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Soil stoichiometry mediates links between tree functional diversity and soil microbial diversity in a temperate forest

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Abstract

Interactions between plants and soil microbial communities underpin soil processes and forest ecosystem function but the links between tree diversity and soil microbial diversity are poorly characterized. Differences in both the taxonomic and functional diversity of trees and microbes can shape soil nutrient status and carbon storage, but the stoichiometry of carbon and nutrients in the soil also influences resource availability to plant and microbial communities. Given the key role of resource availability in plant-soil interactions, we hypothesized that relationships between tree diversity metrics and soil bacterial or fungal diversity are mediated by soil stoichiometry. To test our hypothesis, we measured tree diversity metrics (tree species richness, functional trait diversity and functional trait composition) and soil stoichiometry in a temperate forest in China, and we determined soil microbial diversity by Illumina sequencing. We used structural equation models to assess the relationships between tree diversity metrics and soil bacterial or fungal diversity, and to evaluate the influence of soil stoichiometry. Overall, microbial diversity was strongly related to soil stoichiometry, whereby fungal diversity was associated with high soil N:P ratios, whereas bacterial diversity was related to high soil C:P ratios. Soil bacterial and fungal diversity were more closely related to tree functional trait diversity and composition than to tree species richness, and the links between tree and soil microbial diversity were mediated by soil stoichiometry. The strong links between tree functional traits, soil stoichiometry and soil bacteria or fungi suggest that resource quality plays a key role in plant-microbial interactions. Our results highlight the importance of nutrient stoichiometry in linkages between tree functional diversity and soil microbial diversity.

Key words: *Bacterial and fungal diversity; forest soil stoichiometry; functional trait composition; tree functional trait diversity; tree species richness; plant-soil interactions; soil microbial communities.*

Highlights

- Soil bacterial and fungal diversity responded differently to tree diversity metrics and soil stoichiometry.
- Soil microbial diversity was strongly associated with soil stoichiometry.
- Soil bacterial and fungal diversity were more closely related to tree functional trait diversity and composition than to tree species richness.

1. Introduction

Soil microbes, particularly bacteria and fungi, are key components of forest ecosystems, because they catalyse multiple crucial ecosystem processes (Voříšková and others 2014; Lladó and others 2017). Soil microbial communities are primarily responsible for decomposition processes that underpin forest nutrient and carbon dynamics and can thus influence tree species diversity and productivity (Wardle and others 2004; Van Der Heijden and others 2008; Bardgett and van der Putten 2014). In turn, forest soil microbes are influenced by tree species diversity and functional traits, which modify habitat conditions, diversify resources and facilitate mutualisms (Wardle and others 2004; Pantha and Dassanayake 2020; Prada-Salcedo and others 2021). The diversity and species composition of trees and soil microbial communities are also strongly associated with soil properties and nutrient status (Han and others 2005; Li and others 2020) and thus, numerous interactions between plants, soil properties and microbial communities are crucial for forest ecosystem function (Delgado-Baquerizo and others 2018; Li and others 2020; Yuan and others 2020). However, the diversity and species composition of both trees and soil microbes are being affected by climate change, land-use intensification (Vitali and others 2016; Lladó and others 2017), and nutrient inputs from atmospheric deposition (Zhang and others 2018; Ma and others 2021), all of which could modify plant-soil interactions and influence important forest ecosystem services such as carbon storage and nutrient retention (reviewed by Hyvönen and others 2007). Thus, to improve our understanding of how global changes might influence forest ecosystems in future, we first need to gain a better understanding of the links between soils, trees, and microbial communities.

In forest ecosystems, tree species diversity, community structure and species composition play crucial roles in shaping soil microbial communities (Delgado-Baquerizo and others 2018; Dukunde and others 2019; Prada-Salcedo and others 2021). Diverse tree stands can shape soil microbial community structure because many soil organisms obtain their energy by mineralising organic matter (Hättenschwiler and Jørgensen 2010; Delgado-Baquerizo and others 2017), which in turn releases nutrients for plant uptake (Van Der Heijden and others 2008). Different groups of microorganisms such as bacteria and fungi are ecologically and morphologically distinct, and therefore have distinct resource requirements (Delgado-Baquerizo and others 2018). In general, soil bacteria have faster growth rates and lower C:N biomass stoichiometry than soil fungi, whereas fungi are better able to degrade recalcitrant ‘low-quality’ plant material (Waring and others 2013), although the specific requirements of taxa within these broad groups can also vary widely (Fierer

and others 2007; McGuire and others 2010). The links between soil microbial communities and tree species diversity are thus often explained by the range of resources provided by plant inputs such as leaf or root litter and rhizodeposits (Delgado-Baquerizo and others 2018; Prada-Salcedo and others 2020) because 'functional complementarity' of resources should support a greater diversity of bacteria and fungi (Hättenschwiler and others 2005; Bardgett and Wardle 2010; Sayer and others 2017). There is growing recognition that the resource acquisition traits of trees can shape soil microbial communities because they represent plant inputs that are preferentially utilized by different groups of microorganisms and hence, the functional composition and trait diversity of trees are often better for explaining variation in soil microbial communities than species richness *per se* (Hättenschwiler and others 2005; Prada-Salcedo and others 2021). For example, inputs from fast-growing trees with acquisitive traits, such as high specific leaf area and leaf nitrogen and phosphorus concentrations, are favoured by bacterial communities (Orwin and others 2010; Delgado-Baquerizo and others 2018), because they represent high-quality resources that are rapidly decomposed (Bakker and others 2011). By contrast, conservative traits of slow-growing, stress-tolerant trees, such as high leaf dry matter content and low specific leaf area, are generally preferred by fungal communities (Orwin and others 2010; Boeddinghaus and others 2019). Hence, tree species can govern the structure of a particular soil microbial community via resource inputs with distinct physical and biochemical traits (Urbanová and others 2015; Prada-Salcedo and others 2021). However, microbial communities can also access a range of soil resources, and nutrients in the mineral soil and soil organic matter can support the decomposition of plant litter (reviewed by Krishna and Mohan 2017). Consequently, the strength of associations between plant functional traits and soil microbial communities is likely related to the availability of nutrients and carbon in the soil (Figure 1).

Soil stoichiometry plays an important role in shaping plant and soil microbial diversity in forests because soil nutrient elements, such as carbon (C), nitrogen (N), and phosphorus (P), and their stoichiometric balance (C:N:P) are important for the growth and community composition of both trees and soil microbes (Delgado-Baquerizo and others 2018; Li and others 2020). Soil stoichiometry is strongly influenced by organic C content, reflecting the balance of resources in the soil (Delgado-Baquerizo and others 2017), and soil stoichiometry can provide some indication of nutrient limitation to plants or soil microbial communities (Cleveland and Liptzin 2007; Fan and others 2015). Soil stoichiometry is also strongly linked to plant functional traits and diversity (Schlatter and others 2015) due to the considerable variation in the C, N, and P content of plant inputs to the soil (Han and others 2005). In forests, soil fertility interacts with nutrient cycling by litterfall, whereby plants

growing on nutrient-rich soil tend to produce large quantities of leaf litter with high nutrient content, which in turn provides large nutrient inputs to the soil, whereas plants growing on nutrient-poor soil tend to resorb a higher proportion of foliar nutrients before leaf abscission, resulting in lower nutrient inputs (Zechmeister-Boltenstern and others 2015). In theory, the elemental stoichiometry of plants and soils also link directly to the resource requirements of soil microbes (Chen and others 2019) because bacteria have high P requirements (Güsewell and Gessner 2009), and therefore prefer soils characterized by lower C:P stoichiometry, whereas fungi have high N requirements and therefore prefer soils characterized by higher N:P ratios (Zechmeister-Boltenstern and others 2015). Nonetheless, there is contrasting evidence for the influence of soil N:P stoichiometry on bacterial (Zheng and others 2020) or fungal (Liu and others 2020) communities and soil stoichiometry may instead modulate soil microbial communities indirectly via plant biodiversity and plant traits (Schlatter and others 2015; Carrillo and others 2016).

Despite the importance of tree species identity and richness in shaping forest soil microbial diversity and composition, the role of tree functional trait diversity is still poorly characterised, and the importance of soil properties for mediating interactions between tree functional traits and soil microbial communities is unclear. To advance our understanding of the linkages between tree functional traits diversity and soil microbial communities, we conducted a study at a temperate forest site in Northeast China to assess the linkages between different tree diversity metrics (i.e., tree species richness vs. functional trait diversity and composition) and soil bacterial and fungal diversity, while considersing the potential mediating role of soil stoichiometry (C:P and N:P ratios). We expected that the relationships between tree diversity metrics, soil stoichiometry and soil microbial diversity would differ among microbial groups with distinct resource requirements (Faust and Raes 2012). Specifically, we hypothesized that:

1) Given the distinct resource requirements of bacteria and fungi, bacterial diversity will be greater in soils characterized by lower C:P ratios, whereas fungal diversity will be greater in soils with higher N:P ratios;

2) As plant traits represent resource quality for soil microbial communities, tree functional trait diversity and composition will have a greater influence on soil microbial communities than tree species richness;

3) As both tree species and soil microbial communities are influenced by soil nutrient status, soil stoichiometry will modulate the relationships between tree diversity metrics and soil microbial diversity.

To test our hypotheses, we determined soil C:P and N:P stoichiometry, measured the traits of 52 tree species, and characterized the diversity of soil bacteria and fungi in 120 quadrats across 25-ha of temperate forest.

2. Materials and Methods

2.1. Study forests

The study was conducted in a 25-ha permanent temperate mixed forest megaplot in the Changbai Mountains in Northeast China (41°41′49″ - 42°25′18″N and 127°42′55″ - 128°16′48″E; Figure 2), which is one of the megaplots in the Forest Global Earth Observatory Network (ForestGEO; http://www.forestgeo.si.edu). The vegetation at the study site is characterized as late-successional Broadleaved-Korean pine (*Pinus koraiensis*) mixed forest, with woody plant species belonging to 52 species, 32 genera and 18 families. The study area has a mean annual air temperature of 2.8°C and mean annual rainfall of 700 mm (Yang 1985) and the soil type is dark-brown (FAO soil classification; Yang 1985). The elevation of study area ranges from 793 to 809 m above sea level, and the slope ranges from 0.15° to 19° (Yuan and others 2020).

2.2. Quantification of tree diversity metrics

We assessed tree species richness and tree functional trait diversity and composition in 120 20-m × 20-m quadrats, spaced at least 40 m apart across the 25-ha forest plot. We identified all woody plants with stem diameter at breast height (DBH) ≥ 1 cm in each quadrat and measured seven above- and below-ground tree species traits for at least 10 individuals of 52 species in total. Aboveground traits comprised maximum tree height (H_{max}), leaf phosphorus content (LPC), leaf nitrogen content (LNC), leaf water content (LWC), specific leaf area (SLA), and leaf area (LA), and as a belowground trait we measured specific root length (SRL). We determined maximum tree height (H_{max}) from the height of the ten individuals with the largest DBH, measured using a laser rangefinder (Yuan and others 2016). Leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf area (LA) and specific leaf area (SLA) were calculated using healthy, sun-exposed leaves (Wang and others 2013). Specifically, LNC was estimated by colourimetry after KCl extraction using the Kjeldahl method, LPC was determined by molybdate colorimetry after digestion in H_2SO_4–$HClO_4$ and leaf area was measured using a portable scanning planimeter (LiDE 110, Canon, Tokyo, Japan; Cornelissen and others 2003). We calculated SRL as root dry mass divided by root length. We calculated three tree

diversity metrics for each quadrat: tree species richness, functional trait diversity and functional trait composition, using the *vegan* (Oksanen and others 2015) and *FD* packages (Laliberte and Legendre 2010) in R version 3.6.1 (R Development Core Team 2019). Tree species richness was calculated as the total number of observed species with DBH ≥ 1 cm within a quadrat using the *vegan* package (Oksanen and others 2015). Tree functional trait diversity and functional composition were calculated using the standard protocols recommended by Cornelissen and others (2003) and Paquette and Messier (2011). Functional trait diversity was based on four tree functional traits representing differences in resource acquisition strategies: leaf phosphorus and nitrogen content, specific leaf area and leaf area (Conti and Díaz 2013), using mean trait values for each species rescaled to a mean of 0 with a standard deviation of 1 (Villéger and others 2008). Functional trait diversity (FDis) was then computed as functional dispersion of the four traits (*dbFD* function in FD), which accounts for species abundance within each plot in addition to the distance of each species to the centre of multi-trait functional space (Laliberté and Legendre 2010). Finally, functional trait composition was calculated for each quadrat from the community weighted means (CWM) of all traits, using the proportional basal area of each species to calculate the CWM for each trait in each plot (Garnier and others 2004) using the *dbFD* function in FD package (Laliberté and Legendre 2010).

