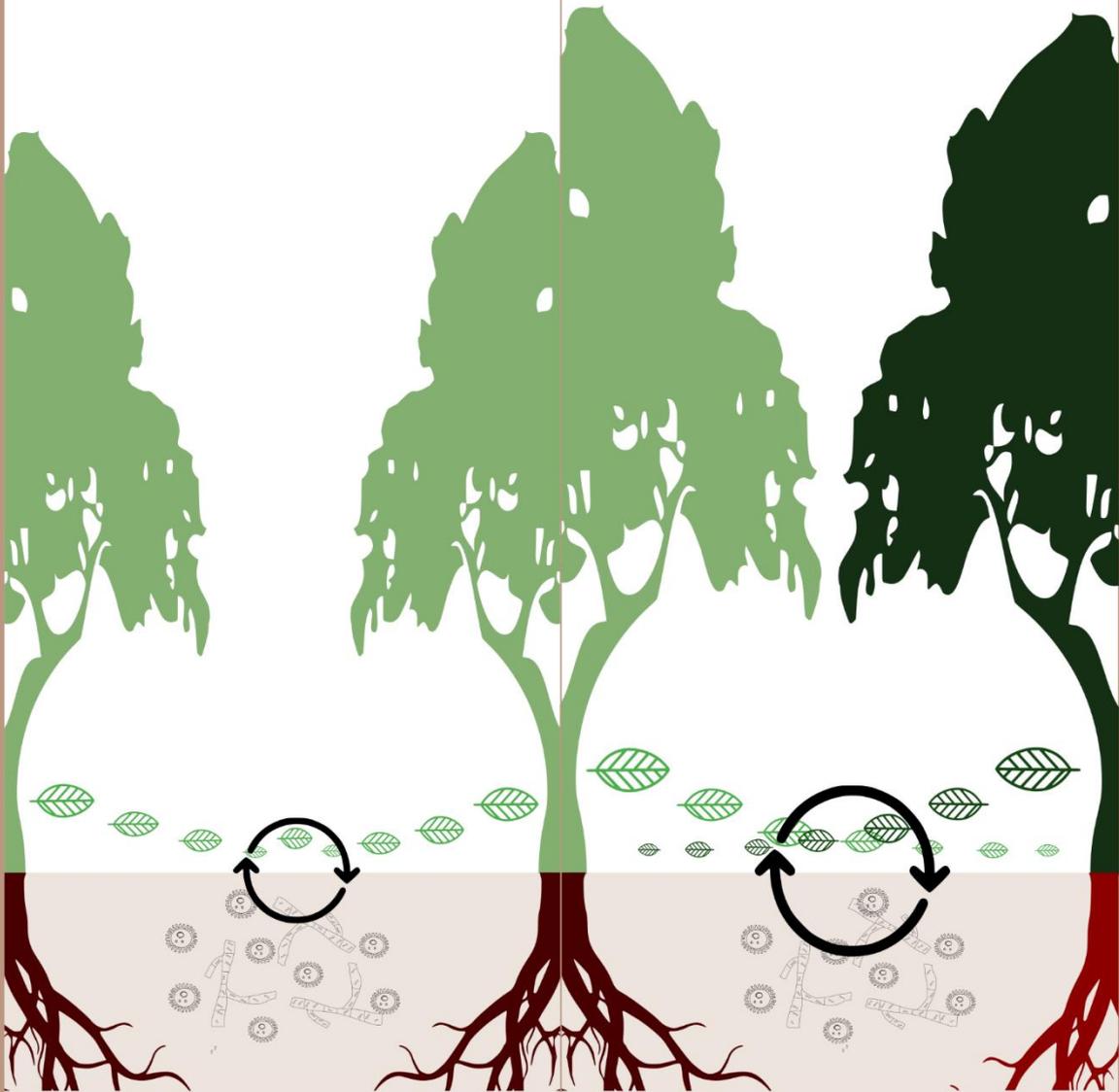




Chapter I



Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

Chapter I - Tree diversity effects on litter decomposition are mediated by litterfall and microbial processes

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Abstract

Forest ecosystems are critical for carbon fixation in both above- and belowground compartments. Increasing tree diversity enhances forest productivity and litter decomposition through soil organisms. Litter diversity increases litter decomposability (i.e., the susceptibility of litter to decomposition) by increasing the diversity of substrates offered to decomposers. However, the relative importance of the litter decomposability and the decomposer community in mediating tree diversity effects on decomposition remains unknown. Moreover, how tree diversity modulates the spatial distribution of litterfall, and consequently, litter decomposition has rarely been tested.

Here, we studied tree diversity effects on decomposition using litter bags with different mesh sizes and how such effects are mediated by the amount of litterfall, litter diversity, decomposability and soil microorganisms in a large-scale tree diversity experiment in subtropical China (BEF-China Experiment). In addition, we examined how leaf litter decomposability is affected by the litter functional identity and diversity. Finally, we tested how leaf functional traits, tree biomass, and forest spatial organization drive the spatial patterns of litterfall.

We found evidence that tree species richness increased litter decomposition by increasing litter species richness and the amount of litterfall. Moreover, we showed that the majority of litter decomposition (84-87%) is performed by soil microorganisms in this subtropical forest. Changes in the amount of litterfall and microbial decomposition explained 19-37% of total decomposition variance with similar effect sizes. In addition, up to 20% of microbial decomposition variance was explained by litter decomposability, while litter decomposability was determined by the litter nutrient content, functional diversity, and species richness. In addition, our results show that tree species richness increased the amount of litterfall (+200% from monoculture to 8-species neighborhood) and litter species richness (1:1 relationship between tree and litter species richness). We further demonstrated that species-specific amount of litterfall increased with increasing tree biomass and proximity to the trees, but not with specific leaf area. These drivers of litterfall increased the spatial heterogeneity of litter distribution in the plot, thus influencing litter decomposability, and thereby litter decomposition. Together, our findings highlight multiple mass- and diversity-mediated effects of tree diversity on ecosystem properties driving forest carbon and nitrogen cycling. Therefore, we conclude that considering spatial variability in biotic properties will improve our mechanistic understanding of biogeochemical cycles and ecosystem functioning.

Introduction

Forest ecosystems have been highlighted for their carbon fixation potential in both above- and belowground compartments (Bastin *et al.* 2019; Lewis *et al.* 2019), especially in species-rich forests (Liang *et al.* 2016; Liu *et al.* 2018; Xu *et al.* 2020). Recycling of tree dead organic matter (e.g., litter or dead wood decomposition) controls the release of carbon and other nutrients from the aboveground compartment into the soil (Seibold *et al.* 2021; Wardle *et al.* 2004), while preventing dead organic matter accumulation (Minderman 1968). Recycling processes become even more important in highly productive ecosystems, such as subtropical Chinese forests (Yu *et al.* 2014), where high amounts of dead organic matter are released (Liu *et al.* 2018), and where it is therefore critical to understand the drivers of decomposition processes.

Decomposition of leaf litter is the main recycling process in forests, including the fragmentation of litter, its incorporation into the soil, and its mineralization due to enzymatic activities (Coûteaux *et al.* 1995; Hättenschwiler 2005; Wardle *et al.* 2002). Tree species richness was shown to increase decomposition (Gartner and Cardon 2004; Gessner *et al.* 2010; Joly *et al.* 2017; Trogisch *et al.* 2016), thus enhancing the incorporation of organic matter into the soil compartment (Gartner and Cardon 2004; Lange *et al.* 2015). Litter decomposition is carried out by meso- and macro-decomposers (García-Palacios *et al.* 2013) interacting with microbial communities (Bradford *et al.* 2002; Joly *et al.* 2018). Tree species richness, and as a consequence litter species richness, is expected to increase decomposer biomass and diversity by providing a higher diversity of substrates and increasing niche partitioning of the decomposer community (Ebeling *et al.* 2014; Finke and Snyder 2008; Hooper *et al.* 2000; Scherber *et al.* 2010). In addition, litter species richness should increase litter decomposition by increasing litter decomposability (Lin and Zeng 2018; Zhou *et al.* 2020); i.e., the ability of litter to decompose when measured in a controlled environment (Freschet *et al.* 2012).

However, the relative contribution of litter decomposability and soil decomposer community in mediating tree diversity effects on litter decomposition remains untested.

Litter decomposability quantifies how decomposition responds to changing substrate; i.e., the effect of litter on decomposition when controlling for the effects on decomposer community or environmental conditions. Litter decomposability is strongly driven by leaf functional trait identity and diversity (Freschet *et al.* 2012; Rosenfield *et al.* 2020; Zhou *et al.* 2020). For example, high-quality litter, related leaf functional traits like nutrient stoichiometry (i.e., high quality litter with lower C:N and C:P ratios), enhances litter decomposition by increasing the availability of limiting nutrients (Fanin *et al.* 2012; Patoine *et al.* 2020; Zhang *et al.* 2018). Moreover, higher litter species richness promotes litter decomposability by increasing litter chemical dissimilarity and favoring nutrient transfer from nutrient-rich leaves to nutrient-poor leaves (Schimel and Hättenschwiler 2007). However, the relative contributions of litter composition and diversity on decomposability remain rarely tested, especially in a large pool of species and species mixtures (Lin *et al.* 2021).

