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Abiotic and biotic drivers of tree trait effects on soil microbial biomass and soil carbon concentration

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# Abstract

Forests are critical ecosystems to understand the global carbon budget, due to their carbon sequestration potential in both above- and belowground compartments, especially in species-rich forests. Soil carbon sequestration is strongly linked to soil microbial communities, and this link is mediated by the tree community, likely due to modifications of micro-environmental conditions (i.e., biotic conditions, soil properties, and microclimate). We studied soil carbon concentration and the soil microbial biomass of 180 local neighborhoods along a gradient of tree species richness ranging from 1 to 16 tree species per plot in a Chinese subtropical forest experiment (BEF-China). Tree productivity and different tree functional traits were measured at the neighborhood level. We tested the effects of tree productivity, functional trait identity and dissimilarity on soil carbon concentrations, and their mediation by the soil microbial biomass and micro-environmental conditions. Our analyses showed a strong positive correlation between soil microbial biomass and soil carbon concentrations. Besides, soil carbon concentration increased with tree productivity and tree root diameter while it decreased with litterfall C:N content. Moreover, tree productivity and tree functional traits (e.g. root fungal association and litterfall C:N ratio) modulated micro-environmental conditions with substantial consequences for soil microbial biomass. We also showed that soil history and topography should be considered in future experiments and tree plantations, as soil carbon concentrations were higher where historical (i.e., at the beginning of the experiment) carbon concentrations were high, themselves being strongly affected by the topography.

Altogether, these results imply that the quantification of the different soil carbon pools is critical for understanding microbial community–soil carbon stock relationships and their dependence on tree diversity and micro-environmental conditions.

## Key Words

BEF-China, biotic conditions, microbial community, microclimate, micro-environment, productivity, root morphology, soil quality, soil carbon stock, subtropical forest, tree diversity

# Main text

## Introduction

The rapid increase in atmospheric carbon is one of the main causes of climate change and becomes a major threat to life on Earth (IPBES 2019). Atmospheric carbon concentrations can be reduced by both reducing carbon emissions and increasing carbon fixation. Forest ecosystems have been identified to be capable of mitigating increases in atmospheric carbon dioxide by capturing and fixing it aboveground and storing it both above and below the ground (Bastin et al. 2019; Lewis et al. 2019). Belowground carbon storage provides a high potential for atmospheric carbon control due to the long residence time of carbon in soil (Trumbore 2009). However, our understanding of the balance between soil carbon influx (e.g., due to photosynthesis) and efflux (e.g., due to soil respiration and erosion) in forest systems is still limited.

Tree diversity can enhance carbon storage in forests (Huang et al. 2018; Liu et al. 2018) via increased productivity, such as tree biomass, litterfall quantity, root biomass, and exudation (Huang et al. 2017; 2018; Xu et al. 2020; Zheng, Chen, and Yan 2019), even though these processes might lead to higher soil respiration. Moreover, tree diversity should decrease soil erosion and thus soil carbon effluxes, by reducing the impact of precipitation on surface soil (Goebes et al. 2015; Seitz et al. 2016), for instance by increasing canopy closure (Perles–Garcia et al. 2021; Williams et al. 2017). Consequently, tree diversity is expected to enhance carbon storage in forests by increasing the ratio of carbon influxes to carbon effluxes (Liu et al. 2018).

Recent studies linked soil carbon concentrations to tree roots (Adamczyk et al. 2019).

Specifically, morphological traits, e.g., root diameter (RD) and specific root length (SRL),

were shown to control the release of root carbon to the soil by root turnover or exudation (Sun et al. 2020) and to drive soil organic matter decomposition (Adamczyk et al. 2019). For example, higher specific root length increases root carbon exudation and root turnover due to a higher density of fine roots (Bergmann et al. 2020; Sun et al. 2020; Wen et al. 2019). Additionally, the mycorrhizal association of tree roots, e.g., with arbuscular and ectomycorrhizal fungi, is a key driver of soil carbon storage (Averill, Turner, and Finzi 2014; Averill and Hawkes 2016; Craig et al. 2018; Crowther et al. 2019), as differences in mycorrhizal associations can lead to variations in fungal metabolic pathways due to different nutrient acquisition strategies (Bonfante and Genre 2010; Crowther et al. 2019), and thus influence soil carbon dynamics. However, the effects of the mycorrhizal association on soil carbon dynamics still remain unclear (Frey 2019). On top of that, mycorrhizal colonization of roots increases with the increase of cortical tissues, themselves being positively correlated with root diameter (Bergmann et al. 2020). Thus, root diameter can determine soil carbon concentrations by modulating fungal colonization.

Soil microorganisms play a central role in soil carbon dynamics by processing soil carbon, thereby being the main driver of carbon sequestration (Lange et al. 2015; Schmidt et al. 2011). As microorganisms are the main consumers of plant-derived and soil organic matter, one would expect them to reduce soil carbon concentrations. However, recent studies highlighted that increased microbial activity could increase soil carbon concentrations by transferring higher amounts of soil organic matter to a stable pool of microbial necromass (Buckeridge et al. 2020; Lange et al. 2015; Miltner et al. 2012; Schmidt et al. 2011; Trumbore 1993). The relative contribution of microbial derivatives in structuring soil organic carbon was underestimated in the past (Simpson et al. 2007; Kästner and Miltner 2018), whereas microbial residues are expected to represent 50 - 80% of the total soil organic carbon (Liang and Balser 2011; Simpson et al. 2007).

Soil microorganisms and the functions provided are strongly influenced by the above-mentioned root traits and thereby by the tree community composition due to species-specific associations (Lareen, Burton, and Schäfer 2016; Pei et al. 2016). Root biomass and litter production can further increase habitat space and substrate availability for soil microorganisms with increasing plant species richness (Bardgett, Mommer, and de Vries 2014; Hooper et al. 2000). Moreover, species-rich plant communities affect soil microorganisms and generally increase soil microbial biomass and diversity (Beugnon et al. 2021; Chapman et al. 2013; Eisenhauer et al. 2010; Lange et al. 2015). Thereby, the positive effect of high plant species diversity on soil microorganisms is suggested to increase soil carbon concentrations (Li et al. 2019; Liang and Balser 2011; Lange et al. 2015). For example, plant species diversity enhances soil microbial biomass and increases soil carbon by enhancing litter diversity (Thoms et al. 2010; Ushio et al. 2008), root biomass (Xu et al. 2020), and the amount and diversity of root exudates (Eisenhauer et al. 2017), and due to the dissimilarity between root traits (Kramer et al. 2016).

Next to root traits, environmental conditions, such as biotic interactions, soil chemistry, and climate, influence soil microbial biomass and community composition (Bernhard et al. 2018; Beugnon et al. 2021; Cesarz et al. 2022; Delgado-Baquerizo et al. 2016; Gottschall et al. 2019). One example of biotic interactions is that understory plant diversity can increase the soil microbial biomass and activity in temperate forests (Eisenhauer et al. 2011); however, empirical evidence remains inconsistent (Xu et al. 2020). Global studies showed that climate and soil chemistry are the two main drivers of microbial biomass and composition in drylands (Delgado-Baquerizo et al. 2016), but also along large climate gradients from arid to humid (Bernhard et al. 2018). Temperature and soil water content increase microbial biomass by increasing microbial activity and growth (Delgado-Baquerizo et al. 2016). Moreover, reduced water availability increases the osmotic pressure which, due to salt concentration and pH,

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constrains microbial biomass and alters community composition pointing to interactions among abiotic drivers (Aciego Pietri and Brookes 2009; Delgado-Baquerizo et al. 2017; Wichern, Wichern, and Joergensen 2006).

In forests, environmental conditions (i.e., biotic interactions, soil chemistry, and microclimate conditions) can be modulated by the tree community. For instance, forest understory plant communities are connected to tree community composition and diversity (Germany, Bruelheide, and Erfmeier 2017). Tree diversity, for example, has been identified to increase the cover of forbs, while the proportion of forest-specific understory species increased with canopy cover (Vockenhuber et al. 2011). However, herb layer productivity is not necessarily affected by tree layer diversity (Germany, Bruelheide, and Erfmeier 2017), or herb layer diversity (Both et al. 2011). Furthermore, tree community composition can also modify soil chemistry, such as soil pH and nutrient availability (Reich et al. 2005), with significant consequences for soil microbial community composition (Delgado-Baquerizo et al. 2017; Thoms et al. 2010). Likewise, soil moisture can be affected by tree-specific root length, as this trait affects the hydraulic lift (Burgess et al. 1998), with consequences for microbial communities (Cesarz et al. 2022). In addition, tree canopies provide a buffering layer between macroclimatic fluctuations and microclimatic fluctuations (de Frenne et al. 2019), as species-rich forests have a higher spatial complementarity in tree crowns and canopy closure (Kunz et al. 2019; Perles-Garcia et al. 2021; Williams et al. 2017). Thereby, tree diversity would stabilize the microclimate and enhance ecosystem functions (Gottschall et al. 2019). In this study, we aim to mechanistically understand the effects of tree diversity, productivity, functional trait identity and dissimilarity on soil carbon concentration and its mediation by the soil microbial biomass and micro-environmental conditions (i.e., biotic interactions, soil chemical properties, and microclimatic conditions; Fig. 1). We based our study on the BEF-China experiment and investigated 180 small-scale neighborhoods distributed with a species



richness gradient ranging from 1 to 16. For each sample location, we measured soil carbon concentration, soil microbial biomass, and environmental conditions to mechanistically describe and understand tree diversity, productivity and functional trait effects on soil carbon concentrations.

We hypothesized **tree diversity, productivity, functional trait (e.g., specific root length, root diameter, mycorrhizal status) identity and dissimilarity between these root traits to drive soil carbon concentrations (hypothesis 1; Fig. 1)**. In addition, **tree diversity, productivity, and functional identity and dissimilarity effects on soil carbon concentrations are mediated by soil microbial biomass (hypothesis 2)**. We further hypothesize that **tree community effects on soil microbial biomass are mediated by micro-environmental conditions (biotic environment, soil chemical properties, and microclimate; hypothesis 3)**. In order to control for soil history and topography effects on erosion and, therefore soil carbon concentration, we considered historical soil carbon concentration (measured before the onset of tree interactions) and plot topography (i.e., plot altitude, slope, and curvature) as covariates in our analyses (Fig. 1).

## Material and methods

### Study site

The study site is located in south-east China nearby the town of Xingangshan (Jiangxi province, 29.08-29.11° N, 117.90-117.93° E). Our experimental site is part of the BEF-China experiment (site A, Bruehlheide et al. 2014), and it was planted in 2009 after a clear-cut of the previous commercial plantation. The region is characterized by a subtropical climate with warm, rainy summers and cool, dry winters with a mean temperature of 16.7°C and a mean annual rainfall of 1,821 mm (Yang et al. 2013). Soils in the region are Cambisols and Cambisol derivatives, with Regosol on ridges and crests (Geißler et al. 2012; Scholten et al.

2017). The natural vegetation consists of species-rich broad-leaved forests dominated by *Cyclobalanopsis glauca*, *Castanopsis eyrei*, *Daphniphyllum oldhamii*, and *Lithocarpus glaber* (Bruehlheide et al. 2011; 2014).

## Study design

We selected 180 small-scale sample locations across five species richness levels (1, 2, 4, 8, and 16 species) per plot, according to the BEF China planting design (Appendix S1). These small-scale locations are local neighborhoods of trees defined as the twelve trees directly adjacent in the planting grid with two central trees (Appendix S1: Figs. S1-S2, see Tree Species Pairs in Trogisch et al. 2021). Each local neighborhood was replicated three times in each richness level when available (see “broken stick” design, Bruehlheide et al. 2014).

## Plot topography

To control for the topography effect on soil carbon concentration, topography measures were calculated from a digital elevation model (DEM). The DEM was interpolated in 2015 from elevation measurements with a differential global positioning system (DGPS) using the ordinary kriging algorithm and a cell size of 5 m x 5 m. Slope, altitude, plan curvature (Curv. PL), and profile curvature (Curv. PR) were calculated from the DEM at the plot level due to the low intra-plot variability (Scholten et al. 2017).

## Microclimate modeling

The daily air temperature was recorded using 35 data loggers (HOBO® Pro v2, U23-001) installed at 1 m height in the center of 35 plots across the experiment, while a meteorological station was set up in the central part of the experimental site (see Appendix S2: Fig. S1 for more details; Bruehlheide et al. 2014). To cover our full experimental area, the air temperature was modeled for all of our experimental plots using the available logger data. We modeled the temperature measurements of the 35 data loggers (i.e., daily minimum, mean, and

maximum temperature) as a function of the meteorological station measurements (i.e., daily temperature, rainfall, and solar radiation), plot topography (i.e., latitude, longitude, altitude, orientation, slope, plot curvature, and mean annual solar radiation), forest vertical stratification (i.e. effective number of layers index, “ENL”, see below) and plot species richness (see Appendix S2 for more details). Spatio-temporal trends for the whole experiment were estimated using Gaussian radial basis functions (functions “auto-basis”, “eval\_basis” from the R package FRK, see Appendix S2: Section S1 and Wikle, Zammit-Mangion, and Cressie 2019). Our model fits explained more than 90% of the loggers' temperature measurement variability. The fitted models were used to predict daily minimum, mean, and maximum temperature for all experimental plots with a standard error from 0°C to 2°C during our sampling period (see Appendix S2 for the complete procedure).

### **Field sampling**

Our field measurements were performed from mid-August to the end of September 2018, before the main litterfall season (from September to December; Huang et al. 2017). To avoid spatio-temporal autocorrelation, each day another sampling area was randomly chosen. To test the effect of biotic conditions on soil microbial biomass and carbon concentrations, understory plant cover in each location was estimated on a five-level factorial scale from 'no understory plant' to 'mainly covered by understory plants'. Although this is a relatively coarse measurement, while being comparable with the Londo scale (Londo 1976), it allows considering the influence of understory vegetation which was shown to be of importance (Vockenhuber et al., 2011). We encourage subsequent studies to assess the understory vegetation in a more detailed way.