2.3. Soil sampling and nutrient analysis

For analyses of soil nutrients, carbon and microbial diversity, we randomly selected two sampling points from the four corners points of each quadrat, took five soil cores (3.8 cm diameter, 10 cm deep) at each sampling point and mixed them thoroughly to create one composite sample per quadrat (Figure 2). Each sample was then separated into two subsamples: one subsample for measuring soil carbon and nutrients, and the second subsample for measuring soil microbial diversity (bacteria and fungi). The subsamples for determination of soil microbial diversity were stored at −80 °C until DNA extraction.

To determine soil stoichiometry, soil samples were sieved (< 2 mm) to remove roots and stones and then air-dried. Total soil nitrogen (TN) was analysed with an automatic Kjeldahl apparatus (N210, Gdana, China), total soil phosphorus (TP) was analysed by molybdate colourimetry using a UV-visible spectrophotometer (SP-2500, Shanghai, China; Sparks 1996) and soil organic carbon (SOC) was measured using the acidified dichromate ($K_2Cr_2O_7$–H_2SO_4) oxidation method (Lu 1999). Soil C:N,

C:P and N:P ratios were then calculated from the ratio of SOC to TN or TP and the ratio of TN to TP, respectively.

2.4. Quantification of soil microbial diversity

Soil bacterial and fungal diversity was determined using the Illumina Miseq platform (Illumina, San Diego, CA, USA) following the manufacturer's instructions. Soil genomic DNA was isolated from 0.25 g of soil using the MoBio PowerSoil® DNA Isolation extraction kit (MoBio Laboratories, USA). The quality of the DNA was assessed based on 260/280 nm and 260/230 nm absorbance ratios obtained using a NanoDrop Life Spectrophotometer (NanoDrop Technologies, USA) and the DNA was stored at −20 °C until further use.

The universal bacterial V4~V5 region of the 16S rRNA gene was amplified using the primers 515F (5'- GTGCCAGCMGCCGCGG-3') and 907R (5'- CCGTCAATTCMTTTRAGTTT-3'; Yusoff and others 2013). The fungal internal transcribed spacer (ITS) sequence of the ITS rRNA gene was amplified using primers ITS_1737F (5'-GGAAGTAA AAGTCGTAACAAGG-3') and ITS_2043R (5'-ATGCAGGCTGCGTTCTTCA TCGATGC-3'; Zhang and others 2016). Polymerase chain reaction (PCR) amplification was carried out using a GeneAmp PCR-System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR analyses were performed in triplicate in a 20 µL mixture containing 4 µL of 5×FastPfu Buffer, 2µL of 2.5 mM dNTPs, 0.8 µL of each primer (5 µM), 0.4 µL of FastPfu Polymerase and 10 ng of template DNA. The thermal cycling conditions of the PCR included an initial denaturation step at 95 ºC for 3 min, followed by 27 (16S rRNA) or 35 (ITS) cycles at 95 ºC for 30 s, annealing at 55 ºC for 30 s, extension at 72 ºC for 45 s, and a final extension at 72 ºC for 10 min. The amplified 16S rRNA gene and ITS region were sequenced on a 300PE MiSeq run.

The 16S and ITS rRNA gene sequencing reads were demultiplexed, filtered and merged using fastp version 0.20.0 (Chen and others 2018) and FLASH version 1.2.7 (Magoč and Salzberg 2011), using the same quality control criteria. In brief: (i) sequences for sites with an average quality score of <20 were truncated over a 50 bp sliding window, and we discarded truncated reads <50 bp or reads containing ambiguous characters; (ii) Overlapping sequences >10 bp length were assembled according to the overlapped sequence, with a maximum mismatch ratio of 0.2 for the overlap region and discarding reads that could not be assembled; (iii) Samples were distinguished according to the primers, and the sequence direction was adjusted. Subsequently, we clustered operational taxonomic units (OTUs) with 97% similarity cut-off (Stackebrandt and Goebel 1994; Edgar 2013) using UPARSE version 7.1 (Edgar 2013), identifying and removing chimeric sequences. The taxonomy

of each OTU representative sequence was determined against relevant databases (Silva v128 for bacteria and unite 7.0 for fungi) using RDP Classifier version 2.2 (Wang and others 2007) with a confidence threshold of 0.7. It is important to note that assignment of OTUs based on sequence matches to reference databases might over- or under-represent actual microbial diversity (Callahan and others 2017) but any bias is likely to be consistent among samples. We used the identified bacterial phyla for subsequent analyses, and identified fungal functional groups using FUNGuild (Nguyen and others 2016a) based on 'highly probable', 'probable' or 'possible' functional guilds, omitting 412 OTUs with multiple guild assignments from further analysis. The number of phylotypes (OTU richness) for bacteria and fungi and for the most common bacterial phyla and fungi guilds were calculated as OTU richness (hereafter: bacterial or fungal diversity). A summary of descriptive statistics for all variables is shown in Table 1.

2.5. Statistical analyses

We assessed the relative importance of plant biodiversity metrics and soil stoichiometry in shaping soil microbial diversity using structural equation models (SEMs; Figure 1), which allow us to link multiple variables and pathways in one ecological model (Grace and others 2010). As individual plant traits can be poor predictors of soil microbial diversity (Eisenhauer and Powell 2017), we used multiple trait combinations based on Principal Component Analysis (PCA) using the *rda* function in the *vegan* package (Oksanen and others 2015) to represent tree functional trait diversity and composition in the SEMs. We first performed separate PCAs for tree functional diversity and functional composition to reduce the number of variables and avoid issues of collinearity, and sampling adequacy was evaluated using the Bartlett test of sphericity and the Kaise-Meyer-Olkin test (Table S1). The first axis of PCA for functional trait diversity (FT PC1) explained 49% of the total variation and was positively correlated with FT_{LPC}, FT_{LNC}, FT_{LA}, and FT_{SLA} and the first axis of PCA for functional trait composition (CWM PC1) explained 65% of the variation and was positively related with CWM_{LWC}, CWM_{SRL}, CWM_{LPC}, CWM_{LNC}, CWM_{LA}, and CWM_{SLA} (Table S1).

To account for spatial autocorrelation in bacterial and fungal diversity prior to conducting SEM analysis, we performed generalized least-square (GLS) analysis (Pinheiro and Bates 2016) to compare models with and without the spatial autocorrelation as an explanatory variable. The models without spatial autocorrelation showed the lower Akaike Information Criterion (Table S2), and we thus did not account for sampling distance in our SEMs. We then constructed SEMs based on theoretical direct and indirect relationships between tree diversity metrics, soil properties and

the diversity of soil bacteria or fungi (Figure 1). We constructed SEMs using the *lavaan* package (Rosseel 2012), using tree species richness and the first PCA axes for functional trait diversity and composition to represent plant diversity, bacterial and fungal OTU richness to represent soil microbial diversity, and we included soil C:N, C:P and N:P ratios to account for the influence of soil stoichiometry. Before analysis, the data were first log-transformed and then standardized (Zuur and others 2009). The overall model fit of alternative SEMs were assessed with *Chi-square* test statistics and associated *P*-values (whereby $P > 0.05$ indicates that expected and observed covariance matrices are statistically indistinguishable). For the best-fit models, the goodness of fit index (GFI) and Bentler's comparative fit index (CFI) were both > 0.95 and the standardized root mean square residual (RMSR) was < 0.05 (Malaeb and others 2000; Rosseel 2012). Soil C:N ratios did not contribute to the overall model fit and was therefore not retained in the final models. The relationships among tree and soil diversity and soil stoichiometry variables were then assessed by pairwise Pearson correlations (Figure S1). In order to assess the relationships between the relative abundances of bacterial or fungal phyla and total bacterial or fungal richness we conducted simple linear regressions for individual bacterial and fungal phyla (Figures S2-S6). The resulting bivariate relationships were then fitted to the postulated paths in the final SEM using linear regression (Rosseel 2012).

3. Results

All measured variables showed substantial variation among sampling quadrats across the 25-ha forest plot. In particular, tree species richness differed up to three-fold among quadrats and tree functional trait diversity or composition also varied widely among quadrats (Table 1). There was a wide range of soil C:N, C:P and N:P ratios across the 25-ha plot (Table 1) and bacterial OTU diversity was generally higher but less variable among quadrats than fungal OTU diversity (Table 1). We identified 9534 bacterial OTUs belonging to 33 phyla, 52 classes, 105 orders, 166 families, 369 genera and 472 species. The dominant bacterial phyla were Proteobacteria (3547 OTUs; 37.2% relative abundance), Acidobacteria (2221 OTUs; 23.3% relative abundance), Actinobacteria (1463 OTUs; 15.4% relative abundance), Planctomycetes (595 OTUs; 6.2% relative abundance), Chloroflexi (413 OTUs; 5.4% relative abundance) and Bacteroidetes (478 OTUs; 5.0% relative abundance; Figure 3). We identified fungi belong to 7 phyla, 27 classes, 86 orders,183 families, 601 genera and 968 species. The dominant fungal phyla were Ascomycota (62% relative abundance), Basidiomycota (24% relative abundance) and Zygomycota (13% relative abundance). Out of a total 10689 fungal

OTUs, we were able to ascribe 4535 OTUs (42.4%) to a fungal guild. The most dominant fungal guild was ectomycorrhizas (2225 OTUs; 49.1% relative abundance), followed by epiphytes (876 OTUs; 19.3% relative abundance), saprotrophs (339 OTUs; 7.5% relative abundance), plant pathogens (339 OTUs; 7.5% relative abundance), lichenized fungi (320 OTUs; 7.1% relative abundance) and animal pathogens (189 OTUs; 4.2% relative abundance; Figure 3).

Tree functional trait composition was related to tree species richness, but functional trait diversity was not (Figures 4 and 5). Tree functional trait diversity and composition were strongly positively associated with soil stoichiometry (C:P and N:P ratios), whereas tree species richness declined with increasing soil C:P ratio (Figures 4 and 5).

The final SEMs showed that tree diversity metrics and soil C:P or N:P ratios explained a greater proportion of the variation in bacterial (24 %) than fungal diversity (11%; Figure 4). In contrast to our first hypothesis, bacterial diversity was strongly associated with high soil C:P ratios (Figure 4a and 4b) and fungal diversity was associated with low C:P ratios; however, as hypothesized, fungal diversity was also strongly and positively associated with high soil N:P ratios (Figure 4c and 4d). In partial support of our second hypothesis, bacterial diversity was significantly and positively associated with tree functional trait diversity and composition, but not tree species richness, (Figure 4a and 4b). However, fungal diversity was not directly associated with any tree diversity metric (Figure 4c). Our third hypothesis was supported by multiple indirect links between tree diversity metrics and soil microbial diversity via differences in soil stoichiometry. Fungal diversity was indirectly linked to tree species richness via the soil C:P ratio (Figure 4c and Tables S4 and S5). Bacterial diversity was indirectly associated with both tree species richness and functional trait composition via the soil C:P ratio, but whereas the indirect relationship with tree species richness was negative, the indirect relationship with tree functional trait composition was positive (Figure 4b and Table S4). Hence, although soil microbial diversity was related to soil stoichiometry and tree diversity metrics, the relationships did not always conform to predictions based on differences in resource requirements between bacteria and fungi.

The SEMs for individual microbial groups demonstrated that the linkages between microbial diversity, tree diversity metrics and soil stoichiometry differed among bacterial phyla and fungal guilds, explaining between 8% and 18% of the variation in the most abundant groups (Figure 5). The diversity of Proteobacteria and Acidobacteria were strongly associated with tree functional trait composition and high soil C:P ratios (Figure 5a and 5b), whereas the diversity of Actinobacteria was positively related to tree functional trait diversity and soil C:P ratios (Figure 5c). Ectomycorrhizal

fungal diversity was strongly associated with tree functional trait diversity but not soil stoichiometry (Figure 5d), whereas the diversity of both saprotrophs and plant pathogens were mainly explained by low soil C:P and high N:P ratios (Figure 5e and 5f).

The diversity of individual microbial groups was also indirectly linked to tree diversity metrics via soil stoichiometry. Among the bacterial phyla, the diversity of Proteobacteria and Actinobacteria were indirectly negatively associated with tree species richness via the soil C:P ratio, but Proteobacterial diversity was also indirectly positively associated with tree functional trait diversity and composition (Figure 6a and 6b and Tables S6 and S8). Among the fungal guilds, only plant pathogen diversity was indirectly linked to greater tree species richness via the soil C:P ratio (Figure 6f and Table S11). Hence, the linkages between microbial diversity, tree diversity metrics and soil stoichiometry clearly differed among microbial groups with distinct ecological niches.

