THE EFFECT OF LAND-USE TYPES ON COMPOSITION OF ABUNDANT AND RARE SOIL MICROBIAL COMMUNITIES IN URBAN AREAS IN CYPRUS

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Abstract. With the rapid development of cities, different types of land-use in and around urban areas dramatically affect the properties and structure of soil, and further change soil microbial community structure and ecological functions. Although studies of microbial change and underlying drivers in urban and peri-urban soil have attracted considerable attention, the relationship among types of land-use, microbial change, and rare species are poorly understood. Here, the relationship among four different types of land use (e.g. forest, agriculture, industry, and school) and microbial community change, abundant, and rare species in soil were investigated in Cyprus. We found that different land-use types significantly impact the richness of abundant and rare species both in soil, while there were differences in the degree of impact. Based on network and cohesion analysis, microbial communities in forest and agricultural soil, which owned higher negative cohesion and modularity than in industrial and school soil, were more stable. Moreover, deterministic processes, especially homogeneous selection, tended to be more important in shaping the assembly of microbial communities in the soil of the four types of land use. This study considerably expanded our understanding of the effects of land use on soil microbial communities. That will provide a scientific basis for sustainable land use management in urban and peri-urban areas.
Keywords: *anthropogenic, community assembly, co-occurrence network, ecological process, richness*

Introduction

Urban areas accommodate 4.2 billion people, which was approximately 55% of the global population in 2018, and this number will rapidly increase to 6.7 billion (68%) by 2050 (SFC, 2018). The rapidly growing population requires more land for urban infrastructure, forcing urban areas to expand. This will cause a series of consequences such as loss of fertile agricultural land (Seto et al., 2004), habitat fragmentation (Müller et al., 2013), local climate change (Kaufmann et al., 2007), soil contamination (Zhao et al., 2019), and biodiversity reduction (McKinney, 2002). As an important part of urban and peri-urban ecosystems, soil ecosystems are mainly affected by land use (Douglas, 2012). For example, with the compaction of soil, irrigation and nutrient input, accumulation of heavy metals, deposition of inorganic or organic compounds, and types of plant species, the physical and chemical properties of urban and peri-urban soil have increased variability (Godswill et al., 2016). Microorganisms, as one of the main active parts of the soil, play an important role in maintaining soil ecosystem functions and services (Wang et al., 2019) and are very sensitive to environmental changes. Understanding the response of the soil microbiome to environmental and land-use changes is important for soil development in urban and peri-urban regions. Recent studies have focused on the influence of land use and its modifying effect on bacterial and protists compositions and their ecological function in decomposition, and nutrient cycling (Malik et al., 2018). Anthropogenic activities, inorganic pollution, and fertilizer use have been shown to affect the diversity and function of soil microbial communities. On the contrary,

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Xu et al. (2014) showed that the bacterial diversity in urban parks has no relationship with land-use related factors. Such conflicting results highlight the complexity of factors influencing the bacterial community structure in urban and peri-urban areas. Therefore, the relationship between microbial change and land use needs to be further investigated.

Rare microbial species represent the majority of Earth's biodiversity (Naeem and Li, 1997), and these rare species are universal in microbial consortia. Previous study has confirmed that rare species play an important role in ecological functions in soil. For instance, rare species are participating in nitrogen cycling (Montoya et al., 2004), responding to carbon assimilation (Stone et al., 2021), and enhancing the functionality of abundant microbes in soil (Jousset et al., 2017). Additionally, rare taxa can drive ecosystem responses to environmental change and "bloom" to abundance under favorable conditions (Shade et al., 2014). Consequently, changes in these rare but functional important microorganisms could lead to substantial consequences on an ecosystem. Compared with microbial rare species, abundant species exhibit much higher relative abundance and greater resilience to environmental stresses (Prosser et al., 2007). For example, abundant species showed a much weak response to environmental factors than rare species (Delgado-Baquerizo et al., 2018). However, several studies have shown that rare and abundant taxa were influenced by the same environmental factors, such as the depth of water for bacterioplankton in ocean (Mo et al., 2018). Obviously, the difference in pattern between rare and high abundance species that responded to environmental factors is still underexplored. Specifically, it is still unclear whether different land-use patterns lead to different patterns of rare and high abundance species in soil.

In this study, we examined soil samples from urban and peri-urban areas which represented different land-use types. The 16S rRNA amplicon sequencing was employed to understand the soil microbial community. Co-occurrence network construction, cohesion analysis, and null model analysis were used to evaluate the effects of land-use types on rare and abundant species of soil microbial community. Our results provide comprehensive insight into microbial community assembly and the pattern of rare and abundant species in different land use, which may support the development of theories and policies for sustainable management of urban land use in populated developing countries.

Methods

Data selection

We explored papers that used high-throughput sequencing for the analysis of prokaryote communities in the soil of different land-use types. Finally, the publicly available soil microbial data for exploring forests, agricultural land, industrial land, and school land in Stephanou et al. (2021) were selected as the data source for this study. The total number of soil samples was 24, including 5 forest and school soil samples, and 7 industrial and agricultural soil samples respectively. These samples were taken from the area of Lefkosia in the Republic of Cyprus (June 2017). For each sampling location, approximately 250 g soil was collected at 10–20 cm soil depth. In the industrialized area, industrial activity was featured by light with small-scale manufacturing. There were free of vegetation for industrialized and school areas. The agricultural ecosystems mainly planted with seasonal crops and *Olea europea*, while forested areas dominated with *Pinus silvestris.* Detailed information on sample sites, sampling, soil DNA extraction, and sequencing of the 16S rRNA gene was described in Stephanou et al. (2021).

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Bioinformatic analysis

The analysis of the raw sequences was done by following the pipeline of the DADA2 package (version 1.6, Callahan et al., 2016) in R software. Briefly, the package includes the following steps: filtering, dereplication, chimera identification, and merging of paired-end reads (Callahan et al., 2016). Amplicon sequence variants (ASVs) were inferred from sequencing data by the DADA2 algorithm. The taxonomy was assigned by using RDP naïve Bayesian classifier (Wang et al., 2007) with the SILVA v132 database (Quast et al., 2012). Respective reads were summarized and converted to relative abundance by dividing by total sample reads and then collapsed to the genus level. The dataset was normalized to 8700 reads per sample to account for a variation in the samples reaching from 8708 to 73967 reads.