Changes in tree diversity affect the amount of litterfall and litter species richness at the plot level (Huang *et al.* 2017). For example, tree species richness was shown to increase forest productivity (Huang *et al.* 2018), including litterfall biomass (Huang *et al.* 2017). In species-rich forests, the spatial arrangement of tree species in the plot (i.e., tree planting pattern) is also expected to influence the spatial distribution of litter and, thus, litter composition and decomposition. Moreover, we could expect litter distribution across space to be affected by species identity and leaf morphological traits. For example, as leaf size increases, leaves should be transported further away from the source tree (Chandler *et al.* 2008). However, little is known about the effects of leaf morphological traits and tree productivity on spatial patterns of litterfall distribution and the consequences for decomposition processes.

In this study, we aim to mechanistically understand tree species richness effects on leaf litter decomposition by considering the amount of litterfall and litter composition, the factors (e.g., tree biomass, leaf traits and tree spatial organization) that affect litter composition, its decomposability, as well as the mediation by microbial processes. We hypothesized that (Fig. I.1) tree species richness would increase litter decomposition (H1), and that litter decomposition would be carried out mainly by the soil microbial community (H2). Further, increasing litter decomposability should increase microbial decomposition (H3), and we expect litter diversity and nutrient availability (e.g., litter N, P content) to increase litter decomposability (H4). Finally, we hypothesized the spatial distribution of litterfall to be driven by tree biomass, leaf morphological traits, and the spatial distribution of the trees in the plot (H5).

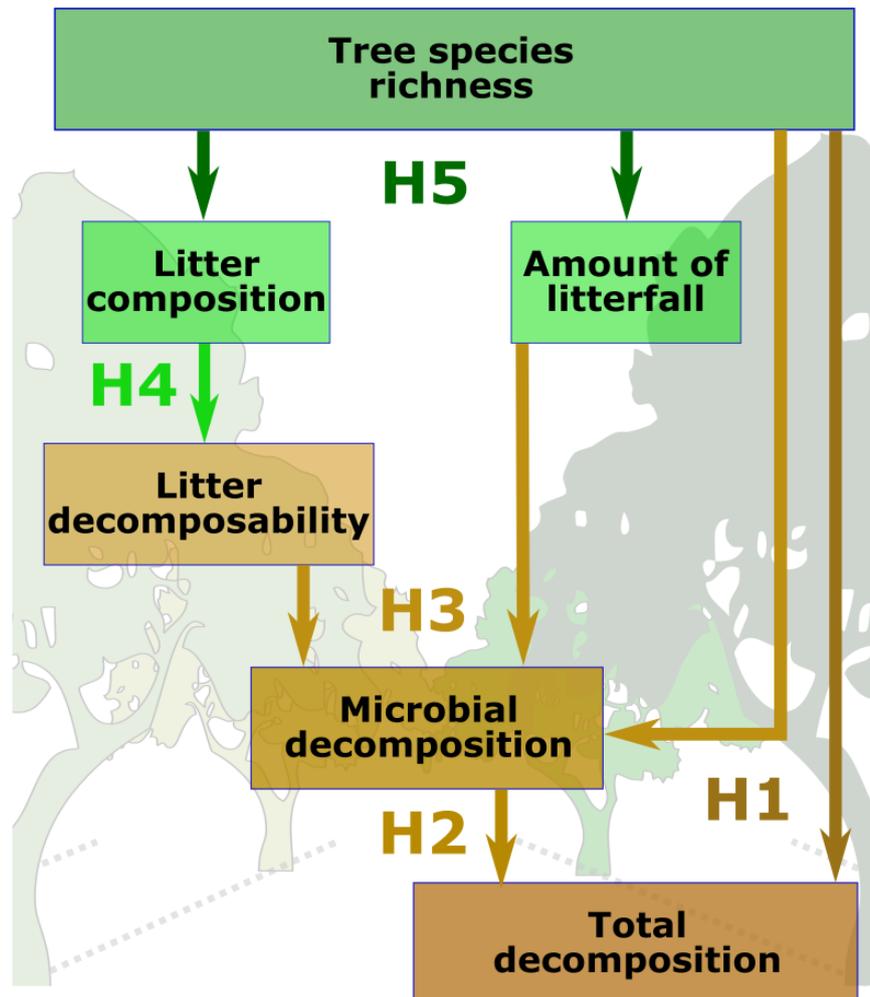


Fig. I.1: Conceptual framework of the study. Relationships between the different hypotheses tested in this study: **H1** - tree species richness increases litter decomposition; **H2** - litter decomposition is carried out mainly by the soil microbial community; **H3** - microbial decomposition increases with litter decomposability (i.e., litter decomposition measured in a controlled environment); **H4** - litter diversity and nutrient availability (e.g., litter C, N, P content) increases litter decomposability; **H5** - the litter composition is driven by tree biomass, leaf morphological traits, and the spatial distribution of the trees in the plot.

Materials and methods

Study site

The study site is located in south-east China near 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; Bruelheide *et al.* 2014), which was planted in 2009 after a clear-cut of the previous commercial plantations. The region is characterized by a subtropical climate with warm, rainy summers and cool, dry winters with a mean annual 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* (Bruelheide *et al.* 2011; Bruelheide *et al.* 2014).

Study design

To identify the effect of tree spatial organization on litterfall distribution and decomposition, we measured litterfall and decomposition between tree species pairs (i.e., TSP) across various neighborhoods. Each TSP consisted of two trees next to each other (1.28 m), and we defined its neighborhood as the ten trees directly adjacent in the planting grid (Trogisch *et al.* 2021). Each TSP was replicated three times in five tree species richness levels (1, 2, 4, 8, and ≥ 16 species), when available according to the experimental design (see "broken stick design"; Bruelheide *et al.* 2014). In total, we surveyed 24 combinations of tree species resulting in a total of 180 TSPs in 52 plots (Suppl. I-S1).

Litterfall sampling

In September 2018, a litter trap of 1 m² was set up at a height of 1 m above the soil surface between each TSP (Suppl. I-S1). Litter was collected in December 2018 to cover the main litterfall season in the region (Huang *et al.* 2017). To measure litterfall composition, each leaf

of the litter trap was sorted and identified to species level. Each species' litter was dried at 40°C for two days and weighed (± 0.1 g). Litter species richness was assessed as the number of species identified in the trap, and the total amount of litterfall was calculated as the sum of the dried biomass of all species.

Litter decomposition experiments

We performed two complementary decomposition experiments: one in the TSPs to measure microbial and total decomposition, and one in a Common Garden experimental field site to assess decomposability (i.e., the susceptibility of litter to decompose measured in controlled conditions Suppl. I-S1).

For both experiments, litterbags (10 cm x 10 cm), with different mesh sizes (see details below) were filled with 2 g (± 0.01 g) of dried litter according to litter trap species composition (i.e., species-specific biomasses) of the different TSPs. Therefore, the litter composition of the litterbags exactly matched the litter composition (i.e., species-specific biomasses) collected in the corresponding TSP. The litterbags for both experiments were installed in December 2018 and collected in September 2019, i.e., after nine months of decomposition. The litterbags were water-cleaned and dried at 40 °C for two days. The residual litter was weighed (± 0.01 g) and milled.

Decomposition experiment in between the TSPs

To assess total litter decomposition (total C and N loss, including fauna-mediated decomposition) and microbial decomposition (microbial C and N loss, excluding fauna-mediated decomposition), two large-mesh (5 mm mesh, total litter decomposition) and two small-mesh (0.054 mm mesh, microbial decomposition) litterbags were set up between the TSPs, respectively, with plot-specific litter. Small-mesh litter bags excluded meso- and macro-detrivores by using a fine mesh size (0.054 mm-mesh) to assess microbial decomposition,

while large-mesh litter bags were built using a 5 mm-mesh in the upper half of the bag to provide access to macro-decomposers, and a 0.054 mm-mesh only at the bottom to prevent loss of fine leaf litter particles to access to total litter decomposition. All litterbags were covered by a 1 m x 1 m grid to prevent heavy rainfalls from dislocating the litterbags (1 cm mesh size, see Suppl. I-S1).

Decomposition experiment in the Common Garden

The Common Garden setting consisted of a monoculture stand of *Schima superba*, a species that was not included in the TSP experiment; thereby, we were able to exclude any home-field advantages (Fanin *et al.* 2021). *Schima superba* was not part of the litter mixtures of the decomposition experiment and was chosen to maximize the phylogenetic distance with our target species and minimize environmental heterogeneity within the plot (i.e., productive species with closed canopy). *Schima superba*'s litter was removed from the ground before deploying the litterbags at a distance of 10 cm from each other in two blocks (one TSP replicate per block, Suppl. I-S1). To measure litter decomposability, two small-mesh litterbags (0.054 mm mesh) representing the litter composition of each TSP were incubated in the Common Garden experiment.