Starting from the center of the two central trees of the local neighborhood, we extracted two soil cores with 5 cm diameter and 10 cm depth, 5 cm away from the center (Appendix S1:

Fig. S2). Two additional cores of the same dimensions were taken 20 cm away from the center in the direction of each tree. A composite soil sample was built for soil analyses from these four soil cores and sieved with a 2 mm mesh. As a first measure of the biotic environment, root fragments contained in the sieving residues were air-dried at 40°C for two days and weighed ( $\pm 0.01$  g), while the composite soil samples were stored at -20°C.

To estimate the effect of biotic conditions and especially nutrient availability effect on soil microbial biomass and soil carbon concentration, the litter cover on the ground between the two central trees of each location was estimated on a five-level factorial scale from 'no-litter' to 'litter layer thicker than five centimeters'. Leaf litter was collected between the central trees from the ground excluding green understory plant residuals, air-dried at 40°C for two days, and milled to powder. Carbon and nitrogen concentrations were measured by micro-combustion from a subsample of 4 mg (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

### **Soil analyses**

Soil moisture was measured from a subset of 25 g soil by drying the soil at 40 °C for two days. A subsample was used to quantify soil pH in a 1:2.5 soil-water solution. Soil total nitrogen (TN) was determined on an auto-analyzer (SEAL Analytical GmbH, Norderstedt, Germany) using the Kjeldahl method (Bradstreet 1954). Soil total phosphorus (TP) was measured after wet digestion with H<sub>2</sub>SO<sub>4</sub> and HClO<sub>4</sub> (Parkinson and Allen 1975) using a UV-VIS spectrophotometer (UV2700, SHIMADZU, Japan). Soil total organic carbon (TOC) was measured by a TOC Analyzer (Liqui TOC II; Elementar Analysensysteme GmbH, Hanau, Germany). TOC in 2010 was quantified in a previous study (Scholten et al. 2017) at the plot level using the micro-combustion method (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

## Soil microbial biomass

Soil microbial biomass was measured using phospholipid fatty acid (PLFA) analysis. PLFAs were extracted from 5 g of frozen soil following Frostegård, Tunlid, and Bååth (1991).

Biomarkers were assigned to microbial functional groups according to Ruess and Chamberlain (2010) using markers to assign bacteria (gram-positive bacteria: i15:0, a15:0, i16:0, i17:0; gram-negative bacteria: cy17:0, cy19:0; general bacteria markers: 16:1 $\omega$ 5; 16:1 $\omega$ 7), arbuscular mycorrhizal fungi (20:1 $\omega$ 9), and saprophytic and ectomycorrhizal fungi (18:1 $\omega$ 9 and 18:2 $\omega$ 6,9, see Appendix S3).

## Tree functional traits

### Tree biomass

Tree biomass was predicted for all neighbor trees using tree basal area (BA) and species-specific allometric relationships estimated on the two central trees. (1) Circumference at breast height (CBH) was measured in September 2018 for all trees in order to calculate the basal area of these trees as  $BA = \frac{(CBH)^2}{4\pi}$ . (2) Tree height was measured for the two central trees using a laser meter ( $4.9 \pm 2.1$  m, PLR 50C, Robert Bosch GmbH, Gerlingen, Germany), and tree biomass was calculated following Huang et al. (2018). BA and biomass of the central trees were used to estimate species-specific allometric BA-biomass relationships (see Appendix S4). (3) These species-specific allometric relationships were used to calculate the neighborhood biomass (i.e., sum of the twelve surrounding trees' biomass).

### Leaf traits

For each tree species of the experiment, ten samples consisting of 10 to 25 pooled fresh leaves were collected across all diversity levels from mid-August to October 2018 (Davrinche and Haider 2021). Each sample was dried at 80°C for two days and milled for 5 min at 26

shakes per second. Carbon and nitrogen concentrations were measured by micro-combustion from a subsample of 5 mg (Elementar Vario El III analyzer, Elementar, Hanau, Germany).

### **Root traits**

Root functional traits were measured from BEF-China Site A from September to October 2013 using two to three tree individuals per species per diversity level. First-order roots were collected, cleaned, scanned, and analyzed by WinRHIZO (Regent Software, Canada). After measurements, roots were air-dried at 60°C for two days and weighed. Average RD (in mm) and SRL (in  $\text{m.g}^{-1}$ ) were calculated from the measurements of each species at all species richness levels (Bu et al. 2017). The mycorrhizal status of the tree species was determined from the literature (Haug et al. 1994; Hawley and Dames 2004; Wang and Qiu 2006). The mycorrhizal status was assumed from the literature and confirmed by recent measurements in the same experiment (Singavarapu et al. 2021). However, intraspecific root functional trait variability can be high and may change over the course of an experiment depending on the biotic context (e.g., Zuppinger-Dingley et al. 2014), which could not be considered in the present study.

### **Root functional trait variables**

We considered three functional root traits that are related to soil processes (Bardgett, Mommer, and de Vries 2014): root diameter (RD), specific root length (SRL), and mycorrhizal tree association (i.e., AM or EM). For each location, trait identity and diversity were calculated at the neighborhood level. At the neighborhood level, we calculated community-weighted means (CWM, Garnier et al. 2004) and functional dispersion (FDis) – defined as the weighted variance of the trait values within the neighborhood (Laliberté and Legendre 2010). All measures were weighted using tree BA. Calculations were made using the 'dbFD' function from the 'FD' package in R (Laliberté et al. 2014).

## Forest vertical stratification

To quantify the forest vertical stratification and estimate crown complementarity, we computed the Effective Number of Layers (ENL, Ehbrecht et al. 2016) using terrestrial laser scanning measurements. A high ENL value indicates more evenly distributed layers, which can be an indication of higher crown complementarity and, thus, increase of canopy packing (Ehbrecht et al. 2016). A terrestrial laser scanning campaign took place in February-March of 2019 using a FARO Focus S120 and a FARO Focus X130 laser scanner (FARO Europe, Korntal-Münchingen, Germany; for more information see Perles–Garcia et al. 2021). The scanner was set up on a tripod at 1.3 m height in the center of each plot and a fully three-dimensional point cloud (360° x 305° field of view) with a spatial resolution of 6 mm at a distance of 10 m was acquired.

For each plot, the Effective Number of Layers (ENL) was computed. First, the scans were filtered using a statistical outlier removal filter (SOR, N=10, SD=3) in CloudCompare 2.9.1 software. Taking into account the dimensions of each plot (~667 m<sup>2</sup>), each point cloud was clipped in a 20 m square around the scan center (~400 m<sup>2</sup>). The point clouds were voxelized into a voxel grid of 5 cm voxels using the R package VoxR (Lecigne, Delagrangue, and Messier 2018). Then, they were grouped in vertical slices of 50 cm and, for each slice, we quantified the proportion of filled voxels. The ENL was the result of calculating the inverse Simpson-Index:  $ENL = 1 / \sum_{i=1}^n p_i^2$ , where n refers to the number of slices, calculated as  $(\text{height}_{\text{max}} - \text{height}_{\text{min}}) / 50\text{cm}$ ; and  $p_i$  is the proportion of filled voxels of the  $i_{\text{th}}$  slice.

## Leaf litterfall measurement

From September to December 2018, the freshly fallen leaf litter between the two central trees of each location was collected in a 1 m<sup>2</sup> litter trap (1 cm mesh). The collected litter was identified to species level, air-dried at 40°C for two days, and weighed ( $\pm 0.01$  g). Annual



amounts of litter carbon (i.e. " $C_{\text{litterfall}}$ ") and nitrogen (i.e. " $N_{\text{litterfall}}$ ") deposited on the ground were calculated using species-specific leaf carbon and nitrogen contents and species-specific table litter mass collected in the traps. We calculated the litterfall carbon to nitrogen ratio ( $CN_{\text{litterfall}}$ ) from these measurements.

## Statistical analyses

A description of all the variables used in this study can be found in Appendix S5: Table S1. All data handling and statistical calculations were performed using the R statistical software version 3.6.1. All R scripts used for this project can be found in our Zenodo release (<https://doi.org/10.5281/zenodo.7225739>).

In order to avoid any deviation due to scale differences between variables, all explanatory variables were centered and divided by two standard deviations for our analyses using the R 'rescale' function from the 'arm' package. Collinearity of root trait indices was inspected by Pearson's correlation (Appendix S6); highly correlated variables were excluded by our both-way step selection algorithm favoring the simplest model (Venables and Ripley 2002), i.e., the R 'step' function from the 'stat' package. We first tested the effects of tree species richness on our productivity and structural variables (i.e., neighborhood biomass, ENL,  $C_{\text{litterfall}}$ , and  $CN_{\text{litterfall}}$ ) using linear models and normal distribution assumptions. Similarly, we used linear models to control for the effects of topography (plot slope, plan curvature, profile curvature and altitude) on soil historical carbon concentration.

**Drivers of soil carbon concentration (H1).** We used linear models and normal distribution assumptions to test the effects of initial soil carbon concentration (i.e.,  $[C]_{2010}$ ), topography, tree productivity variables, litterfall carbon deposition, and C:N ratio, and root functional traits on soil carbon concentration (i.e.,  $[C]_{2018}$ ). Explanatory variables were selected by a both-way step selection based on AIC (R 'step' function from the 'stats' package with back-



and forward selection). We estimated the drivers of soil carbon concentrations from the final model. All significant variables of the model output ( $p$ -value < 0.05) were implemented with the effects of topography on soil historical C concentrations and, when applicable, with tree diversity effects on productivity in a Structural Equation Model (SEM). Our SEM was fitted using the R 'sem' function from the 'lavaan' package (Rosseel 2012). The quality of our model fit on the data was estimated using three complementary indices: (i) the root-mean-squared error of approximation (RMSEA), (ii) the comparative fit index (CFI), and (iii) the standardized root mean squared residuals (SRMR). A model fit was considered acceptable when RMSEA<0.10, CFI>0.9, and SRMR<0.08.

**Drivers of soil carbon concentration mediated by soil microbial biomass (H2).** We used the same procedure to select drivers of microbial biomass. All selected drivers of microbial biomass were implemented in the above-described SEM structure. The relation between microbial biomass and soil carbon concentration (i.e., causal relation direction or correlation) was tested by comparing the models AIC.

**Drivers of microbial biomass mediated by micro-environmental conditions (H3).** Micro-environmental conditions were described by (i) biotic conditions, (ii) soil chemical properties, and (iii) microclimatic conditions. Correlations between micro-environment variables were explored in Appendix S7: Fig. S1.

(i) Biotic conditions were described by using field measurements of understory plant cover, soil root biomass, litter cover, and leaf chemical traits (i.e., litter carbon and nitrogen contents). (ii) To describe soil chemical properties, we used soil carbon to nitrogen ratio ('C:N'), and carbon to phosphorus ratio ('C:P'). (iii) Microclimatic conditions were estimated using both soil humidity (RH) and air temperature. The air temperature was used at the plot level on the day of sampling (minimum, average, and maximal temperature, 'T.min', 'T.mean', 'T.max', respectively) and during the week before sampling (minimum, average, and maximal

temperature, 'T.min.week', 'T.mean.week', 'T.max.week', respectively, see Appendix S7: Fig. S2). The first axis of the PCA projection was negatively correlated with temperature variables (Appendix S7: Fig. S2). Given that the first PCA axis was negatively correlated with temperature indices and to simplify the presentation to the readers, we used the positive value of the vector for the first PCA axis as a proxy for air temperature variables in further analyses.

For each micro-environmental variable, we used linear models and normal distribution assumptions to test the effects of tree productivity, litterfall carbon deposition and C:N ratio, and root functional traits. However, only relationships with a strong biological reason described in the introduction were included in the analyses. We used linear models and normal distribution assumptions to test the effects of micro-environmental variables on soil microbial biomass. Explanatory variables were selected by a both-way step selection based on AIC. We estimated the drivers of microbial biomass from the final model. All variables selected and their relations to tree variables were implemented in our previous SEM. All the statistical assumptions of our linear models were tested using the 'check\_model' function from the R package 'performance' (Appendix S8).

## Results

### Local history and topography effects on soil carbon concentrations

On average, forest soil carbon concentrations were stable across years (mean  $\pm$  sd:  $-0.33 \pm 0.86 \text{ g}_{\text{carbon}} \text{ g}_{\text{soil}}^{-1} \text{ yr}^{-1}$ ), but we observed high variability between the sampled locations (from  $-3.00$  to  $+1.85 \text{ g}_{\text{carbon}} \text{ g}_{\text{soil}}^{-1} \text{ yr}^{-1}$ , Fig. 2.A). Soil carbon concentrations measured in 2018 were higher where historical soil carbon concentrations were high in 2010 before the experiment (estimate  $\pm$  sd:  $0.265 \pm 0.078$ , Fig. 2.D-F, Appendix S9). As historical soil carbon concentrations were affected by local topography (slope: estimate  $\pm$  sd:  $0.175 \pm 0.038$ , plan

curvature:  $0.357 \pm 0.038$ ,  $R^2 = 10\%$ , Fig. 2.B), topography indirectly affected soil carbon concentrations measured in 2018 by the modification of historical soil carbon concentrations (Fig. 2.E-F).

### **Tree species richness effects on tree productivity**

At the neighborhood level, plot tree species richness significantly increased the different aspects of tree productivity: neighborhood tree biomass ( $0.427 \pm 0.073$ ,  $R^2 = 18\%$ ), litterfall production (i.e., "C.litterfall",  $0.416 \pm 0.078$ ,  $R^2 = 17\%$ ), and forest vertical stratification (i.e., ENL,  $0.248 \pm 0.070$ ,  $R^2 = 32\%$  when accounting for topography effects, Fig. 2.C). These different aspects of forest productivity were correlated to each other (Pearson correlation: neighborhood biomass – ENL = 0.38, neighborhood biomass – "C litterfall" = 0.4, "ENL – "C litterfall" = 0.61, see Appendix S6).

### **Tree effects on soil carbon concentrations (H1)**

Plot tree species richness did not directly affect soil carbon concentrations (Fig. 2.D), but tree productivity, especially, forest vertical stratification (i.e., ENL) increased soil carbon concentrations ( $0.256 \pm 0.093$ , Fig. 2.E), and increased with increasing tree species richness (Fig. 2.C). In contrast, increasing litterfall C:N ratio decreased soil carbon concentration ( $-0.187 \pm 0.081$ , Fig. 2.D-F, Appendix S9). Belowground, increasing root diameter (RD) strongly decreased soil carbon concentration ( $-0.183 \pm 0.084$ ), Fig. 2.F, Appendix S9).