Rare ASVs were defined as the ASVs with a relative abundance <0.1% in all samples analyzed, whereas abundant ASVs were defined as the ASVs with a relative abundance >1% in one or more samples (Zhang et al., 2020).

Co-occurrence network construction and cohesion analysis

In microbial network analysis, networks were constructed for both abundance and rare microbial communities of the four style samples. To reduce the complexity of the datasets, only the OTUs presented in ≥20% of each kind of sample were used for subsequent analyses. Network was inferred by SparCC (Friedman et al., 2012). The Significance of correlations between taxa was calculated using 1000 permutations. Only robust ($|r|>0.4$) and statistically significant ($p < 0.01$) correlations were considered. The network-level (mean node degree, clustering coefficient, average path length, modularity, density, diameter, betweenness centralization, and degree centralization) and node-level (degree, transitivity, betweenness centrality, and closeness centrality) topological features of a network were calculated. Network visualization was generated with Gephi version 0.9.1 (Bastian et al., 2009). To assess the possible topological roles of taxa in networks, nodes were classified into four categories based on their among-module connectivity (Pi) and within-module connectivity (Zi) values: network hubs ($Pi \geq 0.62$, $Zi \geq 2.5$; vital to both the network and its own module coherence), module hubs ($Pi < 0.62$, $Zi \geq 2.5$; critical to its own module coherence), connectors ($Pi \geq 0.62$, $Zi < 2.5$; connect modules together and important to network coherence), and peripherals ($Pi < 0.62$, $Zi < 2.5$) (Shi et al., 2016). Network hubs, module hubs, and connectors have been proposed as potential keystone taxa due to their important roles in network topology.

Cohesion was a calculated method developed recently to estimate within-microbiome dynamics by quantifying the connectivity of microbial communities based on the association among taxa and the abundance of taxa (Herren and McMahon, 2017). Cohesion was applied to microbial communities according to the protocol reported by Herren and McMahon (2017). Briefly, correlations between all taxa in a community were calculated using Pearson correlation measurement and a null model was used to verify the strength of these correlations. Expected correlations derived from the null model were then subtracted from the observed correlations to obtain positive and negative connectedness values. These connectedness values were weighted by the relative abundance of taxa and summed to yield both a positive and negative cohesion metric. Microbial communities with larger negative cohesion values tend to be more stable (Herren and McMahon, 2017; Hernandez et al., 2021).

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Community assembly analysis

To better understand the mechanisms underlying the microbial community assembly in different styles of land utilization, a null model analysis framework developed by Stegen et al. (2013, 2015) was used to evaluate the contribution of different ecological processes to prokaryotic community assembly. An important assumption of this framework was that more phylogenetically closely related species were more ecologically similar. Therefore, using this analysis framework called for significant phylogenetic signals in species niches (Stegen et al., 2013; Dini-Andreote et al., 2015). The Mantel correlogram was used to analyze phylogenetic signal by calculating the correlation coefficients between niche differences (inter-taxa differences in environmental optima) and phylogenetic distances in the R "vegan" package (Stegen et al., 2013; Dini-Andreote et al., 2015). To evaluate ecological processes, the β-Nearest Taxon Index (βNTI) was calculated using the R "picante" package (Kembel et al., 2010). βNTI values less than -2 or larger than 2 indicated homogeneous (between-sample phylogenetic distance being significantly lower than expected) and heterogeneous (between-sample phylogenetic distance being significantly higher than expected) selection respectively, which represent the deterministic processes. βNTI values between -2 and 2, which meant that phylogenetic turnover is not significantly different from null expectation, indicated that stochastic processes. To further differentiate stochastic processes, a Bray-Curtis based Raup-Crick index (RCbray) was calculated to investigate the communities that were not structured by selection (Stegen et al., 2013). RCbray values > 0.95 indicated the observed taxonomic turnover is greater than expected by chance as a result of dispersal limitation combined with drift. RCbray values < -0.95 indicated that observed taxonomic turnover is less than expected by chance as a result of homogeneous dispersion. RCbray values between 0.95 and -0.95 indicated community turnovers are not distinguishable from expected by chance, occurring when drift is acting alone (Stegen et al., 2013; Dini-Andreote et al., 2015). Then, we calculated the fraction of values of βNTI and RCbray that fell into different sections as previously described to evaluate the relative importance of different processes.

Correlation and multivariate analyses

The community composition and phylogenetic variations of the rare, abundant, and whole communities were calculated based on the Bray–Curtis dissimilarity distance and the weighted β-MNTD distance matrices to indicate community phylogenetic distance between samples (Ji et al., 2020). The Bray–Curtis dissimilarity was calculated using the "vegan" package (Oksanen, 2015), whereas the β-MNTD distance was calculated using the "Picante" package (Kembel et al., 2010) in R. Mantel tests were conducted to explore the correlations between rare/abundant species subcommunity composition dissimilarity and the whole community composition dissimilarity. PERMANOVA was used to test the significance of rare, abundant, and whole community compositional differences among the four land-use types. All these statistical analyses were performed using the "vegan" package in R software.

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Result

Community composition of rare and abundant prokaryotes in the soil of four land-use types

A total of 17423 amplicon sequence variants (ASVs) were identified from agriculture, forest, industry, and school soil samples. Rare Prokaryote (relative abundance <0.01%) comprised 88.4±1.7%, 87.0±1.7%, 83.5±11.5%, 81.9±2.7% of total prokaryotic richness in agriculture, forest, industry and school soil (*Fig. 1a*), respectively, whereas their total relative abundance accounted for only 28.5%, 17.1%, 21.2% and 20.8% of the whole community (*Fig. 1b*). In contrast, abundant prokaryote comprised only 1% of the total richness, but their abundance reached 36.2%, 57.7%, 47.8%, and 51.0% respectively (*Fig. 1b*). Across all samples, rare subcommunities were dominated by *Proteobacteria*, *Actinobacteria*, *Planctomycetes*, *Chloroflexi*, and *Cyanobacteria*, but the relative abundance of *Proteobacteria*, *Actinobacteria*, and *Chloroflexi* in the soil of industry and school were higher than that in agriculture and forest (*Fig. 1c*). Likewise, abundant subcommunities were also dominated by *Proteobacteria* and *Actinobacteria* (*Fig. 1c*), but *Proteobacteria* in forest soil had a higher abundance compared with agriculture, industry, and school.

