

Article

Mineral Protection Potential and Hydroclimatic Context Modulate Plant Diversity Associations with Soil Organic Carbon Fractions in China's Natural Forests

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Abstract

Plant diversity is often expected to enhance soil organic carbon (SOC) storage through greater and more heterogeneous plant inputs, but its relationships with functionally distinct SOC fractions in natural forests remain uncertain. This study compiled published SOC fraction data from 341 surface soil observations in natural forests across China and spatially matched these records with gridded plant alpha diversity, forest age, climate, topographic and soil properties datasets to evaluate biotic and abiotic associations with SOC, particulate organic carbon (POC), mineral-associated organic carbon (MAOC) and MAOC/SOC. Linear regression, multiple regression, piecewise structural equation modelling and stratified analyses were used to evaluate whether plant diversity was associated with the absolute accumulation and relative stabilization of SOC fractions. Plant alpha diversity was negatively associated with $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$ at the national scale, whereas its bivariate relationship with MAOC/SOC was weak. After accounting for forest age and environmental covariates, plant alpha diversity remained negatively related to the absolute contents of SOC fractions while showing a positive association with MAOC/SOC. Forest age was positively associated with $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, and POC was more strongly related to plant diversity and forest age than MAOC. In contrast, MAOC and MAOC/SOC were more strongly associated with mineral protection potential, soil pH and precipitation background. Structural equation models indicated that mineral protection potential and mean annual precipitation were associated with greater MAOC accumulation and SOC allocation to the mineral-associated fraction, whereas temperature and topography were linked to MAOC partly through indirect associations with soil physicochemical conditions. Stratified analyses showed that plant diversity associations varied among forest types and climatic backgrounds. Additional interaction models showed that mineral protection potential significantly moderated the associations between plant alpha diversity and $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, with negative diversity associations weakening under higher mineral protection potential. These findings indicate that plant diversity associations with SOC fractions in natural forests cannot be interpreted as universally positive input relationships. Instead, their direction and strength depend on hydroclimatic context and soil mineral protection, especially for the absolute accumulation of SOC fractions.



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Keywords: plant diversity; soil organic carbon; particulate organic carbon; mineral-associated organic carbon; natural forest; mineral protection; hydroclimatic context

1. Introduction

Soil organic carbon (SOC) is a major component of the terrestrial carbon reservoir, and even small changes in SOC storage can generate substantial feedback to the global carbon cycle [1]. Forest ecosystems are particularly important in this context because they represent a large and persistent global carbon sink, with carbon stored in both vegetation biomass and soils [2,3]. Beyond climate regulation, SOC supports soil fertility, nutrient cycling, soil structure and water retention, thereby linking carbon sequestration with broader soil health and ecosystem functioning [1,4]. Maintaining forest SOC is therefore relevant not only for climate change mitigation, but also for sustaining long-term forest productivity and ecosystem resilience [3]. However, forest SOC formation and stabilization are jointly regulated by plant-derived inputs, microbial processing, mineral protection and forest developmental stage [5,6]. Total forest SOC estimates alone do not reveal whether organic carbon accumulates mainly in relatively transient particulate pools or is transformed into more persistent mineral-associated pools [6,7]. This limitation constrains the ability to predict how biodiversity conservation, forest development and environmental change jointly regulate SOC formation, allocation and stabilization in natural forests [3,5].

Plant diversity has been widely proposed as a biotic driver of SOC accumulation because diverse plant communities can enhance carbon inputs through complementary resource use [8], more stable productivity and a broader range of litter and root-derived substrates [9,10]. Experimental evidence shows that plant diversity can increase soil microbial activity and soil carbon storage [11], suggesting that diversity effects may accumulate through both plant input and microbial pathways [10]. In forests, tree diversity has been shown to increase decadal soil carbon and nitrogen accrual, but this relationship can vary with site properties and functional trait composition [12,13]. Natural forests differ from short-term biodiversity experiments because their diversity patterns are shaped by long-term succession, environmental filtering and non-random species assembly, while their soils integrate decades to centuries of plant inputs, decomposition and disturbance history [14,15]. These characteristics make natural forests essential systems for testing whether biodiversity effects observed in experiments are maintained under real environmental gradients. Large-scale natural forest studies have shown that tree diversity–SOC relationships may strengthen under colder or more arid conditions, indicating that climatic context can alter the strength and direction of diversity effects [14]. Similarly, grassland evidence shows that the positive relationship between plant diversity and SOC can depend on climate and may be stronger under warm and arid conditions [15]. These findings imply that diversity-driven increases in organic inputs do not necessarily translate into higher SOC storage because climate, site fertility and decomposition conditions can mediate the balance between carbon input and carbon retention [13]. Therefore, the plant diversity–SOC relationship in natural forests should be treated as context-dependent rather than universally positive.

However, interpreting plant diversity effects from bulk SOC alone remains limited because SOC consists of functionally distinct fractions with different formation pathways, turnover rates and persistence mechanisms [6,7]. The particulate and mineral-associated organic carbon (POC/MAOC) framework provides a useful basis for separating relatively input-driven organic matter from mineral-stabilized pools [16]. Although increasing evidence links plant diversity to bulk SOC storage, much less is known about whether plant

diversity preferentially affects POC, MAOC or the relative allocation of SOC between these two fractions [7,17]. This distinction is important because POC is generally associated with relatively undecomposed or partially decomposed plant residues and can function as an active interface for soil carbon persistence [18], whereas MAOC is formed through microbial transformation, dissolved organic matter inputs and organo-mineral interactions that depend on mineral surfaces and soil matrix protection [16,19]. Existing fractionation and biomarker studies suggest that plant diversity can influence SOC through both plant residue pathways and microbial transformation pathways, with their relative importance varying across soil depths and environmental conditions [17,20]. However, most available evidence comes from experiments, single regions or individual forest sites, and large-scale evidence linking plant diversity to POC and MAOC in natural forests remains limited [7,21]. Because POC and MAOC differ in formation pathways and persistence mechanisms, separating these fractions can reveal whether plant diversity affects SOC through direct plant residue inputs, microbial transformation or changes in the relative allocation of SOC to mineral-associated pools [22,23].

The effects of plant diversity on SOC fractions can also be modified by forest developmental stage and abiotic constraints [13,17]. Forest age can influence cumulative carbon inputs, stand structure, root distribution and soil development, and it may covary with plant diversity along natural succession gradients [10,17]. Climate regulates both plant productivity and organic matter decomposition, while temperature and soil moisture jointly influence microbial activity, dissolved organic matter movement and SOC persistence [24,25]. Topography can shape soil water redistribution, erosion risk and local microenvironmental conditions, thereby modifying the spatial distribution and preservation of soil carbon [26]. Soil mineral properties can constrain the retention of plant-derived carbon because fine particles, charged surfaces and reactive mineral–organic interfaces influence organic matter sorption, aggregation and persistence [19,27]. Global estimates of mineral-associated carbon stocks indicate that mineral capacity may set an upper limit for additional stabilized carbon storage in many soils [27]. Together, these abiotic conditions may determine how much plant-derived carbon is decomposed, transported or retained in soils, thereby modifying the apparent relationship between plant diversity and SOC fractions.

