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Research article

Multiple dimensions of phylogenetic diversity are needed to explain the complex aboveground–belowground diversity relationships

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The complex relationship between aboveground and belowground diversity and whether they act as surrogates for one another remains unresolved. Increasing evidence suggests that investigating phylogenetic diversity could provide valuable insights into the interplay between plants and soil microbes, but the proliferation of phylogenetic diversity metrics has hindered comparative studies and the identification of general patterns. To overcome this challenge, we implemented a multi-dimensional framework that classifies phylogenetic diversity metrics into three dimensions: richness, divergence, and regularity, each of which captures different ecological aspects of species differences. Then we applied this framework to investigate the relationship between above and belowground diversity in a subtropical forest in eastern China. We found that phylogenetic diversity of plant and soil microbes, including bacteria and fungi, were more strongly correlated at the richness and regularity dimensions compared with divergence dimension. Further analyses revealed that these observed correlation patterns align with variations in soil total phosphorus content, a key factor influencing both plant and microbial phylogenetic diversity at richness and regularity dimensions. Together, our study demonstrated the necessity of using a multi-dimensional approach to advance our understanding of the complex relationships between plant and soil microbial biodiversity.

Keywords: bacteria, fungi, phylogenetic diversity, phylogeny, plants

Introduction

The linkages between plants and soil microbes are crucial for the maintenance of biodiversity and ecosystem functioning (van der Putten et al. 2016). It is widely assumed that aboveground plant communities are positively associated with belowground soil

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microbes, and their diversity patterns should thus reflect one another (Hooper et al. 2000, Delgado-Baquerizo et al. 2018). However, recent studies have shown that the relationship between plant diversity and soil microbial diversity can also be absent (Cameron et al. 2019) or even negative (Prober et al. 2014).

The majority of studies investigating aboveground–belowground linkages have focused on taxonomic diversity, treating all taxonomic entities equally, despite the important ecological differences among species (Vane-Wright et al. 1991). Incorporating phylogenetic information has significantly broadened our understanding of biodiversity over the past two decades. It has been suggested that the linkages between plants and soil microbes could be stronger at the phylogenetic level than at the taxonomic level (Barberán et al. 2015, Leff et al. 2018). This is not only because plants and microbes have co-evolved together over 450 million years (Delaux and Schornack 2021, Lyu et al. 2021), but also because closely related plant species tend to share similar properties that are important for structuring soil microbial communities (De Deyn and Van der Putten 2005, Gilbert and Parker 2016). Further, ecological processes, such as environmental filtering and competitive hierarchies, may favor the coexistence of closely related taxa for both plant and microbial communities, but these coexisting taxa are not necessarily taxonomically similar (Pillar and Duarte 2010). Therefore, the phylogenetic diversity of plants should be a better predictor of belowground diversity than the number of species and their identities (Staab et al. 2021). Despite this potential, the relationship between plant and microbial phylogenetic diversity remains understudied. Although several empirical studies have incorporated phylogenetic information in recent years, the results were seemingly inconsistent even for the same microbial taxa. For example, Wang et al. (2015) used Faith's PD to quantify the phylogenetic diversity and found a significant positive relationship between phylogenetic diversity of bacteria and plant richness, whereas Goberna et al. (2016) used standardized mean phylogenetic distance (MPD) as phylogenetic diversity measures and found a negative correlation between plant and soil bacterial phylogenetic diversity along a soil fertility gradient. This inconsistency might be due to the use of different phylogenetic diversity metrics without comparing their ecological significance. Specifically, Faith's PD represents the summation of phylogenetic branch lengths, and therefore the total amount of evolutionary accumulation (Faith 1992). MPD captures the average distance among species within a community, reflecting the relatedness among coexisting species across the phylogeny connecting species together (Clarke and Warwick 1998). The application of different metrics from disparate phylogenetic dimensions limits the potential for synthetic studies and the elucidation of general patterns (Tucker et al. 2017).

Currently, there are over 70 metrics available to quantify phylogenetic diversity, but the use of a plethora of phylogenetic diversity metrics has caused much confusion in selecting the most appropriate metric for addressing specific ecological questions. To address this issue, Tucker et al. (2017) proposed a multi-dimensional framework that unifies measures of phylogenetic diversity. This framework categorizes phylogenetic metrics into three dimensions: richness, divergence, and regularity. Each dimension captures different ecological processes and patterns based on the phylogenetic attributes of the metrics. For example, the richness dimension reflects the total evolutionary history of the species within a community, while the divergence dimension captures the phylogenetic dissimilarities among species, and the regularity dimension measures how regularly the species are located along the phylogenetic tree. Although this framework unifies measures of phylogenetic diversity, it has not been applied to the study of aboveground–belowground diversity relationships.

