SYNTHESIS & INTEGRATION

Relationships between plant diversity and soil microbial diversity vary across taxonomic groups and spatial scales

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Abstract.   Plant diversity has long been assumed to predict soil microbial diversity. However, contradictory results have been found when examining their relationships, particularly at broad spatial scales. To address this issue, we conducted a meta-analysis to evaluate the patterns in the correlation between plant diversity and soil microbial diversity and the underlying factors driving the relationship. We collected correlation data from 84 studies covering more than 3900 natural terrestrial samples globally. Using the hierarchical mixed-effects model, we investigated factors including targeted taxonomic group, microbial examination method, sampling extent, biome type, soil type, and environmental factors to assess the patterns of the plant–microbial correlation and the determinants of their variations. We found that microbial richness displayed a modest but positive correlation with plant diversity ($r = 0.333$, CI = 0.220–0.437). In spite of variability among taxonomic groups and their relationship with plant diversity, positive correlations were more pronounced in the intermediate sampling extent of latitude and elevation coverage, and tropical forests. Among examined environmental factors, soil pH was negatively associated with the plant and soil microbial relationships at large spatial scales. The plant–microbial correlation appears more sensitive to edaphic factor variation in the poor nutrients and soil less compact systems. Collectively, our results point to key differences across taxonomic groups, spatial scales and biomes, and the modulating effects of climate and soil. The findings shed light on our deep understanding in plant–microbial diversity relationships at broad spatial scales and ecosystem sensitivity to biodiversity loss and environmental change.

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Introduction

The nature of the relationship between plant diversity and microbial diversity provides insights into the ecological drivers of community structure and function (Wardle et al. 2004, De Deyn and Van der Putten 2005, Allan et al. 2013,

Duhamel and Peay 2015). Although soil microbial groups vary in their functional relationships with plants, they can promote plant community diversity through a variety of mechanisms. For example, symbiotic mutualists can promote plant community diversity by increasing nutrient availability or facilitating niche partitioning (Van

Der Heijden et al. 2006, Bever et al. 2015, Van Der Putten 2017), while soil pathogens can infect and kill plant seedlings directly, or suppress beneficial microbial interactions with plant hosts, which both contribute to the survival of heterospecifics and lead to higher plant diversity (Mangan et al. 2010, Liu et al. 2016b). Plants also serve as the principal suppliers of energy for decomposers, symbionts, and pathogens, thereby governing the niche space for different soil microbes to persist (Facelli and Pickett 1991, Zak et al. 2003, Berg and Smalla 2009, Bulgarelli et al. 2013, Steinauer et al. 2015). Thus, the diversity of plant community and soil microbial community has long been assumed to be closely related (Lavelle et al. 1995, Whitman et al. 2003, Wardle et al. 2004, Falkowski et al. 2008). However, the existing information about the plant–microbial relationship at the global scale is contradictory or inconclusive (Tedersoo et al. 2014, Prober et al. 2015, Ochoa-Hueso et al. 2018).

According to general biogeographic theories (Pianka 1966, Willig et al. 2003), we might expect soil microbial diversity to follow the pattern of vascular plant diversity, which declines with increasing latitude and elevation. However, studies have revealed inconsistent results. Along latitudinal gradients, both tropical forests at low latitude (Mueller et al. 2007, Tedersoo et al. 2014) and temperate forests at midlatitude (Fierer et al. 2012, Shi et al. 2014) contain the highest soil microbial diversity. In contrast, with a few exceptions (Bahram et al. 2018), most studies find no increase in soil microbial diversity from polar to equatorial regions (Fenchel and Finlay 2004, Fuhrman 2009, Fierer et al. 2011, Hendershot et al. 2017). Likewise, soil microbial diversity patterns vary widely along elevation gradients, where monotonic declines (Bryant et al. 2008), unimodal patterns (Liu et al. 2016a), and no relationships (Fierer et al. 2011, Shen et al. 2014) with increasing elevation have all been reported. As a consequence, studies aiming to examine the relationship between plant diversity and soil microbial diversity across biogeographic scales find weak (Bryant et al. 2008, Prober et al. 2015), or even no correlations (Lanzén et al. 2016, Cameron et al. 2019). These conflicting results suggest that the relationship between soil microbial diversity and plant diversity might differ across biomes and spatial scales.

Several factors may explain the dramatic variation in the correlation between microbial diversity and plant diversity. First, the plant–microbial relationship can vary among different microbial taxonomic groups. For example, based on a site-level analysis, the richness of certain bacterial taxa, such as nitrogen-fixing bacteria, was more closely related to plant diversity than were other taxonomic groups (Liang et al. 2016, Zhou et al. 2016). The sampling of soil microbial and plant communities is often conducted at different spatial scales, ranging from local sites (Gömöryová et al. 2009, Navarrocano et al. 2014) to broad geographic regions (Fierer et al. 2012, Zhou et al. 2016), such that variability in abiotic factors such as soil pH (Fierer and Jackson 2006, Lauber et al. 2009, Shen et al. 2013, Siles and Margesin 2016), total organic carbon (Calbrix et al. 2007, Dimitriu and Grayston 2010, Ding et al. 2015), and mean annual temperature (Hobbie 1996, Luo et al. 2014, Zhou et al. 2016) among sites may further complicate the plant–microbial relationship. Therefore, a comprehensive analysis using data across taxonomic groups and spatial scales is needed to quantify the relationship between plant diversity and microbial diversity.

In this study, we synthesized data from 84 studies that included over 3900 samples to determine the relationship between plant diversity and soil microbial diversity at a global scale. We investigated factors including targeted taxonomic group, microbial response type in diversity (richness, abundance, diversity index, and composition), microbial examination method, sampling extent (latitude and elevation cover range), biome type, soil type, and environmental factors (e.g., soil pH, total organic carbon, precipitation, and temperature) to assess the patterns of the plant–microbial correlation and variables explaining their variation. In this meta-analysis, we addressed the following questions: (1) Are plant and microbial diversity positively correlated at the global scale? Based on the functional role of soil microbes as the main decomposer of plant-derived substrates, we expect a positive relationship between them. (2) Are predicated plant-associated taxa, such as mycorrhizal fungi, more strongly correlated with plant diversity than other taxa? The symbiotic microbes, which interact directly with plants,

may enable a stronger correlation. (3) Which ecosystems do plant diversity and microbial diversity show a higher correlation? Tropical forests should have a higher plant–microbial correlation, considering the extraordinary high biodiversity and the strong interaction between plant community and parasitic microbes (Bagchi et al. 2014, Sarmiento et al. 2017). (4) Which environmental factors determine the plant and microbial relationships in biodiversity across taxonomic groups and spatial scales? We expect soil pH to be one of the most important environmental factors at the global scale, and the roles of other soil attribute effects vary among taxonomic groups and spatial scales.

METHODS

Database

We conducted an extensive literature search for studies that analyzed the relationship between soil microbial diversity and plant diversity in natural terrestrial ecosystems. Relevant journal articles from 1990 to March 2019 were searched using both ISI Web of Science and Google Scholar with but not limited to the following search terms "microb*", "fung*", "bacteria", "archaea" or "mycorrhizae" combined with "plant" or "vegetation" and diversity parameters including "richness", "abundance", "diversity", "composition", *etc*. We only included articles that met the following three criteria: (1) studies that reported summary statistics (i.e., r, R^2, F, and t) of plant and soil microbial diversity correlation; (2) studies that were conducted in natural terrestrial ecosystems or recovering ecosystems at least 10 yr after abandonment without obvious disturbance; and (3) studies that sampled microbes from topsoil with sampling depth not exceed 30 cm.

For each selected study, we collected the summary statistics of microbe–plant diversity correlations. These summary statistics of different taxonomic groups in the same work were considered as separate results to avoid subjective decisions and lost information. Further, we gathered the information on the examined taxonomic group, soil microbe detection method, sampling extent (latitude and elevation), biome type, soil type, and most frequently reported environmental variables, including mean annual temperature

(MAT), and mean annual precipitation (MAP), soil pH, total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), soil moist (SM), and bulk density (BD). Since some literature provided information on soil composition of sand, silt, and clay, the widely used United States Department of Agriculture (USDA) soil textural classification system which determines soil types based on the physical texture (i.e., the percentage of sand, silt, and clay) was used. Missing data of soil properties were obtained through referenced literature or from SoilGrids at 250 m spatial resolution (Hengl et al. 2017). MAT and MAP were downloaded from WorldClim at the resolution of 2.5 arc minutes if original literature did not report (Fick and Hijmans 2017). Four of the most frequently used diversity indicators were selected for our analyses: richness, abundance, diversity index, and composition (beta diversity). Richness is a measure of the total number of species/operational taxonomic units (OTU) in a microbial community. Abundance in our dataset represents the relative abundance of a specific phylum (e.g., Wu et al. 2012, Zhang et al. 2015) or taxonomic group (e.g., Álvarez-Sánchez et al. 2012, Liang et al. 2016). Diversity indices include the Shannon index, Simpson index, and Hill number. Hill number or effective numbers of species is a mathematically unified family of diversity indices that incorporate relative abundance and species richness (Jost 2006, Chao et al. 2014). The composition was calculated based on the species/OTUs' relative abundance. The frequently used composition measures such as Bray-Curts distance, Jaccard distance, and UniFrac distance were included. For the further refinement of the dataset, if study sites were analyzed more than once (e.g., Guo et al. 2018, Zhang et al. 2018), only one set of data was used for analysis. If soil microbes were sampled in different seasons (e.g., Slabbert et al. 2010), only the value measured in the summer was selected, to maximize our ability to compare across studies. In total, more than 5000 papers were reviewed, and 84 studies fulfilled our criteria and were included in the subsequent analysis (Appendix S1).