This study integrated publicly available SOC fraction data from natural forests across China with spatially matched open-source datasets on plant alpha diversity, forest age, climate, topography and soil properties. By distinguishing SOC into total SOC, POC, MAOC and MAOC/SOC, this study aimed to evaluate how plant diversity is associated with both the absolute accumulation and relative stabilization of SOC fractions. Specifically, this study addressed three questions: whether plant alpha diversity is positively associated with SOC, POC and MAOC; whether the relationship between plant alpha diversity and SOC fractions differs between POC and MAOC; and whether mineral protection potential and hydroclimatic context modulate these associations, and whether MAOC and MAOC/SOC are more closely linked to soil matrix and hydroclimatic conditions than to plant alpha diversity alone. Three hypotheses were tested. H1: Plant alpha diversity was expected to be positively associated with SOC, POC and MAOC because diverse forests may provide more abundant and heterogeneous organic carbon inputs through litter, roots and rhizosphere processes [9]. H2: The diversity association was expected to differ between POC and MAOC, with a stronger relationship for POC because this fraction is more directly linked to plant residue inputs, whereas MAOC formation additionally requires microbial transformation and mineral protection [17]. H3: Plant diversity associations with SOC fractions were expected to depend on soil mineral protection potential and hydroclimatic context because the retention of plant-derived carbon requires microbial transformation and

protection by the soil matrix [19,27]. MAOC and MAOC/SOC were expected to be more strongly associated with soil mineral properties, soil pH and hydroclimatic background than with plant diversity alone.

2. Materials and Methods

2.1. Integration of SOC Fraction Data from Natural Forests in China

The soil response variables included SOC, POC, MAOC and MAOC/SOC. These data were derived from an integrated POC and MAOC dataset for Chinese natural forest soils [21]. The original dataset was reorganized to retain information on geographic coordinates, publication year, forest type, soil depth, forest age, climate, SOC, POC, MAOC, MAOC/SOC and available soil properties. Forest types were harmonized into coniferous, broadleaf and mixed forests, and soil depth records were classified into surface and deeper layers. MAOC/SOC represents the proportion of SOC occurring as MAOC and was used to indicate the relative allocation of SOC to the mineral-associated carbon pool. The source dataset ensured the comparability of POC and MAOC separation protocols by retaining only field studies that separated SOC into physical fractions using the sodium hexametaphosphate dispersion method [21]. POC and MAOC were defined using a common 53 μm particle-size threshold, with POC representing the $>53\ \mu\text{m}$ fraction and MAOC representing the $<53\ \mu\text{m}$ fraction. Studies using other SOC fractionation or soil texture classification methods were excluded from the original synthesis. Therefore, the present analysis is based on a dataset in which the main POC/MAOC separation protocol had been harmonized before further environmental data matching.

To reduce the influence of differences in sampling depth, this study retained 0–20 cm surface soil observations for the data analysis. Records without valid coordinates, SOC fraction measurements or key covariates were excluded. Forest age, plant alpha diversity, climate, topography and soil properties were then matched to the SOC fraction dataset according to sample coordinates. After final complete-case screening, the dataset used for the main analyses contained 341 natural forest observations (Figure 1). Thus, the final dataset represents an integrated and spatially matched synthesis dataset rather than a new field sampling dataset collected by the authors. These spatial datasets were selected because the original SOC fraction studies did not consistently report plant diversity, forest age, climate, topographic and soil property variables, whereas gridded products provided nationally consistent and reproducible covariates for all sampling locations.

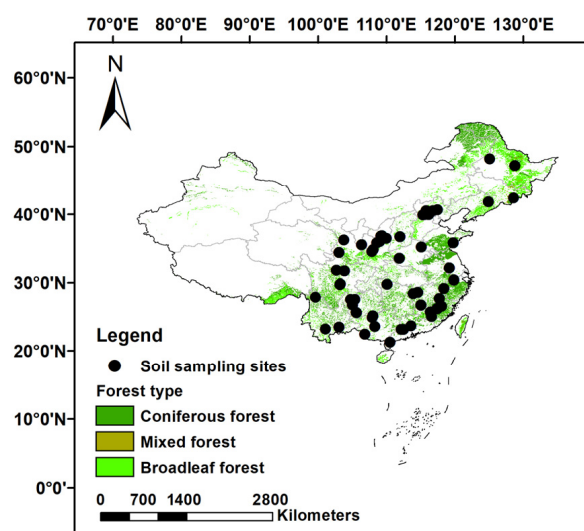


Figure 1. Spatial distribution of soil sampling sites and forest types across China’s natural forests.

2.2. Plant Alpha Diversity, Forest Age and Forest Type

Plant alpha diversity was used as a spatial proxy for plant community diversity around the soil sampling sites. In this study, plant diversity refers to vascular plant alpha diversity, defined as the predicted local species richness of vascular plants at a 1000 m² spatial grain. Alpha diversity variables were extracted from gridded vascular plant alpha diversity products obtained from the iDiv Data Repository (<https://doi.org/10.25829/ividiv.3506-p4c0mo>). For each POC/MAOC sampling point, alpha diversity values were extracted from the raster layers using geographic coordinates.

Forest age was used to represent forest developmental stage. For sites where forest age was reported in the original POC/MAOC soil dataset, the reported value was used preferentially. For sites lacking forest age information, forest age was spatially matched and interpolated using China's Annual Forest Age dataset (CAFA V2.0), which provides annual forest age maps for China from 1986 to 2022 at 30 m spatial resolution. The CAFA dataset was downloaded from Figshare (<https://doi.org/10.6084/m9.figshare.24464170>). Remaining missing values were checked using local neighbourhood information or supplementary imputation procedures when the raster value at the exact sampling location was unavailable. Because forest age was generally right-skewed, and the influence of forest development on soil carbon accumulation may weaken with increasing age [28], the natural logarithm of forest age was used in subsequent models. In the final dataset of 341 observations, forest age was obtained from reported values for 179 observations, CAFA2019-adjusted values for 112 observations, and supplementary proxy or imputed values for 50 observations.

Forest type was used to describe the ecological background and spatial distribution of sites, including coniferous forests, broadleaf forests and mixed forests. Forest type information was taken directly from the forest type records in the original POC/MAOC soil dataset.

2.3. Climate, Topographic and Soil Environmental Covariates

Climate variables included mean annual temperature (MAT) and mean annual precipitation (MAP), which were used to characterize the hydroclimatic conditions of each site. Climate data were obtained from the WorldClim version 2.1 historical climate layers and downloaded from the official WorldClim data portal: <https://www.worldclim.org/data/worldclim21.html> (accessed on 21 July 2026). WorldClim version 2.1 provides high-spatial-resolution global climate grids, and its historical climate data represent long-term mean conditions from 1970 to 2000. MAT and MAP were extracted from the corresponding raster layers according to the coordinates of each soil sampling site. MAT mainly reflects the influence of temperature on plant productivity, organic matter decomposition and microbial processes [29], whereas MAP mainly reflects water availability effects on plant inputs, soil moisture and SOC preservation [30].

Topographic variables included elevation and slope. Elevation data were obtained from the WorldClim version 2.1 elevation layer, downloaded from the official WorldClim data portal (<https://www.worldclim.org/data/worldclim21.html>). This elevation layer was derived from Shuttle Radar Topography Mission elevation data. Slope was calculated from the elevation raster and should therefore be interpreted as a broad scale topographic proxy rather than a plot level field measurement. Elevation can integrate changes in temperature, moisture and regional geomorphic background, whereas slope may influence soil erosion, material transport and water redistribution [31]. All topographic variables were spatially extracted according to sample coordinates.

Soil data were obtained from the ISRIC SoilGrids 2.0 global soil property dataset. SoilGrids provides global digital soil mapping products at 250 m resolution and was

accessed through the official SoilGrids portal and data service: <https://soilgrids.org/> and <https://files.isric.org/soilgrids/latest/data/> (both accessed on 23 July 2026). Soil pH, clay content and cation exchange capacity (CEC) were extracted for the 0–20 cm soil layer. The 0–20 cm values were calculated using depth-weighted information from the 0–5, 5–15 and 15–30 cm SoilGrids layers, with weights of 5, 10 and 5 cm, respectively. Soil pH was used to characterize soil acidity and alkalinity and may influence microbial activity, organic matter decomposition and the association of organic carbon with mineral surfaces [32]. Clay content and CEC were used to represent soil mineral protection potential. Soils with higher clay content generally have a larger specific surface area, which can facilitate organic matter adsorption and aggregate protection [33]. CEC reflects exchangeable sites and charge characteristics and may influence the binding of organic carbon to minerals or cations [34].

