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Effects of Invasive Plant Diversity on Soil Microbial Communities

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Abstract: Native plant communities can be invaded by different numbers of alien plant species or by the same number of alien plant species with different levels of evenness. However, little is known about how alien invasive plant species richness and evenness affect soil microbial communities. We constructed native herbaceous plant communities invaded by exotic plants with different richness (1, 2, 4 and 8 species) and evenness (high and low) and analyzed soil physico-chemical properties and the diversity and composition of soil fungal and bacterial communities by high-throughput Illumina sequencing. Overall, the species richness and evenness of invasive plants had no significant effect on bacterial and fungal alpha diversity (OTUs, Shannon, Simpson, Chao1 and ACE) or the soil physico-chemical properties. However, invasive species richness had a significant impact on the relative abundance of the most dominant fungi, Ascomycota and *Bipolaris*, and the dominant bacteria, Actinobacteriota, which increased with increasing invasive species richness. The relative abundance of the dominant microbial groups was significantly correlated with the relative abundance of some specific invasive plants in the community. This study sheds new light on the effects of plant co-invasion on soil microbial communities, which may help us understand the underlying mechanisms of multiple alien plant invasion processes from the perspective of soil microorganisms.

Keywords: bacterial community; co-invasion; diversity effect; fungal community; invasive species evenness; invasive species richness

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1. Introduction

Invasions by alien plants are a world-wide problem that has received great attention [1–4]. Alien plant invasions may not only displace native plant species and damage local flora and biodiversity but may also negatively influence many other ecosystem functions and services [5–9] in relation to the regional context [10]. Thus, there is a great need to develop measures to efficiently manage and control alien plant invasions [11,12]. To this end, we need to first assess the impacts of alien plant invasions on ecosystem functions such as soil microbial communities [13–16]. Soil microbial communities can alleviate the effects of invasive plants on local plant communities by degrading allelopathic substances [17], promoting further invasion via symbiosis with arbuscular mycorrhizal fungi or inhibiting further invasion via the accumulation of pathogens [18,19].

Previous studies have shown that alien plant invasions can have profound effects on soil microbial communities [14,20,21]. For instance, alien plant invasions can affect the soil properties [22–25], species richness and composition of soil microbial communities [26,27], thus destroying the long-term balance between native plants and soil microorganisms [15,16,27]. Some studies have shown that plant invasions can improve soil microbial diversity by providing more energy sources from secondary metabolites or a greater quantity and quality of litter [26,28–30]. Other studies have found that plant invasions reduce soil microbial diversity (e.g., AM fungi) [31–33] or have no significant effect [33,34].

One overlooked phenomenon in invasion ecology is that a native plant community can be invaded by different numbers of alien plant species [35]. Thus, while many studies have

examined the impacts of alien plant invasions on soil microbial communities, the impacts of alien invasive species richness have never been considered. Recent studies found that increasing invasive plant species richness significantly increased the productivity of alien invasive plants and decreased that of native plant communities [35–38]. This suggests that increasing alien plant species can promote the invasion success of alien plants into native plant communities [35]. Since previous studies have shown that changes in both alien plant productivity and native plant productivity can impact soil microbial communities [39–42], we hypothesize that alien plant richness can influence soil microbial communities.

Another overlooked phenomenon is that a native plant community can be invaded by the same number of alien plant species with different levels of evenness [35]. As an important aspect of species diversity, evenness is often used to explain inconsistencies in species richness effects [43–46]. In several cases, evenness explained more biodiversity effects than species richness [47,48]. For instance, it has been shown that species richness had impacts on bacterial communities through the modulation of plant evenness in native grassland communities [46,49]. To our best knowledge, little is known about the effect of invasive plant evenness on soil microbial communities. We speculate that a high level of invasive plant evenness can result in high microbial diversity due to the different contributions of all invasive plants to soil micro-environment changes. By contrast, when the evenness of alien invasive plants is low, only one or two alien species are dominant, so alien plant diversity has similar effects to a monoculture of the dominant species [49,50].

We constructed native herbaceous plant communities invaded by alien plants with different richness (1, 2, 4 and 8 species) and evenness (high and low) to explore the impacts of invasive plant species diversity on soil fungal and bacterial communities. Specifically, we addressed the following questions: (1) Do alien invasive plant richness and evenness affect the diversity and composition of soil fungal communities? (2) Do alien invasive plant richness and evenness affect the diversity and composition of soil bacterial communities? (3) Do alien invasive plant richness and evenness affect the abundance of some specific microbial taxa?

2. Materials and Methods

2.1. Native and Invasive Species Preparation

The plant species pool used to construct experimental plant communities consisted of 18 native plant species and 10 alien invasive plant species that commonly grow in grasslands around Taizhou city (121.43° E, 28.68° N), Zhejiang Province, China [35]. Eight of the native species were perennials (*Achyranthes bidentata* Blume, *Persicaria filiformis* (Thunb.) Nakai, *Aster trinervius* subsp. *ageratoides* (Turczaninow) Grierson, *Bellis perennis* L., *Carpesium abrotanoides* L., *Patrinia scabiosifolia* Link, *Penthorum chinense* Pursh and *Plantago asiatica* L.), and ten were annual/biennial. The ten invasive species include four perennials (*Alternanthera philoxeroides* (Mart.) Griseb., *Mirabilis jalapa* L., *Solidago canadensis* L., and *Talinum paniculatum* (Jacq.) Gaertn.) and six annuals (*Ageratum conyzoides* L., *Symphyotrichum subulatum* (Michx.) G.L.Nesom, *Bidens frondosa* L., *Bidens pilosa* L., *Celosia argentea* L., and *Sesbania cannabina* (Retz.) Poir.). Detailed information on these species was described by Wang et al. (2022) [35].

Seeds (except *Alternanthera philoxeroides*) of all native and invasive species were collected from field sites around Taizhou city and stored at 4 °C till use. In April 2020, these seeds were sown into plastic containers (30 cm long × 30 cm wide × 30 cm high) filled with a mixture of river sand and peat. The plastic containers were placed in a greenhouse at Taizhou University, Zhejiang Province, China. For *A. philoxeroides*, ramets (asexual individuals) were propagated from stem cuttings. One month later, seedlings with similar sizes were used to construct plant communities. Height differences within the same species were limited to 2 cm.