### **Tree effects on soil microbial biomass (H2)**

Our analyses showed a positive effect of tree species richness on soil microbial biomass (estimate  $\pm$  sd:  $0.202 \pm 0.079$ ,  $R^2 = 3\%$ , Fig. 3.A). By considering tree functional traits and productivity, we got a better understanding of the factors affecting soil microbial biomass ( $R^2 = 11\%$ ,  $AIC_{\text{sp. rich. based model}} = 222$  vs.  $AIC_{\text{trait based model}} = 214$ ). Soil microbial biomass was affected by root morphological traits identity and dissimilarity. Soil microbial biomass

decreased with increasing RD ( $-0.259 \pm 0.088$ ) and decreased with increasing AM:ECM ratio ( $-0.176 \pm 0.086$ ). In addition, soil microbial biomass decreased with increasing functional dissimilarity of SRL ( $-0.235 \pm 0.104$ ) and increased with increasing dissimilarity of tree fungal association ( $0.217 \pm 0.104$ , Fig. 3.B).

## **Relationship between soil microbial biomass and soil carbon concentration (H2)**

We found a strong positive correlation between soil carbon concentration and soil microbial biomass (Pearson-correlation = 62.7%,  $p$ -value < 0.001, Fig. 3.C). Taken together with the other drivers of soil carbon and microbial biomass, we tested the directionality of the relationship between soil carbon concentration and soil microbial biomass (Fig. 3.D). The AIC comparison between the models was in favor of the model with a causal effect from soil carbon concentration to soil microbial biomass and the model took into account both causal links (i.e., soil carbon concentration effect on microbial biomass and *vice versa*). The latter, being the most conservative model, is given in Fig. 3.E. This SEM showed a strong positive effect of soil carbon concentration on microbial biomass ( $0.608 \pm 0.059$ , Fig. 3.E), but a non-significant effect of soil microbial biomass on soil carbon concentration ( $p$ -value = 0.72, Appendix S10). The tree productivity and root functional trait effects on soil microbial biomass were mostly mediated by soil carbon concentration (remaining direct root effect -  $0.147 \pm 0.063$ , Fig. 3.E, Appendix S10).

## **Tree effects on micro-environmental conditions (H3)**

Tree species richness effects on micro-environmental conditions (i.e., biotic conditions, soil chemical properties, and microclimate) were limited to a negative effect on air temperature ( $-0.208 \pm 0.082$ ,  $R^2 = 3\%$ ) and a positive effect on the amount of litter collected on the ground ( $0.168 \pm 0.080$ ,  $R^2 = 2\%$ , Fig. 4.A). However, the trait-based model showed the major role of

trees in controlling environmental conditions. Aboveground, higher forest vertical stratification (i.e., ENL) reduced air temperature ( $-0.406 \pm 0.078$ ), understory plant abundance ( $-0.457 \pm 0.009$ ), root biomass ( $-0.389 \pm 0.091$ ), and amount of litter ( $-0.342 \pm 0.083$ ), but also litter C:N ratio ( $-0.342 \pm 0.086$ ). Increasing litterfall C:N ratio decreased soil humidity ( $-0.197 \pm 0.078$ ), soil nitrogen ( $-0.228 \pm 0.083$ ) and phosphorus contents ( $-0.186 \pm 0.080$ ), and plant abundance ( $-0.173 \pm 0.078$ , Fig. 4.B), while it increased C:N ratio of the residual litter on the ground ( $0.233 \pm 0.077$ ). Belowground, environmental conditions were affected by the root functional traits identity and diversity. While SRL decreased soil humidity ( $-0.285 \pm 0.078$ ), RD increased soil phosphorus contents ( $0.408 \pm 0.097$ ), and AM:ECM fungal association ratio increased root biomass and litter C:N ratio ( $0.276 \pm 0.078$  and  $0.367 \pm 0.081$ , respectively). Moreover, root functional trait dissimilarity played a major role in controlling soil chemical properties and biotic conditions, AM:ECM fungal association dissimilarity increased litter C:N ratio ( $0.192 \pm 0.081$ ), and fungal dissimilarity in root diameter reduced soil phosphorus content ( $-0.446 \pm 0.096$ , Fig. 4.B). In addition, plant cover was positively correlated to root biomass and amount of litter (Pearson correlation: plant cover ~ root biomass = 0.30, plant cover ~ amount of litter = 0.37, Appendix S7).

### **Micro-environmental mediation of tree effects on microbial biomass (H3)**

Microbial biomass was affected by the micro-environment (i.e., biotic conditions, soil chemical properties, and microclimate; Fig. 5.A). Soil microbial biomass decreased with increasing air temperature ( $-0.288 \pm 0.054$ ). In addition, soil microbial biomass increased with increasing litter C:N ratio ( $0.222 \pm 0.055$ , Fig. 5.A and Appendix S8). By adding these drivers to the previous structural equation model, we explained up to 57% of the variability in soil microbial biomass (Fig. 5.B, vs. 47% without environmental drivers). Microbial biomass was mostly affected by variations in soil carbon concentration (total effect: 0.613) and micro-

environmental conditions (total effect: 0.511), which were themselves strongly mediated by tree productivity and functional traits (total effect: on soil carbon concentration = 0.655, on micro-environmental conditions = 1.961, Fig. 5.B, Appendix S11).

## Discussion

The present study revealed strong effects of forest diversity, productivity, and functional traits on soil carbon concentrations as well as the underlying biotic and abiotic drivers in a tree diversity experiment. In addition to the effects of topography, our analyses showed a strong positive effect of tree species richness on tree productivity (i.e., tree biomass, amount of litterfall, and forest vertical stratification). Tree productivity and tree functional traits modulated micro-environmental conditions, such as biotic conditions, soil chemical properties, and microclimate. These changes in micro-environmental conditions had significant consequences for soil microbial biomass (e.g., a decrease in temperature increased soil microbial biomass), in addition, root functional traits modulated soil microbial biomass. Soil microbial biomass was strongly correlated to soil carbon concentration, and our analyses found more support for a positive effect of soil carbon concentration on soil microbial biomass than vice versa. Moreover, soil carbon concentration increased with tree productivity and root morphological traits. Taken together, these findings show how tree diversity, productivity, and functional traits shape forest abiotic and biotic conditions and soil functioning.

### Soil carbon concentration dynamics in BEF-China (H1)

Our analyses showed a slight loss of soil carbon during the first ten years of the experiment in low diversity level plots. Site A of the BEF-China experiment was planted in 2009 after a clear-cut of the previous conifer plantation (Yang et al. 2013). Clear-cut harvestings are known to enhance soil carbon loss during the following decade (Li et al. 2019; Seedre et al.

2014). This is mainly caused by a massive input of deadwood to the soil acting as a primer of soil organic matter decomposition as well as by the removal of litterfall and exudation causing a shift in microbial physiology (Taylor, Wang, and Kurz 2008). However, this average decrease of soil carbon concentrations was accompanied by a large range variability of plot-level values (ranging from -3.33 to 1.85 g yr<sup>-1</sup>), suggesting strong local drivers of soil carbon dynamics. First, we found a positive effect of soil historical carbon concentrations on current soil carbon concentrations. Second, we found that the topography had affected historical carbon concentrations with consequences for the current soil carbon concentration (Liu et al. 2020; Scholten et al. 2017). This result highlights the importance of soil history for *in situ* experiments and the need to consider historical variables in the analyses. Moreover, recent studies have shown the central role of soil history and temporal changes in BEF relationships to better understand ecosystem functions and their underlying drivers (Guerrero-Ramírez et al. 2017; Vogel et al. 2019). Therefore, future research should not only consider the mechanisms behind BEF relationships but also consider their temporal dynamics and evolution over time (Eisenhauer et al. 2019).

### **Neighborhood tree traits and productivity drive soil carbon concentrations**

#### **(H1)**

Once controlling for topography and soil history effects, small-scale tree communities influenced soil carbon concentrations, both through above- and belowground mechanisms. Aboveground, soil carbon concentration was increased by forest vertical stratification, which decreased litter C:N ratio, i.e., increasing litter quality. This emphasizes the central role of the biotic processes transforming the fresh litter into stable carbon forms (Buckeridge et al. 2020). The positive effects of forest vertical stratification can be further related to two independent mechanisms: on the one hand, the increase of tree biomass production and



thereby enhanced inputs to the soil (Liu et al. 2018); on the other hand, the reduction of erosion due to the reduction of the kinetic energy of throughfall with higher crown complementarity (i.e., higher ENL, Goebes et al. 2015; Seitz et al. 2015).

Belowground, root morphological traits, such as RD, have been related to belowground biomass allocation and productivity (Bardgett, Mommer, and de Vries 2014) and were shown to increase soil carbon concentrations (Adamczyk et al. 2019). However, our measurements of root traits were based on species-specific values and did not consider trait plasticity (Sun et al. 2017; Zuppinger-Dingley et al. 2014). Tree diversity and forest productivity have been shown to influence fine root traits, such as RD (Sun et al. 2017). Our study again stresses the need for non-invasive methods and measurements of belowground productivity and root traits (Bu et al. 2017; Sun et al. 2017). Such measures will allow us to consider trait plasticity and disentangle productivity and physiological effects.

## **Soil microbial biomass and soil carbon concentration are strongly related (H2)**

Our analyses highlighted a robust positive correlation between soil microbial biomass and soil carbon concentrations. We expected feedback mechanisms between soil microbial biomass and soil organic carbon (Clemmensen et al. 2013; Kästner and Miltner 2018; Lange et al. 2015). On the one hand, soil microbial growth is maintained and limited by soil organic carbon availability (Bollag and Stotzky 1993). On the other hand, soil organic carbon is consumed and processed by soil microbes and is altered by their activity (Clemmensen et al. 2013; Schmidt et al. 2011). Therefore, soil microbial biomass and soil organic carbon are strongly related to each other across spatial scales (Serna-Chavez, Fierer, and van Bodegom 2013; Xu, Thornton, and Post 2013). However, in the present study, we could only verify the strong positive effect of soil carbon concentration on soil microbial biomass, while the



potential feedback effect of soil microbes on soil carbon accumulation (Kästner and Miltner 2018; Miltner et al. 2012; Lange et al. 2015) was not significant. Microbial necromass accumulation might become relevant on a longer time scale, thus repeated sampling of the experiment might help to better quantify microbial necromass accumulation and positive effects on soil carbon storage. Moreover, measurements of the different soil carbon pools (see von Lützow et al. 2007; Miltner et al. 2012) and more detailed assessments of soil microbial community structure and the activities of main groups therein would be needed to understand the fluxes of carbon between these carbon pools and the role of soil microbes as main consumers and producers of soil carbon (Goto, Sakoda, and Suzuki 1994; Liski et al. 2005).

### **Micro-environmental conditions and root morphological traits drive soil microbial biomass (H2-H3)**

We highlighted the negative effect of AM associated trees on soil microbial biomass, these observation in forest top-soils (0 - 10 cm) are falling in line of previous studies showing higher concentrations of carbon and nitrogen in ECM associated forest top soils in comparison to AM associated forests (Craig et al. 2018). Therefore, microbial biomass and activity would be enhanced by higher nutrient availability (Beugnon et al. 2021; Cesarz et al. 2022; Smith et al. 2021). In addition, we showed that two micro-environmental parameters drove soil microbial biomass: temperature, and litter C:N ratio. In contrast to our expectations, soil microbial biomass decreased with increasing air temperature. Notably, we sampled during summer with an average daily temperature of  $27^{\circ}\text{C} \pm 3^{\circ}\text{C}$  and an average maximum daily temperature of  $35^{\circ}\text{C} \pm 8^{\circ}\text{C}$ . These high temperatures may exceed the thermal activity niche of some microbial taxa and thus repress microbial growth (Barcenas-Moreno et al. 2009). Further efforts are now needed to better grasp the temporal extent of the tree

diversity effect on micro-environmental conditions, thus the consequences for variables with slower dynamics such as soil carbon storage.

### **Tree diversity enhances productivity with consequences for micro-environmental conditions (H3)**

Our analyses confirmed previous results showing increased productivity with tree species richness (Fichtner et al. 2018; Huang et al. 2017; 2018; Kunz et al. 2019). Interestingly, our results highlighted that tree species richness simultaneously enhances tree biomass, litter production, and forest vertical stratification. This positive effect of tree species richness is also expected belowground (Liu et al. 2018; Liu et al. 2020; Xu et al. 2020). However, further efforts are needed to better quantify belowground productivity in space and time (Liu et al. 2020). A major challenge is the development of non-invasive quantification methods to measure belowground biomass and turnover (Clark et al. 2011; Metzner et al. 2014; Mooney et al. 2012).

Tree productivity combined with root functional traits allowed us to explore how tree effects are mediated by micro-environmental conditions: biotic conditions, soil chemical properties, and microclimate. Our results, by showing a negative effect of forest vertical stratification on temperature, confirmed previous findings emphasizing the role of forests as a heat buffer (de Frenne et al. 2019; Zhang et al. 2022). In the same line, we found negative effects of tree-specific root length on soil water availability, which can be explained by increased water uptake with a denser root system (Zhang et al. 2020). This increase in water consumption, consequently decreasing soil water availability, would increase the competition for water between trees and understory plants and would explain the negative effects of specific root length on understory productivity (i.e., plant cover and root biomass). In addition to the belowground competition, our results suggested an aboveground competition for light with

negative effects of forest vertical stratification on understory productivity (Hakkenberg et al. 2020; Mueller et al. 2016). Besides, we confirmed the role of trees in controlling soil nitrogen and phosphorus contents by modifying litter C:N ratio and root morphological traits related to desiccation and exudation (i.e., N and P-rich compounds, Bardgett, Mommer, and de Vries 2014; Sun et al. 2020).

