



Microbial community responses to land-use types and its ecological roles in mining area



Enzong Xiao^a, Yuqi Wang^a, Tangfu Xiao^{a,*}, Weimin Sun^c, Jinmei Deng^a, Shiming Jiang^a, Wenjun Fan^a, Jinfeng Tang^a, Zengping Ning^{b,**}

^a Key Laboratory for Water Quality and Conservation of the Pearl River Delta, Ministry of Education, School of Environmental Science and Engineering, Guangzhou University, Guangzhou 510006, China

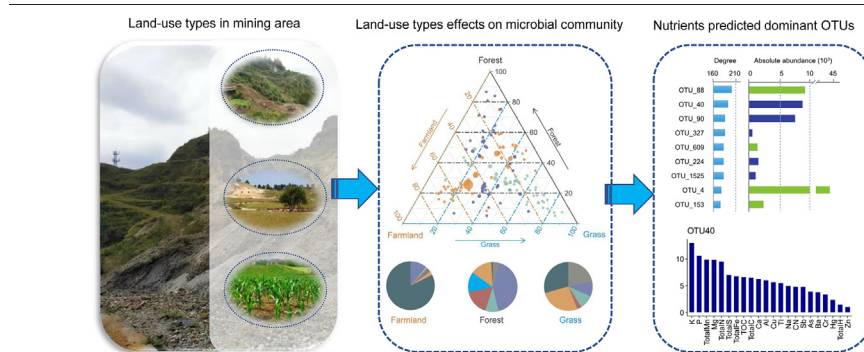
^b State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang 550081, China

^c National-Regional Joint Engineering Research Center for Soil Pollution Control and Remediation in South China, Guangdong Key Laboratory of Integrated Agro-environmental Pollution Control and Management, Institute of Eco-environmental and Soil Sciences, Guangdong Academy of Sciences, Guangzhou 510650, China

HIGHLIGHTS

- Distribution of soil microbiome across land-use types in mining area was examined.
- Land-use types effects on soil bacterial communities and keystone OTUs
- Nutrient contents dominantly predicted changes of soil microbiome across land-use types.
- Soil microbiome maintains nutrient functioning for soil ecological restoration.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 6 January 2021

Received in revised form 5 February 2021

Accepted 5 February 2021

Available online 10 February 2021

Editor: Frederic Coulon

Keywords:

Land-use types
Soil bacterial community
Indicator genera
Co-occurrence network

ABSTRACT

Mining activities result in adverse impacts on soil ecosystems, leading to environmental damage and ecological degradation. Soil microorganisms are considered critical for soil ecosystem restoration. However, questions about how soil microbiomes respond to land-use types and their beneficial roles in soil restoration have received little attention. Here, we collected soils from replicated plots representing three land-use types (forest, grass, and farmland soil) in a mining area to study the distributional pattern of soil microbiome across land-use types and their roles in soil ecological restoration. The results demonstrated that the specific sets of OTUs were divided into three distinct microbial sub-communities, which were thriving across the land-use types, and that this pattern was explained by the nutrient status of the soil samples. We demonstrated that land-use type had a marked influence on the microbial co-occurrence network. We observed that nutrient and metal(loid) parameters, i.e., Tl, Sb, K, P, and Ca, were the main determinants of keystone OTUs, which were linked to network stability. The distribution of microbial taxa is in line with their putative lifestyles, thereby maintaining nutrient cycling across land-use types. This study provides important information on the occurrence and distribution of the soil microbiomes in mining areas and their potentially beneficial roles in soil restoration.

© 2021 Elsevier B.V. All rights reserved.

* Correspondence to: T. Xiao, 230 Waihuanxi Road, Guangzhou, Guangdong, China.

** Correspondence to: Z. Ning, 99 Lincheng Xi Road, Guiyang, Guizhou, China.

E-mail addresses: txiao@gzhu.edu.cn (T. Xiao), ningzengping@mail.gyig.ac.cn (Z. Ning).

1. Introduction

Mining activities result in adverse impacts on the soil ecosystems in mining areas, leading to environmental damage and ecological

degradation. To alleviate such deleterious effects, ecosystem restoration, which aims to establish diverse plant communities that contribute to the recovery of ecosystem functions, has become an essential strategy for mitigating adverse ecological consequences (Barber et al., 2017). Nonetheless, the establishment of diverse plant communities was constrained by soil functions. Microorganisms that inhabit soil ecosystems contribute substantially to a wide range of services, including nutrient cycling (Jing et al., 2020), organic matter decomposition (Shi et al., 2020; Hu et al., 2020), and metal(loid) cycling (Sun et al., 2019; Xiao et al., 2019; Zhang et al., 2019), and thereby influence soil functions. However, there is still unclear about the effects of land use types on soil microbial communities and their beneficial roles on soil restoration. In general, the quality and quantity of carbon supplied by plant litter and root exudates differ across the soils of different land-use types, which results in measurable changes in a set of edaphic factors, such as soil pH, nutrient status, and metal(loid) content (Banerjee et al., 2019; Sun et al., 2020b; Wei et al., 2020). Usually, these factors are identified as strong regulators that are able to alter soil microbial communities (Ma et al., 2020; Poncelet et al., 2014). However, few studies have focused systematic attention on the effect of land-use type-induced changes in these edaphic factors on microbial communities. The main regulator that drives the soil microbial community across land-use types is not clear. For example, are there relationships between changes in edaphic factors introduced by land-use types and the enrichment of specific soil microorganisms across land-use types? If so, what do these relationships have to do with soil restoration functions? Therefore, this study provided a fine-scale dissection of the microbial composition across land-use types to gain an important insight into the distributional pattern of microbial assemblages and their potential roles in soil ecological restoration.

The structure of soil microbiome is important to its ecological functioning (Strogatz, 2001). However, it is challenging to study soil microbiome structures due to the complex and numerous interrelationships among microbial taxa (de Menezes et al., 2014). Recently, works have established that keystone taxa could be a useful tool for gaining insights into the structure of the soil microbiome and its response to environmental changes (de Menezes et al., 2014). It is now well established that the responses of soil microbiomes to environmental factors are facilitated via keystone taxa in mining impacted environments (Aglar et al., 2016). However, studies conducted on the distribution of the keystone taxa across land-use types and their responses to soil ecological restoration in mining area remain unexplored.

Here, we examined the difference in the soil microbial community across three land-use types to investigate the microbial community responses on land-use types and their potential roles in soil restoration. We aimed to address the following questions: (a) Do soils harbor unique bacterial communities across land-use types? (b) Which factor drives the distributional pattern of soil microbiomes across land-use types? (c) Do the dominant taxa have beneficial roles in soil ecological restoration?

2. Materials and methods

2.1. Soil sampling

The sampling site is located a typical Tl—Hg mining area in Guizhou Province, Southwest China. We applied a randomized field design and chose 9 sampling sites with heavily (4 sampling sites) and moderate mining disturbances (5 sampling sites) according to our previous studies (Ning et al., 2020; Ma et al., 2020). At each sampling site, we collected a total of 6 samples from 3 land-use types (farmland soil, forest soil, and grass soil) at different depths (surface (0–10 cm) and bottom (10–20 cm) samples). A total of 54 samples were collected. Each sample was divided into two parts according to their use: one part was used for chemical analysis, and another part was used for microbial analysis. The samples for the chemical and microbial analyses were stored at 4 °C and – 40 °C, respectively.