2.2. Experimental Design

On 27 May 2020, 96 native plant communities were constructed in 96 containers (each 120 cm in diameter × 74 cm in height) with 18 native plant species. In each container, each native species was initially planted with three seedlings. The containers were filled with a mixture of soil (0.62 ± 0.17 g kg^{-1} total N, 0.13 ± 0.03 g kg^{-1} total P, *mean* ± *SE*, $n = 5$), peat and sand at a volume ratio of 2:1:1. Slow release fertilizer (N:P:K = 14:14:14, Osmocote exact standard 3–4 M) was added to the soil at a dose of 3 g L^{-1}. After one week, individuals of invasive plants with four levels of species richness (1, 2, 4 and 8 species) and two levels of evenness (high and low) were introduced to 90 of the 96 native plant communities (Table A1). For the 1-species treatment, individuals of each of the 10 invasive species were planted in three containers, making 30 communities. For each of the 2-species, 4-species and 8-species treatments, 10 different species mixtures were constructed by randomly selecting them from the species pool in such a way that each species had an equal chance of being selected. Each of these mixtures was replicated twice: one was used for high evenness (2-species, 12:12; 4-species, 6:6:6:6; 8-species, 3:3:3:3:3:3:3:3) and the other for low evenness (2-species, 22:2; 4-species, 18:3:2:1; 8-species, 13:3:2:2:1:1:1:1). For communities with invasive plants, the number of individuals of invasive species in each community was equal (i.e., 24 individuals). In the remaining six native plant communities, invasive species were not introduced. For a more detailed description of the experiment, see Wang et al. (2022) [35].

2.3. Soil Sample Collection and Physico-Chemical Analysis

On 11 October 2020, we took five soil samples (0–10 cm deep) under each of the 90 communities invaded by alien plant species [51,52]. The five soil samples from each container were thoroughly homogenized to form a composite sample. Then, a sub-sample of 10 mL was preserved at −80 °C until DNA extraction for soil microbial analysis. Another sub-sample was air-dried for analysis of soil physico-chemical properties. Soil pH was measured in a 1:2.5 soil:water (w:w) mixture using a digital pH meter (Mettler Toledo FE20, Shanghai, China). Soil organic matter was determined by the Walkley-Black acid digestion method. Soil N-NH_4^+, N-NO_3^- (extracted from a 1:5 suspension of soil in 2 M KCl solution) and total N (digested with concentrated H_2SO_4 and $HClO_4$) were measured using a continuous flow analyzer (Auto Analyzer 3, Bran and Luebbe, Norderstedt, Germany). Total P (digested with concentrated H_2SO_4 and $HClO_4$) and available P (extracted with 0.5 M $NaHCO_3$) were determined by an inductively coupled plasma emission spectrometer (Optima 2100DV, PerkinElemer, Waltham, MA, USA).

2.4. Microbial Sample Collection and Sequencing

Soil DNA was extracted using a PowerSoil™ DNA Isolation Kit (MoBio, Carlsbad, CA, USA) following the manufacturer's instructions and then sent to Novogene Co., Ltd., Beijing, China for amplification, library preparation and sequencing. The V4 region of the bacterial 16S rDNA gene was amplified using primers 515F (GTGCCAGCMGCCGCGGTAA) and 806R (GGACTACNNGGGTATCTAAT) [53]. The fungal ITS region rDNA was amplified using primers ITS5-1737F (GGAAGTAAAAGTCGTAACAAGG) and ITS2-2043R (GCTGCGTTCTTCATCGATGC) [54]. The sequencing was done on an Illumina Novaseq 6000 platform, with 250 bp paired-end reads generated. The raw sequencing data have been deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: PRJNA870235 and PRJNA861831).

2.5. Bioinformatic Analysis

Barcode extraction, paired read assembly and quality filtering of the raw data were processed using the Software QIIME v.1.9.1 [55]. Chimeric sequences were identified and removed using UCHIME [56]. Operational taxonomic units (OTUs) were identified at the 97% similarity level with the UPARSE v.7.1b [57]. The taxonomy of each OTU of bacteria and fungi was assigned by the Uclust method using SILVA release 132 (https://www.

arb-silva.de/documentation/release-132, accessed on 5 July 2021) and UNITE database (http://qiime.org/scripts/assign_taxonomy.html, accessed on 5 July 2021), respectively.

2.6. Statistical Analysis

Alpha diversity (Shannon, Simpson, Chao1 and ACE indices) and beta diversity were calculated using the QIIME software (Version 1.9.1) [55]. The effects of invasive plant species richness (log_2 scale), evenness and their interaction on alpha diversity index, soil physico-chemical properties and the relative abundance of the most abundant phyla and genera of soil fungi and bacteria were tested by linear mixed models. In these models, invasive species richness was treated as a fixed continuous term, evenness as a fixed categorical term and species composition as a random term [35]. The treatment with a single invasive species was considered a low evenness treatment because monocultures were on the regression lines of uneven rather than even treatments [35,58]. We performed Principal Co-ordinates Analysis (PCoA) and Adonis to test whether species composition of soil microbial communities differed between different treatments based on Weighted Unifrac distance. Linear regressions were used to assess the relationships of invasive species richness with the alpha diversity index, and relative abundances of phyla and genera of fungi and bacteria. Residuals of all variables were checked for homoscedasticity and normality. All statistical analyses were conducted using R 4.1.2 (https://www.r-project.org/, accessed on 10 June 2022).

3. Results

3.1. Effects of Invasive Species Diversity on Alpha Diversity of Soil Microbial Communities

Alien invasive species richness, evenness or their interaction did not significantly affect alpha diversity (OTUs, Shannon, Simpson, Chao1 and ACE) of either soil fungal communities (Table 1A, Figure 1A–E) or soil bacterial communities (Table 1B, Figure 1F–J).