## Conclusion

First, we highlighted that tree productivity and tree functional traits, modulated micro-environmental conditions with significant consequences for soil microbial biomass. Future studies would therefore gain to consider tree diversity mediation of micro-environmental conditions to better understand tree diversity effects on ecosystem functioning. Second, our analyses showed a strong positive correlation between soil microbial biomass and soil carbon concentration, suggesting a significant interplay between soil microbial communities and soil carbon stocks. Third, we found that soil carbon concentrations increased with historical carbon concentrations, with the latter being strongly affected by the plot topography. These results stress the need to consider topography and the historical baseline to understand soil carbon dynamics. To conclude, future mechanistic studies on the drivers of soil microbial biomass and carbon sequestration need to consider local neighborhood at which the underlying mechanisms act. Moreover, the quantification of the different soil carbon pools is critical to the understanding of microbial community–soil carbon stock relationships.

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## Authors contributions

The authors contributed to the manuscript by i. funding (NE, HB, SH, GvO, YW, TW, KX, SC), ii. field sampling (RB, WB, AD, SH, MK, MPD, MS, TS, SS, BS, ST, TW, BY), iii. lab measurements (RB, WB, AD, JD, MPD, TS, SS, BY, SC), iv. project conceptual framework (RB, NE, HB, JD, SC), v. statistical analyses (RB), vi. manuscript framing (RB, NE, SC) vii. manuscript writing (RB, NE, SC), viii. manuscript revisions (HB, AD, JD, SH, MK, GvO, MPD, MS, TS, SS, BS, ST, YW, TW, KX).

## Conflict of Interest Statement

The authors declare no conflict of interest.

## Literature Citations

- Aciego Pietri, J. C., and P. C. Brookes. 2009. "Substrate Inputs and PH as Factors Controlling Microbial Biomass, Activity and Community Structure in an Arable Soil." *Soil Biology and Biochemistry* 41 (7): 1396–1405. <https://doi.org/10.1016/j.soilbio.2009.03.017>.
- Adamczyk, Bartosz, Outi-Maaria Sietiö, Petra Straková, Judith Prommer, Birgit Wild, Marleena Hagner, Mari Pihlatie, Hannu Fritze, Andreas Richter, and Jussi Heinonsalo. 2019. "Plant Roots Increase Both Decomposition and Stable Organic Matter Formation in Boreal Forest Soil." *Nature Communications* 10 (1): 3982. <https://doi.org/10.1038/s41467-019-11993-1>.
- Averill, Colin, and Christine V. Hawkes. 2016. "Ectomycorrhizal Fungi Slow Soil Carbon Cycling." *Ecology Letters* 19 (8): 937–47. <https://doi.org/10.1111/ele.12631>.
- Averill, Colin, Benjamin L. Turner, and Adrien C. Finzi. 2014. "Mycorrhiza-Mediated Competition between Plants and Decomposers Drives Soil Carbon Storage." *Nature* 505 (7484): 543–45. <https://doi.org/10.1038/nature12901>.
- Barcenas-Moreno, Gema, Maria Gomez-Brandon, Johannes Rousk, and Erland Bååth. 2009. "Adaptation of Soil Microbial Communities to Temperature: Comparison of Fungi and Bacteria in a Laboratory Experiment." *Global Change Biology* 15 (12): 2950–57. <https://doi.org/10.1111/j.1365-2486.2009.01882.x>.
- Bardgett, Richard D., Liesje Mommer, and Franciska T. de Vries. 2014. "Going Underground: Root Traits as Drivers of Ecosystem Processes." *Trends in Ecology & Evolution* 29 (12): 692–99. <https://doi.org/10.1016/j.tree.2014.10.006>.
- Bastin, Jean-Francois, Yelena Finegold, Claude Garcia, Danilo Mollicone, Marcelo Rezende, Devin Routh, Constantin M. Zohner, and Thomas W. Crowther. 2019. "The Global Tree

Restoration Potential.” *Science (New York, N.Y.)* 365 (6448): 76–79.

<https://doi.org/10.1126/science.aax0848>.

Bergmann, Joana, Alexandra Weigelt, Fons van der Plas, Daniel C. Laughlin, Thom W.

Kuyper, Nathaly Guerrero-Ramirez, Oscar J. Valverde-Barrantes, et al. 2020. “The Fungal Collaboration Gradient Dominates the Root Economics Space in Plants.” *Sciences Advances* 6: 1–9.

Bernhard, Nadine, Lisa-Marie Moskwa, Karsten Schmidt, Ralf A. Oeser, Felipe Aburto, Maaiké Y. Bader, Karen Baumann, et al. 2018. “Pedogenic and Microbial Interrelations to Regional Climate and Local Topography: New Insights from a Climate Gradient (Arid to Humid) along the Coastal Cordillera of Chile.” *CATENA* 170: 335–55.

<https://doi.org/10.1016/j.catena.2018.06.018>.

Beugnon, Rémy, Wensheng Bu, Helge Bruehlheide, Andréa Davrinche, Jianqing Du, Sylvia Haider, Matthias Kunz, et al. 2022. “Beugnon-et-al-2022\_Soil-Carbon-and-Microbial-Biomass-Drivers: Data.” DRYAD. <https://doi.org/10.5061/dryad.pvmcvidnqc>.

Beugnon, Rémy, Jianqing Du, Simone Cesarz, Stephanie D. Jurburg, Zhe Pang, Bala Singavarapu, Tesfaye Wubet, Kai Xue, Yanfen Wang, and Nico Eisenhauer. 2021. “Tree Diversity and Soil Chemical Properties Drive the Linkages between Soil Microbial Community and Ecosystem Functioning.” *ISME Communications* 1 (1).

<https://doi.org/10.1038/s43705-021-00040-0>.

Bollag, Jean-Marc. Ed, and G. Ed Stotzky. 1993. *Soil Biochemistry*.

Bonfante, Paola, and Andrea Genre. 2010. “Mechanisms Underlying Beneficial Plant–Fungus Interactions in Mycorrhizal Symbiosis.” *Nature Communications* 1 (1): 48.

<https://doi.org/10.1038/ncomms1046>.

Both, Sabine, Teng Fang, Martin Böhnke, Helge Bruelheide, Christian Geißler, Peter Kühn, Thomas Scholten, Stefan Trogisch, and Alexandra Erfmeier. 2011. “Lack of Tree Layer Control on Herb Layer Characteristics in a Subtropical Forest, China.” *Journal of Vegetation Science* 22 (6): 1120–31. <https://doi.org/10.1111/j.1654-1103.2011.01324.x>.

Bradstreet, R. B. 1954. “Determination of Nitro Nitrogen by Kjeldahl Method.” *Analytical Chemistry* 26 (1): 235–36.

Bruelheide, Helge, Martin Böhnke, Sabine Both, Teng Fang, Thorsten Assmann, Martin Baruffol, Jürgen Bauhus, et al. 2011. “Community Assembly during Secondary Forest Succession in a Chinese Subtropical Forest.” *Ecological Monographs* 81 (1): 25–41. <https://doi.org/10.1890/09-2172.1>.

Bruelheide, Helge, Karin Nadrowski, Thorsten Assmann, Jürgen Bauhus, Sabine Both, François Buscot, Xiao–Yong Chen, et al. 2014. “Designing Forest Biodiversity Experiments: General Considerations Illustrated by a New Large Experiment in Subtropical China.” *Methods in Ecology and Evolution* 5 (1): 74–89. <https://doi.org/10.1111/2041-210X.12126>.

Bu, Wensheng, Bernhard Schmid, Xiaojuan Liu, Ying Li, Werner Härdtle, Goddert von Oheimb, Yu Liang, et al. 2017. “Interspecific and Intraspecific Variation in Specific Root Length Drives Aboveground Biodiversity Effects in Young Experimental Forest Stands.” *Journal of Plant Ecology* 10 (1): 158–69. <https://doi.org/10.1093/jpe/rtw096>.

Buckeridge, Kate M., Kelly E. Mason, Niall P. McNamara, Nick Ostle, Jeremy Puissant, Tim Goodall, Robert I. Griffiths, Andrew W. Stott, and Jeanette Whitaker. 2020. “Environmental and Microbial Controls on Microbial Necromass Recycling, an Important Precursor for Soil Carbon Stabilization.” *Communications Earth & Environment* 1 (1). <https://doi.org/10.1038/s43247-020-00031-4>.

Burgess, Stephen S. O., Mark A. Adams, Neil C. Turner, and Chin K. Ong. 1998. "The Redistribution of Soil Water by Tree Root Systems." *Oecologia* 115 (3): 306–11.

<https://doi.org/10.1007/s004420050521>.

Cesarz, Simone, Dylan Craven, Harald Auge, Helge Bruehlheide, Bastien Castagneyrol, Jessica Gutknecht, Andrew Hector, et al. 2022. "Tree Diversity Effects on Soil Microbial Biomass and Respiration Are Context Dependent across Forest Diversity Experiments."

*Global Ecology and Biogeography*. <https://doi.org/10.1111/geb.13461>.

Chapman, Samantha K., Gregory S. Newman, Stephen C. Hart, Jennifer A. Schweitzer, and George W. Koch. 2013. "Leaf Litter Mixtures Alter Microbial Community Development: Mechanisms for Non-Additive Effects in Litter Decomposition." *PloS One* 8 (4): e62671.

<https://doi.org/10.1371/journal.pone.0062671>.

Clark, Randy T., Robert B. MacCurdy, Janelle K. Jung, Jon E. Shaff, Susan R. McCouch, Daniel J. Aneshansley, and Leon V. Kochian. 2011. "Three-Dimensional Root Phenotyping with a Novel Imaging and Software Platform." *Plant Physiology* 156 (2): 455–65.

<https://doi.org/10.1104/pp.110.169102>.

Clemmensen, K. E., O. Ovaskainen, A. Dahlberg, A. Ekblad, H. Wallander, J. Stenlid, D. A. Finlay, David A. Wardle, and B. D. Lindahl. 2013. "Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest." *Science (New York, N.Y.)* 339 (6127): 1615–18. <https://doi.org/10.1126/science.1232728>.

Craig, Matthew E., Benjamin L. Turner, Chao Liang, Keith Clay, Daniel J. Johnson, and Richard P. Phillips. 2018. "Tree Mycorrhizal Type Predicts Within-Site Variability in the Storage and Distribution of Soil Organic Matter." *Global Change Biology* 24 (8): 3317–30.

<https://doi.org/10.1111/gcb.14132>.



Crowther, T. W., J. van den Hoogen, J. Wan, M. A. Mayes, A. D. Keiser, L. Mo, C. Averill, and D. S. Maynard. 2019. “The Global Soil Community and Its Influence on Biogeochemistry.” *Science* 365 (6455). <https://doi.org/10.1126/science.aav0550>.

Davrinche, Andréa, and Sylvia Haider. 2021. “Intra-Specific Leaf Trait Responses to Species Richness at Two Different Local Scales.” *Basic and Applied Ecology*. <https://doi.org/10.1016/j.baae.2021.04.011>.

Delgado-Baquerizo, Manuel, Fernando T. Maestre, Peter B. Reich, Pankaj Trivedi, Yui Osanai, Yu-Rong Liu, Kelly Hamonts, Thomas C. Jeffries, and Brajesh K. Singh. 2016. “Carbon Content and Climate Variability Drive Global Soil Bacterial Diversity Patterns.” *Ecological Monographs* 86 (3): 373–90.

Delgado-Baquerizo, Manuel, Peter B. Reich, Amit N. Khachane, Colin D. Campbell, Nadine Thomas, Thomas E. Freitag, Waleed Abu Al-Soud, Søren Sørensen, Richard D. Bardgett, and Brajesh K. Singh. 2017. “It Is Elemental: Soil Nutrient Stoichiometry Drives Bacterial Diversity.” *Environmental Microbiology* 19 (3): 1176–88. <https://doi.org/10.1111/1462-2920.13642>.

Ehbrecht, Martin, Peter Schall, Julia Juchheim, Christian Ammer, and Dominik Seidel. 2016. “Effective Number of Layers: A New Measure for Quantifying Three-Dimensional Stand Structure Based on Sampling with Terrestrial LiDAR.” *Forest Ecology and Management* 380: 212–23. <https://doi.org/10.1016/j.foreco.2016.09.003>.

Eisenhauer, N., H. Bessler, C. Engels, G. Gleixner, M. Habekost, A. Milcu, S. Partsch, et al. 2010. “Plant Diversity Effects on Soil Microorganisms Support the Singular Hypothesis.” *Ecology* 91 (2): 485–96. <https://doi.org/10.1890/08-2338.1>.

Eisenhauer, Nico, Arnaud Lanoue, Tanja Strecker, Stefan Scheu, Katja Steinauer, Madhav P. Thakur, and Liesje Mommer. 2017. “Root Biomass and Exudates Link Plant Diversity with Soil Bacterial and Fungal Biomass.” *Scientific Reports* 7: 44641.

<https://doi.org/10.1038/srep44641>.

Fichtner, Andreas, Werner Härdtle, Helge Bruehlheide, Matthias Kunz, Ying Li, and Goddert von Oheimb. 2018. “Neighbourhood Interactions Drive Overyielding in Mixed-Species Tree Communities.” *Nature Communications* 9 (1): 1144. <https://doi.org/10.1038/s41467-018-03529-w>.

Frenne, Pieter de, Florian Zellweger, Francisco Rodríguez-Sánchez, Brett R. Scheffers, Kristoffer Hylander, Miska Luoto, Mark Vellend, Kris Verheyen, and Jonathan Lenoir. 2019. “Global Buffering of Temperatures under Forest Canopies.” *Ecology and Evolution* 3: 744–49.

Frey, Serita D. 2019. “Mycorrhizal Fungi as Mediators of Soil Organic Matter Dynamics.” *Annual Review of Ecology, Evolution, and Systematics* 50 (1): 237–59.

<https://doi.org/10.1146/annurev-ecolsys-110617-062331>.

Frostegård, Å., A. Tunlid, and E. Bååth. 1991. “Microbial Biomass Measured as Total Lipid Phosphate in Soils of Different Organic Content.” *Journal of Microbiological Methods* 14 (3): 151–63. [https://doi.org/10.1016/0167-7012\(91\)90018-L](https://doi.org/10.1016/0167-7012(91)90018-L).

