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Peer reviewed

Tree diversity–soil organic carbon relationships strengthen under colder and more arid conditions

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Summary

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- Soil organic carbon (SOC) plays an essential role in carbon sequestration and climate change mitigation in forest ecosystems. While experimental studies have shown that plant diversity usually increases SOC, it remains unclear whether this positive relationship holds in natural ecosystems across varying climatic conditions.
- Using a global dataset of 15 large and long-term monitored natural forest sites spanning a wide latitudinal range, we assess the relationship between tree diversity and SOC within and across sites in temperate, subtropical, and tropical regions.
- We found an overall positive relationship between tree taxonomic diversity and SOC. The relationships between tree taxonomic or functional diversity and SOC became stronger under

Key words: biodiversity, climate, ForestGEO, functional traits, soil organic carbon, diversity effects.

colder and more arid conditions. Additionally, tree functional composition was linked to SOC only within a subset of sites in more arid climates.

- These findings suggest that warmer and more humid conditions increase decomposition, offsetting diversity-driven carbon inputs, while colder and more arid conditions enhance SOC through low decomposition and increased inputs through abiotic facilitation and biotic interactions in high-diversity communities. Our findings indicate that conserving plant diversity is critical for enhancing carbon sequestration and mitigating the effects of climatic conditions, particularly in cold climates and regions facing an increase in arid conditions.

Introduction

Soil organic carbon (SOC) represents a large carbon reservoir in forests and is crucial for maintaining soil fertility and biodiversity, as well as mitigating global warming (Pan *et al.*, 2011). However, regional studies have reported declines in SOC stocks over recent decades (X. Chen *et al.*, 2020; Chen *et al.*, 2023), particularly in cold regions (García-Palacios *et al.*, 2024), releasing CO₂ back to the atmosphere, which reduces the land C sink. Experimental studies in grasslands and forests have shown that plant diversity usually increases SOC (Lange *et al.*, 2015, 2023; Li *et al.*, 2019; Schnabel *et al.*, 2025). Consequently, the observed decline in plant diversity could be a key driver reducing SOC (Lange *et al.*, 2015; Li *et al.*, 2019; Lange *et al.*, 2023). Yet, the influence of plant diversity on SOC in natural forests remains debated, with studies reporting positive (Chen *et al.*, 2018, 2023), neutral (Lin *et al.*, 2016; Li *et al.*, 2020), or negative (Adair *et al.*, 2018) relationships for different carbon fractions. These divergent outcomes likely reflect both the specific facets of diversity examined and the climatic contexts of the study sites. While previous research has mainly focused on identifying climatic drivers of SOC (Davidson & Janssens, 2006; Chen *et al.*, 2023), an equally critical yet underexplored aspect is how plant diversity–SOC relationships are mediated by climatic conditions (Maestre *et al.*, 2012; Loreau & de Mazancourt, 2013). Unraveling the environmental context dependency of plant diversity–SOC relationships in natural forests is crucial for understanding and predicting ecosystem carbon dynamics under global change.

Plant diversity is a multifaceted concept, encompassing taxonomic diversity, functional diversity, and functional composition. Because the particular facet of diversity under study isolates different aspects of community-trait structure, studies relying on only one metric may report divergent diversity–SOC relationships. Taxonomic diversity (species richness or abundance-weighted indices) quantifies the number of species co-occurring without revealing their functional roles (Tilman *et al.*, 1997). Functional diversity indices such as functional diversity (FDiv, total branch length of a trait dendrogram; Petchey & Gaston, 2002) and functional dispersion (FDis, mean distance of species' traits to the community centroid; Laliberté & Legendre, 2010) go further by providing insights into the influence of the diversity of ecological strategies in the community and of biotic and abiotic filtering or niche complementarity, for example via resource partitioning, abiotic facilitation, or biotic

interactions (Wright *et al.*, 2014; Barry *et al.*, 2019), on ecosystem processes. Additionally, functional composition (CWM, community-weighted mean) reflects whether the dominant trait syndromes drive ecosystem processes (Garnier *et al.*, 2004). Because each metric isolates different ecological processes, they can yield contrasting, yet complementary insights into diversity–SOC relationships. For instance, higher taxonomic diversity may correlate with greater overall biomass inputs – boosting SOC via increased litter and root production (Makkonen *et al.*, 2013; Santonja *et al.*, 2017) – or, alternatively, accelerate SOC loss if diverse litter mixtures stimulate microbial decomposition (Conti & Diaz, 2013; Buzzard *et al.*, 2019). Functional diversity and dispersion can be linked to complementary resource use – species differing in rooting depth or litter chemistry can spatially and chemically partition carbon inputs, enhancing stabilization (Edwards *et al.*, 2018; Chari & Taylor, 2022). Additionally, a high CWM of recalcitrant-litter traits can slow decomposition and promote SOC accumulation. However, labile litter inputs can also contribute to SOC by fueling microbial growth and promoting the formation of mineral-associated organic carbon, especially when microbial carbon dominates this pool (Hartley *et al.*, 2012). Thus, integrating multiple facets can contribute to capturing multiple processes involved in SOC storage, such as input quantity, niche complementarity, or dominant-species effects.

The strength of the relationship between plant diversity and SOC may also vary across climatic conditions, particularly along temperature and aridity gradients, as demonstrated in grasslands (Spohn *et al.*, 2023). Previous studies have suggested that plant diversity–SOC relationships vary along environmental gradients (Chen *et al.*, 2018). The niche complementarity hypothesis predicts a stronger influence of plant diversity on SOC in resource-rich environments, where species differ in resource acquisition strategies and temporal or spatial niches (Tilman *et al.*, 1997; Loreau & Hector, 2001; Dimitrakopoulos & Schmid, 2004). Such complementarity can enhance community productivity and litter and root inputs, thereby increasing soil carbon inputs and SOC, but at the same time can also enhance decomposition processes. More recently, studies have also shown that, despite physiological constraints on plant growth and resource acquisition in colder and more arid conditions (Spohn *et al.*, 2023), the influence of plant diversity on SOC may nevertheless increase under such conditions, due to reduced competition or increased facilitation between plant species (Bertness & Callaway, 1994; Callaway *et al.*, 2002;