4. Discussion

Our study demonstrates clear linkages between tree diversity metrics, microbial diversity, and soil stoichiometry. In partial agreement with our first hypothesis, fungal diversity was linked to soil stoichiometry, with greater fungal diversity at high soil N:P ratios, but bacterial diversity was related to high rather than low soil C:P ratios. Similarly, in partial support of our second hypothesis, bacterial diversity was more closely associated with tree functional diversity than tree species richness (Figure 4), but fungal diversity was not associated with any tree diversity metric. Nonetheless, our results provide evidence to support our third hypothesis that soil stoichiometry plays a role in mediating the linkages between tree and microbial diversity. Overall, the interactions between soil microbial communities, tree functional traits and soil stoichiometry demonstrate the importance of considering the diversity of plant and soil resource pools (Hooper and others 2000; Wardle and others 2004) and many of the patterns we observed can be explained by the distinct resource requirements of different microbial taxa (Faust and Raes 2012).

Direct influence of soil stoichiometry

Soil stoichiometry has recently been identified as a key determinant of variation in microbial communities (Delgado-Baquerizo and others 2017; Li and others 2020; Liu and others 2020) and our findings support the general hypothesis that soil stoichiometry influences microbial diversity. However, whereas other studies demonstrated higher bacterial diversity at a low soil C:P ratio (Delgado-Baquerizo and others 2017), we observed the opposite pattern of greater bacterial

diversity in soils with a high C:P ratio. The temperate forest soils at our site are more likely to be N than P-limited (Xu and others 2017), and thus it is conceivable that bacteria are not P-limited, even in soils with a high C:P ratio. Bacterial diversity also increases with organic C content (Maestre and others 2015), and the indirect effects of tree diversity via the soil C:P ratio could therefore indicate that greater diversity of C-rich soil resources promotes bacterial diversity because specific soil microbial groups have distinct resource preferences (Chen and others 2019; Zhao and others 2020). Interestingly, our analyses of individual bacterial phyla demonstrated that the diversity of the three most abundant phyla was associated with a high soil C:P ratio, even though they are usually assigned to distinct functional groups: Proteobacteria and Actinobacteria are fast-growing copiotrophs, which favour nutrient-rich soils, whereas Acidobacteria are regarded as oligotrophs that tend to dominate in nutrient-poor soils (Fierer and others 2007; Ai and others 2015). Although a strong relationship between soil N:P ratios and bacterial diversity or composition was reported along a steep climatic gradient across 12 forest ecosystems in China (Zheng and others 2020), we found no influence of soil N:P ratio on bacterial diversity within our study forest, despite the wide range of N:P values across our 120 sampling quadrats (Table 1). Hence, it seems likely that bacterial diversity in our soils is not nutrient-limited and the links between bacterial diversity and tree functional traits might suggest that the quality or diversity of carbon sources plays a more important role in shaping soil bacterial communities at our study site (Hättenschwiler and Jørgensen 2010).

As hypothesized, fungal diversity increased with soil N:P ratios, highlighting the higher N compared to P requirements of fungi (Hodge and others 2000), but fungal diversity was also related to low soil C:P ratios, which was unexpected. However, the C:P stoichiometry of fungal tissues varies markedly among taxa, whereas N:P stoichiometry is much more stable (Camenzind and others 2020). Distinct nutrient requirements among fungal guilds could also contribute to the observed relationships between fungal diversity and soil stoichiometry. It is noteworthy that saprotrophs and plant pathogens, which have low tissue C:P and N:P ratios compared to ectomycorrhizal fungi (Zhang and Elser 2017), were most diverse in soils with high N:P but low C:P ratios (Figure S5). By contrast, the lack of a direct relationship between soil stoichiometry and ectomycorrhizal fungi might be explained by C acquisition metabolism from host plants, and their ability to produce enzymes to acquire nutrients from organic matter (Bödeker and others 2016), which plays an important role in decomposition processes in forest ecosystems (Talbot and others 2008; Sterkenburg and others 2018).

Links between tree functional diversity and soil microbial diversity

As hypothesized, we found that the diversity of soil bacteria was more strongly associated with tree functional trait diversity and composition than with tree species richness (Figure 4a). There is mounting evidence that plant trait-based approaches better explain variation in forest soil microbial communities than plant species diversity (Shigyo and others 2019). Plant functional traits that reflect structural, physiological and chemical characteristics of organisms can shape microbial communities (Steinauer and others 2017) and thus drive variation in ecosystem functioning (Violle and others 2007). In our study, we focused on tree traits related to resource acquisition, including leaf nitrogen and phosphorus content, specific leaf area and leaf area (Conti and Díaz 2013) because these also represent the quality of resources available to soil microbial communities (Bardgett and Wardle 2010; Sayer and others 2017). Although our metric for functional trait composition included all measured tree trait variables, the traits that explained most of the variation in tree trait functional composition were resource acquisition traits, but also included leaf water content, which might influence microhabitat conditions at the forest floor, and specific root length, which contributes to C inputs to the rooting zone (Bardgett and others 2014). However, we note that in only considering one root trait, our study would not have detected the associations between soil bacterial diversity and functional dispersion of root traits in forests, which have recently been established (Prada-Salcedo and others 2020). Nonetheless, our analyses of individual bacterial phyla suggest that Proteobacteria and Acidobacteria were largely influenced by tree functional trait composition, whereas Actinobacteria were influenced by tree functional trait diversity (Figure 6a,b,c). Hence, the influence of tree functional traits on bacterial diversity suggests that variation in tree traits, rather than tree species richness, determines bacterial community composition via differences in the range of available resources (Hooper and others 2000; Wardle and others 2004; Delgado-Baquerizo and others 2018).

We expected soil fungal diversity to be highly associated with tree functional diversity, because previous work reports strong links between plant species identity and fungal community composition in forest litter and soils (Urbanová and others 2015; Li and others 2020). Fungal decomposers are often linked to tree traits representing low-quality resources, as fungi tend to have slower growth rate traits and a more conservative C metabolism (Orwin and others 2010; Delgado-Baquerizo and others 2018). The negligible direct effects of tree diversity metrics on fungal diversity in our study are surprising but might suggest that fungal communities are more strongly influenced by tree traits we did not measure (e.g., foliar and root lignin:N ratios; Bray and others 2012; Bardgett

and others 2014). For example, recent work showed that fungal guilds were more associated with root community traits than with tree diversity across European forests (Prada-Salcedo and others 2021). Hence, we may have detected stronger associations between fungal diversity and tree functional diversity by including a wider range of belowground traits. The stronger links to tree functional diversity for bacterial than fungal diversity might be explained by the greater influence of plant trait variation at early stages of decomposition when bacteria play a key role in the rapid turnover of labile plant compounds (Güsewell and Gessner 2009; Bray and others 2012). Alternatively, as ectomycorrhizal fungi and plant pathogens were two of the dominant guilds in our soils, it is conceivable that host plant identity played a more important role in shaping overall fungal diversity than tree trait variation (Ishida and others 2007; Tedersoo and others 2013). However, the tree traits we measured also represent available resource to saprotrophic fungi (Nguyen and others 2016b), so it is unclear why only ectomycorrhizal diversity was directly related to plant functional trait diversity in our study.

Conclusions

Our study demonstrates strong linkages between tree functional diversity and soil microbial diversity, with a role for soil stoichiometry in mediating those linkages. We propose that tree functional diversity is a better predictor of soil microbial diversity than tree species richness because functional diversity represents the range of resources to soil microbial communities. Hence, soil stoichiometry likely modifies the linkages between trees and soil microbes by influencing resource quality and availability to both groups of organisms. Consequently, studies of ecosystem processes in forests might benefit from simultaneously considering the relationships between plant trait diversity, microbial communities, and soil resources. We focused solely on microbial diversity, but our study provides a solid foundation for future work to investigate how the linkages with tree diversity and soil stoichiometry influence soil microbial activity and community composition. In particular, further work assessing the role of belowground plant traits and the relative importance of plant vs. soil resources for microbial decomposers may be particularly illuminating. Given that global change can influence tree functional diversity, soil microbial communities and soil stoichiometry, we suggest that all three aspects need to be taken into account to fully assess how global changes will affect important forest ecosystem processes such as decomposition, nutrient dynamics and carbon storage.

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Table 1. Summary of variables measured in sampling quadrats within a 25-ha mixed temperate forest plot in the Changbai Mountains, Northeast China. Means, standard errors (S.E.), minima (min.) and maxima (max.) are given for *n* = 120 sampling quadrats across the 25-ha plot; where PC1 refers to the fist axis of a principal component analysis, and OTU is operational taxonomic unit.

Variable	Unit	Mean	S.E.	Min.	Max.
Tree species richness (SR)	Spp. per 400 m^{-2}	11	0.22	6	18
Functional dispersion diversity PC1 (FT)	Unitless	0.00	0.13	-3.63	3.79
Functional dispersion based on leaf nitrogen content (LNC)	Unitless	0.38	0.01	0.18	0.69
Functional dispersion based on leaf phosphorous content (LPC)	Unitless	0.43	0.01	0.15	0.69
Functional dispersion based on specific leaf area (SLA)	Unitless	0.52	0.01	0.15	0.82
Functional dispersion based on leaf area (LA)	Unitless	0.51	0.01	0.17	0.84
Community weighted means (CWM) PC1 (TC)	Unitless	0.00	0.22	-7.77	5.42
CWM of tree maximum height (Hmax)	meter	26.66	0.14	21.59	30.77
CWM of leaf phosphorus content (LPC)	%	1.73	0.01	1.52	1.88
CWM of leaf nitrogen content (LNC)	%	2.00	0.01	1.72	2.25
CWM of specific leaf area (SLA)	$cm^2\ g^{-1}$	195.82	1.79	131.78	247.50
CWM of leaf area (LA)	cm^2	30.82	0.58	15.89	46.50
CWM of leaf water content (LWC)	%	0.65	0.002	0.60	0.69
CWM of specific root length (SRL)	$m\ g^{-1}$	2904.29	30.57	2159.09	3660.51
Soil organic carbon (C)	$g\ kg^{-1}$	9.40	0.21	4.24	20.42
Total soil nitrogen (N)	$g\ kg^{-1}$	6.34	0.16	3.02	12.42
Total soil phosphorus (P)	$g\ kg^{-1}$	1.24	0.03	0.58	2.11
Soil C:P ratio	Unitless	12.56	0.27	8.15	27.84
Soil N:P ratio	Unitless	5.23	0.09	3.50	10.35
Total bacterial OTU richness	No. of OTUs	2424	13	2133	2737
Proteobacteria	No. of OTUs	719	5	603	841
Acidobacteria	No. of OTUs	322	1	276	370
Actinobacteria	No. of OTUs	260	2	188	313
Total fungal OTU richness	No. of OTUs	921	19	949	1760
Ectomycorrhizas	No. of OTUs	159	3	82	244
Saprotrophs	No. of OTUs	153	4	60	312
Plant pathogens	No. of OTUs	49	1	22	97

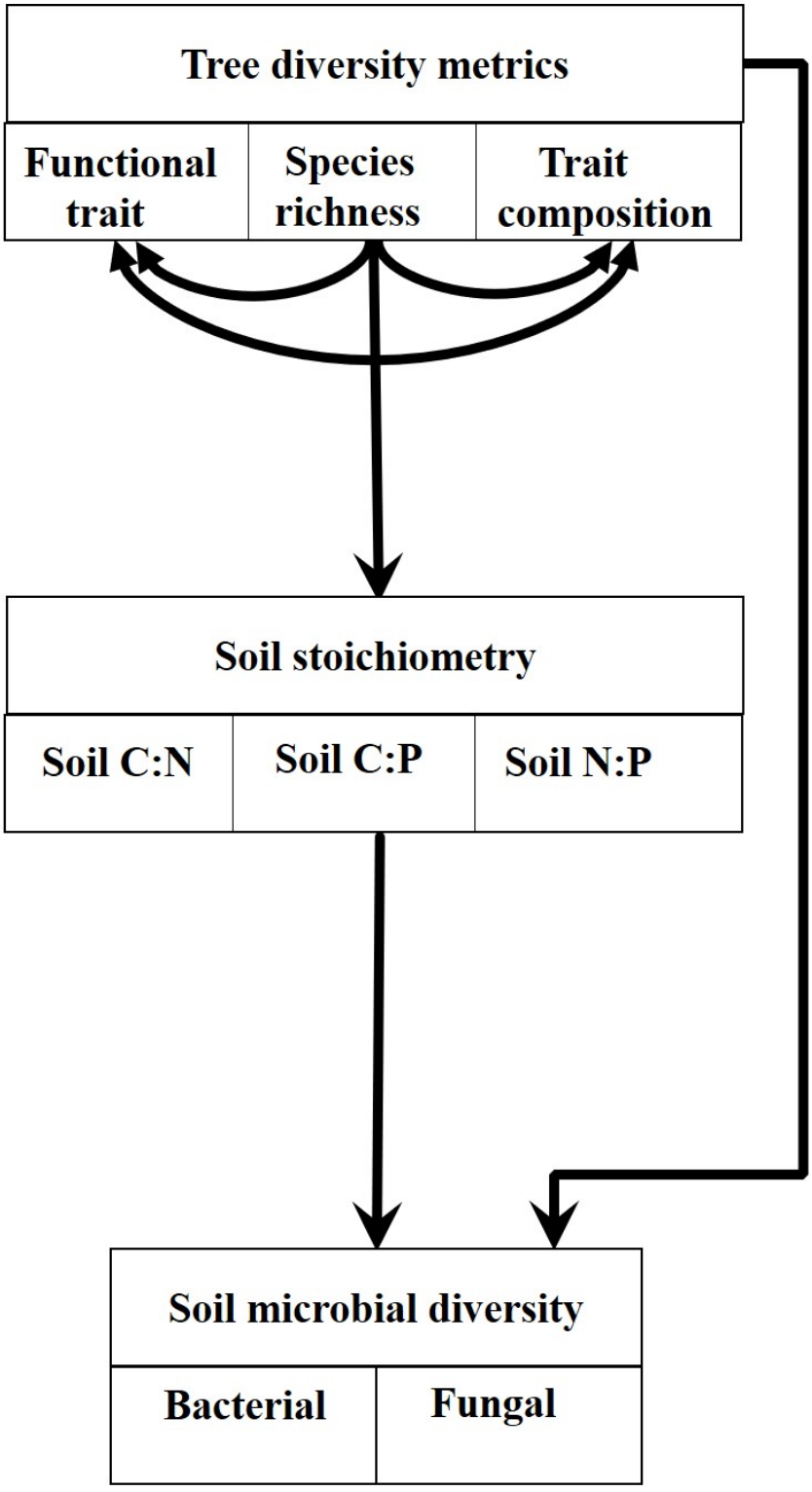

Figure 1 Initial conceptual model illustrating the hypothesized linkages between tree diversity metrics, soil microbial diversity and the modulating effects of soil stoichiometry, represented by the ratios of carbon to nitrogen (C:N), carbon to phosphorus (C:P) and nitrogen to phosphorus (N:P).