Leaf and litter trait measurements

Leaf functional traits were assessed at the species- and plot-level in September 2018, following Davrinche and Haider (2021). For each TSP species in each plot, several leaf samples were collected, and the reflectance spectra were measured using ASD FieldSpec® 4 High-Resolution Spectroradiometer (Malvern Panalytical Ltd., Malvern, United Kingdom). Leaf functional traits were predicted from the reflectance spectra of a calibration dataset of the same species, where both reflectance spectra and leaf functional traits were measured. For leaf morphological traits – specific leaf area (SLA, leaf area divided by dry weight) and leaf dry matter content (LDMC, ratio of leaf dry mass to fresh mass – fresh and dry weights were

measured before and after drying for 72 h at 80°C. To obtain SLA, leaf areas were measured from scans with a resolution of 300 dpi of the fresh leaves using the WinFOLIA software (Regent Instruments, Quebec, Canada). Leaf chemical contents; carbon (C), nitrogen (N), phosphorus (P) contents; were measured from dried leaves ground into a fine powder (Mixer Mill 400, Retsch, Haan, Germany). About 5 mg of leaf powder was used to determine C and N content with an elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany); a 200 mg subsample was used to measure P content via nitric acid digestion and spectrophotometry using the acid molybdate technique. The filtrate resulting from nitric acid digestion was analyzed with atomic absorption spectrometry (ContrAA 300 AAS, Analytik Jena, Jena, Germany) for magnesium (Mg), calcium (Ca) and potassium (K) content. The relation between the leaf spectra of the calibration samples and the leaf traits was analyzed in the software Unscrambler X (version 10.1, CAMO Analytics, Oslo, Norway) to predict species- and plot-specific leaf functional traits. For each litterbag, we calculated the total amount of nutrients (i.e., C, N, P, Mg, Ca, K) as the sum of all species contribution, and leaf morphological traits (i.e., SLA and LDMC) community weighted means (Garnier *et al.* 2004). In addition, we calculated the variance of each functional trait (i.e., C, N, P, Mg, Ca, K, SLA, LDMC) within the litterbags.

Litter C and N content after decomposition were measured from the residual litter with an elemental analyzer (Vario EL Cube, Elementar, Langenselbold, Germany). To estimate soil contamination, the ash content of the sample was measured using the loss on ignition method as:

$$\text{soil content } [g_{\text{soil}}/g_{\text{sample}}] = \frac{\text{ash}_{\text{sample}} \left[\frac{g_{\text{ash}}}{g_{\text{sample}}} \right]}{\text{ash}_{\text{soil}} \left[\frac{g_{\text{ash}}}{g_{\text{soil}}} \right]} = \frac{\text{ash} \left[\frac{g_{\text{ash}}}{g_{\text{sample}}} \right]}{1 - \text{SOM} \left[\frac{g_{\text{SOM}}}{g_{\text{soil}}} \right]}, \text{ where } \text{ash}_{\text{soil}} = (1 - \text{SOM})$$

The carbon and nitrogen content in the litter sample were corrected for soil contamination after:

$$[C]_{litter} = [C]_{sample} - [C]_{soil} \times soil\ content$$

$$[N]_{litter} = [N]_{sample} - [N]_{soil} \times soil\ content$$

See Suppl. I-S2 for details

Decomposition measures

C and N loss (%) in the litterbags between December 2018 and September 2019 were used as a measure of the total decomposition (i.e., measured via the large mesh-size in the TSP experiment), microbial decomposition (i.e., using small mesh-size in the TSP experiment), and litter decomposability (i.e., using small mesh-size in the Common Garden experiment).

Statistical methods

A description of all the variables used in this study can be found in Suppl I-S1. All data handling and statistical calculations were performed using the R statistical software version 4.1.0 (R Core Team 2021). All R scripts used for this project can be found in our GitHub repository (https://github.com/remybeugnon/Beugnon-et-al-2021_Tree-diversity-effects-on-litter-decomposition). All following linear multiple-predictors models were tested in R using the 'lm' function (R Core Team, 2021), and statistical hypotheses (i.e., residuals normality, homoscedasticity, homogeneity of variance) of the following linear models were tested in Suppl. I-S3 using the 'model_check' function from the 'performance' package (Lüdtke *et al.* 2020).

Tree diversity effect on carbon and nitrogen loss (H1)

We used linear models and normal distribution assumptions to test the effects of neighborhood tree species richness on total decomposition ("C loss" and "N loss" measured between the TSPs) and microbial decomposition ("C loss" and "N loss" measured between the TSPs when soil meso- and macro-fauna were excluded). In addition, we used linear models and normal

distribution assumptions to test the effects of litter species richness on litter decomposability ("C loss" and "N loss" measured in the Common Garden Experiment).

Tree diversity effect on the amount of litterfall and litter species richness

We used linear models and normal distribution assumptions to test the effect of neighborhood tree species richness on the amount of litterfall, and litter species richness.

Mediation of tree species richness effects on litter decomposition

To test the effects of litter species richness on litter decomposability ("C loss" and "N loss" in the Common Garden experiment), we used linear models and normal distribution assumptions. To test the effects of litter species richness, amount of litterfall, and decomposability ("C loss" and "N loss" in the Common Garden experiment) on litter microbial decomposition ("C loss" and "N loss" between the TSPs when soil meso- and macro-fauna were excluded), we used linear multiple predictor models and normal distribution assumptions where all predictors values were rescales using the R function 'scale' (R Core Team 2021). To test the effects of litter species richness, amount of litterfall, and litter microbial decomposition ("C loss" and "N loss" between the TSP when soil meso- and macro-fauna were excluded) on litter decomposition ("C loss" and "N loss" between the TSP when soil meso- and macro-fauna were included), we used linear multiple predictor models and normal distribution assumptions where all predictors values were rescales using the R function 'scale' (R Core Team 2021 - H2). All previously cited model output can be found in Suppl. I-S3.

To test the mediation of tree species richness effects on litter decomposition by litterfall abundance and species richness effects on decomposability, we implemented the previous relationships in a Structural Equation Model (SEM) framework (see Suppl. I-S3 for model structure). 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 $SRMR < 0.08$.

Litterfall composition effect on litter decomposability (H4)

To test the effects on litter functional identity and diversity on litter decomposability: first, we summarized changes in litter functional identity (i.e., total amount of C, N, P, Mg, Na, K, and the CWM of the litter SLA and LDMC in the litterbag) using a principal component analysis (PCA); second, we summarized changes in litter functional diversity (i.e., variance of C, N, P, Mg, Na, K, SLA and LDMC in the litterbag) using a PCA, and third, we tested the effects of litter species richness and litter functional identity and diversity on litter decomposability.

The first two axes of the litter functional identity PCA covered 76% of the litter functional identity variance between the litterbags (Suppl. I-S3). The first axis (i.e., "Litter nutrient content" axis) was correlated with the chemical content (total amount of C, N, P, Mg, Na, K) of material in the litterbag, while the second axis (i.e., "Litter morphology" axis) was correlated with the litter morphological traits (i.e., CWM of SLA and LDMC within the litterbag). We extracted the first two axes of the PCA ("Litter nutrient content" and "Litter morphology") for the following analyses. The first two axes of the litter functional diversity PCA explained 91% of the variance in litter functional diversity between the litterbags (Suppl. I-S3). We extracted the first two axes of the PCA ("Litter fun. diversity 1" and "Litter fun. diversity 2") for the following analysis. To test the effects of litter species richness, litter nutrient content, morphology and functional diversity on litter decomposability (i.e., "C loss" and "N loss" in the Common Garden experiment), we used linear multiple predictor models and normal distribution assumptions where all explanatory variables were rescaled using the R function 'scale' (R Core Team 2021). Explanatory variables were selected using forward and backward step selection based on AIC, R 'step' function from 'stats' package (R Core Team 2021).