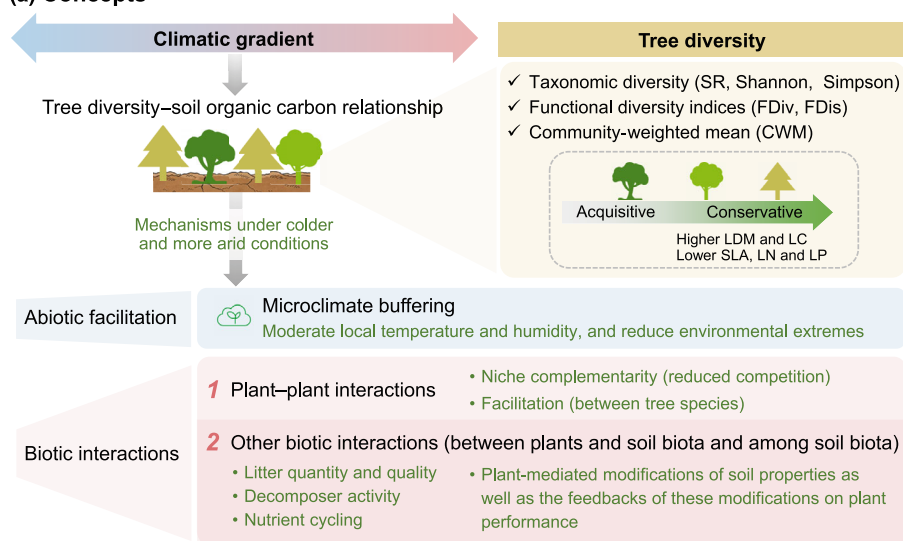
Maestre *et al.*, 2009; Guerrero-Ramírez & Eisenhauer, 2017; Yan *et al.*, 2022). Diversity effects on SOC may operate through both abiotic facilitation and biotic interactions (Fig. 1a). Abiotic facilitation includes microclimate buffering, which arises from canopy shading, reduced wind penetration, and increased litter accumulation that moderate local temperature and humidity and reduce environmental extremes. Biotic interactions consist of plant–plant interactions (between species competition and facilitation) (Callaway *et al.*, 2002; Maestre *et al.*, 2009; Wright *et al.*, 2014), as well as other biotic interactions, such as litter quantity and quality (Guerrero-Ramírez *et al.*, 2016), decomposer activity, nutrient cycling, and plant-mediated modifications of soil properties, as well as the feedbacks of these modifications on plant performance (Lange *et al.*, 2015; Chen *et al.*, 2018; X. Chen *et al.*, 2020).

Recent studies provide a conceptual framework for interpreting how biodiversity–ecosystem functioning relationships may strengthen under more extreme conditions (Pretzsch *et al.*, 2010; Wright *et al.*, 2021; Chen *et al.*, 2025). In forest ecosystems, this may partly arise from abiotic facilitation, particularly microclimate buffering (Fig. 1a). Higher tree diversity

can increase canopy structural complexity and maintain higher air and soil humidity (Wright *et al.*, 2014, 2015; Seidelmann *et al.*, 2016; Guimarães-Steinicke *et al.*, 2021; Zhang *et al.*, 2022, 2024). Such microclimate buffering may mitigate negative effects of cold and drought, thereby promoting plant growth and enhancing plant inputs to SOC in more diverse forest stands even under colder or more arid macroclimatic conditions.

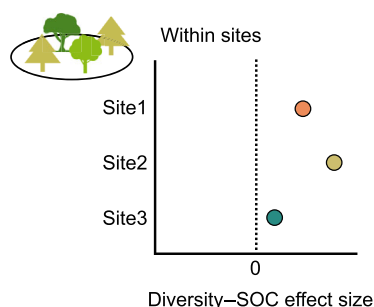
Here, we examine the relationship between tree diversity and SOC in natural temperate, subtropical, and tropical forests across broad climatic gradients. In addition to taxonomic diversity, we adopt a functional perspective by using trait data directly measured at the field sites. Specifically, we obtained data from 15 long-term monitored large forest sites from two continents (Fig. 2), including forest inventory variables, species functional traits (specific leaf area (SLA), leaf dry matter (LDM) content, leaf carbon (LC) content, leaf nitrogen (LN) content, and leaf phosphorus (LP) content), and soil measurements (SOC and soil bulk density (SBD) (Supporting Information Table S1)). A higher CWM indicates that conservative species dominate the community, that is communities with overall higher LDM and

(a) Concepts



(b) Hypothesis

H1: Higher tree diversity are positively associated with SOC



H2: Tree diversity–SOC relationships are strengthened under colder and more arid conditions

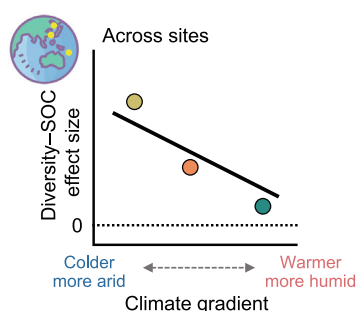


Fig. 1 Hypothesized relationships between tree diversity and soil organic carbon (SOC). (a) Multifaceted tree diversity and mechanisms underlying the tree diversity–SOC relationship under colder and more arid conditions. (b) Hypothesized within- (H1) and across-site (H2) relationships between tree diversity and soil organic carbon.

