New Phytologist

Research

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

Haoru Yan[1,2,3], Xiaojuan Liu[1,4,5], Bernhard Schmid[6], Yi Li[1], Kristina J. Anderson-Teixeira[7,8], Sabine Both[9], Norman A. Bourg[7], David F. R. P. Burslem[10], Chengjin Chu[11], Keith Clay[12], Hu Du[13], Nathaly R. Guerrero-Ramírez[14], Hua Huang[15], Daniel J. Johnson[16], Guangze Jin[17,18], Luxiang Lin[19,20], Feng Liu[21], Yankun Liu[22], William J. McShea[7], Xiangcheng Mi[1], Jonathan A. Myers[23], Jinyao Nie[1], Michael J. O'Brien[24], Richard P. Phillips[25], Xiujuan Qiao[26,27], Glen Reynolds[28], Guochun Shen[29,30], Marko J. Spasojevic[31], Hongxin Su[32], Shangwen Xia[20], Xuehong Xu[1,33], Enrong Yan[29,34,35], Xiaodong Yang[19,36], Jie Yang[19,37], Yan Zhu[1], Keping Ma[1] and Yann Hautier[3]

[1]State Key Laboratory of Forage Breeding-by-Design and Utilization, Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China; [2]Nanjing Institute of Environmental Sciences, Ministry of Ecology and Environment of China, Nanjing, 210042, China; [3]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, Utrecht, 3584 CH, the Netherlands; [4]Zhejiang Qianjiangyuan Forest Biodiversity National Observation and Research Station, Beijing, 100093, China; [5]China National Botanical Garden, Beijing, 100093, China; [6]Remote Sensing Laboratories, Department of Geography, University of Zurich, Zurich, 8057, Switzerland; [7]Conservation Ecology Center, Smithsonian's National Zoo and Conservation Biology Institute, Front Royal, VA 22630, USA; [8]Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Panama City, Panama, Republic of Panama; [9]School of Environmental and Rural Science, University of New England, Armidale, 2351, Australia; [10]School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK; [11]School of Ecology and State Key Laboratory of Biological Control, Sun Yat–sen University, Guangzhou, 510275, China; [12]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA; [13]Huanjiang Observation and Research Station for Karst Ecosystem, Guangxi Key Laboratory of Karst Ecological Processes and Services, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha, 410125, China; [14]Biodiversity, Macroecology and Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Göttingen, 37077, Germany; [15]Lijiang Alpine Botanic Garden, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, 650201, China; [16]School of Forest, Fisheries, & Geomatics Sciences, University of Florida, Gainesville, FL 32611, USA; [17]Center for Ecological Research, Northeast Forestry University, Harbin, China; [18]Key Laboratory of Sustainable Forest Ecosystem Management–Ministry of Education, Northeast Forestry University, Harbin, 150040, China; [19]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, 666303, China; [20]National Forest Ecosystem Research Station at Xishuangbanna, Mengla, Yunnan, 666303, China; [21]Yunnan Academy of Forestry and Grassland, Kunming, 650204, China; [22]Heilongjiang Ecological Institute, Harbin, 150081, China; [23]Department of Biology, Washington University in St. Louis, St. Louis, MO 63130, USA; [24]Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Almería, 04120, Spain; [25]Department of Biology, Indiana University, Bloomington, IN 47405, USA; [26]Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, 430074, China; [27]Center of Conservation Biology, Core Botanical Gardens, Chinese Academy of Sciences, Wuhan, 430074, China; [28]Southeast Asia Rainforest Research Partnership, Danum Valley Field Centre, Sabah, 60282, Malaysia; [29]Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China; [30]Shanghai Institute of Pollution Control and Ecological Security, Shanghai, 200092, China; [31]Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, CA 92521, USA; [32]Key Laboratory of Environment Change and Resources Use in Beibu Gulf, Ministry of Education, Nanning Normal University, Nanning, 530001, China; [33]Biodiversity committee, Chinese Academy of Science, 100093, Beijing, China; [34]Zhejiang Zhoushan Island Observation and Research Station, East China Normal University, Shanghai, 200241, China; [35]Institute of Eco–Chongming (IEC), Shanghai, 200241, China; [36]National Field Scientific Observation and Research Station of Forest Ecosystem in Ailao Mountain, Mengla, 666303, China; [37]Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla, 666303, China

Author for correspondence:
Xiaojuan Liu
Email: liuxiaojuan06@ibcas.ac.cn

Received: *11 February 2026*
Accepted: *9 April 2026*

New Phytologist (2026)
doi: 10.1111/nph.71242

Summary

- 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 CO_2 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; Laliberte & 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-Ramirez *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