We propose that applying this framework to the study of aboveground–belowground diversity relationships can provide insights into the ecological processes underlying these relationships (Fig. 1). For example, a positive relationship for the richness dimension indicates that the total evolutionary history of plant and microbial communities is correlated, which may reflect that the total niche spaces occupied by plants and microbes are correlated. For beta diversity at the richness dimension, such a correlation suggests that if both plant and microbial communities are more dissimilar then they are both exhibiting substantial compositional turnover such that different sites have many new phylogenetic branches. A positive relationship for the divergence dimension suggests that phylogenetically distantly related plants promote the co-occurrence of phylogenetically distantly related microbes, which would be the signal of coevolution between plants and microbes (Bitomský et al. 2022, Kohli et al. 2022). For the beta diversity level, such correlation indicates that if plant and microbial communities are both more phylogenetically dissimilar then turnover between sites is occurring deeper in the phylogeny, likely reflecting an underlying selection gradient. A positive relationship for the regularity dimension indicates that plants with more evenly distributed phylogenies also exhibit greater evenness in the distribution of evolutionary history among microbes, which could reflect the balance of underlying mechanisms that might select for species with a minimum phylogenetic distance separating them (e.g. competitive exclusion) on both plant and microbial communities (Tucker et al. 2017, Bitomský et al. 2022). For beta diversity, such a correlation suggests that similar changes in structuring mechanisms influence both plants and microbes across sites. Therefore, given that different phylogenetic dimensions represent different ecological patterns and processes, using multi-dimensional approaches is necessary to resolve potentially inconsistent aboveground–belowground diversity relationships found in previous studies.

We explored the correlation in plant–microbe diversity patterns across multiple phylogenetic dimensions in a subtropical forest in eastern China. We collected 80 soil samples from 16 permanent plots with a clear gradient in plant diversity, allowing us to investigate the strength of correlations for the three dimensions and determine at which dimension plant diversity is a better predictor of soil microbial diversity. According to the ecological meaning of above–underground relationship at

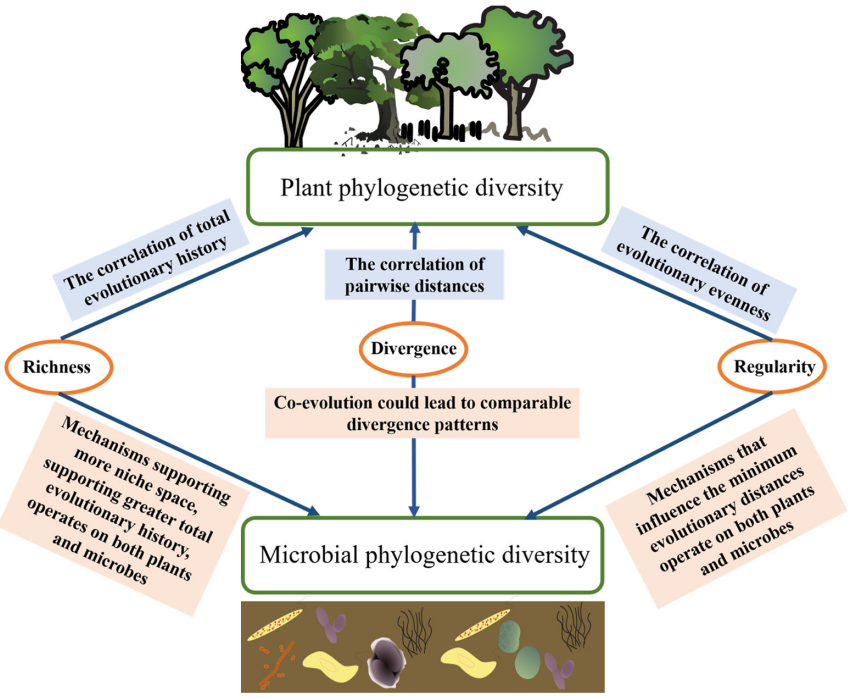

Figure 1. A conceptual framework describing the linkage between plant and microbial phylogenetic diversity at the richness, divergence, and regularity dimensions, with the relationships at different dimensions having different ecological significance.

three dimensions described above, we hypothesized that: 1) there will be a stronger relationship for the richness dimension if the plant and microbes were influenced by mechanisms determining the total niche spaces (the total contents of resources) simultaneously; 2) if the coevolution between plants and microbes plays central role, we hypothesize that the relationship between plant and microbial phylogenetic divergence are stronger than the relationships for the richness and regularity dimensions; 3) if underlying mechanisms select for species with a minimum phylogenetic distance separating them on both plant and microbial communities, the relationship between plant and microbial phylogenetic regularity will be strongest. Moreover, to account for potential environmental influences on plant and microbial diversity, we also measured a range of edaphic variables to assess whether the phylogenetic diversities of plants and soil microbes at the three dimensions are driven by similar or different environmental factors. By taking this multi-dimensional approach, we aim to provide a more comprehensive understanding of the complex relationships between aboveground and belowground diversity in subtropical forest ecosystems.

Material and methods

Study site and soil sampling

This study was conducted in a subtropical forest located in Ningbo City, Zhejiang Province, eastern China in 2017, with a subtropical monsoon climate characterized by an average annual temperature of 16.2°C and an average annual precipitation of 1700 mm. Dominant tree species in the area include *Pinus massoniana*, *Schima superba* and *Cunninghamia lanceolata*. Our study comprised 16 plots situated in three different locations, dominated by various tree species (Supporting information, 40–60-year-old stand), including both unmanaged secondary forests and forests that underwent close-to-nature silviculture treatment. In total, we obtained 16 plots, representing a clear diversity gradient and different composition structure across sites (Supporting information).

For each plot, five bulk-soil cores (3.8 cm in diameter, 0–10 cm depth), excluding litter and organic horizons, were collected using a five-point sampling method and placed in separate sterile plastic bags. We obtained a total of 80 soil samples from the 16 plots in October 2019. The samples were stored on ice and transported to the laboratory on the same day of collection. Prior to analysis, the soil samples were sieved through 2 mm sieves to homogenize them and remove plant residues and rocks. We then subsampled 10 g of soil from each sample and stored them at −80°C before DNA extraction. The remaining soils were air-dried for soil property analyses.