2.4. Statistical Analyses

All analyses were conducted in R 4.5.2 (R Development Core Team, Vienna, Austria, 2025). Data processing, model fitting, multicollinearity assessment, structural equation model (SEM) analysis and figure preparation were mainly performed using the R packages dplyr 1.2.1, ggplot2 4.0.3, car 3.1-5 and piecewiseSEM 2.3.1. All analyses were based on the final complete-case dataset containing 341 observations. SOC, POC and MAOC were ln-transformed to reduce strong right-skewness in their distributions. MAOC/SOC was retained on its original scale because it was much less skewed and is directly interpretable as the relative contribution of MAOC to total SOC.

To compare differences in SOC fractions among ecological backgrounds, sampling sites were grouped by forest type and eco-climatic region. Forest types included coniferous (sampling points: 97), broadleaf (198) and mixed forests (46). Climatic background was determined by spatially overlaying sampling coordinates with the Chinese eco-geographical regionalization layer and combining the temperature zone with the humidity zone [35]. To retain the main hydroclimatic gradient while ensuring sufficient sample size for stratified analyses, six climatic groups were defined: Temperate semi-arid (31), Temperate semi-humid (84), Middle temperate humid (29), North subtropical humid (30), Middle subtropical humid (136) and South subtropical/tropical humid (31). Differences in SOC, POC, MAOC and MAOC/SOC among forest types and among climatic groups were tested separately using Kruskal–Wallis tests, followed by Dunn’s post hoc tests with Holm adjustment for multiple comparisons. Different lowercase letters were used in Figure 2 to indicate significant differences among groups at $p < 0.05$.

Linear regressions were first used to test the bivariate relationships between plant alpha diversity and ln[SOC], ln[POC], ln[MAOC] and MAOC/SOC, with fitted uncertainty represented by 95% confidence intervals. Multiple linear regression models were then built separately for the four response variables to compare the relative importance of different predictors. Explanatory variables included plant alpha diversity, ln(forest age), MAT, MAP, soil pH, clay content, CEC, elevation and slope. All continuous explanatory variables were standardized before modelling because they were measured in different units. This standardization allowed the direct comparison of standardized regression coefficients and relative contributions among variable groups. Multicollinearity was assessed using variance inflation factor (VIF) [36], and predictors were iteratively screened until all retained variables had VIF values below 5. When variables within the same environmental group showed high collinearity, variables with clearer ecological interpretation and stronger relevance to the study hypotheses were preferentially retained [37]. We conducted robustness and diagnostic checks for publication-level clustering and residual spatial autocorrelation. The main regression models were refitted using cluster robust standard errors by reference number, and Moran’s I was calculated after residuals were averaged by unique sampling

coordinates. Because these checks did not alter the main conclusions for the absolute SOC fractions, the original regression framework was retained.

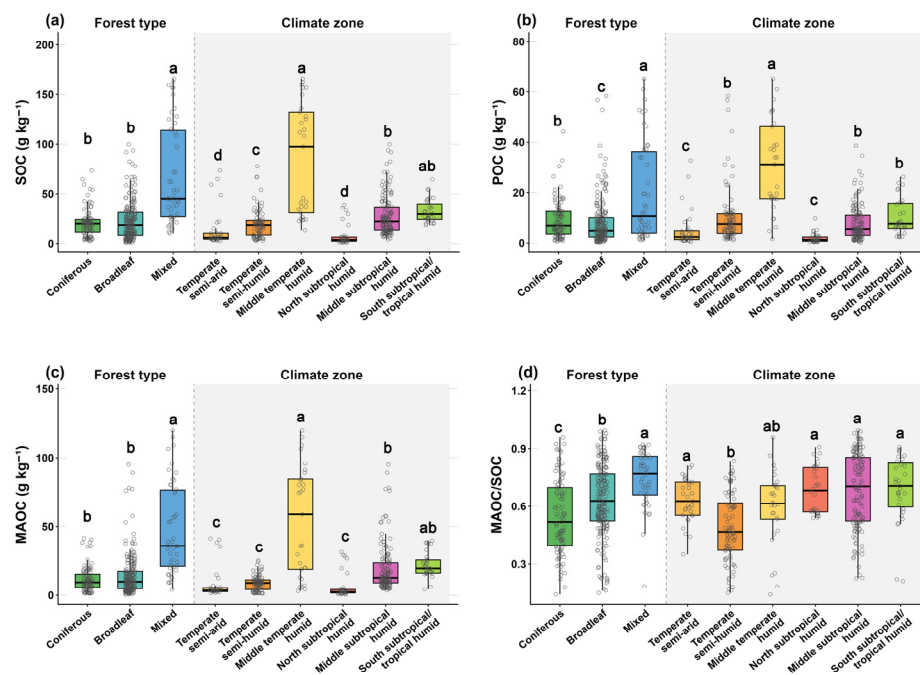


Figure 2. Distribution of SOC fractions across forest types and eco-climatic backgrounds in natural forests of China. Panels show SOC (a), POC (b), MAOC (c) and MAOC/SOC (d) across three forest types and six climate zones. The forest-type section is shown on a white background and the climate-zone section on a light grey background. Boxes show medians and interquartile ranges, whiskers indicate $1.5 \times$ interquartile range, and points indicate individual samples. SOC, POC and MAOC are shown as raw values in g kg^{-1} , and MAOC/SOC is shown as a ratio. Different lowercase letters indicate significant differences among groups based on Dunn's post hoc tests with Holm adjustment at $p < 0.05$. Forest types and climatic groups were tested separately.

Piecewise SEM was used as an exploratory path analysis to evaluate whether the observed covariance structure was consistent with the proposed biotic and abiotic pathways. Because this study was observational and based on spatially matched datasets, the SEM results were not interpreted as proof of causality. Component models were specified a priori according to the conceptual framework and included linear models linking climate, topography, soil pH, mineral protection potential, forest age and SOC fractions. For SEM analysis, soil mineral protection potential was represented by the first principal component of standardized clay content and CEC [38]. The SEMs were constructed according to the three hypotheses of this study and the formation mechanisms of SOC fractions. Climate and topography were treated as exogenous environmental background variables that may first influence soil pH and mineral protection potential [39]. Soil pH and mineral protection potential represented the soil chemical environment and mineral protection conditions. Forest age represented forest developmental stage and could be influenced by environmental background, while also affecting plant inputs and SOC accumulation. Plant alpha diversity was positioned at the biological-process level and could be jointly affected by environment and forest age, while influencing SOC fractions through changes in litter, roots and rhizosphere inputs [9,17]. POC, MAOC and MAOC/SOC were set as final response variables.

Based on this conceptual pathway hierarchy, two SEM models were constructed. The first model used POC and MAOC as dual-response variables to examine pathways regu-

lating absolute SOC fraction accumulation and allowed an association between POC and MAOC to reflect synchronous variation between SOC fractions. The second model used MAOC/SOC as the response variable to examine pathways regulating the relative stabilization of SOC in the mineral-associated fraction. Both models included paths from climate and topography to soil pH and mineral protection potential, paths from environmental factors and soil properties to forest age, and paths from environmental factors, forest age and plant alpha diversity to SOC fractions. Soil pH and mineral protection potential were allowed to covary because both represent soil physicochemical conditions, and POC and MAOC were allowed to covary because they are related SOC fractions. Model fit was evaluated using Fisher's C, degrees of freedom, p value and AICc. When the p value of Fisher's C test was greater than 0.05, the model structure was considered not to deviate significantly from the observed data. Path coefficients were standardized to compare the relative strength of different pathways.