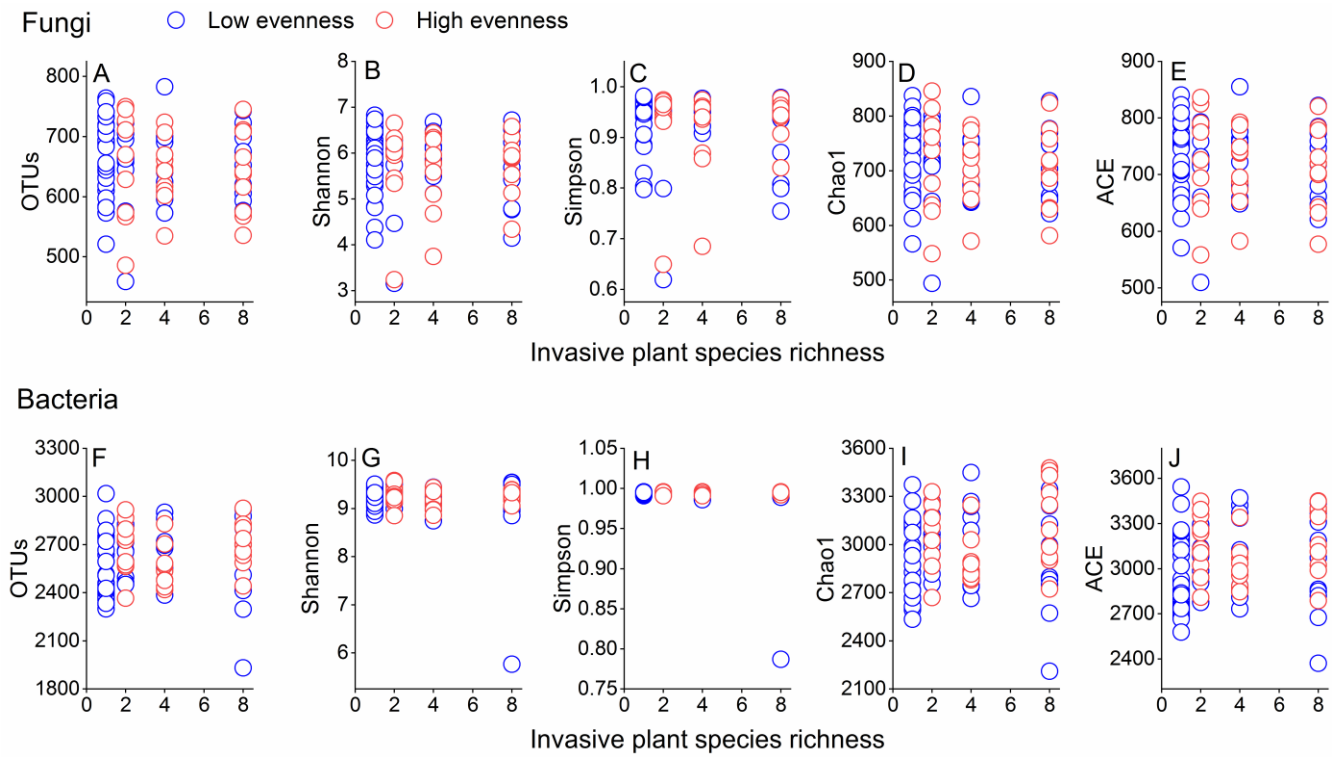

Figure 1. Effects of invasive species richness and evenness on the OTUs, Shannon, Simpson, Chao1 and ACE of soil fungal communities (**A**–**E**) and soil bacterial communities (**F**–**J**). Raw data points are shown. See Table 1A,B for the results of the linear mixed models.

Table 1. Summary of linear mixed models testing the effects of invasive species richness, evenness and their interaction on alpha diversity of soil fungal communities (**A**), soil bacterial communities (**B**) and soil physico-chemical properties (**C**). Species composition was included as a random term. Degrees of freedom are (1, 38), (1, 48) and (1, 48) for the effects of richness, evenness and their interaction, respectively.

	Richness (R)		**Evenness (E)**		**R′ E**	
Variable	***F***	***P***	***F***	***P***	***F***	***P***
(A) Soil fungal communities						
OTUs	0.515	0.477	0.337	0.564	0.298	0.588
Shannon	0.555	0.461	0.007	0.933	0.292	0.592
Simpson	0.286	0.596	0.033	0.857	0.781	0.381
Chao1	0.284	0.597	0.170	0.682	0.357	0.553
ACE	0.341	0.563	0.128	0.722	0.316	0.577
(B) Soil bacterial communities						
OTUs	0.585	0.449	1.344	0.252	0.008	0.931
Shannon	0.568	0.456	1.856	0.180	0.768	0.385
Simpson	2.155	0.150	2.204	0.144	1.433	0.237
Chao1	1.668	0.204	2.688	0.108	0.587	0.447
ACE	1.232	0.274	2.529	0.118	0.150	0.701
(C) Soil physico-chemical properties						
pH	0.012	0.913	0.004	0.951	0.448	0.506
Organic matter	0.019	0.891	0.724	0.399	1.317	0.257
Total N	1.508	0.227	1.257	0.268	2.303	0.136
NH_4_N	0.021	0.886	1.835	0.182	0.843	0.363
NO_3_N	0.005	0.944	2.427	0.126	2.755	0.104
Total P	0.475	0.495	0.277	0.602	0.037	0.849
Available P	0.058	0.811	2.977	0.091	0.801	0.375
Available K	0.023	0.882	0.884	0.352	3.272	0.077

3.2. Effects of Invasive Species Diversity on Soil Physico-Chemical Properties

Alien invasive species richness, evenness or their interaction had no significant effect on any of the soil physico-chemical properties (soil pH, organic matter, total N, NH_4_N, NO_3_N, total P, available P and available K; Table 1C, Table 2).

Table 2. Soil physico-chemical properties under communities with different levels of invasive plant species richness and evenness (mean ± SE). See Table 1C for the results of the linear mixed models.

Richness	**Evenness**	**pH**	**Organic matter (g/kg)**	**Total N (mg/g)**	**NH_4_N (mg/kg)**	**NO_3_N (mg/kg)**	**Total P (mg/g)**	**Available P (mg/kg)**	**Available K (mg/kg)**
1	Low	7.27 ± 0.04	285.05 ± 17.48	0.77 ± 0.07	10.45 ± 1.20	33.76 ± 3.24	3.45 ± 0.06	122.05 ± 7.49	163.27 ± 8.90
2	Low	7.35 ± 0.05	303.00 ± 37.82	0.78 ± 0.08	11.90 ± 2.29	37.29 ± 6.68	3.43 ± 0.14	125.64 ± 17.72	182.28 ± 31.35
	High	7.34 ± 0.06	328.04 ± 27.28	0.58 ± 0.06	8.74 ± 1.33	35.72 ± 7.62	3.48 ± 0.11	122.13 ± 15.25	189.38 ± 24.27
4	Low	7.34 ± 0.05	275.48 ± 37.52	0.67 ± 0.09	9.96 ± 1.69	36.20 ± 6.91	3.32 ± 0.10	132.27 ± 12.46	180.98 ± 27.74
	High	7.26 ± 0.09	303.12 ± 18.88	0.65 ± 0.06	8.21 ± 0.61	31.32 ± 3.71	3.47 ± 0.12	105.33 ± 11.21	161.78 ± 13.50
8	Low	7.27 ± 0.04	296.57 ± 27.73	0.66 ± 0.05	11.12 ± 2.22	43.31 ± 6.00	3.39 ± 0.20	139.36 ± 13.88	191.89 ± 18.65
	High	7.29 ± 0.05	278.40 ± 11.35	0.70 ± 0.05	11.11 ± 1.48	26.67 ± 4.40	3.37 ± 0.20	115.02 ± 16.12	150.62 ± 16.54

3.3. Effects of Invasive Species Diversity on Soil Microbial Community Composition

Soil fungal communities in the 1-, 2- and 4-species treatments were separated from those in the 8-species treatment along the first axis of PCoA (Figure 2A). Results of the Adonis test also confirmed that species composition of soil fungal communities differed between the lower (1-, 2- and 4-species) and the higher (8-species) species richness treatments (Table 3A). For soil bacterial communities, the 1- and 8-species treatments were distinguished from the 2- and 4-species treatments along the first axis of PCoA (Figure 2B), and the results of the Adonis test also confirmed that the differences were significant (Table 3A). However, the Adonis test showed that neither the species compositions of soil fungal

communities nor soil bacterial communities differ significantly between the high and the low evenness treatment within each level of species richness (Table 3B).