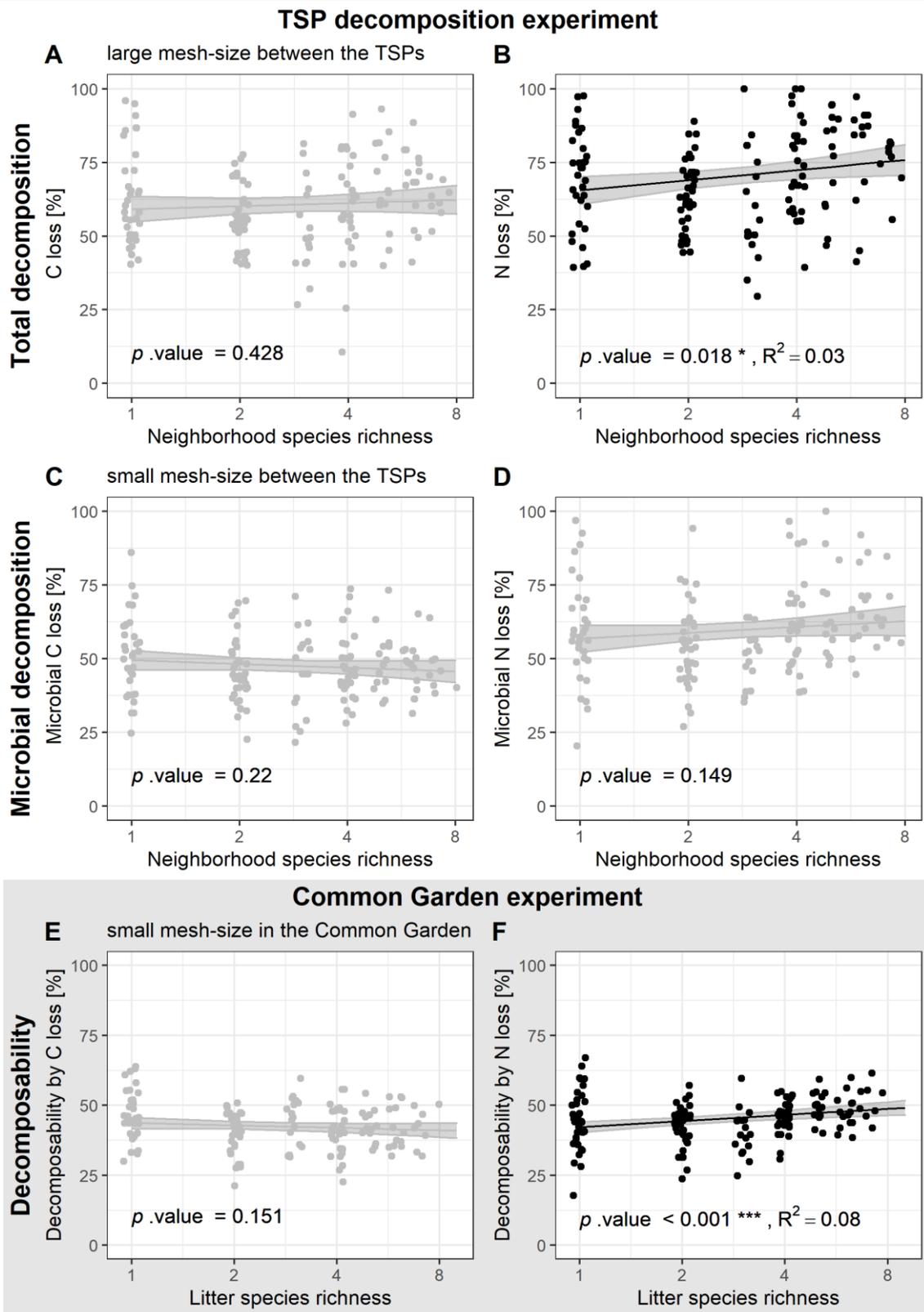


Fig. I.2: Neighborhood tree species richness effect on total litter decomposition using large mesh-size litterbags (5 mm mesh, A & B), microbial decomposition using small mesh-size litterbags (0.054 mm mesh, C & D), and litter species richness effect on litter decomposability measured under controlled conditions in the Common Garden experiment using small-mesh size litterbags (0.054 mm mesh, E & F). The values represent carbon and nitrogen loss (in %) after nine months of decomposition in a subtropical Chinese forest. For better readability, the values were jittered and non-significant relationships (i.e., p -value > 0.05) were grayed. Significance levels: “.”: p -value < 0.1, “*”: p -value < 0.05, “***”: p -value < 0.01, and “****”: p -value < 0.001).

Tree biomass, functional traits and planting pattern effects on litterfall composition (H5)

To test the effects of tree biomass ("log(biomass)"), leaf morphology ("SLA", LDMC was removed from the model due to the high correlation with SLA, Suppl. I-S3), the tree proximity to the traps ("1/dist") on amount of species-specific litterfall in our traps, we fitted linear mixed effect multiple predictor models with normal distribution assumptions using the R 'lmer' function from 'lmerTest' package (Kuznetsova *et al.* 2017). Species identity was used as random factor and the total amount of litter from other species in the litter trap was used as a covariate to control for TSP productivity. Explanatory variables were rescaled using the R function 'scale' (R Core Team 2021) and selected using forward and backward step selection based on AIC (R 'step' function from 'lmerTest' package, Kuznetsova *et al.* 2017).

Results

Tree species richness increases decomposition

Our analyses showed that after nine months of decomposition, neighborhood tree species richness did not affect carbon loss (p -value = 0.428, Fig. I.2.A), but significantly increased litter nitrogen loss significantly (estimate \pm SE = 5.00 ± 2.08 , p -value = 0.018, Fig. I.2.B). However, tree species richness did not affect carbon nor nitrogen loss during microbial decomposition (p -value = 0.220, Fig. I.2.C, and p -value = 0.149, Fig. I.2.D). In addition, litter species richness increased litter decomposability measured in the controlled environment. In detail, litter species richness did not affect carbon loss (p -value = 0.151, Fig. I.2.D) but increased nitrogen loss (3.15 ± 0.85 , p -value < 0.001, Fig. I.2.F).

Tree species richness affects litterfall with consequences for litter decomposition

Our model revealed a positive effect of neighborhood tree species richness on the amount litterfall and litter species richness (estimate \pm SE = 52.3 ± 8.24 , p -value < 0.001; 1.00 ± 0.05 , p -value < 0.001, respectively; Fig. I.3.A). In the Common Garden experiment, where litter decomposability was investigated, litter species richness of the litterbags increased litter N loss

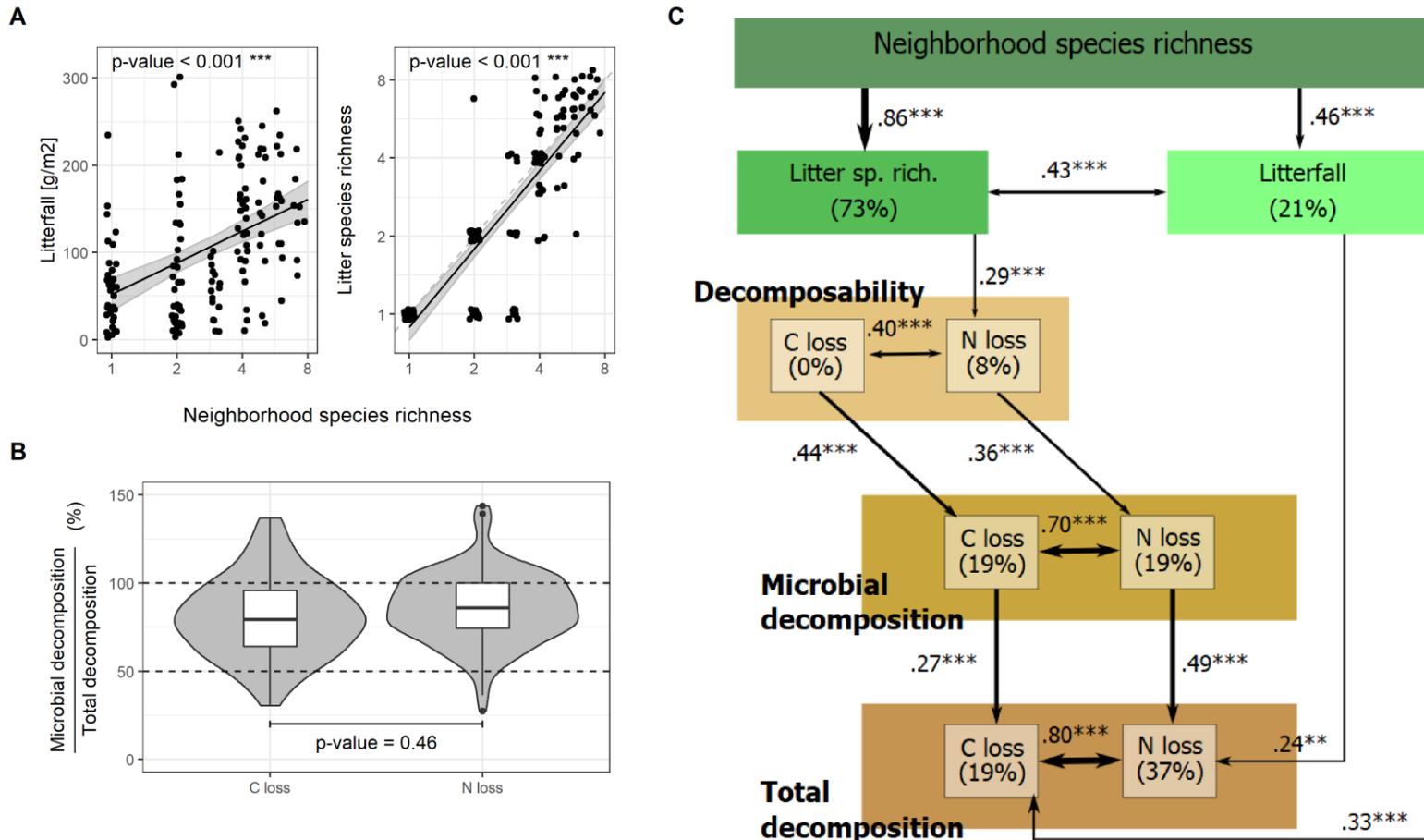


Fig. I.3 Tree species effect on the amount of litterfall and litter species richness, as well as consequences for litter decomposition. A. Neighborhood species richness effect on the amount of litterfall and litter species richness (values were jittered for better readability). B. Percentage of total decomposition carried out by the microbial community. C. Structural equation model linking neighborhood species richness, litterfall (i.e., litter species richness: "Litter sp. rich.", and amount of litterfall: "Litterfall") and decomposition processes (i.e., Decomposability in terms of litter "C loss" and "N loss" in a Common Garden experiment, microbial decomposition in terms of litter "C loss" and "N loss", and total decomposition in terms of "C loss" and "N loss"). Only significant paths (p -value < 0.05) are reported with an arrow in the figure (see the whole model structure in Suppl. I-S3). Arrow widths were scaled by the standardized effect size of significant relations. Correlations between nodes were drawn with double-headed arrows, while causal relations were drawn with one-way arrows. The variance explained by the model (R^2 , in %) is shown after each node name. Significance levels: ".": p -value < 0.1, "*": p -value < 0.05, "***": p -value < 0.01, and "****": p -value < 0.001).