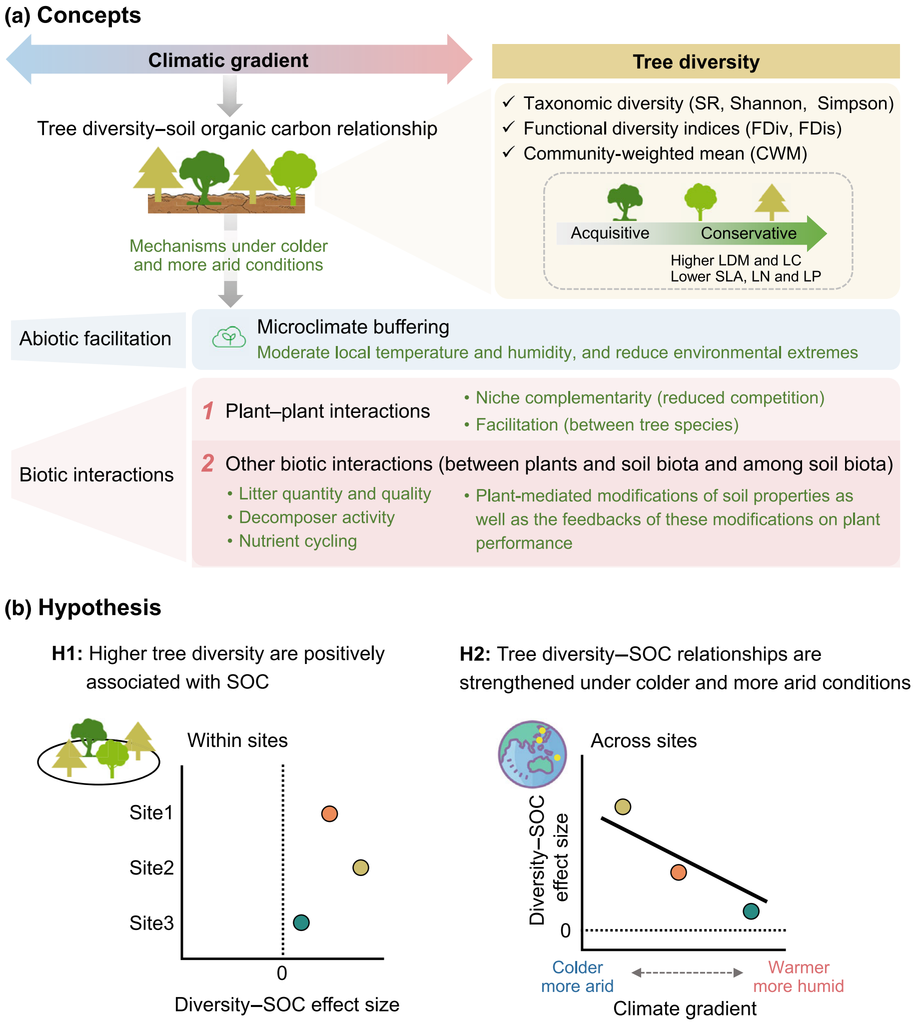

Fig. 1 Hypothesized relationships between tree diversity and soil organic carbon (SOC). (a) Multifaceted tree diversity and mechanisms underlying the tree diversity–SOC relationship under colder and more arid conditions. (b) Hypothesized within- (H1) and across-site (H2) relationships between tree diversity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

