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Title page

Trophic interactions in soil micro-food webs drive ecosystem multifunctionality along tree species richness

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Running title: Soil micro-food webs regulate ecosystem multifunctionality

Abstract

Rapid biodiversity loss under global climate change threaten forest ecosystem function. However, the drivers of soil micro-food web on ecosystem functions across biodiversity gradients remains equivocal. We measured responses of multiple ecosystem functions to tree species richness in a subtropical forest. Tree species richness had negligible effects on nutrient cycling, organic matter decomposition, and plant productivity, but carbon stocks and multifunctionality increased with tree species richness. Soil organisms, particularly arbuscular mycorrhizal fungi and soil nematodes, elicited the greatest relative effects on multifunctionality. Structural equation models revealed indirect effects of functional diversity on multifunctionality mediated by trophic interactions in soil micro-food webs. There was a significant negative effect of G^+ bacteria on soil nematode abundance, and a significant positive effect of fungal biomass on soil nematode abundance. Our study emphasizes the significance of a multitrophic perspective in elucidating biodiversity-multifunctionality relationships and highlights the conservation of functioning soil micro-food webs to maintain multiple ecosystem functions.

Keywords: functional diversity; nematodes; niche complementarity; phylogenetic diversity; soil biodiversity; trophic interactions

1 Introduction

Anthropogenic activities and associated changes in climate have triggered major declines in biodiversity (Tilman et al., 2006; Isbell et al., 2023), with implications for ecosystem function and service provision. Forest ecosystems regulate organic matter decomposition and carbon sequestration, and support nutrient cycling (Gamfeldt et al., 2013; Yuan et al., 2021; Augusto and Boča, 2022) that contribute to the mitigation of effects of global climate change (Eisenhauer et al., 2013; Messier et al., 2022). Multifunctionality research enables us to simultaneously evaluate the ability of ecosystems to deliver multiple functions and provide policy-relevant recommendations (van der Plas et al., 2018; Messier et al., 2022). Increasing evidence from boreal and temperate forests has shown positive biodiversity and ecosystem functioning relationships (BEFs) (Gamfeldt et al., 2013; van der Plas et al., 2016; Ratcliffe et al., 2017). However, recent studies emphasized the importance of environmental conditions in shaping the pattern of BEFs (Ratcliffe et al., 2017; Eisenhauer et al., 2018; Liu et al., 2023). It thus remains largely unknown whether the findings from the relatively species-poor regions are transferrable to the subtropical regions with species-rich forests.

Although plant species richness is often the most commonly used indicator for biodiversity, the BEFs tend to level off when plant species richness is at higher levels (Gamfeldt et al., 2013). In this regard, understanding the impacts of different metrics of biodiversity is crucial to predict BEFs under changing environmental conditions (Schuldt et al., 2018). The functional diversity of plant traits might be a more meaningful predictor than plant species richness alone (Craven et al., 2018; Xiao et al., 2020), due to the effects of niche partitioning and modification of microenvironmental conditions (Loreau and Hector. 2001; Sanaei et al., 2022). Furthermore, phylogenetic diversity could also be an important indicator of complementarity effects in ecosystem functions (Flynn et al., 2011; Xiao et al., 2020). It is increasingly recognized that evolutionarily distant species are more likely to show niche differentiation and exhibit facilitation (Xiao et al., 2020; Srivastava et al., 2012). Besides, phylogenetic diversity can capture species interactions within communities that affect ecosystem functions

(Srivastava et al., 2012), for instance, by representing interactions with higher trophic levels like pathogens and herbivores (Craven et al., 2018). And yet, limited studies have simultaneously evaluated the contributions of taxonomic, functional, and phylogenetic diversity of subtropical tree communities to ecosystem multifunctionality.

The presence and abundance of soil organisms are crucial drivers of terrestrial ecosystem multifunctionality (Wagg et al., 2014; Schuldt et al., 2018; Shi et al., 2021; Wang et al., 2023), and a global meta-analysis has shown positive relations between natural and managed tree species diversity and levels of biomass of soil microbes, bacteria, and fungi (Chen et al., 2019), with great implications for soil microbe-driven ecosystem function. However, significant knowledge gaps exist with respect to the relative importance of different groups of soil organisms across trophic levels for driving ecosystem multifunctionality. While the role of soil bacteria and fungi in regulating forest ecosystem functions has been widely documented (Shi et al., 2021; Yuan et al., 2021; Wang et al., 2023), most studies ignore the contribution of higher trophic-level organisms, such as nematodes, to modifying ecosystem functions, despite their key position within complex soil micro-food webs, and interactions with other trophic and functional group types (Wagg et al., 2014; Jiang et al., 2023). It is thus imperative to incorporate different trophic levels into multifunctionality research and explore the extent to which the higher trophic-level organisms affect ecosystem multifunctionality through trophic interactions.

The overarching aim of this 3-year manipulated field experiment, therefore, is to understand the patterns and drivers of ecosystem multifunctionality (nutrient cycling, soil carbon stocks, organic matter decomposition, plant productivity) across multiple facets of tree biodiversity (taxonomic, functional, and phylogenetic diversity) in a highly diverse subtropical forest. We hypothesized that (1) increasing levels of tree diversity, particularly functional and phylogenetic diversity, promote ecosystem multifunctionality, due to increased niche complementarity (Hooper et al., 2005; Srivastava et al., 2012; Schuldt et al., 2018), and (2) soil micro-food webs with more representatives of higher trophic levels (Cesarz et al., 2017) directly drive changes in ecosystem multifunctionality, due to greater community coexistence (Xiao et al., 2020) and modulation effects (Schuldt et al., 2018) (Fig. S1).

2. Results and Discussion

2.1 Effects of tree diversity on ecosystem functions

There were no significant effects of tree species richness on nutrient cycling, organic matter decomposition, or plant productivity (Figure 1). In contrast, soil carbon stocks and ecosystem multifunctionality significantly increased with tree species richness. Soil carbon stocks were significantly greater in the 32-species tree mixtures than in the four-species mixtures ($P < 0.05$) (Figure S2). Additionally, there was no change in the impacts of tree species richness on the ecosystem functions between models that included or excluded monocultures, showing that tree diversity effects on ecosystem multifunctionality were also apparent when diversity increased from four to 32 species.

Losses in biodiversity have triggered studies of relations between measures of diversity and ecosystem function (Tilman et al., 2006; Isbell et al., 2023). Although the positive relationship between biodiversity and ecosystem functioning has been established mostly based on individual functions like primary productivity (Erskine et al., 2006; Liang et al., 2016; Huang et al., 2018), the patterns of ecosystem multifunctionality across tree diversity gradients and underlying drivers are less well studied in subtropical forest ecosystems (Schuldt et al., 2018). In support of our first hypothesis, we found that tree species richness was positively related to ecosystem multifunctionality, where levels of soil carbon stocks, as an indicator of carbon sequestration, were significantly greater with the higher number of tree species. This observation agrees with previous findings that forest ecosystem soil carbon storage was positively affected by plant species richness (Chen et al., 2019; Xu et al., 2020; Augusto and Boča, 2022). Long-term field experiments revealed that root biomass production was significantly enhanced along a plant species richness gradient of 1–16 (Ravenek et al., 2014; Eisenhauer et al., 2018). The positive effect of tree species richness on soil carbon stocks we found may be attributed to a rise in root-derived carbon inputs, such as root exudates (Xu et al., 2020; Lange et al., 2015), due to strengthened vertical root differentiation and resource use complementarity that consequently contributed to belowground overyielding (Mueller et al., 2013).

2.2 Ecosystem properties linked to ecosystem functioning

Linear mixed-effect models indicated that of the three groups of ecosystem properties, soil organisms elicited the greatest relative effects on ecosystem multifunctionality (Figure 2), where there were positive effects of nematodes ($P = 0.004$) and SWC ($P = 0.014$) and negative effects of AMF ($P = 0.011$) (Table 1, Figure 2). Nutrient cycling was positively related to soil microbial biomass ($P = 0.026$) and negatively related to the biomass of soil fungi and AMF ($P < 0.001$) and soil pH ($P = 0.004$) (Figure 3, Figure S3 and S5). Soil carbon stocks were positively related to the abundance of soil nematodes ($P = 0.032$). Organic matter decomposition was positively related to SWC ($P = 0.023$; Figure S3). Plant productivity was positively related to the biomass of soil microbes ($P = 0.027$), G^{-} bacteria ($P = 0.016$), fungi ($P = 0.011$), and AMF ($P < 0.001$), and soil pH ($P < 0.001$) and SWC ($P = 0.011$). Ecosystem multifunctionality was positively related to soil nematode abundance ($P = 0.004$) and SWC ($P = 0.005$) (Figure S4).