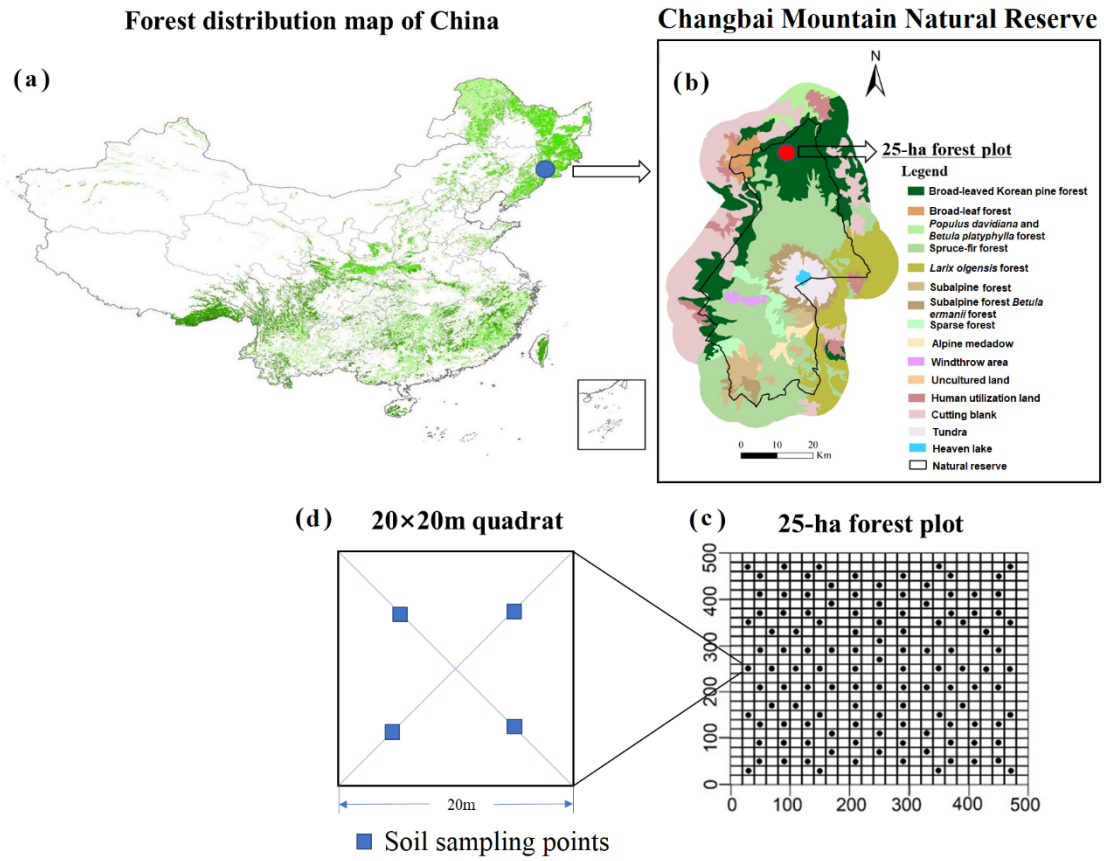

Figure 2 Maps showing the location of the temperate forest study site; a) the location of the Changbai mountains in China, b) the location of the 25-ha forest plot within the Changbai Mountain Natural Reserve, c) the sampled quadrats within the forest plot, and d) the soil sampling points in each quadrat.

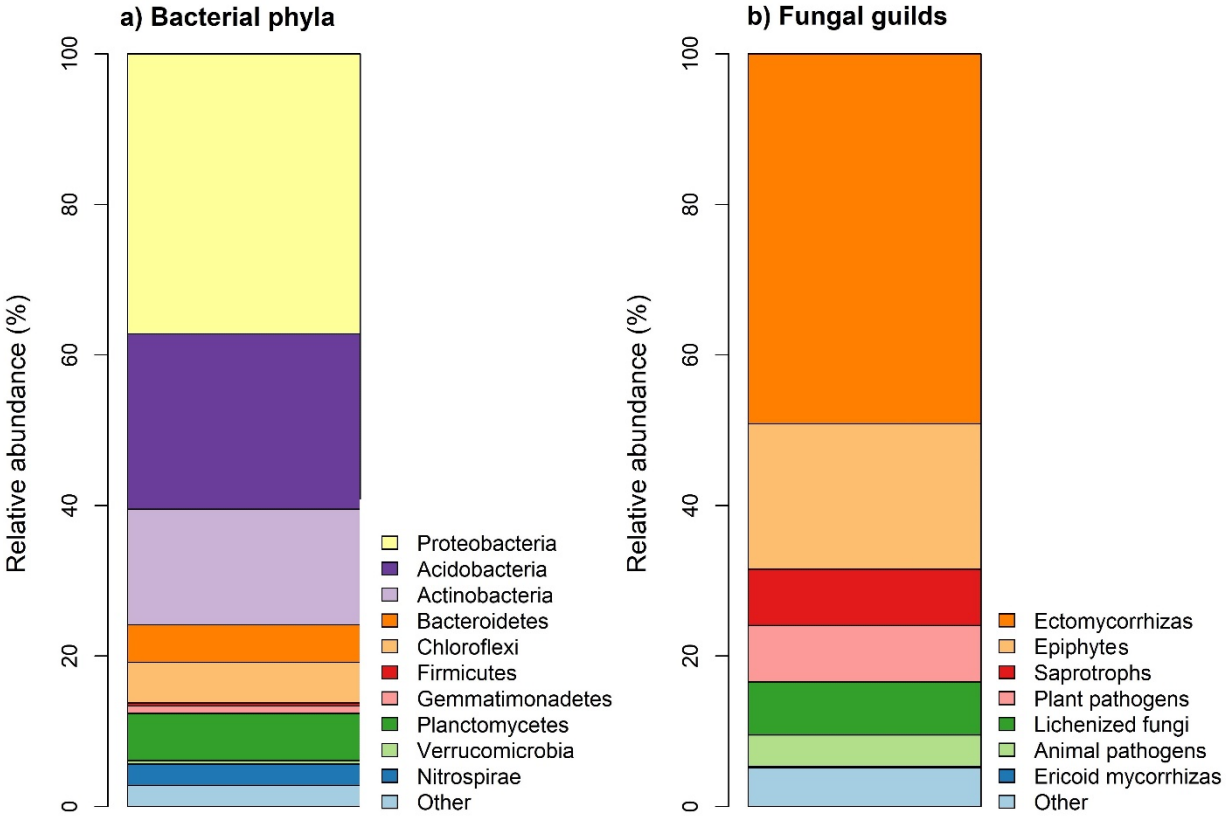

Figure 3 Relative abundances of (a) soil bacterial phyla and (b) fungal guilds in 120 sampling quadrats across a 25-ha temperate forest site in north-east China.

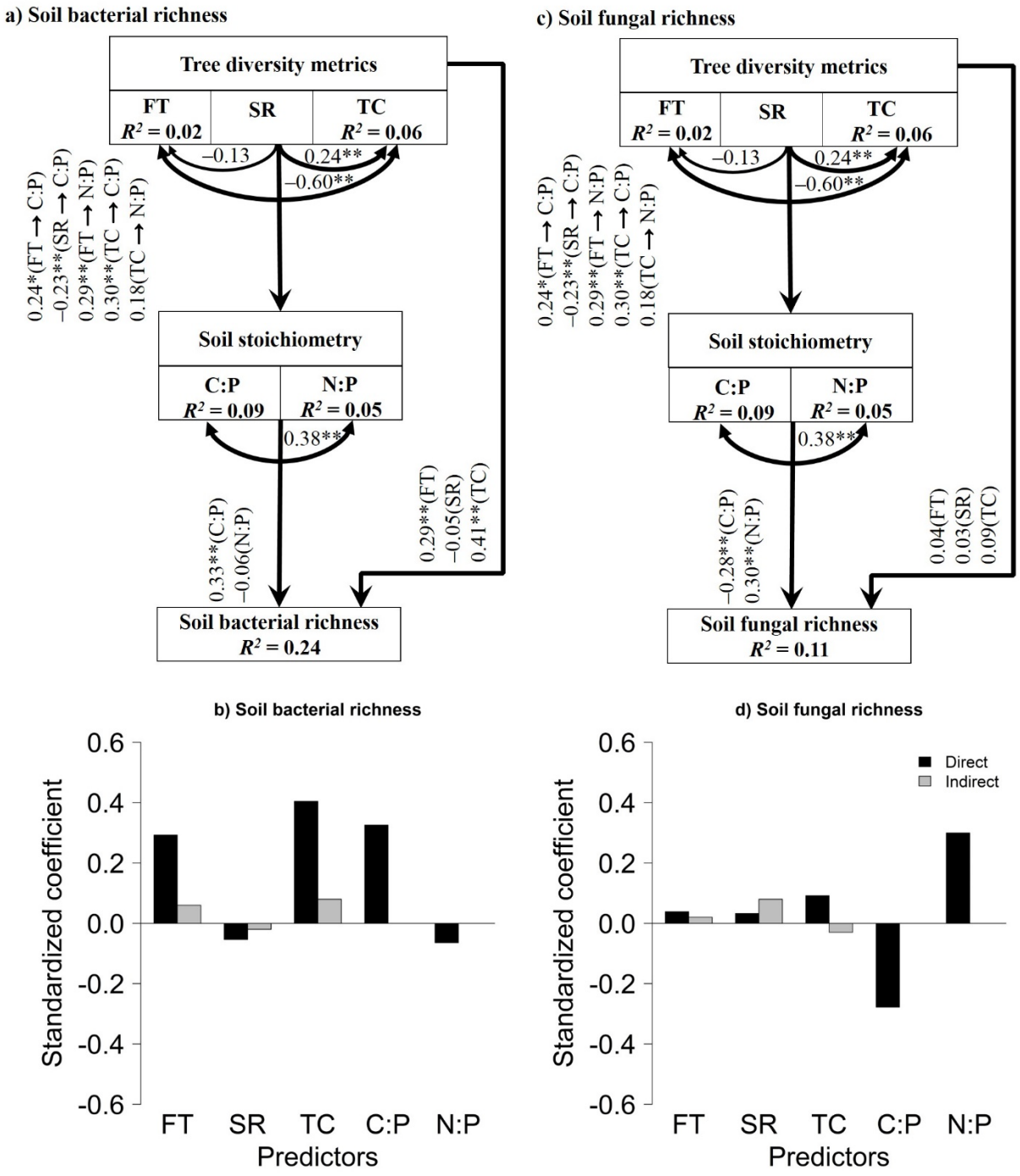

Figure 4 Final structural equation models (SEMs) illustrating the pathways by which a,b) soil bacterial and c,d) fungal diversity are linked to tree diversity metrics and soil stoichiometry in 120 sampling quadrats across a 25-ha temperate forest site in north-east China. In b) and d), the magnitude of direct and indirect relationships is shown as standardized coefficients, where 0 indicates no relationship. SR is tree species richness, FT is functional trait diversity, TC is functional trait composition, C:P and N:P indicate the ratios of soil carbon to phosphorus and soil nitrogen to phosphorus, respectively. Significance levels are shown as $^{**}P < 0.01$, $^{*}P < 0.05$ and pathways without asterisks are not significant.