Finally, stratified analyses were conducted to test whether the associations between plant alpha diversity and SOC fractions varied among forest types and climatic backgrounds. Simple linear models were fitted separately within each forest type and each climatic group using the model form $\text{response} \sim \text{plant alpha diversity}$. This analysis was used to describe the direction and strength of plant diversity effects under different ecological backgrounds. To further evaluate hydroclimatic regulation at a broader regional scale, sites were divided into Temperate and Subtropical regions. Within each region, plant alpha diversity, MAT and MAP were standardized, and the model $\text{response} \sim \text{plant alpha diversity} \times \text{MAT} \times \text{MAP}$ was fitted to test whether temperature and precipitation modulated the relationships between plant diversity and SOC fractions. We also considered the annual heat moisture index (AHMI), calculated as $(\text{MAT} + 10)/(\text{MAP}/1000)$, as an aridity indicator. However, because AHMI was derived from MAT and MAP and was strongly correlated with MAP in our dataset ($r = -0.80$), it was not included in the main models together with MAT and MAP to avoid collinearity. To test whether mineral protection potential moderated plant diversity associations with SOC fractions, additional interaction models were fitted for each response variable. The model form was $\text{response} \sim \text{plant alpha diversity} \times \text{mineral protection potential} + \ln(\text{forest age}) + \text{MAT} + \text{MAP} + \text{soil pH} + \text{elevation} + \text{slope}$. Simple slopes of plant alpha diversity were then estimated at low, mean and high mineral protection potential, corresponding to -1 SD, mean and $+1$ SD of mineral protection potential, respectively.

3. Results

3.1. Spatial Variation in SOC Fractions and Their Relationships with Plant Alpha Diversity

Among the 341 surface soil samples from natural forests in China, SOC, POC, MAOC and MAOC/SOC all showed substantial spatial variation (Table 1; Figures 1 and 2). Specifically, the mean values and coefficients of variation (CV) were 28.24 g kg^{-1} and 1.04 for SOC, 10.03 g kg^{-1} and 1.16 for POC, 18.02 g kg^{-1} and 1.17 for MAOC, and 0.62 and 0.31 for the MAOC/SOC ratio. SOC fractions showed significant differences among forest types and among eco-climatic backgrounds, although the patterns differed among SOC, POC, MAOC and MAOC/SOC (Figure 2). Among forest types, mixed forests had significantly higher SOC, POC and MAOC concentrations than coniferous and broadleaf forests. Mean SOC, POC and MAOC concentrations in mixed forests were 67.88 , 20.14 and 47.75 g kg^{-1} , respectively. For SOC and MAOC, coniferous and broadleaf forests did not differ significantly from each other. For POC, coniferous forests had significantly higher values than broadleaf forests. MAOC/SOC also differed significantly among the three forest types, with the highest value in mixed forests, followed by broadleaf forests and coniferous forests. Across climatic backgrounds, middle temperate humid sites had the highest SOC, POC

and MAOC concentrations and were significantly higher than most other climatic groups. North subtropical humid and temperate semi-arid sites generally had the lowest absolute SOC fraction concentrations. For SOC and MAOC, south subtropical/tropical humid sites were not significantly different from middle temperate humid or middle subtropical humid sites, indicating partly overlapping carbon accumulation patterns among these humid forest regions. For MAOC/SOC, temperate semi-humid sites had the lowest values, whereas the other climatic groups generally showed higher and partly overlapping values.

Table 1. Descriptive statistics for SOC fractions and explanatory variables in Chinese natural forests, showing mean, maximum (Max.), median, minimum (Min.), standard deviation (SD), and coefficient of variation (CV) for $n = 341$ sampling sites.

Variances	Mean	Max	Median	Min	SD	CV
SOC (g kg^{-1} soil)	28.24	166.05	21.17	1.09	29.37	1.04
POC (g kg^{-1} soil)	10.03	65.33	5.86	0.19	11.68	1.16
MAOC (g kg^{-1} soil)	18.02	119.68	11.16	0.61	21.02	1.17
MAOC/SOC	0.62	0.99	0.63	0.14	0.19	0.31
Plant alpha diversity (species per 1000 m^2)	37.88	56.00	39.00	17.00	8.85	0.23
Forest age (yr)	50.41	400.00	41.00	1.00	46.47	0.92
MAT ($^{\circ}\text{C}$)	13.66	23.00	16.20	−0.30	5.77	0.42
MAP (mm)	1097.85	2100.00	836.00	263.00	540.18	0.49
Elevation (m)	966.40	3425.00	891.00	10.00	777.09	0.80
Slope ($^{\circ}$)	4.24	13.23	3.01	0.02	3.50	0.82
Soil pH	6.30	8.38	6.00	4.80	0.97	0.15
Clay (%)	25.80	38.60	24.98	14.97	6.42	0.25
CEC (cmol(c) kg^{-1})	18.67	27.38	18.32	10.90	3.04	0.16

Note: $\text{CV} = \text{SD}/\text{Mean}$.

The relationships between plant alpha diversity and SOC fractions did not support the positive relationship predicted in H1 (Figure 3). Across all observations, plant alpha diversity was significantly negatively related to $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, with R^2 values of 0.15, 0.14 and 0.11 and slopes of −0.04, −0.05 and −0.04, respectively. In contrast, the relationship between plant alpha diversity and MAOC/SOC was weak and non-significant. Because the same gridded plant diversity value may correspond to multiple soil observations with different SOC fraction contents, these national-scale relationships should be interpreted as broad patterns rather than site-level causal effects. The relationships may also reflect the uneven distribution of observations among forest types and climatic backgrounds. Therefore, the relationship between plant diversity and SOC fractions was evaluated within a multifactorial framework that accounted for forest age, climate, topography and soil properties.

3.2. Relative Associations and Contributions of Plant Diversity, Forest Age and Environmental Factors on SOC Fractions

Multiple regression models showed that plant diversity, forest age, climate, topography and soil properties jointly explained the spatial variation in SOC fractions, and all four models were statistically significant ($p < 0.001$; Figure 4). The model explained the largest proportion of variation in $\ln[\text{MAOC}]$, with $R^2 = 0.55$, followed by $\ln[\text{SOC}]$ with $R^2 = 0.49$. The R^2 values for $\ln[\text{POC}]$ and MAOC/SOC were 0.31 and 0.28, respectively. Standardized regression coefficients showed that plant alpha diversity had significant negative associations with $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, with β values of −0.44, −0.57 and −0.36, respectively, but it had a significant positive association with MAOC/SOC, with $\beta = 0.04$. Forest age was positively associated with $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, with β values of 0.13, 0.18 and 0.13, respectively, but its effect on MAOC/SOC was weak and

non-significant. Among climatic variables, MAT was negatively associated with $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, with β values of -0.32 , -0.33 and -0.33 , whereas MAP was positively associated with $\ln[\text{SOC}]$, $\ln[\text{MAOC}]$ and MAOC/SOC , with β values of 0.16 , 0.31 and 0.08 .