Contrary to our expectation, we found that G^{+} bacteria and fungi were negatively related to all three metrics of tree diversity (taxonomic, functional, and phylogenetic diversity) (Figure 4). Indeed, this finding contrasts with previous studies showing that high levels of diversity among tree communities stimulated microbial growth, due to habitat and plant-derived resource diversity (Chen et al., 2019; Beugnon et al., 2021). Nevertheless, our results align with those reported by Cesarz et al. (2022) and Schittko et al. (2022), who illustrated the weak and negative tree diversity effects on soil microbial biomass, possibly reflecting the context-dependent diversity effects. The observed negative tree diversity impacts might be explained by the resource acquisition strategies of G^{+} bacteria and fungi (stress-tolerant) and their relatively slow growth rates (Denef et al., 2009). Unlike copiotrophic microbes that are associated with recent photosynthetic carbon under increasing tree species richness, growth of G^{+} bacteria and fungi tends to be associated with mature, stabilized organic carbon (Mellado-Vázquez et al., 2016; Wang et al., 2021). Thus, our findings indicate that the magnitude and direction of diversity impacts on belowground organisms may be largely dependent on specific microbial taxa. Moreover, plant diversity effects on soil microbial communities may need a longer time to materialize (Eisenhauer et al., 2012; Thakur et al., 2015; Cesarz et al., 2022).

2.3 Effects of soil multitrophic organisms on ecosystem multifunctionality

Different tree diversity metrics, taxonomic, functional, and phylogenetic diversity significantly decreased the biomass of G^+ bacteria and fungi ($P < 0.05$; Figure 4). Structural equation models confirmed the direct effects of aforementioned factors on ecosystem multifunctionality. Additionally, it revealed that tree species richness was positively associated with functional and phylogenetic diversity, where functional trait diversity was a negative driver of the biomass of G^+ bacteria (Figure 5). Meanwhile, the biomass of AMF was positively associated with soil nematode abundance (a bottom-up effect), and the biomass of G^+ bacteria was negatively associated with soil nematode abundance (a top-down effect). The abundance of soil nematodes, in turn, significantly promoted ecosystem multifunctionality.

Soil organisms have been shown to be important drivers of ecosystem multifunctionality (Wagg et al., 2014; Delgado-Baquerizo et al., 2020; Shi et al., 2021). However, much attention has tended to be focused on the role of single microbial groups, such as bacteria and fungi, in the regulation of ecosystem functions (Yuan et al., 2021; Li et al., 2022). Nevertheless, a multitrophic perspective is particularly crucial for low-latitude forests, where trophic interactions of highly diverse communities influence ecosystem functions (Schuldt et al., 2018). In the soil micro-food webs, nematodes are an integral component and are central to the regulation of multiple ecosystem functions (van den Hoogen et al., 2019; Wang et al., 2023) and, in support of our second hypothesis, we found that soil organisms, particularly nematodes, played a predominant role in the regulation of plant productivity and soil carbon stocks. This finding is consistent with previous studies showing that bacterivore nematodes can enhance plant productivity and stabilization of soil organic carbon (Bonkowski, 2004; Martin and Sprunger, 2021). Bottom-up and top-down effects are important regulators of soil microbial communities (Liu et al., 2016; Asiloglu et al., 2021) and in this study, we found a positive association between the biomass of arbuscular mycorrhizal fungi and soil nematode abundance, indicating strong bottom-up effects of arbuscular mycorrhizal fungi on soil nematodes. Bottom-up processes prevail when organisms are resource-limited, leading to the shaping of trophic levels within communities by resource availability (Eisenhauer et al., 2013). In this regard, the positive effect of arbuscular mycorrhizal fungi on nematodes may derive from arbuscular mycorrhizal fungi-mediated reductions in nitrogen losses and increases in soil nutrient availability (Chen et al., 2022; Shi et al., 2023).

In addition, we observed top-down effects of soil nematodes on G^+ bacteria that then led to greater ecosystem multifunctionality, supporting studies that reported the influence on soil bacterial community composition by nematode grazing (Mesel et al., 2004; Flues et al., 2017). While it is considered that the G^- bacteria affiliated with Proteobacteria and Bacteroidetes were preferred prey of soil nematodes (Flues et al., 2017; Asiloglu et al., 2021), we found a strong top-down effect of soil nematodes on G^- bacteria, possibly reflecting a decrease in nematode predation of G^- bacteria, due to higher levels of motility, biofilm formation, and intracellular resistance to digestion reported for G^- bacteria (Asiloglu et al., 2021). Given that the predation of bacteria can lead to reductions in pathogen, and enhanced soil fertility, and plant productivity (Gao et al., 2019; Jiang et al., 2023), it is possible that nematode grazing of G^+ bacteria may have contributed to the increase in ecosystem multifunctionality in this study. It is worth noting that no direct paths between tree species richness and ecosystem multifunctionality were supported by the structural equation models. Thus, our results demonstrated the importance of functional trait diversity and interactions across trophic levels in the regulation of ecosystem multifunctionality. However, the relevance of the suggested bottom-up and top-down effects needs to be tested in future experimental work by manipulating the trophic structure of soil micro-food webs.

Our results showed that soil microbial biomass positively affected the function of nutrient cycling and plant productivity, possibly due to the breakdown of complex organic polymers, such as nucleic acids and chitin, that require extracellular enzymes produced by soil microorganisms (Baldrian, 2014), and increases in the mineralization of organic nitrogen monomers (Elrys et al., 2021) that accelerated nutrient cycling and plant growth. However, we found that soil fungal biomass negatively impacted nutrient cycling, likely reflecting the close association of soil fungi-dominated microbial communities with low rates of nutrient cycling (Wardle et al., 2004), such as in acidic soils with high organic matter content and low resource quality (van der Heijden et al., 2008). Likewise, we observed negative impacts of arbuscular mycorrhizal fungi on nutrient cycling, supporting a recent study showing that arbuscular mycorrhizal fungi-mediated decreases in soil nitrification rates in subtropical forests (Shi et al., 2023).

We found that biomass of arbuscular mycorrhizal fungi was positively associated with plant productivity, likely due to symbiotic associations with plant roots and greater plant uptake of phosphorus (Smith et al., 2004) that is particularly limiting in subtropical forest (Shi et al., 2020), and increased plant resistance to pathogens and environmental stress (Chen et al., 2022). Furthermore, arbuscular mycorrhizal fungi can potentially improve nutrient use efficiency (van der Heijden et al., 1998) through the inhibition of nitrous oxide emissions (Bender et al., 2014). This might be due to the advantage of arbuscular mycorrhizal fungi over the slow-growing nitrifiers in competing for soil ammonium (Storer et al., 2018).

Overall, tree species richness was positively related to ecosystem multifunctionality, as indicated by higher levels of soil carbon stocks, likely as a result of increased root biomass production and rhizodeposition. In contrast to our expectation, the taxonomic, functional, and phylogenetic metrics of tree diversity led to decreased biomass of G^+ bacteria and fungi, possibly due to their oligotrophic affinity. This result indicates that the magnitude and direction of tree diversity impacts on belowground organisms may be largely dependent on microbial taxonomic composition. Although our results reveal the underlying mechanisms of tree diversity effects on ecosystem multifunctionality by stressing the role of trophic interactions among soil bacteria, fungi, and nematodes, additional research by manipulating the trophic structure of soil micro-food webs is needed to test the suggested bottom-up and top-down effects.

3. Material and methods

3.1 Experimental design

The study was carried out on the experimental research platform of NaBEF-China

(Nutrient addition and Biodiversity Ecosystem Function) located in southeastern China, Baisha Forest Farm, Fujian Province (25°05′N, 116°42′E), where the subtropical climate is characterized by an average annual temperature of 19.8 °C and an average annual precipitation of 1637 mm. Vegetation in a 13-ha area that had previously been planted with *Cunninghamia lanceolata* was slash-burned in 2018, prior to the establishment of 300, 12 × 12 m plots in which 256 one-year-old seedlings were planted in rows 75 cm apart, with a gradient of native tree species richness (1, 4, 8, 16, 32) in March 2019 (Shi et al., 2023). For the tree species richness gradient, we randomly selected 81, 32, 15, 110, and 4 plots, respectively, where each tree species occurred with the same probability (Table S1).

3.2 Metrics of tree biodiversity

We measured seven plant functional traits in monocultures associated with plant resource use strategies, comprising specific leaf area (SLA), leaf dry matter content (LDMC), specific root length (SRL), root tissue density (RTD), specific root surface area (SRA), and leaf and root nitrogen (N) content (Table S2), following the methods described by Pérez-Harguindeguy et al. (2013) and Cornelissen et al. (2003). Briefly, SLA (m^2 kg^{-1}) and SRA (cm^2 g^{-1}) were measured by scanning leaf and root material using an Epson Expression 10000XL scanner (Epson, Japan). LDMC (mg g^{-1}) was measured following drying fresh leaf material at 60 °C for 48 h. SRL (m g^{-1}) and RTD (g cm^{-3}) of fine roots (< 2 mm) were analyzed using WINRHIZO software (Regents Instrument, Canada). Leaf and root N content of finely ground oven-dried tissue was measured using an Elementar analyzer (Elemental EL MAX, Germany).