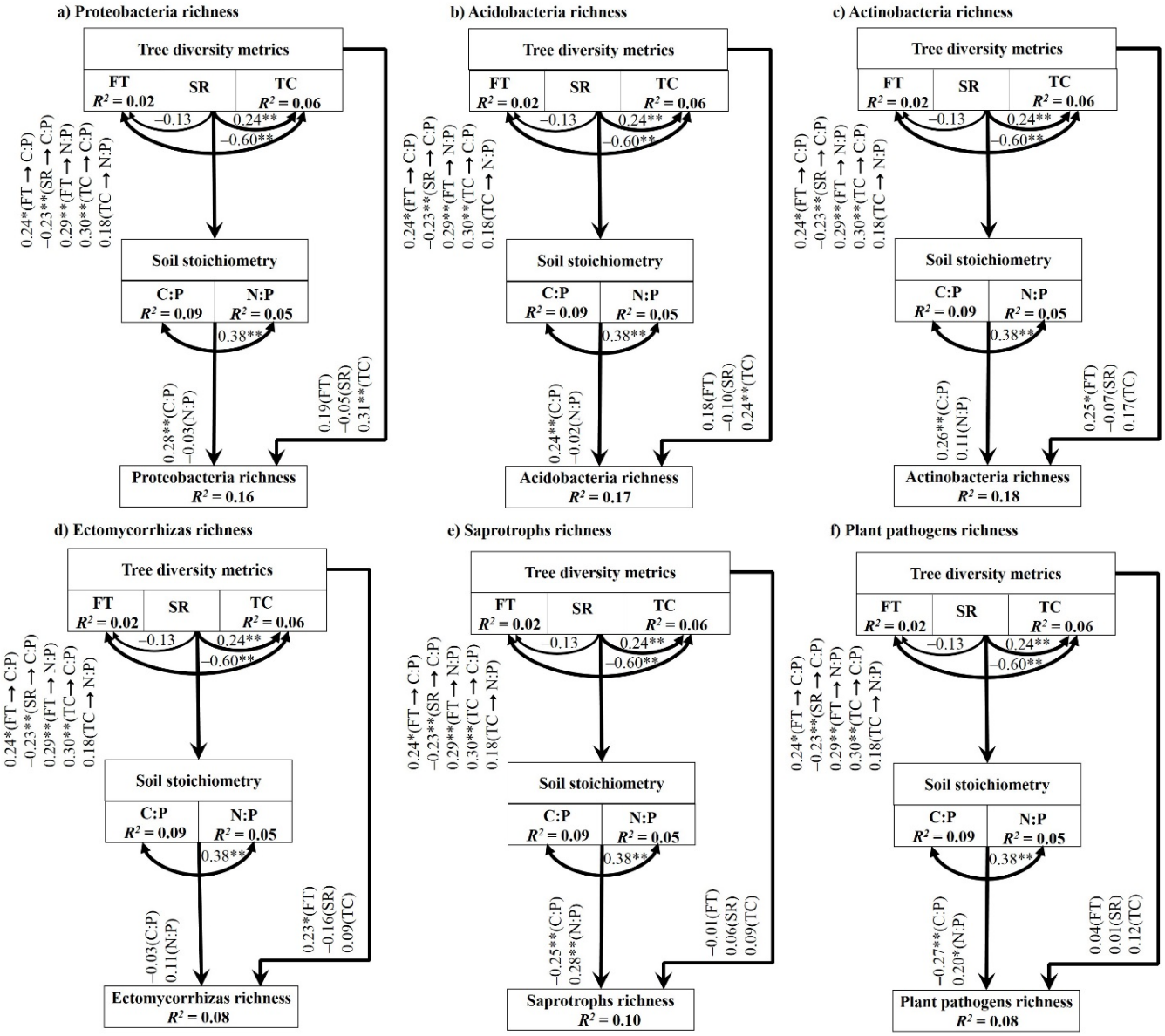

Figure 5 Final structural equation models (SEMs) illustrating the pathways by which the most common (a, b and c) bacterial phyla and (d, e and f) fungal guilds are linked to plant diversity metrics and soil stoichiometry in 120 sampling quadrats across a 25-ha temperate forest site in north-east China. Model-fit statistics are shown in Table S3. Abbreviations and symbols follow the legend to Figure 4.

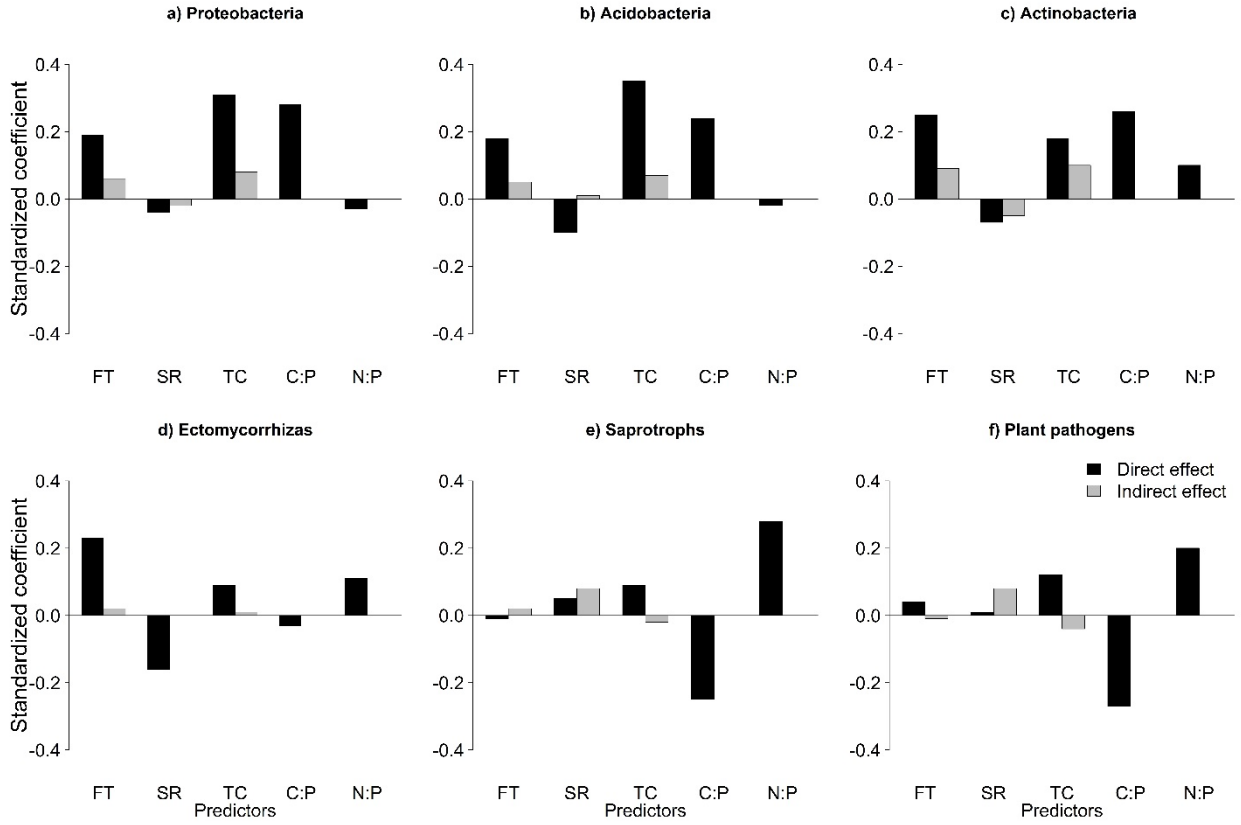

Figure 6 Standardized coefficients showing the magnitude of direct and indirect linkages between a-c) the most common bacterial phyla, or d-f) the most common fungal guilds and plant diversity metrics or soil stoichiometry in 120 sampling quadrats across a 25-ha temperate forest site in north-east China. Model-fit statistics are shown in Table S3. Abbreviations and symbols follow the legend to Figure 4.

Appendix A: Supplementary information

Table S1. Results of the principal component analyses (PCA) based on parameters representing plant functional trait diversity and composition in a temperate forest in China, showing the variation explained by the first principal component (PC 1), and the results of the Kaise-Meyer-Olkin (KMO) test and Bartlett's test of sphericity (BS) for the variables used in each PCA. The plus (+) and minus (-) symbols in parentheses refer to positive or negative correlations, respectively, between PC1 and the individual variables, where LNC is leaf nitrogen content; LPC is leaf phosphorus content; SLA is specific leaf area; LA is leaf area; H_{max} is maximum tree height; SRL is specific root length and LWC is leaf water content.

	Parameters	PC 1 (%)	KMO values	BS test
Functional trait diversity	LNC (+), LPC (+), SLA (+), LA (+)	49	0.64	$\chi^2 = 116$, $p < 0.05$
Functional trait composition	LNC (+), LPC (+), SLA (+), LA (+), Hmax (-), SRL (+), LWC (+)	65	0.80	$\chi^2 = 1054$, $p < 0.05$

Table S2. Summary statistics of the generalized least-squares (GLS) models of the relationships between bacterial or fungal richness and the explanatory variables tree functional trait diversity (FT), tree functional trait composition (TC), tree species richness (SR), and ratios of soil organic carbon to total phosphorus (Soil C:P) and total soil nitrogen to soil phosphorus (Soil N:P); showing the coefficients, t-statistic, significance, pseudo R^2 value and Akaike Information Criterion (AIC) for alternative GLS models including or excluding spatial autocorrelation (spatial or non-spatial, respectively).

GLS model	Model	Coefficient	*t*-value	*P*-value	AIC	R^2 pseudo
Bacterial richness						
Bacterial richness ~ FT	Non-spatial	0.069	0.757	0.451	352.363	0.0004
	Spatial	0.049	0.750	0.454	355.534	0.0004
Bacterial richness ~ TC	Non-spatial	0.100	2.700	0.008	346.127	0.003
	Spatial	0.100	2.700	0.008	350.127	0.003
Bacterial richness ~ SR	Non-spatial	-0.067	-0.734	0.464	350.894	0.01
	Spatial	-0.067	-0.734	0.464	354.894	0.01
Bacterial richness ~ Soil C:P	Non-spatial	0.378	4.439	<0.001	333.211	0.02
	Spatial	0.378	4.439	<0.001	337.211	0.02
Bacterial richness ~ Soil N:P	Non-spatial	0.139	1.520	0.131	349.143	0.03
	Spatial	0.139	1.520	0.131	353.143	0.03
Fungal richness						
Fungal richness ~ FT	Non-spatial	0.005	0.071	0.943	352.091	0.0004
	Spatial	-0.001	-0.105	0.917	353.579	0.0004
Fungal richness ~ TC	Non-spatial	0.021	0.562	0.574	352.885	0.003
	Spatial	0.022	0.582	0.562	354.394	0.003
Fungal richness ~ SR	Non-spatial	0.075	0.815	0.417	350.769	0.01
	Spatial	0.069	0.757	0.451	352.363	0.01
Fungal richness ~ Soil C:P	Non-spatial	-0.151	-1.655	0.100	348.723	0.02
	Spatial	-0.174	-1.867	0.064	349.556	0.02
Fungal richness ~ Soil N:P	Non-spatial	0.183	2.020	0.046	347.420	0.03
	Spatial	0.194	2.144	0.034	348.491	0.03

Table S3. Model fit statistics for the structural equation models (SEMs) shown in Figures 3 and 4, where *df* is degrees of freedom, CFI is the comparative fit index, GFI is the goodness of fit index, SRMR is standardized root mean square residual, AIC is Akaike Information Criterion and χ^2 is the Chi-square test statistic.