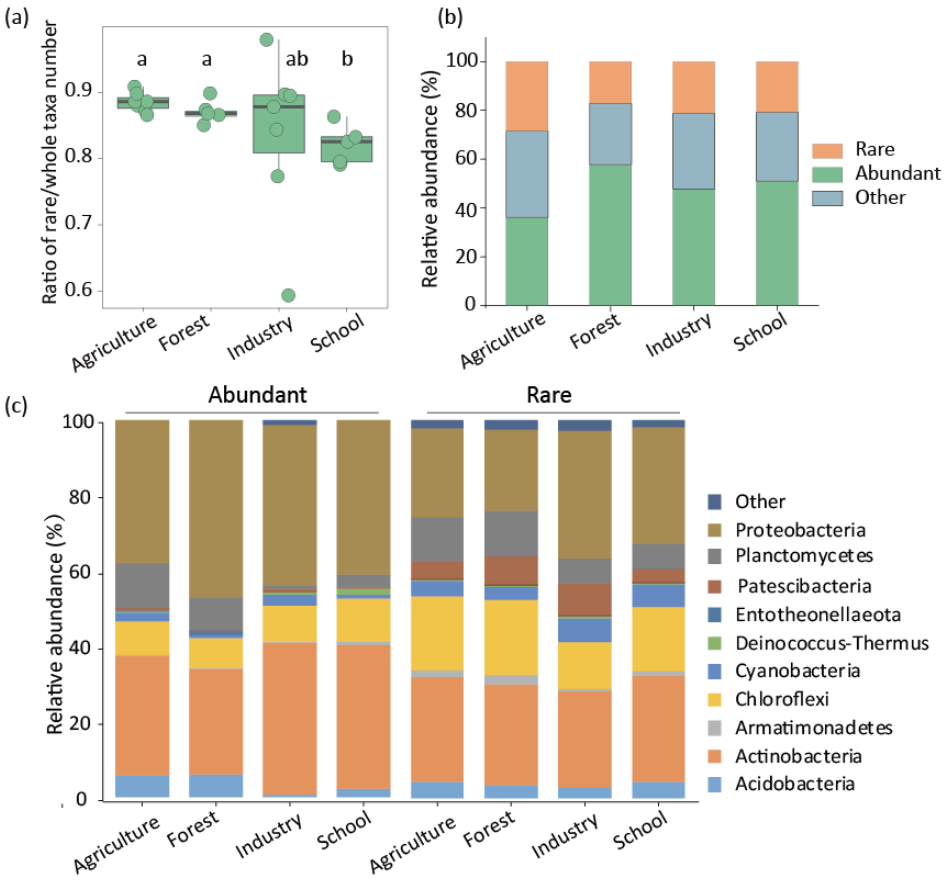

Figure 1. *Microbial communities' composition in the soils of different land-use. The samples were collected from the area of Lefkosia in Cyprus in 2017. a, The ratio of rare/whole taxa numbers. Letters (a,b) indicated the multiple comparison results. Same letters indicated no significant difference, different letters indicated significant differences in statistics. Significance level was 0.05. b, The relative abundance of rare and abundant taxa in the soil of different land-use types. c, The community composition of rare and abundant taxa in soil*

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To understand the effect of abundant and rare community on the whole community, principal coordinate analysis (PCoA) were conducted to evaluate the similarities among communities of agriculture, forest, industry, and school. The result showed that communities of agriculture and forest were clustered together while industry and school communities had a closed relationship (*Fig. 2a,b,* and *c*). Interestingly, the abundant communities presented an almost consistent pattern with the whole communities while rare communities kept the same trend with whole communities, suggesting that the abundant communities played a vital role in shaping whole communities. To assess the contribution of the abundant and rare community to the whole community structure, a mental test was performed between the abundant or rare community and the whole community. Except for the school community, R^2 values of the abundant community were higher than the rare community in the soil of agriculture, forest, and industry (*Fig. 2d*), which could further confirm abundant community dominated the whole community structure.

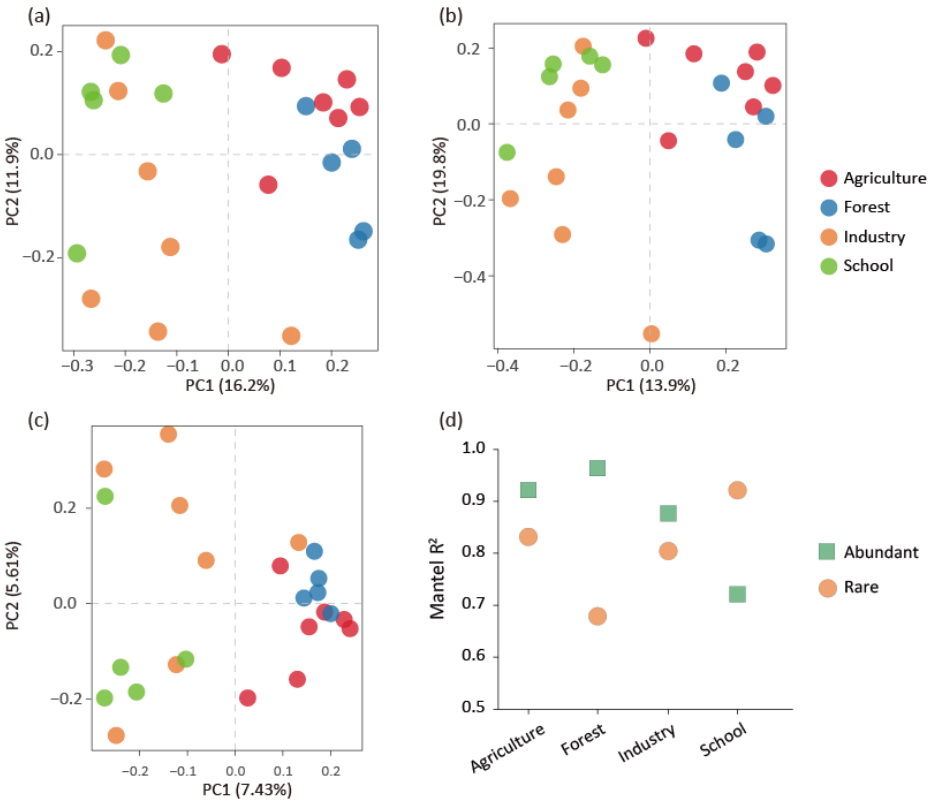

Figure 2. *Principal coordinates analysis (PCoA) of the rare (a), abundant (b), and whole (c) microbial community composition. d, Mantel test between rare/abundant and whole community in the soils of different land-use types*