We quantified the study plot functional diversity using the functional dispersion index (FDis), based on the ‘dbFD’ function in the FD package (Laliberté et al., 2015). The phylogenetic diversity was calculated using the mean phylogenetic distance, based on the PICANTE package (Kembel et al., 2010). The functional and phylogenetic diversity of the mixed experimental plots were weighed by the initial relative abundance of each tree species (Shi et al., 2023).

3.3 Soil physiochemical properties

Ten samples of soil (0–10 cm) were collected at random points equidistant between saplings to ensure full plot representation (Wan et al., 2022) using a 3.5-cm diameter auger in August 2021. The ten samples were combined to form a single composite sample per plot. Soil samples were passed through a 2-mm sieve to remove roots and stones. Soil water content (SWC) was determined following drying soil samples at 105 °C for 24 h. Bulk density was determined using the core method. Soil pH was determined using a soil-to-water ratio of 1:2.5. Soil content of total C and N was determined using an elemental analyzer (Elemental EL MAX, Germany). Soil mineral N (extractable ammonium and nitrate) was extracted from soil and 1 M KCl (1: 5) and determined using an automated ion analyzer (Skalar San++, Netherlands). Soil mineralization and nitrification rates were measured as the changes in total mineral and nitrate N content, respectively, between the start and end of a 28-d period of incubation at 25 °C (Shi et al., 2018). Soil enzyme activity measured as μmol g^{-1} dry $soil^{-1}$ h^{-1} of β-glucosidase, cellobiohydrolase, peroxidase, phenol oxidase, N-acetylglucosaminidase, and acid phosphatase, was measured using methods described by Saiya-Cork et al. (2002).

3.4 Soil organisms

Soil microbial biomass was estimated following chloroform fumigation, where biomass of total bacteria and fungi, including gram-positive (G^+) and gram-negative (G^-) bacteria, and arbuscular mycorrhizal fungi (AMF) was determined using phospholipid fatty acid analysis. We measured G^+ bacteria on the basis of i14:0, i15:0, a15:0, i16:0, i17:0, and a17:0, and G^- bacteria were measured on the basis of 16:1ω9, 16:1ω7, 18:1ω7, 18:1ω5, cy17:0, and cy19:0 (Tedersoo et al., 2016); the sum of 18:2ω6,9 and 18:1ω9 was used as a fungal marker, and lipid fatty acid 16:1ω5 was used as a marker for AMF. Soil nematodes were extracted from 100 g of fresh soil samples using a Baermann funnel and identified using a Motic microscope (Wang et al., 2023).

3.5 Ecosystem multifunctionality

We measured indicators of four ecosystem functions (nutrient cycling, soil carbon stocks, organic matter decomposition, plant productivity) to calculate ecosystem multifunctionality (Table S3). Soil mineralization and nitrification rates, and total and mineral N indicators of nutrient cycling (Wang et al., 2019). Soil total carbon content corrected by soil bulk density indicated carbon stocks (Wang et al., 2019). Soil enzyme activities of β-glucosidase, cellobiohydrolase, peroxidase, phenol oxidase, N-acetylglucosaminidase, and acid phosphatase were indicators of organic matter decomposition (Shi et al., 2021), and tree height, ground basal area, and annual litterfall yield indicated plant productivity (Shi et al., 2021). We measured tree height and ground basal diameter after two experiment years and annual litterfall yield was calculated from monthly litter traps (47 cm × 47 cm × 20 cm) every month from April 2021 to March 2022. We standardized the four ecosystem functions using min-max normalization (0-1) (Wang et al., 2019) and then calculated the ecosystem multifunctionality index as the average of the four standardized scores (Eisenhauer et al., 2018). We used weighted ecosystem multifunctionality to down-weight highly correlated functions, as described by Manning et al. (2018).

3.6 Statistical analysis

At first, the individual ecosystem functions and ecosystem multifunctionality were analyzed separately using statistical models including linear, log-linear, and exponential models with tree species richness as the explanatory variable. Meanwhile, differences in tree species richness-level means of ecosystem functions were tested using a one-way analysis of variance, with the comparison of means using the Duncan test at $P < 0.05$.

Secondly, we used linear mixed-effect models to evaluate the relative importance of ecosystem properties in affecting ecosystem multifunctionality using the lme4 package. The models were established with tree species composition as a random factor (Shi et al., 2023). In addition, we classified the ecosystem properties into three groups including tree diversity metrics (taxonomic, functional, and phylogenetic diversity), soil organisms (G^+ bacteria, G^- bacteria, fungi, AMF, nematodes), and environmental factors. The model averaging approach was then performed to quantify the relative importance of the three groups as predictors of ecosystem multifunctionality (Huang et al., 2022). Before this analysis, we controlled the variance inflation factor to < 10, to avoid multicollinearity among variables. The regression analysis was used to investigate the relationship between ecosystem properties and ecosystem functions.

Finally, Structural equation models (SEMs) were used to estimate the direct and indirect effects of tree diversity on ecosystem multifunctionality using the piecewiseSEM package (Lefcheck, 2016), and overall fit was examined using the Fisher's C statistic and *P* value. Prior to analysis, all of the variables were standardized by subtracting the mean from observed values and dividing standard deviations. A priori hypotheses including all potential relationships are provided in Figure S1. The statistical analyses were performed using R4.2.0 (R Core Team, 2021).

Author contributions

XS led the writing and improvement of the original manuscript. JW contributed ideas to the study and data analysis. NE, JP, YC, SL and MELB greatly improved the manuscript. YF performed data analysis. LH and LW collected the data. ZH conceived the ideas and experimental design, and all authors gave final approval for publication.

Conflict of interest

The authors have no conflict of interest.

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Table 1 Linear mixed-effect models evaluating the relative importance of ecosystem properties in affecting ecosystem multifunctionality.

Predictors	Estimates	F value	*P* value
Tree diversity			
Functional trait diversity	-0.01	1.18	0.280
Phylogenetic diversity	0.02	3.03	0.084
Soil organisms			
Microbial biomass	0.01	2.64	0.107
AMF	-0.04	6.65	**0.011**
Nematodes	0.02	8.61	**0.004**
Fungi	0.02	1.52	0.220
Gram-negative bacteria	-0.01	0.70	0.405
Gram-positive bacteria	0.02	2.33	0.129
Soil properties			
Soil water content	0.02	6.18	**0.014**
Soil pH	0.01	0.63	0.428

The marginal R^2 and conditional R^2 were 0.162 and 0.316, respectively. Tree species richness was removed from the final model to reduce collinearity. AMF: arbuscular mycorrhizal fungi.

Figure 1 Effects of tree species richness on indicators of nutrient cycling, carbon stocks, organic matter decomposition, plant productivity, and ecosystem multifunctionality. The line and shaded area represent the fitted regression and the 95% confidence interval of the fit, respectively.

Figure 2 The relative effects of indicators of tree diversity metrics (yellow), soil organisms (green), and soil physiochemical properties (blue) on ecosystem multifunctionality. The model averaging shows the relative importance of the three groups of explanatory variables (left panel) and linear mixed-effect model parameter estimates (right panel) were standardized regression coefficients ± 95% CIs, with $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Figure 3 Linear regression analyses of the relationship between soil organisms and individual ecosystem functions. The fitted relationship (solid line) was shown with 95% CIs (shaded area). AMF: arbuscular mycorrhizal fungi.

Figure 4 Linear regression analyses of relationships between tree diversity metrics and soil organisms. The fitted relationship (solid line) was shown with 95% CIs (shaded area).

Figure 5 Structural equation model estimates of direct and indirect effects of tree diversity on ecosystem multifunctionality. Standardized path coefficients are shown against arrows, where black and red arrows indicate positive and negative relationships, respectively, at $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$; R^2-values indicate the contribution of explanatory variables to the relationship; Fisher's C = 39.43, $P = 0.17$, AIC = 1227.12. AMF: arbuscular mycorrhizal fungi.