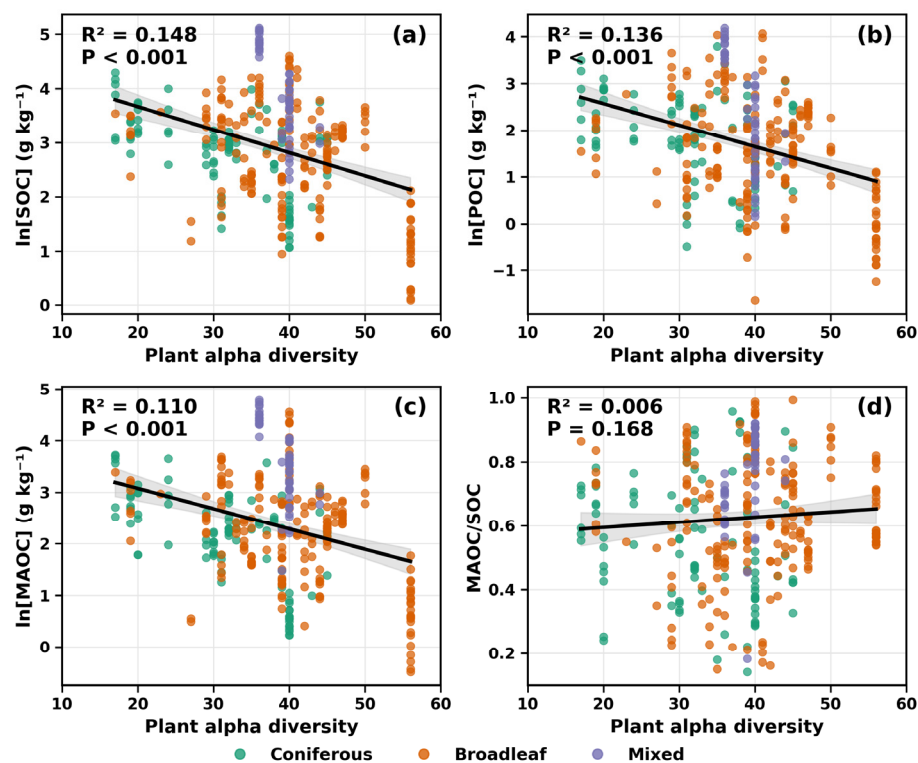


Figure 3. Relationships between plant alpha diversity and $\ln[\text{SOC}]$ (a), $\ln[\text{POC}]$ (b), $\ln[\text{MAOC}]$ (c), and MAOC/SOC (d). Points are colored by forest type. Shaded areas indicate 95% confidence intervals, and solid black lines indicate fitted linear regressions based on all observations. Significance levels and R^2 values are shown in each panel.

The dominant factors and relative contributions differed clearly among SOC fractions (Figure 4). For $\ln[\text{SOC}]$, plant diversity and forest age together contributed 30.5%, climate contributed 25.8%, soil properties contributed 26.2% and topography contributed 17.5%. For $\ln[\text{POC}]$, plant diversity and forest age had the highest contribution, accounting for 35.5%, with plant alpha diversity alone contributing 27.1%. For $\ln[\text{MAOC}]$, climate and soil properties made similar contributions, accounting for 32.0% and 30.3%, respectively. Clay content was the strongest positive predictor, with $\beta = 0.44$ and an individual contribution of 22.1%. For MAOC/SOC , soil properties had the highest contribution, accounting for 51.5%. Soil pH, clay content and CEC all had significant positive effects, with β values of 0.05 , 0.06 and 0.06 , respectively. These results indicate that POC was more closely associated with plant diversity and forest age, whereas MAOC and MAOC/SOC were more strongly associated with mineral protection conditions and the soil chemical environment. This pattern was consistent with H2 and H3, indicating divergent controls over plant input-related and mineral-associated SOC fractions.

3.3. Direct and Indirect Pathways Regulating SOC Fraction Formation and Stabilization

The SEMs supported the hypothesized pathway framework linking climate, topography, soil properties, forest age and plant alpha diversity to SOC fraction formation and stabilization (Figure 5). The dual-response POC–MAOC model showed good fit (Fisher's $C = 2.27$, $df = 4$, $p = 0.69$; Figure 5a) and explained 29% and 53% of the variation in POC

and MAOC, respectively. The direct paths were broadly consistent with the multiple regression results and showed contrasting controls over the two SOC fractions. POC was negatively associated with plant alpha diversity ($\beta = -0.47$), soil pH ($\beta = -0.29$), MAT ($\beta = -0.28$) and elevation ($\beta = -0.23$), whereas forest age had a weak positive effect on POC ($\beta = 0.13$). In contrast, MAOC was positively affected by mineral protection potential ($\beta = 0.39$), MAP ($\beta = 0.32$) and forest age ($\beta = 0.10$), but negatively affected by plant alpha diversity ($\beta = -0.31$), MAT ($\beta = -0.28$) and elevation ($\beta = -0.26$). POC and MAOC also showed a strong positive residual association ($\beta = 0.55$), indicating synchronous spatial variation between the two SOC fractions after accounting for the specified environmental, edaphic and biological pathways. The indirect paths indicated that climate and topography were linked to POC and MAOC through their effects on soil pH, mineral protection potential, forest age and plant alpha diversity. MAP indirectly promoted MAOC accumulation by increasing mineral protection potential ($\beta = 0.45$), whereas MAT and slope indirectly constrained MAOC through negative effects on mineral protection potential ($\beta = -0.18$ and -0.30 , respectively). Environmental background could also influence SOC fractions through plant diversity, as plant alpha diversity was negatively associated with elevation ($\beta = -0.38$) and mineral protection potential ($\beta = -0.18$) but positively associated with slope ($\beta = 0.38$).

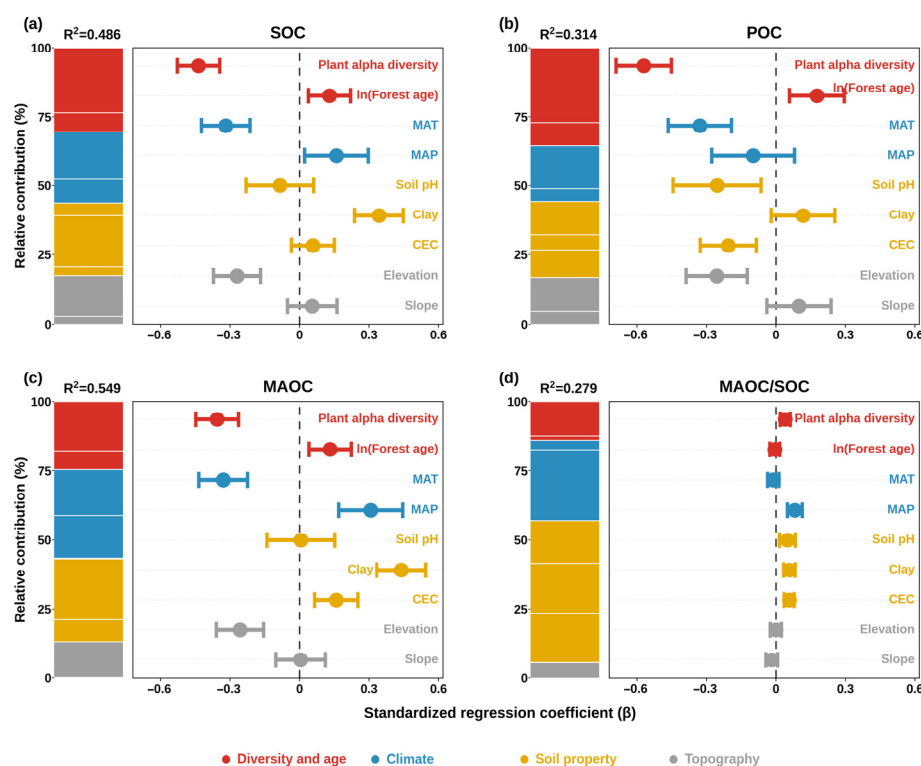


Figure 4. Standardized regression coefficients (β) and relative contributions of explanatory variables to $\ln[\text{SOC}]$ (a), $\ln[\text{POC}]$ (b), $\ln[\text{MAOC}]$ (c), and MAOC/SOC (d). Points and horizontal lines represent parameter estimates and 95% confidence intervals. Stacked bars indicate the relative contribution of each predictor to the summed absolute standardized regression coefficients. R^2 values indicate the proportion of total variance explained by the full model.

The MAOC/SOC stabilization model also showed good fit (Fisher's $C = 9.04$, $df = 8$, $p = 0.34$; Figure 5b) and explained 27% of the variation in MAOC/SOC. The direct paths showed that MAOC/SOC increased with mineral protection potential ($\beta = 0.46$), MAP ($\beta = 0.42$), soil pH ($\beta = 0.32$) and plant alpha diversity ($\beta = 0.19$), with mineral protection potential showing the strongest positive effect. The indirect paths further suggested that

climate and topography could shape the proportion of SOC in the mineral-associated fraction through their effects on soil pH and mineral protection potential. Soil pH and mineral protection potential showed a significant negative residual association in both SEM models ($\beta = -0.29$), indicating that these two soil physicochemical dimensions represented related but distinct constraints on SOC stabilization. Overall, plant alpha diversity was negatively associated with the absolute contents of POC and MAOC but positively associated with MAOC/SOC. MAOC accumulation and the proportion of SOC stabilized in the mineral-associated fraction were more strongly regulated by mineral protection potential, soil acid–base conditions and precipitation background than by plant diversity, consistent with H3.