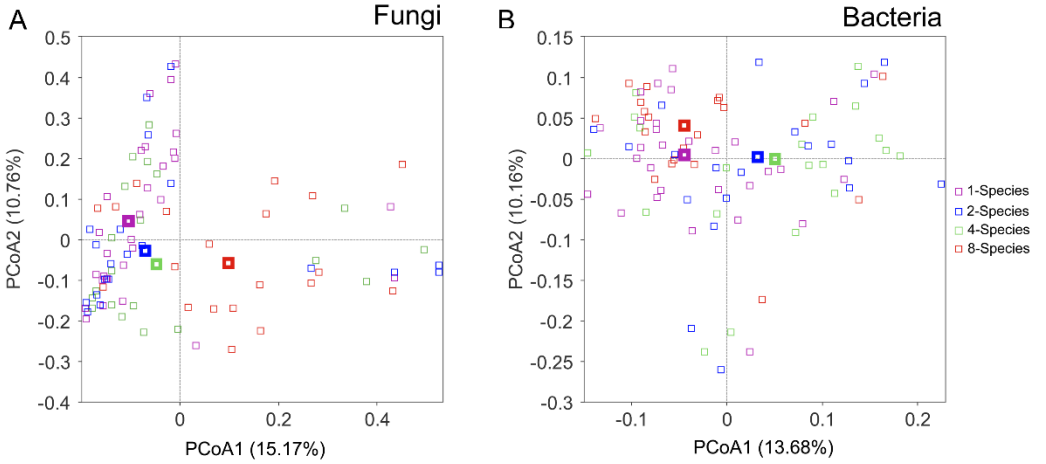

Figure 2. Results of PCoA for soil fungal (**A**) and bacterial (**B**) communities. See Table 3A for the results of Adonis test. The bold boxes indicate the central location of the sample points under different richness treatments.

Table 3. Adonis test for differences in community composition of fungi and bacteria between different richness and evenness treatments of invasive species based on Bray-Curtis distance.

		df	*F*	R^2	*P*
	(A) Comparison among different richness of alien invasive plant species				
Fungi					
	1 vs. 2 species	1 (48)	0.704	0.014	0.872
	1 vs. 4 species	1 (48)	1.135	0.023	0.291
	1 vs. 8 species	1 (48)	3.048	0.060	0.001
	2 vs. 4 species	1 (38)	0.747	0.019	0.807
	2 vs. 8 species	1 (38)	1.803	0.045	0.030
	4 vs. 8 species	1 (38)	1.967	0.049	0.016
Bacteria					
	1 vs. 2 species	1 (48)	1.333	0.027	0.113
	1 vs. 4 species	1 (48)	1.767	0.036	0.017
	1 vs. 8 species	1 (48)	1.149	0.023	0.242
	2 vs. 4 species	1 (38)	0.763	0.020	0.812
	2 vs. 8 species	1 (38)	1.595	0.040	0.026
	4 vs. 8 species	1 (38)	1.791	0.045	0.021
	(B) Comparison among different evenness of alien invasive plant species				
Fungi					
	Low vs. high evenness of the 2 species	1 (18)	0.910	0.048	0.517
	Low vs. high evenness of the 4 species	1 (18)	0.637	0.034	0.929
	Low vs. high evenness of the 8 species	1 (18)	0.737	0.039	0.844
Bacteria					
	Low vs. high evenness of the 2 species	1 (18)	0.694	0.037	0.930
	Low vs. high evenness of the 4 species	1 (18)	0.814	0.043	0.593
	Low vs. high evenness of the 8 species	1 (18)	0.958	0.051	0.501

3.4. Effects of Invasive Species Diversity on Relative Abundances of Soil Microbial Taxa

Regarding soil fungal taxa, Ascomycota, Basidiomycota and Rozellomycota were the three most abundant phyla (Figure 3A). Among them, invasive plant species richness had a significant effect on Ascomycota and Rozellomycota (Table 4); with increasing invasive plant species richness, the relative abundance of Ascomycota increased significantly, while that of Rozellomycota decreased (Figures 3A and 4A). Among the 20 most abundant

fungal genera, invasive plant species richness had a significant effect on *Bipolaris*, unidentified_*Rozellomycota*_sp and *Clitopilus* (Table 4A); with increasing invasive plant species richness, the relative abundance of *Bipolaris*, the most abundant genus, increased significantly, while that of unidentified_*Rozellomycota*_sp and *Clitopilus* decreased (Figures 3C and 4A).