Correlation relationship between community composition and phylogeny of four land-use styles

Significant correlations between community composition and phylogeny were observed in rare, abundant, and whole communities of agriculture, industry, and school, except for forest (*Fig. 3*). The correlations in abundant and whole communities were much stronger than that in rare communities (*Fig. 3*). In agriculture and industry soil, the

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observed increase in the community composition was accompanied by a relatively weak change in the community phylogeny until the community compositional dissimilarity further increased to approximately 99.75%, 60%, and 90% for rare, abundant, and whole communities. After passing these thresholds, exponential increases in the community phylogenetic distance have then occurred. In contrast, exponential increases were not observed in school soil communities. This observed delay in the community phylogenetic variation was smaller for rare subcommunities than that in abundant subcommunities.

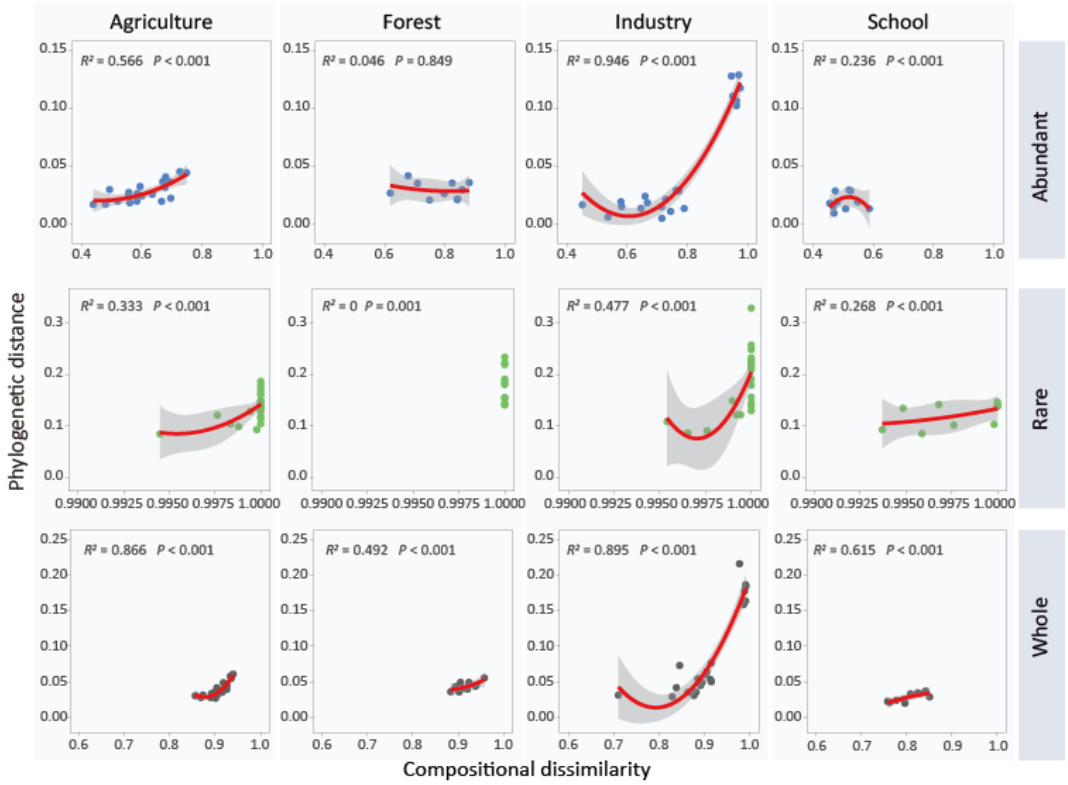

Figure 3. *Correlations between the community composition and phylogeny for rare, abundant, and whole communities. The correlations are fitted by power-law correlations*

Co-occurrence networks of abundant and rare subcommunities

The effect analysis of abundant and rare communities on the whole community raises the question of which species tend to co-exist in the abundant and rare communities. To answer this question, abundant and rare subcommunity co-occurrence networks were built based on correlation relationship (*Fig. 4*). Results showed *Proteobacteria* and *Actinobacteria* played an important role in the network of abundant subcommunities in agriculture, forest, industry, and school soils. For example, *Proteobacteria* was identified as module hubs in abundant subcommunities of agriculture and school (*Fig. A1*, *Table A1*). Meanwhile, *Proteobacteria* and *Actinobacteria* were major connectors in all abundant subcommunities (*Table A1*). In addition, *Planctomycetes* took an important place in the network of abundant subcommunities in agriculture and forest, while *Chloroflexi* had a higher abundance in industry and school subcommunities (*Fig. 4*). This suggested that the abundant subcommunity network between agriculture and forest was more similar than that between industry and school. Similar to abundant subcommunities,

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the network of rare subcommunities had an analogous pattern in industry and school (*Fig. 4*; *Fig. A1*). Compared with industry and school, nevertheless, there were fewer nodes, edges, and taxa abundance in the rare subcommunity networks of agriculture and forest (*Fig. 4*).