Data analysis

The summary statistics of plant and microbial diversity correlation in these 84 studies were

transformed into effect size (Z_r) and conditional variance (Z_{VAR}) using Fisher's (1921) transformation:

$$Z_r = 0.5 \times \ln\left[\frac{1+r}{1-r}\right] \text{ and } Z_{VAR} = \frac{1}{n-3},$$

where r is the correlation coefficient and n is the sample size. Since the variance is inversely related to n, studies with larger sample sizes were assigned with larger weights. Other summary statistics (i.e., R^2, F) were converted to r using

$$r = R^2 - \frac{p(1-R^2)}{n-p-1} \text{ and } r = \sqrt{\frac{F}{F+\text{dferror}}},$$

from Cohan and Perry (2007) and Rosenthal et al. (1994).

We performed a hierarchical mixed-effects meta-analysis, which allows specification of the fixed predictor variables and nested random effects to account for variation across and within studies (Rossetti et al. 2017). Multiple effect sizes obtained within a given study violated the assumption of independence (Hedges et al. 2010). The nested random effects (study/taxonomic group) took into account hierarchical dependence and also publication-level variation that incorporates the dependency of multiple outcomes within study observations (Stevens and Taylor 2009). The method has been recently used in meta-analysis to account for hierarchical dependence between multiple observations within studies (Harbord and Whiting 2009, Tuck et al. 2014, Rossetti et al. 2017). Our preliminary analysis revealed that most frequently used measures of microbial diversity showed no difference in their correlations with plant diversity (with the exception of Shannon diversity, Appendix S2: Fig. S1). To consider the different ecological implications (Stirling and Wilsey 2001), we applied the diversity measures as the second random effect to account for variations among them. The statistic Q_M which quantifies the variation explained by the predictor variable and the residual (Q_E) was calculated (Deeks et al. 2008, Viechtbauer 2010). Significant Q_M indicated obvious differences within predictor variables, while Q_E represented unaccounted variability by variables included in models. Specifically, we examined the P values of Q_M statistics. A significant Q_M describes that the variation in effect sizes can be attributed to differences among categories of each predictor variable (e.g., biome type and taxonomic group). Models with categorical predictor variables were also run without the intercept to obtain the parameter estimates (mean effect sizes) of each level. Within each level, two mean effect sizes were considered to differ significantly if confidence intervals did not overlap. Effect size was considered significant if the confidence interval did not include 0.

We first examined the distribution of the effect sizes along latitude and elevation gradients to identify whether the plant–microbial correlations showed obvious patterns (Appendix S2: Fig. S2). Subsequently, we subdivided our data into different spatial scales according to their sampling extent and biome. The sampling extent of latitude and elevation coverage varied greatly among studies, ranging from <0.05° (one local site) to >100° in latitude and <100 m to over 3200 m in elevation. To evaluate how plant–microbial relationship varied across different spatial scales, data were sorted to six-grid size classes according to the latitude cover range (<0.05°, 0.05°–1°, 1°–5°, 5°–15°, 15°–20°, and ≥20°, respectively), and elevation cover range (<100 m, 100–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m, and ≥2000 m, respectively). For biomes, we sorted all study sites into ten categories: tropical forests, subtropical forests, temperate forests, temperate grasslands, boreal forests, shrublands, savannas, deserts, tundra (Ramankutty and Foley 1999), and across biomes that included several biome types. The mean effect size among sampling extents, biomes, and soil types was assessed separately by the hierarchical mixed-effects models. The same model determined the overall mean effect size without a fixed effect.

To determine microbial taxonomic group and the microbial examination method's impact on the plant–microbial diversity relationship, we assessed hierarchical mixed-effects models with those variables as the fixed predictors. We classified the data into microbial taxonomic groups following the original studies. Microbes indicate studies that analyzed the whole microbial community, the groups of bacteria and fungi consisted of data from studies that were directly targeting overall bacteria or fungi (e.g., high-throughput sequencing of bacterial 16S rRNA

gene or the fungal nuclear ribosomal internal transcribed spacer ITS region). For the microbial examination methods, next-generation sequencing such as Hiseq and Miseq, other DNA-based approaches such as PLFA, T-RFLP, and DGGE, and morphological identification were used to examine microbial diversity in studies. From culture-dependent, biochemical-based, molecular-based to high-throughput sequencing techniques, the specificity and accuracy of methods are varied (see the discussions in Kirk et al. 2004, Thies 2008), and thus, employed methods may contribute to the lack of correspondence across studies. We assessed taxonomic groups and different methods' impacts by the hierarchical mixed-effects models separately. But categories with less than five data points were not included in the individual analysis. Diversity measures, including richness, abundance, and diversity index, may provide insights on how microbes are responding to plant diversity. Therefore, we tried to isolate each measure's relationship with plant diversity. However, due to limited available data, only the correlations of microbial richness and Shannon diversity with plant diversity were assessed. Subset data in the correlation between plant and bacteria, and plant and fungi were examined separately as well. Due to limited data and a nonsignificant difference in the plant diversity matrices on the plant–microbial correlation (richness, abundance, diversity index, and composition; $P = 0.222$), plant diversity parameters did not separately analyze. In addition, we examined the impact of environmental factors using differences in soil pH (ΔpH), soil TOC (ΔTOC), MAP (ΔMAP), and MAT (ΔMAT) for individual correlations. Each continuous (log-transformed) predictor was separately run in the hierarchical mixed-effects model.

To detect publication bias of the meta-analysis, we examined the relationship between effect size and sample size, funnel plots, Rosenthal's fail-safe number, and Egger's regression. A negative relationship between sample size and effect sizes implies a publication bias (Palmer 2000, Cassey et al. 2004). Rosenthal's fail-safe number was calculated to detect whether nonsignificant, unpublished, or missing studies would change the results. A fail-safe number larger than $5k + 10$ (where k is the number of studies) indicate no publication bias (Rosenthal 1979). Egger's

regression (Egger et al. 1997), where an intercept different from zero is an indication of asymmetry and publication bias, was also conducted. All analyses were performed in R language using the package metafor (Viechtbauer 2010, R Development Core Team 2016). R codes were attached in Appendix S2.

RESULTS

Data structure

In total, we evaluated 176 correlations between plant diversity and soil microbial diversity from 84 studies covering 3992 samples (Fig. 1; Appendix S1). The distribution of sampling sites showed that most studies were conducted in subtropical and temperate biomes with subtropical forests and temperate grasslands accounted for about 23% and 25% of the dataset, respectively. For fungi (Fig. 1c), a number of sampling sites distributed in tropical regions were from a single study by Tedersoo et al. (2014). For the sampling coverage, over 60% of the studies focused on a specific local site or smaller regions with a latitudinal coverage of fewer than 1° in spite of increasing attention on plant–microbial relationships at large spatial scales (Tedersoo et al. 2014, Prober et al. 2015, Delgado-Baquerizo et al. 2016, Ochoa-Hueso et al. 2018).

For the sensitivity analysis of publication bias, the relationship between the standardized effect size and the sample size was nonsignificant (overall dataset $P_{\text{overall}} = 0.804$, plant diversity and microbial richness $P_{\text{richness}} = 0.968$). Although Egger's tests produced an intercept of 1.733 and 4.053, indicating the existence of an asymmetry which may lead to potential publication bias, the funnel plot showed no visual asymmetry (Appendix S2: Fig. S3). Meanwhile, Rosenthal's fail-safe number was large enough (overall $n_{\text{fs}} = 28{,}471$ and microbial richness $n_{\text{fs}} = 7563$) to be confident about the reliability of the overall and microbial richness dataset estimation.

Impacts of biome and sampling extent on the correlations of plant diversity and microbial diversity

Among the evaluated 176 correlations, about 75% (132) were positive, 12% showed no clear relationship (22), and 12% reported negative (22)

(a) Overall

(b) Bacteria

(c) Fungi

- ● Tropical forest
- ● Subtropical forest
- ● Temperate forest
- ● Temperate grassland
- ● Boreal forest
- ● Shrubland
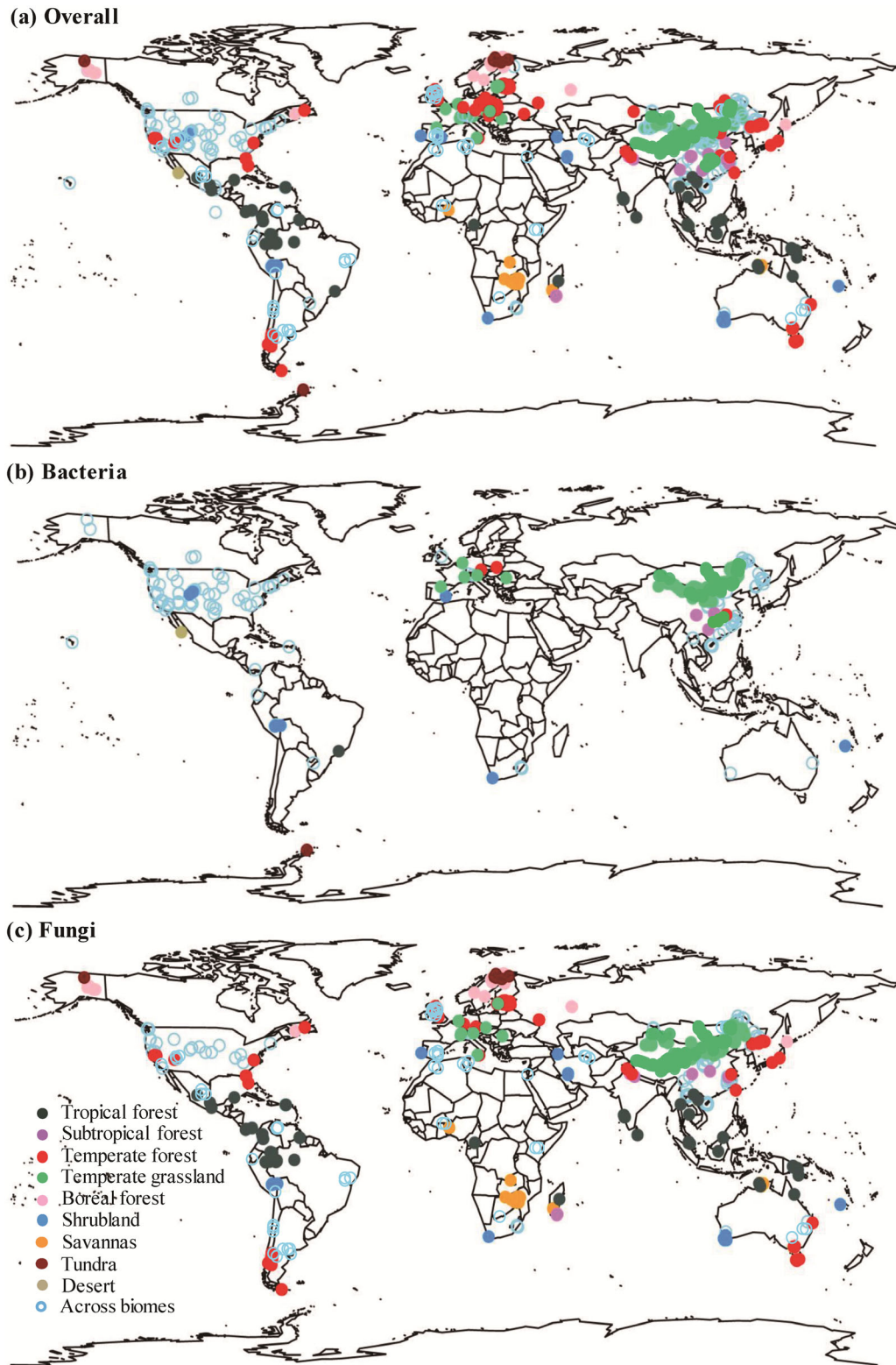- ● Savannas
- ● Tundra
- ● Desert
- ○ Across biomes