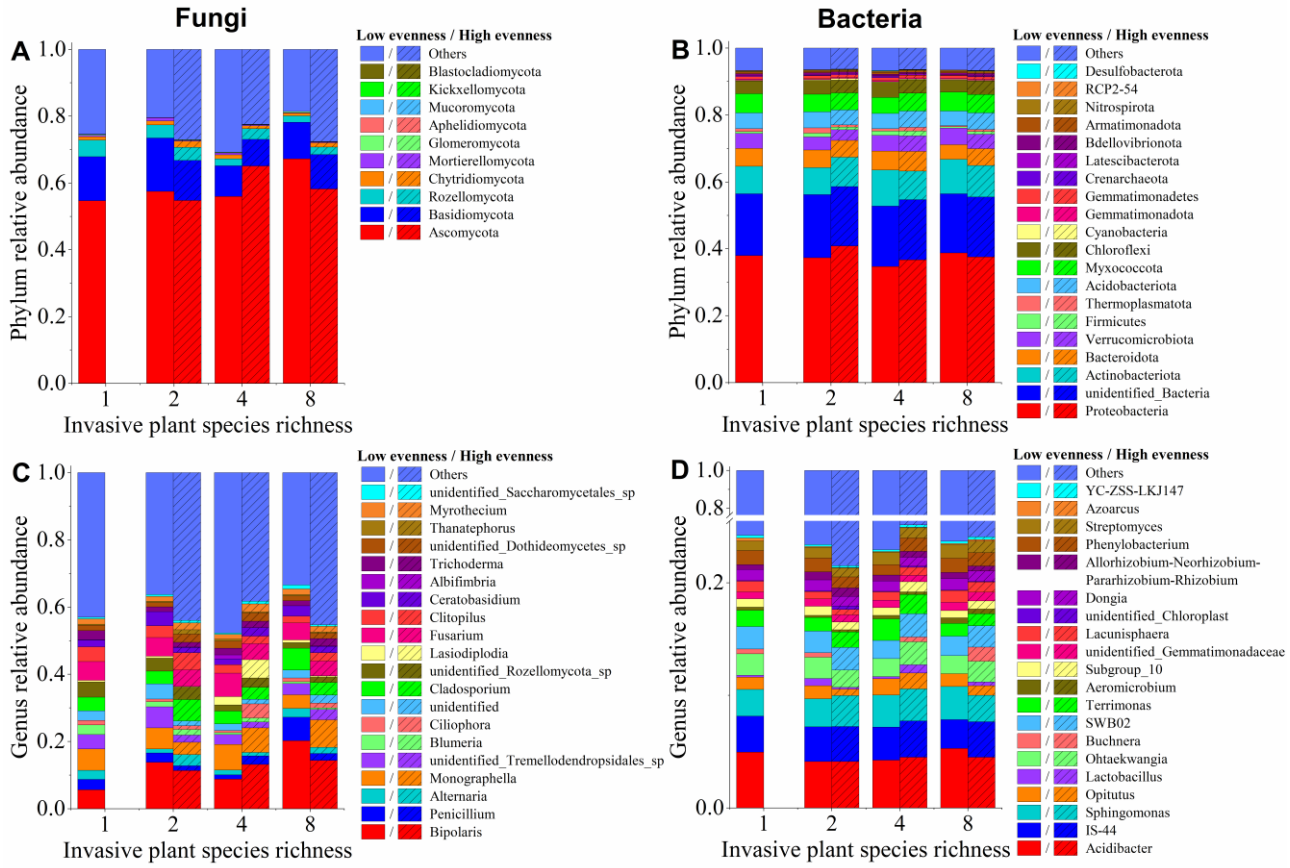

Figure 3. Relative abundance of the 10 most abundant phyla of soil fungi (**A**), the 20 most abundant phyla of soil bacteria (**B**) and the 20 most abundant genera of soil fungi (**C**) and bacteria (**D**) under the communities with different invasive plant species richness and evenness.

Table 4. Summary of linear mixed models testing the effects of invasive species richness, evenness and their interaction on the relative abundance of (**A**) soil fungal and (**B**) soil bacterial taxa. Values are in bold when $p < 0.05$. Species composition was included as a random term. Degrees of freedom are (1, 38), (1, 48) and (1, 48) for the effects of richness, evenness and their interaction, respectively.

Variable	Richness (R)		Evenness (E)		R × E	
	F	*P*	*F*	*P*	*F*	*P*
(A) Fungi						
Phylum						
Ascomycota	4.896	0.033	0.119	0.732	0.894	0.349
Rozellomycota	7.365	0.010	0.093	0.762	0.180	0.673
Genus						
Bipolaris	5.203	0.028	0.022	0.883	0.275	0.602
unidentified_*Rozellomycota*_sp	7.835	0.008	0.043	0.836	0.011	0.918
Clitopilus	6.076	0.018	0.606	0.440	0.222	0.639

Table 4. *Cont.*

Variable	Richness (R)		Evenness (E)		R × E	
	F	***P***	***F***	***P***	***F***	***P***
(B) Bacteria						
Phylum						
Actinobacteriota	4.920	0.033	1.838	0.182	0.844	0.363
Bdellovibrionota	0.252	0.619	0.210	0.649	7.782	0.008
Armatimonadota	1.065	0.309	4.358	0.042	0.018	0.894
Genus						
Sphingomonas	1.465	0.234	0.067	0.796	4.576	0.038
Buchnera	0.314	0.579	0.918	0.343	7.560	0.008
Streptomyces	8.822	0.005	6.024	0.018	0.126	0.724

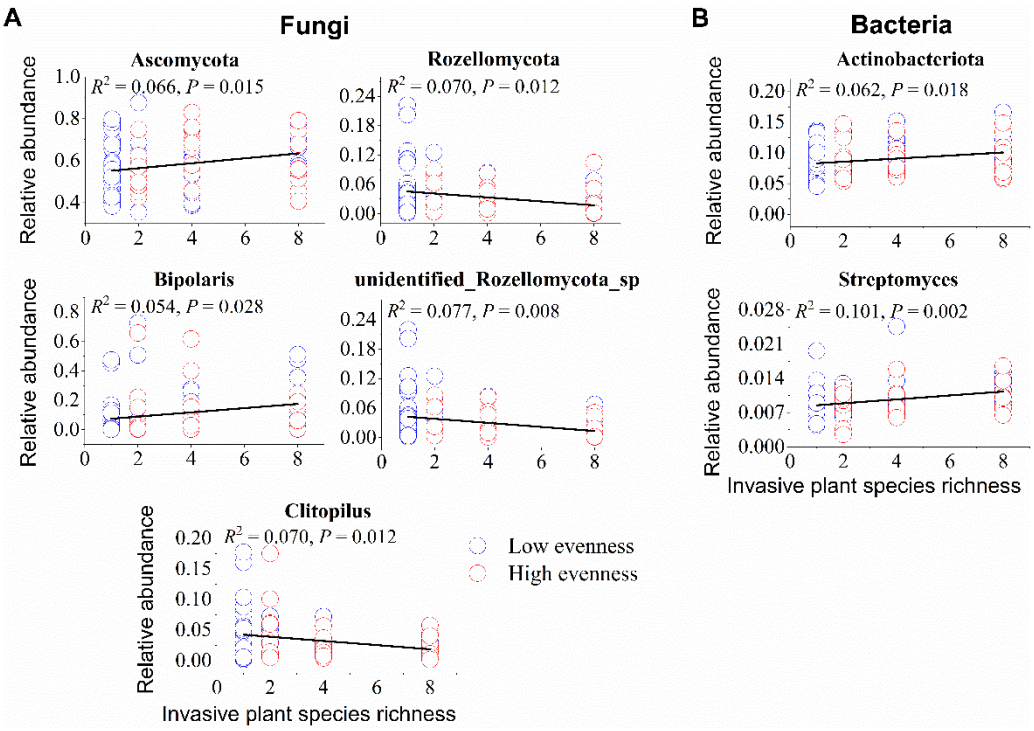

Figure 4. Relationships of the relative abundance of the fungal phylum of Ascomycota and Rozellomycota, the fungal genus of *Bipolaris*, unidentified_*Rozellomycota*_sp and *Clitopilus* (**A**), the bacterial phylum of Actinobacteriota and the bacterial genus of *Streptomyces* (**B**) with invasive plant richness. Raw data points are shown. See Table 4 for the results of the linear mixed models.