Dataset	*df*	Model fit statistics					Model fit	SEM
		CFI	GFI	SRMR	AIC	χ^2 (*P*-value)		
Overall soil microbial diversity								
Bacterial richness	1	0.982	0.989	0.038	1890.77	3.257 (0.071)	Accepted	Fig. 4a
Fungal richness	1	0.979	0.989	0.038	1909.93	3.257 (0.071)	Accepted	Fig. 4c
Dominant soil bacteria								
Proteobacteria	1	0.980	0.989	0.038	1902.13	3.257 (0.071)	Accepted	Fig. 5a
Acidobacteria	1	0.980	0.989	0.038	1901.03	3.257 (0.071)	Accepted	Fig. 5b
Actinobacteria	1	0.981	0.989	0.038	1898.22	3.257 (0.071)	Accepted	Fig. 5c
Dominant soil fungi								
Ectomycorrhizas	1	0.978	0.989	0.038	1912.32	3.257 (0.071)	Accepted	Fig. 5d
Saprotrophs	1	0.978	0.989	0.038	1911.18	3.257 (0.071)	Accepted	Fig. 5e
Plant pathogens	1	0.978	0.989	0.038	1913.75	3.257 (0.071)	Accepted	Fig. 5f

Table S4. The relationships between soil bacterial richness and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 4a, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Bacterial richness	-----	Direct	FT	a	0.08	**0.005**	**0.29**
Bacterial richness	-----	Direct	SR	b	0.08	0.528	-0.05
Bacterial richness	-----	Direct	TC	c	0.04	**<0.001**	**0.40**
Bacterial richness	-----	Direct	Soil C:P	d	0.09	**<0.001**	**0.33**
Bacterial richness	-----	Direct	Soil N:P	e	0.09	0.470	-0.06
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Bacterial richness	FT	Indirect	SR	ka	0.03	0.191	-0.04
Bacterial richness	TC	Indirect	SR	lc	0.04	**0.027**	**0.10**
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Bacterial richness	Soil C:P	Indirect	FT	fd	0.03	0.061	0.08
Bacterial richness	Soil N:P	Indirect	FT	ge	0.02	0.486	-0.02
Bacterial richness	Soil C:P	Indirect	SR	hd	0.03	**0.027**	**-0.08**
Bacterial richness	Soil C:P	Indirect	TC	id	0.02	**0.034**	**0.10**
Bacterial richness	Soil N:P	Indirect	TC	je	0.01	0.509	-0.01
Bacterial richness	-----	Total	FT	a+(f*d)+(g*e)	0.08	**0.001**	**0.35**
Bacterial richness	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Bacterial richness	-----	Total	TC	c+(j*e)+(i*d)	0.04	**<0.001**	**0.49**
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

Table S5. The relationships between soil fungal richness and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 4c, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Fungal richness	-----	Direct	FT	a	0.08	0.733	0.04
Fungal richness	-----	Direct	SR	b	0.09	0.720	0.03
Fungal richness	-----	Direct	TC	c	0.05	0.426	0.09
Fungal richness	-----	Direct	Soil C:P	d	0.10	**0.005**	**-0.28**
Fungal richness	-----	Direct	Soil N:P	e	0.10	**0.002**	**0.30**
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Fungal richness	FT	Indirect	SR	ka	0.02	0.740	-0.01
Fungal richness	TC	Indirect	SR	lc	0.03	0.445	0.02
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Fungal richness	Soil C:P	Indirect	FT	fd	0.03	0.083	-0.07
Fungal richness	Soil N:P	Indirect	FT	ge	0.03	**0.045**	**0.09**
Fungal richness	Soil C:P	Indirect	SR	hd	0.03	**0.046**	**0.06**
Fungal richness	Soil C:P	Indirect	TC	id	0.02	0.053	-0.08
Fungal richness	Soil N:P	Indirect	TC	je	0.02	0.146	0.06
Fungal richness	-----	Total	FT	a+(f*d)+(g*e)	0.08	0.607	0.06
Fungal richness	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Fungal richness	-----	Total	TC	c+(j*e)+(i*d)	0.05	0.582	0.06
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

Table S6. The relationships between taxonomic (operational taxonomic unit) richness of soil Proteobacteria and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5a, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Proteobacteria	-----	Direct	FT	a	0.08	0.080	0.19
Proteobacteria	-----	Direct	SR	b	0.09	0.613	-0.04
Proteobacteria	-----	Direct	TC	c	0.05	**0.006**	**0.31**
Proteobacteria	-----	Direct	Soil C:P	d	0.10	**0.003**	**0.28**
Proteobacteria	-----	Direct	Soil N:P	e	0.09	0.780	-0.03
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Proteobacteria	FT	Indirect	SR	ka	0.02	0.258	-0.03
Proteobacteria	TC	Indirect	SR	lc	0.04	0.052	0.07
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Proteobacteria	Soil C:P	Indirect	FT	fd	0.03	0.079	0.07
Proteobacteria	Soil N:P	Indirect	FT	ge	0.02	0.781	-0.01
Proteobacteria	Soil C:P	Indirect	SR	hd	0.03	**0.042**	**-0.06**
Proteobacteria	Soil C:P	Indirect	TC	id	0.02	**0.050**	**0.08**
Proteobacteria	Soil N:P	Indirect	TC	je	0.01	0.783	-0.005
Proteobacteria	-----	Total	FT	a+(f*d)+(g*e)	0.08	**0.022**	**0.25**
Proteobacteria	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Proteobacteria	-----	Total	TC	c+(j*e)+(i*d)	0.05	**0.001**	**0.39**
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

Table S7. The relationships between taxonomic (operational taxonomic unit) richness of soil Acidobacteria and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5b, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Acidobacteria	-----	Direct	FT	a	0.08	0.109	0.18
Acidobacteria	-----	Direct	SR	b	0.09	0.277	-0.10
Acidobacteria	-----	Direct	TC	c	0.05	**0.001**	**0.35**
Acidobacteria	-----	Direct	Soil C:P	d	0.10	**0.010**	**0.24**
Acidobacteria	-----	Direct	Soil N:P	e	0.09	0.857	-0.02
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.21	**0.007**	**0.24**
TC	-----	Direct	SR	l	0.13	0.139	-0.13
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Acidobacteria	FT	Indirect	SR	ka	0.05	0.168	0.04
Acidobacteria	TC	Indirect	SR	lc	0.02	0.179	-0.05
Soil C:P	FT	Indirect	SR	kf	0.06	0.088	0.06
Soil N:P	FT	Indirect	SR	kg	0.07	0.060	0.07
Soil N:P	TC	Indirect	SR	li	0.01	0.272	-0.02
Soil C:P	TC	Indirect	SR	lj	0.02	0.197	-0.04
Acidobacteria	Soil C:P	Indirect	FT	fd	0.03	0.095	0.06
Acidobacteria	Soil N:P	Indirect	FT	ge	0.02	0.857	-0.005
Acidobacteria	Soil C:P	Indirect	SR	hd	0.03	0.058	-0.06
Acidobacteria	Soil C:P	Indirect	TC	id	0.02	0.065	0.07
Acidobacteria	Soil N:P	Indirect	TC	je	0.01	0.857	-0.003
Acidobacteria	-----	Total	FT	a+(f*d)+(g*e)	0.08	**0.035**	**0.23**
Acidobacteria	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.08	**0.004**	**0.34**
Acidobacteria	-----	Total	TC	c+(j*e)+(i*d)	0.05	**<0.001**	**0.42**
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.08	**0.004**	**0.34**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.08	**0.004**	**0.34**

Table S8. The relationships between taxonomic (operational taxonomic unit) richness of soil Actinobacteria and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5c, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Actinobacteria	-----	Direct	FT	a	0.08	**0.022**	**0.25**
Actinobacteria	-----	Direct	SR	b	0.09	0.437	-0.07
Actinobacteria	-----	Direct	TC	c	0.05	0.105	0.18
Actinobacteria	-----	Direct	Soil C:P	d	0.09	**0.005**	**0.26**
Actinobacteria	-----	Direct	Soil N:P	e	0.09	0.256	0.10
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.21	**0.007**	**0.24**
TC	-----	Direct	SR	l	0.13	0.139	-0.13
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Actinobacteria	FT	Indirect	SR	ka	0.06	0.080	0.06
Actinobacteria	TC	Indirect	SR	lc	0.01	0.274	-0.02
Soil C:P	FT	Indirect	SR	kf	0.06	0.088	0.06
Soil N:P	FT	Indirect	SR	kg	0.07	0.060	0.07
Soil N:P	TC	Indirect	SR	li	0.01	0.272	-0.02
Soil C:P	TC	Indirect	SR	lj	0.02	0.197	-0.04
Actinobacteria	Soil C:P	Indirect	FT	fd	0.03	0.084	0.06
Actinobacteria	Soil N:P	Indirect	FT	ge	0.02	0.298	0.03
Actinobacteria	Soil C:P	Indirect	SR	hd	0.03	**0.047**	**-0.06**
Actinobacteria	Soil C:P	Indirect	TC	id	0.02	0.054	0.08
Actinobacteria	Soil N:P	Indirect	TC	je	0.01	0.351	0.02
Actinobacteria	-----	Total	FT	a+(f*d)+(g*e)	0.08	**0.002**	**0.34**
Actinobacteria	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.08	**0.004**	**0.34**
Actinobacteria	-----	Total	TC	c+(j*e)+(i*d)	0.05	**0.014**	**0.28**
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.08	**0.004**	**0.34**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.08	**0.004**	**0.34**

Table S9. The relationships between taxonomic (operational taxonomic unit) richness of ectomycorrhizal fungi and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5d, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Ectomycorrhizas	-----	Direct	FT	a	0.08	**0.045**	**0.23**
Ectomycorrhizas	-----	Direct	SR	b	0.09	0.083	-0.16
Ectomycorrhizas	-----	Direct	TC	c	0.05	0.451	0.09
Ectomycorrhizas	-----	Direct	Soil C:P	d	0.10	0.795	-0.03
Ectomycorrhizas	-----	Direct	Soil N:P	e	0.10	0.241	0.11
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Ectomycorrhizas	FT	Indirect	SR	ka	0.03	0.234	-0.03
Ectomycorrhizas	TC	Indirect	SR	lc	0.03	0.467	0.02
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Ectomycorrhizas	Soil C:P	Indirect	FT	fd	0.02	0.796	-0.01
Ectomycorrhizas	Soil N:P	Indirect	FT	ge	0.02	0.285	0.03
Ectomycorrhizas	Soil C:P	Indirect	SR	hd	0.02	0.795	0.01
Ectomycorrhizas	Soil C:P	Indirect	TC	id	0.01	0.796	-0.01
Ectomycorrhizas	Soil N:P	Indirect	TC	je	0.01	0.340	0.02
Ectomycorrhizas	-----	Total	FT	a+(f*d)+(g*e)	0.08	**0.021**	**0.26**
Ectomycorrhizas	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Ectomycorrhizas	-----	Total	TC	c+(j*e)+(i*d)	0.05	0.373	0.10
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

Table S10. The relationships between taxonomic (operational taxonomic unit) richness of saprotrophic fungi and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5e, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Saprotrophs	-----	Direct	FT	a	0.08	0.965	-0.01
Saprotrophs	-----	Direct	SR	b	0.09	0.551	0.05
Saprotrophs	-----	Direct	TC	c	0.05	0.427	0.09
Saprotrophs	-----	Direct	Soil C:P	d	0.10	**0.012**	**-0.25**
Saprotrophs	-----	Direct	Soil N:P	e	0.10	**0.003**	**0.28**
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Saprotrophs	FT	Indirect	SR	ka	0.02	0.965	0.001
Saprotrophs	TC	Indirect	SR	lc	0.03	0.446	0.02
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Saprotrophs	Soil C:P	Indirect	FT	fd	0.03	0.098	-0.06
Saprotrophs	Soil N:P	Indirect	FT	ge	0.03	0.051	0.08
Saprotrophs	Soil C:P	Indirect	SR	hd	0.03	0.061	0.06
Saprotrophs	Soil C:P	Indirect	TC	id	0.02	0.069	-0.07
Saprotrophs	Soil N:P	Indirect	TC	je	0.02	0.152	0.05
Saprotrophs	-----	Total	FT	a+(f*d)+(g*e)	0.08	0.874	0.02
Saprotrophs	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Saprotrophs	-----	Total	TC	c+(j*e)+(i*d)	0.05	0.545	0.07
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

Table S11. The relationships between taxonomic (operational taxonomic unit) richness of plant pathogenic fungi and tree diversity metrics (FT, SR and TC) or soil stoichiometry (soil C:P and N:P ratio) for the structural equation model shown in Figure 5f, showing direct, indirect and total standardized effects with standard errors; significant effects are indicated in bold ($P < 0.05$) and abbreviations follow the legend to Table S2.