Figure 1

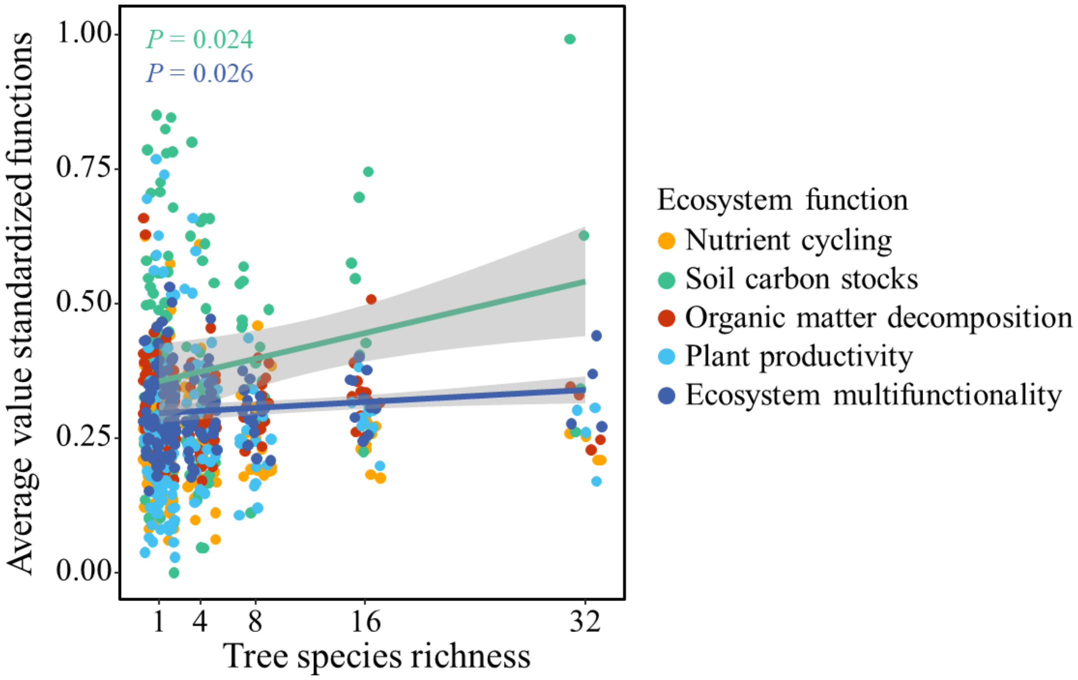

P = 0.024
P = 0.026
Average value standardized functions
1.00
0.75
0.50
0.25
0.00
1
4
8
16
32
Tree species richness
Ecosystem function
● Nutrient cycling
● Soil carbon stocks
● Organic matter decomposition
● Plant productivity
● Ecosystem multifunctionality

Figure 2

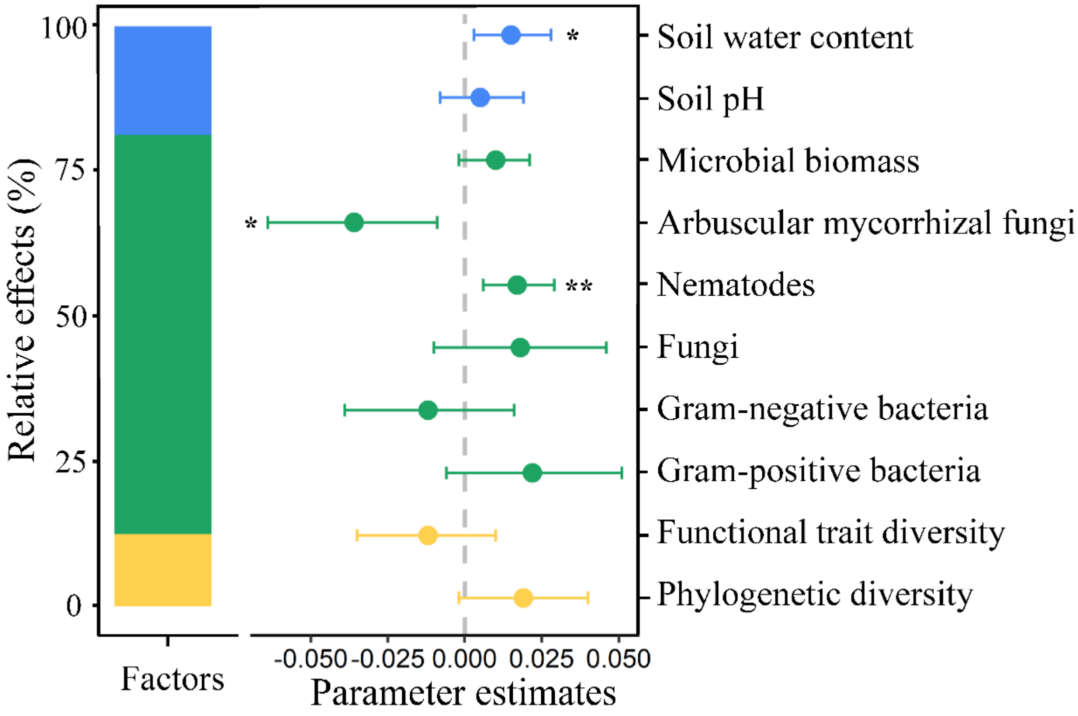

100
75
50
25
0
Relative effects (%)
Factors
Soil water content
Soil pH
Microbial biomass
Arbuscular mycorrhizal fungi
Nematodes
Fungi
Gram-negative bacteria
Gram-positive bacteria
Functional trait diversity
Phylogenetic diversity
*
*
**
-0.050
-0.025
0.000
0.025
0.050
Parameter estimates