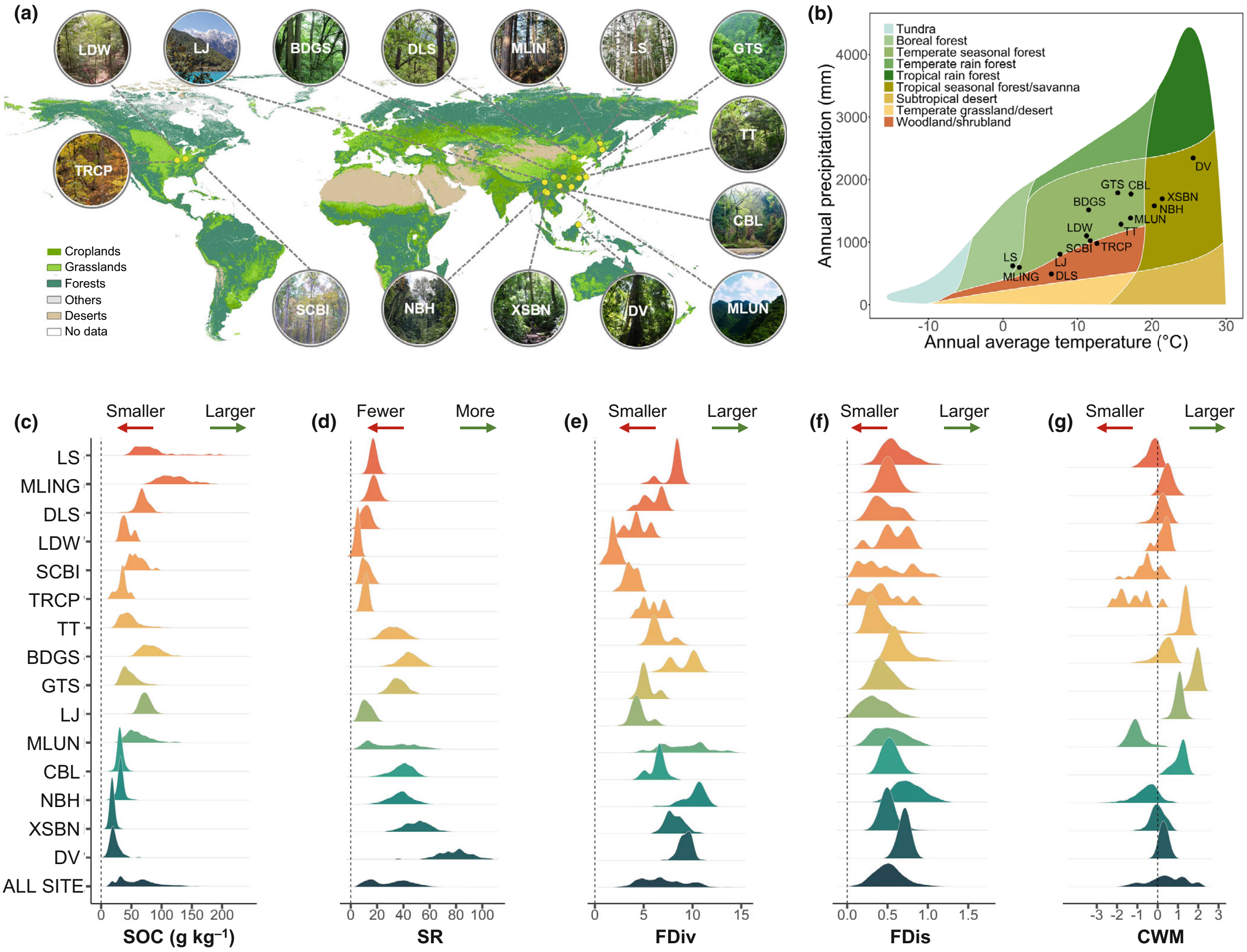

Fig. 2 Site overview and ridge density plots of soil organic carbon (SOC), tree species richness (SR), functional diversity (FDiv), functional dispersion (FDis), and community-weighted mean (CWM of first PC axis extracted from principal component analysis of five traits; see the Materials and Methods 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; Laliberte & Legendre, 2010), and CWM (Laliberte & 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; Laliberte & 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 (Laliberte & 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 ($r_{\mathrm{SR-FDiv}} = 0.63$, $r_{\mathrm{SR-FDis}} = 0.34$), as expected and CWM was uncorrelated with SR ($r_{\mathrm{SR-CWM}} = 0.002$), 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 ($r_{\mathrm{FDiv-FDis}} = 0.60$, $r_{\mathrm{FDiv-CWM}} = -0.55$, $r_{\mathrm{FDis-CWM}} = -0.44$).

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

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

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 *c.* 3.8 g kg^{-1} in SOC (*c.* 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 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 METAFOR 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 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;