Response	Mediator	Pathway	Predictor	label	S.E.	*P*-value	Effect
Plant pathogens	-----	Direct	FT	a	0.08	0.713	0.04
Plant pathogens	-----	Direct	SR	b	0.09	0.905	0.01
Plant pathogens	-----	Direct	TC	c	0.05	0.307	0.12
Plant pathogens	-----	Direct	Soil C:P	d	0.10	**0.006**	**-0.27**
Plant pathogens	-----	Direct	Soil N:P	e	0.10	**0.042**	**0.20**
Soil C:P	-----	Direct	FT	f	0.08	**0.028**	**0.24**
Soil N:P	-----	Direct	FT	g	0.08	**0.009**	**0.29**
Soil C:P	-----	Direct	SR	h	0.08	**0.005**	**-0.23**
Soil C:P	-----	Direct	TC	i	0.05	**0.008**	**0.30**
Soil N:P	-----	Direct	TC	j	0.05	0.101	0.18
FT	-----	Direct	SR	k	0.13	0.139	-0.13
TC	-----	Direct	SR	l	0.21	**0.007**	**0.24**
TC	-----	Covariance	FT	m	0.34	**<0.001**	**-0.61**
Soil C:P	-----	Covariance	Soil N:P	n	0.09	**<0.001**	**0.38**
Plant pathogens	FT	Indirect	SR	ka	0.02	0.721	-0.01
Plant pathogens	TC	Indirect	SR	lc	0.03	0.339	0.03
Soil C:P	FT	Indirect	SR	kf	0.03	0.220	-0.03
Soil N:P	FT	Indirect	SR	kg	0.03	0.198	-0.04
Soil N:P	TC	Indirect	SR	li	0.03	0.161	0.04
Soil C:P	TC	Indirect	SR	lj	0.04	0.058	0.07
Plant pathogens	Soil C:P	Indirect	FT	fd	0.03	0.087	-0.07
Plant pathogens	Soil N:P	Indirect	FT	ge	0.03	0.109	0.06
Plant pathogens	Soil C:P	Indirect	SR	hd	0.03	**0.050**	**0.06**
Plant pathogens	Soil C:P	Indirect	TC	id	0.02	0.057	-0.08
Plant pathogens	Soil N:P	Indirect	TC	je	0.01	0.202	0.04
Plant pathogens	-----	Total	FT	a+(f*d)+(g*e)	0.08	0.767	0.03
Plant pathogens	-----	Total	SR	b+(k*b)+(l*b)+(h*d)	0.06	**0.036**	**0.30**
Plant pathogens	-----	Total	TC	c+(j*e)+(i*d)	0.05	0.523	0.08
Soil C:P	-----	Total	SR	h+(k*f)+(l*i)	0.06	**0.036**	**0.30**
Soil N:P	-----	Total	SR	i+(k*g)+(l*j)	0.06	**0.036**	**0.30**

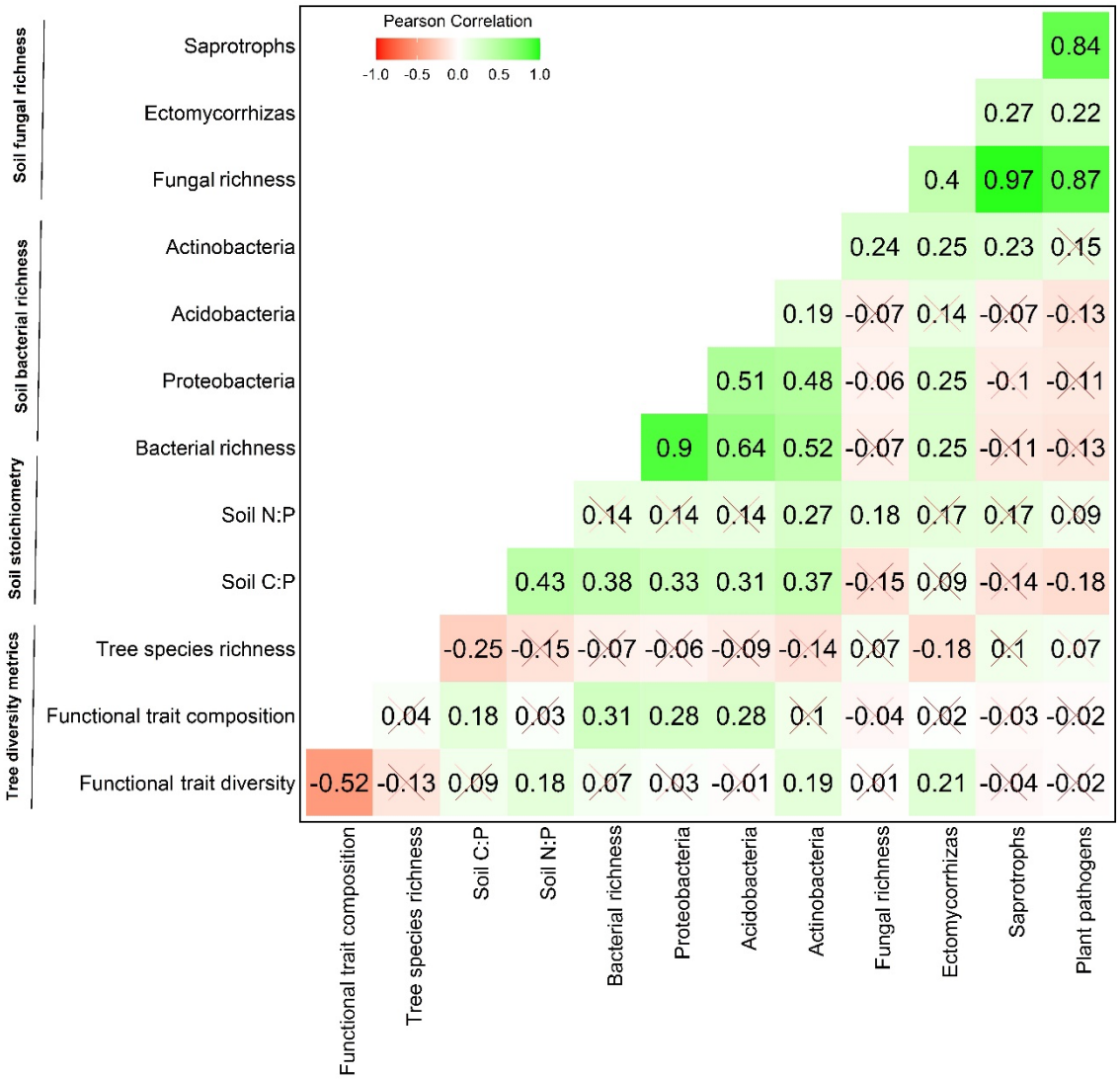

Figure S1. Pearson's correlation coefficients for the relationships between each pair of variables used in this study, the heat map indicates negative (red) to positive (green) correlations, the numbers within each square represent correlation coefficients (*r*) and insignificant correlations ($P > 0.05$) are crossed out. Abbreviations follow the legend for Table S2.

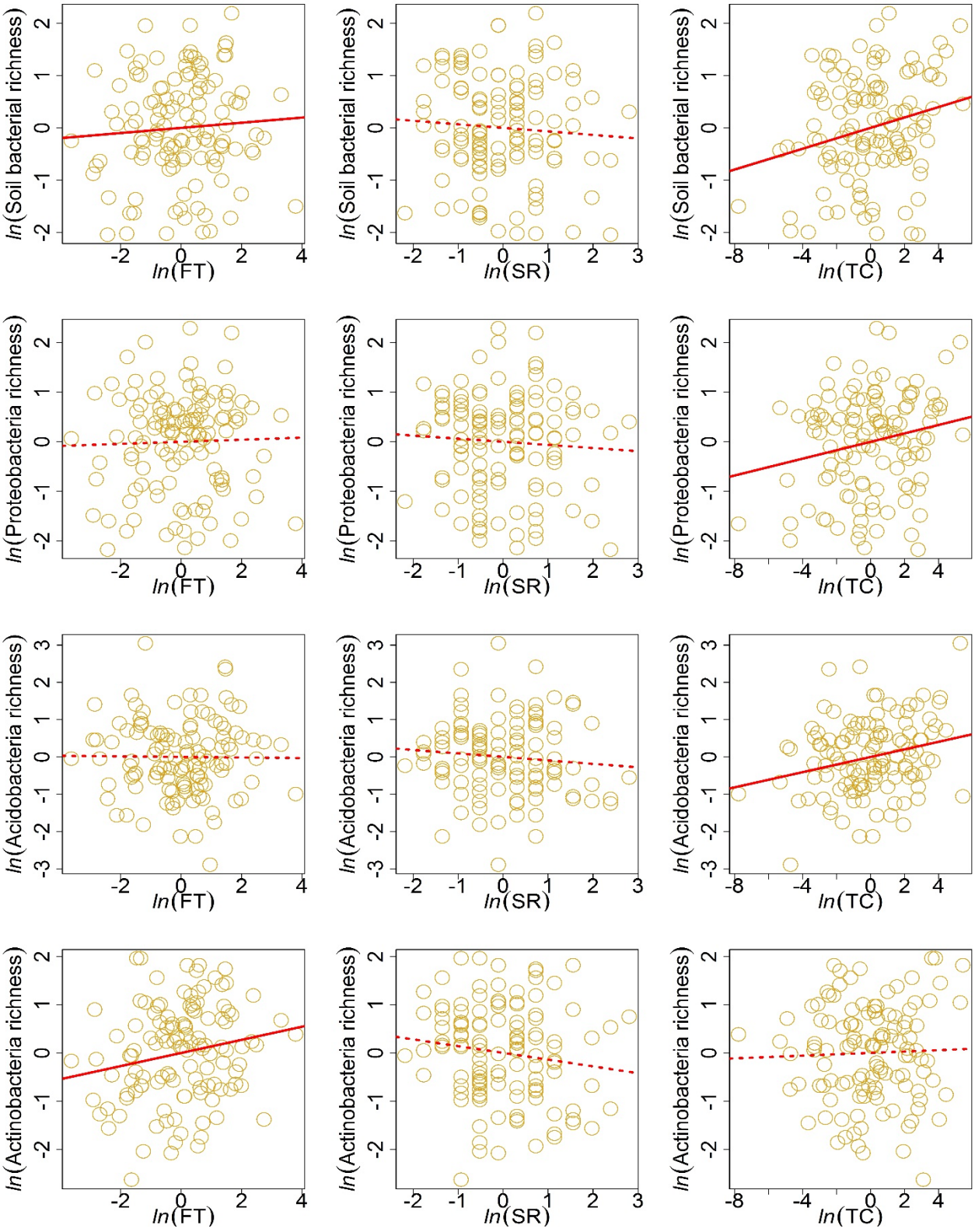

Figure S2. Bivariate relationships between bacterial taxonomic (operational taxonomic unit) richness and tree diversity metrics from the structural equation models (SEMs) shown in Figures 4a and 5a,b,c. All variables were natural-logarithm transformed and standardized. Solid lines indicate significant relationships at $P < 0.05$ and dashed lines are non-significant relationships at $P > 0.05$. All abbreviations follow the legend to Table S2.

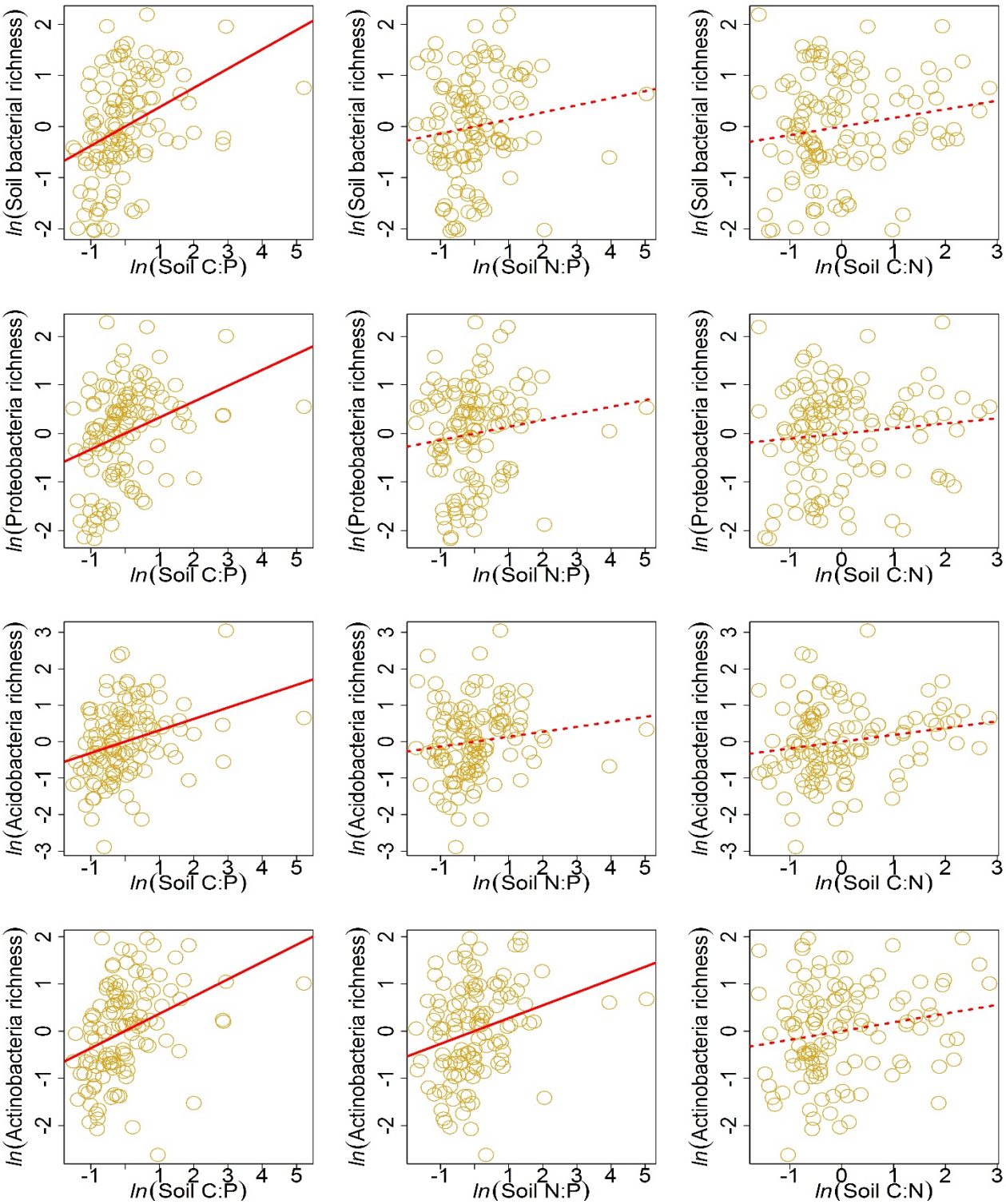

Figure S3. Bivariate relationships between bacterial taxonomic (operational taxonomic unit) richness and soil stoichiometry in the structural equation models (SEMs) shown in Figures 4a and 5a,b,c. All variables were natural-logarithm transformed and standardized. Solid lines indicate significant relationships at $P < 0.05$ and dashed lines are non-significant relationships at $P > 0.05$. All abbreviations follow the legend to Table S2.