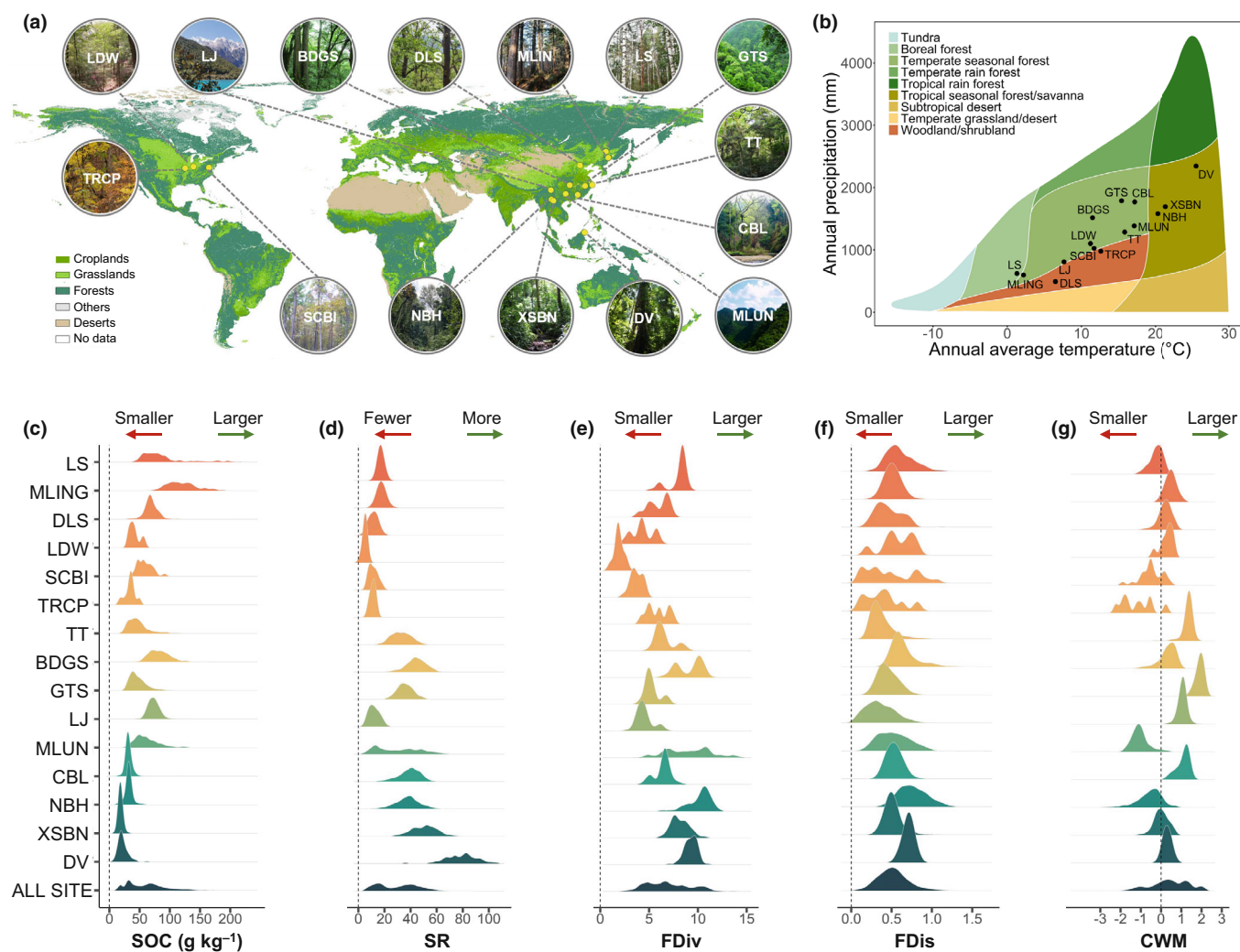


Fig. 2 Site overview and ridge density plots of soil organic carbon (SOC), tree species richness (SR), functional diversity (FDiv), functional dispersion (FDis), and community-weighted mean (CWM of first PC axis extracted from principal component analysis of five traits; see the [Materials and Methods](#) section). Locations of the 15 long-term monitored large forest sites (a) and their distribution on Whittaker's classic climate–biomes diagram (b). Ridge density plots showing the distribution within site and all site together of SOC (c), SR (d), FDiv (e), FDis (f) and CWM (g). The ordering of sites from top to bottom is according to their latitude from high to low. BDGS, Badagongshan; CBL, Chebaling; DLS, Donglingshan; DV, Danum valley; GTS, Gutianshan; LDW, Lilly dickey woods; LJ, Lijiang; LS, Liangshui; MLUN, Mulun; MLING, Muling; NBH, Nabanhe; SCBI, Smithsonian conservation biology institute; TRCP, Tyson research center plot; TT, Tiantong; XSBN, Xishuangbanna.

LC and lower SLA, LN, and LP. SOC refers to the mass of carbon per kilogram of soil (g C kg^{-1}). Our data allow us to test the within-site tree diversity–SOC relationship across sites and whether it strengthens as site conditions become colder and more arid. Given the complementary insights into ecosystem processes, we test whether the diversity–SOC relationship differs across facets (taxonomic diversity: species richness and Shannon diversity and Simpson diversity; functional diversity indices: functional diversity and functional dispersion; CWM trait values). Using meta-regression approaches, we tested two hypotheses. (H1) Higher taxonomic and functional diversity indices (e.g. FDis, FDiv) are positively associated with SOC, consistent with mechanisms of niche complementarity (Fig. 1b). By contrast, communities with higher CWMs of conservative traits (e.g. high

LDM or low SLA) have higher SOC due to slower decomposition and more persistent carbon inputs. (H2) The relationship between tree diversity and SOC is strengthened under colder and more arid conditions due to microclimatic buffering and/or reduced competition and increased facilitation between tree species increasing plant productivity and litter inputs and generally slower decomposition rates.

Materials and Methods

Study sites

We obtained data from 15 large natural forest-dynamics sites provided by the Forest Global Earth Observatory (ForestGEO,

Anderson-Teixeira *et al.*, 2015) and the Chinese Forest Biodiversity Monitoring Network (CforBio, Feng *et al.*, 2016). These two networks include long-term monitored forest dynamics sites spanning major forest biomes of the world. The sites in this study cover a latitudinal range from 47.18° N (Liangshui, China) to 5.10° N (Danum valley, Malaysia; Fig. 2a,b; Table S1). The annual mean temperature gradient ranges from 1.3°C (Liangshui) to 25°C (Danum valley) and the annual precipitation gradient from 493 mm (Donglingshan) to 2346 mm (Danum valley). The area of the sites varies between 9 ha (Liangshui) and 50 ha (Danum valley). Each site was split into 20 × 20 m plots without overlap for measurements. All trees with a diameter at breast height ≥ 1 cm across all sites were tagged, identified to species, measured, and mapped according to the CTFS–ForestGEO protocol. In total, there were 1214 212 trees from 1872 species, 541 genera, and 128 families included in this study.

Taxonomic diversity, functional diversity, and composition

Taxonomic diversity was represented by Hill number with orders $q = 0, 1$, and 2 to evaluate species richness, Shannon diversity, and Simpson diversity, respectively (Jost, 2006; Chao *et al.*, 2014). The Hill number, expressed as the effective number of species—a community in which species have equal abundance—allows for direct comparison of the importance of rare and dominant species. Here, $q = 0$ (species richness) weights all species equally, $q = 1$ (Shannon diversity, refer to Shannon's entropy index) accounts for species relative abundances, and $q = 2$ (Simpson diversity, refer to Simpson's concentration index) gives greater weight to dominant species. Considering the high correlation of the three indices, we only include species richness to represent taxonomic diversity in the analysis of the main text (Figs S1, S2).

Five species-level functional traits—SLA, LDM, LC, LN, and LP—were measured at all sites, except at Lilly Dickey Woods, in which trait values were obtained from measurements of the same tree species in a nearby site within the same region (the Tyson Research Center plot; Table S2). These traits can be related to fast and slow resource acquisition strategies of species, affecting SOC through litter quality and soil bacterial decomposition (Buzzard *et al.*, 2019). We obtained trait measures for most species (90.75% for SLA, 86.30% for LDM, 86.02% for LC, 88.06% for LN, and 86.54% for LP), representing the proportion of species with measured traits among all recorded species. Missing trait values were imputed using genus-level means across sites (Table S3). We further used 1000 runs of predictive mean matching of multivariate imputation from the mice package in R to fill the rest of missing traits data in which no other species of the same genus were available for imputation (Groothuis-Oudshoorn, 2011). We calculated principal component analyses (PCA) for both imputed traits and measured traits (Fig. S3; Tables S4, S5). The two types of PCAs gave similar results, and thus, we used the first component of imputed trait PCA for all further analyses presented in the main text.

Functional diversity indices (FDs) and composition were calculated per 20 × 20 m unit area, including functional diversity (total branch length of the functional dendrogram, FDiv; Petchey & Gaston, 2002), functional dispersion (distance of all species traits to the mean trait value, FDis; Laliberté & Legendre, 2010), and CWM (Laliberté & Legendre, 2010). We used both FDiv and FDis to represent complementarity effects, with FDiv emphasizing the overall resource space occupied by a community and FDis emphasizing the average difference between species within a community. Note that FDiv generally increases with species richness while FDis does not (Petchey & Gaston, 2002; Laliberté & Legendre, 2010). The CWM is the abundance-weighted mean of the species traits within a community. A high CWM value indicates that the community is dominated by species with conservative traits (e.g. low SLA and high LDM content), whereas a low CWM value indicates dominance by species with acquisitive traits (e.g. high SLA and low LDM content). Therefore, CWM captures the mean functional strategy of the dominant species in the community, while FDiv/FDis reflects the diversity of plant strategies among all species. The FD indices were calculated with the PICANTE package (Kembel *et al.*, 2010) and the FD package (Laliberté & Legendre, 2010) in R (R Core Team, 2023). All functional diversity indices were calculated using the first principal component (PC1) of a PCA that combined five key traits (Fig. S3). In our dataset, FDiv was more highly correlated with SR than with FDis ($r_{\text{SR-FDiv}} = 0.63$, $r_{\text{SR-FDis}} = 0.34$), as expected and CWM was uncorrelated with SR ($r_{\text{SR-CWM}} = 0.002$), indicating that presumed species loss leading to reduced richness was random with regard to species traits (Y. Chen *et al.*, 2020). The correlations between the different indices of FDs were slightly higher ($r_{\text{FDiv-FDis}} = 0.60$, $r_{\text{FDiv-CWM}} = -0.55$, $r_{\text{FDis-CWM}} = -0.44$).