Fig. 1. Maps of sampling sites included 84 studies on the relationship between plant diversity and microbial

(Fig. 1. *Continued*)

diversity. Figures show site locations for (a) the overall dataset and studies on (b) bacteria and (c) fungi. Blue circles show the locations of sampling sites for studies that examined the plant–microbial relationships across biomes. For fungi, a number of sampling sites distributed in tropical regions were obtained from Tedersoo et al. (2014).

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correlations (Fig. 2). The current meta-analysis showed an overall insignificant correlation between plant diversity and soil microbial diversity (Fig. 3a, $r = 0.173$, CI = -0.006–0.341). Among the metrics of microbial diversity, microbial richness and Shannon diversity showed modest but positive correlation with plant diversity (Fig. 4, $r_{richness} = 0.273$, CI = 0.193–0.350; $r_{Shannon} = 0.197$, CI = 0.052–0.333).

Our results showed that plant–microbial correlations were impacted by biomes and sampling extents (Figs. 3 and 4; Appendix S2: Table S1) rather than latitude or elevation gradients (Appendix S2: Fig. S2) and soil types (Figs. 3–5). Among biomes, we observed significant variation in the correlation between the plant diversity and microbial diversity ($Q = 18.763$, df = 6, $P = 0.005$), microbial richness ($Q = 27.202$, df = 4, $P = < 0.001$), and Shannon diversity ($Q = 13.224$, df = 2, $P = 0.001$). The strongest plant–microbial diversity correlations were generally observed in tropical forests. For instance, the relation between plant diversity and microbial richness was 0.656 in tropical forests (Fig. 4a), which was more than twice as strong as other biomes such as subtropical forests and shrublands ($r = 0.183$ and $r = 0.304$, respectively). When examining the Shannon diversity index, temperate grasslands showed a relatively higher
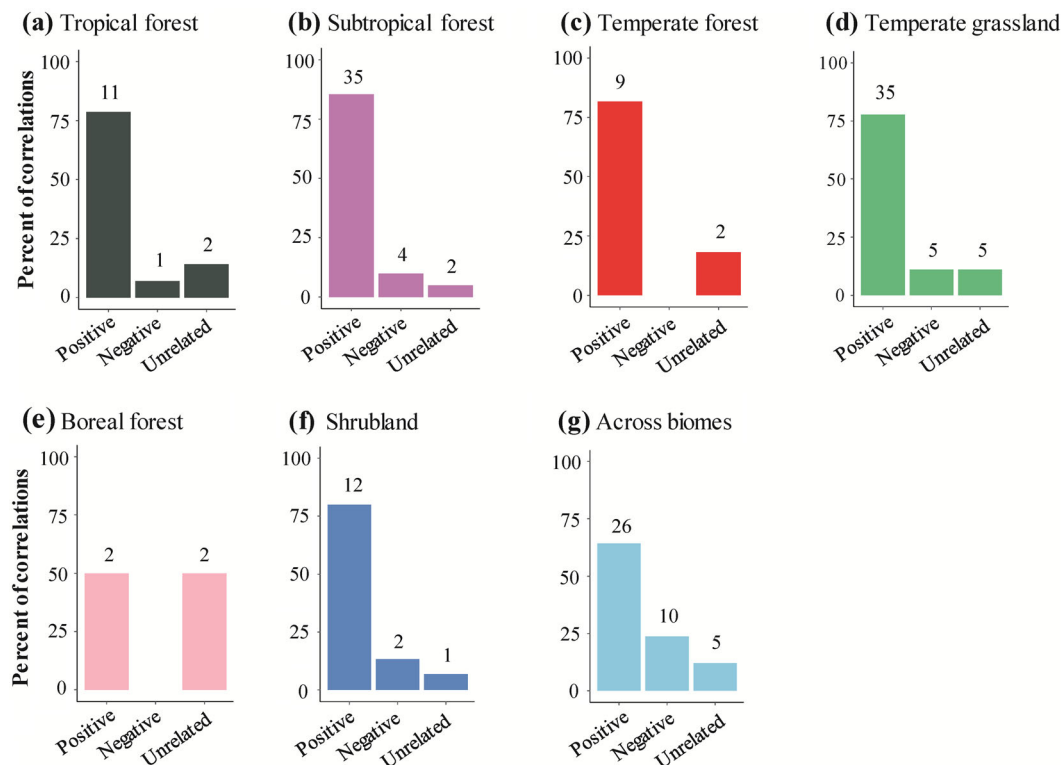

Fig. 2. Percentage distribution of positive, negative, and unrelated correlations between plant diversity and soil microbial diversity across biome types. The number of correlations is shown at the top.
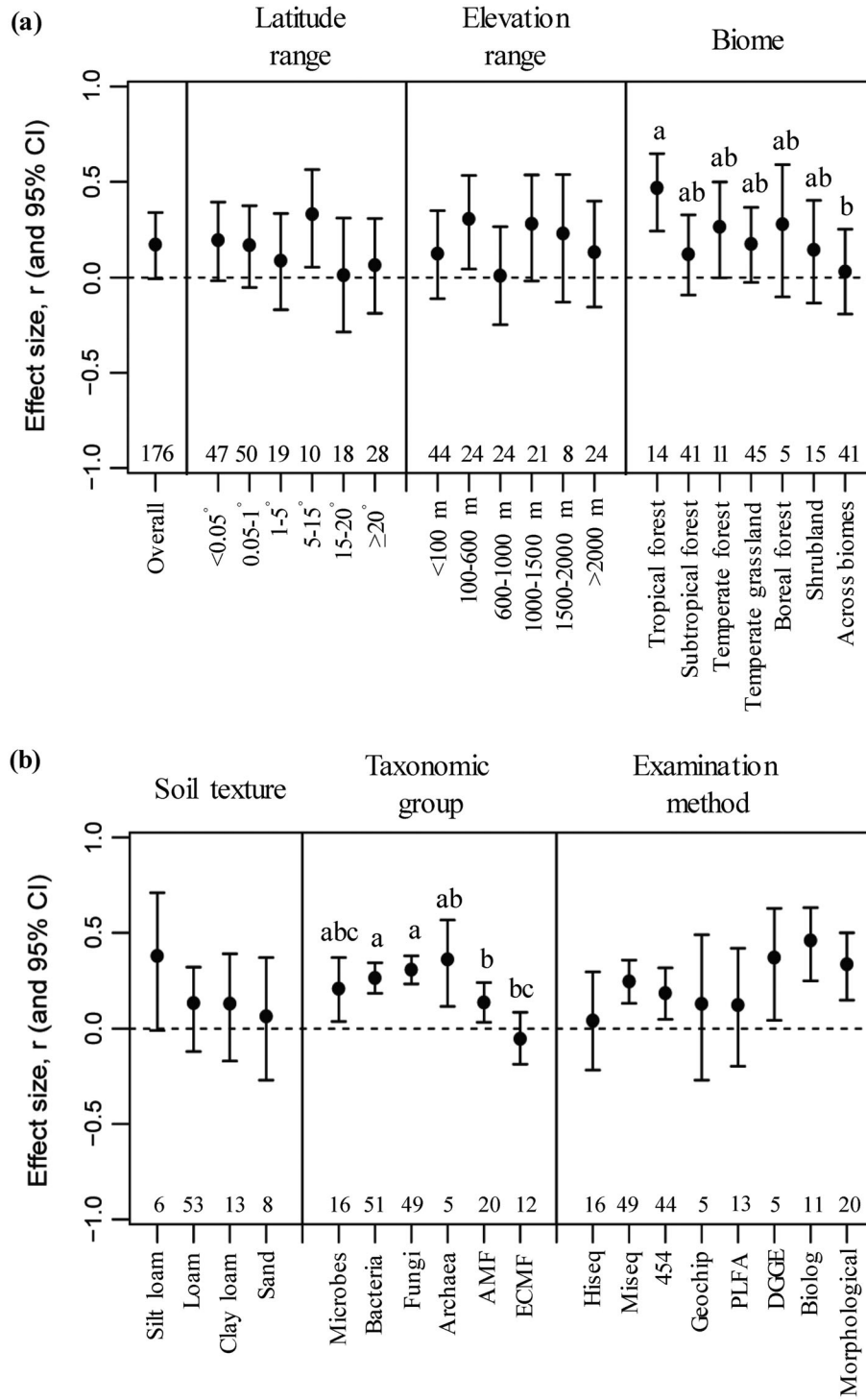
Fig. 3. The impact of variables on the correlation of the plant diversity–soil microbial diversity, including (a) the overall relationship, sampling extent and biome type, (b) soil type, taxonomic groups, and microbial examination method. For different sampling extents, data were sorted into six-grid size classes according to the latitudinal cover range (<0.05°, 0.05°–1°, 1°–5°, 5°–15°, 15°–20°, and ≥20° respectively), and elevational cover range

(Fig. 3. *Continued*)

(<100 m, 100–600 m, 600–1000 m, 1000–1500 m, 1500–2000 m, and ≥2000 m respectively). Plant–microbial correlations estimated from several biomes are grouped as across biomes. Categories with fewer than five correlations were not included. Within subsets, categories with the same lowercase letters do not differ significantly from each other. The number of observations used to calculate the mean effect sizes is shown.

correlation with plant diversity compared with subtropical forests (Fig. 4b, $r = 0.669$).