Regarding soil bacterial taxa, Proteobacteria, unidentified_Bacteria and Actinobacteriota were the three most abundant phyla (Figure 3B). Invasive plant richness has a significant influence on Actinobacteriota, which increased significantly with the increase of invasive plant species richness (Table 4 and Figures 3B and 4B). Invasive plant evenness had a significant effect on Armatimonadota, and invasive plant richness and evenness had a significant interactive effect on Bdellovibrionota (Table 4B, Figure 3B). Among the 20 most abundant genera of bacteria, invasive plant species richness and evenness had a significant effect on *Streptomyces*, which increased significantly with the increase of invasive species richness (Table 4B, Figures 3D and 4B). In addition, the interaction of invasive plant richness and evenness had a significant effect on *Sphingomonas* and *Buchnera* (Table 4B, Figure 3D).

4. Discussion

A large body of studies has investigated the effects of alien plant invasions on soil microbial communities [14–16,20,21], but few have considered the effects of invasive species diversity (richness and evenness). While we found no significant effect of alien invasive plant species richness and evenness on the alpha diversity of soil fungal and bacterial communities, there was a significant effect of invasive species richness on the community composition of both soil fungi and bacteria and on the relative abundances of some specific microbial taxa.

4.1. Effects of Invasive Species Diversity on Alpha Diversity of Soil Microbial Communities

Although, in the same experimental setup, increasing invasive species richness was found to significantly change the species compositions of the plant communities by increasing the productivity of alien invasive plant species and decreasing that of native plant species [35], it had no impact on alpha diversity of either soil fungal or bacterial communities. Previous studies testing the role of native plant richness showed that alpha diversity of soil fungal communities can have a positive [16,59,60], negative [61,62] or no relationship [63–67] with native plant species richness. The positive relationship could be because of more diverse microhabitats and/or resources created by the higher richness of plant species [16,63,68]. For example, soil fungal richness increased with native plant richness through the increase of soil total carbon [16]. The negative relationship results from the greater impact of context (e.g., plant biomass, soil pH and plant species identity) [61,62]. For example, soil resources and plant species had a stronger effect on soil biota than plant species richness [69].

The neutral effect of invasive plant species richness on soil microbial diversity in this study may be related to the antagonistic effects among different invasive plants on soil microorganisms [20]. This can be explained from two aspects: different invasive plants have opposite effects on the same microbial group, and the same invasive plant communities have opposite effects on different microbial groups. In this study, the first aspect can be confirmed by the opposite effects of the relative abundance of different invasive plants on specific microbial groups (Table A2). For example, the relative abundance of the invasive plants *Alternanthera philoxeroides*, *Sesbania cannabina* and *Talinum paniculatum* was significantly negatively correlated with the relative abundance of *Bipolaris*, the genus with the highest relative abundance of fungi, while the relative abundance of *Bidens frondosa* showed the opposite trend (Table A2).

For the second aspect, when multiple invasive plants co-exist, some species favor some particular microbial taxa and inhibit others, with the result that there is no significant change, as reported before [23]. In this study, this explanation can be evidenced by the opposite trend of the effect of invasive species diversity on the relative abundance of some fungal taxa (i.e., Ascomycota vs. Rozellomycota and *Bipolaris* vs. unidentified_*Rozellomycota*_sp and *Clitopilus;* Figure 4A). The same situation is present in soil bacterial communities, i.e., increasing invasive species richness increased the relative abundance of Actinobacteriota and decreased that of *Streptomyces* (Figure 4B).

Soil is an important environmental factor for microbial life. Many studies on the effects of plant richness on microbial life have found that this relationship is ultimately explained not only by plant species richness but also by soil physico-chemical properties, such as soil pH [70,71]. In this study, although soil microbial diversity was significantly negatively correlated with some soil physico-chemical properties (Table A3), invasive species richness and evenness had no significant effect on soil physico-chemical properties. Therefore, invasive species diversity may not change soil microbial diversity via altering soil physico-chemical properties.

4.2. Effects of Invasive Species Diversity on Soil Microbial Taxa and Community Composition

Specific taxa of microorganisms play an important role in maintaining microbial community structure and affecting ecosystem functions [72,73] (In this study, invasive species richness and evenness have significant effects on some specific taxa of fungi and bacteria (Table 4; Figure 4). Our results revealed that high invasive plant richness promoted the most abundant fungal phylum of Ascomycota and the most abundant fungal genus of *Bipolaris* and suppressed the fungal phylum of Rozellomycota and fungal genus of unidentified_*Rozellomycota*_sp and *Clitopilus*.

Ascomycota is one of the most common phyla among soil fungi and is the most abundant phyla in the soil of many invasive sites [16,29]. Similarly, Ascomycota possessed more than 50% relative abundance in each treatment of this study and increased significantly with increasing invasive species richness. As Ascomycota contained a wide diversity of fungal taxa, ranging from pathogens to mutualists, its ecological function depends on the comprehensive effect of each member. The increasing tendency of relative abundance of Ascomycota with invasive species richness in this study may be partly explained by its member *Bipolaris*, the most abundant genus of fungi, which also increased significantly with increasing invasive species richness. The genus of *Bipolaris* includes more than 20 species of pathogens that can infect a broad range of grasses [74–76], including invasive plants (e.g., *Microstegium*) [77]. Our results suggest that increasing invasive species richness may facilitate pathogen emergence and amplification, and these effects may inhibit native plant growth and promote further invasions. On the other hand, the accumulation of pathogens may also inhibit the invasion of alien plants [77].

For soil bacterial communities, Actinobacteriota, one of the largest taxonomic units of bacteria, increased significantly with increasing invasive species richness. As plant growth-promoting rhizobacteria, Actinobacteriota constitute important drivers of rhizosphere nutrient cycling and play a role as biocontrol agents against a range of pathogenic fungi and promote plant growth by phosphate solubilization, secondary metabolite production and antimicrobial synthesis [78–80]. Our results agreed with the findings of a previous study, which showed that increasing native crop diversity increased the relative abundance of Actinobacteriota [81]. In this study, the increased relative abundance of Actinobacteriota in more diverse invasive plant communities has the same trend with its member *Streptomyces*, which is the most abundant and arguably the most important actinomycetes, and is a good source of bioactive compounds, antibiotics, and extracellular enzymes [79,80,82]. Although studies have shown that plant invasion (e.g., *Ageratina adenophora*) increases the relative abundance of *Streptomyces* [83], the relative abundances of Actinobacteriota and *Streptomyces* were all negatively related to the relative abundance of the invasive plants *Sesbania cannabina* and *Talinum paniculatum* (Table A2). Therefore, invasive species richness may affect this microbe (Actinobacteriota and *Streptomyces*) through species-species interactions and species-environment interactions, and this effect may be beneficial to the growth and competitiveness of invasive plants themselves [83].