Soil measurements

SOC (g C kg^{-1}) and SBD (g soil cm^{-3}) were measured in the same 20 × 20 m plots as the diversity indices, following the ForestGEO soil sampling protocol (John *et al.*, 2007; Zhang *et al.*, 2011). Cores of the mineral soil were taken after removing the surface litter (recognizable leaves and twigs). The total number of plots containing soil carbon data for 15 sites is presented in Table S1. For 11 sites, all plots had soil measurements, while four sites not all plots had soil measurements (nine for Lilly Dickey woods, 24 for Smithsonian conservation biology institute, nine for Tyson research center, and 79 for Danum valley). For 12 sites, SOC was measured, whereas for the remaining three sites—Smithsonian Conservation Biology Institute (soil pH = 5.1), Xishuangbanna (soil pH = 4.9), and Danum Valley (soil pH = 5.4)—total carbon (TC) in the soil was measured. Because the soil pH values of these three sites were below 6.2, the soils were classified as acidic, making it reasonable to assume that TC and SOC were effectively equivalent (Scholten *et al.*, 2017). Considering that the uppermost soil layer was the most active layer regarding the interaction between plant roots and soil, we took soil samples for 12 sites at 0–10 cm, for the Lilly Dickey

Woods and Tyson research center sites at 0–5 cm, and for the Chebaling site at 0–20 cm depth. Finally, for the eight sites with SBD data, we calculated SOC stocks as

$$\text{SOC stocks} = \text{SOC}(\text{g C kg}^{-1}) \times \text{soil bulk density}(\text{g soil cm}^{-3}) \\ \times \text{sample depth}(\text{cm})$$

Climate data

We extracted mean annual temperature (MAT) from the World Clim 2.1 database (<https://worldclim.org/>) for all 15 sites. Aridity data were extracted from the Global Aridity Index and Potential Evapotranspiration Database (Zomer *et al.*, 2022). We used the Aridity Index (AI) calculated as mean annual precipitation divided by potential evapotranspiration (PET), which increases with decreasing aridity. Pearson correlations between all measured variables are given in the Figs S1 and S2. We performed principal component analysis (PCA) using MAT and AI, with PC1 representing a ‘Combined temperature and aridity gradient’ in which higher values indicate warmer and more humid conditions and lower values indicate colder and more arid conditions (Fig. S4; Table S6). Lower MAT and lower AI impose stronger environmental constraints on plant growth and soil carbon processes rather than direct physiological stress on locally adapted species.

Statistical analysis

First, to investigate the relationship between SR, FDs, or CWM and SOC within sites (H1), we fitted simple linear regression models with SOC or SOC stocks as a function of each diversity index (within-site effects). We extracted the regression slopes to represent tree diversity effect sizes on SOC or SOC stocks for each site. We then used these regression slopes as dependent variables in meta-regression models to assess the overall across-site relationship for H1. We applied two meta-regression approaches: a linear mixed effects (LME) meta-regression model and a meta-regression using the METAFOR package (Viechtbauer, 2010). In both approaches, site variances are used as weights, and the residual variance is set to 1. Using both approaches allowed us to evaluate the robustness of the model results. Additionally, to evaluate the contribution of different facets of tree diversity to variation in SOC, we calculated multiple linear regression models for each site with SOC or SOC stocks as dependent variables and the four tree diversity indices (SR, FDiv, FDis, and CWM) as explanatory variables for each site. We calculated partial R^2 values by dividing the sum of squares (SS) for each of the four tree diversity indices by the total SS. This allowed us to quantify the proportion of SOC variance uniquely explained by each diversity metric. In the case of multiple linear regression, percent SS correspond to increments of multiple R^2 and can be used to partition the total variance explained. To quantify the overall contribution of each facet of tree diversity to SOC or SOC stocks, we fitted a linear model for each diversity facet, in which the response variable was the proportion of SOC variance uniquely explained by

each diversity metric. Each model included only an intercept term; the variance of the linear model within site was used as weights.

Second, to test whether the relationship between tree diversity and SOC would strengthen under colder and more arid conditions (H2), we fitted meta-regressions with LME models and the METAFOR package with each climatic condition as the explanatory variable. Specifically, the site-level effect sizes of tree diversity on SOC or SOC stocks—calculated as the slopes from the within-site linear regressions described previously—were used as the dependent variable. Climatic conditions (MAT, AI, or Combined temperature and aridity gradient) were included as fixed effects. Because meta-regressions using the LME model and meta-regression using the METAFOR package use the same statistical methodology (Viechtbauer, 2010) yet differ in output features (F-tests from analysis of variance tables in the LME model vs likelihood-ratio tests in the METAFOR package), we report the LME model in the main text, while the meta-regression results obtained with the METAFOR package are presented in the Supporting Information. We used meta-regression in addition to ordinary LME models because the 15 studies did not follow a common design, thus violating assumptions of homoscedasticity, that is similar within-site variances across sites. All the analyses were conducted with R 4.3.2 (R Core Team, 2023).

Results

Relationships between multifaceted tree diversity and SOC within and across sites

We found an overall positive species richness–SOC relationship, while the relationships of FDs and CWM with SOC were overall neutral (i.e. nonsignificant; Fig. 3e–h; Table S7). For example, doubling species richness, for example from 10 to 20 species, corresponds to an increase of $\approx 3.8 \text{ g kg}^{-1}$ in SOC ($\approx 6.2\%$ of the mean SOC). Within sites, species richness–SOC relationships were positive at six sites, neutral at seven sites and negative at two sites (Fig. 3e; Table S8). Results obtained using Shannon diversity or Simpson diversity yielded similar outcomes to species richness (Fig. S5). Within sites, functional diversity and composition–SOC relationships were positive at five sites for FDiv, five sites for FDis, and three sites for CWM; neutral at eight sites for FDiv, eight sites for FDis, and 10 sites for CWM; and negative at two sites for FDiv, two sites for FDis, and two sites for CWM (Fig. 3f–h; Table S9).

Moreover, we found that different facets of tree diversity contributed to SOC variation differently among sites (Fig. 3i). For each site, although the total variance of SOC explained by the different facets of tree diversity was modest, multiregression models demonstrated significant diversity contributions to SOC variation at the majority (nine of 15) of sites.