2.2. Chemical analysis

The freeze-dried samples were thoroughly ground and then passed through a 200-mesh sieve before chemical analysis. Using an elemental analyzer (Vario MACRO cube, Elementar, Hanau, Germany), we tested the contents of total sulfur (TS), total carbon (TC), and total organic carbon (TOC) according to our previous study (Xiao et al., 2016). The samples were digested by using concentrated HF and HNO₃ (1:5, v:v) before trace element analysis (Edgell, 1989). After digestion, an inductively coupled plasma mass spectrometry (ICP-MS, Agilent, 7700×, California, USA) was used to measure the contents of metal(loid)s. To increase the reliability of the measurements, the certified reference materials including SLRS-5 (National Research Council, Canada) and GBW07310 (Chinese soil reference) were used (Xiao et al., 2016).

2.3. Analysis of soil bacterial communities

We employed the FastDNA® spin kit (MP bio, Santa Ana, USA) to extract total genomic DNA from the samples according to the manufacturer's protocol. The bacterial V4–V5 regions were amplified with primers 515f/907r (Kuczynski et al., 2012). High-throughput sequencing was performed on an Illumina MiSeq platform at Ecogene Bioinformatics Company (Shenzhen, China). Using FLASH, the raw reads were merged (Magoč and Salzberg, 2011) and then filtered by QIIME (Quantitative Insights into Microbial Ecology) (V1.7.0) (Bokulich et al., 2013). The raw sequence was obtained by comparing with the GOLD database. Next, we used UCHIME (http://www.drive5.com/usearch/manual/uchime_algo.html) to remove chimeric sequences (Haas et al., 2011). Using UPARSE with a criterion of 97% similarity, we obtained the operational taxonomic units (OTUs). The phylogenetic taxonomy of OTUs was assigned by using the RDP classifier and Greengenes (Wang et al., 2007).

2.4. Statistical analysis

With the packages “tidyverse” and “DESeq2” in R software, we analyzed the enrichment of the differentially abundant OTUs in farmland, forest, and grass soils (Robinson et al., 2010). OTUs with relative abundances >0.5% were chose to construct three co-occurrence networks across the farmland soil, forest soil, and grass soil samples (Xiao et al., 2021). The procedures for constructing co-occurrence network were followed previous studies conducted by Barberán et al. (2014) and Delgado-Baquerizo et al. (2018). The visualization of co-occurrence networks was performed in Gephi software (Bastian et al., 2009). Finally, the properties of the network were obtained from Gephi with default parameters. Keystone taxa, i.e., taxa that have a large influence in a community (Barberán et al., 2012; Lauber et al., 2013), confer high connectivity and thus can be indicators of microbial community shifts (Herren and McMahon, 2018). In the current study, the keystone species were classified as those that accounted for the highest average degree (top 1%) (Fan et al., 2018; Fisher and Mehta, 2014). To determine the relative importance of environmental predictors for microbial attributes such as diversity and keystone species, we employed random forest analysis with the randomForest package (version 3.0.2) (<http://cran.r-project.org/>) (Breiman, 2001; Trivedi et al., 2016) and rfPermute package (Delgado-Baquerizo et al., 2018) in R statistical software. The indicator taxa across three land-use types were identified by using the indicspecies package in R statistical software (Team, 2013).

3. Results

3.1. Geochemical parameters

In the current study, the results showed that edaphic factors demonstrate distinct ranges across land-use types. For example, metal(loid)s, such as Hg, Tl, and As, were significantly enriched in the farmland and

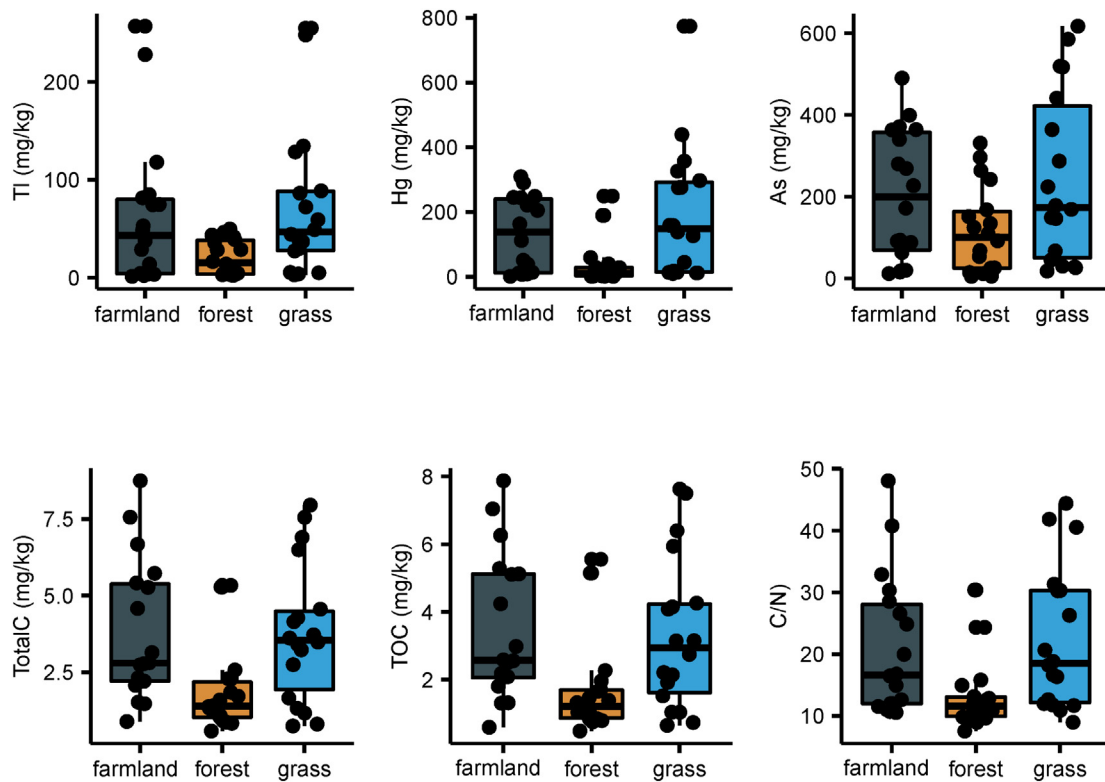


Fig. 1. Distributional pattern of geochemical parameters across land-use types.

grass soil samples compared with the forest soil samples (Fig. 1). Nutrient parameters, such as total C, TOC, total S, and C/N, were significantly enriched in the farmland soil and grass soil samples compared with the forest soil samples (Table S1). In addition, total N was significantly enriched in the farmland soil samples compared with the forest soil samples. Notably, we also identified diverse associations between edaphic factors. For example, the metal(loid)s (Hg, TI, and As) were significantly correlated with the total C, TOC, total S, C/N, Ba, Al, total S, and total Fe ($p < 0.05$) (Fig. S2). In addition, Hg was significantly correlated to total N and Ca; As was correlated with total Mn and P; and Ca was correlated with total N, total C, and TOC ($p < 0.05$) (Fig. S2).