Microbial richness showed varied relationships with plant diversity among sampling ranges (Fig. 4a). The intermediate latitude range of about 500–1500 km (5°–15°, $r = 0.515$, $P = 0.040$) and elevation range of 1–1.5 km ($r = 0.605$, df = 4, $P = 0.034$) showed relatively higher correlation with plant diversity. Likewise, bacterial relationship with plant diversity was associated with elevation range (Fig. 5a). The elevation extent of 1–1.5 km displayed the strongest correlations in the plant–bacterial diversity with back-transformed effect sizes reaching 0.679.

Correlations between plant diversity and microbial diversity varied among taxonomic groups

We detected significant differences across microbial taxonomic groups in the correlations between plant diversity and microbial diversity (Fig. 3b, Q = 44.212, df = 5, $P < 0.001$), and microbial richness (Fig. 4a, Q = 37.429, df = 4, $P < 0.001$). The results showed that both fungi and bacteria held the strongest correlations with plant diversity, particularly in the linkage between microbial richness and plant diversity ($r_{bacteria} = 0.319$ and $r_{fungi} = 0.364$), while ectomycorrhizal fungi (ECMF) and arbuscular mycorrhizal fungi (AMF) possessed the relative weaker relationships with plant diversity ($r = -0.036$ and $r = 0.119$). The significant impact of the examination method was only detected in the relationship between plant diversity and bacterial diversity (Fig. 5a; Appendix S2: Table S1). Biochemical methods such as Biolog ($r = 0.641$) produced relatively higher correlations than the next-generation sequencing such as Miseq ($r = 257$).

Impacts of climatic and edaphic factors

Among examined environmental factors, soil pH was the major factor associated with the plant–microbial diversity correlation over large sampling extents, including the latitude range >20°, elevation range >2000 m, and across biomes (Fig. 6e, i, m; Appendix S2: Table S2), and in bacterial relationship with plant diversity (Fig. 6a; Appendix S2: Table S2).

The plant–microbial correlations declined with increased environmental differences in most cases, but the positive associations were observed in the TOC's effect in tropical forests (Fig. 6n, $P = 0.032$), TN's effect in elevation range of 100–600 m and 1000–1500 m (Appendix S2: Table S2), MAT's effect in temperate grasslands (Fig. 6o, $P = 0.039$), and MAP's effects at a latitude sampling range of >20° (Fig. 6h, $P < 0.001$). Edaphic factor-impacted scales seem to hold relatively lower soil nutrients in TOC and TN, except for total organic carbon's impacts in the temperate forest where a large standard error was detected (Appendix S2: Fig. S4a–c). The higher mean phosphorus content was detected in the phosphorus significantly impacted plant–microbial relationship sites (Appendix S2: Fig. S4d). In addition, a lower BD was found to associate with plant–bacterial correlation (Appendix S2: Fig. S4e-f).