Tree diversity–SOC relationships under climatic conditions

The relationships between tree diversity and SOC strengthened under harsh climatic conditions (Fig. 4). Specifically, the species

richness–SOC relationship and FDiv–SOC relationship strengthened under colder (Fig. 4a,b), more arid conditions (marginally for species richness–SOC relationship; Fig. 4e,f), and both colder and more arid conditions (Fig. 4i,j). For example, doubling

species richness, for example from 10 to 20 species, corresponds to an increase of *c.* 6.2% in SOC under colder conditions, but only *c.* 1.5% under conditions that are 5°C warmer, indicating a weaker diversity effect in warmer environments. Results obtained

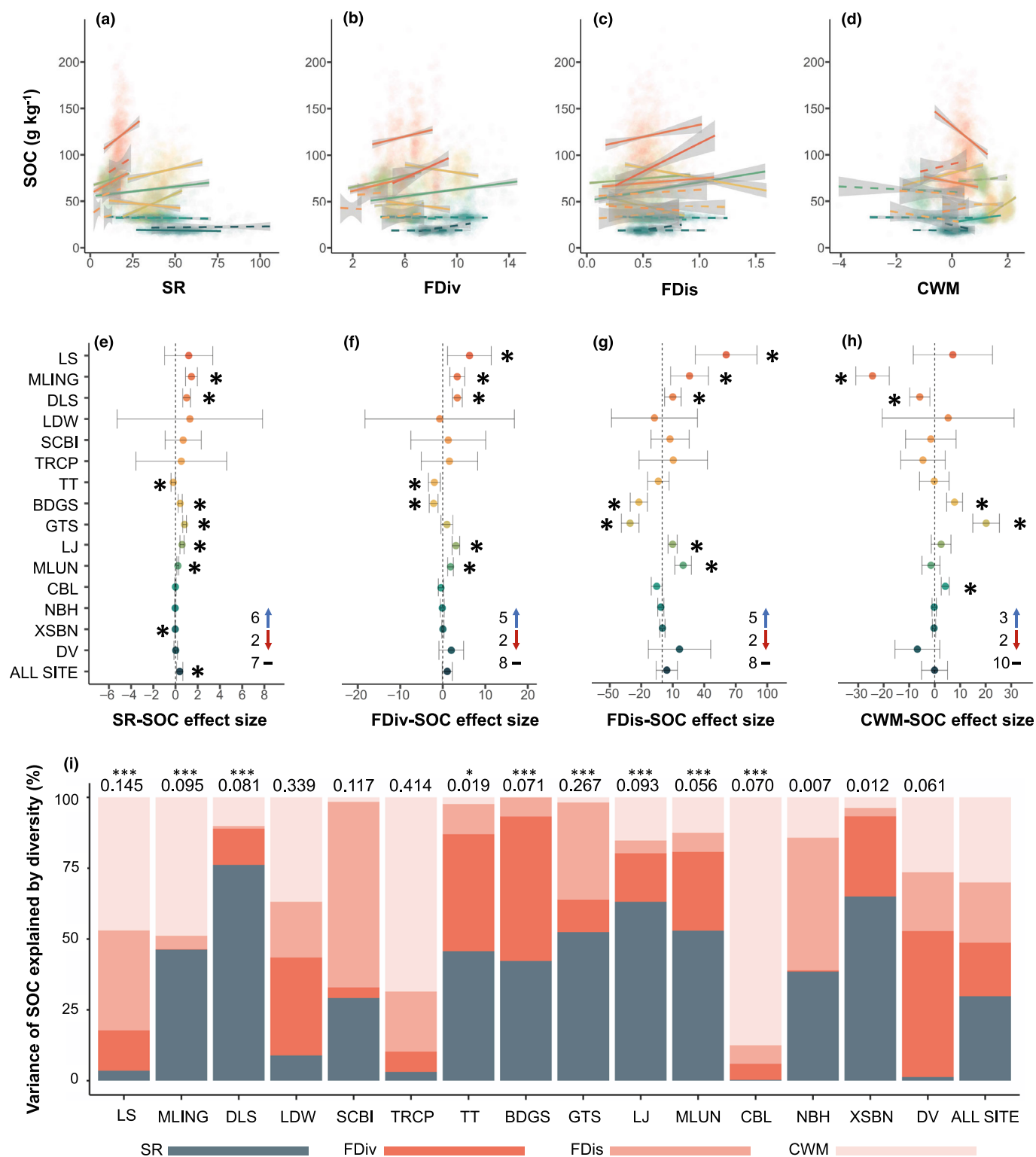


Fig. 3 Relationship between tree diversity and soil organic carbon (SOC) for each site. Simple linear regressions of species richness (SR), functional diversity (FDiv), functional dispersion (FDis), and community-weighted mean (CWM) on SOC are shown from a to d. Dashed lines indicate nonsignificant ($P > 0.05$) relationships. The effect size within each site, calculated as the slope from the simple linear regressions, is shown from e to h. The overall effect size across all sites shown in 'ALL SITE' is calculated as the slope of a meta-regression using a linear mixed effect (LME) model. Error bars represent 95% confidence intervals (± 1.96 SE). Significant relationships with $P < 0.05$ are indicated with a star (*). The numbers and arrows on the lower right of panels e–h represent the number of positive (blue arrows), negative (red arrows), and neutral (i.e. non-significant, black lines) relationships between tree diversity and SOC. The ordering of the sites from top to bottom in panels e–h is according to latitude from high to low. All tests can be found in Supporting Information Tables S7–S9. The contribution of tree diversity on SOC based on filled traits (i). The ordering of the sites from left to right is according to latitude from high to low. R^2 -values are from the multiple regression model of SOC as dependent variable on four diversity facets as explanatory variables for each site. The percentage explained is calculated with 100% as the total variation in SOC explained by the four explanatory variables together. The overall variance explained by meta-regression is shown in 'ALL SITE'. SR, species richness; FDiv, functional diversity; FDis, functional dispersion; CWM, community-weighted mean. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

using Shannon diversity or the Simpson diversity yielded similar outcomes to species richness (Table S10). The FDis–SOC relationship and CWM–SOC relationship strengthened only under more arid conditions (Fig. 4g,h), but not under colder conditions (Fig. 4c,d). The FDis–SOC relationship strengthened under colder and more arid conditions (Fig. 4k). These results remained when we used SOC stocks instead of SOC (Figs S6–S8; Tables S11–S14), when we used measured traits instead of imputed traits (see the Materials and Methods section; Figs S9–S12; Tables S15–S17), and in meta-regressions using the META-FOR package (Tables S18–S20).

Discussion

Assessing the relationship between plant diversity and soil carbon across large scales, and understanding how it varies with climate variables, is vital for conservation and carbon sequestration. However, previous results for this relationship – whether positive, negative, or neutral – remain unclear and not well-defined. Our dataset, including census data of over a million trees, functional traits, and plot-level (20×20 m) soil carbon measurements, offers an opportunity to explore the generality and context dependency of tree diversity–SOC relationships. We found that the relationships between tree diversity and SOC strengthen as the environment becomes colder or more arid, suggesting a potential role of tree diversity in mitigating the impacts of colder and more arid conditions. Our results provide insights into the generality and context dependency of tree diversity–SOC relationships, with implications for maintaining SOC and SOC stocks under colder and more arid conditions.