Figure 3

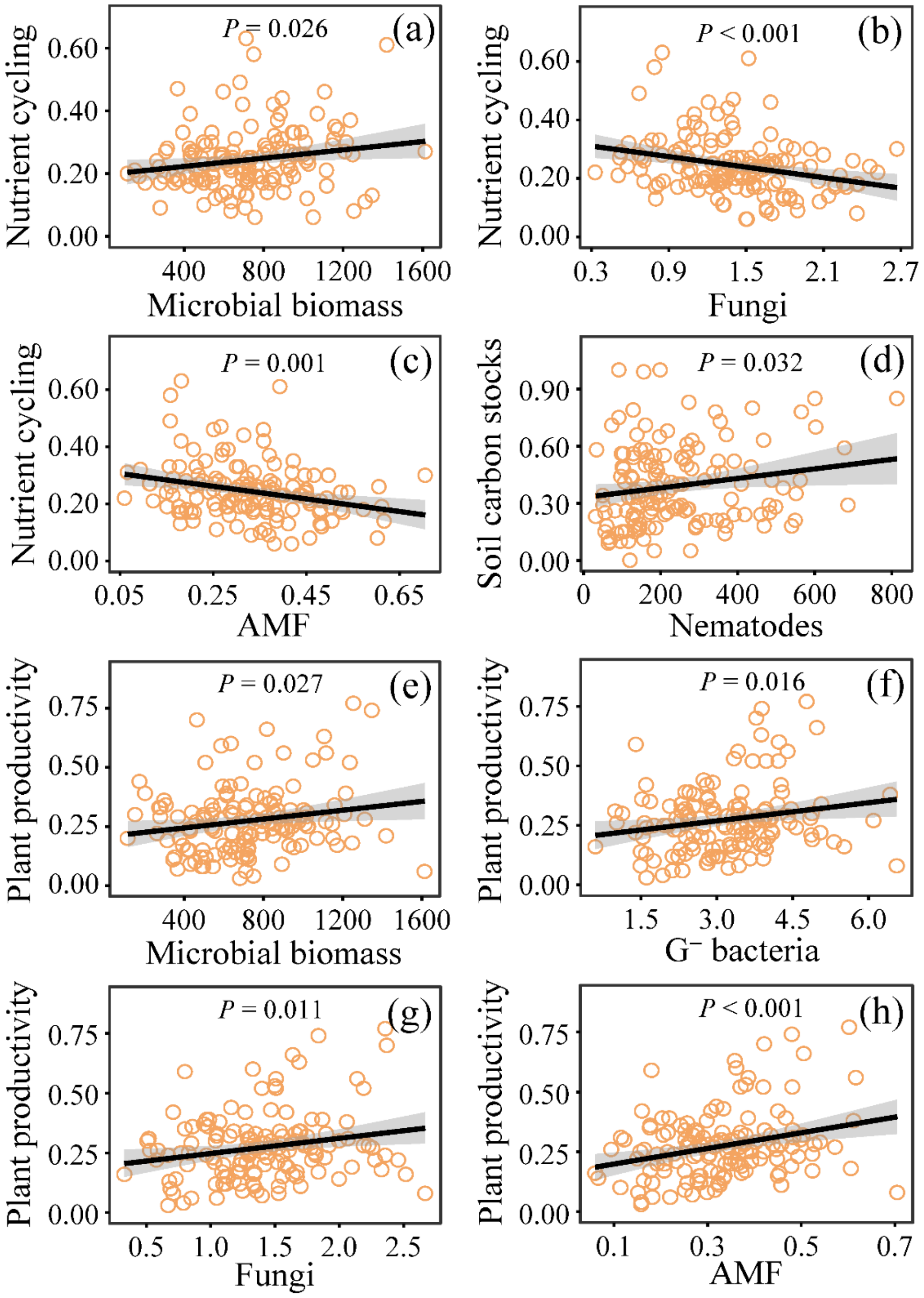
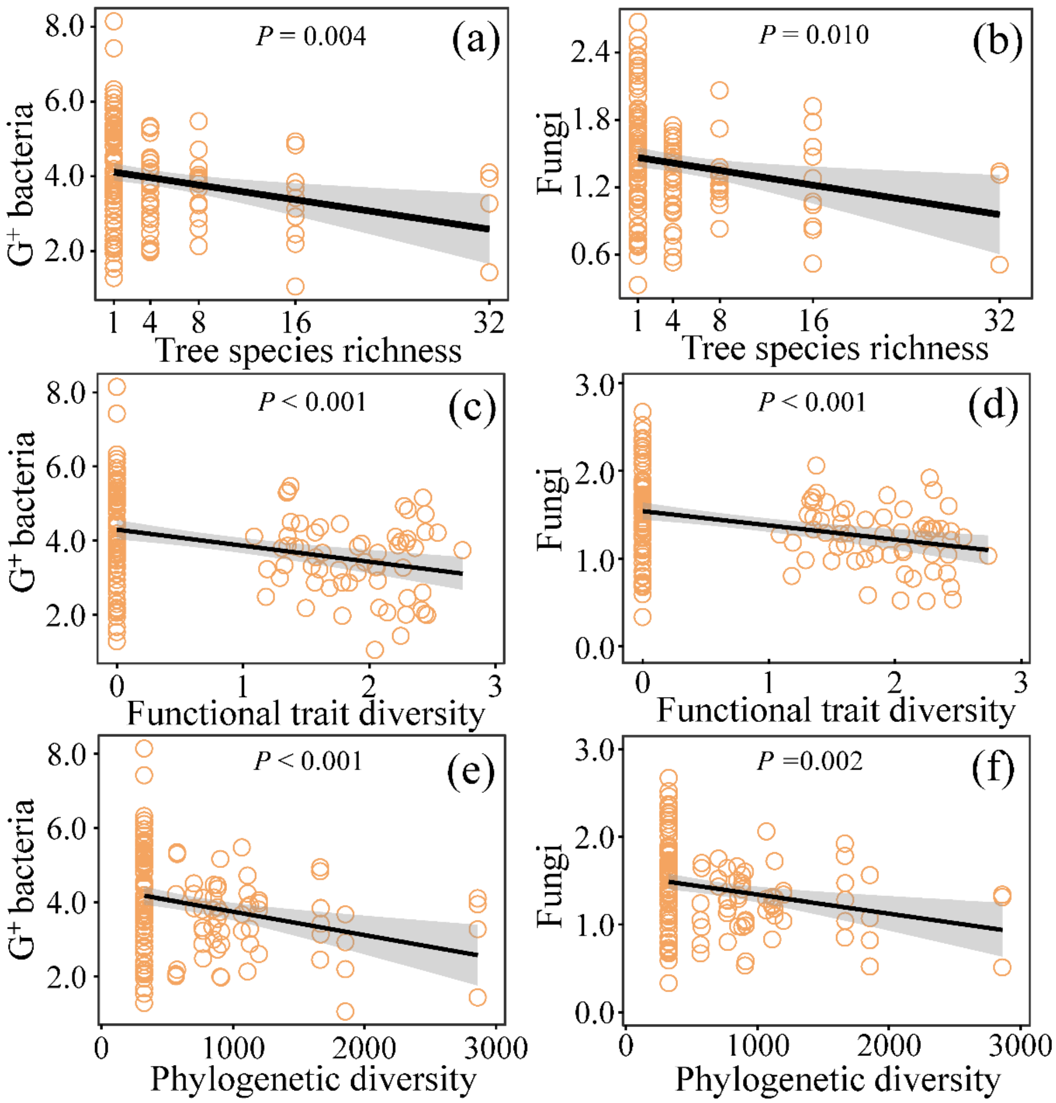
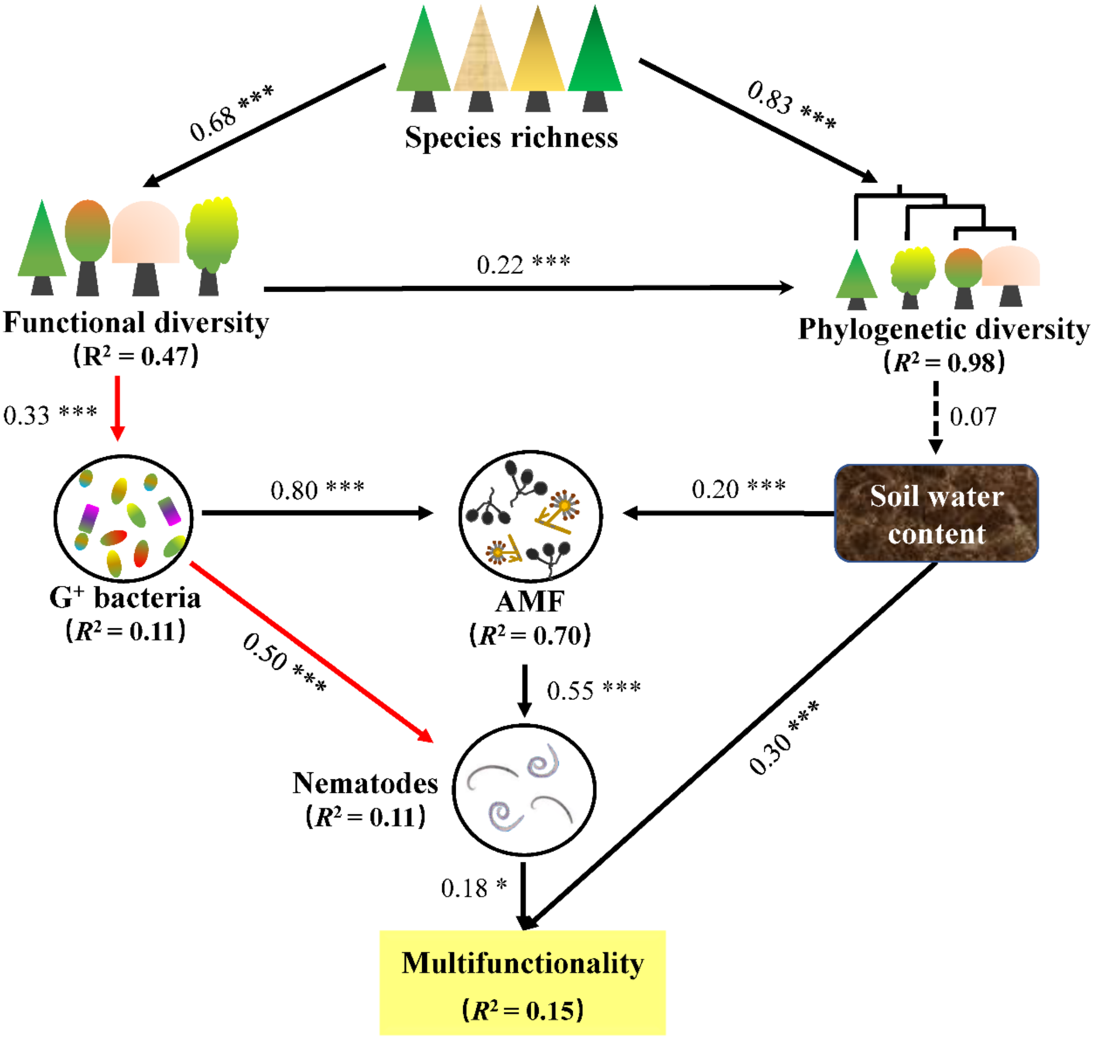

(a)
P = 0.026
Nutrient cycling
0.00
0.20
0.40
0.60
400
800
1200
1600
Microbial biomass
(b)
P < 0.001
Nutrient cycling
0.00
0.20
0.40
0.60
0.3
0.9
1.5
2.1
2.7
Fungi
(c)
P = 0.001
Nutrient cycling
0.00
0.20
0.40
0.60
0.05
0.25
0.45
0.65
AMF
(d)
P = 0.032
Soil carbon stocks
0.00
0.30
0.60
0.90
0
200
400
600
800
Nematodes
(e)
P = 0.027
Plant productivity
0.00
0.25
0.50
0.75
400
800
1200
1600
Microbial biomass
(f)
P = 0.016
Plant productivity
0.00
0.25
0.50
0.75
1.5
3.0
4.5
6.0
G⁻ bacteria
(g)
P = 0.011
Plant productivity
0.00
0.25
0.50
0.75
0.5
1.0
1.5
2.0
2.5
Fungi
(h)
P < 0.001
Plant productivity
0.00
0.25
0.50
0.75
0.1
0.3
0.5
0.7
AMF

Figure 4



(a)
P = 0.004
G$^+$ bacteria
8.0
6.0
4.0
2.0
1
4
8
16
32
Tree species richness
(b)
P = 0.010
Fungi
2.4
1.8
1.2
0.6
1
4
8
16
32
Tree species richness
(c)
P < 0.001
G$^+$ bacteria
8.0
6.0
4.0
2.0
0
1
2
3
Functional trait diversity
(d)
P < 0.001
Fungi
3.0
2.0
1.0
0.0
0
1
2
3
Functional trait diversity
(e)
P < 0.001
G$^+$ bacteria
8.0
6.0
4.0
2.0
0
1000
2000
3000
Phylogenetic diversity
(f)
P =0.002
Fungi
3.0
2.0
1.0
0.0
0
1000
2000
3000
Phylogenetic diversity

665 **Figure 5**



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Supplementary Information

Trophic interactions in soil micro-food webs drive ecosystem multifunctionality along tree species richness

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Running title: Soil micro-food webs regulate ecosystem multifunctionality

The supplementary information includes three tables and five figures.