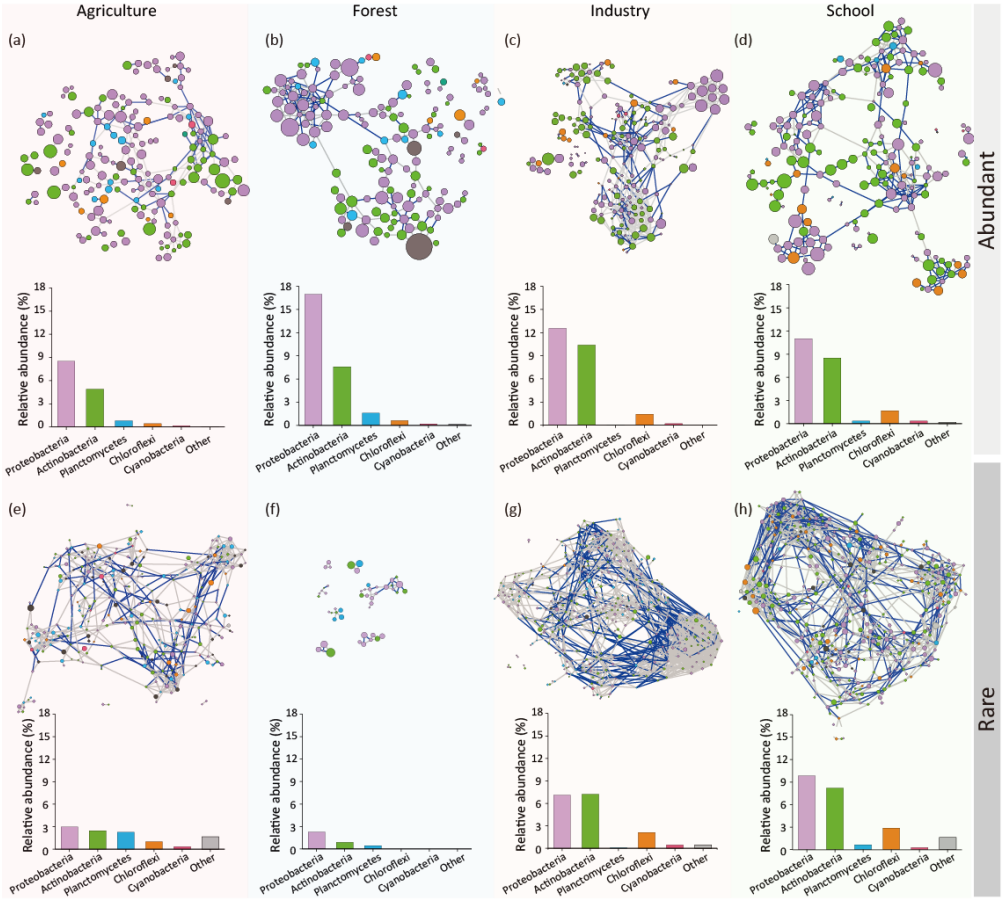

Figure 4. *Co-occurrence networks of rare and abundant microbial taxa in the soils of different land-use types. The node color and size correspond to lineages of the same phylum and the abundance of taxa, respectively*

Based on the microbial network analyses, high negative (competitive interactions) and low positive (cooperative interactions) associations can be employed to depict a stable community. Therefore, the negative:positive cohesion was utilized to evaluate and compare the prokaryotic community stability in agriculture, forest, industry, and school (*Fig. 5a*). Interestingly, the negative:positive cohesion of prokaryotic communities in agriculture and forest were comparable, but higher than that in industry and school (*Fig. 5a*), possibly due to stronger disturbance in industry and school soils. Modularity as another network property of microbial communities as well can be used to describe a stable community. Communities with high modularity tend to be more stable because effects from changes in the abundance of one species are more strongly limited to that species' module. Results showed that microbial communities in forest soil had the largest modularity, followed by agriculture, industry, and school soils (*Fig. 5b*). This indicated that prokaryotic communities in agriculture and forest soils were more stable than in industry and school soils.

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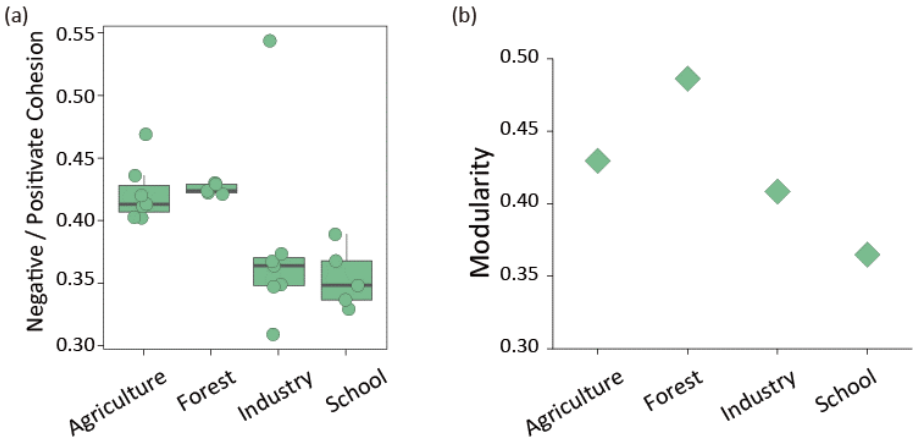

Figure 5. *Microbial network properties in soils of different land-use types. a, Modularity of microbial networks. b, Negative:positive cohesion across the soils of different land-use types*

The prokaryotic communities' assembly in four land-use style soil

βNTI values were calculated to assess the relative importance of two types of prokaryotic community assembly (deterministic and stochastic) in the four land-use style soils (*Fig. 6*). Since most of the βNTI values of all samples were less than -2, deterministic processes were the main force influencing microbial community assembly for all tested samples. To quantitatively assess the key process(es) in governing microbial community assembly in the soil of agriculture, forest, industry, and school, weighted βNTI and Bray-Curtis-based Raup-Crick (RCbray) were used in combination to approximate the relative contributions of five different ecological processes, i.e., Heterogeneous Selection, Homogeneous Selection, Dispersal Limitation, Homogenizing Dispersal, and Drift. Based on the quantitative estimation of the ecological processes that drive the community assembly, 61.9%, 42.8%, 80.0%, and 100.0% of turnover in soil prokaryotic community composition in agriculture, forest, industry, and school, respectively, was primarily due to Homogeneous Selection. In addition, Heterogeneous selection was also an important ecological process in the soil prokaryotic communities of agriculture and forest and explained 19.0% and 33.3% of community turnover, respectively. This indicated selection processes primarily governed prokaryotic community assembly in the soil of urban land.