Garnier, Eric, Jacques Cortez, Georges Billès, Marie-Laure Navas, Catherine Roumet, Max Debussche, Gérard Laurent, et al. 2004. “Plant Functional Markers Capture Ecosystem Properties during Secondary Succession.” *Ecology* 85 (9): 2630–37.

<https://doi.org/10.1890/03-0799>.

Geißler, C., P. Kühn, M. Böhnke, H. Bruelheide, X. Shi, and T. Scholten. 2012. “Splash Erosion Potential under Tree Canopies in Subtropical SE China.” *CATENA* 91: 85–93. <https://doi.org/10.1016/j.catena.2010.10.009>.

Germany, Markus S., Helge Bruelheide, and Alexandra Erfmeier. 2017. “Limited Tree Richness Effects on Herb Layer Composition, Richness and Productivity in Experimental Forest Stands.” *Journal of Plant Ecology* 10 (1): 190–200. <https://doi.org/10.1093/jpe/rtw109>.

Goebes, Philipp, Steffen Seitz, Peter Kühn, Ying Li, Pascal A. Niklaus, Goddert von Oheimb, and Thomas Scholten. 2015. “Throughfall Kinetic Energy in Young Subtropical Forests: Investigation on Tree Species Richness Effects and Spatial Variability.” *Agricultural and Forest Meteorology* 213: 148–59. <https://doi.org/10.1016/j.agrformet.2015.06.019>.

Goto, Naohiro, Akiyoshi Sakoda, and Motoyuki Suzuki. 1994. “Modelling of Soil Carbon Dynamics as a Part of Carbon Cycle in Terrestrial Ecosystems.” *Ecological Modelling* 74 (3–4): 183–204. [https://doi.org/10.1016/0304-3800\(94\)90119-8](https://doi.org/10.1016/0304-3800(94)90119-8).

Gottschall, Felix, Sophie Davids, Till E. Newiger-Dous, Harald Auge, Simone Cesarz, and Nico Eisenhauer. 2019. “Tree Species Identity Determines Wood Decomposition via Microclimatic Effects.” *Ecology and Evolution* 9 (21): 12113–27. <https://doi.org/10.1002/ece3.5665>.

Hakkenberg, Christopher R., Robert K. Peet, Thomas R. Wentworth, Kai Zhu, and Michael P. Schafale. 2020. “Tree Canopy Cover Constrains the Fertility-Diversity Relationship in Plant Communities of the Southeastern United States.” *Ecology* 101 (10): e03119. <https://doi.org/10.1002/ecy.3119>.

Haug, Ingeborg, Roswitha Weber, Franz Oberwinkler, and Johannes Tschen. 1994. “The Mycorrhizal Status of Taiwanese Trees and the Description of Some Ectomycorrhizal Types.” *Trees* 8 (5). <https://doi.org/10.1007/BF00196628>.

Hawley, Greer L., and Joanna F. Dames. 2004. “Mycorrhizal Status of Indigenous Tree Species in a Forest Biome of the Eastern Cape, South Africa.” *South African Journal of Science* 100 (11): 633–37.

Hooper, David U., David E. Bignell, Valerie K. Brown, Lijbert Brussard, Mark J. Dangerfield, Diana H. Wall, David A. Wardle, et al. 2000. “Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks.” *BioScience* 50 (12): 1049.

Huang, Yuanyuan, Yuxin Chen, Nadia Castro-Izaguirre, Martin Baruffol, Matteo Brezzi, Anne Lang, Ying Li, et al. 2018. “Impacts of Species Richness on Productivity in a Large-Scale Subtropical Forest Experiment.” *Science (New York, N.Y.)* 362 (6410): 80–83. <https://doi.org/10.1126/science.aat6405>.

Huang, Yuanyuan, Yinlei Ma, Ke Zhao, Pascal A. Niklaus, Bernhard Schmid, and Jin-Sheng He. 2017. “Positive Effects of Tree Species Diversity on Litterfall Quantity and Quality along a Secondary Successional Chronosequence in a Subtropical Forest.” *Journal of Plant Ecology* 10 (1): 28–35. <https://doi.org/10.1093/jpe/rtw115>.

IPBES. 2019. “Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.” Zenodo. <https://doi.org/10.5281/ZENODO.3831673>.

Kästner, Matthias, and Anja Miltner. 2018. "SOM and Microbes—What Is Left From Microbial Life." In *The Future of Soil Carbon*, 125–63. Elsevier.  
<https://doi.org/10.1016/B978-0-12-811687-6.00005-5>.

Kramer, Susanne, Dörte Dibbern, Julia Moll, Maike Huenninghaus, Robert Koller, Dirk Krueger, Sven Marhan, et al. 2016. "Resource Partitioning between Bacteria, Fungi, and Protists in the Detritosphere of an Agricultural Soil." *Frontiers in Microbiology* 7: 1524.  
<https://doi.org/10.3389/fmicb.2016.01524>.

Kunz, Matthias, Andreas Fichtner, Werner Härdtle, Pasi Raumonen, Helge Bruehlheide, and Goddert von Oheimb. 2019. "Neighbour Species Richness and Local Structural Variability Modulate Aboveground Allocation Patterns and Crown Morphology of Individual Trees." *Ecology Letters* 22 (12): 2130–40. <https://doi.org/10.1111/ele.13400>.

Laliberté, E., P. Legendre, B. Shipley, and M. E. Laliberté. 2014. "Package 'FD': Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology."

Laliberté, Etienne, and Pierre Legendre. 2010. "A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits." *Ecology* 91 (1): 299–305.  
<https://doi.org/10.1890/08-2244.1>.

Lange, Markus, Nico Eisenhauer, Carlos A. Sierra, Holger Bessler, Christoph Engels, Robert I. Griffiths, Perla G. Mellado-Vázquez, et al. 2015. "Plant Diversity Increases Soil Microbial Activity and Soil Carbon Storage." *Nature Communications* 6: 6707.  
<https://doi.org/10.1038/ncomms7707>.

Lareen, Andrew, Frances Burton, and Patrick Schäfer. 2016. "Plant Root-Microbe Communication in Shaping Root Microbiomes." *Plant Molecular Biology* 90 (6): 575–87.  
<https://doi.org/10.1007/s11103-015-0417-8>.

Lecigne, Bastien, Sylvain Delagrangé, and Christian Messier. 2018. “Exploring Trees in Three Dimensions: VoxR, a Novel Voxel-Based R Package Dedicated to Analysing the Complex Arrangement of Tree Crowns.” *Annals of Botany* 121 (4): 589–601.

<https://doi.org/10.1093/aob/mcx095>.

Lewis, Simon L., Charlotte E. Wheeler, Edward T. A. Mitchard, and Alexander Koch. 2019. “Restoring Natural Forests Is the Best Way to Remove Atmospheric Carbon.” *Nature* 568 (7750): 25–28. <https://doi.org/10.1038/d41586-019-01026-8>.

Li, Yin, Helge Bruelheide, Thomas Scholten, Bernhard Schmid, Zhenkai Sun, Naili Zhang, Wensheng Bu, Xiaojuan Liu, and Keping Ma. 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 (5): 882–93. <https://doi.org/10.1093/jpe/rtz026>.

Liang, Chao, and Teri C. Balser. 2011. “Microbial Production of Recalcitrant Organic Matter in Global Soils: Implications for Productivity and Climate Policy.” *Nature Reviews Microbiology* 9 (1): 75–75. <https://doi.org/10.1038/nrmicro2386-c1>.

Liski, Jari, Taru Palosuo, Mikko Peltoniemi, and Risto Sievänen. 2005. “Carbon and Decomposition Model Yasso for Forest Soils.” *Ecological Modelling* 189 (1–2): 168–82. <https://doi.org/10.1016/j.ecolmodel.2005.03.005>.

Liu, Cong, Wenhua Xiang, Binggeng Xie, Shuai Ouyang, Yelin Zeng, Pifeng Lei, and Changhui Peng. 2020. “Decoupling the Complementarity Effect and the Selection Effect on the Overyielding of Fine Root Production Along a Tree Species Richness Gradient in Subtropical Forests.” *Ecosystems*. <https://doi.org/10.1007/s10021-020-00538-z>.

Liu, Xiaojuan, Stefan Trogisch, Jin-Sheng He, Pascal A. Niklaus, Helge Bruelheide, Zhiyao Tang, Alexandra Erfmeier, et al. 2018. “Tree Species Richness Increases Ecosystem Carbon

Storage in Subtropical Forests.” *Proceedings. Biological Sciences* 285 (1885).

<https://doi.org/10.1098/rspb.2018.1240>.

Lützow, Margit von, Ingrid Kögel-Knabner, Klemens Ekschmitt, Heinz Flessa, Georg Guggenberger, Egbert Matzner, and Bernd Marschner. 2007. “SOM Fractionation Methods: Relevance to Functional Pools and to Stabilization Mechanisms.” *Soil Biology and Biochemistry* 39 (9): 2183–2207. <https://doi.org/10.1016/j.soilbio.2007.03.007>.

Metzner, Ralf, Dagmar van Dusschoten, Jonas Bühler, Ulrich Schurr, and Siegfried Jahnke. 2014. “Belowground Plant Development Measured with Magnetic Resonance Imaging (MRI): Exploiting the Potential for Non-Invasive Trait Quantification Using Sugar Beet as a Proxy.” *Frontiers in Plant Science* 5: 469. <https://doi.org/10.3389/fpls.2014.00469>.

Miltner, Anja, Petra Bombach, Burkhard Schmidt-Brücken, and Matthias Kästner. 2012. “SOM Genesis: Microbial Biomass as a Significant Source.” *Biogeochemistry* 111 (1–3): 41–55. <https://doi.org/10.1007/s10533-011-9658-z>.

Mooney, S. J., T. P. Pridmore, J. Helliwell, and M. J. Bennett. 2012. “Developing X-Ray Computed Tomography to Non-Invasively Image 3-D Root Systems Architecture in Soil.” *Plant and Soil* 352 (1–2): 1–22. <https://doi.org/10.1007/s11104-011-1039-9>.

Mueller, Kevin E., Nico Eisenhauer, Peter B. Reich, Sarah E. Hobbie, Oliver A. Chadwick, Jon Chorover, Tomasz Dobies, et al. 2016. “Light, Earthworms, and Soil Resources as Predictors of Diversity of 10 Soil Invertebrate Groups across Monocultures of 14 Tree Species.” *Soil Biology and Biochemistry* 92: 184–98. <https://doi.org/10.1016/j.soilbio.2015.10.010>.



Parkinson, J. A., and S. E. Allen. 1975. "A Wet Oxidation Procedure Suitable for the Determination of Nitrogen and Mineral Nutrients in Biological Material." *Communications in Soil Science and Plant Analysis* 6 (1): 1–11. <https://doi.org/10.1080/00103627509366539>.

Pei, Zhiqin, David Eichenberg, Helge Bruelheide, Wenzel Kröber, Peter Kühn, Ying Li, Goddert von Oheimb, et al. 2016. "Soil and Tree Species Traits Both Shape Soil Microbial Communities during Early Growth of Chinese Subtropical Forests." *Soil Biology and Biochemistry* 96: 180–90. <https://doi.org/10.1016/j.soilbio.2016.02.004>.

Perles–Garcia, Maria D., Matthias Kunz, Andreas Fichtner, Werner Härdtle, and Goddert von Oheimb. 2021. "Tree Species Richness Promotes an Early Increase of Stand Structural Complexity in Young Subtropical Plantations." *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.13973>.

Reich, Peter B., Jacek Oleksyn, Jerzy Modrzynski, Pawel Mrozinski, Sarah E. Hobbie, David M. Eissenstat, Jon Chorover, Oliver A. Chadwick, Cynthia M. Hale, and Mark G. Tjoelker. 2005. "Linking Litter Calcium, Earthworms and Soil Properties: A Common Garden Test with 14 Tree Species." *Ecology Letters* 8 (8): 811–18. <https://doi.org/10.1111/j.1461-0248.2005.00779.x>.

remybeugnon. 2022. remybeugnon/Beugnon-et-al-2021\_Soil-carbon-and-microbial-biomass-drivers: Major revision of the analyses during review process (manuscript-update). Zenodo. <https://doi.org/10.5281/zenodo.7225739>

Rosseel, Y. 2012. "Lavaan: An R Package for Structural Equation Modeling and More. Version 0.5–12 (BETA)." *Journal of Statistical Software* 48 (2): 1–36.



Ruess, Liliane, and Paul M. Chamberlain. 2010. "The Fat That Matters: Soil Food Web Analysis Using Fatty Acids and Their Carbon Stable Isotope Signature." *Soil Biology and Biochemistry* 42 (11): 1898–1910. <https://doi.org/10.1016/j.soilbio.2010.07.020>.

Schmidt, Michael W. I., Margaret S. Torn, Samuel Abiven, Thorsten Dittmar, Georg Guggenberger, Ivan A. Janssens, Markus Kleber, et al. 2011. "Persistence of Soil Organic Matter as an Ecosystem Property." *Nature* 478 (7367): 49–56. <https://doi.org/10.1038/nature10386>.

Scholten, Thomas, Philipp Goebes, Peter Kühn, Steffen Seitz, Thorsten Assmann, Jürgen Bauhus, Helge Bruelheide, 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 (1): 111–27. <https://doi.org/10.1093/jpe/rtw065>.

Seedre, Meelis, Anthony R. Taylor, Brian W. Brassard, Han Y. H. Chen, and Kalev Jõgiste. 2014. "Recovery of Ecosystem Carbon Stocks in Young Boreal Forests: A Comparison of Harvesting and Wildfire Disturbance." *Ecosystems* 17 (5): 851–63. <https://doi.org/10.1007/s10021-014-9763-7>.

Seitz, S., P. Goebes, Z. Song, H. Bruelheide, W. Härdtle, P. Kühn, Y. Li, and T. Scholten. 2016. "Tree Species and Functional Traits but Not Species Richness Affect Interrill Erosion Processes in Young Subtropical Forests." *SOIL* 2 (1): 49–61. <https://doi.org/10.5194/soil-2-49-2016>.