Table S1 Tree species composition of study plots, ranked by species richness.

Species richness	Study plot	Tree species composition
1	27	*Cunninghamia lanceolata*
1	248	*Cunninghamia lanceolata*
1	258	*Cunninghamia lanceolata*
1	259	*Cunninghamia lanceolata*
1	28	*Pinus massoniana*
1	50	*Pinus massoniana*
1	51	*Pinus massoniana*
1	134	*Pinus massoniana*
1	108	*Cyclocarya paliurus*
1	220	*Cyclocarya paliurus*
1	88	*Fokienia hodginsii*
1	89	*Fokienia hodginsii*
1	107	*Fokienia hodginsii*
1	136	*Fokienia hodginsii*
1	235	*Taxus wallichiana*
1	236	*Taxus wallichiana*
1	237	*Taxus wallichiana*
1	91	*Cryptomeria japonica*
1	142	*Cryptomeria japonica*
1	143	*Cryptomeria japonica*
1	166	*Cryptomeria japonica*
1	96	*Alnus trabeculosa*
1	144	*Alnus trabeculosa*
1	23	*Castanopsis carlesii*
1	247	*Castanopsis carlesii*
1	274	*Castanopsis carlesii*
1	275	*Castanopsis carlesii*
1	120	*Castanopsis fissa*
1	185	*Castanopsis fissa*
1	186	*Castanopsis hystrix*
1	187	*Castanopsis hystrix*
1	270	*Castanopsis hystrix*
1	8	*Castanopsis sclerophylla*
1	9	*Castanopsis sclerophylla*
1	62	*Castanopsis sclerophylla*
1	170	*Castanopsis sclerophylla*
1	44	*Cinnamomum camphora*
1	86	*Cinnamomum camphora*
1	160	*Elaeocarpus sylvestris*

1	218	*Elaeocarpus sylvestris*
1	52	*Euscaphis japonica*
1	224	*Euscaphis japonica*
1	17	*Hovenia acerba*
1	18	*Hovenia acerba*
1	241	*Hovenia acerba*
1	35	*Liquidambar formosana*
1	146	*Liquidambar formosana*
1	266	*Liquidambar formosana*
1	267	*Liquidambar formosana*
1	99	*Lithocarpus glaber*
1	121	*Lithocarpus glaber*
1	80	*Manglietia yuyuanensis*
1	296	*Manglietia yuyuanensis*
1	182	*Michelia macclurei*
1	211	*Michelia macclurei*
1	31	*Michelia maudiae*
1	162	*Michelia maudiae*
1	36	*Mytilaria laosensis*
1	169	*Mytilaria laosensis*
1	228	*Mytilaria laosensis*
1	229	*Mytilaria laosensis*
1	292	*Ormosia hosiei*
1	90	*Ormosia hosiei*
1	22	*Osmanthus fragrans*
1	126	*Osmanthus fragrans*
1	74	*Phoebe bournei*
1	161	*Phoebe bournei*
1	176	*Phoebe bournei*
1	177	*Phoebe bournei*
1	7	*Phoebe chekiangensis*
1	207	*Phoebe chekiangensis*
1	153	*Quercus variabilis*
1	225	*Quercus variabilis*
1	226	*Quercus variabilis*
1	284	*Quercus variabilis*
1	114	*Sapindus saponaria*
1	299	*Sapindus saponaria*
1	171	*Schima superba*
1	281	*Schima superba*
1	46	*Schima superba*
1	1	*Schima superba*

4	2	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*
4	55	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*
4	56	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*
4	5	*Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba*
4	6	*Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba*
4	16	*Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba*
4	14	*Celtis sinensis, Quercus variabilis , Acer palmatum, Lithocarpus glaber*
4	154	*Celtis sinensis, Quercus variabilis , Acer palmatum, Lithocarpus glaber*
4	41	*Castanopsis hystrix, Cunninghamia lanceolata , Cryptomeria japonica, Castanopsis carlesii*
4	42	*Castanopsis hystrix, Cunninghamia lanceolata , Cryptomeria japonica, Castanopsis carlesii*
4	105	*Castanopsis hystrix, Cunninghamia lanceolata , Cryptomeria japonica, Castanopsis carlesii*
4	69	*Cunninghamia lanceolata , Pinus massoniana, Taxus wallichiana, Mytilaria laosensis*
4	116	*Cunninghamia lanceolata , Pinus massoniana, Taxus wallichiana, Mytilaria laosensis*
4	103	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis*
4	104	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis*
4	109	*Celtis sinensis, Quercus variabilis , Acer palmatum, Lithocarpus glaber*
4	110	*Celtis sinensis, Quercus variabilis , Acer palmatum, Lithocarpus glaber*
4	12	*Cryptomeria japonica, Celtis sinensis, Phoebe bournei, Acer palmatum*
4	112	*Cryptomeria japonica, Celtis sinensis, Phoebe bournei, Acer palmatum*
4	113	*Cryptomeria japonica, Celtis sinensis, Phoebe bournei, Acer palmatum*
4	117	*Cryptomeria japonica, Castanopsis carlesii, Phoebe bournei, Schima superba*

4	118	*Cryptomeria japonica, Castanopsis carlesii, Phoebe bournei, Schima superba*
4	139	*Cryptomeria japonica, Castanopsis carlesii, Phoebe bournei, Schima superba*
4	122	*Castanopsis hystrix, Liquidambar formosana, Fokienia hodginsii, Castanopsis sclerophylla*
4	130	*Castanopsis hystrix, Liquidambar formosana, Fokienia hodginsii, Castanopsis sclerophylla*
4	131	*Castanopsis hystrix, Liquidambar formosana, Fokienia hodginsii, Castanopsis sclerophylla*
4	132	*Castanopsis hystrix, Cunninghamia lanceolata, Fokienia hodginsii, Taxus wallichiana*
4	25	*Castanopsis hystrix, Cunninghamia lanceolata, Fokienia hodginsii, Taxus wallichiana*
4	194	*Castanopsis hystrix, Cunninghamia lanceolata, Fokienia hodginsii, Taxus wallichiana*
4	137	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis*
4	155	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis*
4	217	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis*
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8	58	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei, Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa,*
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8	11	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*

8	269	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
8	141	*Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
8	75	*Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi, Phoebe chekiangensis*
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16	33	*Castanopsis hystrix, Cunninghamia lanceolata , Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei , Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi , Phoebe chekiangensis*
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16	179	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
16	181	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
16	193	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis, Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
16	277	*Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis, Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
16	250	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*

16	198	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*
16	199	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber*
32	57	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei, Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi, Phoebe chekiangensis, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
32	157	*Castanopsis hystrix, Cunninghamia lanceolata , Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei, Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi , Phoebe chekiangensis, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*

32	175	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei, Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi , Phoebe chekiangensis, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*
32	238	*Castanopsis hystrix, Cunninghamia lanceolata, Cryptomeria japonica, Castanopsis carlesii, Michelia macclurei, Euscaphis japonica, Manglietia yuyuanensis, Alnus trabeculosa, Fokienia hodginsii, Taxus wallichiana, Phoebe bournei, Schima superba, Ormosia hosiei, Michelia maudiae, Machilus pauhoi, Phoebe chekiangensis, Liquidambar formosana, Pinus massoniana, Celtis sinensis, Quercus variabilis , Hovenia acerba, Castanopsis fissa, Cyclocarya paliurus, Sapindus saponaria, Castanopsis sclerophylla, Mytilaria laosensis, Acer palmatum, Lithocarpus glaber, Cinnamomum camphora, Elaeocarpus sylvestris, Lagerstroemia indica, Osmanthus fragrans*

Table S2 Definition and justification for measurement of plant functional traits.

