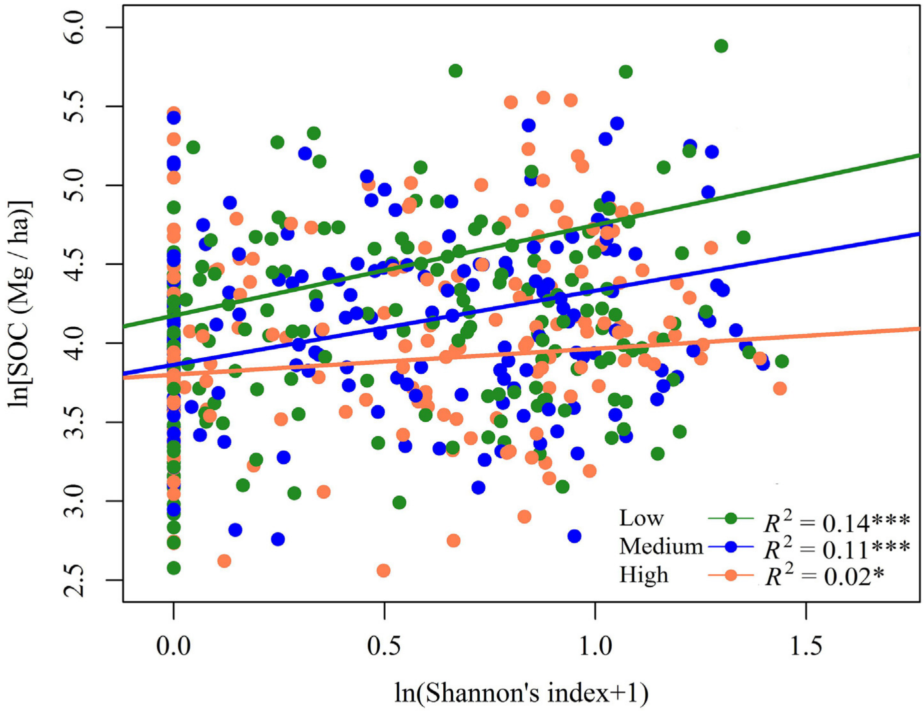

Fig. 3. The relationship between Shannon's index and SOC storage across plots at low (green circles), medium (blue circles) and high (orange circles) MAP levels. All plots were divided into three similar-sized groups according to the MAP, with MAP ≤ 1100 mm, 1100 mm < MAP < 1400 mm, and MAP ≥ 1400 mm indicating low, medium, and high MAP, respectively. These thresholds were defined in such a way that the different environmental categories had comparable sample sizes (following Guo et al., 2019). Significant effects are at $P < 0.05$ (*), < 0.01 (**), and < 0.001 (***). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of linear model for the effects of Shannon's index, MAP and their interaction on SOC storage.

Term	DF	*MS*	*p*-value
Shannon's index	1	7.305	< 0.001
MAP	2	15.380	< 0.001
Shannon's index × MAP	2	1.293	0.008
Residuals	517	0.265	

Abbreviations: DF, degree of freedom; MS, mean square

storage. More detailed information about the direct and indirect effects of all the variables on SOC storage is shown in Table 3.

The results of the separate SEMs for each soil depth (0–10, 10–20 and 20–30 cm) were similar to the result for the full 0–30 cm soil profile (Fig. S3–S5, Fig. 4). However, species diversity had only a positive direct effect on SOC storage in the top 0–10 cm soil depth (Fig. S3–S5).

4. Discussion

About half of the organic carbon in global forests is stored in soils (Pan et al., 2011). Tropical and subtropical forests, which account for the largest area of global forest biomes, have an important role in the global carbon cycle (Pan et al., 2011) and biodiversity conservation (Bonan, 2008). Only a few studies were conducted in natural forests to address the question whether biodiversity is correlated with SOC storage (Gamfeldt et al., 2013; Liu et al., 2018). In our study, we related SOC storage to biodiversity and environmental drivers in subtropical forests at a broad scale, and found that species diversity enhanced SOC storage in subtropical forests, even after controlling for environmental conditions. Our study underscores the importance of species diversity as a driver of SOC storage in subtropical forests and provides comprehensive evidence for biodiversity mediated SOC storage.