Seitz, Steffen, Philipp Goebes, Pascale Zumstein, Thorsten Assmann, Peter Kühn, Pascal A. Niklaus, Andreas Schuldt, and Thomas Scholten. 2015. "The Influence of Leaf Litter Diversity and Soil Fauna on Initial Soil Erosion in Subtropical Forests." *Earth Surface Processes and Landforms* 40 (11): 1439–47. <https://doi.org/10.1002/esp.3726>.

Serna-Chavez, Hector M., Noah Fierer, and Peter M. van Bodegom. 2013. “Global Drivers and Patterns of Microbial Abundance in Soil.” *Global Ecology and Biogeography* 22 (10): 1162–72. <https://doi.org/10.1111/geb.12070>.

Simpson, André J., Myrna J. Simpson, Emma Smith, and Brian P. Kelleher. 2007. “Microbially Derived Inputs to Soil Organic Matter: Are Current Estimates Too Low?” *Environmental Science & Technology* 41 (23): 8070–76. <https://doi.org/10.1021/es071217x>.

Singavarapu, Bala, Rémy Beugnon, Helge Bruehlheide, Simone Cesarz, Jianqing Du, Nico Eisenhauer, Liang–Dong Guo, et al. 2021. “Tree Mycorrhizal Type and Tree Diversity Shape the Forest Soil Microbiota.” *Environmental Microbiology*. <https://doi.org/10.1111/1462-2920.15690>.

Smith, Linnea C., Alberto Orgiazzi, Nico Eisenhauer, Simone Cesarz, Alfred Lochner, Arwyn Jones, Felipe Bastida, et al. 2021. “Large-Scale Drivers of Relationships between Soil Microbial Properties and Organic Carbon across Europe.” *Global Ecology and Biogeography* 30 (10): 2070–83. <https://doi.org/10.1111/geb.13371>.

Sun, Lijuan, Mioko Ataka, Mengguang Han, Yunfeng Han, Dayong Gan, Tianle Xu, Yanpei Guo, and Biao Zhu. 2020. “Root Exudation as a Major Competitive Fine-Root Functional Trait of 18 Coexisting Species in a Subtropical Forest.” *The New Phytologist*. <https://doi.org/10.1111/nph.16865>.

Sun, Zhenkai, Xiaojuan Liu, Bernhard Schmid, Helge Bruehlheide, Wensheng Bu, and Keping Ma. 2017. “Positive Effects of Tree Species Richness on Fine-Root Production in a Subtropical Forest in SE-China.” *Journal of Plant Ecology* 10 (1): 146–57. <https://doi.org/10.1093/jpe/rtw094>.

- Taylor, Anthony R., Jian R. Wang, and Werner A. Kurz. 2008. "Effects of Harvesting Intensity on Carbon Stocks in Eastern Canadian Red Spruce (*Picea Rubens*) Forests: An Exploratory Analysis Using the CBM-CFS3 Simulation Model." *Forest Ecology and Management* 255 (10): 3632–41. <https://doi.org/10.1016/j.foreco.2008.02.052>.
- Thoms, Carolin, Andreas Gattinger, Mascha Jacob, Frank M. Thomas, and Gerd Gleixner. 2010. "Direct and Indirect Effects of Tree Diversity Drive Soil Microbial Diversity in Temperate Deciduous Forest." *Soil Biology and Biochemistry* 42 (9): 1558–65. <https://doi.org/10.1016/j.soilbio.2010.05.030>.
- Trogisch, Stefan, Xiaojuan Liu, Gemma Rutten, Kai Xue, Jürgen Bauhus, Ulrich Brose, Wensheng Bu, et al. 2021. "The Significance of Tree-Tree Interactions for Forest Ecosystem Functioning." *Basic and Applied Ecology*. <https://doi.org/10.1016/j.baae.2021.02.003>.
- Trumbore, Susan. 2009. "Radiocarbon and Soil Carbon Dynamics." *Annual Review of Earth and Planetary Sciences* 37 (1): 47–66. <https://doi.org/10.1146/annurev.earth.36.031207.124300>.
- Ushio, Masayuki, Rota Wagai, Teri C. Balser, and Kanehiro Kitayama. 2008. "Variations in the Soil Microbial Community Composition of a Tropical Montane Forest Ecosystem: Does Tree Species Matter?" *Soil Biology and Biochemistry* 40 (10): 2699–2702. <https://doi.org/10.1016/j.soilbio.2008.06.023>.
- Venables, W. N., and Brian D Ripley. 2002. *Modern Applied Statistics with S*. Springer.
- Vockenhuber, Elke A., Christoph Scherber, Christina Langenbruch, Meik Meißner, Dominik Seidel, and Teja Tschardt. 2011. "Tree Diversity and Environmental Context Predict Herb Species Richness and Cover in Germany's Largest Connected Deciduous Forest."

*Perspectives in Plant Ecology, Evolution and Systematics* 13 (2): 111–19.

<https://doi.org/10.1016/j.ppees.2011.02.004>.

Wang, B., and Y-L Qiu. 2006. “Phylogenetic Distribution and Evolution of Mycorrhizas in Land Plants.” *Mycorrhiza* 16 (5): 299–363. <https://doi.org/10.1007/s00572-005-0033-6>.

Wichern, Jannike, Florian Wichern, and Rainer Georg Joergensen. 2006. “Impact of Salinity on Soil Microbial Communities and the Decomposition of Maize in Acidic Soils.” *Geoderma* 137 (1–2): 100–108. <https://doi.org/10.1016/j.geoderma.2006.08.001>.

Wikle, Christopher K., Andrew Zammit-Mangion, and Noel A. C. Cressie. 2019. *Spatio-Temporal Statistics with R*. Chapman & Hall/CRC the R Series. Boca Raton, FL: CRC Press.

Williams, Laura J., Alain Paquette, Jeannine Cavender-Bares, Christian Messier, and Peter B. Reich. 2017. “Spatial Complementarity in Tree Crowns Explains Overyielding in Species Mixtures.” *Nature Ecology & Evolution* 1 (4): 63. <https://doi.org/10.1038/s41559-016-0063>.

Xu, Shan, Nico Eisenhauer, Olga Ferlian, Jinlong Zhang, Guoyi Zhou, Xiankai Lu, Chengshuai Liu, and Deqiang Zhang. 2020. “Species Richness Promotes Ecosystem Carbon Storage: Evidence from Biodiversity-Ecosystem Functioning Experiments.” *Proceedings. Biological Sciences* 287 (1939): 20202063. <https://doi.org/10.1098/rspb.2020.2063>.

Xu, Xiaofeng, Peter E. Thornton, and Wilfred M. Post. 2013. “A Global Analysis of Soil Microbial Biomass Carbon, Nitrogen and Phosphorus in Terrestrial Ecosystems.” *Global Ecology and Biogeography* 22 (6): 737–49. <https://doi.org/10.1111/geb.12029>.

Yang, Xuefei, Jürgen Bauhus, Sabine Both, Teng Fang, Werner Härdtle, Wenzel Kröber, Keping Ma, et al. 2013. “Establishment Success in a Forest Biodiversity and Ecosystem Functioning Experiment in Subtropical China (BEF-China).” *European Journal of Forest Research* 132 (4): 593–606. <https://doi.org/10.1007/s10342-013-0696-z>.

Zhang, Shengmin, Dries Landuyt, Kris Verheyen, and Pieter De Frenne. 2022. “Tree Species Mixing Can Amplify Microclimate Offsets in Young Forest Plantations.” *Journal of Applied Ecology*, March, 1365-2664.14158. <https://doi.org/10.1111/1365-2664.14158>.

Zhang, Zhijie, Yanjie Liu, Caroline Brunel, and Mark van Kleunen. 2020. “Evidence for Elton’s Diversity-Invasibility Hypothesis from Belowground.” *Ecology*, e03187. <https://doi.org/10.1002/ecy.3187>.

Zuppinger-Dingley, Debra, Bernhard Schmid, Jana S. Petermann, Varuna Yadav, Gerlinde B. De Deyn, and Dan F. B. Flynn. 2014. “Selection for Niche Differentiation in Plant Communities Increases Biodiversity Effects.” *Nature* 515 (7525): 108–11. <https://doi.org/10.1038/nature13869>.

## Figures caption

**Figure 1: Conceptual framework of the study.** Relationship between the different hypotheses tested in the study: **H1** - tree productivity and functional trait identity and dissimilarity drive soil carbon concentration; **H2** - tree productivity and functional identity and dissimilarity effects on soil carbon concentrations are expected to be mediated by soil microbial biomass; **H3** - tree community effects on soil microbial biomass are mediated by micro-environmental conditions (microclimate, soil chemical properties, and biotic environment).

**Figure 2: Tree diversity effects on tree productivity and consequences for soil carbon concentration, while controlling for soil history and topography effects. A. Soil carbon balance between 2010 and 2018. B. Topography effect on historical soil carbon concentrations.** For each driver of soil historical carbon concentration on the y-axis (i.e., slope, plan curvature: “Curvature PL”, profile curvature: “Curvature PR”, altitude), the dot represents the estimated effect of the driver on historical soil carbon concentration, the line represents the 95% confidence interval for a given estimated value. The drivers excluded during model selection have neither estimates nor confidence intervals. **C. Tree species richness effect on tree productivity.** For each response variable on the y-axis – neighborhood biomass (i.e. "neigh. biomass"), forest vertical stratification (i.e., “ENL”), and litterfall carbon deposition (i.e. "C litterfall") – the standardized estimate of plot tree species richness (i.e. “Sp. Rich.”) was shown with the significance of the relationship. *N.B.* ENL model controlled for topography effects. **Tree species richness (D.), tree productivity, and functional traits effects (E.) on soil carbon concentration (“Soil C 2018”) controlling for soil history (“Soil C 2010”) and topography effects (i.e. "Slope", profile curvature: "Curvature PR", plan curvature: "Curvature PL" and "Altitude").** For each driver on

the y-axis, the dot represents the estimated effect of the driver on soil carbon concentrations; the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver on soil carbon concentration was non-significant (i.e.  $p$ -values  $> 0.05$ ). The drivers excluded during model selection have neither estimates nor confidence intervals. Six groups of explanatory variables were built: species richness variables (i.e. plot species richness: "Sp. rich."), soil history variables (i.e. "Soil C 2010"), plot topography (i.e. "Slope", "Curvature PR", "Curvature PR", "Altitude"), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), aboveground productivity and traits (i.e. neighbor biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). **F. Structural equation model showing the relationships between topography (i.e. "Slope", "Curv. PR" and "Curv. PL"), soil history (i.e. "[C]<sub>2010</sub>"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall") and root functional traits (i.e. "RD"), and soil carbon concentration (i.e. "[C]<sub>2018</sub>").** Each node represents a group of variables (selected from panels B.-E.), and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations between all variables of the two nodes. When non-significant relations were found between any variables of two nodes, the arrows were drawn with dashed lines. The variance in soil carbon concentration explained by the model ( $R^2$ , in %) was added after the node name, see Appendix S9 for detailed output. The significance levels were standardized across the panel ( $p$ -value  $> 0.05$ : "n.s.",  $p$ -value  $< 0.05$ : \*,  $p$ -value  $< 0.01$ : \*\* and  $p$ -value  $< 0.001$ : \*\*\*).



**Figure 3: Biotic drivers of soil microbial biomass (A.-B.) and relationship with soil carbon concentrations (C.-E.). Tree species richness (A.), and tree productivity and functional trait effects (B.) on soil microbial biomass.** For each driver on the y-axis, the dot represents the estimated effect of the driver on soil microbial biomass; the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver on soil microbial biomass was non-significant (i.e. p-values > 0.05). The drivers excluded during model selection have neither estimates nor confidence intervals. Four groups of explanatory variables were built: species richness variables (i.e. plot species richness: "Sp. rich."), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), aboveground productivity and traits (i.e. neighbor biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). **C. Linear regression between soil carbon concentration and soil microbial biomass. D. Directionality of the relationship between soil carbon concentration and soil microbial biomass tested in the SEM including the drivers of soil microbial biomass (A.-B.) and soil carbon concentration (Fig. 2.F.). F. Structural equation model showing the relationships between topography (i.e. "Slope", profile curvature: "Curv. PR" and plan curvature: "Curv. PL"), soil history (i.e. "[C]<sub>2010</sub>"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall"), root functional traits (i.e. "RD"), soil carbon concentration (i.e. "[C]<sub>2018</sub>"), and soil microbial biomass.** Each node represents a group of variables (selected from A.B. and Fig. 2.F.) and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations

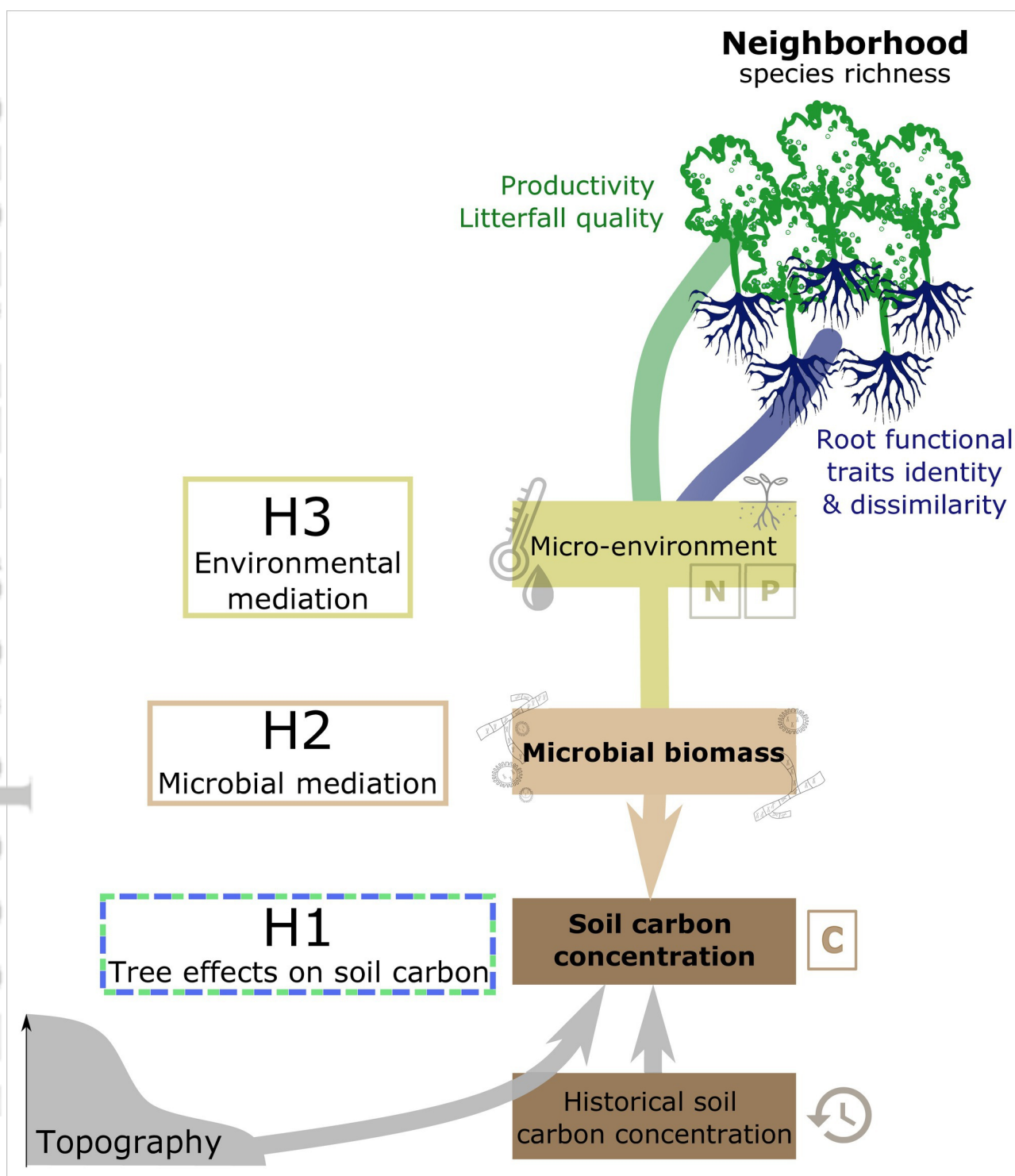


between all variables of the two nodes. When no significant relations were found between any variables of two nodes, the arrows were drawn with dashed lines. The variance in soil carbon concentration and microbial biomass explained by the model ( $R^2$ , in %) were added after the node name, see Appendix S10 for detailed output. The significance levels were standardized across the panel (p-value > 0.05: “n.s.”, p-value < 0.05: \*, p-value < 0.01: \*\* and p-value < 0.001: \*\*\*).

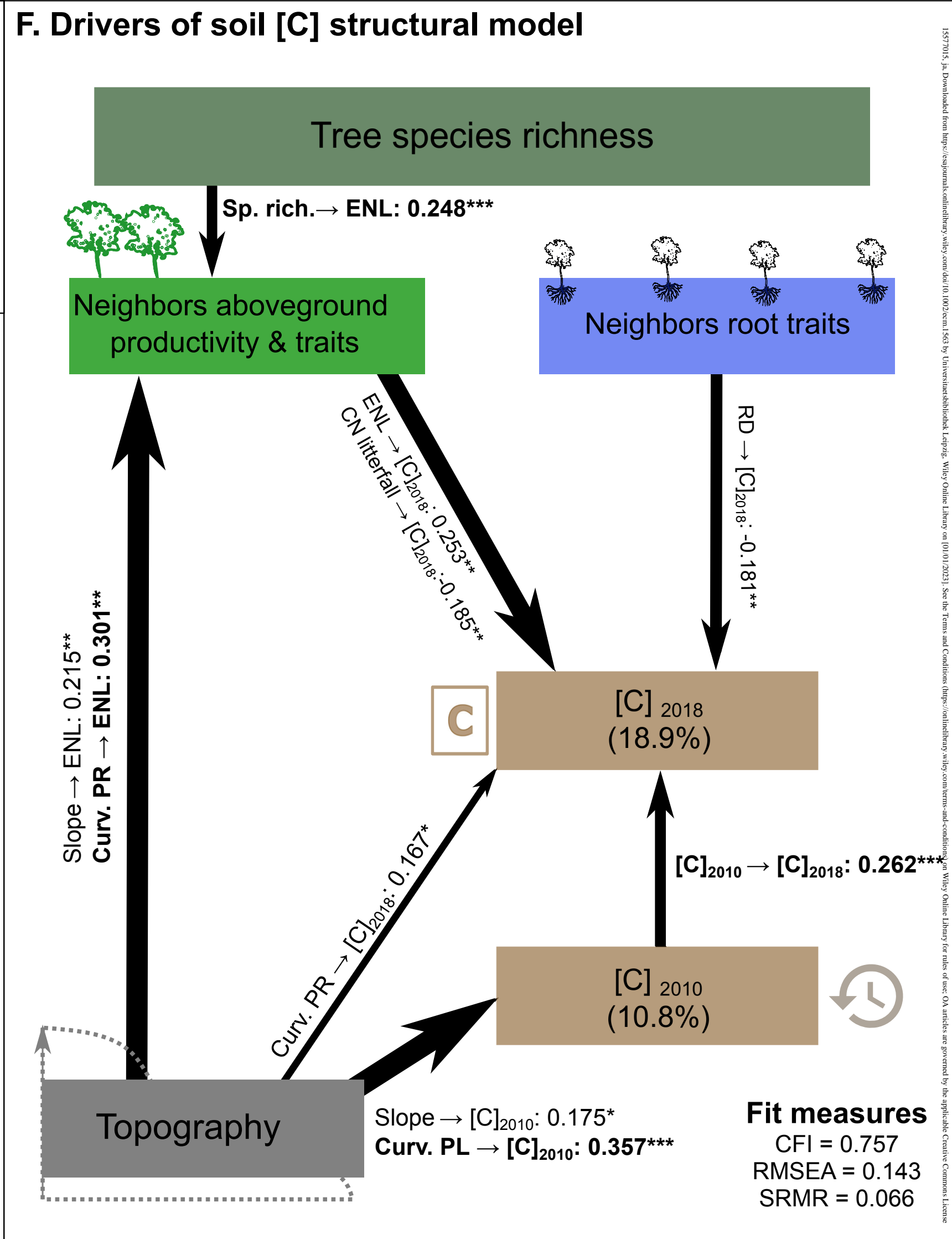
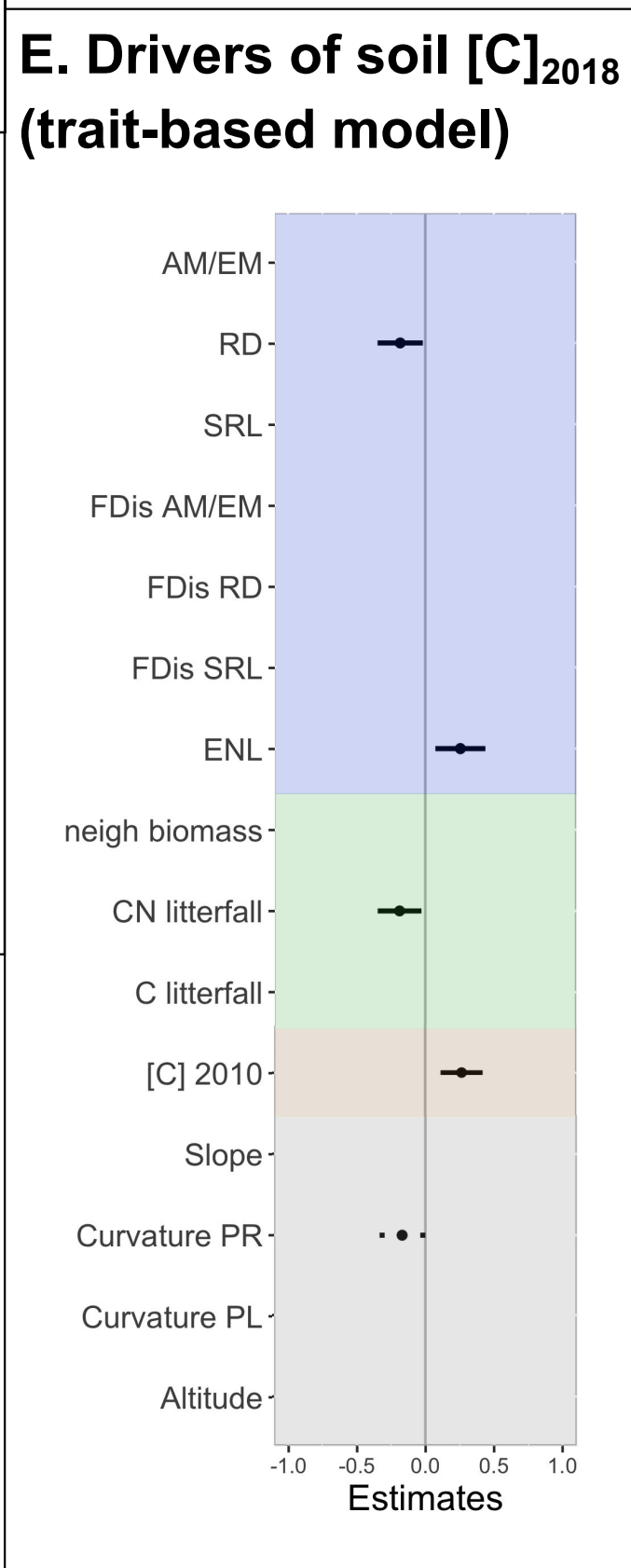
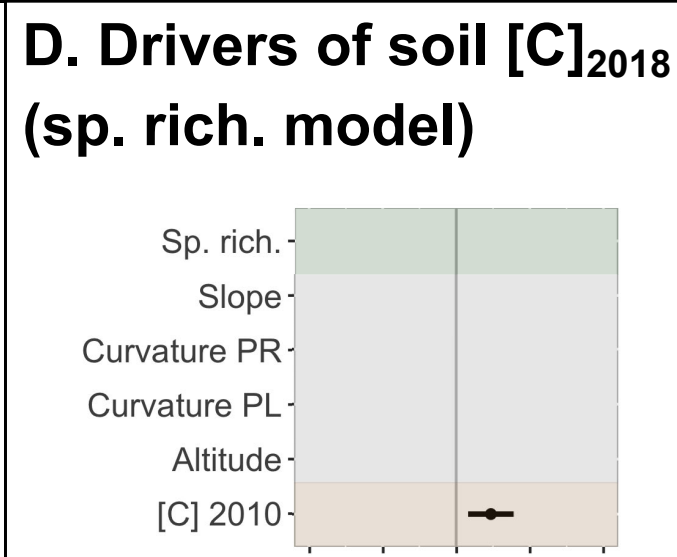
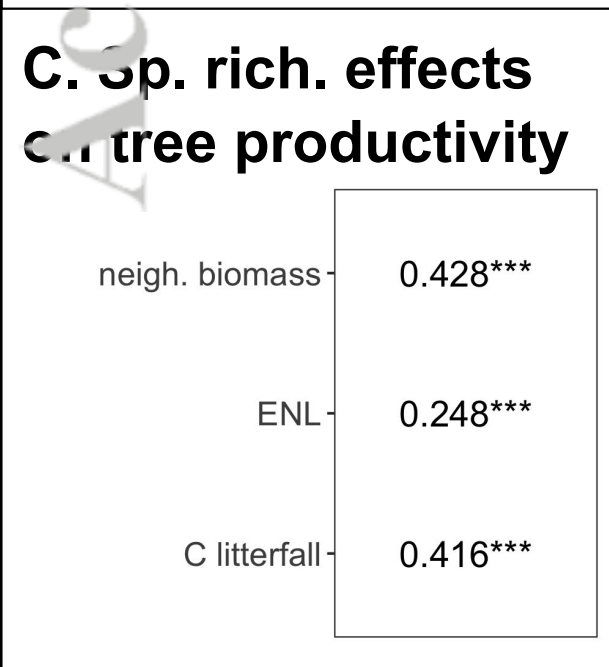
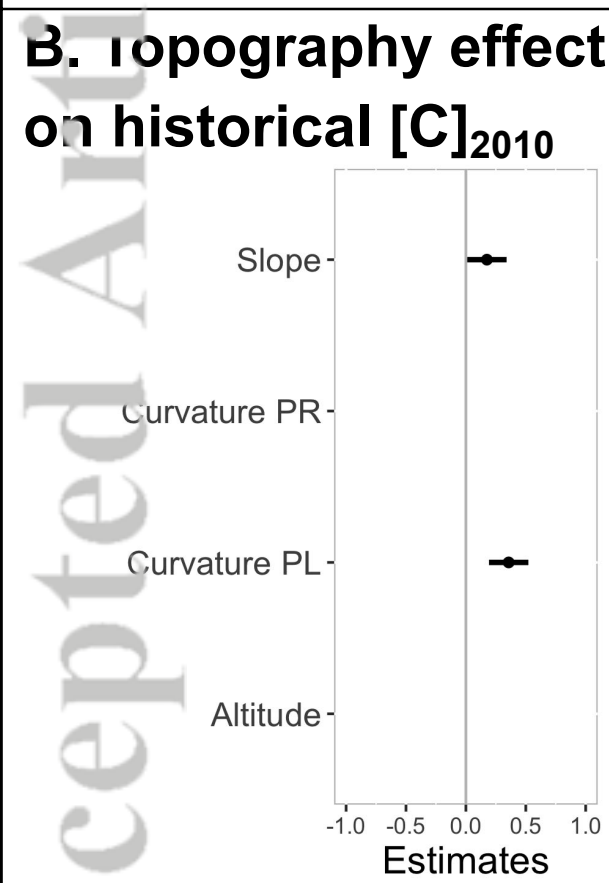
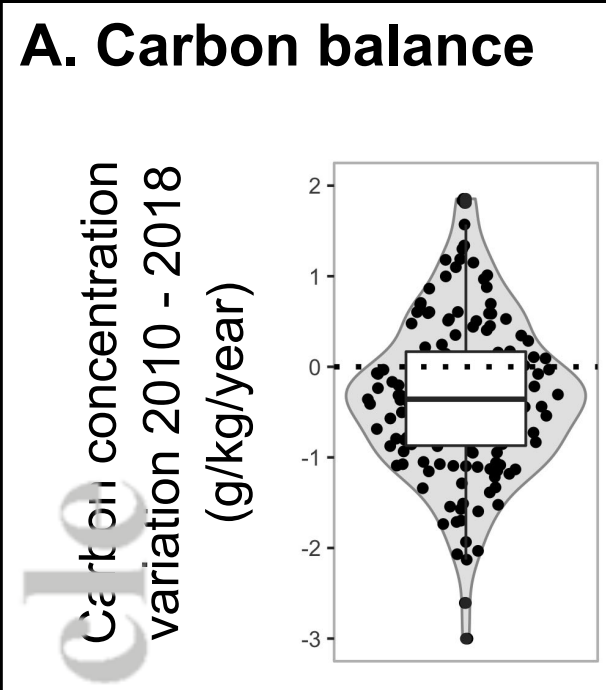
**Figure 4: Tree species richness (A.), and tree productivity and functional traits effects (B.) on micro-environmental variables.** For each driver on the y-axis, the dot represents the estimated effect of the driver on the micro-environmental variable, the line represents the 95% confidence interval for a given estimate value. Estimates and confidence intervals were drawn in dashed lines when the effect of the driver was non-significant (i.e., p-values > 0.05). The drivers excluded during model selection have neither estimates nor confidence intervals. Four groups of explanatory variables were built: species richness variables (i.e. plot species richness: "Sp. rich."), neighborhood root trait indices (i.e. neighbors' AM versus EM tree association: "AM/EM", community weighted mean of root diameter and specific root length: "RD" and "SRL", functional dissimilarity of tree fungal association, root diameter, and specific root length: "FDis AM/EM", "FDis RD", and "FDis SRL", respectively), aboveground productivity and traits (i.e. forest vertical stratification: “ENL”, neighbors biomass: "neigh biomass", litterfall C:N ratio: "CN litterfall", litterfall carbon deposition: "C litterfall"). In the case of air temperature (i.e. "Temperature"), only tree aboveground productivity and functional traits were considered in the trait-basal model.