Microbial analyses

Microbial diversity was assessed through high-throughput sequencing methods. DNA was extracted from each soil sample using Advanced Soil DNA Kit (*m*ChipBiotech CO., Guangzhou, China). We sequenced the V4 region of the 16S rRNA gene for bacteria using the 515 (GTGCCAGCMGCCGCGGTAA) and 806 (GGACTACHVGGGTWTCTAAT) priming pair (Fierer et al. 2012). Similarly, we sequenced the second internal transcribed spacer (ITS2) region of the rRNA for fungi using the gITS7ngs (GTGARTCATCRARTYTTTG) and

ITS4ngs (TCCTSCGCTTATTGATATGC) priming pair (Nilsson et al. 2019). The primers included the appropriate adapters for Illumina and error-correcting 12-bp barcoded specific to each sample to permit multiplexing of samples. Genes from each sample were amplified with 50 μl reactions containing 25 μl 2× Premix Taq, 1 μl of each primer (10 μm), 1 μl g-DNA and 22 μl nuclease-free water. PCR was carried out under the following conditions: initial denaturation for 5 min at 94°C, then 30 cycles of denaturation for 30 s at 94°C, annealing at 53°C for 30 s and elongation for 30 s at 72°C, and a final step for 8 min at 72°C. Purified PCR products from all samples were pooled together in equimolar concentrations and subsequently sequenced on an Illumina NovaSeq platform with separate sequencing runs for the 16S rRNA and ITS2 amplicon pools. The raw sequence data was deposited into the National Centre for Biotechnology Information (NCBI) Sequence Read Archive (SRA) database (PRJNA 850164 and PRJNA 850274).

Raw sequences were processed using the software USEARCH for merging and quality filtering as well as deduplication (Edgar 2010). Then the high-quality sequences were clustered into operational taxonomic units (OTUs) at the 100% similarity threshold using UNOISE3 command (Edgar 2016). We then determined taxonomy assignment of each 'zero noise OTUs' (zOTUs) using the Ribosomal Database Project (RDP) classifier against the SILVA database (Quast et al. 2012) and UNITE database (Abarenkov et al. 2010) for bacteria and fungi with a confidence threshold of 0.8, respectively. Finally, we used the zOTUs classified into bacteria and fungi for further analyses. To consider differences in sequencing depths, samples were rarefied to 40 310 and 44 763 sequences per sample for bacteria and fungi, respectively.

The phylogenetic trees of both bacteria and fungi were constructed by FastTree software with the maximum-likelihood method (Price et al. 2009), following the alignment of representative sequences using software MAFFT (auto mode) and PASTA (default parameters), respectively (Katoh and Standley 2013, Mirarab et al. 2015). PASTA uses the divide-and-conquer algorithm to align sequences, which is suitable for the alignment of fungal ITS sequences whose lengths are highly variable (Wang et al. 2020). However, existing alignment methods still have some serious challenges, which need more research in the future. In addition, we classified the fungi into three main functional guilds (i.e. pathotroph, saprotroph and symbiotroph) according to FUNGuild and FungalTraits database (Nguyen et al. 2016, Põlme et al. 2020). We only retained zOTUs with a confidence designation of 'probable' or 'highly probable' in FUNGuild, and excluded zOTUs belonging to multiple functional guilds (Delgado-Baquerizo et al. 2020).

Plant survey and phylogenetic tree

Trees, especially large trees, play an important role in forest ecosystem functions and services. In our research, we focus specifically on the correlation relationship between trees and soil microbes, which is crucial for a comprehensive understanding of ecosystem dynamics. The plant composition of all plots was investigated in August 2019. Every tree stem with a diameter at breast height (DBH) ≥ 5 cm in the plot was sampled. We found 117 plant species in total across all the study plots, both gymnosperms and angiosperms were included. We then produced a species-level phylogenetic tree of these species form a mega-tree (i.e. GBOTB.extended.tre) reported by Smith and Brown (2018), using R package 'V.PhyloMaker' (www.r-project.org, Jin and Qian 2019). GBOTB.extended is the largest dated phylogenetic tree for seed plants, which is well resolved at the genus level, thereby ensuring the robustness of our community phylogenetics analysis. Phylogenetic information for all species from our dataset was received from the mega-tree.

Phylogenetic diversity metrics

We first calculated the phylogenetic alpha diversity of plants and microbes at the three dimensions. We calculated Faith's PD and MPD to represent the richness and divergence dimension, respectively. They were calculated by *pd* and *mpd* function in the R 'picante' package (Kembel et al. 2010). For the regularity dimension, we calculated the evolutionary distance (Eed), which quantifies how evenly spaced species are across a community phylogeny (Cadotte et al. 2010). The Eed was calculated using the *.eed* function in the R package 'pez' (Pearse et al. 2015). Then to examine whether phylogenetic beta diversity of plants and microbes were associated with each other, we calculated unweighted Unifrac dissimilarity index and inter-community MPD (betaMPD) for the richness and divergence dimensions, respectively. Unifrac is defined as the percent of branch length unique to any pair of assemblages (Lozupone and Knight 2005). BetaMPD measured the mean pairwise phylogenetic distance separating taxa across communities, which is an MPD-based measure of beta diversity (Fine and Kembel 2011). They were estimated using the *unifrac.query* and *cd.query* function in the R package 'PhyloMeasures' (Tsirogiannis and Sandel 2016). For the regularity dimension at beta level, we used the D(p)β, which calculated by dividing the gamma component by the alpha component using the regularity dimension (Scheiner et al. 2017). Besides phylogenetic diversity, we also calculated the taxonomic diversity of plants, bacteria, and fungi, with alpha diversity was measured as species or zOTU richness, and beta diversity was measured as Bray–Curtis and Jaccard dissimilarity index, using *vegdist* function of 'vegan' package (Oksanen et al. 2019). For soil microbes, we calculated their phylogenetic alpha and beta diversity at both sample and plot levels. The estimate of plot phylogenetic alpha diversity was obtained by calculating the average microbial alpha diversity of five samples within each plot. The beta diversity at the plot level was estimated by calculating the average of beta diversity between samples among sites.