4.1. Effects of biodiversity on SOC storage

How biodiversity influences SOC storage in naturally assembled forest communities remains unclear and controversial (van der Plas, 2019). Our results from species-rich subtropical forests showed that SOC storage was related to species diversity, whether the effects of climate and soil conditions were accounted for or not. This supports our hypothesis and is in line with findings in other studies that greater species diversity increases SOC storage in natural and planted forest systems (Li et al., 2019; Liu et al., 2018). Species diversity effects on SOC storage have often been attributed to differences in the quantity (e.g. leaf litter biomass, root biomass and root exudates) and quality (e.g. leaf litter C/N) of litter inputs and their microbial decomposition (Lange et al., 2015; Chen et al., 2018; Zhou et al., 2019). Indeed, we found that species diversity indirectly influenced SOC storage through increased root biomass and decreased leaf litter C/N. We also found

Table 2
Summary of the best linear mixed-effects model showing the effects of mean annual precipitation (MAP), mean annual temperature (MAT), Shannon's index, leaf litter C/N and root biomass on SOC storage.

Fixed effects	Std. Est.	Std. Error	d.f.	*t*	*P*	Marginal R^2	Conditional R^2
MAT	−0.293	0.047	489.8	−6.26	< 0.001	0.31	0.33
MAP	−0.145	0.056	337.0	−2.57	0.011		
Shannon's index	0.140	0.052	223.7	2.67	0.008		
Leaf litter C/N	−0.181	0.051	501.2	−3.58	< 0.001		
Root biomass	0.102	0.041	513.0	2.51	0.012		

Abbreviations: Std. Est., Standardized estimates; Std. Error, Standard error; d.f., degree of freedom.
The best 5 models are provided in Table S3.

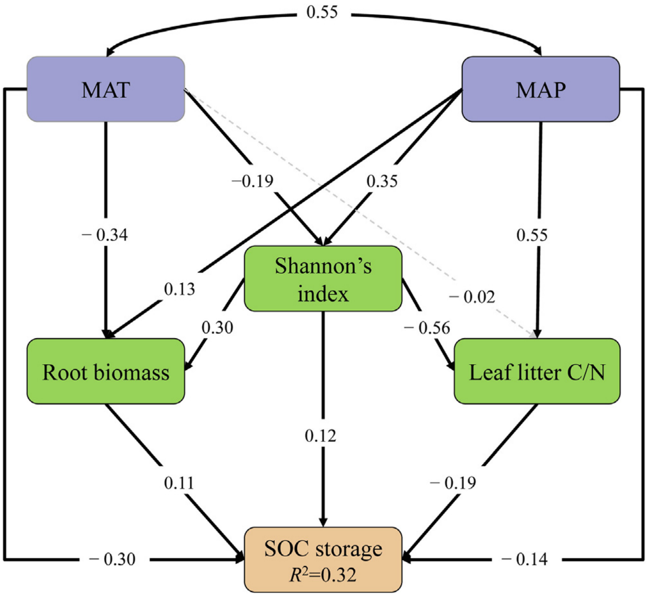

Fig. 4. The most parsimonious structure equation model illustrating the potential direct and indirect effects of MAT, MAP, Shannon's index, leaf litter C/N and root biomass on SOC storage (0–30 cm) in subtropical forests. Solid lines indicate significant relationships ($P < 0.05$), dotted lines indicate non-significant relationships ($P > 0.05$). The coefficients are standardized prediction coefficients for each causal path. R^2 indicates the total variation of the dependent variable explained by all independent variables. Model-fit statistics: $\chi^2 = 0.018$, $P = 0.894$, $df = 1$, $n = 523$.

Table 3
Direct, indirect and total standardized effects of MAT, MAP, Shannon's index, leaf litter C/N and root biomass on SOC storage based on a structural equation model (SEM). Significant effects are at $P < 0.05$ (*), < 0.01 (**), and < 0.001 (***).