3.2. Microbial diversity and dominant phyla across land-use types

According to the random forest analysis, edaphic factors, including Ca, K, total N, Mg, C/N, and total S, were important predictors of bacterial diversity (Fig. 2). Specifically, Ca was the most important predictor of the microbial diversity indices including Chao1 and Shannon. In addition, total N, Mg, C/N, and total S were the most important predictors of these diversity indices. In this study, we found diverse and significant

associations between edaphic factors and diversity indices (Fig. 2). For example, the Shannon index was significantly correlated with As, total N, total S, Ca, and Mg; the Chao1 and ACE indices were significantly related to total S, C/N, Ca, and Mg (Fig. S3).

3.3. Taxonomic features across land-use types

The taxonomic assignments revealed that *Proteobacteria*, *Acidobacteria*, and *Firmicutes* were the dominant phyla in the current study (Fig. 3). We used a linear model analysis to examine microbial diversification and identify significantly enriched OTUs across the land-use types. There were 47, 42, and 50 enriched OTUs in the farmland, forest, and grass soil samples, respectively (Fig. 4A). The phylum-level taxonomic assignments revealed that the bacteria in the farmland soil samples were consisted to *Acidobacteria*, *Proteobacteria*, and *Actinobacteria*. The samples from the forest soils were dominated by *Proteobacteria*, *Chloroflexi*, and *Actinobacteria*. The samples from the grass soil were dominated by *Acidobacteria*, *Actinobacteria*, and *Verrucomicrobia* (Fig. 4B). PERMANOVA showed that the distributional pattern of the microbial composition was significantly altered by mining

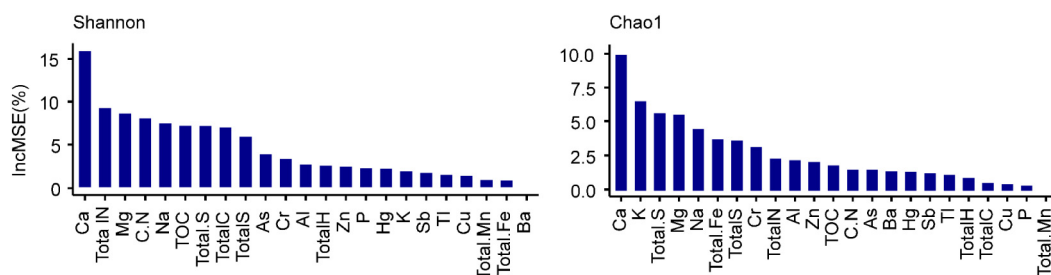


Fig. 2. Random Forest analysis of microbial diversity indices (Chao1 and Shannon) predicted by nutrients and metal(loid)s.

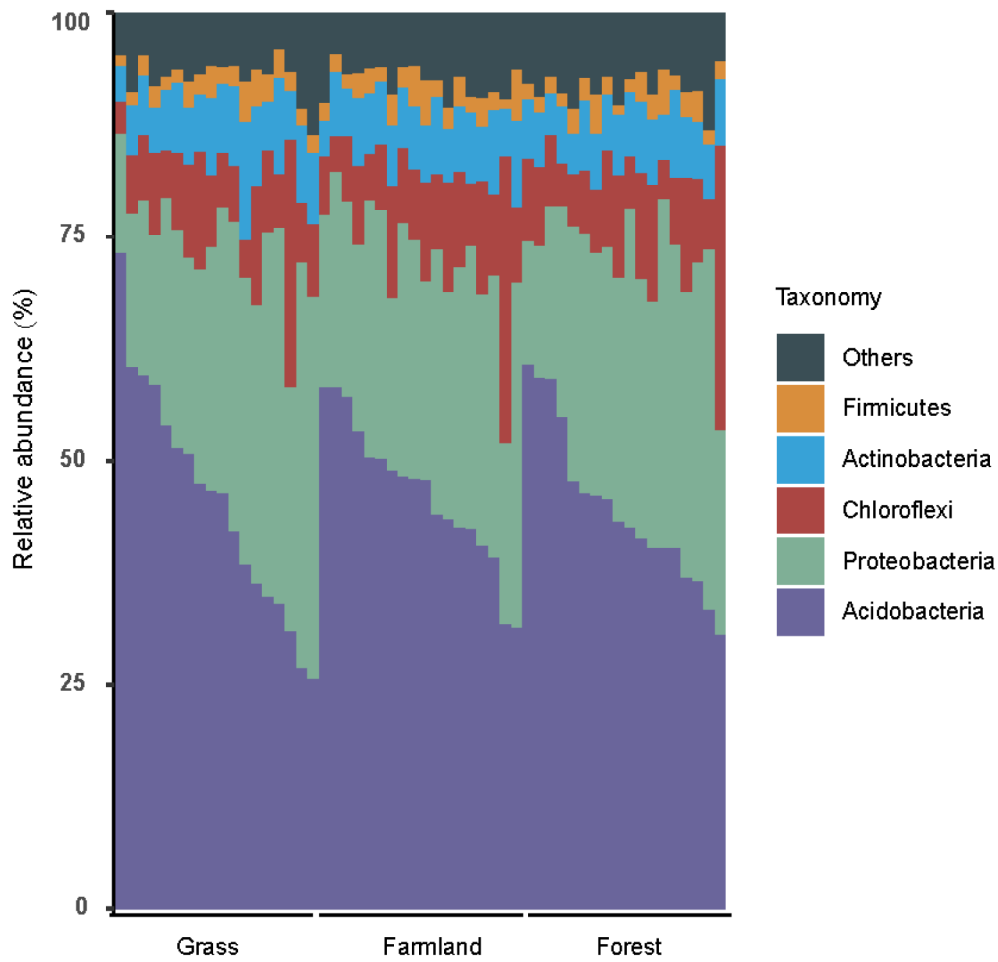


Fig. 3. Distributional pattern of dominant phyla across grass, farmland, and forest soil ecosystem.