The relationships between tree diversity and SOC are site-specific

We found that the tree diversity–SOC relationships are site-specific. This aligns with previous studies, which have shown predominantly positive (Chen *et al.*, 2018; Chen *et al.*, 2023), occasionally neutral (Lin *et al.*, 2016; Li *et al.*, 2020), and rarely negative effects for a range of soil carbon fractions (Adair *et al.*, 2018). A positive relationship between taxonomic diversity (linked to higher species richness or abundance) and SOC can reflect increased biomass input (Huang *et al.*, 2018), which promotes litter quantity and quality (Makkonen *et al.*, 2013;

Santonja *et al.*, 2017) and microbial carbon-use efficiency (Duan *et al.*, 2023), but still exceeds SOC losses. By contrast, a neutral or negative relationship may arise when increased diversity accelerates decomposition and microbial respiration, leading to higher carbon losses that offset or even outweigh increased biomass inputs (Handa *et al.*, 2014; García-Palacios *et al.*, 2021). Adair *et al.* (2018) did not quantify SOC directly, focusing instead on carbon in the organic soil layer and in the aboveground biomass. Furthermore, differences in our study may also have arisen because Adair *et al.* relied on trait data extracted from databases, whereas here, we used site-measured trait data. Consistent with earlier studies from grasslands (Chen *et al.*, 2018; X. Chen *et al.*, 2020), our results indicate a broadly positive relationship between taxonomic diversity and SOC across forests along a large climatic gradient. Higher tree diversity may influence SOC positively because of plant–plant interactions (i.e. reduced competition and increased facilitation) and thus outweigh SOC loss driven by soil microbial communities, including microbial respiration (Lange *et al.*, 2015; Palandrani & Alberti, 2019; Duan *et al.*, 2023).

The relationship between functional diversity indices and SOC showed greater variability and site-dependence. Positive relationships of FDs with SOC suggest that trait complementarity in rooting depth and litter chemistry promote SOC via complementary resource use (Laliberte & Legendre, 2010; Chen *et al.*, 2018; Chen *et al.*, 2023), outweighing carbon losses. Conversely, neutral or negative relationships suggest that greater complementarity leads to higher decomposition relative to carbon inputs (Handa *et al.*, 2014; Adair *et al.*, 2018). We note that our set of functional traits likely does not fully capture complementarity effects relevant for SOC inputs and decomposition; in particular, we lacked information about additional belowground root traits (Lin *et al.*, 2016; Li *et al.*, 2020).

We observed that except for cold or arid sites, where decay rates of carbon inputs are expected to be low even for acquisitive species, higher CWM of conservative traits was associated with higher SOC, which is consistent with previous studies (Lin *et al.*, 2016; Adair *et al.*, 2018). This indicates that at the more beneficial side of the climatic gradient, communities dominated by conservative species tend to accumulate more soil carbon (Hartley *et al.*, 2012). Conversely, in some cases, acquisitive traits in communities – those linked to rapid resource uptake – also contributed to SOC, likely through increased productivity and

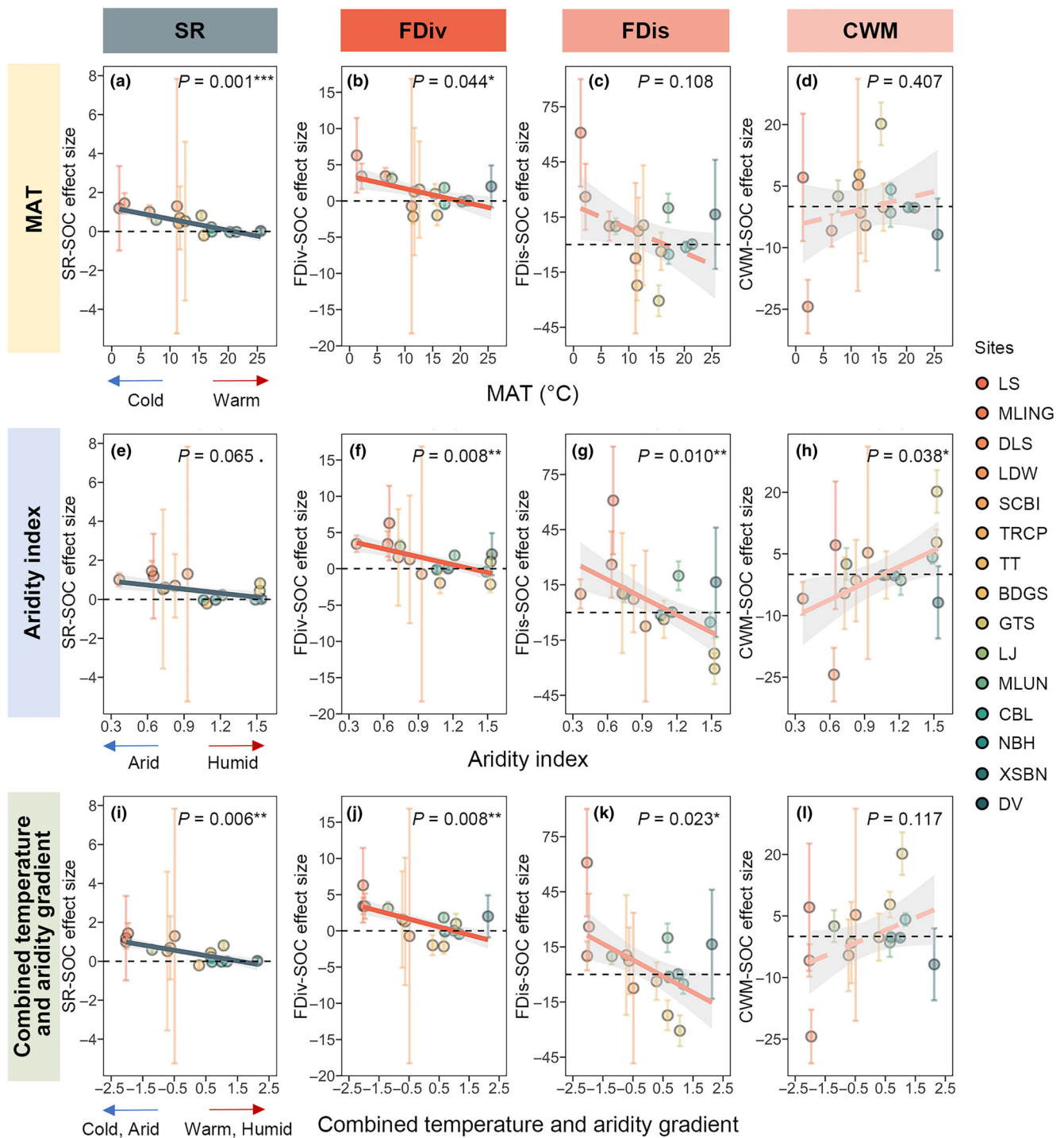


Fig. 4 Relationships between climate and effect sizes of tree diversity–soil organic carbon (SOC) relationships. The relationship between mean annual temperature (MAT) and effect size of SR–SOC (a), FDiv–SOC (b), FDis–SOC (c), and CWM–SOC (d). The relationship between aridity index and effect size of SR–SOC (e), FDiv–SOC (f), FDis–SOC (g), and CWM–SOC (h). The relationship between combined temperature and aridity gradient and effect size of SR–SOC (i), FDiv–SOC (j), FDis–SOC (k), and CWM–SOC (l). Lower values on the x-axes indicate colder, more arid conditions, or both colder and more arid conditions (Combined temperature and aridity gradient). Solid lines show significant ($P < 0.05$) relationships and dashed lines show non-significant ($P > 0.05$) relationships. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. The statistical significances were estimated from meta-regression with MAT, Aridity index or combined temperature and aridity gradient as fixed and site as random term. The black dashed line is $y = 0$. All tests can be found in Supporting Information Table S10. CWM, community-weighted mean; FDis, functional dispersion; FDiv, functional diversity; SOC, soil organic carbon; SR, species richness.

greater litter and root density (Cotrufo *et al.*, 2015; Chen *et al.*, 2022; Ridgeway *et al.*, 2023).