DISCUSSION

Based on a meta-analysis of more than 3900 samples globally, we found that microbial richness showed a moderate but positive correlation with plant diversity ($r = 0.273$, CI = 0.193–0.350). The results imply that microbes, even at the global scale, are responding to resource composition driven by variations in plant composition and identity (De Deyn et al. 2010). Diverse chemical and physical attributes of plant detritus, which enter the belowground ecosystem, could lead to discrete niches for specific decomposers (Hooper et al. 2000, Gessner et al. 2010). Or plant community with higher diversity may be more productive (Tilman et al. 2014, Lange et al. 2015) and provides more resource input
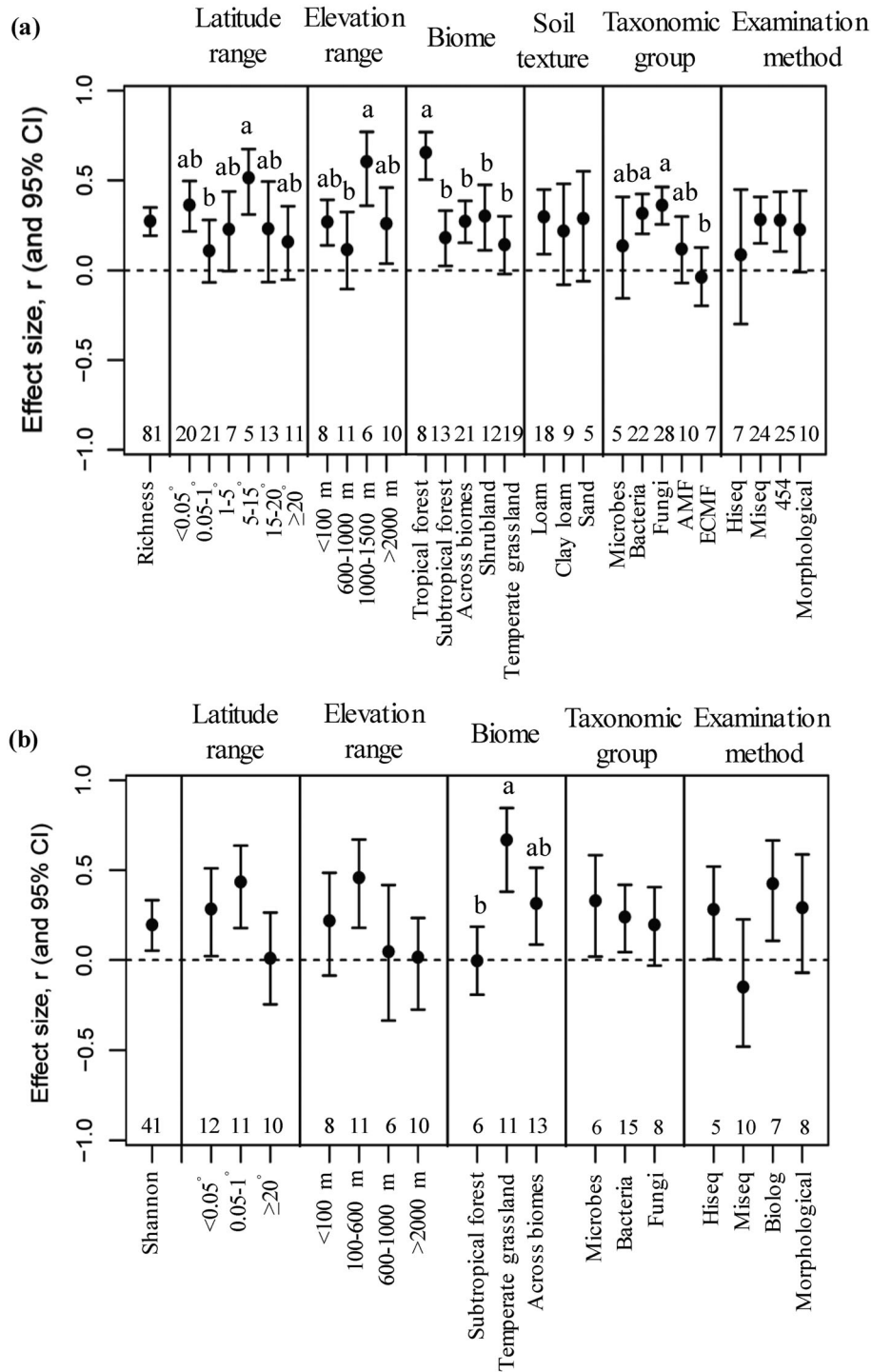
Fig. 4. The impact of variables on the correlation of (a) the plant diversity–microbial richness and (b) plant diversity–microbial Shannon diversity. Categories are identical to Fig. 3. Subset groups with fewer than five data points were not assessed. Categories with the same lowercase letters do not differ significantly from each other. The number of observations used to calculate the mean effect sizes is shown.
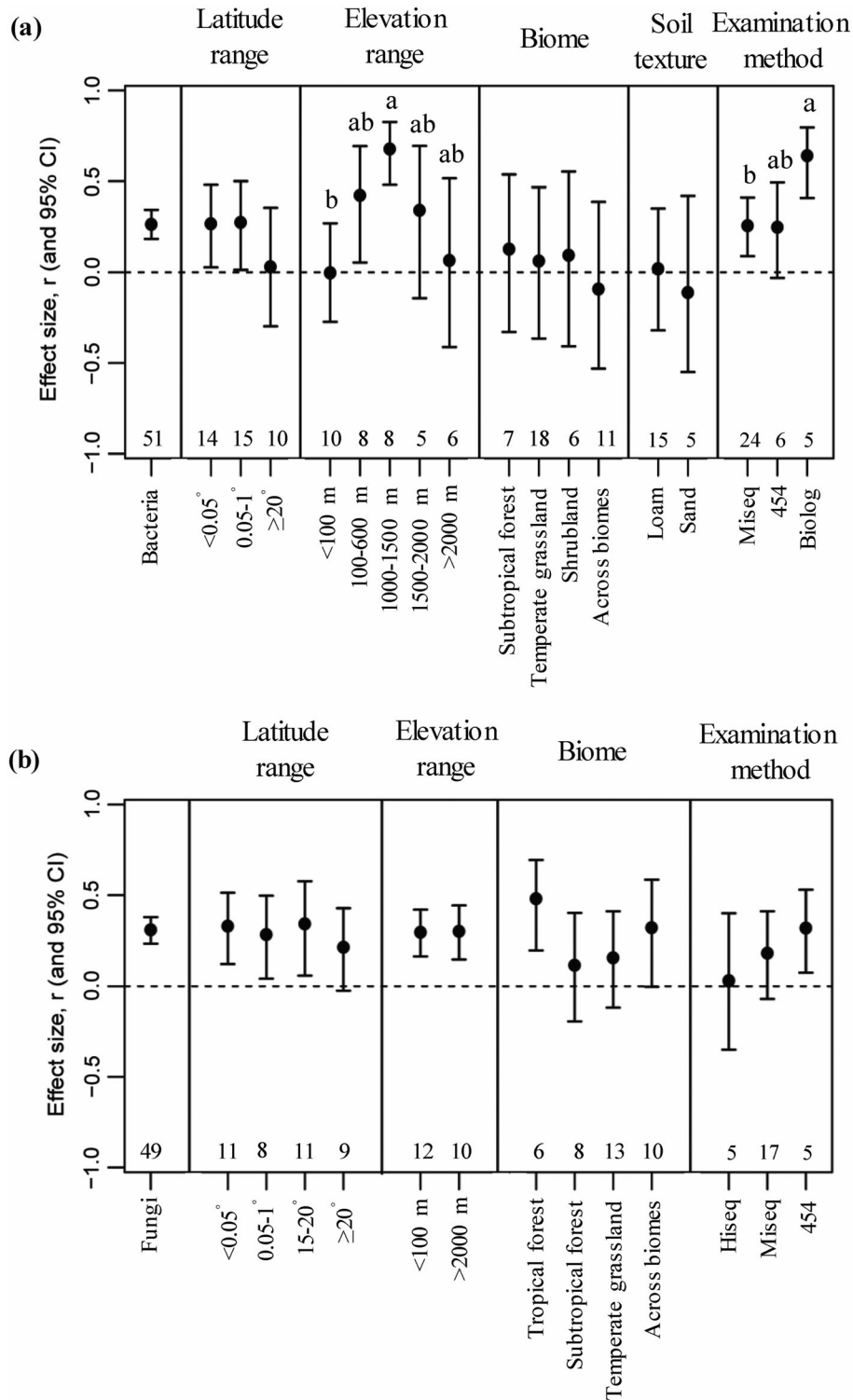
Fig. 5. The impact of variables on the correlation of plant and (a) bacterial and (b) fungal diversity. Categories are identical to Fig. 3. Within subsets, categories with the same lowercase letters do not differ significantly from each other. The number of observations used to calculate the mean effect sizes is shown.
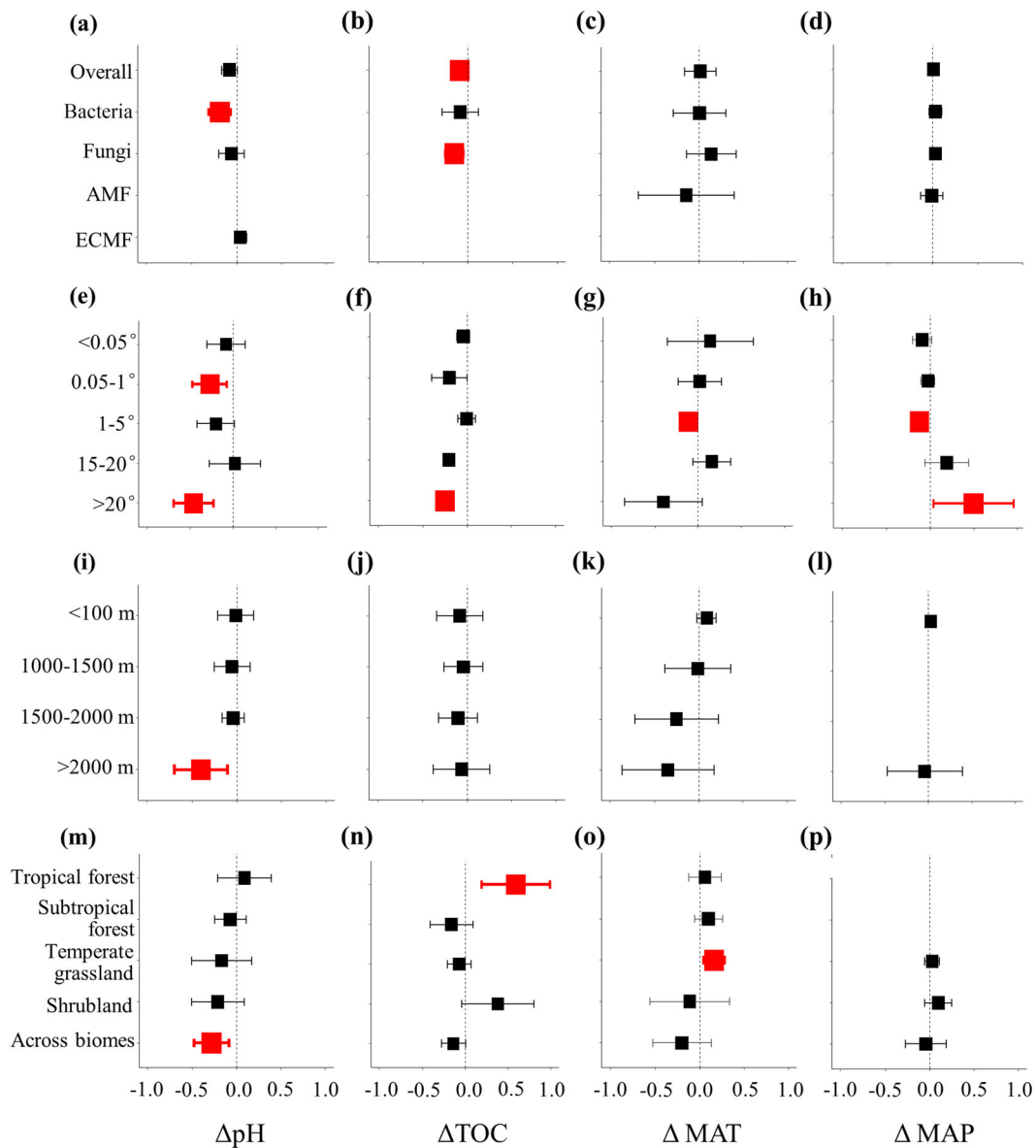
Fig. 6. The potential effects of environmental factors on the correlations of plant diversity and microbial richness among taxonomic groups (a–d), latitude (e–h) and elevation (i–l) cover range, and biome types (m–p) from hierarchical mixed-effects models. A significant association of environmental factors on examined moderators indicated in red ($P < 0.05$). Variation in TN, TP, soil moist, and soil bulk density's impacts on the correlation included in support information (Appendix S2: Tables S1–S2).

that promotes microbial diversity (Hätten-schwiler et al. 2005, Bardgett and Van Der Putten 2014). Although there is a possibility that soil condition enables a greater diversity of both plant and soil microbes, the associations between plant–microbial correlation and soil properties

we found do not support it (Appendix S2: Tables S2–S3 and below discussion). However, the plant–microbial relationship is impacted by taxonomic groups and spatial scales.

We observed the stronger plant–microbial relationships in the overall fungal community, as

well as the overall bacterial community (Fig. 3a; Fig. 4a). Saprophytic microbes have a wide range of functional abilities, and most soils contain most functional guilds of saprophytes (Hätten-schwiler et al. 2005, Grau et al. 2017, Semchenko et al. 2018). The positive relationship, thus, supports the idea of a functional relationship between plants and microbes at the global scale (Fierer and Jackson 2006, Chen et al. 2019). Contrary to our expectation, a weak plant–mycorrhizal fungal (AMF and ECMF) correlation was observed. Such results indicate diverse plant community will not directly contribute to the mycorrhizal fungal diversity at the global scales, may be due to the mismatched host density and plant community diversity (Gilbert et al. 2002, Cameron et al. 2019). For example, some ECM-dominated ecosystems (e.g., boreal and tropical monodominant forests) tend to have low plant diversity despite the high richness in these fungal communities (McGuire 2007, Corrales et al. 2016, Garcia et al. 2018). Moreover, it was reported that host plant genus-level diversity might be a better predictor of the ECMF diversity (Gao et al. 2013), whereas most studies examined the overall plant community correlations with ECMF (Peay et al. 2010, Shi et al. 2014). There are likely to be some strong correlations at finer taxonomic resolution or for some specific microbial functional groups. For instance, nitrogen fixation bacteria seem to hold a stronger correlation with plant diversity (Liang et al. 2016, Zhou et al. 2016). With increasing available data, further studies on certain microbial functional groups and with identified hosts from the plant community could largely improve the global scale estimation of the plant–microbial relationship.

Our results suggest that sampling extent is an important factor in explaining patterns in the relationship between soil microbial diversity and plant diversity. The plant–microbial correlation was strongest at the intermediate sampling extent rather than the local or global scales, especially at the intermediate elevation coverage (Fig. 4a and 5a). The intermediate scale we found is consistent with previous studies that found a significant distance effect on microbial assemblages at spatial scales of about 10–3000 km (Green et al. 2004, Ranjard et al. 2013, Ma et al. 2016), indicating a potential role of dispersal limitation on microbes and its correlation with plant

community. Alternatively, such spatial dependency of the plant–microbial diversity relationship may be explained by historical or contemporary environmental factors that drive the spatial distribution of both plants and microbes (Martiny et al. 2006), and thus their relationship with each other. Or the spatial dependency may arise if the mechanism by which plant and microbial communities facilitate each other (i.e., by promoting environmental heterogeneity, or structural complexity, as described above) is strongest at intermediate spatial scale (Angers and Caron 1998). Future work is needed to disentangle the mechanisms underlying the intermediate spatial scale effects and to understand whether and why plant–microbial facilitation effects are weaker at more local and broader spatial scales.