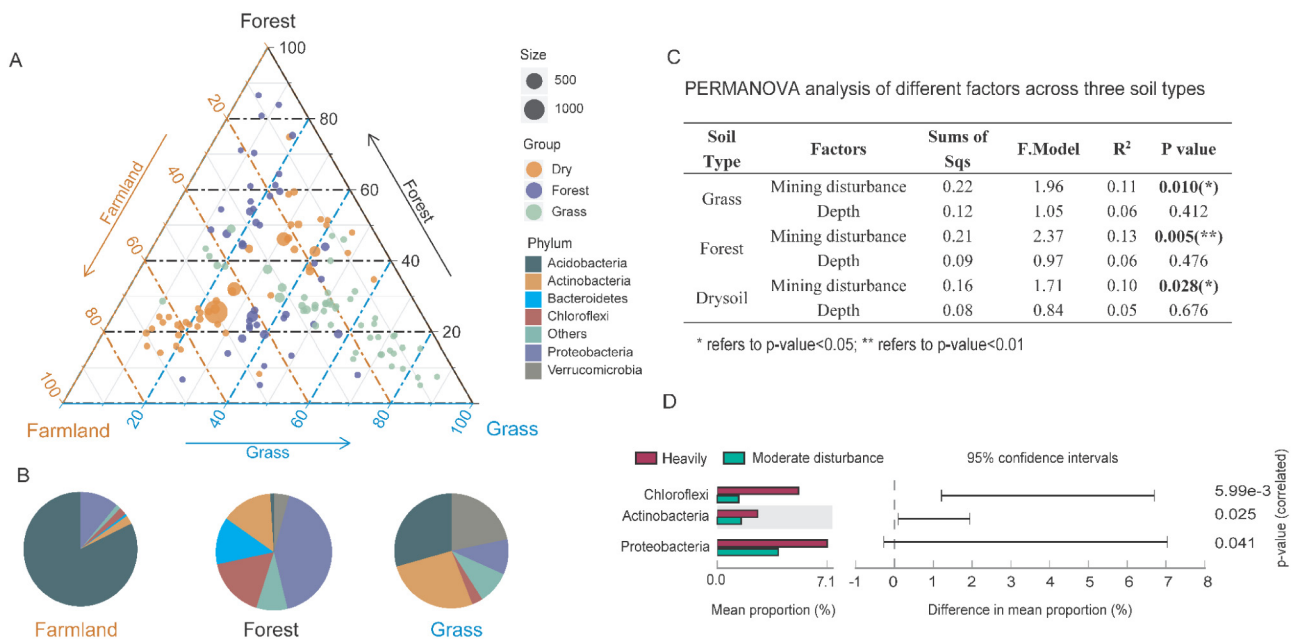


Fig. 4. Distributional pattern of microbial community across Forest, farmland, and grass soils. (A) the distribution of dominant OTUs across land-use types; (B) taxonomic composition of enriched OTUs across land-use types; (C) PERMANOVA analysis to detect the contributions of different factors to microbial community; (D) The significant different of dominant phyla between extensively and less mining disturbance soils.

disturbance (Fig. 4C). Consistently, the distributional patterns of these phyla were influenced by mining disturbance. For example, we found that in the forest soils, *Chloroflexi* was significantly enriched in areas with heavy mining disturbances compared to areas with less disturbance. Furthermore, in the farmland soils, *Proteobacteria* was significantly enriched in areas with heavy mining disturbances compared to areas with less disturbance. *Acidobacteria* and *Proteobacteria* in the grass soil samples were significantly enriched in the surface soil compared with the lower soil (Fig. 4D).

3.4. Bacterial co-occurrence network structures and keystone taxa across land-use types

In the current study, we constructed three bacterial networks (one for each land-use type). The constructed networks displayed distinct differences in their topological parameters. The farmland, forest, and grass soil networks consisted of 41,535, 47,851, and 43,270 edges (associations between taxa), respectively (Fig. 5). The average degree and closeness centrality parameters appeared to be higher in the forest soil network than in the other two networks. In contrast, the betweenness centralization and diameter appeared to be lower in the forest soil network than in the other two networks (Fig. 5). We identified 9 keystone OTUs for each land-use type in this study. These OTUs were taxonomically affiliated with different phyla. Specifically, *Acidobacteria* and *Proteobacteria* were dominant in the farmland

and grass soil network structures, and *Acidobacteria*, *Proteobacteria*, *Chloroflexi*, and *Firmicutes* were dominant in the forest soil network (Fig. 5). The random forest analysis revealed that the environmental parameters of K, P, Mn, Mg, and Sb best explained the distributional pattern of the keystone taxa in the farmland soil ecosystems; K, P, Mn, and Sb best explained the occurrence of the keystone taxa in the forest soil ecosystems; and Tl, total N, total C, and Ca best explained the distributional pattern of the keystone taxa in the grass soil ecosystems (Fig. 6).

3.5. Distributional pattern of indicator genera across land-use types

Prior study showed that indicator taxa could be useful for predicting microbial community responses to specific environmental conditions (Bier et al., 2015). In the current study, we identified indicator species to study their responses to different land-use types. For the farmland soil ecosystems, the indicator genera consisted of *Aquicola*, *Rickettsiaceae*, and *Roseococcus* (Fig. 7). The indicator genera of the grass soil ecosystem were *Chthoniobacter*, *Pedospaera*, *Labrys*, *Bradyrhizobium*, *Sorangium*, and *Proteiniborus*. The indicator genus of the forest soils was *Paracoccus*. Notably, we found that the distributional patterns of these genera were also influenced by mining disturbance. *Aquicola* was significantly enriched in heavily disturbed soils, whereas *Proteiniborus* was significantly enriched in moderately disturbed mining areas ($p < 0.05$) (Fig. 7).