5. Conclusions

We conclude that alien invasive plant species diversity had no effect on the alpha diversity of both soil fungal and bacterial communities, likely because the dominant microbial groups showed opposite responses to alien invasive species diversity. One caveat is that the soil samples were collected only after one growing season of invasion, so the impact of invasive species diversity on the alpha diversity of soil microbial communities may not be big enough. Thus, future studies could test the longer-term effect of alien invasive plant species diversity on the alpha diversity of soil microbes. Given the important effects of soil microbial communities on plant growth, especially pathogens, it is possible that soil microorganisms may have important effects on native plants or invasive plants to alter community composition. Therefore, it is worth further researching if invasive plant diversity can affect the plant community composition through the influence of soil pathogens.

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Appendix A

Table A1. Species composition ratio in different richness levels and evenness levels.

	1-species										2-species																					
											High evenness										Low evenness											
Invasive species	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10				
Bidens pilosa	24										12					12					22					2							
Bidens frondosa		24												12					12					22				22				
Ageratum conyzoides			24								12							12				2						22				
Sesbania cannabina				24											12	12									2	22						
Talinum paniculatum					24									12							12			2					2			
Celosia argentea						24						12					12					2					22					
Solidago canadensis							24								12			12							22			2				
Mirabilis jalapa								24				12									12		22						22			
Alternanthera philoxeroides									24				12				12							22			2					
Aster subulatus										24			12						12					2				22				

	4-species																								8-species															
	High evenness										Low evenness										High evenness										Low evenness									
1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	9	10
6	6	6	6							18	3	2	1									3	3	3	3	3	3	3	3			1	3	2	1	13	1	1	2
6				6	6	6				3				3	18	1					3	3			3	3	3	3	3	3	13	1			1	2	1	1	2	3
			6		6	6			6				18		1	2			3			3	3		3	3	3	3	3	3		13	3		1	1	1	2	2	1
	6	6	6					6			2	3	2					18			3	3		3	3	3		3	3	3	3	1		1	1	13		3	1	1
6	6						6		6	2	1						2		18	3		3	3	3		3	3	3	3	2		1	13	2		2	2	3	2
				6	6		6	6						1	3	18	18	2		3	3	3	3	3	3	3	3			2	1	2	2	13	3	1	1		
		6		6	6		6						18		2	2	3	3			3	3	3	3	3	3	3		3		1	1	2	1	1	1	1		13	
						6	6	6	6								1	3	2	3	3	3	3		3	3	3		3	1	3	1	1		1	2	13		1
6				6		6			6	1				18					1	3	3	3	3			3	3	3	3	1	2	1	1			3	1	1	13
	6	6	6					6			18	1	3					1		3	3	3	3	3	3			3	3	1	2	13	2	3	2			1	1

The numbers in the third row represent the number of experiment replicates. For 1-species, there are three replicates for each species, which was not shown in the table. Other numbers represent the seedling number of different species planted in each community.

Table A2. Pearson correlation analysis between top 20 predominant phyla and genus and percentage of initial plant number for 10 invasive plants.

	Bidens pilosa	*Bidens frondosa*	*Ageratum conyzoides*	*Sesbania cannabina*	*Talinum paniculatum*	*Celosia argentea*	*Solidago canadensis*	*Mirabilis jalapa*	*Alternanthera philoxeroides*	*Aster subulatus*
Fungi										
Phylum										
Ascomycota	**−0.375** *	0.265	***−0.328***	**−0.465** **	−0.248	0.052	−0.241	***0.337***	**−0.474** **	***−0.340***
Basidiomycota	0.195	0.124	0.080	**0.531** **	0.179	−0.114	0.202	−0.219	**0.367** *	−0.182
Rozellomycota	0.265	−0.225	**0.541** **	**0.391** *	0.066	0.065	0.099	0.186	**0.481** **	0.174
Chytridiomycota	−0.178	−0.281	***0.314***	−0.166	−0.007	0.243	−0.106	−0.152	0.229	0.044
Mortierellomycota	−0.151	−0.037	0.293	***0.352***	−0.102	−0.278	***0.331***	−0.256	**0.370** *	**0.598** **
Glomeromycota	0.126	0.206	0.145	−0.220	0.237	***−0.312***	0.066	**0.382** *	−0.173	−0.045
Mucoromycota	−0.001	−0.078	−0.126	**0.492** **	0.174	0.069	0.102	−0.100	0.018	0.148
Monoblepharomycota	0.255	−0.122	0.052	−0.189	**0.549** **	0.063	−0.005	−0.077	−0.100	−0.079
Genus										
Bipolaris	***−0.309***	**0.419** *	***−0.352***	**−0.389** *	**−0.426** *	−0.350	−0.139	0.197	**−0.429** *	−0.282
Alternaria	0.026	**−0.366** *	−0.225	−0.090	0.094	**0.380** *	−0.043	0.161	−0.281	0.068
Monographella	−0.181	−0.242	**0.514** **	−0.155	0.174	0.297	−0.045	−0.083	−0.213	−0.155
unidentified_*Tremellodendropsidales_sp*	0.038	−0.007	−0.162	***0.323***	0.101	−0.076	0.128	***−0.340***	**0.398** *	−0.196
Blumeria	0.028	−0.182	−0.142	**0.388** *	0.270	0.153	−0.106	**0.516** **	**0.417** *	0.160
unidentified	−0.026	−0.058	−0.148	0.288	0.075	−0.089	0.156	***−0.304***	**0.366** *	−0.191
Cladosporium	−0.020	***−0.317***	−0.230	0.051	0.006	0.101	−0.116	0.280	−0.187	−0.078
unidentified_*Rozellomycota_sp*	0.279	−0.237	**0.588** **	**0.445** *	0.048	0.097	0.056	0.298	**0.476** **	0.124
Clitopilus	**0.668** **	0.195	0.293	**0.570** **	0.157	−0.035	0.187	0.113	0.256	0.137
Albifimbria	−0.124	−0.164	−0.114	−0.153	0.037	0.266	0.090	−0.096	−0.123	***0.346***
Trichoderma	−0.050	0.093	**0.440** *	0.112	***0.329***	−0.164	−0.034	−0.178	0.137	0.121
unidentified_*Dothideomycetes_sp*	***0.335***	−0.038	0.049	−0.051	0.289	−0.089	−0.181	0.104	−0.058	−0.167
Bacteria										
Phylum										
Proteobacteria	−0.013	0.207	−0.139	0.197	0.267	−0.062	0.225	0.058	0.060	**−0.498** **
unidentified_Bacteria	0.242	−0.147	0.221	0.229	−0.186	−0.024	0.027	0.062	**0.488** **	−0.113
Actinobacteriota	**−0.431** *	0.061	−0.180	**−0.478** **	**−0.358** *	−0.117	−0.271	0.152	−0.277	0.169
Verrucomicrobiota	−0.001	−0.100	0.212	−0.209	0.142	0.056	−0.115	−0.295	**−0.357** *	−0.055
Firmicutes	0.006	−0.019	−0.008	−0.185	−0.133	−0.055	−0.176	−0.064	−0.182	**0.506** **
Thermoplasmatota	0.149	−0.269	**0.394** *	0.068	0.013	0.294	−0.203	−0.066	0.159	**0.527** **
Acidobacteriota	0.132	**−0.400** *	−0.139	0.109	0.055	0.158	0.233	−0.186	−0.060	0.172
Myxococcota	−0.029	−0.169	−0.056	**0.490** **	0.244	**0.421** *	−0.021	−0.028	−0.165	−0.228
Gemmatimonadota	−0.005	−0.192	***0.349***	***−0.353***	−0.219	−0.022	0.055	−0.190	0.106	0.065
Gemmatimonadetes	−0.024	**0.363** *	−0.019	**−0.438** *	−0.241	−0.270	***0.339***	−0.178	0.007	0.076
Latescibacterota	0.228	−0.286	−0.155	***0.332***	**0.406** *	0.218	0.152	−0.081	−0.017	0.023
Bdellovibrionota	0.045	−0.092	0.249	0.221	0.188	0.191	0.020	−0.038	−0.047	**−0.377** *
Nitrospirota	−0.106	−0.036	0.042	−0.123	−0.063	−0.065	**0.381** *	−0.287	0.005	**−0.383** *
RCP2-54	−0.005	−0.025	0.121	***0.333***	−0.034	0.107	0.118	0.172	**0.374** *	−0.164
Desulfobacterota	0.072	0.097	0.146	−0.221	−0.056	−0.025	−0.092	−0.039	−0.138	**0.723** **
Genus										
Acidibacter	−0.086	−0.271	0.227	0.010	**0.386** *	0.113	0.037	−0.116	***−0.328***	−0.067
IS-44	***0.341***	**−0.424** *	−0.105	**0.376** *	***0.354***	0.116	−0.180	0.125	0.035	0.094
Sphingomonas	−0.284	***0.313***	−0.165	***−0.302***	−0.239	***−0.341***	**0.373** *	−0.099	0.102	−0.296
Opitutus	0.089	0.071	***0.320***	***−0.309***	0.048	−0.014	−0.237	−0.189	***−0.325***	0.171
Lactobacillus	−0.059	−0.068	−0.010	−0.033	−0.065	−0.097	−0.045	−0.130	−0.111	**0.469** **
Ohtaekwangia	0.146	−0.278	−0.272	**0.430** *	0.084	0.142	−0.021	0.037	0.088	−0.062