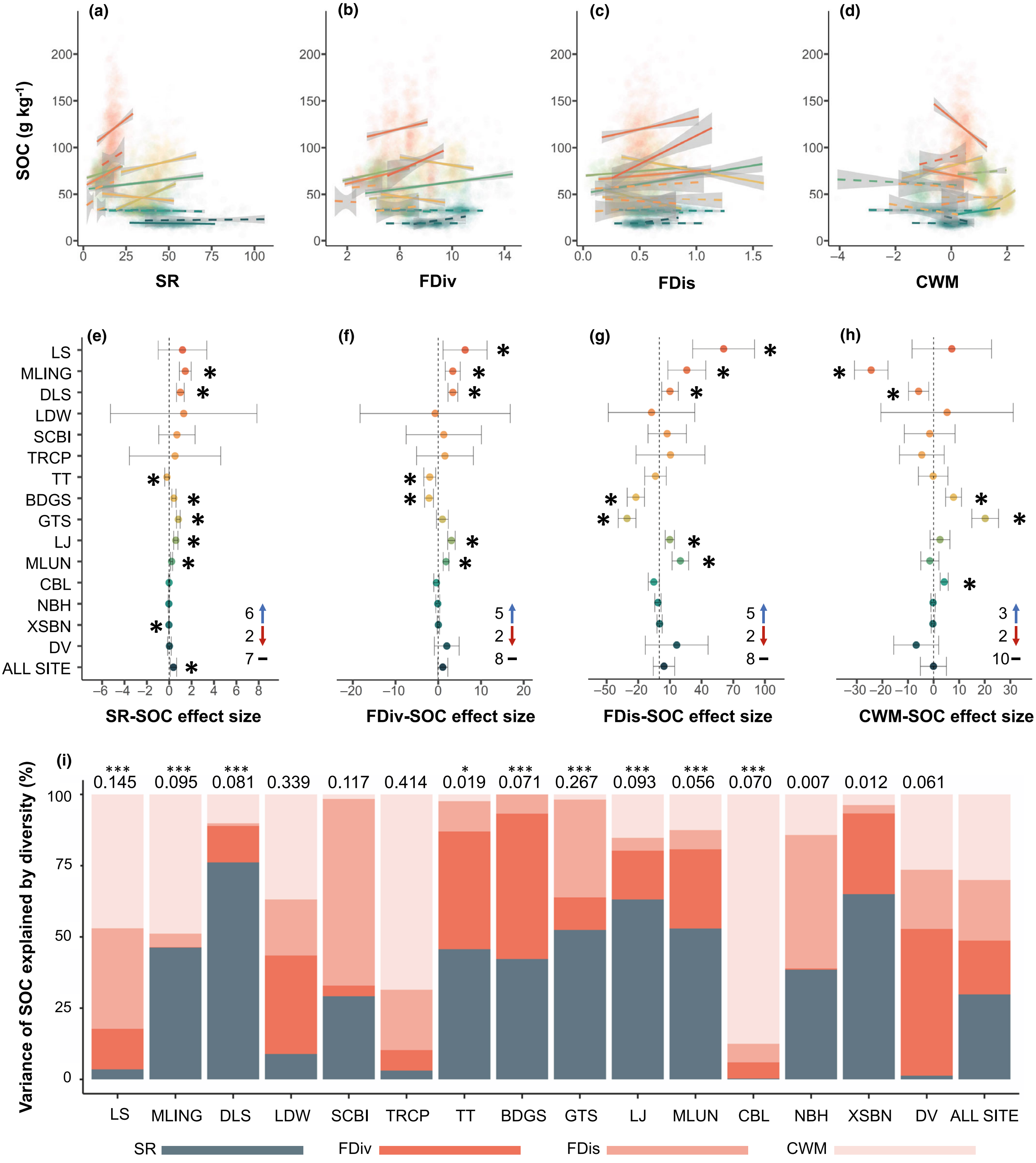

Fig. 3 Relationship between tree diversity and soil organic carbon (SOC) for each site. Simple linear regressions of species richness (SR), functional diversity (FDiv), functional dispersion (FDis), and community-weighted mean (CWM) on SOC are shown from a to d. Dashed lines indicate nonsignificant ($P > 0.05$) 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. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

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 a*l., 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.