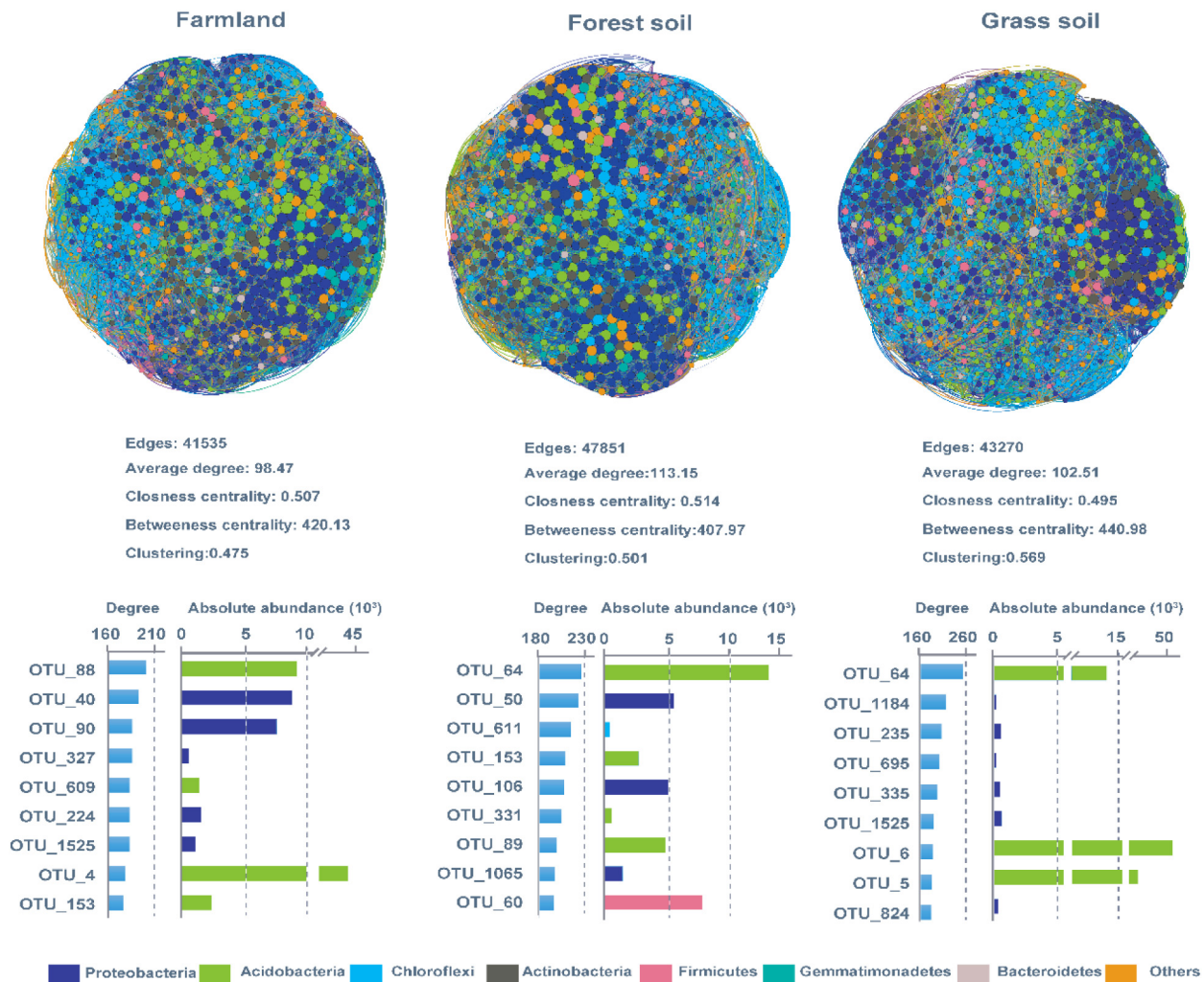


Fig. 5. Microbial co-occurrence network across land-use types. The parameters of structure of networks (Edges, average degree, closeness centrality, betweenness centrality, and clustering) were shown. The top 10 degree of OTUs and their absolute abundance were show (each OTUs were colored by phyla).

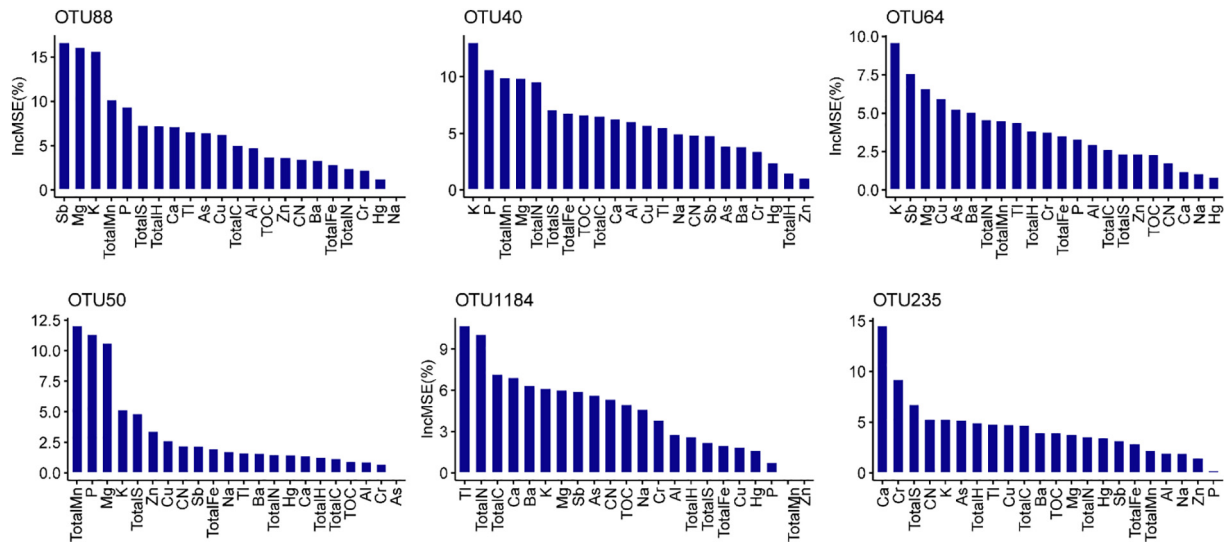


Fig. 6. Random Forest analysis of dominant OTUs (Listed on Fig. 5) predicted by nutrients and metal(loid)s parameters.

4. Discussion

4.1. Land-use type effects on microbial communities

The specific sets of OTUs (with relative abundances >0.05%) were divided into three distinct microbial subcommunities, which thrived across the land-use types. This observation indicates that land-use type exerted a crucial role in recruiting soil microorganisms. The distinctiveness of the soil microbiome was also found in prior studies across land-use types (Dassen et al., 2017; Schlatter et al., 2015). Existing evidence indicates that the distinctive distributional patterns of soil microbial communities are likely to be related to differences in plant species across land-use types (Dassen et al., 2017; Schlatter et al., 2015). Generally, root exudates secreted from plants can change the status of edaphic factors, and microbial communities can be sensitive to these changes (Broeckling et al., 2008; Shahzad et al., 2015). We identified distinctly different nutrient statuses across the three land-use types studied, with a significantly higher relative concentration of nutrients, such as TC, TOC, and C/N, in the farm and grass soils than in the forest soils (Fig. 1). We assume that variations in the nutrient status of the soil samples could explain the differential responses of soil microbiomes to the land-use types. We see support for this idea, as there is a significant relationship between the microbial diversity indices and measured nutrient parameters (Fig. S2). Furthermore, the

random forest analysis demonstrated that bacterial community composition is mainly predicted by nutrient parameters, such as Ca, K, total N, total C, TOC, and Mg (Fig. 2). Likewise, the prevalence of the dominant bacterial taxonomic groups is reflected in the changes in soil nutrient status occurring across land-use types. For example, the taxonomic assignments of the dominant OTUs at the phylum level revealed that *Acidobacteria* was significantly enriched in both the farmland and grass soil samples compared with the forest soil samples, whereas *Proteobacteria* was enriched in the forest soil samples (Fig. 4B). The phyla *Acidobacteria* and *Proteobacteria* are considered abundant and ubiquitous bacterial phyla and are typically found in diverse mining impacted environments, such as agricultural soils (Zhang et al., 2020a), forest soils (Shi et al., 2015), peat soils (Sun et al., 2014), tailing soils (Xiao et al., 2019), and river system (He et al., 2020; Wang et al., 2020). *Acidobacteria* has been reported to be a versatile heterotroph with an oligotrophic (more K-selected) lifestyle (de Castro et al., 2013; Yao et al., 2017), whereas *Proteobacteria* has been reported to be a fast-growing bacterium with the ability to utilize a variety of carbon sources (i.e., a copiotroph) (Yao et al., 2017). The enrichment of *Acidobacteria* in the farmland and grass soil samples was consistent with its capacity to colonize nutrient-limited soils, in which this phylum contributes to enhancing soil nutrients (de Castro et al., 2013; Yao et al., 2017). In this study, we hypothesized that across land-use types, soil microbial community structure would change with soil depth and