Predictor	Pathway to SOC storage	Effect
MAT	Direct effect	− 0.30***
	Indirect through Shannon's index	− 0.05*
	Indirect through leaf litter C/N	− 0.00
	Indirect through root biomass	− 0.04**
	Total effect	− 0.39
MAP	Direct effect	− 0.14***
	Indirect through Shannon's index	0.09*
	Indirect through leaf litter C/N	− 0.10**
	Indirect through root biomass	0.01**
	Total effect	− 0.14
Shannon's index	Direct effect	0.12**
	Indirect through leaf litter C/N	0.11**
	Indirect through root biomass	0.03**
	Total effect	0.26
Leaf litter C/N	Direct effect	− 0.19**
	Indirect effect	–
	Total effect	− 0.19**
Root biomass	Direct effect	0.11*
	Indirect effect	–
	Total effect	0.11*

that species diversity can directly increase SOC storage. This means that species diversity may influence SOC storage by other mechanisms besides affecting litter quantity and quality. For example, species diversity could promote microbial growth and turnover and increase microbial biomass and necromass, leading to SOC accumulation (Prommer et al., 2020). Additionally, species diversity may increase tree canopy stratification and biological soil crusts that consequently reduce soil erosion (Song et al., 2019), and therefore enhance SOC storage. Our large-scale study suggests that the generality of the positive species diversity effect on SOC storage that is found in experimental studies (Lange et al., 2015; Li et al., 2019) and in boreal and temperate forests (Gamfeldt et al., 2013) could be extended to natural, species-rich subtropical forest ecosystems.

In our study, we found weaker species diversity effects on SOC storage in the 10–20 and 20–30 cm soil depths compared to the effect in the top 0–10 cm soil depth. This agrees with previous studies that showed that species diversity had stronger effects in the top soil depth in forest ecosystems (Li et al., 2019; Zhou et al., 2019). Our results indicate that species diversity may have smaller effects on SOC storage in deeper soil depths. Therefore, soil depth should be considered in future research to better understand the consequences of biodiversity loss on SOC storage.

We found that the relationship between species diversity and SOC storage changed along MAP gradients, with a stronger relationship at the low MAP level. This is consistent with previous studies that have found strengthened positive BEF relationships under more stressful environments (Paquette and Messier, 2011; Chen and Chen, 2019; Guo et al., 2019). For instance, Chen and Chen (2019) found that species diversity had more pronounced effect on soil carbon under drier climates. This stronger positive relationship between species diversity and SOC storage in lower MAP may be partly explained by the shift in soil biological activity (Chen and Chen, 2019). We should point out, however, that a series of grassland experiments (He et al., 2002; Fridley, 2003; Wacker et al., 2009; Yin et al., 2017) found that the positive BEF relationships become weaker under more stressful conditions.

Plant functional traits could influence SOC storage through interspecific variation in litter quality (e.g., decomposability) and quantity (De Deyn et al., 2008). While species diversity was positively related to SOC storage, functional diversity had only a weak positive effect in the bivariate relationship (Fig. 2), and was exclued in the best model after other variables were accounted for. Our result was also supported by some other studies indicating that functional diversity had minimal effects on SOC storage in natural forests (Lin et al., 2016; Adair et al., 2018). A possible explanation was that the ecological meaningful traits that related to SOC storage, such as minimum rooting depth, root carbon content and leaf nitrogen content, were not considered in this study due to the lack of accessibility. However, it is also possible that functional traits are not good predictors of ecosystem functioning (van der Plas et al., 2019).

4.2. Effects of litter quantity and quality on SOC storage

Generally, SOC storage represents the balance of carbon inputs and outputs (Jobbágy and Jackson, 2000; Jastrow et al., 2007; Jackson et al., 2017). On the one hand, increased plant derived litter carbon input would result in more carbon input to soil and thus enhance SOC storage (Jackson et al., 2017). On the other hand, increased litter inputs may reduce SOC storage, partly due to positive priming effects (i.e. enhanced decomposition of existing SOC when microorganisms are stimulated by increased fresh organic matter) (Sayer et al., 2011). We hypothesized that increased leaf litter and root biomass inputs would enhance SOC storage. As expected, we found that root biomass had a significant positive effect on SOC storage. Plant root derived carbon has been recognized as a main source of SOC (Lange et al., 2015; Chen et al., 2018), due to high chemical recalcitrance of root tissues, physicochemical protection, and chemical interactions with metal ions (Jastrow et al., 2007; Jackson et al., 2017). Root exudates, as an important root related carbon input, may favor microbial carbon use efficiency and in turn promote microbial growth and carbon stabilization in mineral soil (Manzoni et al., 2012; Jackson et al., 2017), and finally would increase SOC storage (Poirier et al., 2018). We should point out that this study only considered standing root biomass, and lacked data on specific fine root biomass. However, a large number of studies have found a close relationship between root biomass and fine root biomass (Kurz et al., 1996; Litton et al., 2003; Jagodziński and Kałucka, 2011). Not withstanding this limitation, our study still yields some useful insights into the effect of root biomass on SOC storage.