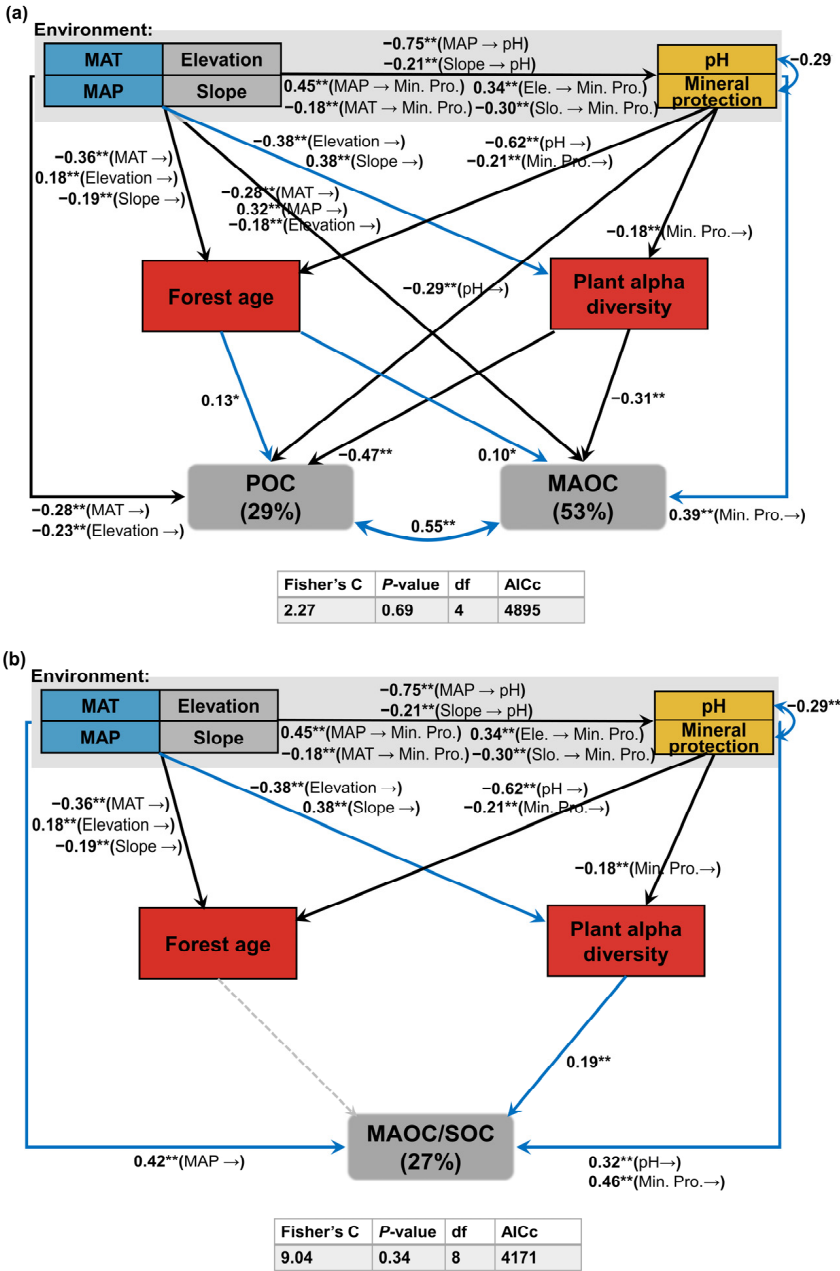


Figure 5. Structural equation models for SOC fraction formation and stabilization. Panel (a) shows the direct and indirect pathways associated with POC and MAOC, and panel (b) shows the pathways regulating MAOC/SOC. Blue and black arrows indicate positive and negative paths, respectively. Grey dashed arrows indicate non-significant paths. Path coefficients are standardized. $p < 0.05$, * and $p < 0.01$, **. Fisher's C, degrees of freedom, p value and AICc are shown below each panel.

3.4. Differences in Plant Alpha Diversity Associations Among Forest Types and Climatic Backgrounds

Stratified regression analyses showed that the relationships between plant alpha diversity and SOC fractions varied strongly among forest types and climatic backgrounds (Figure 6). Across forest types, plant alpha diversity was generally negatively associated with the absolute contents of SOC fractions, with the strongest associations in mixed forests for $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$ (slopes = -0.30 , -0.43 and -0.27 , respectively). However, plant alpha diversity had a positive association with MAOC/SOC in mixed forests (slope = 0.03), suggesting that diversity associations with absolute SOC fraction contents and the relative allocation of SOC to MAOC could differ in direction. Across climatic backgrounds, the strongest negative relationship occurred in north subtropical humid sites, where plant alpha diversity was significantly negatively related to all four response variables. Negative diversity associations were also observed for several SOC fractions in temperate semi-arid and temperate semi-humid sites, whereas middle temperate humid sites showed no significant relationships. In contrast, middle subtropical humid sites showed positive relationships for $\ln[\text{MAOC}]$ and MAOC/SOC, indicating that the direction and strength of diversity associations depended strongly on hydroclimatic background. Forest types were unevenly distributed among climatic groups. North subtropical humid sites were represented only by broadleaf forests, whereas middle subtropical humid sites included broadleaf, coniferous and mixed forests. This uneven distribution indicates that the stratified diversity slopes should be interpreted as climate-associated patterns that may also include differences in forest type composition.

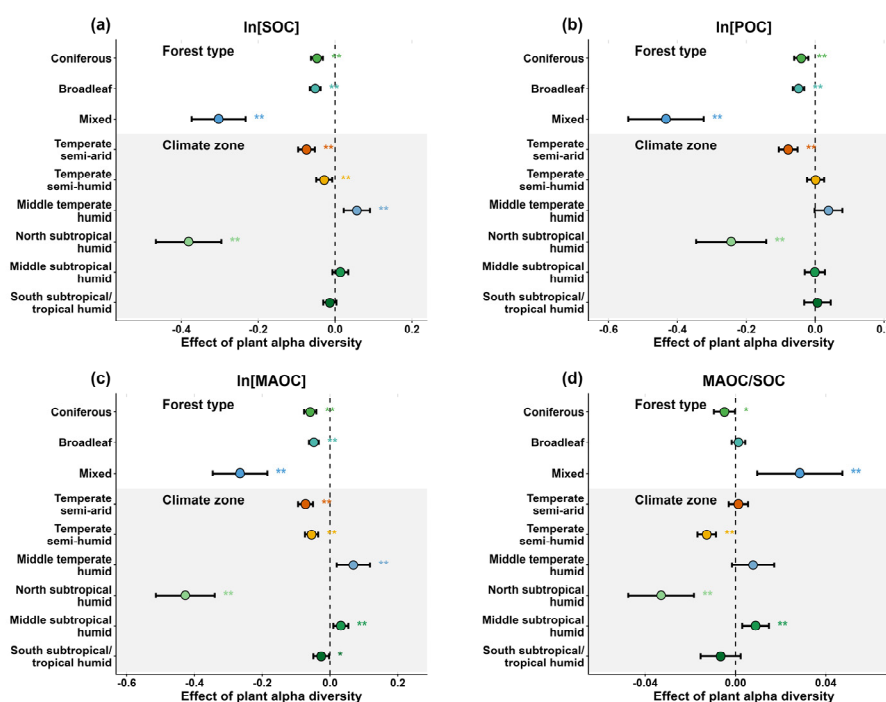


Figure 6. Forest type- and climate zone-dependent associations of plant alpha diversity with SOC fractions. Points indicate within-group slopes of plant alpha diversity, and horizontal lines indicate 95% confidence intervals. The vertical dashed line indicates zero effect. The forest type section is shown on a white background and the climate zone section on a light grey background. Response variables are $\ln[\text{SOC}]$ (a), $\ln[\text{POC}]$ (b), $\ln[\text{MAOC}]$ (c) and MAOC/SOC (d). Different colors are used to visually distinguish the forest types and climatic groups used in the stratified analyses. $p < 0.05$, * and $p < 0.01$, **.