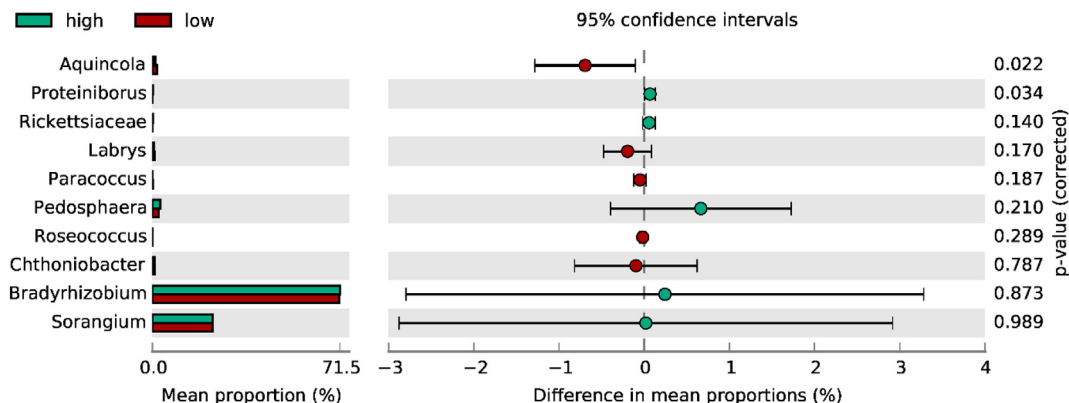


Fig. 7. Distribution of indicator genera from different land-use types and their difference between extensive and less mining disturbance ($p < 0.05$), high refers heavily disturbance and low refers moderate disturbance.

mining-induced disturbances, which involve several soil perturbations (Kane et al., 2020; Zhao et al., 2019). Using PERMANOVA, we tested the contributions of soil depth and mining disturbances to the distributional patterns of the bacterial communities within three land-use types (Fig. 4C). The results showed that the microbial communities were strongly driven by mining disturbance within land-use types, irrespective of the soil depth. Consistently, we found that *Proteobacteria*, and *Chloroflexi* were significantly enriched from sites heavily disturbed by mining (Fig. 4D). This variation is consistent with the soil chemistry data, which shows that there are higher metal(loid)s and lower nutrient contents in areas with heavily mining disturbances than in areas with moderate mining disturbances. Taken together, these results raise the possibility that mining disturbance-induced environmental stresses influence the selective enrichment of soil microbiota within each land-use type.

4.2. Land-use type effects on the microbial co-occurrence network

Soil microorganisms form complex association networks, which are important for understanding the structure of microbial communities and their responses to environmental changes (de Menezes et al., 2014). Given the differences in the edaphic factors among the three land-use types, it is reasonable to suggest that the network structures are distinct across the land-use types. Indeed, we observed that the samples from the forest soil ecosystem have many more highly connected taxa (nodes) than the farmland or grass soil samples, which indicates that the forest soil ecosystem harbors a more complex microbial network (de Vries et al., 2018). Evidence has shown that complex networks are more robust than simple networks to environmental perturbations (Anje-Margriet et al., 2007; Shade et al., 2012). Therefore, we deduced that the microbial communities in the forest soil ecosystems, which had more complex networks, are more resilient than those in the other ecosystems to environmental stresses. This deduction is rational because the nutrient contents in the farmland and grass ecosystems were higher than that in the forest ecosystem (Fig. 1). Typically, elevated nutrient contents foster the growth of some microbes and results in lower selection pressure for other microbes (Button, 1985). In contrast, low nutrient contents could act as a selective force on the assembly of the soil microbiome and increase the chance for coevolution (Button, 1985).

Keystone taxa are thought to frequently interact with other taxa, thereby playing critical roles in maintaining the stability of co-occurrence networks (Herren and McMahon, 2018). We found that the distributional patterns of the keystone OTUs differed among the land-use types. Therefore, it is reasonable to suggest that land-use type can manipulate the assembly of microbes in soil ecosystems. This is consistent with prior studies conducted across 10 landscapes (Barnett et al., 2019). Importantly, we observed that nutrient and metal(loid) parameters, i.e., Tl, Sb, K, P, and Ca, were the main determinants of keystone OTUs, which are linked to network stability (Fig. 6). Given that mining disturbances could significantly influence the statuses of soil nutrients and metal(loid)s within land-use types (Fig. 1), it is reasonable to propose that mining disturbances can modulate the soil co-occurrence networks in each land-use type. Intriguingly, we demonstrated that the relative abundance of the individual OTUs is inconsistent with their importance in the soil microbial network. For instance, OTU_88, OTU_50, and OTU_64 were characterized as having the highest degrees in the farmland, forest, and grass soil samples, respectively; however, none of these OTUs were among the top 20 most abundant OTUs in any of the networks. A similar pattern has previously been observed in human (Tapio et al., 2017) and plant (van der Heijden and Hartmann, 2016) microbiome networks. These facts remind us that low-abundance microorganisms should not be neglected in ecological restorations. Interestingly, we found that OTU_64 was the most well-connected node in both the forest soil and grass soil ecosystems. The consistent identification of OTU_64 as a keystone OTU across land-use

types suggests its vital roles in manipulating the soil microbiome. The taxa in OTU_64 belong to the *Solibacterales* order, which was also characterized as a keystone group by Xue et al. (2017) in karst rocky desertification areas. Members of the *Solibacterales* in soils are considered indicators of soil degradation (Soman et al., 2017) and they can participate in the biogeochemical cycling of phosphorus (P) in alpine soil ecosystems (Sun et al., 2020a). *Solibacterales* is also capable of chitin degradation, which is involved in carbon and nitrogen cycling in soil ecosystems (Hui et al., 2020). The capacity of *Solibacterales* species to perform key biogeochemical nutrient processes may explain their central role as keystone species in the microbial networks of areas with mining disturbances. Nonetheless, it is important to bear in mind that the identification of the keystone OTUs was based on the analysis of correlations (associations) among the OTUs. Future studies are now needed to verify the impact of keystone taxa on microbiome composition and functioning (Herren and McMahon, 2018; Paine, 2010).

4.3. Distribution of indicator genera and their roles in nutrient cycling

Recent evidence recognized that microbial indicators could represent specific environmental settings and the responses of the taxa to environmental conditions (Chen et al., 2020; Guo et al., 2018). The indicator genera identified herein overlap with those identified in previous studies of diverse land-use types, such as forest (Sun et al., 2014), tilling (Xiao et al., 2019), and agricultural soils (Zhang et al., 2020a), suggesting that factors driving the assembly of the soil microbiome may be common across diverse land-use types. Although the taxonomy of the indicator genera changed greatly across the three land-use types, we found that most of these indicator genera were involved in nutrient cycling. For example, members of *Paracoccus*, an indicator genus of the forest soil, have been widely identified as aerobic denitrifying bacteria (Zhang et al., 2020b) and therefore participate in nitrogen recycling in terrestrial ecosystems. In addition, *Paracoccus* can also perform chemolithotrophic carbon fixation (Ye et al., 2020). Similarly, some indicator genera from grass and farmland soils, including *Labrys* and *Bradyrhizobium*, are assigned to the phylum *Proteobacteria* and have been suggested to be involved in nutrient cycling. *Bradyrhizobium* was found to minimize oxidative stress and enhance nitrogen fixation in particular plants (Rodrigues et al., 2013). *Labrys* has been suggested to solubilize phosphate minerals and improve IAA production activities from soils under sugarcane cultivation (Rosangela et al., 2012). These examples suggest that the distribution of soil taxa across land-use types is in line with their putative lifestyles, which helps to maintain nutrient cycling in nutrient-poor soil ecosystem disturbed by mining.