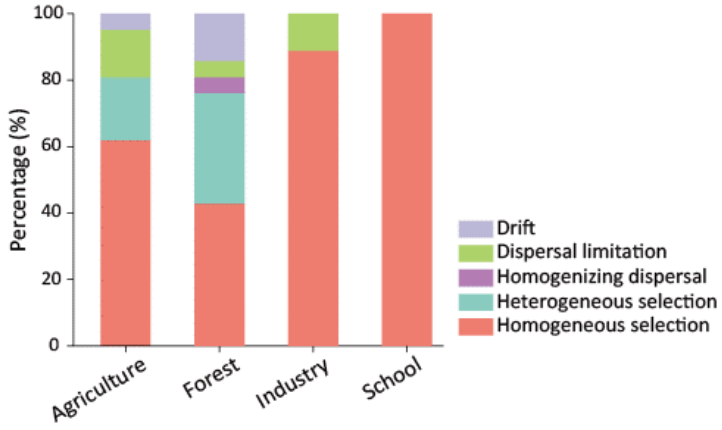

Figure 6. *Microbial community assembly processes in the soil of different land-use types*

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Discussion

In contrast to Stephanou et al. (2021) mainly focused on changed in bacterial community composition and functional guilds involved in N cycling, this study investigated the effects of different land-use on rare and abundant species, community assembly, stability, and network of soil microorganisms. The result showed that land-use types effectively shape soil biota by significantly changing the richness of taxa (*Fig. 1*). This result was in accordance with previous studies in which different land-use types could affect soil biota (Hu et al., 2018; George et al., 2019; Jurburg et al., 2020). Land-use did not directly change the soil microbial community, but indirectly changed taxa's richness by effected on soil moisture, clay, and nutrient contents (Liu et al., 2022). For instance, in our study, *Proteobacteria* and *Actinobacteria* were the dominant phyla, and their abundance varied across land-use types. The abundance of *Proteobacteria* was the highest in forest soil and the lowest in agricultural soil. This might be due to the less human disturbance in forest soil. Compared with forest soil, agricultural soil was often affected by nutrient addition, irrigation, and soil loosening (Ben-Noah and Friedman, 2018), which made *Proteobacteria* unable to adapt to environmental changes that resulted in the decline of its abundance, and then some other microbial species occupying its niche.

In general, microbial communities in soil consisted of a few dominant taxa and low abundant species with long tails pattern (Jia et al., 2018). The same is true for soil microbial communities in the different land-use types that we studied. However, there were significant differences in the richness and abundance of not only abundant taxa but also rare taxa in soils of different land-use types (*Fig. 1a* and *1c*). The richness of rare species in agricultural soil was the highest, reaching 88.4±1.7%, while the abundance of rare species in the school soil was only 81.9±2.7%. This may be due to stronger anthropogenic effects on school soils, compared with agricultural soils. Similarly, Dopheide et al. (2020) showed that the richness of rare species in forest soil was the highest, while that in urban green land soil was the lowest. In addition, compared with rare species, the relationship between the species composition and phylogenetic distance of abundant species could better reflect the overall change of community (*Fig. 3*). Moreover, the species composition of abundant and rare species was more strongly associated with community phylogenetic distance changes in both industrial and school soils than that in agricultural and forest soils (*Fig. 3*). These results showed that the microbial community composition of forest soil changed at a smaller phylogenetic distance, while that of industrial soil was disturbed by large changes at a large phylogenetic distance. This further confirms that microbial communities in forest soil have a stronger ability to maintain stability (Lladó et al., 2018). Therefore, different land-use types both had a significant impact on the richness of abundant and rare species in soil, while the degree of impact was different.

Microbial co-occurrence networks usually reflect the interactions between species within a community (Faust et al., 2021). Abundant species in the soil of all land-use types form complex networks (*Fig. 4*). Compared to agricultural, industrial, and school soils, rare species in forests had a simpler network, and the overall abundance of rare species that form networks was lower. However, Xue et al. (2020) found that the network formed by rare species in forest soil was complex and dominated the whole forest ecological network. In this case, it might be due to the strong homogeneity of the soil in the forest, which made the abundance of rare microbial communities in the soil to keep relatively stable, and the interaction of rare microbial communities in the soil was not strong. The microbial co-occurrence network reflected not only the interactions between species but

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also the stability of the community (Hernandez et al., 2021). Generally, the networks with more negative interactions have stronger stability, while those with more positive relationships have poorer stability (Herren et al., 2017). Herein, forest and agricultural soil microbial communities had higher negative cohesion and modularity, while industrial and school soil microbial communities had lower negative cohesion and modularity (*Fig. 5*). This further confirmed more stability of microbial communities in forest and agricultural soils. Obviously, land-use styles not only affected the composition and structure of the soil microbial community but also affected its stability by changing the interaction network.

Microbial community assembly was determined by stochastic and deterministic processes (Stegen et al., 2012). Based on the results of our analysis, the microbial communities in the soil of these four land-use types were dominated by deterministic processes (*Fig. 6*). Among them, the effects on microbial communities in the forest by the homogeneous selection and the heterogeneous selection were comparable, while the school soil microbial communities were completely dominated by the heterogeneous selection. In less disturbed forests or grassland soils, stochastic processes often dominated the microbial assembly processes (Zhang et al., 2016). This indicates that the soil microbial communities of the four land-use styles were seriously disturbed, and the school soil microbial community suffered the most serious disturbance. Therefore, soils in different land-use styles had a varied extent of disturbance and were directly reflected in the microbial community of the soil.

Conclusions

In this study, different land-use types both had a significant impact on the richness of abundant species and rare species in soil, while there were differences in the degree of impact. Land-use styles not only affected the composition and structure of the soil microbial community but also affected its stability by changing the interaction network. In addition, deterministic processes, especially homogeneous selection, tended to be more important in shaping the assembly of microbial communities in the soil of different land-use types. This study considerably expanded our understanding of the effects of land use on soil microbial communities. That will provide a scientific basis for sustainable land use management in urban and peri-urban areas.