While SOC storage was positively associated with root biomass, we did not detect a significant association with leaf litter biomass, which is inconsistent with our hypothesis and other studies (Li et al., 2019b). One possibility is that higher amounts of fresh and easily decomposable organic matter input might enhance decomposition of existing SOC through positive priming effects (Sayer et al., 2011), thus counteracting the positive litter input effect on SOC storage.

Litter with low C/N will increase microbial substrate use efficiency (Cotrufo et al., 2013), resulting in a higher microbial biomass and a higher proportion of dissolved organic carbon and fine residues, which can be transported and incorporated effectively into deeper soils and be stabilized, and thus enhance SOC storage (Zhou et al., 2019). However, litter with low C/N may also promote decomposition and thus lead to C losses in soils (García-Palacios et al., 2016). In this study, we found a strong negative effect of leaf litter C/N on the SOC storage, which is in line with other studies (Huang et al., 2011; Zhou et al., 2019). Theoretical and experimental studies also demonstrated that litter inputs with lower C/N or that are less recalcitrant (that is, easiser to decompose) lead to more SOC storage than stable inputs due to higher microbial carbon use efficiency (Cotrufo et al., 2013; Frey et al., 2013).

4.3. *Environmental effects on SOC storage*

Climatic factors, such as temperature and precipitation, are usually key regulators of SOC at large spatial scales (Jobbágy and Jackson, 2000; Jackson et al., 2017; Wiesmeier et al., 2019). Precipitation and temperature generally have positive effects on plant productivity (Beer et al., 2010), and thus lead to high amount of plant derived carbon inputs into soil, enhancing SOC storage. However, high temperature would also increase microbial decomposition and therefore may reduce SOC storage (Jackson et al., 2017; Wiesmeier et al., 2019). As we expected, climatic factors had stronger effects on SOC storage than species diversity. We found a strong negative effect of temperature on SOC storage, probably due to increased microbial decomposition and thus high carbon losses in warm areas, confirming what has been shown in previous studies (Jobbágy and Jackson, 2000; Chen et al., 2018). While we found that precipitation had a direct negative influence on SOC storage, it had indirect positive effects on SOC storage through species diversity and root biomass. These indirect positive effects thus could offset the direct negative effect of precipitation on SOC storage.

Soil properties (e.g. CEC and clay content) are expected to have impacts on SOC storage through the effects of soil geochemistry and physical structures (Doetterl et al., 2015; Rasmussen et al., 2018). In contrast to our expectation, no significant effects of soil properties on SOC storage were found in our study, in line with the results of other studies (Wynn et al., 2006; Zhou et al., 2019). This finding suggests that soil properties may have limited effects on SOC storage at large spatial scales despite its critical importance at local or small scales (Jackson et al., 2017; Singh, 2018; Wiesmeier et al., 2019).

5. Conclusions

Using observational data from 523 plots distributed across subtropical forests in China, our results indicate that species diversity (Shannon's index), climatic factors (MAT and MAP) and litter quantity (root biomass) and quality (leaf litter C/N) all affect SOC storage. Among all predictors, SOC storage was most strongly influenced by climatic factors, followed by leaf litter C/N. We found that species diversity enhanced SOC storage in subtropical forests, even after controlling for environmental conditions. Species diversity also indirectly influenced SOC storage through its effects on root biomass and leaf litter C/N. Our findings suggest that planting more multi-species stands could increase SOC storage in China, with the potential to contribute to climate change mitigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118479.

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