5. Conclusion

Soil microorganisms contribute substantially to a wide range of services and thereby improve recovery in ecosystem restoration. However, there is relatively limited information on how microbial communities respond to land-use types with different intensities of mining disturbance and their potential roles in supporting soil restoration in mining areas. Here, we examined the distributional patterns of soil bacterial communities across three land-use types. We showed that land-use types strongly regulated microbial attributes, including diversity indices, dominant taxa, co-occurrence network structure, and keystone OTUs. We found that the occurrence of soil taxa is in line with their putative lifestyles, which thereby maintains soil nutrient functioning for ecological restoration. This study provides important information on the occurrence and distribution of the soil microbiome across land-use types in mining areas and their potential beneficial roles in soil restoration.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.145753>.

CRedit authorship contribution statement

Enzong Xiao: Writing – original draft, Writing – review & editing, Investigation. **Yuqi Wang:** Resources, Writing – review & editing. **Tangfu Xiao:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Weimin Sun:** Writing – review & editing. **Jinmei Deng:** Writing – review & editing. **Shiming Jiang:** Formal analysis, Writing – review & editing. **Wenjun Fan:** Writing – review & editing. **Jinfeng Tang:** Writing – review & editing. **Zengping Ning:** Writing – review & editing, Project administration.

Declaration of competing interest

The authors declare that they have no current or potential competing financial interests.

Acknowledgement

This research was funded by the National Natural Science Foundation of China (41807127, 41830753, U1612442) and the Science and Technology Planning Project of Guangzhou (No. 202002020072).