The continuous climate interaction models for the temperate and subtropical regions also supported the hydroclimatic context dependency of plant diversity associations

(Table 2). In the temperate region, the Diversity $\times$ MAP interaction was significantly positive for $\ln[\text{SOC}]$ and $\ln[\text{POC}]$, whereas the Diversity $\times$ MAT interaction was not significant, indicating that the relationships between diversity and SOC fractions in temperate forests were more sensitive to precipitation background. For MAOC/SOC, the Diversity $\times$ MAP interaction was significantly negative, suggesting that increasing precipitation may alter the direction of the diversity association with SOC stabilization proportion. In contrast, in the subtropical region, both Diversity $\times$ MAT and Diversity $\times$ MAP interactions were significant for $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, and the estimates for Diversity $\times$ MAP were generally larger. These results indicate that plant diversity associations in subtropical forests were jointly regulated by temperature and precipitation, with water availability remaining an important dimension shaping the responses of SOC fractions.

Table 2. Moderating effects of the interactions between plant alpha diversity and MAT or MAP on SOC fractions within temperate and subtropical regions.

Zone	Response	Diversity $\times$ MAT	<i>p</i>	Diversity $\times$ MAP	<i>p</i>
Temperate	$\ln[\text{SOC}]$	−0.17	0.24	0.28	0.02
Temperate	$\ln[\text{POC}]$	−0.21	0.20	0.51	<0.001
Temperate	$\ln[\text{MAOC}]$	−0.11	0.49	0.06	0.606
Temperate	MAOC/SOC	0.02	0.39	−0.10	<0.001
Subtropical	$\ln[\text{SOC}]$	−0.19	0.02	0.41	<0.001
Subtropical	$\ln[\text{POC}]$	−0.22	0.04	0.339	<0.001
Subtropical	$\ln[\text{MAOC}]$	−0.21	0.01	0.47	<0.001
Subtropical	MAOC/SOC	−0.01	0.51	0.032	0.041

Note: The model form was response~plant alpha diversity $\times$ MAT $\times$ MAP. Plant alpha diversity, MAT and MAP were standardized within the temperate or subtropical regions. Only the two-way interaction terms between plant diversity and MAT or MAP are shown.

The mineral protection interaction models further showed that mineral protection potential significantly moderated the associations between plant alpha diversity and the absolute contents of SOC fractions (Table 3). The Diversity $\times$ mineral protection potential interaction was significantly positive for $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$, but was not significant for MAOC/SOC. Simple slope analyses showed that the negative associations between plant alpha diversity and $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$ were strongest under low mineral protection potential and weakened as mineral protection potential increased. At high mineral protection potential, the diversity slopes for $\ln[\text{SOC}]$ and $\ln[\text{MAOC}]$ were no longer significant. These results indicate that mineral protection potential buffered the negative diversity associations with absolute SOC fraction contents, whereas the diversity association with MAOC/SOC was not significantly moderated by mineral protection potential.

Table 3. Moderating effect of mineral protection potential on plant diversity associations with SOC fractions.

Response	Diversity $\times$ Mineral Protection β (95% CI)	<i>p</i>	Low Mineral Protection Slope	Mean Mineral Protection Slope	High Mineral Protection Slope	Adj. R ²
$\ln[\text{SOC}]$	0.27 (0.18, 0.36)	<0.01	−0.65 **	−0.38 **	−0.11 ns	0.50
$\ln[\text{POC}]$	0.240 (0.12, 0.36)	<0.01	−0.76 **	−0.52 **	−0.28 **	0.31
$\ln[\text{MAOC}]$	0.244 (0.15, 0.34)	<0.01	−0.55 **	−0.31 **	−0.06 ns	0.55
MAOC/SOC	−0.01 (−0.03, 0.01)	0.33	0.05 **	0.04 **	0.03 ns	0.26

Note: Low, mean and high mineral protection indicate −1 SD, mean and +1 SD of mineral protection potential, respectively. Simple slopes indicate the association between plant alpha diversity and each SOC fraction at each mineral protection level. ** $p < 0.01$; ns, not significant. Models included plant alpha diversity, mineral protection potential, their interaction, $\ln(\text{forest age})$, MAT, MAP, soil pH, elevation and slope.

4. Discussion

Our study revealed significant associations of plant alpha diversity, forest age, climate, topography and soil properties with SOC fractions across natural forests in China, and it showed that biotic and abiotic controls contributed differently to SOC accumulation and stabilization. After accounting for forest age and environmental factors, our analyses showed that plant alpha diversity was negatively associated with the absolute contents of SOC, POC and MAOC, whereas it was positively associated with MAOC/SOC. In addition, POC was more strongly related to plant diversity and forest age, while MAOC and MAOC/SOC were more strongly associated with mineral protection potential, soil pH and precipitation background. These results suggest that plant diversity associations with soil carbon in natural forests should not be interpreted simply as positive input effects. Instead, the direction and magnitude of diversity effects appear to depend on how plant-derived inputs interact with forest development, microbial transformation and soil mineral protection under different environmental backgrounds. Taken together, our findings indicate that the accumulation of SOC fractions and the relative stabilization of SOC in the mineral-associated pool are governed by partially distinct mechanisms. Here, we discuss how the interplay among plant diversity, forest development, climate and soil physicochemical constraints may explain the observed patterns of SOC, POC, MAOC and MAOC/SOC in natural forests across China.

4.1. Environment-Dependent Relationships Between Plant Alpha Diversity and SOC Fractions

The negative national-scale relationships between plant alpha diversity and the absolute contents of SOC, POC and MAOC observed in this study suggest that biodiversity effects on soil carbon in natural forests are strongly shaped by environmental context [14]. Although plant diversity is often expected to promote SOC accumulation by increasing plant productivity, litter heterogeneity, root inputs and rhizosphere activity [9,40,41], such positive effects are not always consistently expressed across large environmental gradients [13,15]. In natural forests, plant diversity often covaries with forest type, successional stage, climatic regime and soil conditions, all of which can simultaneously influence carbon input, decomposition and stabilization [14,41]. Consequently, the large-scale relationship between plant diversity and SOC fractions may reflect the combined outcome of multiple interacting processes rather than a direct biodiversity effect alone. This interpretation is consistent with recent evidence showing that tree diversity–SOC relationships vary with resource availability and climatic background and become stronger under colder, drier or otherwise more environmentally constrained conditions [14,15,41].

This perspective helps explain why the present results differ from studies that reported positive diversity effects on soil carbon accumulation [12,40,41]. The stratified analyses showed that the negative diversity–SOC fraction relationships were not uniformly stronger across all warm and humid environments. The strongest negative slopes occurred in north subtropical humid forests, whereas middle subtropical humid forests showed positive relationships for $\ln[\text{MAOC}]$ and MAOC/SOC, and middle temperate humid forests showed no consistent negative pattern. This contrast suggests that the national-scale negative relationships were not caused by a general warm-humid effect, but reflected the combined influence of climatic background, forest type composition and the distribution of high diversity observations [14,15]. Forest types were also unevenly distributed among climatic groups, with north subtropical humid sites represented only by broadleaf forests, whereas middle subtropical humid sites included broadleaf, coniferous and mixed forests. Therefore, current SOC fractions may still carry strong effects of environmental filtering, long-term soil development, historical vegetation composition and disturbance history, which can obscure the direct effects of plant diversity [12,41,42]. Recent conceptual work also suggests

that biodiversity effects on POM, MAOM and total SOM depend on whether soils are limited by carbon inputs, microbial transformation or mineral stabilization capacity [7,42]. Thus, the negative diversity–SOC relationships observed here should not be interpreted as evidence that plant diversity intrinsically suppresses SOC formation. Rather, they indicate that the sign and strength of biodiversity associations are filtered by climatic background, forest type distribution and the prevailing stabilization context in natural forests [7].