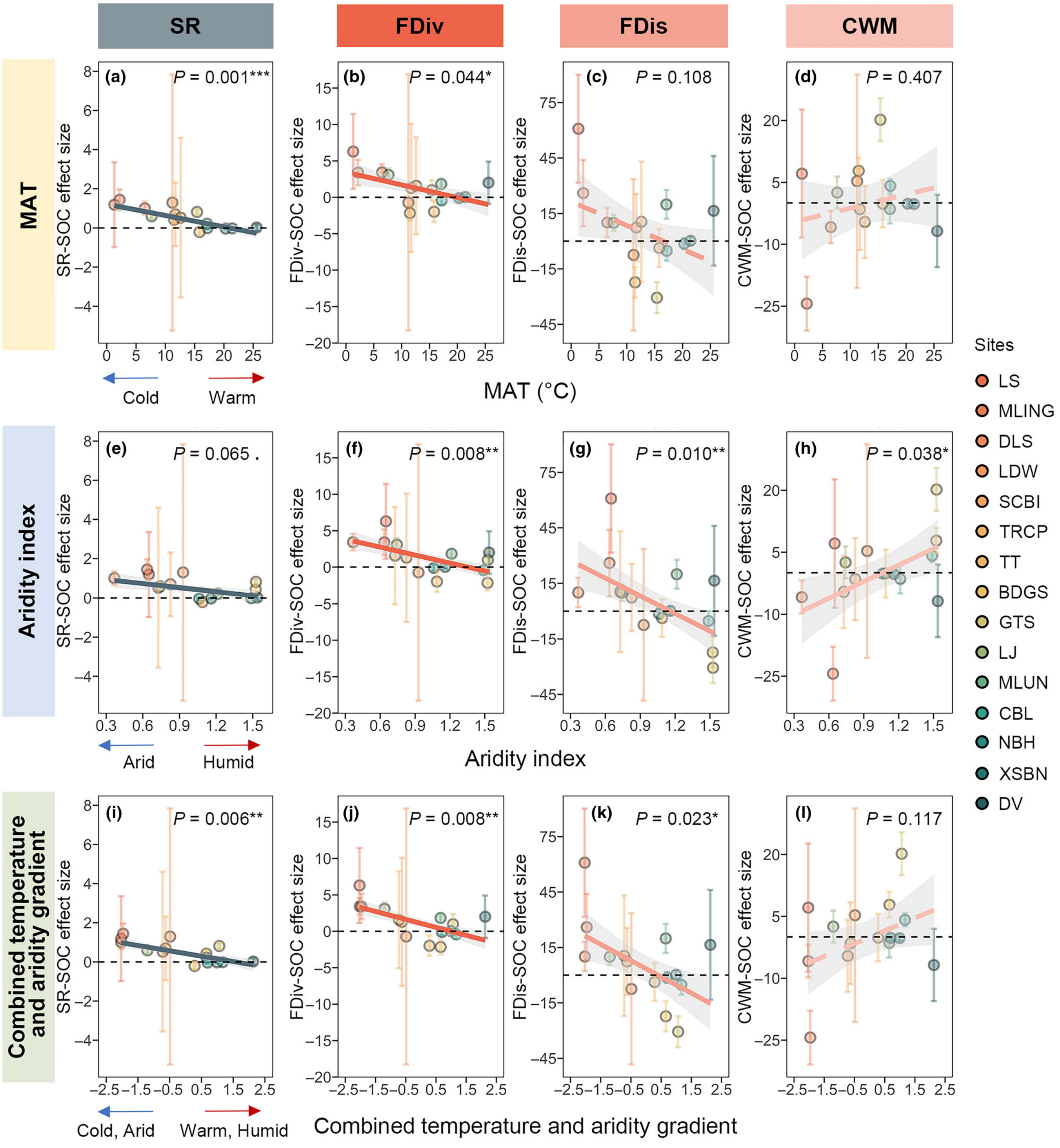

Fig. 4 Relationships between climate and effect sizes of tree diversity–soil organic carbon (SOC) relationships. The relationship between mean annual temperature (MAT) and effect size of SR-SOC (a), FDiv-SOC (b), FDis-SOC (c), and CWM-SOC (d). The relationship between aridity index and effect size of 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 nonsignificant ($P > 0.05$) 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.

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.

Acknowledgements

We thank the CForBo and ForestGEO platforms for allowing us to use their data. This study was financially supported by the National Natural Science Foundation of China (32525042), National Key Research Development Program of China (2022YFF0802300), and the Youth Innovation Promotion Association CAS (2023019). BS was funded by the University Research Priority Program 'Global Change and Biodiversity' of the University of Zurich. LL was funded by the Key Research and Development Program of Yunnan Province (202303AC100009). For site-specific acknowledgements, please refer to Table S21.

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.

ORCID

Kristina J. Anderson-Teixeira https://orcid.org/0000-0001-8461-9713
Sabine Both https://orcid.org/0000-0003-4437-5106
Norman A. Bourg https://orcid.org/0000-0002-7443-1992
David F. R. P. Burslem https://orcid.org/0000-0001-6033-0990
Chengjin Chu https://orcid.org/0000-0002-0606-449X
Keith Clay https://orcid.org/0000-0002-3956-0887
Hu Du https://orcid.org/0000-0002-9645-399X
Nathaly R. Guerrero-Ramírez https://orcid.org/0000-0001-7311-9852

Yann Hautier https://orcid.org/0000-0003-4347-7741
Guangze Jin https://orcid.org/0000-0002-9852-0965
Daniel J. Johnson https://orcid.org/0000-0002-8585-2143
Yi Li https://orcid.org/0000-0001-8878-4249
Luxiang Lin https://orcid.org/0000-0003-2727-0871
Xiaojuan Liu https://orcid.org/0000-0002-9292-4432
Keping Ma https://orcid.org/0000-0001-9112-5340
William J. McShea https://orcid.org/0000-0002-8102-0200
Xiangcheng Mi https://orcid.org/0000-0002-2971-5881
Jonathan A. Myers https://orcid.org/0000-0002-2058-8468
Jinyao Nie https://orcid.org/0009-0006-4510-2272
Michael J. O'Brien https://orcid.org/0000-0003-0943-8423
Richard P. Phillips https://orcid.org/0000-0002-1345-4138
Xiujuan Qiao https://orcid.org/0000-0003-4647-399X
Glen Reynolds https://orcid.org/0000-0002-6792-8589
Bernhard Schmid https://orcid.org/0000-0002-8430-3214
Guochun Shen https://orcid.org/0000-0001-9853-6062
Marko J. Spasojevic https://orcid.org/0000-0003-1808-0048
Xuehong Xu https://orcid.org/0000-0002-5998-3705
Enrong Yan https://orcid.org/0000-0002-8064-3334
Haoru Yan https://orcid.org/0000-0002-6016-0300
Jie Yang https://orcid.org/0000-0002-4444-8240

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.

References

Adair EC, Hooper DU, Paquette A, Hungate BA. 2018. Ecosystem context illuminates conflicting roles of plant diversity in carbon storage. *Ecology Letters* **21**: 1604–1619.

Anderson-Teixeira KJ, Davies SJ, Bennett AC, Gonzalez-Akre EB, Muller-Landau HC, Wright SJ, Abu Salim K, Almeyda Zambrano AM, Alonso A, Baltzer JL *et al.* 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* **21**: 528–549.

Angst Š, Angst G, Mueller KE, Lange M, Eisenhauer N. 2025. Un(der)explored links between plant diversity and particulate and mineral-associated organic matter in soil. *Nature Communications* **16**: 5548.

Augusto L, Boca A. 2022. Tree functional traits, forest biomass, and tree species diversity interact with site properties to drive forest soil carbon. *Nature Communications* **13**: 1097.

Barry KE, Mommer L, van Ruijven J, Wirth C, Wright AJ, Bai YF, Connolly J, De Deyn GB, de Kroon H, Isbell F *et al.* 2019. The future of complementarity: disentangling causes from consequences. *Trends in Ecology & Evolution* **34**: 167–180.