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APPENDIX

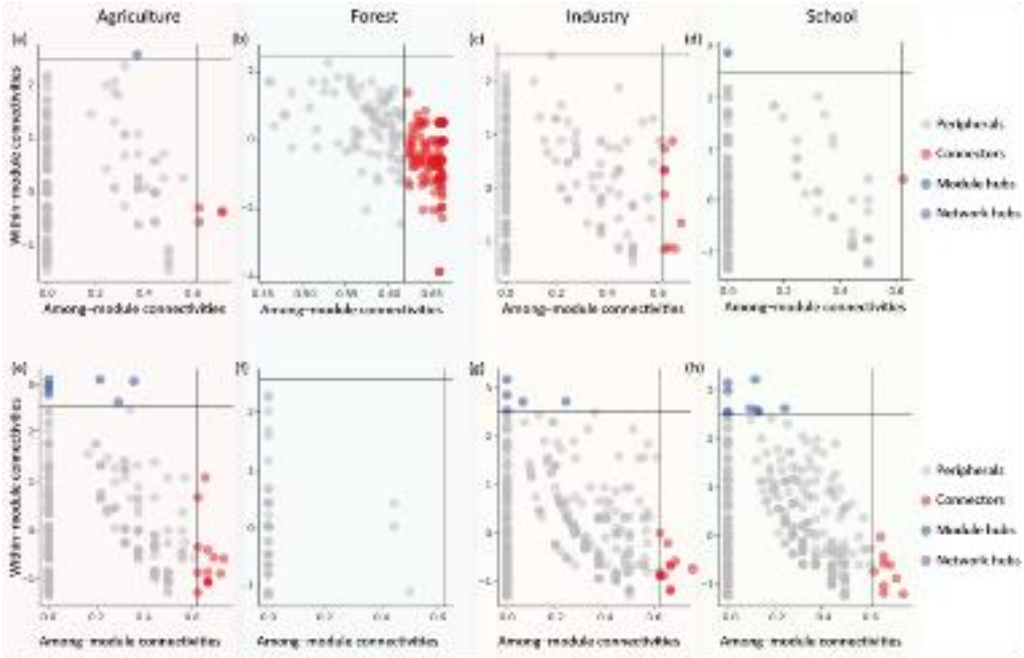

Figure A1. *Z-P plot showing the distribution of rare and abundant ASVs based on their topological roles. Detailed information on connectors and module hubs see Table A1*

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Table A1. *Detailed information on connectors and module hubs*

Categories	Subcommunity	Land-used style	Nodes id	Zi values	Pi values	Phylum
Module hubs	Abundant	Agriculture	ASV_133	2.57	0.37	Proteobacteria
		School	ASV_24	2.88	0.00	Proteobacteria
	Rare	Agriculture	ASV_1407	2.75	0.00	Proteobacteria
			ASV_2575	2.86	0.00	Actinobacteria
			ASV_321	2.58	0.29	Chloroflexi
			ASV_497	3.05	0.00	Actinobacteria
			ASV_570	3.02	0.36	Cyanobacteria
			ASV_666	2.94	0.00	Actinobacteria
			ASV_974	3.05	0.21	Proteobacteria
			ASV_1019	2.72	0.24	Actinobacteria
		Industry	ASV_152	2.85	0.00	Actinobacteria
			ASV_213	3.17	0.00	Actinobacteria
			ASV_262	2.54	0.00	Proteobacteria
			ASV_829	2.71	0.06	Actinobacteria
			ASV_1236	2.97	0.00	Proteobacteria
			ASV_1276	2.54	0.00	Proteobacteria
			ASV_1740	2.61	0.24	Actinobacteria
		School	ASV_323	3.20	0.12	Proteobacteria
			ASV_436	2.54	0.13	Actinobacteria
			ASV_471	2.61	0.10	Proteobacteria
			ASV_569	3.13	0.00	Proteobacteria
			ASV_789	2.57	0.12	Actinobacteria
			ASV_860	2.50	0.00	Proteobacteria
Connectors	Abundant	Agriculture	ASV_126	-0.56	0.63	Proteobacteria
			ASV_37	-0.29	0.63	Proteobacteria
			ASV_47	-0.36	0.72	Actinobacteria
			ASV_618	-0.36	0.72	Planctomycetes
		Forest	ASV_1	0.55	0.66	Proteobacteria
			ASV_10	-1.18	0.65	Actinobacteria
			ASV_108	-0.74	0.63	Actinobacteria
			ASV_118	-0.52	0.63	Actinobacteria
			ASV_121	0.00	0.67	Proteobacteria
			ASV_122	0.55	0.66	Proteobacteria
			ASV_123	0.55	0.64	Proteobacteria
			ASV_125	-0.07	0.63	Proteobacteria
			ASV_128	0.21	0.63	Proteobacteria
			ASV_130	-0.63	0.66	Acidobacteria
			ASV_133	-1.18	0.64	Proteobacteria
			ASV_135	-3.83	0.66	Planctomycetes
			ASV_137	0.55	0.66	Proteobacteria
			ASV_1375	-1.09	0.66	Actinobacteria
			ASV_139	0.55	0.66	Proteobacteria
			ASV_141	-3.83	0.66	Proteobacteria
			ASV_144	-1.92	0.66	Proteobacteria
			ASV_157	0.55	0.64	Actinobacteria
			ASV_159	-1.18	0.62	Proteobacteria
			ASV_166	-1.09	0.66	Planctomycetes
			ASV_168	-1.60	0.66	Proteobacteria
			ASV_17	-0.49	0.64	Proteobacteria
			ASV_170	0.12	0.64	Proteobacteria
			ASV_171	-0.95	0.65	Proteobacteria
			ASV_174	-2.02	0.64	Proteobacteria
			ASV_179	0.55	0.64	Proteobacteria
			ASV_18	-0.07	0.65	Actinobacteria
			ASV_183	-0.63	0.64	Proteobacteria
			ASV_187	-0.09	0.62	Proteobacteria
			ASV_1924	-0.35	0.63	Proteobacteria
			ASV_2	0.00	0.66	Proteobacteria
			ASV_201	-1.18	0.66	Proteobacteria
			ASV_206	-0.55	0.67	Proteobacteria
			ASV_21	0.55	0.66	Actinobacteria