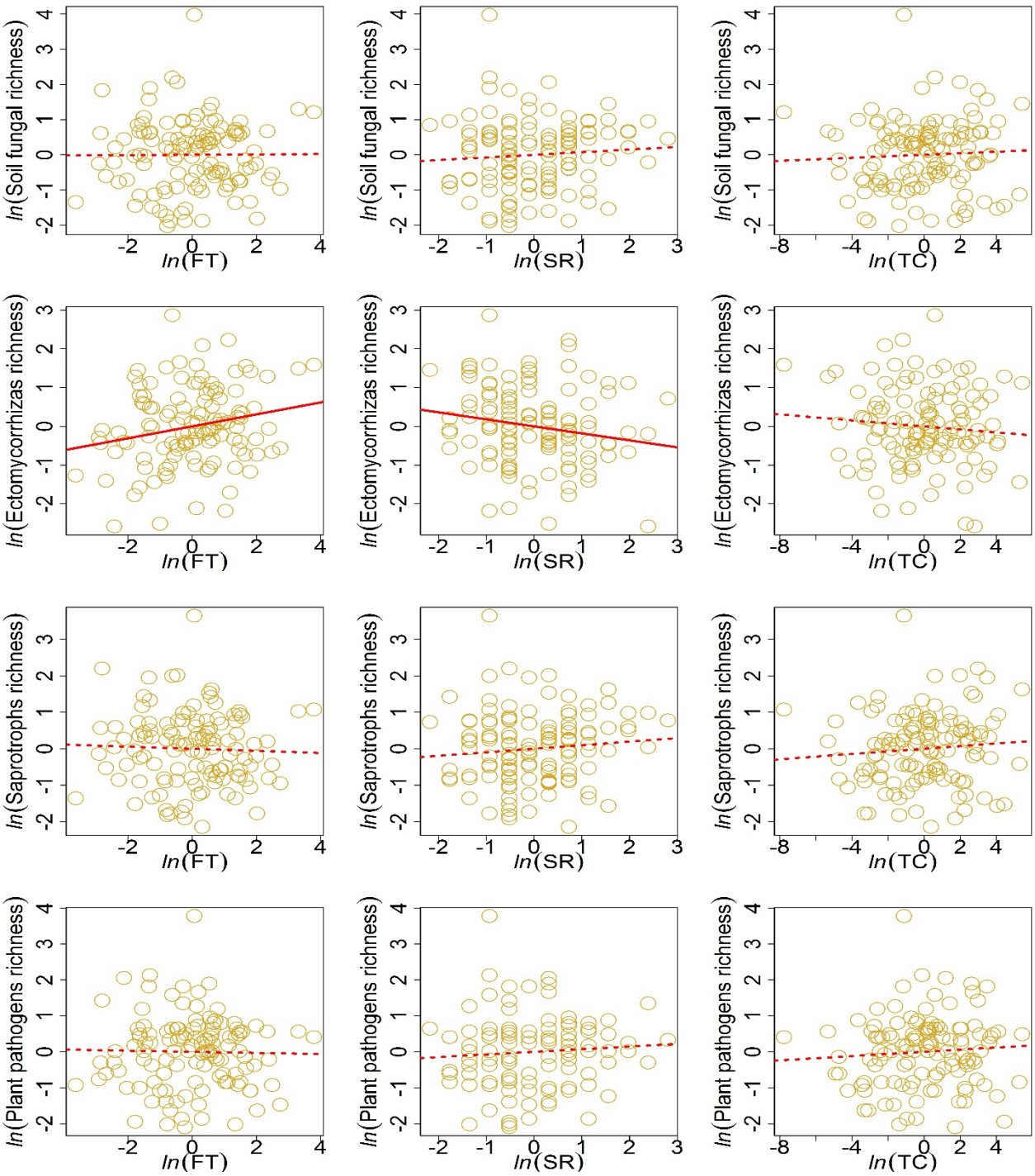

Figure S4. Bivariate relationships between fungal taxonomic (operational taxonomic unit) richness and tree diversity metrics in the structural equation models (SEMs) shown in Figures 4c and 5d,e,f. All variables were natural-logarithm transformed and standardized. Solid lines indicate significant relationships at $P < 0.05$ and dashed lines are non-significant relationships at $P > 0.05$. All abbreviations follow the legend to Table S2.

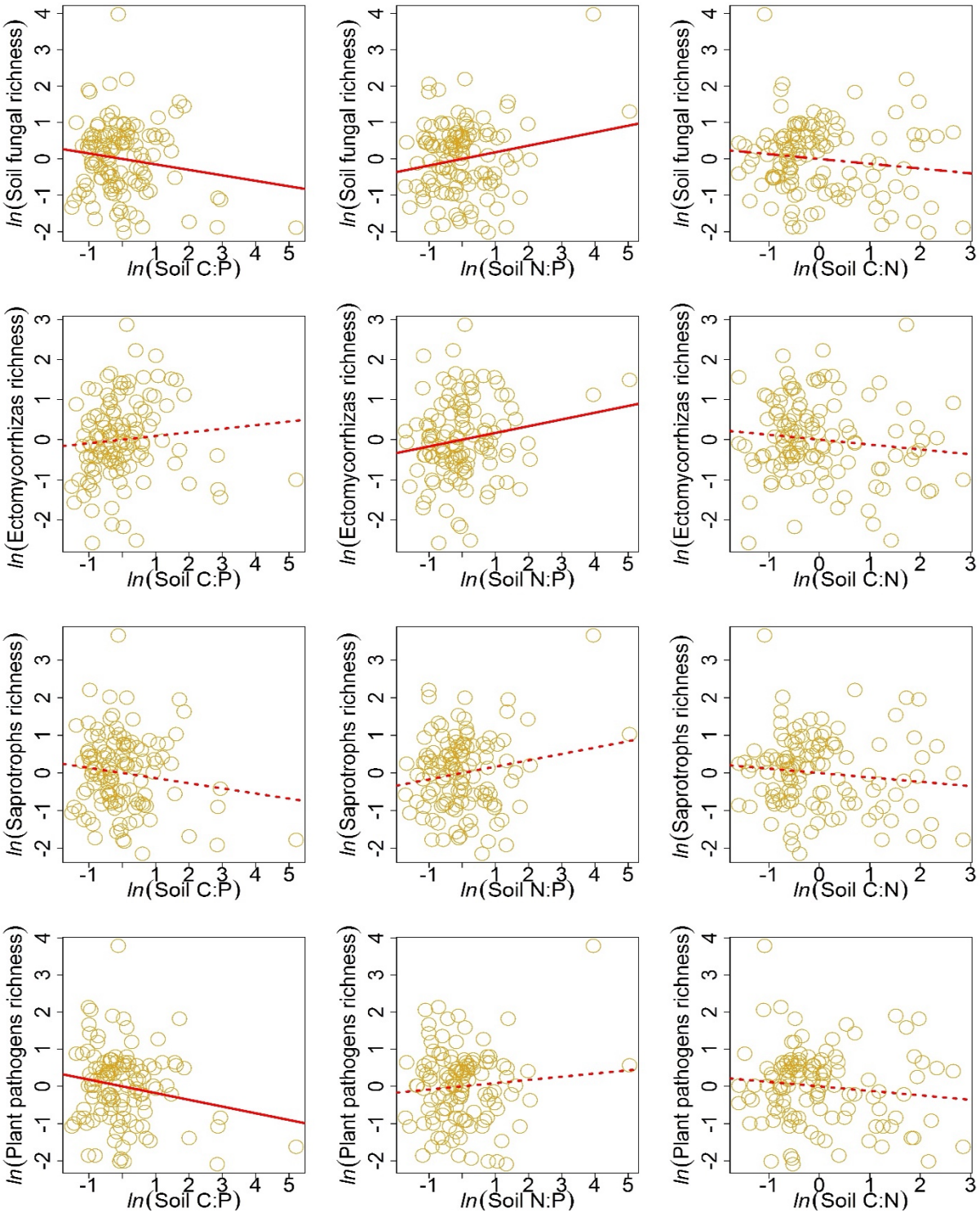

Figure S5. Bivariate relationships between fungal taxonomic (operational taxonomic unit) richness and soil stoichiometry in the structural equation models (SEMs) shown in Figures 4c and 5d,e,f. All variables were natural-logarithm transformed and standardized. Solid lines indicate significant relationships at $P < 0.05$ and dashed lines are non-significant relationships at $P > 0.05$. All abbreviations follow the legend to Table S2.

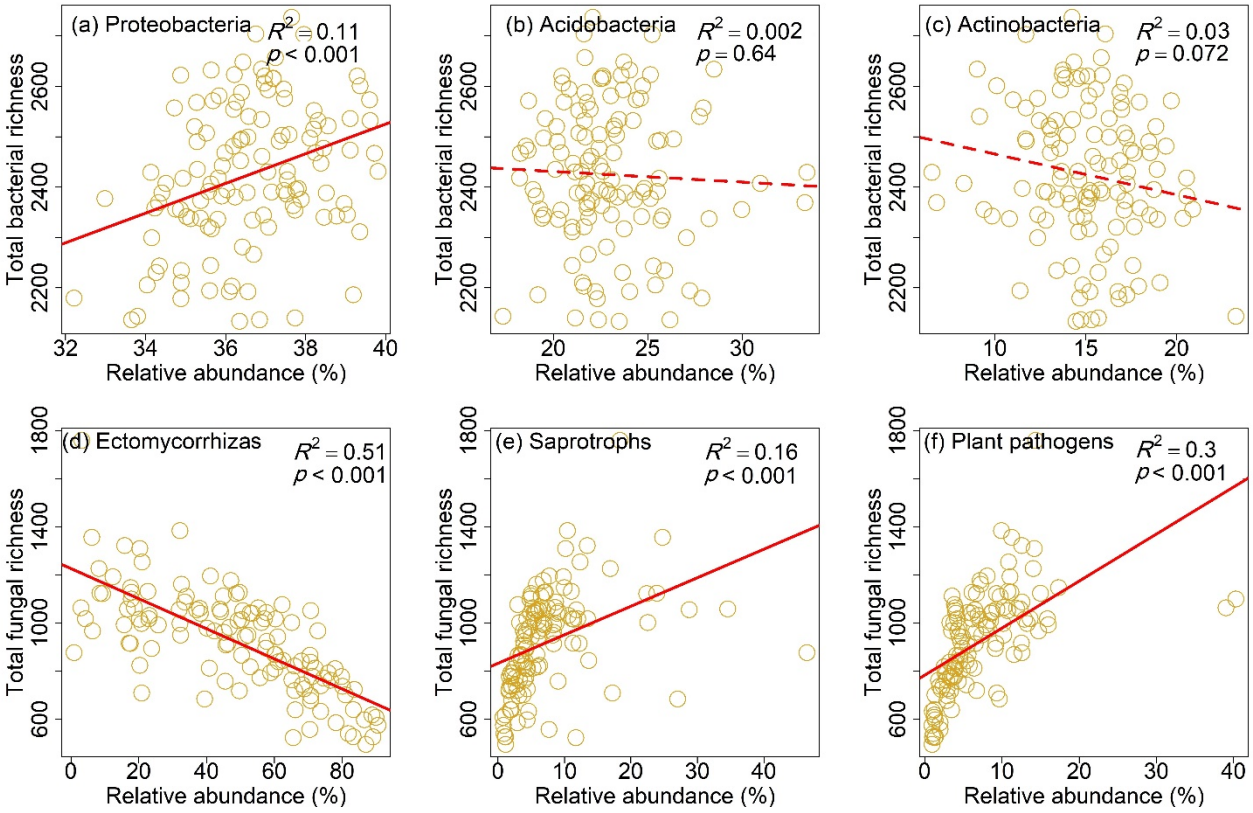

Figure S6. Bivariate relationships between the relative abundances of the most dominant (a-c) bacterial phyla or (d-f) fungal guilds and bacterial or fungal operational taxonomic unit richness; solid red lines represent significant relationships at $P < 0.05$ and dashed lines show non-significant relationships at $P > 0.05$.