Bertness MD, Callaway R. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* **9**: 191–193.

Buzzard V, Michaletz ST, Deng Y, He ZL, Ning DL, Shen LN, Tu QC, Van Nostrand JD, Voordeckers JW, Wang JJ *et al.* 2019. Continental scale structuring of forest and soil diversity via functional traits. *Nature Ecology & Evolution* **3**: 1298–1308.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET *et al.* 2002. Positive interactions among alpine plants increase with stress. *Nature* **417**: 844–848.

Canessa R, van den Brink L, Berdugo MB, Hättenschwiler S, Rios RS, Saldaña A, Tielbörger K, Bader MY. 2022. Trait functional diversity explains mixture effects on litter decomposition at the arid end of a climate gradient. *Journal of Ecology* **110**: 2219–2231.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs* **84**: 45–67.

Chari NR, Taylor BN. 2022. Soil organic matter formation and loss are mediated by root exudates in a temperate forest. *Nature Geoscience* **15**: 1011–1016.

Chen C, Bongers FJ, Schmid B, Ma K, Liu X. 2025. Ecosystem consequences of functional diversity in forests and implications for restoration. *New Phytologist* **247**: 1081–1097.

Chen SP, Wang WT, Xu WT, Wang Y, Wan HW, Chen DM, Tang ZY, Tang XL, Zhou GY, Xie ZQ *et al.* 2018. Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences, USA* **115**: 4027–4032.

Chen X, Chen HYH, Chen C, Ma Z, Searle EB, Yu Z, Huang Z. 2020. Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biological Reviews* **95**: 167–183.

Chen X, Hisano M, Taylor AR, Chen HYH. 2022. The effects of functional diversity and identity (acquisitive versus conservative strategies) on soil carbon stocks are dependent on environmental contexts. *Forest Ecology and Management* **503**: 119820.

Chen X, Taylor AR, Reich PB, Hisano M, Chen HYH, Chang SX. 2023. Tree diversity increases decadal forest soil carbon and nitrogen accrual. *Nature* **618**: 94–101.

Chen Y, Huang Y, Niklaus PA, Castro-Izaguirre N, Clark AT, Bruelheide H, Ma K, Schmid B. 2020. Directed species loss reduces community productivity in a subtropical forest biodiversity experiment. *Nature Ecology & Evolution* **4**: 550–559.

Conti G, Diaz S. 2013. Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. *Journal of Ecology* **101**: 18–28.

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Perez-Harguindeguy N *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**: 1065–1071.

Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix ML, Wall DH, Parton AJ. 2015. Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience* **8**: 776–779.

Cowles JM, Wragg PD, Wright AJ, Powers JS, Tilman D. 2016. Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology* **22**: 741–749.

Crowther TW, van den Hoogen J, Wan J, Mayes MA, Keiser AD, Mo L, Averill C, Maynard DS. 2019. The global soil community and its influence on biogeochemistry. *Science* **365**: eaav0550.

Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**: 165–173.

Dawud SM, Raulund-Rasmussen K, Ratcliffe S, Domisch T, Finer L, Joly FX, Hattenschwiler S, Vesterdal L. 2017. Tree species functional group is a more important driver of soil properties than tree species diversity across major European forest types. *Functional Ecology* **31**: 1153–1162.

Dimitrakopoulos PG, Schmid B. 2004. Biodiversity effects increase linearly with biotope space. *Ecology Letters* **7**: 574–583.

Duan PP, Fu RT, Nottingham AT, Domeignoz-Horta LA, Yang XY, Du H, Wang KL, Li DJ. 2023. Tree species diversity increases soil microbial carbon use efficiency in a subtropical forest. *Global Change Biology* **29**: 7131–7144.

Edwards KR, Kastovská E, Borovec J, Santrucková H, Picek T. 2018. Species effects and seasonal trends on plant efflux quantity and quality in a spruce swamp forest. *Plant and Soil* **426**: 179–196.

Feng G, Mi X, Yan H, Li FY, Svenning J-C, Ma K. 2016. CForBio: a network monitoring Chinese forest biodiversity. *Science Bulletin* **61**: 1163–1170.

García-Palacios P, Bradford MA, Benavente-Ferraces I, de Celis M, Delgado-Baquerizo M, García-Gil JC, Gaitán JJ, Goñi-Urtiaga A, Mueller CW, Panettieri M *et al.* 2024. Dominance of particulate organic carbon in top mineral soils in cold regions. *Nature Geoscience* **17**: 145–150.

García-Palacios P, Crowther TW, Dacal M, Hartley IP, Reinsch S, Rinna R, Rousk J, van den Hoogen J, Ye JS, Bradford MA. 2021. Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming. *Nature Reviews Earth & Environment* 2: 507–517.

Garnier E, Cortez J, Billès G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A *et al.* 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85: 2630–2637.

Groothuis-Oudshoorn B. 2011. mice: multivariate imputation by chained equations in R. *Journal of Statistical Software* 45: 1–67.