Consistent with our expectation, tropical forest did harbor a relatively higher correlation in plant–microbial diversity. Previous studies have shown that microbial biogeographic distribution was associated with ecosystem types (Cornwell et al. 2008, Bradford et al. 2017). The less stressed environments in the tropics may enable a high diversity of soil microbes, thus a higher concurrence of both plant and microbial communities. Or diverse litter quality fosters more divergent microbial communities in tropical forests (Cornwell et al. 2008, Bradford et al. 2017). Moreover, the pronounced association emphasizes the importance of considering the functional nature of plant–microbial interactions across biomes. For example, the strong correlation may relate to the interactions of plant community with parasitic microbes in tropical forests (Bagchi et al. 2014, Sarmiento et al. 2017), whereas symbiotic fungi may contribute to the stronger plant–microbial correlation in temperate forests (Bréda et al. 2006, Brzostek et al. 2015). The long-term coevolution of soil microbes with plants in the tropics, at the same time, may favor a stronger above- and belowground linkage (Mittelbach et al. 2007).

Our results showed that the examined climatic and edaphic factors, including soil pH, total organic carbon, total nitrogen, total phosphorus, and soil moisture, were negatively related to the plant–microbial relationship in most cases (Fig. 6; Appendix S2: Table S3). For example, we found that soil pH is the major factor negatively

associated with the plant–microbial correlations at the large spatial scales, including latitude extent, elevation extent, and across biomes, and suggested that bacteria were most sensitive to the soil pH variations (Fig. 6), which was consistent with other studies (Lauber et al. 2009, Shen et al. 2013, Prober et al. 2015). Large spatial scales could capture large pH gradients. There is greater potential for extreme pH conditions to impose limits on microbial survival and fitness (Tripathi et al. 2018), and thus plant–microbial interactions.

Microbes and microbial diversity are likely to have bigger impacts on plant communities in poor nutrient ecosystems. Using the mean value as an indicator, most sites that showed a significant response to edaphic factor variation were associated with a lower soil nutrient (Appendix S2: Fig. S4). For example, we found that tropical forest holds a lower mean total organic carbon (Appendix S2: Fig. S5b). Tropical forests are organic maters limited ecosystems (Insam and Domsch 1988, Wardle et al. 2004), and the ways that organic matter can both retain and release the other nutrients, such as nitrogen and phosphorus, depend on microbial function and activity (Vitousek 1984, Cleveland and Liptzin 2007). It is likely that plant growing in those low-nutrient environments forged stronger relationships with microbes through direct symbiosis or nutrient recycle-related feedback (Aerts and Chapin 2000). The higher mean phosphorus content in the phosphorus significantly impacted plant–microbial correlated sites may reflect the fact that mineral resource of phosphorus nutrient is limited in soil; thus, poor and high phosphorus could directly inhibit microorganisms that can naturally improve phosphorus availability in soils (Gyaneshwar et al. 2002, Garcia et al. 2015). The finding suggests that nutrient variation caused by global change might induce more pronounced impacts on the poor nutrient ecosystems, possibly through the plant–microbial interaction.

A lower BD was found in scales that showed a sensitive plant–microbial correlation to soil condition (Appendix S2: Fig. S4e, f), indicating soil BD might impact the plant–microbial correlation. Negative impacts of BD on plant–microbial interaction are well-documented, particularly in agricultural soil (Young and Ritz 2000, Beylich et al.

2010). More compact soil is likely impairing activity of both microbes and plants (Young and Ritz 2000, Beylich et al. 2010). At the same time, BD could contribute to soil types' effects on plant–microbial interaction (Li et al. 2002, Gossen et al. 2016). Depending on the dominant plant community (e.g., grasses vs. trees, and annuals vs. perennials), variations in root system might modify soil structure, which in turn contributes to its own turnover (Cook and Hesterberg 2013). Future studies need to take those factors into consideration using fine-scale data.

The plant–microbial correlation among environmental gradients provides an opportunity to detect critical environmental factors and the sensitivity of the correlation to variability within each factor. Climatic changes' impacts on biodiversity are widely discussed, but less is known about the potential effects on the plant–microbial relationship (Classen et al. 2015, Terrer et al. 2018). The significant associations between climatic factors with plant–microbial correlation indicate intense impacts of further climatic changes on ecosystems in certain spatial scales and biomes. For example, the positive association between the plant–microbial correlations and the temperature's changes in temperate grasslands implies a potential exacerbation of elevated temperature's impacts in this area under the global warming (Jones and Donnelly 2004, Piao et al. 2006, Kreyling 2010).

We are aware of the distinct ecological implications of the various microbial attributes (e.g., richness, abundance, and diversity index) assessed in our study. For the overall plant–microbial diversity relationship and factors affecting it, we could take into account the differences among diversity measures by including them as the second random effect (Appendix S2: Fig. S1). Due to limited data, we were unable to isolate factors that affect each diversity parameter's relationship with plant diversity, except for microbial richness and Shannon diversity. The relationship between plant diversity and microbial richness might reflect the heterogeneity of soil that could further affect plant richness via niche partitioning of resources (Angers and Caron 1998, Dejonghe et al. 2001). Diversity indices such as the Shannon diversity index take into account both richness and abundance, potentially masking the individual importance of one over the

other. Therefore, further studies are needed to disentangle factors that potentially affect each parameter's relationship with plant diversity, which could help to differentiate microbial responses to changes in plant diversity.

Our study confirms a modest but positive correlation between plant diversity and microbial richness, but perhaps more importantly, our analysis provides critical insight into the nature of plant–microbial relationships. The positive microbial richness and plant diversity relationship imply functional significance between plants and microbes, and while the precise mechanism that maintains this is unclear, our findings suggest that future efforts consider differences across taxonomic groups, spatial scales in modulating these differences. Most broadly, our findings raise the question of how plant–microbial diversity relationships and their environmental drivers might reflect sensitivity to biodiversity loss or environmental change on the structure and functioning of terrestrial ecosystems.

Acknowledgments

Literature Cited

Aerts, R., and F. Chapin III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30:1–67.

Allan, E., W. W. Weisser, M. Fischer, E. D. Schulze, A. Weigelt, C. Roscher, J. Baade, R. L. Barnard, H. Beßler, and N. Buchmann. 2013. A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173:223–237.

Álvarez-Sánchez, J., N. C. Johnson, A. Antoninka, V. B. Chaudhary, M. K. Lau, S. M. Owen, I. Sánchez-Gallen, P. Guadarrama, and S. Castillo. 2012. Large-scale diversity patterns in spore communities of arbuscular mycorrhizal fungi. Pages 29–47 in M. Pagan, editor. Mycorrhiza: occurrence in Natural and Restored (o, Ed.). Nova Science Publishers, New York, New York, USA.

Angers, D. A., and J. Caron. 1998. Plant-induced changes in soil structure: processes and feedbacks. Biogeochemistry 42:55–72.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506:85–88.

Bahram, M., F. Hildebrand, S. K. Forslund, J. L. Anderson, N. A. Soudzilovskaia, P. M. Bodegom, J. Bengtsson-Palme, S. Anslan, L. P. Coelho, and H. Harend. 2018. Structure and function of the global topsoil microbiome. Nature 560:233–237.

Bardgett, R. D., and W. H. Van Der Putten. 2014. Belowground biodiversity and ecosystem functioning. Nature 515:505–511.

Berg, G., and K. Smalla. 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. FEMS Microbiology Ecology 68:1–13.

Bever, J. D., S. A. Mangan, and H. M. Alexander. 2015. Maintenance of plant species diversity by pathogens. Annual Review of Ecology, Evolution, and Systematics 46:305–325.

Beylich, A., H.-R. Oberholzer, S. Schrader, H. Höper, and B.-M. Wilke. 2010. Evaluation of soil compaction effects on soil biota and soil biological processes in soils. Soil and Tillage Research 109:133–143.

Bradford, M. A., G. C. Veen, A. Bonis, E. M. Bradford, A. T. Classen, J. H. C. Cornelissen, T. W. Crowther, R. Jonathan, G. T. Freschet, and P. Kardol. 2017. A test of the hierarchical model of litter decomposition. Nature Ecology & Evolution 1:1836–1845.

Bréda, N., R. Huc, A. Granier, and E. Dreyer. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63:625–644.

Bryant, J. A., C. Lamanna, H. Morlon, A. J. Kerkhoff, B. J. Enquist, and J. L. Green. 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. Proceedings of the National Academy of Sciences of the United States of America 105:11505–11511.

Brzostek, E. R., D. Dragoni, Z. A. Brown, and R. P. Phillips. 2015. Mycorrhizal type determines the magnitude and direction of root-induced changes in decomposition in a temperate forest. New Phytologist 206:1274–1282.

Bulgarelli, D., K. Schlaeppi, S. Spaepen, E. V. L. van Themaat, and P. Schulze-Lefert. 2013. Structure and functions of the bacterial microbiota of plants. Annual Review of Plant Biology 64:807–838.

Calbrix, R., S. Barray, O. Chabrerie, L. Fourrie, and K. Laval. 2007. Impact of organic amendments on the

dynamics of soil microbial biomass and bacterial communities in cultivated land. Applied Soil Ecology 35:511–522.

Cameron, E. K., I. S. Martins, P. Lavelle, J. Mathieu, L. Tedersoo, M. Bahram, F. Gottschall, C. A. Guerra, J. Hines, and G. Patoine. 2019. Global mismatches in aboveground and belowground biodiversity. Conservation Biology 33:1187–1192.

Cassey, P., J. G. Ewen, T. M. Blackburn, and A. P. Møller. 2004. A survey of publication bias within evolutionary ecology. Proceedings of the Royal Society of London B: Biological Sciences 271:S451–S454.

Chao, A., N. J. Gotelli, T. Hsieh, E. L. Sander, K. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45–67.

Chen, C., H. Y. Chen, X. Chen, and Z. Huang. 2019. Meta-analysis shows positive effects of plant diversity on microbial biomass and respiration. Nature Communications 10:1332.

Classen, A. T., M. K. Sundqvist, J. A. Henning, G. S. Newman, J. A. Moore, M. A. Cregger, L. C. Moorhead, and C. M. Patterson. 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: What lies ahead? Ecosphere 6:1–21.

Cleveland, C. C., and D. Liptzin. 2007. C: N: P stoichiometry in soil: Is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85:235–252.