Soil properties

Soil physical and chemical factors have important influences on both plant and microbial diversity and composition by

influencing habitat and resources availability, resource limitation and ultimately exploitative competition (Bardgett et al. 2005, Wang et al. 2019). In order to quantify whether plant and microbial phylogenetic diversity were associated with shared edaphic variables, we measured five soil properties (Supporting information), including pH, soil total organic carbon (TOC), total N (TN), total P (TP), available P (AP) of each sample. Soil pH was measured by a pH meter in distilled water (1:5, weight/volume), whereas soil TOC was estimated using the potassium dichromate external heating oxidation-volumetric method. TN and TP were determined by Kjeldaha procedure and molybdenum antimony blue colorimetry. The AP content was determined by the $NaHCO_3$ extraction–molybdenum antimony anti-colorimetric. Prior to analysis, the five soil properties and alpha diversities were standardized to have a mean value of 0 and variance of 1.

Statistical analyses

To evaluate the relationship between plant and microbial phylogenetic diversity for alpha diversity, we used Spearman's correlations, as it is robust to nonlinear relationships, deviations from normality and outliers (Tucker et al. 2017). Moreover, we also used the generalized additive models (GAMs) to capture the non-linear relationships based on the *gam* function in the R package 'mgcv' (Wood 2017). For beta diversity, PROTEST analyses were performed using the *protest* function from the 'vegan' package, which assesses the correlations between the phylogenetic dissimilarity of plant and microbes for each dimension through permutation, it is robust for the nonlinear relationships between distance matrixes (Peres-Neto and Jackson 2001). We also used GAMs to fit the trend lines and their confidence interval between plant and microbial beta diversities. Since plant and microbial diversity increase with spatial scale (Green and Bohannan 2006), we performed correlation analyses at both the plot (n = 16) and sample (n = 80) levels to confirm the robustness of our correlation patterns.

To further investigate whether the observed diversity patterns were jointly explained by the influence of shared soil edaphic variables, we used Spearman's correlation analysis to test the relationship between individual soil edaphic variables and plant or microbial alpha diversity for each phylogenetic dimension. Moreover, we used standardized edaphic variables to calculate Euclidian distances among plots, and then used the PROTEST analysis to assess the relationships between edaphic variables and plant or microbial phylogenetic beta diversity for each dimension.

Results

Phylogenetic alpha diversity

For alpha diversity, both bacteria and fungi were more strongly correlated with plants at the richness and regularity dimensions compared with the divergence dimension. For the richness dimension (i.e. Faith's PD), soil bacterial diversity showed a significant positive correlation with plant diversity (Spearman's correlation rho = 0.58, p = 0.019, Fig. 2a), whereas the correlation was marginally significant for fungi (rho = 0.48, p = 0.058, Fig. 2d). Conversely, bacterial and fungal diversity showed weaker correlations with plant diversity at the divergence dimension (i.e. MPD) (Spearman's correlation, rho= −0.42, p = 0.107 for bacteria, Fig. 2b; rho = 0.45, p = 0.078 for fungi; Fig. 2e). Similar to the richness dimension, plant and microbial phylogenetic alpha diversity for the regularity dimension (i.e. Eed) were positively correlated (Spearman's correlation, rho = 0.64, p = 0.008 for bacteria, Fig. 2c; rho = 0.47, p = 0.064 for fungi, Fig. 2f). These patterns were consistent at the sample level (Supporting information). Upon excluding gymnosperms from the plant community, similar relationships were observed for soil bacteria, but the positive correlation between plant and fungal phylogenetic richness and regularity became nonsignificant (Supporting information). Moreover, when we divided soil fungi into three functional guilds (i.e. saprotroph, symbiotroph and pathogen), phylogenetic diversity of all three functional guilds were significantly positively correlated with plants at the richness and regularity dimensions, but not at the divergence dimension (Supporting information). Further, the generalized additive models (GAMs) also revealed non-linear relationships at the divergence dimension but positive relationships at the richness and regularity dimensions between plant and soil microbes.