Guerrero-Ramirez NR, Craven D, Messier C, Potvin C, Turner BL, Handa IT. 2016. Root quality and decomposition environment, but not tree species richness, drive root decomposition in tropical forests. *Plant and Soil* 404: 125–139.

Guerrero-Ramírez NR, Eisenhauer N. 2017. Trophic and non-trophic interactions influence the mechanisms underlying biodiversity–ecosystem functioning relationships under different abiotic conditions. *Oikos* 126: 1748–1759.

Guimarães-Steinicke C, Weigelt A, Proulx R, Lanners T, Eisenhauer N, Duque-Lazo J, Reu B, Roscher C, Wagg C, Buchmann N *et al.* 2021. Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities. *Journal of Ecology* 109: 1969–1985.

Handa IT, Aerts R, Berendse F, Berg MP, Bruder A, Butenschoen O, Chauvet E, Gessner MO, Jabiol J, Makkonen M *et al.* 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509: 218–221.

Hartley IP, Garnett MH, Sommerkorn M, Hopkins DW, Fletcher BJ, Sloan VL, Phoenix GK, Wookey PA. 2012. A potential loss of carbon associated with greater plant growth in the European Arctic. *Nature Climate Change* 2: 875–879.

He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16: 695–706.

Hong P, Schmid B, De Laender F, Eisenhauer N, Zhang X, Chen H, Craven D, De Boeck HJ, Hautier Y, Petchey OL *et al.* 2022. Biodiversity promotes ecosystem functioning despite environmental change. *Ecology Letters* 25: 555–569.

Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang AN, Li Y, Hardtle W, Oheimb G, Yang X *et al.* 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362: 80–83.

John R, Dalling JW, Harms KE, Yavitt JB, Stallard RF, Mirabello M, Hubbell SP, Valencia R, Navarrete H, Vallejo M *et al.* 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences, USA* 104: 864–869.

Jost L. 2006. Entropy and diversity. *Oikos* 113: 363–375.

Jousset A, Schmid B, Scheu S, Eisenhauer N. 2011. Genotypic richness and dissimilarity opposingly affect ecosystem functioning. *Ecology Letters* 14: 537–545.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.

Laliberte E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.

Lange M, Eisenhauer N, Chen H, Gleixner G. 2023. Increased soil carbon storage through plant diversity strengthens with time and extends into the subsoil. *Global Change Biology* 29: 2627–2639.

Lange M, Eisenhauer N, Sierra CA, Bessler H, Engels C, Griffiths RI, Mellado-Vazquez PG, Malik AA, Roy J, Scheu S *et al.* 2015. Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications* 6: 6707.

Laughlin DC, Mommer L, Sabatini FM, Bruelheide H, Kuyper TW, McCormack ML, Bergmann J, Freschet GT, Guerrero-Ramirez NR, Iversen CM *et al.* 2021. Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution* 5: 1123–1134.

Lemoine NP, Budny ML, Rose E, Lucas J, Marshall CW. 2024. Seasonal soil moisture thresholds inhibit bacterial activity and decomposition during drought in a tallgrass prairie. *Oikos* 2024: e10201.

Li Y, Bruelheide H, Scholten T, Schmid B, Sun Z, Zhang N, Bu W, Liu X, Ma K. 2019. Early positive effects of tree species richness on soil organic carbon accumulation in a large-scale forest biodiversity experiment. *Journal of Plant Ecology* 12: 882–893.

Li Y, Liu XJ, Xu WB, Bongers FJ, Bao WK, Chen B, Chen GK, Guo K, Lai JS, Lin DM *et al.* 2020. Effects of diversity, climate and litter on soil organic carbon storage in subtropical forests. *Forest Ecology and Management* 476: 118479.

Lin D, Anderson-Teixeira KJ, Lai J, Mi X, Ren H, Ma K. 2016. Traits of dominant tree species predict local scale variation in forest aboveground and topsoil carbon stocks. *Plant and Soil* 409: 435–446.

Loreau M, de Mazancourt C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* 16(s1): 106–115.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.

Maestre FT, Callaway RM, Valladares F, Lortie CJ. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199–205.

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker MA, Soliveres S, Escolar C *et al.* 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335: 214–218.

Makkonen M, Berg MP, van Logtestijn RSP, van Hal JR, Aerts R. 2013. Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. *Oikos* 122: 987–997.

Niklaus PA, Baruffol M, He J-S, Ma K, Schmid B. 2017. Can niche plasticity promote biodiversity-productivity relationships through increased complementarity? *Ecology* 98: 1104–1116.

O'Brien MJ, Reynolds G, Ong R, Hector A. 2017. Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. *Nature Ecology & Evolution* 1: 1643–1648.

Palandrani C, Alberti G. 2019. Tree derived soil carbon is enhanced by tree species richness and functional diversity. *Plant and Soil* 446: 457–469.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG *et al.* 2011. A large and persistent carbon sink in the world's forests. *Science* 333: 988–993.