Cohan, F. M., and E. B. Perry. 2007. A systematics for discovering the fundamental units of bacterial diversity. Current Biology 17:R373–R386.

Cook, R. L., and D. Hesterberg. 2013. Comparison of trees and grasses for rhizoremediation of petroleum hydrocarbons. International Journal of Phytoremediation 15:844–860.

Cornwell, W. K., J. H. Cornelissen, K. Amatangelo, E. Dorrepaal, V. T. Eviner, O. Godoy, S. E. Hobbie, B. Hoorens, H. Kurokawa, and N. Pérez-Harguindeguy. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Corrales, A., S. A. Mangan, B. L. Turner, and J. W. Dalling. 2016. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. Ecology Letters 19:383–392.

De Deyn, G. B., H. Quirk, and R. D. Bardgett. 2010. Plant species richness, identity and productivity differentially influence key groups of microbes in grassland soils of contrasting fertility. Biology Letters 7:75–78.

De Deyn, G. B., and W. H. Van der Putten. 2005. Linking aboveground and belowground diversity. Trends in Ecology and Evolution 20:625–633.

Deeks, J. J., D. G. Altman, and M. J. Bradburn. 2008. Statistical methods for examining heterogeneity and combining results from several studies in meta-analysis. Pages 285–312 in M. Egger, D. G. Smith, and D. G. Altman, editors. Systematic reviews in health care: meta-analysis in context. BMJ Publishing, London, UK.

Dejonghe, W., N. Boon, D. Seghers, E. M. Top, and W. Verstraete. 2001. Bioaugmentation of soils by increasing microbial richness: missing links. Environmental Microbiology 3:649–657.

Delgado-Baquerizo, M., F. T. Maestre, P. B. Reich, T. C. Jeffries, J. J. Gaitan, D. Encinar, M. Berdugo, C. D. Campbell, and B. K. Singh. 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7:10541.

Dimitriu, P. A., and S. J. Grayston. 2010. Relationship between soil properties and patterns of bacterial β-diversity across reclaimed and natural boreal forest soils. Microbial Ecology 59:563–573.

Ding, J., Y. Zhang, M. Wang, X. Sun, J. Cong, Y. Deng, H. Lu, T. Yuan, J. D. Van Nostrand, and D. Li. 2015. Soil organic matter quantity and quality shape microbial community compositions of subtropical broadleaved forests. Molecular Ecology 24:5175–5185.

Duhamel, M., and K. G. Peay. 2015. Does microbial diversity confound general predictions? Trends in Plant Science 20:695–697.

Egger, M., G. D. Smith, M. Schneider, and C. Minder. 1997. Bias in meta-analysis detected by a simple, graphical test. British Medical Journal 315:629–634.

Facelli, J. M., and S. T. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical Review 57:1–32.

Falkowski, P. G., T. Fenchel, and E. F. Delong. 2008. The microbial engines that drive Earth's biogeochemical cycles. Science 320:1034–1039.

Fenchel, T., and B. J. Finlay. 2004. The ubiquity of small species: patterns of local and global diversity. American Institute of Biological Sciences Bulletin 54:777–784.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Fierer, N., and R. B. Jackson. 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America 103:626–631.

Fierer, N., J. W. Leff, B. J. Adams, U. N. Nielsen, S. T. Bates, C. L. Lauber, S. Owens, J. A. Gilbert, D. H. Wall, and J. G. Caporaso. 2012. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. Proceedings of

the National Academy of Sciences of the United States of America 109:21390–21395.

Fierer, N., C. M. McCain, P. Meir, M. Zimmermann, J. M. Rapp, M. R. Silman, and R. Knight. 2011. Microbes do not follow the elevational diversity patterns of plants and animals. Ecology 92:797–804.

Fisher, R. A. 1921. On the probable error of a coefficient of correlation deduced from a small sample. Metron 1:3–32.

Fuhrman, J. A. 2009. Microbial community structure and its functional implications. Nature 459:193–199.

Gao, C., N. N. Shi, Y. X. Liu, K. G. Peay, Y. Zheng, Q. Ding, X. C. Mi, K. P. Ma, T. Wubet, and F. Buscot. 2013. Host plant genus-level diversity is the best predictor of ectomycorrhizal fungal diversity in a Chinese subtropical forest. Molecular Ecology 22:3403–3414.

Garcia, K., P. M. Delaux, K. R. Cope, and J. M. Ané. 2015. Molecular signals required for the establishment and maintenance of ectomycorrhizal symbioses. New Phytologist 208:79–87.

Garcia, D. E., B. R. Lopez, L. E. de-Bashan, A. M. Hirsch, M. Maymon, and Y. Bashan. 2018. Functional metabolic diversity of the bacterial community in undisturbed resource island soils in the southern Sonoran Desert. Land Degradation & Development 29:1467–1477.

Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25:372–380.

Gilbert, G. S., A. Ferrer, and J. Carranza. 2002. Polypore fungal diversity and host density in a moist tropical forest. Biodiversity and Conservation 11:947–957.

Gömöryová, E., R. Hrivnák, M. Janišová, K. Ujházy, and D. Gömöry. 2009. Changes of the functional diversity of soil microbial community during the colonization of abandoned grassland by a forest. Applied Soil Ecology 43:191–199.

Gossen, B. D., H. Kasinathan, A. Deora, G. Peng, and M. R. Mcdonald. 2016. Effect of soil type, organic matter content, bulk density and saturation on clubroot severity and biofungicide efficacy. Plant Pathology 65:1238–1245.

Grau, O., J. Geml, A. Pérez-Haase, J. M. Ninot, T. A. Semenova-Nelsen, and J. Peñuelas. 2017. Abrupt changes in the composition and function of fungal communities along an environmental gradient in the High Arctic. Molecular Ecology 26:4798–4810.

Green, J. L., A. J. Holmes, M. Westoby, I. Oliver, D. Briscoe, M. Dangerfield, M. Gillings, and A. J. Beattie. 2004. Spatial scaling of microbial eukaryote diversity. Nature 432:747–750.

Guo, Y., X. Chen, Y. Wu, L. Zhang, J. Cheng, G. Wei, and Y. Lin. 2018. Natural revegetation of a semiarid habitat alters taxonomic and functional diversity of soil microbial communities. Science of the Total Environment 635:598–606.

Gyaneshwar, P., G. N. Kumar, L. Parekh, and P. Poole. 2002. Role of soil microorganisms in improving P nutrition of plants. Plant and Soil 245:83–93.

Harbord, R. M., and P. Whiting. 2009. Metandi: meta-analysis of diagnostic accuracy using hierarchical logistic regression. Stata Journal 9:211–229.

Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36:191–218.

Hedges, L. V., E. Tipton, and M. C. Johnson. 2010. Robust variance estimation in meta-regression with dependent effect size estimates. Research Synthesis Methods 1:39–65.

Hendershot, J., Q. Read, J. Henning, N. Sanders, and A. Classen. 2017. Consistently inconsistent drivers of patterns of microbial diversity and abundance at macroecological scales. Ecology 98:1757–1763.

Hengl, T., J. M. de Jesus, G. B. Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, M. N. Wright, X. Geng, and B. Bauer-Marschallinger. 2017. SoilGrids250 m: global gridded soil information based on machine learning. PLOS ONE 12: e0169748.

Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs 66:503–522.

Hooper, D. U., D. E. Bignell, V. K. Brown, L. Brussard, J. M. Dangerfield, D. H. Wall, D. A. Wardle, D. C. Coleman, K. E. Giller, and P. Lavelle. 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience 50:1049–1061.

Insam, H., and K. Domsch. 1988. Relationship between soil organic carbon and microbial biomass on chronosequences of reclamation sites. Microbial Ecology 15:177–188.

Jones, M., and A. Donnelly. 2004. Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. New Phytologist 164:423–439.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Kirk, J. L., L. A. Beaudette, M. Hart, P. Moutoglis, J. N. Klironomos, H. Lee, and J. T. Trevors. 2004. Methods of studying soil microbial diversity. Journal of Microbiological Methods 58:169–188.

Kreyling, J. 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 91:1939–1948.

Lange, M., N. Eisenhauer, C. A. Sierra, H. Bessler, C. Engels, R. I. Griffiths, P. G. Mellado-Vázquez, A. A. Malik, J. Roy, and S. Scheu. 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nature Communications 6:6707.

Lanzén, A., L. Epelde, F. Blanco, I. Martín, U. Artetxe, and C. Garbisu. 2016. Multi-targeted metagenetic analysis of the influence of climate and environmental parameters on soil microbial communities along an elevational gradient. Scientific Reports 6:28257.

Lauber, C. L., M. Hamady, R. Knight, and N. Fierer. 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Applied and Environmental Microbiology 75:5111–5120.

Lavelle, P., C. Lattaud, D. Trigo, and I. Barois. 1995. Mutualism and biodiversity in soils. Pages 23–33 in H. P. Collins, G. P. Robertson and M. J. Klug, editors. The significance and regulation of soil biodiversity. Springer, Dordrecht, The Netherlands.

Li, C. H., B. L. Ma, and T. Q. Zhang. 2002. Soil bulk density effects on soil microbial populations and enzyme activities during the growth of maize (*Zea mays* L.) planted in large pots under field exposure. Canadian Journal of Soil Science 82:147–154.

Liang, Y., F. Pan, X. He, X. Chen, and Y. Su. 2016. Effect of vegetation types on soil arbuscular mycorrhizal fungi and nitrogen-fixing bacterial communities in a karst region. Environmental Science and Pollution Research 23:18482–18491.

Liu, D., X. Wu, S. Shi, H. Liu, and G. Liu. 2016a. A hollow bacterial diversity pattern with elevation in Wolong Nature Reserve, Western Sichuan Plateau. Journal of Soils and Sediments 16:2365–2374.

Liu, L., S. Yu, Z. P. Xie, and C. Staehelin. 2016b. Distance-dependent effects of pathogenic fungi on seedlings of a legume tree: impaired nodule formation and identification of antagonistic rhizosphere bacteria. Journal of Ecology 104:1009–1019.