(0.29 ± 0.07 , p -value < 0.001 , Fig. I.3.C), and explained up to 8% of its variance but did not affect litter C loss. The total and microbial litter decompositions were investigated in the TSP where the litter was collected. Microbial C loss increased with C loss measured in controlled conditions (i.e., decomposability, 0.43 ± 0.05 , p -value < 0.001), explaining 19% of the variance in microbial C loss (Fig. I.3.C). Similarly, microbial N loss increased with increasing litter decomposability (0.36 ± 0.06 , p -value < 0.001), explaining up to 19% of the variance in microbial N loss. Microbial decomposition represented the major part of litter decomposition: 84% ($\pm 40\%$) of C loss and 87% ($\pm 22\%$) of N loss were carried out by the microbial community (Fig. I.3.B). Litter microbial C loss and the amount of litterfall explained up to 19% of litter C loss, both increasing litter C loss (0.31 ± 0.09 , p -value < 0.001 , and 0.26 ± 0.05 , p -value < 0.001 , respectively, Fig. I.3.C). Similarly, microbially-mediated N loss and the amount of litterfall increased total litter N loss (0.50 ± 0.05 , p -value < 0.001 , and 0.23 ± 0.08 , p -value = 0.003), explaining 37% of the variance in litter N loss.

Litter decomposability is leaf trait based

Our analyses showed that, in controlled environmental conditions, litter species richness and functional trait identity and diversity (Fig. I.3.A) explained up to 2% and 17% of litter carbon and nitrogen loss variance, respectively (Fig. I.3.B., Suppl. I-S3). Our models showed that only N loss increased with litter species richness (estimate \pm SE = 2.55 ± 0.73 , p -value < 0.001) and with increasing litter functional diversity (0.45 ± 0.19 , p -value = 0.017). Moreover, both C and N loss increased with increasing litter nutrient content (1.02 ± 0.39 , p -value = 0.009; 2.10 ± 0.51 , p -value < 0.001 , respectively).

Amount and composition of litterfall is affected by tree biomass, and tree spatial organization

Our analyses of litterfall composition highlighted the effect of tree biomass and the spatial arrangements of the trees at the locations of litter collection (Fig. I.4.C),

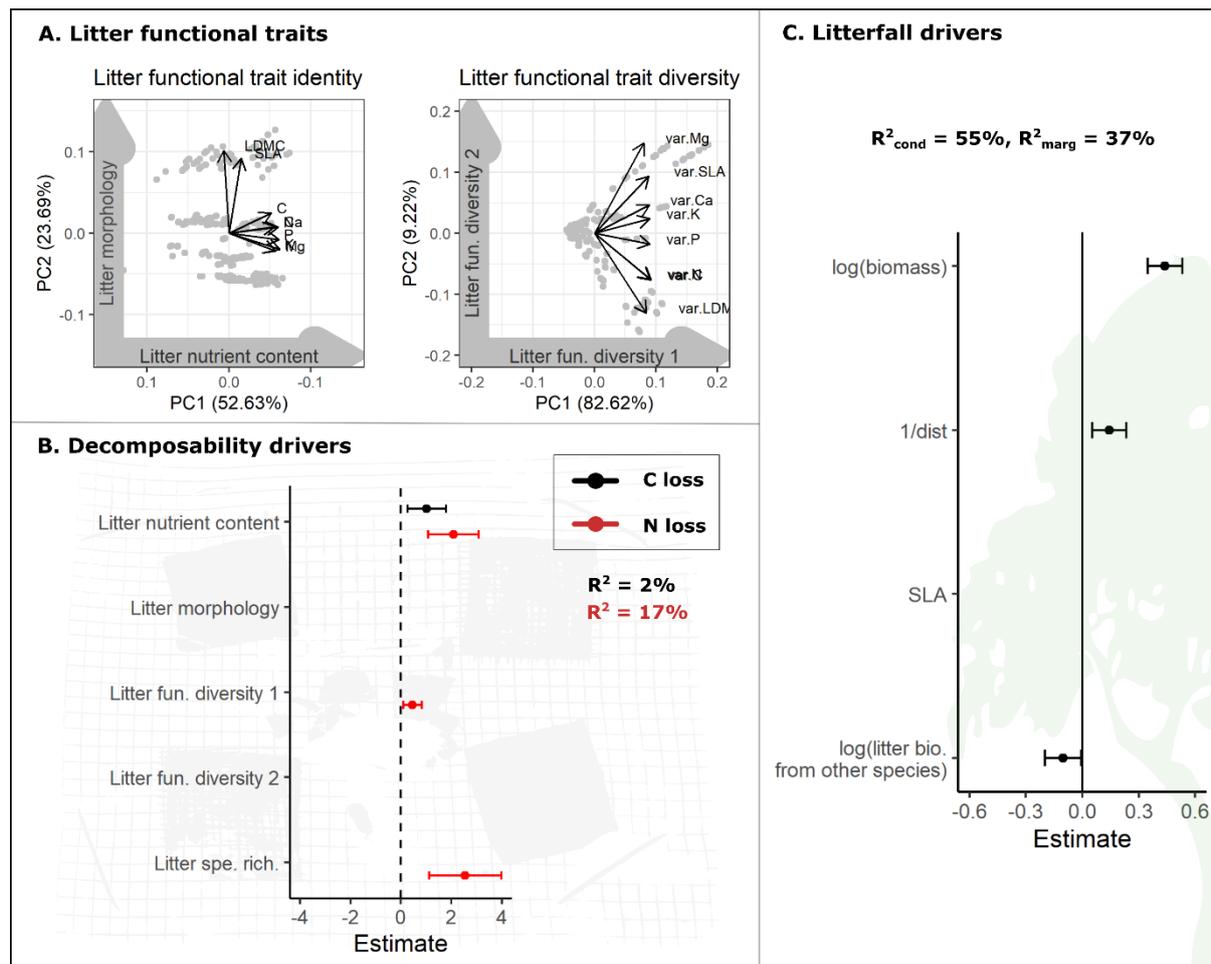


Fig. I.4: Litter functional trait identity and diversity (A), decomposability drivers (B), and drivers of the amount of species-specific litterfall (C). A. Primary Component Analysis (PCA) of litter functional trait identity and diversity. Litter functional trait identity consisted of litter chemical composition (litterbag C, N, P, Mg, Na, K content) and litter leaf morphological traits (litterbag community weighted mean SLA and LDMC), and litter functional trait diversity consisted of litter leaf functional trait variance within the litterbags (C, N, P, Mg, Na, K, SLA and LDMC variances). B. Effect of litter nutrient content (PCA litter functional identity first axis), morphology (PCA litter functional identity second axis), functional diversity (PCA litter functional diversity first two axes), and litter species richness ("Litter spe. rich.") on litter decomposability (in term of carbon and nitrogen loss in black and red, respectively). The plot shows the results of the multi-predictor model fit after a step AIC selection procedure. For selected variables, confidence intervals (95%) were drawn around the standardized effect estimate with a full line for significant effects (p -value < 0.05) and a dashed line for non-significant effects. C. Effect of tree biomass ("log(biomass)"), tree closeness to the litter-trap ("1/dist"), leaf morphology (i.e., SLA) and other species litter biomass in the trap ("log(litter bio. from other species)") on species-specific litterfall amount collected in the trap. The plot shows the results of the multi-predictor linear mixed effect model, using litter species as a random factor, after a step AIC selection procedure. For selected variables, confidence intervals (95%) were drawn around the standardized effect estimate with a full line for significant effects (p -value < 0.05) and a dashed line for non-significant effects.

as these three aspects together explained up to 45% of the variance in species-specific litter biomass. Species-specific litter biomass increased with tree biomass (estimate \pm SE = 0.43 ± 0.05 , p -value < 0.001) and the proximity to the trees (0.14 ± 0.05 , p -value = 0.002), but was not affected by leaf morphology (i.e., SLA was excluded during model selection). In addition, the amount of litter from other species in the litter trap reduced species-specific litter biomass (-0.10 ± 0.05 , p -value = 0.038).

Discussion

We studied the effects of tree species richness on leaf litter decomposition considering the amount of litterfall and its composition, litter decomposability, and the role of the microbial community in the decomposition process. Our results confirmed our hypotheses by showing that tree species richness promoted litter decomposition (H1) and was mainly carried out by microbial decomposers (H2). Microbial decomposition increased with litter decomposability (H3), with the latter being driven by litter species richness and leaf functional trait identity and diversity (H4). In addition, we showed a positive effect of tree species richness on the amount of litterfall and litter species richness (H5), while litter species-specific biomass increased with increasing proximity to the trees as well as with tree biomass (H5). Notably, these findings highlight the complex interplay among tree litter diversity, leaf traits related to litter decomposability, and the spatial arrangement of trees in determining microbial decomposition processes in subtropical forest ecosystems.

Relationship between litter decomposition and soil microorganisms

We found that litter decomposition is mostly performed by soil microbial communities in this studied Chinese subtropical forest (H2). This observation is in contrast with previous measurements of woody litter decomposition, made in the same experiment, showing the significant role of soil meso- and macrofauna (Pietsch *et al.* 2019). However, it could be explained by the low abundance of soil meso- and macrofauna we observed during the

experiment (Suppl. I-S4) and in the respective region (Wang *et al.* 2007; Xu *et al.* 2006). Therefore, changes in litter decomposition were primarily explained by changes in microbial decomposition. Notably, soil fauna removal even increased the decomposition rate in some samples (Fig. 3.B), suggesting top-down control of microbial decomposers by meso- and macrofauna communities (Patoine *et al.* 2020). For instance, the presence of bacterial and fungal feeders could reduce microbial biomass (Crowther *et al.* 2013; Tobias-Hünefeldt *et al.* 2021), and/or the disturbance of fungal hyphae in the early stage of decomposition could reduce fungal activity (Ristok *et al.* 2019).