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Categories	Subcommunity	Land-used style	Nodes id	Zi values	Pi values	Phylum
			ASV_210	-1.04	0.64	Proteobacteria
			ASV_214	-0.21	0.63	Proteobacteria
			ASV_216	-1.32	0.66	Actinobacteria
			ASV_22	-0.52	0.66	Proteobacteria
			ASV_223	-1.32	0.66	Proteobacteria
			ASV_23	0.00	0.67	Actinobacteria
			ASV_231	0.55	0.66	Proteobacteria
			ASV_232	-1.09	0.66	Proteobacteria
			ASV_24	0.88	0.64	Proteobacteria
			ASV_243	-0.55	0.66	Proteobacteria
			ASV_244	0.55	0.67	Proteobacteria
			ASV_25	0.55	0.67	Proteobacteria
			ASV_26	0.55	0.67	Proteobacteria
			ASV_269	0.55	0.67	Proteobacteria
			ASV_27	0.55	0.65	Proteobacteria
			ASV_273	-0.09	0.64	Actinobacteria
			ASV_277	-0.63	0.66	Proteobacteria
			ASV_283	-0.09	0.66	Proteobacteria
			ASV_286	0.55	0.66	Proteobacteria
			ASV_293	-0.63	0.64	Proteobacteria
			ASV_296	0.55	0.66	Proteobacteria
			ASV_30	-1.18	0.66	Actinobacteria
			ASV_306	-2.03	0.66	Actinobacteria
			ASV_312	-0.52	0.65	Cyanobacteria
			ASV_322	-1.92	0.66	Proteobacteria
			ASV_326	0.55	0.66	Proteobacteria
			ASV_33	-0.63	0.65	Proteobacteria
			ASV_339	-1.09	0.67	Proteobacteria
			ASV_34	-1.28	0.64	Proteobacteria
			ASV_36	-0.77	0.65	Proteobacteria
			ASV_385	-0.74	0.66	Proteobacteria
			ASV_414	0.77	0.64	Proteobacteria
			ASV_42	0.02	0.65	Actinobacteria
			ASV_43	0.00	0.67	Proteobacteria
			ASV_449	0.55	0.67	Planctomycetes
			ASV_451	0.07	0.63	Proteobacteria
			ASV_455	-0.77	0.66	Chloroflexi
			ASV_47	-0.42	0.66	Actinobacteria
			ASV_487	-0.35	0.65	Proteobacteria
			ASV_488	-0.55	0.66	Proteobacteria
			ASV_498	0.35	0.63	Proteobacteria
			ASV_5	-0.77	0.63	Proteobacteria
			ASV_50	-0.35	0.63	Proteobacteria
			ASV_59	-1.32	0.63	Actinobacteria
			ASV_6	0.55	0.66	Actinobacteria
			ASV_61	-0.21	0.65	Proteobacteria
			ASV_618	0.55	0.67	Planctomycetes
			ASV_62	-0.49	0.64	Actinobacteria
			ASV_67	-0.63	0.63	Proteobacteria
			ASV_675	-0.85	0.66	Proteobacteria
			ASV_69	0.55	0.66	Proteobacteria
			ASV_70	-0.77	0.65	Actinobacteria
			ASV_71	-2.02	0.65	Planctomycetes
			ASV_73	-0.95	0.66	Proteobacteria
			ASV_741	-0.55	0.66	Proteobacteria
			ASV_75	-0.49	0.63	Proteobacteria
			ASV_758	-0.52	0.66	Actinobacteria
			ASV_760	0.00	0.67	Planctomycetes
			ASV_761	-0.52	0.66	Planctomycetes
			ASV_777	-0.31	0.66	Actinobacteria
			ASV_796	0.00	0.66	Actinobacteria
			ASV_8	0.55	0.67	Proteobacteria
			ASV_80	1.42	0.62	Actinobacteria

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Categories	Subcommunity	Land-used style	Nodes id	Zi values	Pi values	Phylum
			ASV_81	0.00	0.66	Proteobacteria
			ASV_820	0.02	0.66	Proteobacteria
			ASV_83	-2.25	0.67	Proteobacteria
			ASV_84	-0.95	0.66	Proteobacteria
			ASV_85	0.00	0.66	Actinobacteria
			ASV_9	-1.49	0.66	Proteobacteria
			ASV_90	0.45	0.63	Proteobacteria
			ASV_92	-0.74	0.66	Proteobacteria
			ASV_931	0.55	0.66	Planctomycetes
			ASV_98	-1.06	0.66	Planctomycetes
			ASV_108	0.33	0.63	Actinobacteria
			ASV_156	-1.16	0.63	Proteobacteria
			ASV_160	-0.67	0.69	Actinobacteria
			ASV_226	-1.15	0.67	Proteobacteria
		Industry	ASV_308	-1.13	0.64	Actinobacteria
			ASV_37	0.88	0.66	Proteobacteria
			ASV_416	-0.13	0.63	Proteobacteria
			ASV_49	0.32	0.63	Acidobacteria
			ASV_57	0.73	0.63	Proteobacteria
		School	ASV_270	0.41	0.63	Proteobacteria
	Rare		ASV_1075	-0.91	0.72	Proteobacteria
			ASV_1183	-1.29	0.63	Acidobacteria
			ASV_1528	-0.37	0.63	Proteobacteria
			ASV_1560	-0.58	0.69	Planctomycetes
			ASV_1653	-0.43	0.67	Proteobacteria
			ASV_1908	-1.08	0.67	Proteobacteria
		Agricultrue	ASV_2060	0.65	0.63	Actinobacteria
			ASV_2156	-0.88	0.67	Actinobacteria
			ASV_2585	-1.08	0.67	Actinobacteria
			ASV_489	-1.08	0.67	Proteobacteria
			ASV_526	-0.60	0.73	Actinobacteria
			ASV_608	1.05	0.66	Proteobacteria
			ASV_895	-0.89	0.63	Planctomycetes
			ASV_1008	-1.18	0.67	Proteobacteria
			ASV_1056	-0.81	0.63	Proteobacteria
			ASV_1116	-0.67	0.67	Proteobacteria
			ASV_185	0.00	0.63	Actinobacteria
			ASV_192	-0.58	0.69	Proteobacteria
			ASV_290	-0.21	0.66	Proteobacteria
		Industry	ASV_396	-0.88	0.63	Actinobacteria
			ASV_519	-0.67	0.67	Proteobacteria
			ASV_584	-0.58	0.72	Proteobacteria
			ASV_788	-0.88	0.64	Proteobacteria
			ASV_876	-1.18	0.67	Proteobacteria
			ASV_923	-0.88	0.63	Actinobacteria
			ASV_109	-0.74	0.63	Chloroflexi
			ASV_1258	-1.04	0.67	Actinobacteria
			ASV_250	-0.58	0.67	Chloroflexi
			ASV_254	-1.21	0.75	Proteobacteria
		School	ASV_3121	-0.89	0.72	Proteobacteria
			ASV_430	-0.61	0.69	Actinobacteria
			ASV_552	-0.03	0.65	Proteobacteria
			ASV_765	-1.19	0.67	Chloroflexi
			ASV_811	-0.43	0.67	Chloroflexi

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