Luo, C. W., L. M. Rodriguez-R, E. R. Johnston, L. Wu, L. Cheng, K. Xue, Q. Tu, Y. Deng, Z. He, and J. Z. Shi. 2014. Soil microbial community responses to a decade of warming as revealed by comparative metagenomics. Applied and Environmental Microbiology 80:1777–1786.

Ma, B., H. Wang, M. Dsouza, J. Lou, Y. He, Z. Dai, P. C. Brookes, J. Xu, and J. A. Gilbert. 2016. Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. ISME Journal 10:1891–1901.

Mangan, S. A., S. A. Schnitzer, E. A. Herre, K. M. Mack, M. C. Valencia, E. I. Sanchez, and J. D. Bever. 2010. Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466:752–755.

Martiny, J. B. H., B. J. M. Bohannan, J. H. Brown, R. K. Colwell, J. A. Fuhrman, J. L. Green, M. C. Horner-devine, M. D. Kane, J. A. Krumins, and C. R. Kuske. 2006. Microbial biogeography: putting microorganisms on the map. Nature Reviews Microbiology 4:102–112.

McGuire, K. L. 2007. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology 88:567–574.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, and H. A. Lessios. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331.

Mueller, G. M., J. P. Schmit, P. R. Leacock, B. Buyck, J. Cifuentes, D. E. Desjardin, R. E. Halling, K. Hjortstam, T. Iturriaga, and K. H. Larsson. 2007. Global diversity and distribution of macrofungi. Biodiversity and Conservation 16:37–48.

Navarrocano, J. A., M. Goberna, A. Valientebanuet, A. Montesinosnavarro, C. Garcia, and M. Verdu. 2014. Plant phylodiversity enhances soil microbial productivity in facilitation-driven communities. Oecologia 174:909–920.

Ochoa-Hueso, R., D. J. Eldridge, M. Delgado-Baquerizo, S. Soliveres, M. A. Bowker, N. Gross, L. Bagousse-Pinguet, J. L. Quero, M. García-Gómez, and E. Valencia. 2018. Soil fungal abundance and plant functional traits drive fertile island formation in global drylands. Journal of Ecology 106:242–253.

Palmer, A. R. 2000. Quasi-replication and the contract of error: lessons from sex ratios, heritabilities and fluctuating asymmetry. Annual Review of Ecology and Systematics 31:441–480.

Peay, K. G., P. G. Kennedy, S. J. Davies, S. Tan, and T. D. Bruns. 2010. Potential link between plant and fungal distributions in a dipterocarp rainforest: community and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and soil ecotone. New Phytologist 185:529–542.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100:33–46.

Piao, S., A. Mohammat, J. Fang, Q. Cai, and J. Feng. 2006. NDVI-based increase in growth of temperate grasslands and its responses to climate changes in China. Global Environmental Change 16:340–348.

Prober, S. M., J. W. Leff, S. T. Bates, E. T. Borer, J. Firn, W. S. Harpole, E. M. Lind, E. W. Seabloom, P. B. Adler, and J. D. Bakker. 2015. Plant diversity

predicts beta but not alpha diversity of soil microbes across grasslands worldwide. Ecology Letters 18:85–95.

R Development Core Team. 2016. R: a language and environment for statistical computing [Computer software]. R Foundation for Statistical Computing. Vienna, Austria.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. Global Biogeochemical Cycles 13:997–1027.

Ranjard, L., S. Dequiedt, N. C. Prévostbouré, J. Thiou-louse, N. P. A. Saby, M. Lelievre, P. A. Maron, F. E. R. Morin, A. Bispo, and C. Jolivet. 2013. Turnover of soil bacterial diversity driven by wide-scale environmental heterogeneity. Nature Communications 4:1434.

Rosenthal, R. 1979. The file drawer problem and tolerance for null results. Psychological Bulletin 86:638–641.

Rosenthal, R., H. Cooper, and L. Hedges. 1994. Parametric measures of effect size. Pages 231–244 in H. Cooper and L. V. Hedges, editors. Handbook of research synthesis. Russel Sage Foundation, New York, New York, USA.

Rossetti, M. R., T. Tscharntke, R. Aguilar, and P. Batáry. 2017. Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecology Letters 20:264–272.

Sarmiento, C., P.-C. Zalamea, J. W. Dalling, A. S. Davis, S. M. Stump, J. M. U'Ren, and A. E. Arnold. 2017. Soilborne fungi have host affinity and host-specific effects on seed germination and survival in a lowland tropical forest. Proceedings of the National Academy of Sciences of the United States of America 114:11458–11463.

Semchenko, M., J. W. Leff, Y. M. Lozano, S. Saar, J. Davison, A. Wilkinson, B. G. Jackson, W. J. Pritchard, R. Jonathan, and S. Oakley. 2018. Fungal diversity regulates plant-soil feedbacks in temperate grassland. Science. Advances 4:eaau4578.

Shen, C. C., W. J. Liang, Y. Shi, X. Lin, H. Y. Zhang, X. Wu, G. Xie, P. Chain, P. Grogan, and H. Chu. 2014. Contrasting elevational diversity patterns between eukaryotic soil microbes and plants. Ecology 95:3190–3202.

Shen, C. C., J. B. Xiong, H. Y. Zhang, Y. Z. Feng, X. Lin, X. Y. Li, W. J. Liang, and H. Chu. 2013. Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. Soil Biology and Biochemistry 57:204–211.

Shi, L. L., P. E. Mortimer, J. W. F. Slik, X. M. Zou, J. Xu, W. T. Feng, and L. Qiao. 2014. Variation in forest soil fungal diversity along a latitudinal gradient. Fungal Diversity 64:305–315.

Siles, J. A., and R. Margesin. 2016. Abundance and diversity of bacterial, archaeal, and fungal communities along an altitudinal gradient in alpine forest soils: What are the driving factors? Microbial Ecology 72:207–220.

Slabbert, E., R. Y. Kongor, K. J. Esler, and K. Jacobs. 2010. Microbial diversity and community structure in Fynbos soil. Molecular Ecology 19:1031–1041.

Steinauer, K., D. Tilman, P. D. Wragg, S. Cesarz, J. M. Cowles, K. Pritsch, P. B. Reich, W. W. Weisser, and N. Eisenhauer. 2015. Plant diversity effects on soil microbial functions and enzymes are stronger than warming in a grassland experiment. Ecology 96:99–112.

Stevens, J. R., and A. M. Taylor. 2009. Hierarchical dependence in meta-analysis. Journal of Educational and Behavioral Statistics 34:46–73.

Stirling, G., and B. Wilsey. 2001. Empirical relationships between species richness, evenness, and proportional diversity. American Naturalist 158:286–299.

Tedersoo, L., M. Bahram, S. Polme, U. Koljalg, N. S. Yorou, R. L. C. Wijesundera, L. V. Ruiz, A. M. Vascopalacios, P. Q. Thu, and A. Suija. 2014. Global diversity and geography of soil fungi. Science 346:1–11.

Terrer, C., S. Vicca, B. D. Stocker, B. A. Hungate, R. P. Phillips, P. B. Reich, A. C. Finzi, and I. C. Prentice. 2018. Ecosystem responses to elevated CO_2 governed by plant–soil interactions and the cost of nitrogen acquisition. New Phytologist 217:507–522.

Thies, J. E. 2008. Molecular methods for studying microbial ecology in the soil and rhizosphere. Pages 411–436 in A. Varma, editor. Molecular mechanisms of plant and microbe coexistence. Springer, Berlin, Germany.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology, Evolution, and Systematics 45:471–493.

Tripathi, B. M., J. C. Stegen, M. Kim, K. Dong, J. M. Adams, and Y. K. Lee. 2018. Soil pH mediates the balance between stochastic and deterministic assembly of bacteria. ISME Journal 12:1072–1083.

Tuck, S. L., C. Winqvist, F. Mota, J. Ahnström, L. A. Turnbull, and J. Bengtsson. 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. Journal of Applied Ecology 51:746–755.

Van Der Heijden, M. G., R. Streitwolf-Engel, R. Riedl, S. Siegrist, A. Neudecker, K. Ineichen, T. Boller, A. Wiemken, and I. R. Sanders. 2006. The mycorrhizal contribution to plant productivity, plant nutrition and soil structure in experimental grassland. New Phytologist 172:739–752.

Van Der Putten, W. H. 2017. Belowground drivers of plant diversity. Science 355:134–135.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36:1–48.

Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285–298.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. Van Der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Whitman, W. B., D. C. Coleman, and W. J. Wiebe. 1998. Prokaryotes: the unseen majority. Proceedings of the National Academy of Sciences 95:6578–6583.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Wu, Y. T., J. Gutknecht, K. Nadrowski, C. Geißler, P. Kühn, T. Scholten, S. Both, A. Erfmeier, M. Böhnke, and H. Bruelheide. 2012. Relationships between soil microorganisms, plant communities, and soil characteristics in Chinese subtropical forests. Ecosystems 15:624–636.

Young, I., and K. Ritz. 2000. Tillage, habitat space and function of soil microbes. Soil and Tillage Research 53:201–213.

Zak, D. R., W. E. Holmes, D. C. White, A. D. Peacock, and D. Tilman. 2003. Plant diversity, soil microbial communities, and ecosystem function: Are there any links? Ecology 84:2042–2050.

Zhang, Y. G., J. Cong, H. Lu, G. Li, Y. Xue, Y. Deng, H. Li, J. Zhou, and D. Li. 2015. Soil bacterial diversity patterns and drivers along an elevational gradient on Shennongjia Mountain, China. Microbial Biotechnology 8:739–746.

Zhang, C., G. Liu, Z. Song, J. Wang, and L. Guo. 2018. Interactions of soil bacteria and fungi with plants during long-term grazing exclusion in semiarid grasslands. Soil Biology and Biochemistry 124:47–58.

Zhou, J. Z., Y. Deng, L. Shen, C. Q. Wen, Q. Y. Yan, D. L. Ning, Y. J. Qin, K. Xue, L. Y. Wu, and Z. L. He. 2016. Temperature mediates continental-scale diversity of microbes in forest soils. Nature Communications 7:12083.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2999/full