While some studies reported predominantly positive (Chen *et al.*, 2023), occasionally neutral, or rarely negative (Chen *et al.*, 2022) FDs–SOC relationships, we found a generally neutral relationship. This may be because communities with greater complementarity enhanced microbial decomposition rates (Hartley *et al.*, 2012; Conti & Diaz, 2013; Buzzard *et al.*, 2019), potentially offsetting the positive effects of biotic interactions on soil organic carbon inputs such as greater litter inputs, stronger root–microbial interactions (Makkonen *et al.*, 2013; Santonja *et al.*, 2017; Zhang *et al.*, 2023), and enhanced root exudation (Edwards *et al.*, 2018; Chari & Taylor, 2022). When using taxonomic instead of functional diversity indices, we found a positive overall relationship between taxonomic diversity and SOC. Together, our results suggest that the influence of taxonomic diversity, functional diversity indices, and composition on SOC is site-specific, largely driven by abiotic and biotic conditions, including climatic conditions.

Our results also revealed that multiple facets of tree diversity contribute to SOC variation, which highlights the site-specific nature of SOC dynamics and the multifaceted influence of plant diversity. The explanatory power of tree diversity as a predictor of SOC, measured with R^2 values, ranged from 0.007 to 0.414 (Fig. 3i). This is understandable given that SOC dynamics are shaped by numerous variables such as soil conditions, soil microbial activity, and soil–plant interactions (Adair *et al.*, 2018; Augusto & Boca, 2022). For example, previous studies have shown that soil conditions and regional climate can influence the relationship between plant diversity and SOC (Augusto & Boca, 2022; Spohn *et al.*, 2023). Nevertheless, even when tree diversity explains only a fraction of SOC variation, integrating multiple diversity facets into forest management and restoration and conservation planning can help optimize carbon storage and ecosystem resilience across diverse environmental contexts (X. Chen *et al.*, 2020; Angst *et al.*, 2025).

Consistent with previous findings (Dawud *et al.*, 2017; X. Chen *et al.*, 2020), we found that both taxonomic diversity and functional diversity indices contribute to SOC variation. However, while prior studies emphasized either taxonomic diversity (Adair *et al.*, 2018) or functional diversity indices (Dawud *et al.*, 2017) as more influential, our research highlights the collective significance of multifaceted diversity on SOC. This underscores the importance of considering multifaceted diversity in the efforts aimed at enhancing soil carbon sequestration. While different facets of tree diversity varied in their contributions across sites, they played complementary roles in explaining SOC variation.

Climatic conditions strengthen tree diversity–SOC relationships

Although our study and previous meta-analyses reported positive (Chen *et al.*, 2020; Chen *et al.*, 2023; Augusto & Boca, 2022; Hong *et al.*, 2022) or negative (Chen *et al.*, 2022) relationships between tree diversity and SOC, our multisite analysis revealed

that these apparently conflicting results may be explained by different climatic conditions across sites, with the strongest positive influence of tree diversity on SOC occurring under colder and more arid conditions.

The underlying mechanisms likely involve both microclimate buffering (abiotic facilitation) and biotic interactions. Species-rich and structurally complex forests can create warmer and more humid local environments (Wright *et al.*, 2014; Seidelmann *et al.*, 2016; Zhang *et al.*, 2022; Schnabel *et al.*, 2025), thereby buffering colder and more arid conditions and increasing SOC inputs more than decreasing SOC losses. Such microclimate buffering (abiotic facilitation) may therefore contribute to the enhanced role of tree diversity in maintaining SOC under colder and more arid macroclimatic conditions.

Tree diversity further explains variation in SOC along climatic gradients. Under colder conditions, communities with greater species richness and higher functional diversity tend to have higher SOC. Temperature constrains the distribution range and reproductive success of plant species, indirectly influencing carbon sequestration via changes in species occurrence and relative abundance (Svenning *et al.*, 2015). In line with previous studies (Ratcliffe *et al.*, 2017; Spohn *et al.*, 2023), we found higher taxonomic diversity led to marginal increases in SOC under more arid conditions. Under colder and more arid conditions, increased tree diversity likely enhanced SOC inputs through microclimate buffering (abiotic facilitation), reduced competition, and increased facilitation (Bertness & Callaway, 1994; He *et al.*, 2013; Yan *et al.*, 2022), while decomposition rates remained low across all levels of diversity. The lower slope of this relationship in warm and humid sites could also be explained by higher decomposition rates at these sites, driven by stronger complementarity effects under benign conditions (Dimitrakopoulos & Schmid, 2004; Pretzsch *et al.*, 2010; Jousset *et al.*, 2011). In summary, warm and humid conditions likely increased decomposition, thereby offsetting the increased carbon inputs. By contrast, lower temperatures or limited water availability reduce decomposition (Davidson & Janssens, 2006; Canessa *et al.*, 2022; Lemoine *et al.*, 2024), while carbon inputs can still increase in high-diversity communities due to abiotic facilitation, plant–plant interactions (i.e. reduced competition and increased facilitation) (Callaway *et al.*, 2002; Maestre *et al.*, 2009; Wright *et al.*, 2014), and other biotic interactions (Soliveres *et al.*, 2016; O'Brien *et al.*, 2017; Ratcliffe *et al.*, 2017; Duan *et al.*, 2023).

Under more arid conditions, environmental filtering tends to favor slow-growing species with sclerophyllous or tough leaves, which decompose more slowly and prolong carbon residence time in soils (Cornwell *et al.*, 2008; Laughlin *et al.*, 2021). However, in our study, CWM values that reflect the dominance of conservative strategies were negatively associated with SOC in more arid regions. This suggests that, although conservative species produce decay-resistant litter, they may contribute lower total biomass and root exudates, providing insufficient carbon inputs to sustain high SOC values. Alternatively, current trait composition may be decoupled from soil organic carbon, especially in forests where SOC reflects long-term processes rather than present-day trait structure.

In general, SOC in topsoil is at high risk of loss under future climatic conditions, particularly in high-latitude regions (Wang *et al.*, 2022). This suggests that tree diversity may be critical for maintaining SOC under changing environmental conditions (Cowles *et al.*, 2016). Future research should also analyze biodiversity–SOC relationships along resource gradients as a complementary approach to better understand the mechanisms by which biodiversity influences ecosystem functioning—either by reducing competition or by enhancing biotic interactions. Our findings can guide soil carbon restoration strategies by highlighting the importance of enhancing tree diversity to mitigate SOC degradation under changing climatic conditions.