Functional trait	Definition and measurement
Specific leaf area (SLA)	SLA (m^2 kg^{-1}) is the area of one side of a fresh leaf divided by its oven-dried mass.
	SLA is positively related to an acquisitive resource use strategy, and reflects a positive relation with growth rate (Cornelissen et al., 2003; Shi et al., 2020).
	In May 2021, fully developed leaves without herbivore or pathogen damage were cut from the stem and assayed following the methods described by Cornelissen et al. (2003). Leaves were scanned using a scanner (Epson Expression 10000XL scanner) and then oven-dried at 60 °C for 48 h.
Leaf dry matter content (LDMC)	LDMC (mg g^{-1}) is the oven-dried mass of a leaf divided by its water-saturated fresh mass.
	Leaves with high LDMC tend to be tough, and negatively correlate with growth rate. LDMC tends to scale with 1/SLA.
	Fully developed leaves without herbivore or pathogen damage were cut from the stem and assayed for LDMC, as described by Cornelissen et al. (2003). Briefly, water-saturated fresh mass was measured and then dry mass was measured after oven-drying at 60 °C for 48 h.
Leaf N content	Leaf N content (mg g^{-1}) is the total amount of N per unit of dry leaf mass.
	Leaf N content tends to be closely associated with high nutritional quality to the consumers in food webs (Cornelissen et al., 2003).
	Leaf N content was measured from finely ground oven-dried leaf using an Elementar analyzer (Elementar Analysensysteme Co., Hanau, Germany).
Specific root length (SRL)	SRL (m g^{-1}) is the ratio of root length to mass.
	High SRL usually refers to faster root elongation rates and higher rates of nutrient and water uptake capacity, and is therefore positively related to relative growth rates (Cornelissen et al., 2003; Weemstra et al., 2020).

	Surface soil (0–20 cm) at the base of the trees was carefully excavated to expose the main lateral roots, and roots (< 2 mm) were gently washed in deionized water to remove adhered soil. Total length of roots was analyzed using WINRHIZO software (Regents Instrument, Canada), and dry mass was measured following oven-drying at 60 °C for 48 h.
Root tissue density (RTD)	RTD (g cm^{-3}) is the root dry mass over volume.
	RTD is positively related to root longevity and negatively associated with nutrient uptake.
	Total length and diameter of roots were analyzed using WINRHIZO software (Regents Instrument, Canada). Dry mass was measured following oven-drying at 60 °C for 48 h.
Specific root surface area (SRA)	SRA (cm^{2} g^{-1}) is the amount of root surface per gram of root.
	SRA is a surrogate of plant nutrient uptake strategy (Hodge et al., 2009). High SRA is related to greater contact with soil nutrient, and higher N uptake potential (Cornelissen et al., 2003).
	SRA was assayed by scanning washed roots using a scanner (Epson Expression 10000XL scanner) after oven-drying at 60 °C for 48 h.
Root N content	Root N content (mg g^{-1}) is the total amount of N per unit of dry leaf mass.
	Root N content tends to be closely associated with high nutritional quality to the consumers in food webs (Cornelissen et al., 2003).
	Root N content was measured from finely ground oven-dried leaf using an elementar analyzer (Elementar Analysensysteme Co., Hanau, Germany).

Table S3 Indicators of ecosystem function.

Ecosystem function	**Indicator**
Soil carbon stocks	Soil total carbon corrected by bulk density
Nutrient cycling	Soil mineralization and nitrification rates, total N, mineral N
Organic matter decomposition	Enzyme activities of β-glucosidase, cellobiohydrolase, peroxidase, phenol oxidase, N-acetylglucosaminidase, acid phosphatase
Plant productivity	Tree height, ground basal area, annual litterfall yield

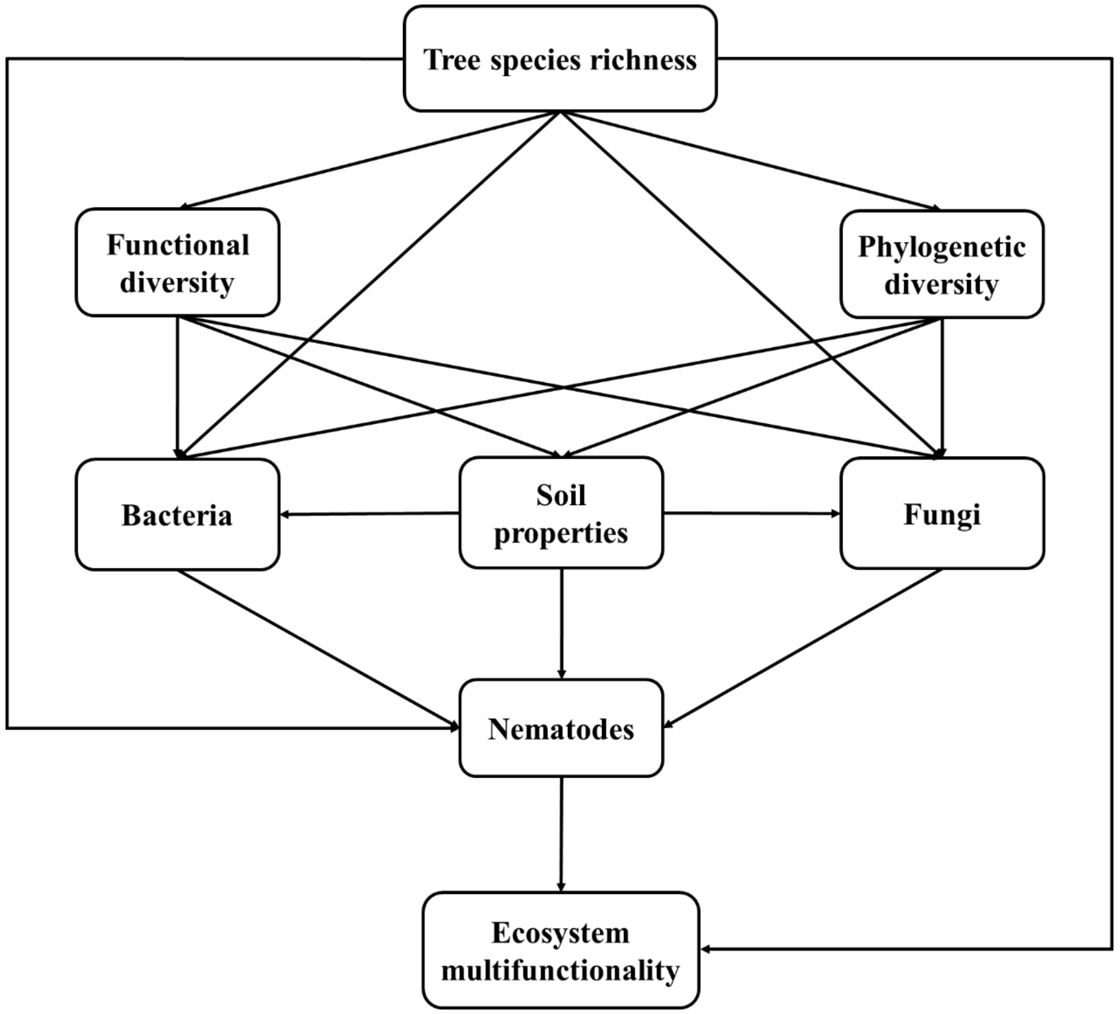

Figure S1 A priori structural equation model assumptions of direct and indirect effects of tree diversity on ecosystem multifunctionality.