Tree diversity mass and diversity effects on decomposition

Our results showed a positive effect of the amount of litter on total decomposition but not microbial decomposition. Increasing the litter cover on the ground may favor other groups of decomposers such as meso- and macro-fauna decomposer by providing suitable environmental conditions (Gottschall *et al.* 2019; Joly *et al.* 2017; Korboulewsky *et al.* 2016). Therefore, more investigation is needed to better understand the interplay between soil microbial community, meso-/macro-fauna community, and litter decomposition. In particular, we need to understand how soil microbial community and soil fauna detritivores interact (Joly *et al.* 2020; Ristok *et al.* 2019) as well as their environmental drivers (Cesarz *et al.* 2020; Phillips *et al.* 2021) to better understand their combined effects on soil carbon dynamics. Interestingly, we showed that both diversity effect pathways – (i) diversity effects on litter decomposition by increasing litterfall (i.e., mass effect), and (ii) diversity effects on litter decomposition through litter species richness and microbial decomposition – had similar effect size, highlighting the concurrence of tree diversity mass (i) and diversity (ii) effects on litter decomposition through litterfall (Sonkoly *et al.* 2019). Together, tree diversity effects on ecosystem functions are multicausal due to combined mass and diversity effects, both being equivalent driving forces of ecosystem function.

Nutrient content and litter diversity drive litter decomposability

Litter decomposability measurements allowed us to isolate the litter effect on decomposition from decomposer and environmental effects (García-Palacios *et al.* 2013; Lin *et al.* 2021; Zhang *et al.* 2018). Consistent with our expectations, we observed a positive effect of litter decomposability on microbial decomposition. Moreover, we estimated that up to 20% of litter decomposition is driven by variations in litter decomposability. These results support previous observations showing that litter is a driving force in litter decomposition (e.g., Fanin *et al.* 2012; Joly *et al.* 2017; Rosenfield *et al.* 2020; Zhang *et al.* 2018).

Together, litter nutrient content and litter diversity are driving litter effects on decomposition which was also observed in earlier studies (Fanin *et al.* 2012; Joly *et al.* 2017; Liu *et al.* 2020; Zhou *et al.* 2020). Two main mechanisms can explain these observations: increasing leaf nutrient contents provided to the decomposer community reduce stoichiometric limitations (Fanin *et al.* 2012; Rosenfield *et al.* 2020), and increasing substrate diversity leads to a higher niche partitioning of the decomposer community (Ebeling *et al.* 2014; Hooper *et al.* 2000). In addition, litter species richness could favor nutrient transfer between species-specific litter (Liu *et al.* 2020), for example, by transferring nutrients such as nitrogen from nitrogen-rich species to nitrogen-poor species through the fungal hyphae (Schimel and Hättenschwiler 2007). However, only a small fraction of the litter decomposability was explained by our models (i.e., 2% of C loss and 17% of N loss); thus other key aspects are still missing in our models to better predict decomposability drivers. These missing litter properties may include chemical components like polyphenols and tannins contents (Ristok *et al.* 2019) or structural components such as celluloses, hemicelluloses or lignin (Austin and Ballaré 2010; Fioretto *et al.* 2005; Hättenschwiler *et al.* 2005).

Tree diversity and functional drivers of litterfall spatial distribution

Litterfall is the significant carbon flux from the canopy to the forest floor; therefore, an increase in litterfall increases litter decomposition and soil carbon storage (Xu *et al.* 2018). We demonstrated that tree species richness increased the amount of litterfall, confirming previous findings (Huang *et al.* 2017). Moreover, species-specific litterfall increased with increasing tree biomass and proximity to the trees. These results provide some of the first empirical evidence of tree diversity effects on the spatial heterogeneity of litterfall composition at small spatial scales (i.e., a fraction of meters around the sampling point) and suggest a trait- and distance-based mediation of litterfall effects on decomposition in forests. Thus, our results emphasize the importance of considering small-scale processes and plot spatial heterogeneity to understand ecosystem functioning. Moreover, these small-scale processes and their drivers are potentially vital in understanding above- and belowground drivers of biodiversity, on top of plot-, field- and landscape-level drivers (Le Provost *et al.* 2021).

Spatially heterogeneous distribution of litter composition and leaf trait effects on decomposition may cause spatial heterogeneity in litter decomposition and thus nutrient cycling. The distance-based mediation of litterfall will promote litter decomposition at two levels: on the one hand, a small part of litter originating from more distant trees could enhance decomposition by increasing litter diversity (Gessner *et al.* 2010; Joly *et al.* 2017; Trogisch *et al.* 2016; Zhang *et al.* 2018). On the other hand, the most litter will accumulate close to the source tree, increasing litter decomposition due to increased litterfall and homefield advantages (Fanin *et al.* 2021; Vogel *et al.* 2013). The accumulation of species-specific litter close to each tree may favor species-specific decomposer communities (such as found in grassland soils; Bezemer *et al.* 2010). Therefore, spatial heterogeneity of litter at the plot level will sustain a high decomposer meta-community diversity (Hooper *et al.* 2000). A diverse meta-community is expected to promote ecosystem functioning (Grman *et al.* 2018; Häussler *et al.* 2020; Mori

et al. 2018) and stability (Mougi and Kondoh 2016; Wang *et al.* 2021). However, these novel insights need further theoretical and empirical investigation to map and predict litter composition, decomposition, and decomposer meta-community dynamics at the plot level. Therefore, spatial experiments and modeling at small-scales are essential to understand litter dispersal and the consequences for decomposition and mineralization processes that determine nutrient availability for plants.

Conclusion

The present study provides new mechanistic insights into the impact of tree diversity on litter decomposition in subtropical forests and its consequences for carbon and nitrogen cycling. We showed that tree diversity enhances litter decomposition by increasing the amount of litterfall and litter species richness, highlighting the multiple effects of tree diversity on litter decomposition. Moreover, we suggest that litter mass and diversity effects of tree diversity are two significant pathways to understand tree diversity effects on ecosystem functioning, and thus, both aspects of tree diversity should be better explored in the future. Moreover, we showed the key role of the spatial distribution of litterfall and thus the consequences for litter decomposition. Further research should consider the spatial distribution of trees to understand the spatial heterogeneity of tree products such as litterfall and root exudates, and thus the consequences for ecosystem functions like carbon and nitrogen cycling in forests.

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References

- Austin, Amy T.; Ballaré, Carlos L. (2010): Dual role of lignin in plant litter decomposition in terrestrial ecosystems. In *Proceedings of the National Academy of Sciences* 107 (10), pp. 4618–4622. DOI: 10.1073/pnas.0909396107.
- Bastin, Jean-Francois; Finegold, Yelena; Garcia, Claude; Mollicone, Danilo; Rezende, Marcelo; Routh, Devin et al. (2019): The global tree restoration potential. In *Science (New York, N.Y.)* 365 (6448), pp. 76–79. DOI: 10.1126/science.aax0848.
- Bezemer, T. M.; Fountain, M. T.; Barea, J. M.; Christensen, S.; Dekker, S. C.; Duyts, H. et al. (2010): Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. In *Ecology* 91 (10), pp. 3027–3036. DOI: 10.1890/09-2198.1.
- Bradford, Mark A.; Tordoff, George M.; Eggers, Till; Jones, T. Hefin; Newington, John E. (2002): Microbiota, fauna, and mesh size interactions in litter decomposition. In *Oikos* 99 (2), pp. 317–323. DOI: 10.1034/j.1600-0706.2002.990212.x.
- Bruelheide, Helge; Böhnke, Martin; Both, Sabine; Fang, Teng; Assmann, Thorsten; Baruffol, Martin et al. (2011): Community assembly during secondary forest succession in a Chinese subtropical forest. In *Ecological Monographs* 81 (1), pp. 25–41. DOI: 10.1890/09-2172.1.
- Bruelheide, Helge; Nadrowski, Karin; Assmann, Thorsten; Bauhus, Jürgen; Both, Sabine; Buscot, François et al. (2014): Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. In *Methods in Ecology and Evolution* 5 (1), pp. 74–89. DOI: 10.1111/2041-210X.12126.
- Cesarz, Simone; Craven, Dylan; Auge, Harald; Bruelheide, Helge; Castagneyrol, Bastien; Hector, Andy et al. (2020): Biotic and abiotic drivers of soil microbial functions across tree diversity experiments. In *bioRxiv*. DOI: 10.1101/2020.01.30.927277.
- Chandler, J. R.; Schmidt, M. G.; Dragicevic, S. (2008): Spatial patterns of forest floor properties and litterfall amounts associated with bigleaf maple in conifer forest of southwestern British Columbia. In *Canadian Journal of Soil Science* 88 (3), pp. 295–313. DOI: 10.4141/CJSS07040.
- Coûteaux, Marie-Madeleine; Bottner, Pierre; Berg, Björn (1995): Litter decomposition, climate and litter quality. In *Trends in Ecology & Evolution* 10 (2), pp. 63–66. DOI: 10.1016/s0169-5347(00)88978-8.
- Crowther, Thomas W.; Stanton, David W. G.; Thomas, Stephen M.; A'Bear, A. Donald; Hiscox, Jennifer; Jones, T. Hefin et al. (2013): Top-down control of soil fungal community composition by a globally distributed keystone consumer. In *Ecology* 94 (11), pp. 2518–2528. DOI: 10.1890/13-0197.1.
- Davrinche, Andréa; Haider, Sylvia (2021): Intra-specific leaf trait responses to species richness at two different local scales. In *Basic and Applied Ecology*. DOI: 10.1016/j.baae.2021.04.011.
- Ebeling, Anne; Meyer, Sebastian T.; Abbas, Maike; Eisenhauer, Nico; Hillebrand, Helmut; Lange, Markus et al. (2014): Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. In *PloS one* 9 (9), e106529. DOI: 10.1371/journal.pone.0106529.