Petchey OL, Gaston KJ. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5: 402–411.

Pretzsch H, Block J, Dieler J, Dong PH, Kohnle U, Nagel J, Spellmann H, Zingg A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science* 67: 712.

R Core Team. 2023. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.R-project.org/.

Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, Verheyen K, Allan E, Benavides R, Bruelheide H, Ohse B *et al.* 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters* 20: 1414–1426.

Ridgeway J, Kane J, Morrissey E, Starcher H, Brzostek E. 2023. Roots selectively decompose litter to mine nitrogen and build new soil carbon. *Ecology Letters* 27: e14331.

Santonja M, Rancon A, Fromin N, Baldy V, Hattenschwiler S, Fernandez C, Montes N, Mirleau P. 2017. Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland. *Soil Biology & Biochemistry* 111: 124–134.

Schmid B. 1992. Phenotypic variation in plants. *Evolutionary Trends in Plants* 6: 45–60.

Schnabel F, Beugnon R, Yang B, Richter R, Eisenhauer N, Huang Y, Liu X, Wirth C, Cesarz S, Fichtner A *et al.* 2025. Tree diversity increases forest temperature buffering via enhancing canopy density and structural diversity. *Ecology Letters* 28: e70096.

Schnabel F, Guillemot J, Barry KE, Brunn M, Cesarz S, Eisenhauer N, Gebauer T, Guerrero-Ramirez NR, Handa IT, Madsen C *et al.* 2025. Tree diversity increases carbon stocks and fluxes above-but not belowground in a tropical forest experiment. *Global Change Biology* 31: e70089.

Scholten T, Goebes P, Kühn P, Seitz S, Assmann T, Bauhus J, Bruelheide H, Buscot F, Erfmeier A, Fischer M *et al.* 2017. On the combined effect of soil fertility and topography on tree growth in subtropical forest ecosystems-a study from SE China. *Journal of Plant Ecology* 10: 111–127.

Seidelmann KN, Scherer-Lorenzen M, Niklaus PA. 2016. Direct vs. microclimate-driven effects of tree species diversity on litter decomposition in young subtropical forest stands. *PLoS ONE* **11**: e0160569.

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J *et al.* 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* **536**: 456–459.

Spasojevic MJ, Turner BL, Myers JA. 2016. When does intraspecific trait variation contribute to functional beta-diversity? *Journal of Ecology* **104**: 487–496.

Spohn M, Bagchi S, Biederman LA, Borer ET, Brathen KA, Bugalho MN, Caldeira MC, Catford JA, Collins SL, Eisenhauer N *et al.* 2023. The positive effect of plant diversity on soil carbon depends on climate. *Nature Communications* **14**: 6624.

Svenning J-C, Eiserhardt WL, Normand S, Ordonez A, Sandel B. 2015. The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **46**: 551–572.

Tilman D, Lehman CL, Thomson KT. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences, USA* **94**: 1857–1861.

Viechtbauer W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**: 1–48.

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* **27**: 244–252.

Wang M, Guo X, Zhang S, Xiao L, Mishra U, Yang Y, Zhu B, Wang G, Mao X, Qian T *et al.* 2022. Global soil profiles indicate depth-dependent soil carbon losses under a warmer climate. *Nature Communications* **13**: 5514.

Wright A, Schnitzer SA, Reich PB. 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* **95**: 2213–2223.

Wright A, Schnitzer SA, Reich PB. 2015. Daily environmental conditions determine the competition–facilitation balance for plant water status. *Journal of Ecology* **103**: 648–656.

Wright AJ, Mommer L, Barry K, van Ruijven J. 2021. Stress gradients and biodiversity: monoculture vulnerability drives stronger biodiversity effects during drought years. *Ecology* **102**: e03193.

Yan GY, Bongers FJ, Trogisch S, Li Y, Chen GK, Yan HR, Deng XL, Ma KP, Liu XJ. 2022. Climate and mycorrhizae mediate the relationship of tree species diversity and carbon stocks in subtropical forests. *Journal of Ecology* **110**: 2462–2474.

Zhang L, Mi X, Shao H, Ma K. 2011. Strong plant-soil associations in a heterogeneous subtropical broad-leaved forest. *Plant and Soil* **347**: 211–220.

Zhang S, Landuyt D, Dhiedt E, De Frenne P, Verheyen K. 2024. Tree species diversity affects litter decomposition via modification of the microenvironment. *Ecosystems* **27**: 508–522.

Zhang S, Landuyt D, Verheyen K, De Frenne P. 2022. Tree species mixing can amplify microclimate offsets in young forest plantations. *Journal of Applied Ecology* **59**: 1428–1439.

Zhang WP, Fornara D, Yang H, Yu RP, Callaway RM, Li L. 2023. Plant litter strengthens positive biodiversity-ecosystem functioning relationships over time. *Trends in Ecology & Evolution* **38**: 473–484.

Zomer RJ, Xu J, Trabucco A. 2022. Version 3 of the global aridity index and potential evapotranspiration database. *Scientific Data* **9**: 409.

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.