Phylogenetic beta diversity

For beta diversity, significant correlations were detected between plants and microbes within the richness dimension. PROTEST analyses revealed that both bacterial and fungal beta diversity at the richness dimension were significantly related to plant beta diversity at the same dimension (PROTEST analysis, r = 0.71, p = 0.001 for bacteria, Fig. 3a; r = 0.63, p = 0.002 for fungi, Fig. 3d). Conversely, bacterial and fungal beta diversity were not significantly correlated with plant beta diversity at the divergence dimension (PROTEST analysis, r = 0.19, p = 0.798 for bacteria, Fig. 3b; r = 0.04, p = 0.995 for fungi, Fig. 3e). At the regularity dimension, a significant correlation was observed between plant and fungal beta diversity (PROTEST analysis, r = 0.56, p = 0.010, Fig. 3f), while the correlation between plant and bacterial beta diversity was nonsignificant (PROTEST analysis, r = 0.37, p = 0.235, Fig. 3c). These results were consistently observed at both the plot level (Fig. 3) and the sample level (Supporting information). Notably, at the sample level, both bacteria and fungi exhibited significant correlations with plant beta diversity at the regularity dimension (PROTEST analysis, r = 0.50, p = 0.001, Supporting information). One exception is there was also a significant relationship between plant and fungal phylogenetic divergence at the sample level (PROTEST analysis, r = 0.27, p = 0.007, Supporting information). These patterns generally persisted even when gymnosperms were excluded from the analysis (Supporting

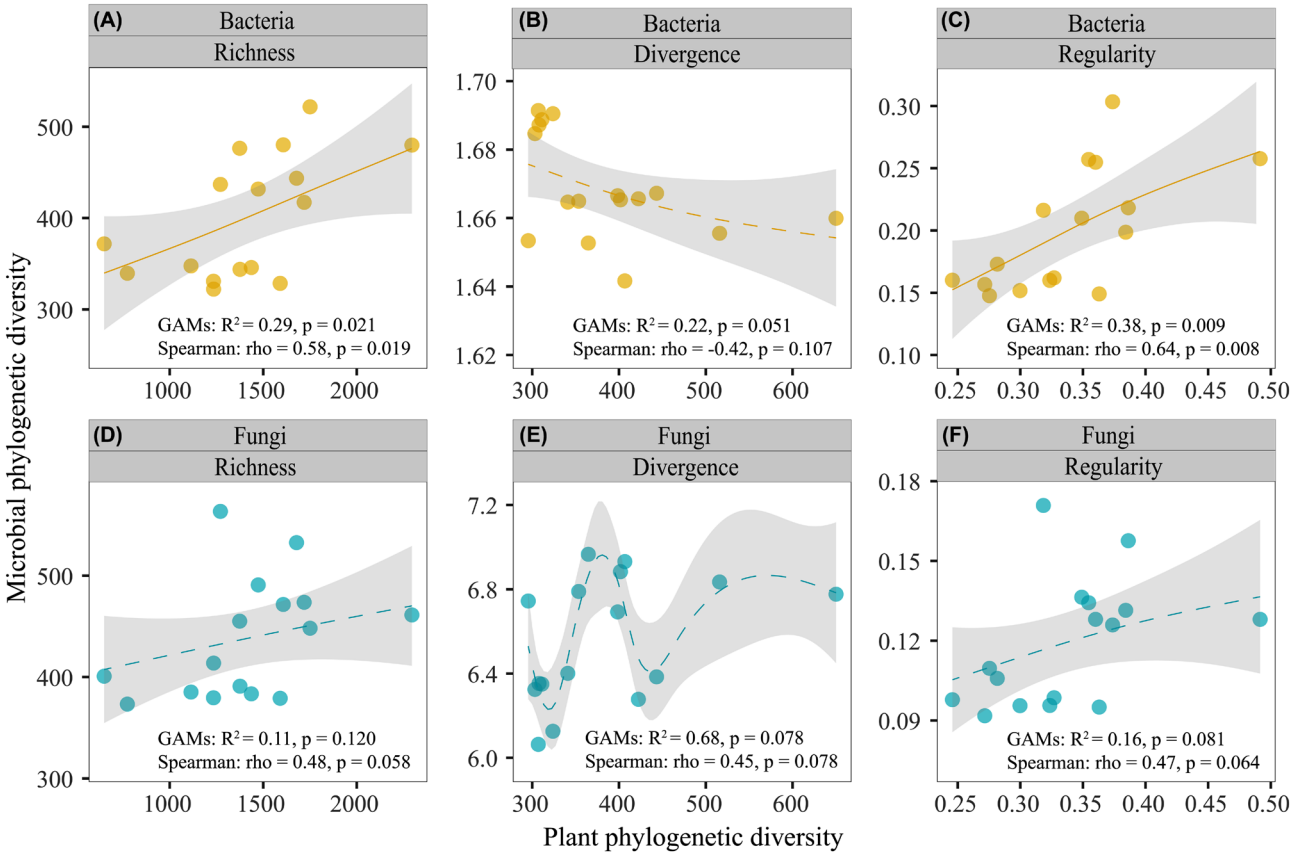

Figure 2. The relationship between plant and microbial phylogenetic alpha diversity for the three dimensions. For the richness (a, d), divergence (b, e) and regularity (c, f) dimensions, phylogenetic diversity was measured as Faith's PD, mean phylogenetic distances (MPD), and evolutionary distance (Eed), respectively. Solid and dashed trend lines represent significant ($p < 0.05$) and marginally significant ($p < 0.1$) generalized additive models (GAMs), respectively. The shaded areas show the 95% confidence interval of the GAMs fits. The correlation coefficients (rho) and p-values were obtained from Spearman's correlation analyses.

information). Additionally, all three fungal functional guilds (i.e. saprotroph, symbiotroph and pathogen) showed positive relationships with plant beta diversity for the richness dimension, but not for the divergence and regularity dimensions (Supporting information). Further, the GAMs also highlighted that the positive correlation between plant and microbial phylogenetic beta diversity was more pronounced at the richness dimension (Fig. 3).