- Fanin, Nicolas; Barantal, Sandra; Fromin, Nathalie; Schimann, Heidy; Schevin, Patrick; Hättenschwiler, Stephan (2012): Distinct microbial limitations in litter and underlying soil revealed by carbon and nutrient fertilization in a tropical rainforest. In *PloS one* 7 (12), e49990. DOI: 10.1371/journal.pone.0049990.
- Fanin, Nicolas; Lin, Dunmei; Freschet, Grégoire T.; Keiser, Ashley D.; Augusto, Laurent; Wardle, David A.; Veen, G. F. Ciska (2021): Home-field advantage of litter decomposition: from the phyllosphere to the soil. In *The New phytologist*. DOI: 10.1111/nph.17475.
- Finke, Deborah L.; Snyder, William E. (2008): Niche Partitioning Increases Resource Exploitation by Diverse Communities. In *Science (New York, N.Y.)* 321 (5895), pp. 1488–1490. DOI: 10.1126/science.1161833.
- Fioretto, Antonietta; Di Nardo, Carmelina; Papa, Stefania; Fuggi, Amodio (2005): Lignin and cellulose degradation and nitrogen dynamics during decomposition of three leaf litter species in a Mediterranean ecosystem. In *Soil Biology and Biochemistry* 37 (6), pp. 1083–1091. DOI: 10.1016/j.soilbio.2004.11.007.
- Freschet, Grégoire T.; Aerts, Rien; Cornelissen, Johannes H. C. (2012): A plant economics spectrum of litter decomposability. In *Functional Ecology* 26 (1), pp. 56–65. DOI: 10.1111/j.1365-2435.2011.01913.x.
- García-Palacios, Pablo; Maestre, Fernando T.; Kattge, Jens; Wall, Diana H. (2013): Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. In *Ecology Letters* 16 (8), pp. 1045–1053. DOI: 10.1111/ele.12137.
- Garnier, Eric; Cortez, Jacques; Billès, Georges; Navas, Marie-Laure; Roumet, Catherine; Debussche, Max et al. (2004): Plant functional markers capture ecosystem properties during secondary succession. In *Ecology* 85 (9), pp. 2630–2637. DOI: 10.1890/03-0799.
- Gartner, Tracy B.; Cardon, Zoe G. (2004): Decomposition dynamics in mixed-species leaf litter. In *Oikos* 104 (2), pp. 230–246. DOI: 10.1111/j.0030-1299.2004.12738.x.
- Geißler, C.; Kühn, P.; Böhnke, M.; Bruelheide, H.; Shi, X.; Scholten, T. (2012): Splash erosion potential under tree canopies in subtropical SE China. In *CATENA* 91, pp. 85–93. DOI: 10.1016/j.catena.2010.10.009.
- Gessner, Mark O.; Swan, Christopher M.; Dang, Christian K.; McKie, Brendan G.; Bardgett, Richard D.; Wall, Diana H.; Hättenschwiler, Stephan (2010): Diversity meets decomposition. In *Trends in Ecology & Evolution* 25 (6), pp. 372–380. DOI: 10.1016/j.tree.2010.01.010.
- Gottschall, Felix; Davids, Sophie; Newiger-Dous, Till E.; Auge, Harald; Cesarz, Simone; Eisenhauer, Nico (2019): Tree species identity determines wood decomposition via microclimatic effects. In *Ecology and Evolution* 9 (21), pp. 12113–12127. DOI: 10.1002/ece3.5665.
- Grman, Emily; Zirbel, Chad R.; Bassett, Tyler; Brudvig, Lars A. (2018): Ecosystem multifunctionality increases with beta diversity in restored prairies. In *Oecologia* 188 (3), pp. 837–848. DOI: 10.1007/s00442-018-4248-6.
- Hättenschwiler, S. (2005): Effects of Tree Species Diversity on Litter Quality and Decomposition. In Michael Scherer-Lorenzen, Christian Körner, Ernst-Detlef Schulze (Eds.): *Forest Diversity and Function*, vol. 176. Berlin/Heidelberg: Springer-Verlag (Ecological Studies, 176), pp. 149–164.

Hättenschwiler, Stephan; Tiunov, Alexei V.; Scheu, Stefan (2005): Biodiversity and Litter Decomposition in Terrestrial Ecosystems. In *Annual Review of Ecology, Evolution, and Systematics* 36 (1), pp. 191–218. DOI: 10.1146/annurev.ecolsys.36.112904.151932.

Häussler, Johanna; Barabás, György; Eklöf, Anna (2020): A Bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions. In *Ecology Letters* 23 (12), pp. 1849–1861. DOI: 10.1111/ele.13607.

Hooper, David U.; Bignell, David E.; Brown, Valerie K.; BRUSSARD, LIJBERT; Dangerfield, Mark J.; Wall, Diana H. et al. (2000): Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks. In *BioScience* 50 (12), p. 1049.

Huang, Yuanyuan; Chen, Yuxin; Castro-Izaguirre, Nadia; Baruffol, Martin; Brezzi, Matteo; Lang, Anne et al. (2018): Impacts of species richness on productivity in a large-scale subtropical forest experiment. In *Science (New York, N.Y.)* 362 (6410), pp. 80–83. DOI: 10.1126/science.aat6405.

Huang, Yuanyuan; Ma, Yinlei; Zhao, Ke; Niklaus, Pascal A.; Schmid, Bernhard; He, Jin-Sheng (2017): Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest. In *Journal of Plant Ecology* 10 (1), pp. 28–35. DOI: 10.1093/jpe/rtw115.

Joly, François-Xavier; Coq, Sylvain; Coulis, Mathieu; David, Jean-François; Hättenschwiler, Stephan; Mueller, Carsten W. et al. (2020): Detritivore conversion of litter into faeces accelerates organic matter turnover. In *Communications Biology* 3 (1), p. 660. DOI: 10.1038/s42003-020-01392-4.

Joly, François-Xavier; Coq, Sylvain; Coulis, Mathieu; Nahmani, Johanne; Hättenschwiler, Stephan (2018): Litter conversion into detritivore faeces reshuffles the quality control over C and N dynamics during decomposition. In *Functional Ecology* 32 (11), pp. 2605–2614. DOI: 10.1111/1365-2435.13178.

Joly, François-Xavier; Milcu, Alexandru; Scherer-Lorenzen, Michael; Jean, Loreline-Katia; Bussotti, Filippo; Dawud, Seid Muhie et al. (2017): Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. In *The New phytologist* 214 (3), pp. 1281–1293. DOI: 10.1111/nph.14452.

Korboulewsky, Nathalie; Perez, Gabriel; Chauvat, Matthieu (2016): How tree diversity affects soil fauna diversity: A review. In *Soil Biology and Biochemistry* 94, pp. 94–106. DOI: 10.1016/j.soilbio.2015.11.024.

Lange, Markus; Eisenhauer, Nico; Sierra, Carlos A.; Bessler, Holger; Engels, Christoph; Griffiths, Robert I. et al. (2015): Plant diversity increases soil microbial activity and soil carbon storage. In *Nature communications* 6, p. 6707. DOI: 10.1038/ncomms7707.

Le Provost, Gaëtane; Thiele, Jan; Westphal, Catrin; Penone, Caterina; Allan, Eric; Neyret, Margot et al. (2021): Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. In *Nature communications* 12 (1), p. 3918. DOI: 10.1038/s41467-021-23931-1.

Lewis, Simon L.; Wheeler, Charlotte E.; Mitchard, Edward T. A.; Koch, Alexander (2019): Restoring natural forests is the best way to remove atmospheric carbon. In *Nature* 568 (7750), pp. 25–28. DOI: 10.1038/d41586-019-01026-8.