Table A2. *Cont.*

	Bidens pilosa	*Bidens frondosa*	*Ageratum conyzoides*	*Sesbania cannabina*	*Talinum paniculatum*	*Celosia argentea*	*Solidago canadensis*	*Mirabilis jalapa*	*Alternanthera philoxeroides*	*Aster subulatus*
SWB02	0.184	−0.178	−0.121	***0.337***	0.066	0.214	0.158	−0.025	−0.057	0.063
Terrimonas	0.192	−0.019	**0.368** *	0.007	0.190	−0.172	0.100	0.235	0.044	0.165
Aeromicrobium	−0.237	***0.331***	−0.242	−0.237	−0.240	−0.144	***−0.343***	−0.199	−0.283	−0.202
Subgroup_10	−0.053	−0.186	0.018	−0.188	−0.071	−0.131	0.252	−0.076	−0.010	**0.445** *
Lacunisphaera	−0.109	−0.113	0.225	−0.065	0.194	0.078	−0.061	***−0.307***	−0.241	**−0.380** *
Dongia	−0.073	−0.065	−0.052	0.075	0.244	−0.118	0.229	−0.044	0.216	***−0.342***
Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium	***−0.324***	**0.401** *	−0.002	0.080	***−0.343***	−0.288	−0.062	0.154	0.239	**−0.358** *
Streptomyces	−0.268	−0.017	−0.089	**−0.524** **	**−0.363** *	−0.199	**−0.410** *	−0.160	**−0.372** *	−0.070
Azoarcus	**0.383** *	0.007	−0.210	0.247	**0.359** *	***0.344***	−0.224	0.077	0.288	***−0.307***
YC-ZSS-LKJ147	0.059	−0.290	***0.315***	***−0.314***	−0.232	−0.010	−0.034	−0.252	0.039	−0.112

Only significant or critical significant results are shown here. Values in the table are correlation coefficients, with bold font indicating a significant correlation and bold and italic font indicating critical significance. Asterisk indicates a significant correlation. "*" represents $0.01 \leq p < 0.05$; "**" represents $p < 0.01$.

Table A3. Pearson correlation analysis between soil physico-chemical properties and fungal and bacterial diversity indices.

	Fungi					**Bacteria**				
	OTUs	**Shannon**	**Simpson**	**Chao1**	**ACE**	**OTUs**	**Shannon**	**Simpson**	**Chao1**	**ACE**
pH	0.069	0.092	0.101	0.070	0.065	−0.009	0.060	0.044	0.030	−0.005
Organic matter	0.004	0.066	0.009	−0.013	−0.004	0.054	−0.154	***−0.191***	0.044	0.063
Total N	0.012	0.002	−0.012	−0.009	−0.010	−0.008	−0.063	−0.046	−0.011	0.028
NH_4_N	−0.080	−0.043	−0.066	−0.082	−0.079	0.006	0.073	0.052	−0.047	−0.052
NO_3_N	**−0.275** **	−0.106	−0.033	**−0.239** *	**−0.241** *	−0.067	0.042	0.065	−0.140	−0.124
Total P	**−0.252** *	***−0.191***	−0.123	**−0.265** **	**−0.240** *	0.039	0.074	0.073	0.029	0.051
Available P	**−0.225** *	**−0.207** *	***−0.182***	***−0.188***	***−0.178***	**−0.225** *	−0.068	0.017	**−0.261** *	**−0.250** *
Available K	−0.039	−0.097	−0.139	−0.025	−0.015	−0.158	−0.034	−0.020	**−0.208** *	**−0.203** *

Values in the table are correlation coefficients, with bold font indicating a significant correlation and bold and italic font indicating critical significance. Asterisk indicates a significant correlation. "*" represents $0.01 \leq p < 0.05$; "**" represents $p < 0.01$.

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