Future perspectives

Our study provides insights for future research on the relationships between biodiversity and soil carbon, particularly in the context of varying climatic conditions. First, we relied on species-level functional traits at each site, potentially overlooking site-level variations in trait expression influenced by local environmental conditions, such as soil properties and microclimate. Intraspecific trait variation, which reflects local adaptation or plasticity of species to local environmental conditions, likely plays a crucial role in fine-scale responses (Schmid, 1992; Violle *et al.*, 2012; Niklaus *et al.*, 2017). Considering this variation may expand our understanding of how tree species adjust to environmental gradients (Spasojevic *et al.*, 2016). Second, the role of plant roots in soil carbon sequestration is crucial yet understudied. Roots have a direct link to soil carbon processes and are vital for understanding the complex dynamics between belowground functional diversity and soil carbon relationships (Li *et al.*, 2019). Roots also contribute to soil carbon by transferring undecomposed or partially decomposed organic matter into more stable aggregate-occluded soil organic matter (Ridgeway *et al.*, 2023). Third, soil organisms including bacteria, fungi, and archaea need to be considered, because they are key drivers of SOC decomposition and turnover (Crowther *et al.*, 2019). Their activity is strongly influenced by abiotic factors, such as climate, plant communities, and soil characteristics (Davidson & Janssens, 2006). Notably, high temperature increases soil microbial decomposition rates, leading to a decrease in SOC (García-Palacios *et al.*, 2021). Fourth, we only had data on SOC in topsoil, making it difficult to assess SOC stocks. For example, it is conceivable that tree diversity also increases soil volume; thus, only by taking soil samples down to the bedrock can we be sure to assess total SOC stocks; just adjusting for bulk density would be misleading in this case. Future research should focus on trait plasticity, plant root traits and soil organism activity to mitigate uncertainties and enhance predictions of how diversity influences SOC along environmental gradients. Furthermore, to assess the influences of tree diversity on SOC stocks, sampling of full soil profiles will be necessary.

Conclusions

By collecting data from 15 long-term monitored large natural forest sites across various climatic conditions, our findings

highlight the significant role of tree diversity in shaping SOC along environmental gradients. Different facets of tree diversity play distinct roles in promoting SOC, with generally positive influence observed across most sites. This highlights the importance of considering a multifaceted approach to tree diversity when optimizing strategies for soil carbon preservation and sequestration. Moreover, our results demonstrate that the positive relationships between tree diversity and SOC can be strengthened under colder and more arid conditions. Efforts and strategies aimed at enhancing belowground carbon sequestration should integrate multiple aspects of diversity while also considering their interaction with local climatic conditions to effectively enhance SOC.

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Competing interests

None declared.

Author contributions

XL and YH designed the study. YL, KJA, SB, NAB, DFRPB, CC, KC, HD, NRG, HH, DJJ, GJ, LL, FL, YL, WJM, XM, JAM, JN, MJO, RPP, XQ, GR, GS, MJS, HS, SX, XX, EY, XY, JY and YZ provide data. HY and XL performed data analysis and wrote the first draft with substantial input from KM, YH, BS, YL, NRG, JAM, MJS, MJO, KJA and RPP helped improve the study design and finalize the data analysis. All authors provided intellectual input and edits.

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Data availability

The data and code that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.26983147>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Histograms and correlations of climatic conditions, tree diversity and soil organic carbon (SOC).

Fig. S2 Histograms and correlations of climatic conditions, tree diversity, and soil organic carbon stocks.

Fig. S3 Principal component analysis plot for the five filled and measured functional traits.

Fig. S4 Principal component analysis plot for the Mean annual temperature and Aridity index.

Fig. S5 The within site and overall effect size of the relationships between taxonomic diversity and soil organic carbon.

Fig. S6 The contribution of tree diversity indices on soil organic carbon stocks based on filled traits.

Fig. S7 The relationship between tree diversity and soil organic carbon stocks for each site.

Fig. S8 The relationships between climate and effect sizes of tree diversity–soil organic carbon stocks relationships from meta-regression using linear mixed effect model based on filled traits.

Fig. S9 The within site and overall effect size of the relationship between tree diversity and soil organic carbon based on measured traits.

Fig. S10 The within site and overall effect size of the relationship between tree diversity and soil organic carbon stocks based on measured traits.

Fig. S11 The relationships between climate and effect sizes of tree diversity–soil organic carbon relationships from meta-regression using linear mixed effect model based on measured traits.

Fig. S12 The relationships between climate and effect sizes of tree diversity–soil organic carbon stocks relationships from meta-regression using linear mixed effect model based on measured traits.

Table S1 Basic information for the 15 large forest sites included in the study.

Table S2 Overview of species-level functional traits measured locally across study sites.

Table S3 Number of species with functional traits values before and after genus mean value filling for 2496 species records of 15 sites.

Table S4 Principal component analysis results of filled functional traits for 15 sites.

Table S5 Principal component analysis results of measured traits for 15 sites.

Table S6 Principal component analysis results of Mean annual temperature and Aridity index.

Table S7 The overall effect size of tree diversity indices on soil organic carbon from meta-regression using linear mixed effect model based on filled traits.

Table S8 Summary of the linear model for each site's taxonomic diversity indices and soil organic carbon relationship based on filled traits.

Table S9 Summary of the linear model for each site's functional diversity indices and soil organic carbon relationship based on filled traits.

Table S10 Summary of the meta-regression using linear mixed effect model for each site's climatic conditions and effect size of tree diversity–soil organic carbon relationships based on filled traits.

Table S11 ANOVA table of the overall relationship between tree diversity indices and soil organic carbon stocks from meta-regression using linear mixed effect model based on filled traits.

Table S12 Summary of the linear model for each site's taxonomic diversity indices and soil organic carbon stocks relationship based on filled traits.

Table S13 Summary of the linear model for each site's functional diversity indices and soil organic carbon stocks relationship based on filled traits.

Table S14 Summary of the meta-regression using linear mixed effect model for each site's climatic conditions and effect size of tree diversity–soil organic carbon stocks relationships based on filled traits.

Table S15 ANOVA table of the overall relationship between tree diversity indices and soil organic carbon/soil organic carbon

stocks from meta-regression using linear mixed effect model (LME) based on measured traits.

Table S16 Summary of the meta-regression using linear mixed effect model for each site's climatic conditions and effect size of tree diversity–soil organic carbon relationships based on measured traits.

Table S17 Summary of the meta-regression using linear mixed effect model for each site's climatic conditions and effect size of tree diversity–soil organic carbon stocks relationships based on measured traits.

Table S18 ANOVA table of the overall relationship between tree diversity indices and soil organic carbon/soil organic carbon stocks from meta-regression using METAFOR package.

Table S19 Summary of the meta-regression using METAFOR package for each site's climatic conditions and effect size of tree diversity–soil organic carbon/soil organic carbon stocks relationships based on filled traits.

Table S20 Summary of the meta-regression using METAFOR package for each site's climatic conditions and effect size of tree diversity–soil organic carbon/soil organic carbon stocks relationships based on measured traits.

Table S21 Site-specific acknowledgements.

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