4.2. Plant Diversity May Alter SOC Allocation Toward MAOC Rather than Simply Increase SOC Fraction Contents

In addition to the negative relationships with SOC fractions, separating bulk SOC into POC and MAOC revealed that plant diversity was associated differently with the absolute accumulation of carbon fractions and with the relative allocation of SOC to the mineral-associated pool [6,7]. This distinction was evident in the present results because POC and MAOC showed different associations with plant diversity, forest age and abiotic controls. POC was more strongly associated with plant diversity and forest age than MAOC, suggesting that this fraction was more responsive to biological inputs and stand developmental processes [6,16,17]. By contrast, MAOC was more closely linked to mineral protection potential, precipitation background and soil pH, indicating stronger control by soil physicochemical conditions and hydroclimatic context [16,17,19]. This pattern agrees with the general view that plant-derived carbon first enters relatively input-related pools before being progressively transformed into more stabilized forms [6,16]. It is also consistent with recent work showing that particulate organic matter is not merely a transient and labile carbon pool, but an active functional interface where fresh litter, microbial processing, aggregation and organo-mineral interactions occur simultaneously [18]. Thus, biodiversity effects in natural forests may be more clearly reflected in the input-related POC pool than in MAOC, whose accumulation depends more strongly on microbial transformation and mineral protection.

Notably, we found that plant alpha diversity was positively related to MAOC/SOC despite its negative relationships with SOC, POC and MAOC contents. This pattern suggests that plant diversity may influence the partitioning of SOC between particulate and mineral-associated pools more strongly than the absolute size of those pools [7,17,43,44]. More specifically, plant diversity may alter SOC allocation by changing the diversity and continuity of litter, root and rhizosphere inputs, which can influence microbial processing, dissolved organic matter production and the transfer of plant-derived carbon toward mineral-associated forms [40,45]. A subtropical forest study supports this mechanism by showing that plant species richness affected SOC accumulation differently in topsoil and subsoil, with topsoil SOC being more closely linked to plant-derived materials and subsoil SOC being more closely linked to microbe-derived materials and MAOM formation through dissolved organic matter pathways [17]. This mechanism is also consistent with evidence that higher plant diversity can increase microbial growth, biomass turnover and microbial carbon use efficiency, thereby increasing the production of microbial-derived compounds that can be stabilized on mineral surfaces [40,45,46]. These changes may increase the probability that plant-derived carbon enters more stable SOC forms. Recent review papers also show that the balance between POM and MAOM depends on carbon inputs, microbial processing and access to mineral surfaces [7,43,47]. Therefore, the present results do not mean that high-diversity forests always produce more MAOC in absolute terms. Instead, they suggest that plant diversity may shift SOC toward mineral-associated forms when soil and environmental conditions favour such stabilization [7,17].

4.3. Mineral Protection and Hydroclimatic Context Modulate Plant Diversity Associations with SOC Fractions

Mineral protection potential and soil pH helped explain why plant diversity associations with SOC fractions depended on soil matrix conditions [27]. In our study, plant alpha diversity was negatively associated with the absolute contents of POC and MAOC, but positively associated with MAOC/SOC. The additional interaction models showed that mineral protection potential significantly moderated the associations between plant alpha diversity and $\ln[\text{SOC}]$, $\ln[\text{POC}]$ and $\ln[\text{MAOC}]$. The negative diversity associations were strongest under low mineral protection potential and weakened as mineral protection potential increased. This pattern suggests that mineral protection potential buffered the negative relationships between plant diversity and absolute SOC fraction contents [33,34]. A plausible explanation is that clay content and CEC, used here as a proxy for mineral protection potential, may represent the capacity of the soil matrix to retain plant-derived and microbially processed carbon through sorption, aggregation and mineral interactions [19,27,48]. Soil pH may further influence this retention by regulating microbial activity, dissolved organic matter chemistry, surface charge and cation bridging [19,32]. Therefore, plant diversity may modify organic carbon inputs and microbial processing, but whether these inputs are retained as SOC fractions depends strongly on mineral protection potential and the soil chemical environment [7,17,27].

Hydroclimatic background also modified plant diversity associations with SOC fractions. In our study, MAT was negatively associated with SOC, POC and MAOC, whereas MAP was positively associated with SOC, MAOC and MAOC/SOC. Higher temperature may have promoted decomposition and carbon turnover more strongly than plant carbon inputs, thereby reducing net SOC fraction accumulation [22,25]. By contrast, greater precipitation may have supported plant production, dissolved organic matter movement and the formation and retention of mineral-associated carbon [22,23,27]. The SEM results also showed that climate affected MAOC not only directly, but also indirectly through soil pH and mineral protection potential, suggesting that hydroclimatic effects were partly mediated by the soil environment [23,39]. The stratified interaction models further showed that the plant diversity $\times$ MAP interaction was significant for $\ln[\text{SOC}]$ and $\ln[\text{POC}]$ in temperate forests, whereas both plant diversity $\times$ MAT and plant diversity $\times$ MAP interactions were significant for absolute SOC fractions in subtropical forests. Together with the mineral protection interaction models, these results indicate that the strength and direction of plant diversity associations with SOC fractions were filtered by both hydroclimatic context and soil mineral protection [14,15].

4.4. Limitations and Future Directions

In our study, spatially matched predictor variables were partly derived from gridded datasets and may therefore involve scale mismatch with the original soil sampling locations. Accordingly, the observed plant diversity associations mainly represent national scale spatial patterns rather than direct local ecological processes. Similarly, slope was derived from a gridded elevation product and may not capture fine-scale terrain conditions or slope aspect at the original field plots. Mineral protection potential was represented by clay content and CEC and should be interpreted as a proxy for soil matrix conditions rather than a direct measurement of mineral associated stabilization capacity. In addition, the piecewise SEM should be interpreted as an exploratory pathway framework because the analysis was based on observational data and spatially matched covariates. Future studies that combine site level vegetation surveys, direct measurements of soil mineral properties and repeated SOC fraction measurements would help test the mechanisms proposed here more directly.

5. Conclusions

This study shows that SOC fraction accumulation and relative stabilization in China's natural forests are associated with partly distinct biotic and abiotic factors. Across 341 observations, plant alpha diversity was negatively associated with SOC, POC and MAOC, but positively associated with MAOC/SOC after environmental covariates were considered. Forest age was positively associated with SOC, POC and MAOC, while POC showed stronger links with plant diversity and forest development than MAOC. By contrast, MAOC and MAOC/SOC were more closely associated with mineral protection potential, soil pH and precipitation background. Mineral protection potential weakened the negative associations between plant alpha diversity and absolute SOC fractions, indicating that soil matrix conditions can modify biodiversity–SOC relationships. Hydroclimatic context also modified these associations, as the strength and direction of plant diversity relationships with SOC fractions varied with temperature and precipitation background, especially across temperate and subtropical forests. These findings suggest that bulk SOC alone is insufficient for evaluating biodiversity associations with soil carbon persistence. Instead, biodiversity–SOC relationships should be interpreted within a SOC fraction framework that considers both mineral protection potential and hydroclimatic context. Future studies combining field vegetation surveys, microbial indicators, direct measurements of mineral properties and repeated SOC fraction measurements would help clarify the processes linking plant inputs, microbial transformation and mineral protection across forest developmental stages.

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