The influences of soil edaphic variables

Further analysis showed that shared edaphic drivers contribute to the correlations between soil microbial and plant phylogenetic diversity. For bacteria, we found that TP was the significant shared edaphic factor in the relationships at alpha (richness and regularity dimensions) and beta (richness dimension) level (Fig. 4a, c, d). For fungi, TP also played the important role in the relationships at alpha (regularity dimension) and beta (richness dimension) levels, while TOC, TN and pH also shaped regularity at beta level (Fig. 4c, d, f). In contrast, for the divergence dimension, plant and microbial phylogenetic diversity were influenced by different edaphic variables, reinforcing the inference of a weak relationship for this dimension. In particular, plant phylogenetic diversity at the divergence dimension was positively affected by soil nutrient content (e.g. TOC, TN) at alpha and beta levels, while bacterial diversities were positively affected by TP and soil pH at the alpha level (Fig. 4b, e). For beta divergence dimension, we did not find that any factors affected microbial phylogenetic diversity (Fig. 4e).

Discussion

Our study provides compelling evidence that the aboveground–belowground diversity relationships are contingent upon the phylogenetic diversity dimensions being measured. Specifically, we observed that the phylogenetic diversity of plants and soil microbes are more strongly correlated at the richness and regularity dimensions. These dimensions are thought to reflect the total amount of ecological niches and the outcome of interactions that influence minimum dissimilarity between species (e.g. limiting similarity), respectively. Thus, our findings suggest that plant communities with larger and more evenly distributed evolutionary history also harbor microbial communities with larger and

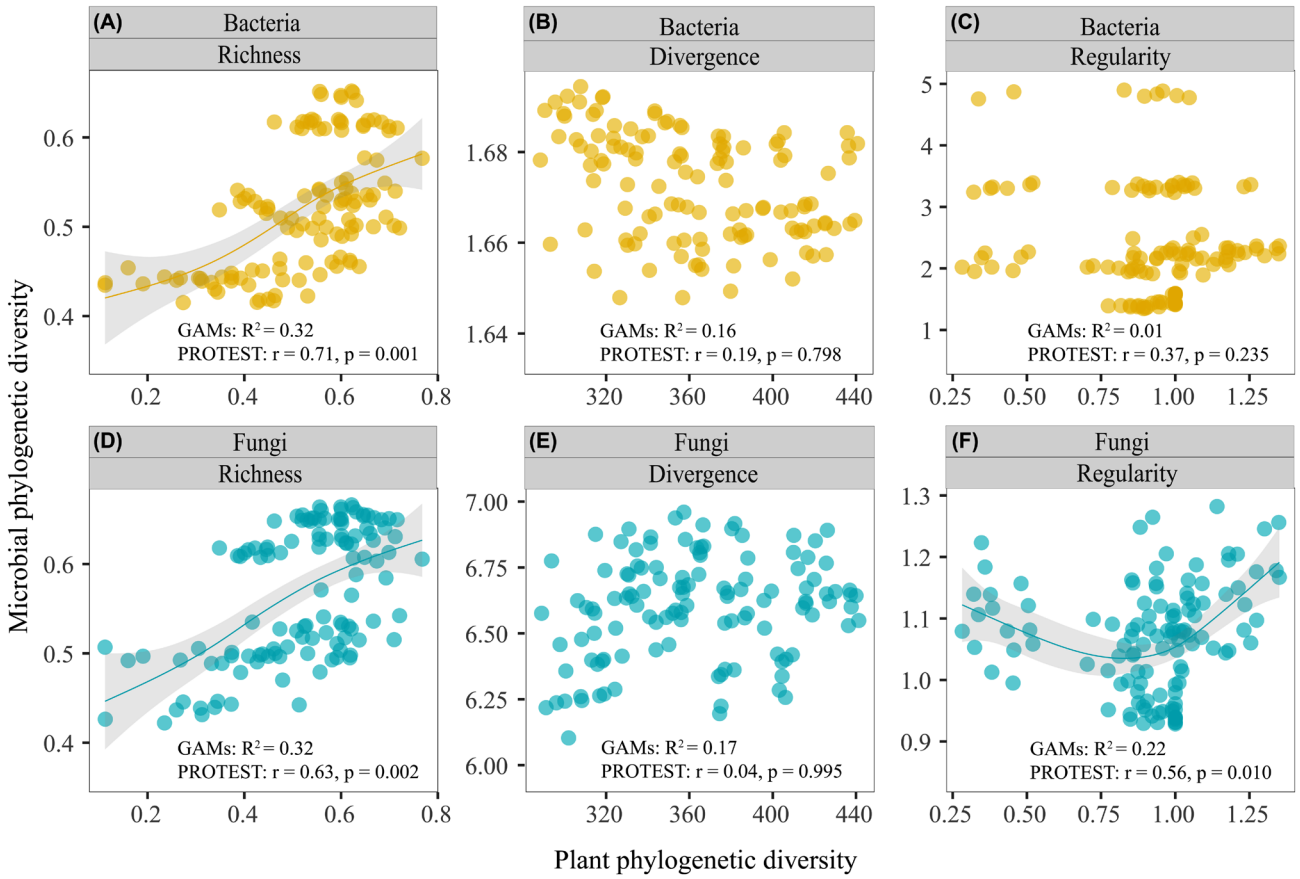

Figure 3. The relationships of plant and soil microbial phylogenetic beta diversity for the richness, divergence and regularity dimensions, which were measured by Unifrac, betaMPD and $D(p)_{\beta}$, respectively. The trend lines were fitted by generalized additive models (GAMs). The shaded areas show the 95% confidence interval of the GAMs fits. The correlation coefficients r and p-values were obtained from PROTEST analyses. Solid lines represent significant (PROTEST' $p < 0.05$) correlation relationships.