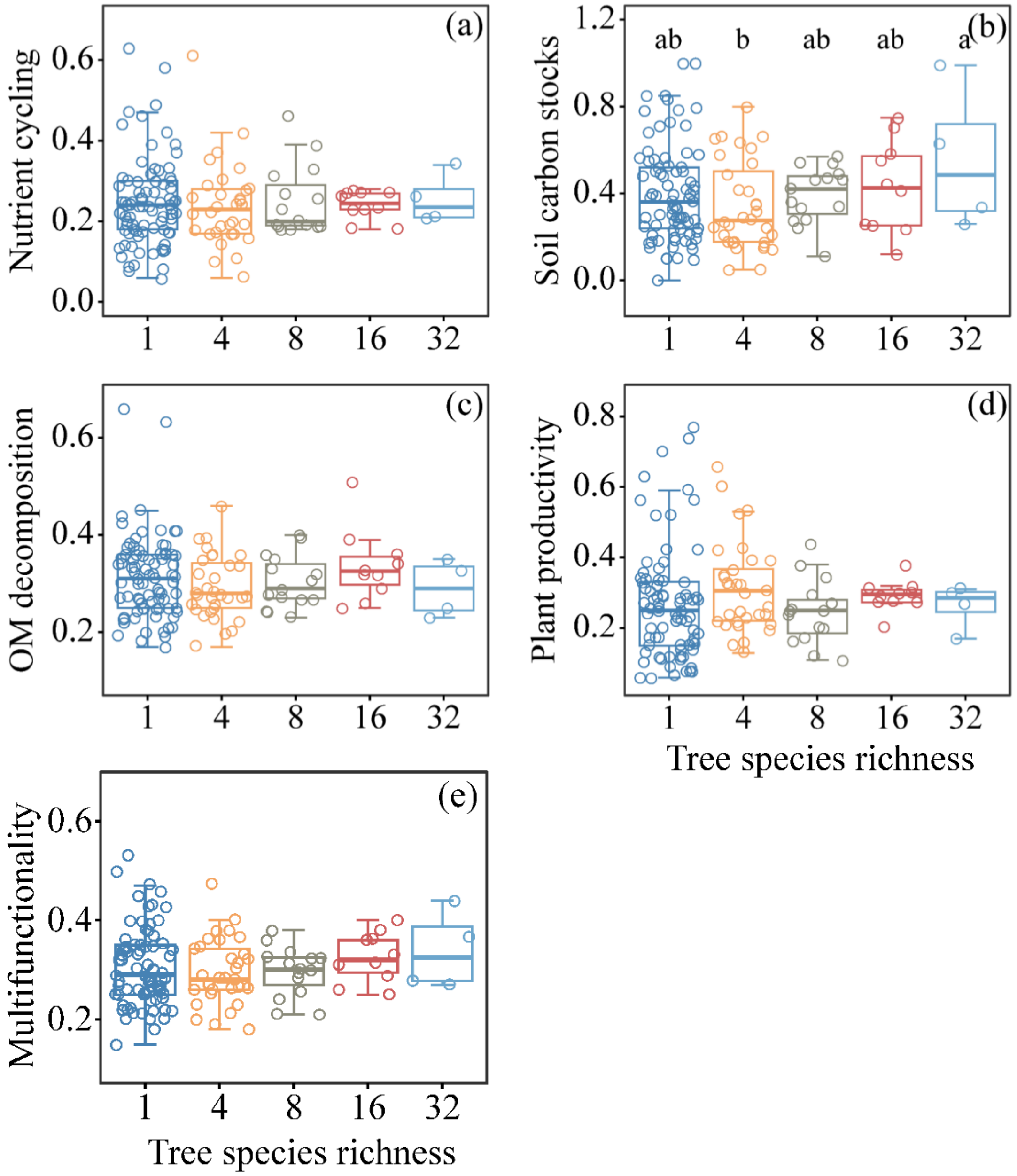

Figure S2 Effects of tree species richness on indicators of nutrient cycling (a), soil carbon stocks (b), organic matter decomposition (c), plant productivity (d) and ecosystem multifunctionality (e). Values for boxplots are medians, with 75% of observations in the boxes, and whiskers above and below the boxes indicating the 95th and 5th percentiles. Different letters indicate statistical differences at $P < 0.05$ using the one-way analysis of variance based on the Duncan test.

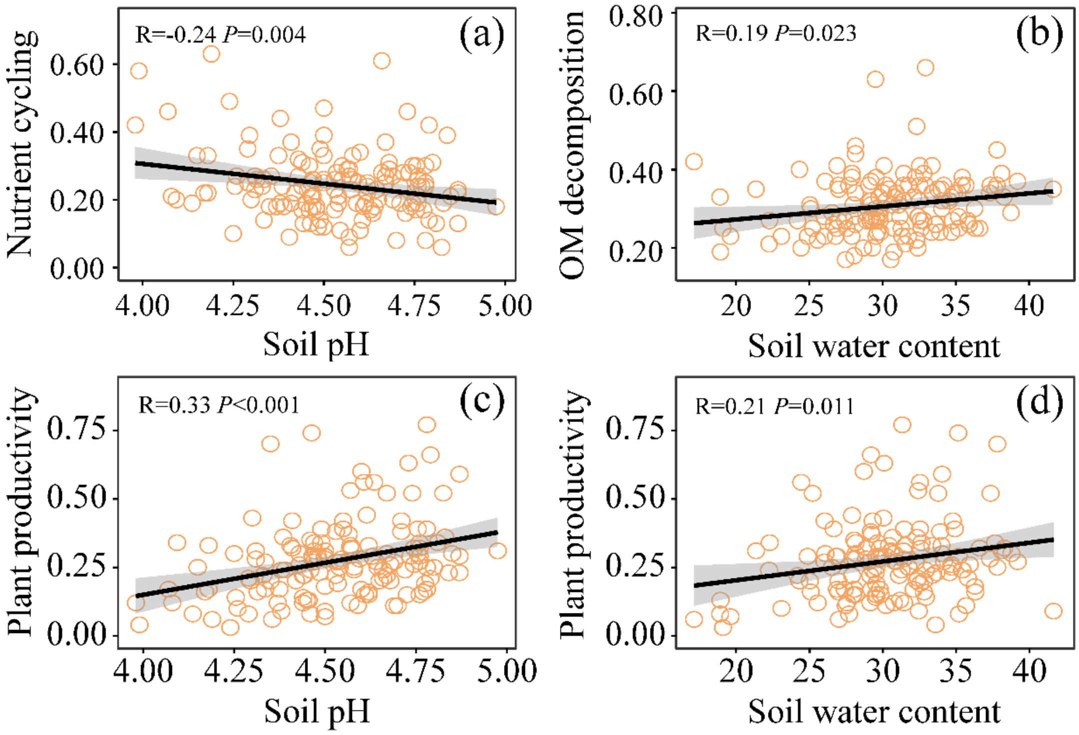

Figure S3 Linear regression analysis of the relationship between soil properties and ecosystem function. The fitted relationship (solid line) is shown with 95% CIs (shaded area). OM decomposition: organic matter decomposition.

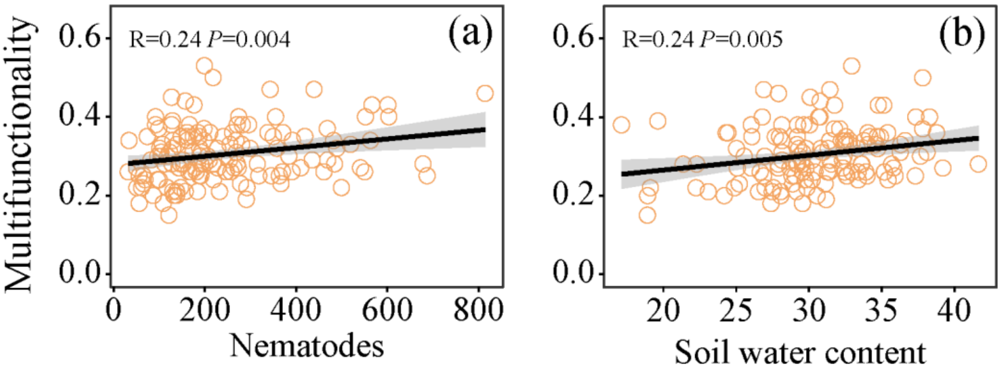

Figure S4 Linear regression analysis of the relationships between soil nematode abundance and soil water content with ecosystem multifunctionality. The fitted relationship (solid line) is shown with 95% CIs (shaded area).

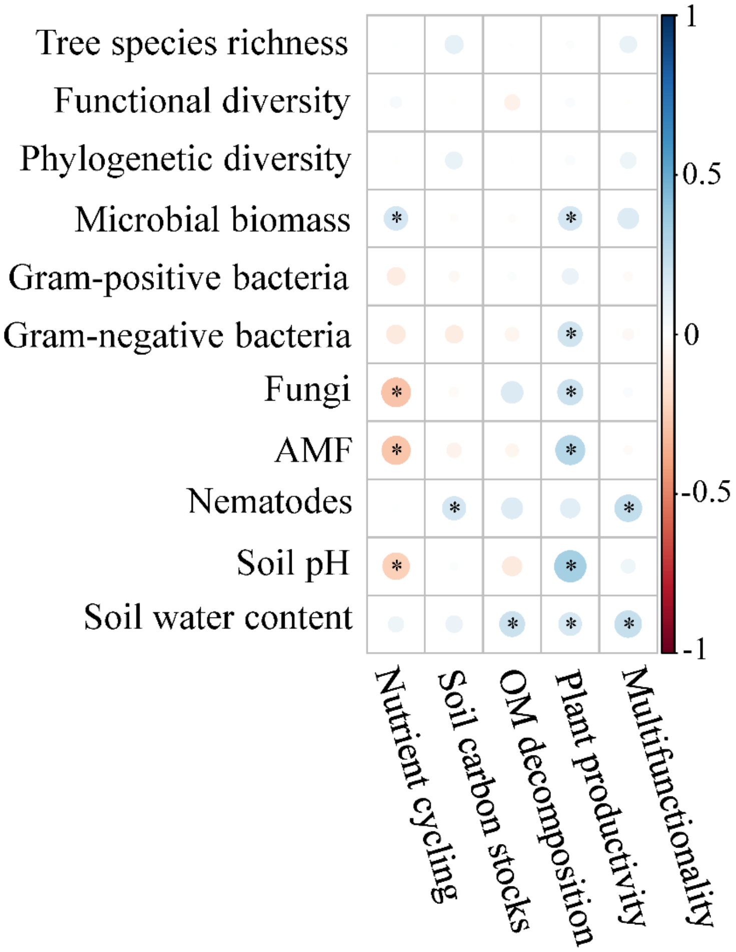

Figure S5 Correlation between ecosystem properties and ecosystem functions. Blue and red circles with asterisks indicate significant (*P* < 0.05) positive and negative effects, respectively. Circle size scales with the predictors' correlation estimate. AMF: arbuscular mycorrhizal fungi, OM decomposition: organic matter decomposition.

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