- Liang, Jingjing; Crowther, Thomas W.; Picard, Nicolas; Wisser, Susan; Zhou, Mo; Alberti, Giorgio et al. (2016): Positive biodiversity-productivity relationship predominant in global forests. In *Science (New York, N.Y.)* 354 (6309). DOI: 10.1126/science.aaf8957.
- Lin, Guigang; Zeng, De-Hui (2018): Functional identity rather than functional diversity or species richness controls litter mixture decomposition in a subtropical forest. In *Plant and Soil* 428 (1-2), pp. 179–193. DOI: 10.1007/s11104-018-3669-7.
- Lin, Hong; Li, Yinong; Bruelheide, Helge; Zhang, Sirong; Ren, Haibao; Zhang, Naili; Ma, Keping (2021): What drives leaf litter decomposition and the decomposer community in subtropical forests – The richness of the above-ground tree community or that of the leaf litter? In *Soil Biology and Biochemistry* 160, p. 108314. DOI: 10.1016/j.soilbio.2021.108314.
- Liu, Jun; Liu, Xiaoyu; Song, Qingni; Compson, Zacchaeus G.; LeRoy, Carri J.; Luan, Fenggang et al. (2020): Synergistic effects: a common theme in mixed-species litter decomposition. In *The New phytologist* 227 (3), pp. 757–765. DOI: 10.1111/nph.16556.
- Liu, Xiaojuan; Trogisch, Stefan; He, Jin-Sheng; Niklaus, Pascal A.; Bruelheide, Helge; Tang, Zhiyao et al. (2018): Tree species richness increases ecosystem carbon storage in subtropical forests. In *Proceedings. Biological sciences* 285 (1885). DOI: 10.1098/rspb.2018.1240.
- Lüdecke, Daniel; Makowski, Dominique; Waggoner, Philip; Patil, Indrajeet (2020): performance: Assessment of Regression Models Performance. In *CRAN*. DOI: 10.5281/zenodo.3952174.
- Minderman, G. (1968): Addition, Decomposition and Accumulation of Organic Matter in Forests. In *Journal of Ecology* 56 (2), p. 355. DOI: 10.2307/2258238.
- Mori, Akira S.; Isbell, Forest; Seidl, Rupert (2018): β -Diversity, Community Assembly, and Ecosystem Functioning. In *Trends in ecology & evolution* 33 (7), pp. 549–564. DOI: 10.1016/j.tree.2018.04.012.
- Mougi, A.; Kondoh, M. (2016): Food-web complexity, meta-community complexity and community stability. In *Scientific reports* 6, p. 24478. DOI: 10.1038/srep24478.
- Patoine, Guillaume; Bruelheide, Helge; Haase, Josephine; Nock, Charles; Ohlmann, Niklas; Schwarz, Benjamin et al. (2020): Tree litter functional diversity and nitrogen concentration enhance litter decomposition via changes in earthworm communities. In *Ecology and Evolution* 68 (10), p. 2201. DOI: 10.1002/ece3.6474.
- Phillips, Helen R. P.; Bach, Elizabeth M.; Bartz, Marie L. C.; Bennett, Joanne M.; Beugnon, Rémy; Briones, Maria J. I. et al. (2021): Global data on earthworm abundance, biomass, diversity and corresponding environmental properties. In *Scientific Data* 8 (1), p. 136. DOI: 10.1038/s41597-021-00912-z.
- Pietsch, Katherina A.; Eichenberg, David; Nadrowski, Karin; Bauhus, Jürgen; Buscot, François; Purahong, Witoon et al. (2019): Wood decomposition is more strongly controlled by temperature than by tree species and decomposer diversity in highly species rich subtropical forests. In *Oikos* 128 (5), pp. 701–715. DOI: 10.1111/oik.04879.
- R Core Team (2021): R: A Language and Environment for Statistical Computing. Vienna, Austria. Available online at <https://www.R-project.org/>.
- Ristok, Christian; Leppert, Katrin N.; Scherer-Lorenzen, Michael; Niklaus, Pascal A.; Bruelheide, Helge (2019): Soil macrofauna and leaf functional traits drive the decomposition of secondary metabolites in leaf litter. In *Soil Biology and Biochemistry* 135, pp. 429–437. DOI: 10.1016/j.soilbio.2019.06.007.

- Rosenfield, Marc V.; Keller, Jason K.; Clausen, Catrina; Cyphers, Kimberlee; Funk, Jennifer L. (2020): Leaf traits can be used to predict rates of litter decomposition. In *Oikos* 129 (10), pp. 1589–1596. DOI: 10.1111/oik.06470.
- Rosseel, Y. (2012): Lavaan: An R package for structural equation modeling and more. Version 0.5–12 (BETA). In *Journal of statistical software* 48 (2), pp. 1–36.
- Scherber, Christoph; Eisenhauer, Nico; Weisser, Wolfgang W.; Schmid, Bernhard; Voigt, Winfried; Fischer, Markus et al. (2010): Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. In *Nature* 468 (7323), pp. 553–556. DOI: 10.1038/nature09492.
- Schimel, Joshua P.; Hättenschwiler, Stephan (2007): Nitrogen transfer between decomposing leaves of different N status. In *Soil Biology and Biochemistry* 39 (7), pp. 1428–1436. DOI: 10.1016/j.soilbio.2006.12.037.
- Scholten, Thomas; Goebes, Philipp; Kühn, Peter; Seitz, Steffen; Assmann, Thorsten; Bauhus, Jürgen et al. (2017): On the combined effect of soil fertility and topography on tree growth in subtropical forest ecosystems—a study from SE China. In *Journal of Plant Ecology* 10 (1), pp. 111–127. DOI: 10.1093/jpe/rtw065.
- Seibold, Sebastian; Rammer, Werner; Hothorn, Torsten; Seidl, Rupert; Ulyshen, Michael D.; Lorz, Janina et al. (2021): The contribution of insects to global forest deadwood decomposition. In *Nature* 597 (7874), pp. 77–81. DOI: 10.1038/s41586-021-03740-8.
- Sonkoly, Judit; Kelemen, András; Valkó, Orsolya; Deák, Balázs; Kiss, Réka; Tóth, Katalin et al. (2019): Both mass ratio effects and community diversity drive biomass production in a grassland experiment. In *Scientific reports* 9 (1), p. 1848. DOI: 10.1038/s41598-018-37190-6.
- Tobias-Hünefeldt, Sven P.; Wenley, Jess; Baltar, Federico; Morales, Sergio E. (2021): Ecological drivers switch from bottom-up to top-down during model microbial community successions. In *The ISME journal* 15 (4), pp. 1085–1097. DOI: 10.1038/s41396-020-00833-6.
- Trogisch, Stefan; He, Jin-Sheng; Hector, Andy; Scherer-Lorenzen, Michael (2016): Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. In *Plant and Soil* 400 (1-2), pp. 337–350. DOI: 10.1007/s11104-015-2737-5.
- Vogel, Anja; Eisenhauer, Nico; Weigelt, Alexandra; Scherer-Lorenzen, Michael (2013): Plant diversity does not buffer drought effects on early-stage litter mass loss rates and microbial properties. In *Global Change Biology* 19 (9), pp. 2795–2803. DOI: 10.1111/gcb.12225.
- Wang, Xi-Hua; Kent, Martin; Fang, Xiao-Feng (2007): Evergreen broad-leaved forest in Eastern China: Its ecology and conservation and the importance of resprouting in forest restoration. In *Forest Ecology and Management* 245 (1-3), pp. 76–87. DOI: 10.1016/j.foreco.2007.03.043.
- Wang, Ying; Chen, Liang; Xiang, Wenhua; Ouyang, Shuai; Zhang, Taidong; Zhang, Xiulan et al. (2021): Forest conversion to plantations: A meta-analysis of consequences for soil and microbial properties and functions. In *Global Change Biology*. DOI: 10.1111/gcb.15835.
- Wardle, D. A.; Bonner, K. I.; Barker, G. M. (2002): Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. In *Functional Ecology* 16 (5), pp. 585–595. DOI: 10.1046/j.1365-2435.2002.00659.x.

Wardle, David A.; Bardgett, Richard D.; Klironomos, John N.; Setälä, Heikki; van der Putten, Wim H.; Wall, Diana H. (2004): Ecological linkages between aboveground and belowground biota. In *Science (New York, N.Y.)* 304 (5677), pp. 1629–1633. DOI: 10.1126/science.1094875.

Xu, Guo-Liang; Mo, Jiang-Ming; Zhou, Guo-Yi; Fu, Sheng-Lei (2006): Preliminary Response of Soil Fauna to Simulated N Deposition in Three Typical Subtropical Forests. In *Pedosphere* 16 (5), pp. 596–601. DOI: 10.1016/S1002-0160(06)60093-3.

Xu, Shan; Eisenhauer, Nico; Ferlian, Olga; Zhang, Jinlong; Zhou, Guoyi; Lu, Xiankai et al. (2020): Species richness promotes ecosystem carbon storage: evidence from biodiversity-ecosystem functioning experiments. In *Proceedings. Biological sciences* 287 (1939), p. 20202063. DOI: 10.1098/rspb.2020.2063.

Xu, Shan; Li, Ping; Sayer, Emma J.; Zhang, Beibei; Wang, Jing; Qiao, Chunlian et al. (2018): Initial Soil Organic Matter Content Influences the Storage and Turnover of Litter, Root and Soil Carbon in Grasslands. In *Ecosystems* 21 (7), pp. 1377–1389. DOI: 10.1007/s10021-018-0227-3.

Yu, Guirui; Chen, Zhi; Piao, Shilong; Peng, Changhui; Ciais, Philippe; Wang, Qiufeng et al. (2014): High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. In *Proceedings of the National Academy of Sciences* 111 (13), pp. 4910–4915. DOI: 10.1073/pnas.1317065111.

Zhang, Naili; Li, Yinong; Wubet, Tesfaye; Bruelheide, Helge; Liang, Yu; Purahong, Witoon et al. (2018): Tree species richness and fungi in freshly fallen leaf litter: Unique patterns of fungal species composition and their implications for enzymatic decomposition. In *Soil Biology and Biochemistry* 127, pp. 120–126. DOI: 10.1016/j.soilbio.2018.09.023.

Zhou, Shixing; Butenschoen, Olaf; Barantal, Sandra; Handa, Ira Tanya; Makkonen, Marika; Vos, Veronique et al. (2020): Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. In *Journal of Ecology* 108 (6), pp. 2283–2297. DOI: 10.1111/1365-2745.13452.