more evenly distributed evolutionary history. However, the lack of correlation at the divergence dimension indicates that plots with phylogenetically distantly related plants do not necessarily contain phylogenetically distantly related soil microbes, despite the expectation that certain microbial taxa, such as mycorrhizal fungi, would show tight coevolution with plants. Therefore, our study highlights the importance of considering different phylogenetic dimensions when studying aboveground–belowground diversity relationships, as the relationships at different dimensions address distinct ecological questions and may be driven by different ecological processes.

Phylogenetic richness reflects the total evolutionary history of taxa, and the high concordance between plant and microbial phylogenetic richness likely reflects that plant communities with greater total evolutionary history can provide more total niche space for microbes. It is worth noting that phylogenetic richness is often strongly correlated with species richness (Tucker et al. 2017). In line with this idea, we found a consistent positive relationship between phylogenetic alpha diversity at the richness dimension (Faith's PD) and taxonomic alpha diversity (species richness) for plants, bacteria, and fungi (Supporting information). Similarly, phylogenetic beta diversity at the richness dimension (Unifrac dissimilarity index) also showed a positive relationship with taxonomic beta diversity (Jaccard dissimilarity index) for all three groups (Supporting information). Therefore, the strong aboveground–belowground diversity relationships at the richness dimension observed in our study are associated with the positive correlation between plants and microbes at the taxonomic level (Fig. 2–3, Supporting information). In addition to taxonomic diversity, shared edaphic drivers were also found to contribute to the positive aboveground–belowground diversity relationships for the richness dimension. Our analysis revealed that TP was the significant shared predictor for phylogenetic alpha and beta diversity for both plant and microbial communities (Fig. 4a, d). This is consistent with previous studies suggesting that TP plays crucial roles in shaping microbial communities in subtropical China (Dong et al. 2014, Zhang et al. 2022). Therefore, the shared edaphic influences of plant and soil microbes could drive patterns of total diversity and turnover and therefore generate the positive aboveground–belowground diversity relationships for the richness dimension.

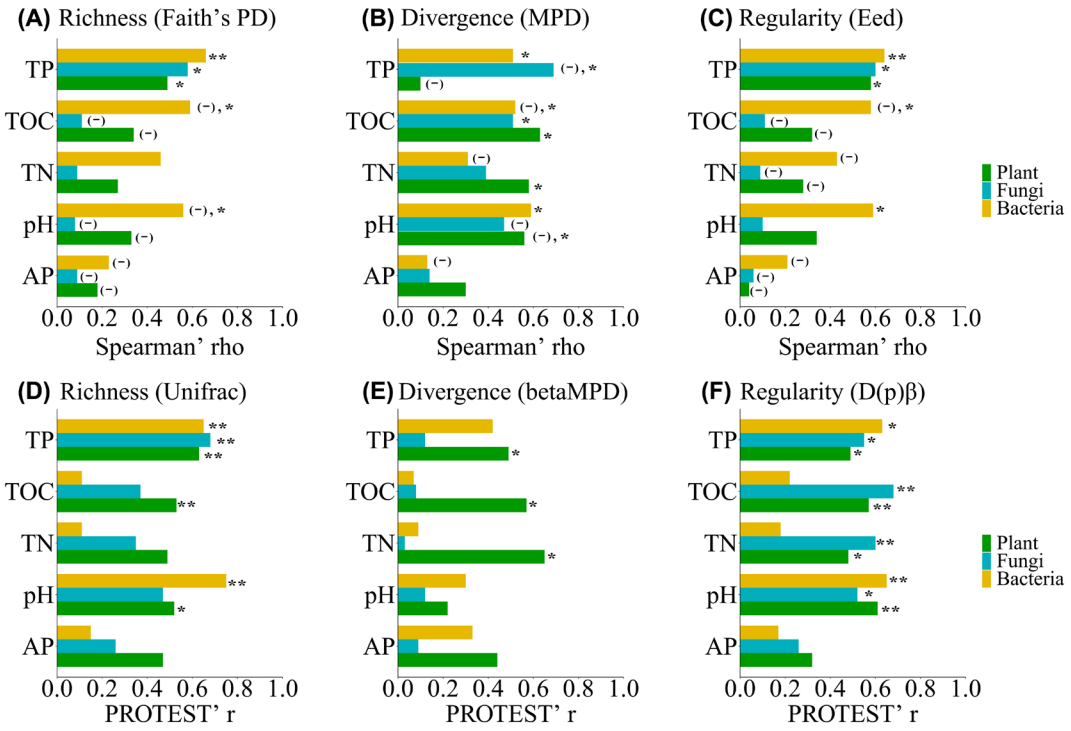

Figure 4. Relationships of plant, fungi and bacteria with individual soil edaphic factors. (a–c: alpha diversity; d–f: beta diversity). The rho or r values of alpha and beta diversities were tested by Spearman's correlation and PROTEST analysis, respectively. The stars represent significant relationships (*p < 0.05, ** p < 0.01, *** p < 0.001), and (−) represent negative correlation relationships. Notes: TOC, soil total organic carbon; TN, soil available nitrogen; TP, soil total phosphorus; AP, soil available phosphorus; pH, soil pH.