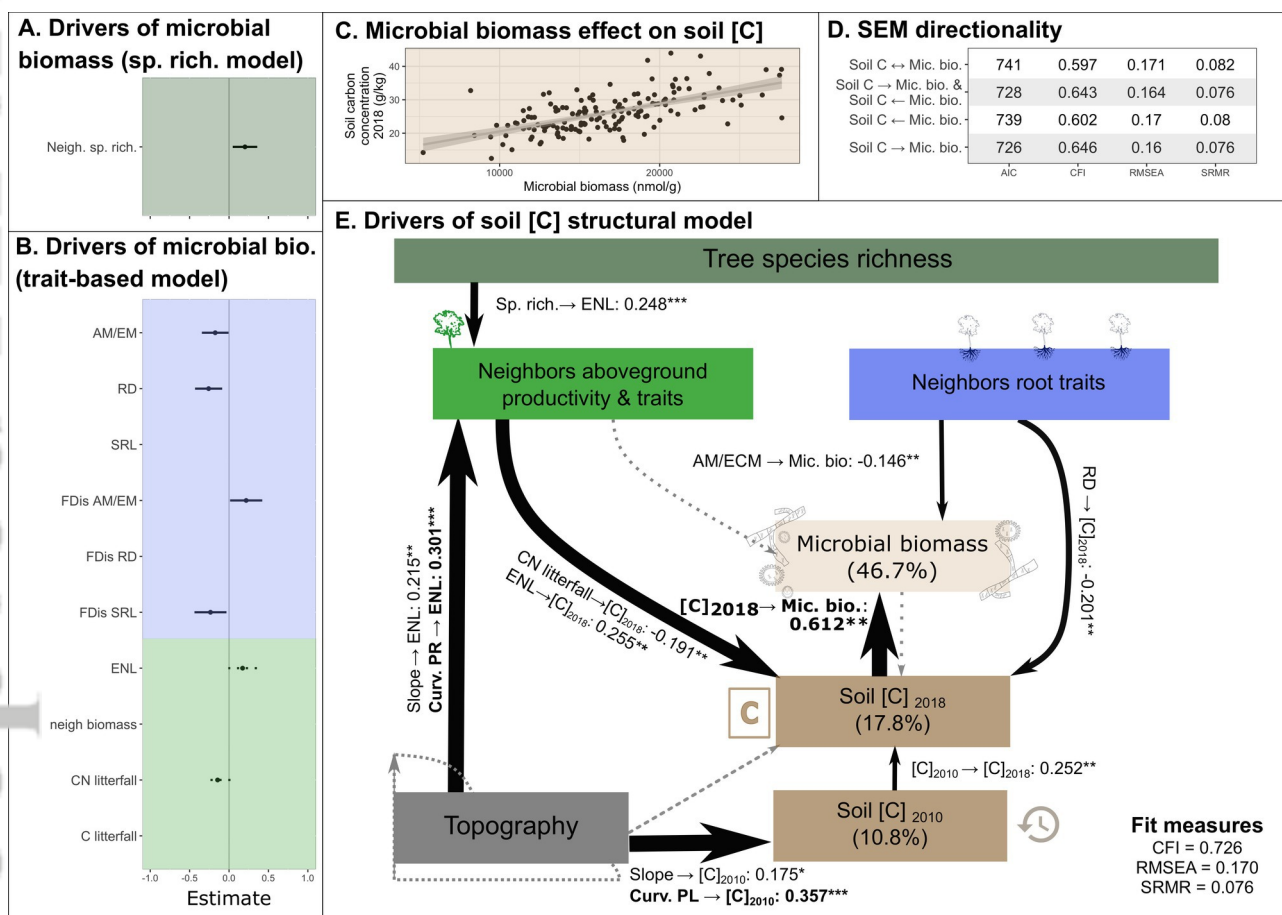
**Figure 5: Mediation of tree effects on soil microbial biomass by micro-environmental conditions. A. Effects of micro-environmental conditions on microbial biomass.** For each driver of microbial biomass on the y-axis, the dot represents the estimated effect of the driver on microbial biomass, the line represents the 95% confidence interval for a given estimated

value. The drivers excluded during model selection have neither estimates nor confidence intervals. **B. Structural equation model showing the relationships between topography (i.e. "Slope", profile curvature: "Curv. PR" and plan curvature: "Curv. PL"), soil history (i.e. "[C]<sub>2010</sub>"), tree species richness, tree aboveground productivity and functional traits (i.e. "ENL" and "CN.litterfall") and root functional traits (i.e. "RD"), soil carbon concentration (i.e. "[C]<sub>2018</sub>"), soil microbial biomass, and microclimatic conditions (i.e., "temperature", soil relative humidity: "RH", Soil nitrogen concentration: "Soil N 2018", litter collected on the ground C:N ratio: "Litter CN").** Each node represents a group of variables (selected from A., Fig. 3.E., and Fig. 4.B.) and each arrow summarizes all the significant effects between all the variables of two nodes. Arrow widths were sized by the sum of the standardized effect size of significant relations between all variables of the two nodes. When no significant relations were found between any variables of two nodes, the arrows are drawn with dashed lines. The variance in soil carbon concentration and microbial biomass explained by the model ( $R^2$ , in %) were added after the node name, see Appendix S11 for detailed output. The significance levels were standardized across the panels (p-value > 0.05: "n.s.", p-value < 0.05: \*, p-value < 0.01: \*\* and p-value < 0.001: \*\*\*).



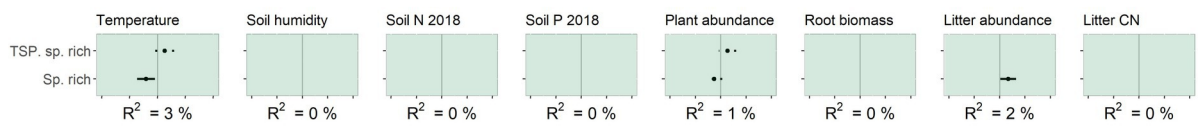
ecm\_1563\_figure1.eps



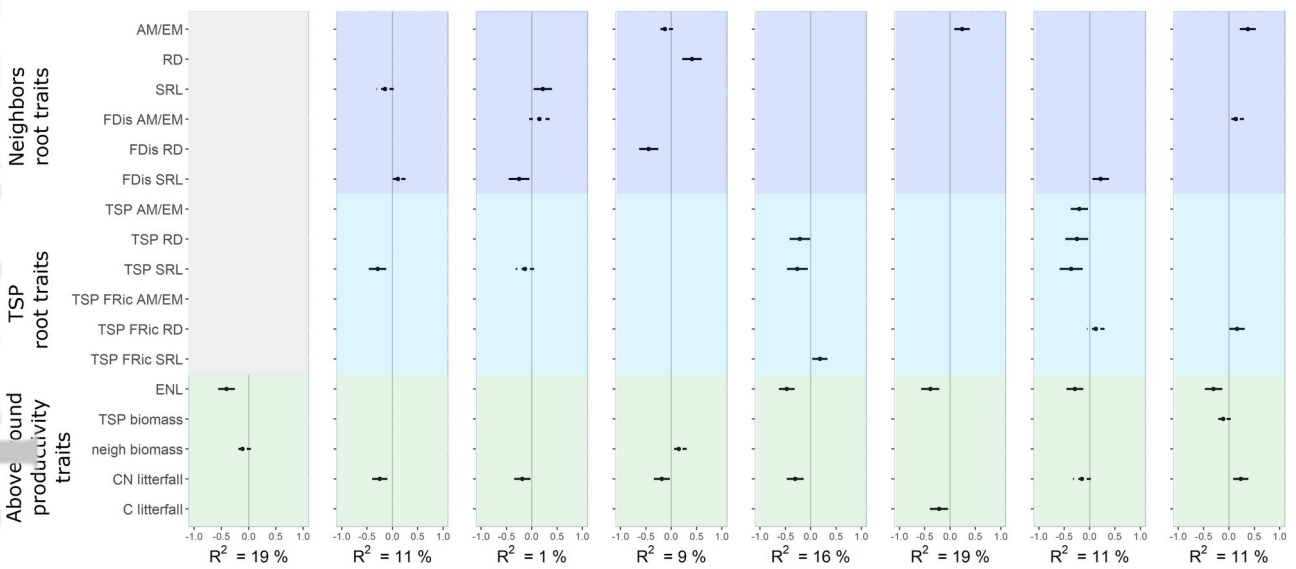


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### A. Tree species richness effects on environmental conditions



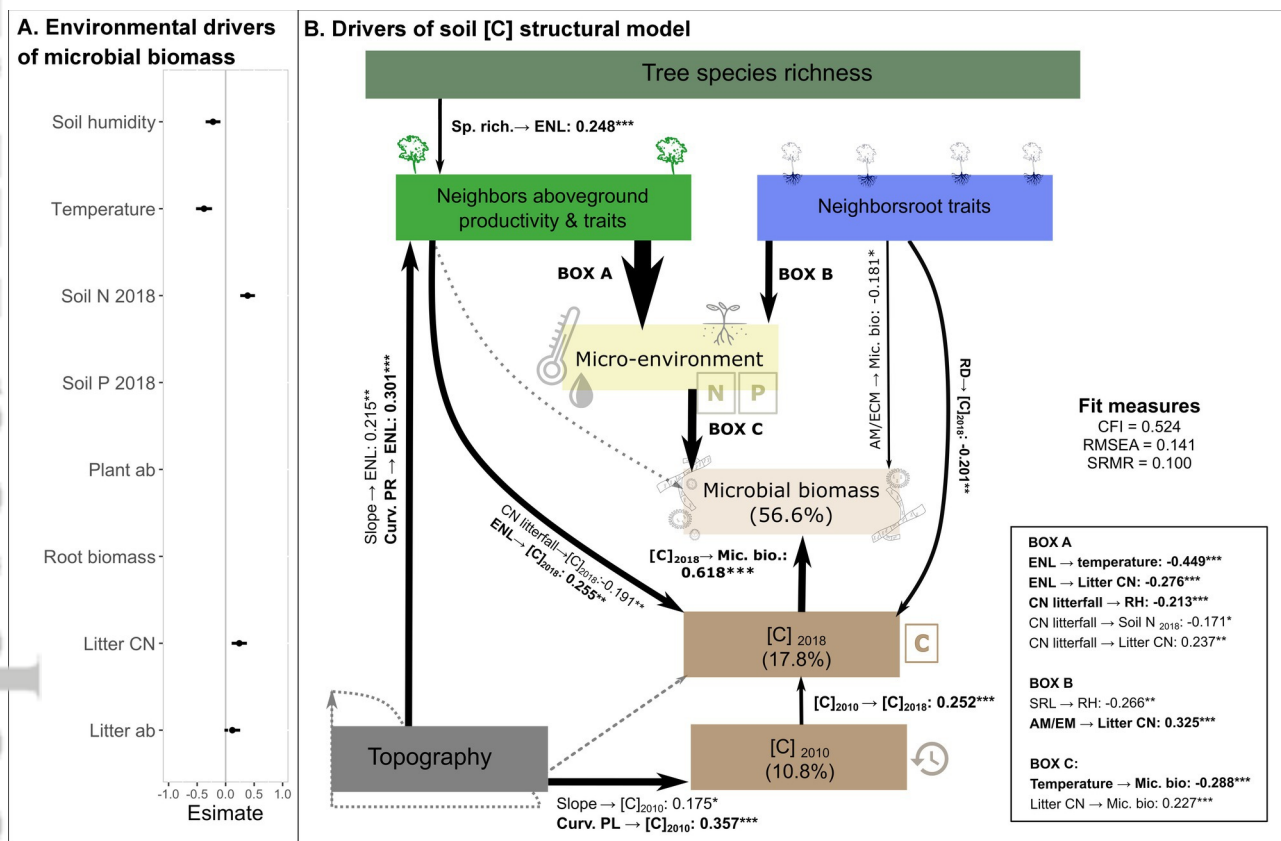
### B. Functional trait effects on environmental conditions



Estimates

ecm\_1563\_figure4.eps





ecm\_1563\_figure5.eps