The measurement of phylogenetic diversity at the divergence dimension provides information on how distantly related taxa are within or among communities. In the case of plant–microbiome associations, these relationships are thought to be the result of millions of years of co-evolution, leading to the expectation that phylogenetically distantly related plants would harbor phylogenetically distantly related microbes (Liu et al. 2016). However, our findings challenge this notion, as we observed little to no significant correlation between MPD and betaMPD of plants and soil microbial community (Fig. 2b, e, 3b, e). One possible explanation is that the free-living generalist soil microbes in bulk soil we studied show little coevolutionary association with plants, compared to the more specialized mutualists and pathogens that are found in the rhizosphere or leaf tissue (Yang et al. 2017). Thus, any phylogenetic coevolutionary signal could be diluted in our study. Future studies should investigate whether the phylogenetic distances of rhizosphere or endophytic microbes within and among communities are more influenced by the phylogenetic distance of plants, as they are more dependent on direct symbiotic relationships with plants (Chen et al. 2019). We also found that the edaphic drivers of microbial phylogenetic divergence typically differed from those of plant phylogenetic divergence, further emphasizing their decoupling. Specifically, soil nutrient contents (e.g. TOC, TN) were significant predictors of plant phylogenetic divergence, while soil TP and pH were the major drivers of microbial phylogenetic divergence (Fig. 4b, e).

The regularity dimension reflects the evenness of phylogenetic distances among taxa and provides complementary information to the divergence dimension about the distribution of species across the phylogeny. Although no study has directly quantified the relationship between aboveground and belowground phylogenetic diversity at the regularity dimension, our findings provide the first evidence that plant and microbes are correlated in the regularity dimension at the alpha level (Fig. 2c, f). Specifically, we observed that plots with both closely and distantly related plants (i.e. low regularity) were more likely to host both closely and distantly related soil microbes. Low regularity in the distribution of phylogenetic similarity among species has often been interpreted as evidence for environmental filtering (Kraft et al. 2008) or perhaps the influence of an ecosystem engineer that restructures the functional make of communities that selects for more dissimilar species (Sodhi et al. 2019). Therefore, the positive correlation for the regularity dimension could reflect that plants and microbe are responding to similar ecological mechanisms, namely, from sites with low regularity (say from environmental filters) to sites where both taxa exhibit greater regularity (perhaps from greater limiting similarity). Consistent with this interpretation, we found that shared TP was the most important shared factor of the phylogenetic regularity of plant, bacterial and fungal communities (Fig. 4c). Soil TP can influence plant and soil microbial communities by affecting the intensity of competition, since competition can play

an important role in shaping plant and soil microbial communities in mature and stable environments (Eldridge et al. 2017, Hortal et al. 2017). However, similar phylogenetic patterns could be driven by multiple assembly mechanisms, the ecological mechanisms underlying the correlation remain to be further explored.

Although our study provides compelling evidence that incorporating the three phylogenetic dimensions is crucial for comprehending the aboveground–belowground diversity relationships, there are several limitations worth noting. First, our research focuses primarily on tree species, which does not encompass the entire spectrum of aboveground diversity by including both tree and herbaceous species. Therefore, we need to apply our framework to diverse plant group, such as herbaceous species. Second, aboveground–belowground diversity relationships vary widely among various ecosystem types and spatial scales (Liu et al. 2020). Therefore, focusing solely on single ecosystem might not adequately resolve these complex relationships. We hope that future studies will utilize this multidimensional approach on different ecosystems (e.g. forests, grasslands and wetlands) across various spatial scales to determine whether any general patterns emerge. Third, our study concentrates on phylogenetic diversity, it is worth noting that functional diversity metrics could also be classified into these three dimensions following the same unified scheme (Mammola et al. 2021), and might not provide concordant results because functional and phylogenetic diversities could be influenced by different ecological mechanisms (Cadotte et al. 2019). Therefore, an important next step is to quantify both phylogenetic and functional diversity at the three dimensions, to gain a comprehensive understanding of the aboveground–belowground diversity relationships. Forth, due to our sampling design, the effect of site is strong in our study, which likely reflects that there are large environmental differences among sites which overwhelm plot differences within site. A broader and more continuous sampling is required to better disentangling spatial patterns. Finally, there is a large literature on plant–soil feedbacks that shows that plants and soil microbial communities have reciprocal influences on one another (Bever 1994, van der Putten et al. 2013). Our work is not able to assess these feedbacks, but it would be extremely valuable to design experiments to see if differences in plant or microbial phylogenetic diversity alter the strength of plant–soil feedback.

Our findings provide insight into comprehending the intricate relationships between plants and soil microbes, namely, that such relationships largely depend on the phylogenetic dimensions we considered. We found phylogenetic diversity of plant and soil microbes, including bacteria and fungi, are more correlated at the richness and regularity dimensions compared with divergence dimension. Although the generality of our findings needs to be further accessed across diverse communities and for different taxonomic groups and spatial scales, our study highlights the importance of considering different dimensions to better understand the aboveground and belowground diversity relationships. It is crucial to avoid treating different phylogenetic dimensions interchangeably since they represent diverse information and effectively test distinct hypotheses.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjt9d (Lu et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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