References

- Agler, M., Ruhe, J., Kroll, S., Morhenn, C., Kim, S., Weigel, D., Kemen, E., 2016. Microbial hub taxa link host and abiotic factors to plant microbiome variation. *PLoS Biol.* 14 (1), e1002352.
- Anje-Margriet, N., Johan, A.P.H., Johan, V.K., Guido, H., An, Vos, Coen, K., Frank, Berendse., Peter, C.R., 2007. Reconciling complexity with stability in naturally assembling food webs. *Nature* 449 (7162), 599–602.
- Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A., Gattinger, A., Keller, T., Charles, R., van der Heijden, M., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. *ISME J* 13 (7), 1722–1736.
- Barber, N.A., Chantos-Davidson, K.M., Amel Peralta, R., Sherwood, J.P., Swingle, W.D., 2017. Soil microbial community composition in tallgrass prairie restorations converge with remnants across a 27-year chronosequence. *Environ. Microbiol.* 19 (8), 3118–3131.
- Barberán, A., Bates, S., Casamayor, E., Fierer, N., 2012. Using network analysis to explore co-occurrence patterns in soil microbial communities. *ISME J* 6 (2), 343–351.
- Barberán, A., Casamayor, E., Fierer, N., 2014. The microbial contribution to macroecology. *Front. Microbiol.* 5, 203.
- Barnett, S.E., Youngblut, N.D., Buckley, D.H., 2019. Soil characteristics and land-use drive bacterial community assembly patterns. *FEMS Microbiol. Ecol.* 96 (1), 194.
- Bastian, M., Heymann, S., Jacomy, M., 2009. Gephi: an open source software for exploring and manipulating networks. Third international AAAI conference on weblogs and social media 3, 1.
- Bier, R., Voss, K., Bernhardt, E., 2015. Bacterial community responses to a gradient of alkaline mountaintop mine drainage in Central Appalachian streams. *ISME J* 9 (6), 1378–1390.
- Bokulich, N., Subramanian, S., Faith, J., Gevers, D., Gordon, J.I., Knight, R., Mills, D., Caporaso, J., 2013. Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. *Nat. Methods* 10 (1), 57–59.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45 (1), 5–32.
- Broeckling, C., Broz, A., Bergelson, J., Manter, D., Vivanco, J., 2008. Root exudates regulate soil fungal community composition and diversity. *Appl. Environ. Microbiol.* 74 (3), 738–744.
- Button, D.K., 1985. Kinetics of nutrient-limited transport and microbial growth. *Microbiol. Rev.* 49 (3), 270–297.
- Chen, Q., Ding, J., Zhu, D., Hu, H., Delgado-Baquerizo, M., Ma, Y., He, J., Zhu, Y., 2020. Rare microbial taxa as the major drivers of ecosystem multifunctionality in long-term fertilized soils. *Soil Biol. Biochem.* 141, 107686.
- Dassen, S., Cortois, R., Martens, H., de Hollander, M., Kowalchuk, G., van der Putten, W., de Deyn, G., 2017. Differential responses of soil bacteria, fungi, archaea and protists to plant species richness and plant functional group identity. *Mol. Ecol.* 26 (15), 4085–4098.
- de Castro, V., Schroeder, L., Quirino, B., Kruger, R., Barreto, C., 2013. Acidobacteria from oligotrophic soil from the Cerrado can grow in a wide range of carbon source concentrations. *Can. J. Microbiol.* 59 (11), 746–753.
- de Menezes, A., Prendergast-Miller, M., Richardson, A., Toscas, P., Farrell, M., Macdonald, L., Baker, G., Wark, T., Thrall, P., 2014. Network analysis reveals that bacteria and fungi form modules that correlate independently with soil parameters. *Environ. Microbiol.* 17 (8), 2677–2689.
- de Vries, F.T., Griffiths, R.I., Bailey, M., Craig, H., Girlanda, M., Gweon, H.S., Hallin, S., Kaisermann, A., Keith, A.M., Kretzschmar, M., Lemanceau, P., Lumini, E., Mason, K.E., Oliver, A., Ostle, N., Prosser, J.I., Thion, C., Thomson, B., Bardgett, R.D., 2018. Soil bacterial networks are less stable under drought than fungal networks. *Nat. Commun.* 9 (1), 3033.
- Delgado-Baquerizo, M., Reith, F., Dennis, P., Hamonts, K., Powell, J., Young, A., Singh, B., Bissett, A., 2018. Ecological drivers of soil microbial diversity and soil biological networks in the southern hemisphere. *Ecology* 99 (3), 583–596.
- Edgell, K., 1989. USEPA Method Study 37 SW-846 Method 3050 Acid Digestion of Sediments, Sludges, and Soils. US Environmental Protection Agency, Environmental Monitoring Systems Laboratory, Washington, DC, USA.
- Fan, K., Weisenhorn, P., Gilbert, J., Chu, H., 2018. Wheat rhizosphere harbors a less complex and more stable microbial co-occurrence pattern than bulk soil. *Soil Biol. Biochem.* 125, 251–260.
- Fisher, C., Mehta, P., 2014. Identifying keystone species in the human gut microbiome from metagenomic timeseries using sparse linear regression. *PLoS One* 9 (7), e102451.
- Guo, J., Liu, W., Zhu, C., Luo, G., Kong, Y., Ling, N., Wang, M., Dai, J., Shen, Q., Guo, S., 2018. Bacterial rather than fungal community composition is associated with microbial activities and nutrient-use efficiencies in a paddy soil with short-term organic amendments. *Plant Soil* 424, 335–349.
- Haas, B., Gevers, D., Earl, A., Feldgarden, M., Ward, D., Giannoukos, G., Ciulla, D., Tabbaa, D., Highlander, S., Sodergren, E., 2011. Chimeric 16S rRNA sequence formation and detection in sanger and 454-pyrosequenced PCR amplicons. *Genome Res.* 21 (3), 494–504.
- He, C., Zhang, B., Lu, J., Qiu, R., 2020. A newly discovered function of nitrate reductase in chemoautotrophic vanadate transformation by natural mackinawite in aquifer. *Water Res.* 189, 116664.
- Herren, C., McMahon, K., 2018. Keystone taxa predict compositional change in microbial communities. *Environ. Microbiol.* 20 (6), 2207–2217.
- Hu, Y., Zheng, Q., Noll, L., Zhang, S., Wanek, W., 2020. Direct measurement of the in situ decomposition of microbial-derived soil organic matter. *Soil Biol. Biochem.* 141, 107660.
- Hui, C., Jiang, H., Liu, B., Wei, R., Zhang, Y., Zhang, Q., Liang, Y., Zhao, Y., 2020. Chitin degradation and the temporary response of bacterial chitinolytic communities to chitin amendment in soil under different fertilization regimes. *Sci. Total Environ.* 705, 136003.
- Jing, X., Chen, X., Fang, J., Ji, C., Shen, H., Zheng, C., Zhu, B., 2020. Soil microbial carbon and nutrient constraints are driven more by climate and soil physicochemical properties than by nutrient addition in forest ecosystems. *Soil Biol. Biochem.* 141, 107657.
- Kane, J., Morrissey, E., Skousen, J., Freedman, Z., 2020. Soil microbial succession following surface mining is governed primarily by deterministic factors. *FEMS Microbiol. Ecol.* <https://doi.org/10.1093/femsec/iaa114>.
- Kuczynski, J., Stombaugh, J., Walters, W., González, A., Caporaso, J., Knight, R., 2012. Using QIIME to analyze 16S rRNA gene sequences from microbial communities. *Curr. Protocbioinform.* 36, 10.7.1–10.7.20.
- Lauber, C., Ramirez, K., Aanderud, Z., Lennon, J., Fierer, N., 2013. Temporal variability in soil microbial communities across land-use types. *ISME J* 7 (8), 1641–1650.
- Ma, L., Xiao, T.F., Ning, Z.P., Liu, Y.Z., Chen, H.Y., Peng, J.Q., 2020. Pollution and health risk assessment of toxic metal(loid)s in soils under different land use in sulphide mineralized areas. *Sci. Total Environ.* 724, 138176.
- Magoč, T., Salzberg, S., 2011. FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics* 27 (21), 2957–2963.
- Ning, Z.P., Liu, E.G., Yao, D.J., Xiao, T.F., Ma, L., Liu, Y.Z., Li, H., Liu, C.S., 2020. Contamination, oral bioaccessibility and human health risk assessment of thallium and other metal (loid)s in farmland soils around a historic Ti-hg mining area. *Sci. Total Environ.* 758, 143577.
- Poncelet, D., Cavender, N., Cutright, T., Senko, J., 2014. An assessment of microbial communities associated with surface mining-disturbed overburden. *Environ. Monit. Assess.* 186 (3), 1917–1929.
- Robinson, M., McCarthy, D., Smyth, G., 2010. edgeR: a Bioconductor package for differential expression analysis of digital gene expression data. *Bioinformatics* 26 (1), 139–140.
- Rodrigues, A., Bonifacio, A., Antunes, J., Silveira, J., Figueiredo, M., 2013. Minimization of oxidative stress in cowpea nodules by the interrelationship between Bradyrhizobium sp. and plant growth-promoting bacteria. *Appl. Soil Ecol.* 64, 245–251.
- Rosangela, N., Inui-Kishi, L., Kishi, S., Picchi, J., Lemos, M., 2012. Phosphorus solubilizing and IAA production activities in plant growth promoting rhizobacteria from Brazilian soils under sugarcane cultivation. *ARPN J Engineer Appl Sci* 7, 1446–1454.
- Schlatter, D., Bakker, M., Bradeen, J., Kinkeel, L., 2015. Plant community richness and microbial interactions structure bacterial communities in soil. *Ecology* 96 (1), 134–142.
- Shade, A., Peter, H., Allison, S., Baho, D., Berga, M., Buergermann, H., Handelsman, J., 2012. Fundamentals of microbial community resistance and resilience. *Front. Microbiol.* 3, 417.
- Shahzad, T., Chenu, C., Genet, P., Barot, S., Perveen, N., Mougin, C., Fontaine, S., 2015. Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species. *Soil Biol. Biochem.* 80, 146–155.
- Shi, C., Wang, C., Xu, X., Huang, B., Wu, L., Yang, D., 2015. Comparison of bacterial communities in soil between nematode-infected and nematode-uninfected Pinus massoniana pinewood forest. *Appl. Soil Ecol.* 85, 11–20.
- Shi, J., Zhang, B., Cheng, Y., Peng, K., 2020. Microbial vanadate reduction coupled to co-metabolic phenanthrene biodegradation in groundwater. *Water Res.* 186, 116354.
- Soman, C., Li, D., Wander, M., Kent, A., 2017. Long-term fertilizer and crop-rotation treatments differentially affect soil bacterial community structure. *Plant Soil* 413 (1–2), 145–159.
- Strogatz, S., 2001. Exploring complex networks. *Nature* 410 (6825), 268–276.
- Sun, H., Terhonen, E., Koskinen, K., Paulin, L., Kasanen, R., Asiégub, F., 2014. Bacterial diversity and community structure along different peat soils in boreal forest. *Appl. Soil Ecol.* 74, 37–45.

- Sun, W., Sun, X., Li, B., Häggblom, M., Han, F., Xiao, E., Zhang, M., Wang, Q., Li, F., 2019. Bacterial response to antimony and arsenic contamination in rice paddies during different flooding conditions. *Sci. Total Environ.* 675, 273–285.
- Sun, H., Wu, Y., Zhou, J., Bing, H., Chen, Y., Li, N., 2020a. Labile fractions of soil nutrients shape the distribution of bacterial communities towards phosphorus recycling systems over elevation gradients in Gongga Mountain, SW China. *Eur. J. Soil Biol.* 98, 103185.
- Sun, T., Wang, Y., Hui, D., Jing, X., Feng, W., 2020b. Soil properties rather than climate and ecosystem type control the vertical variations of soil organic carbon, microbial carbon, and microbial quotient. *Soil Biol. Biochem.* 148, 107905.
- Tapio, I., Fischer, D., Blasco, L., Tapio, M., Vilkkii, J., 2017. Taxon abundance, diversity, co-occurrence and network analysis of the ruminal microbiota in response to dietary changes in dairy cows. *PLoS One* 12 (7), e0180260.
- Team, R., 2013. R: A Language and Environment for Statistical Computing.
- Trivedi, P., Delgado-Baquerizo, M., Trivedi, C., Hu, H., Anderson, I., Jeffries, T., Zhou, J., Singh, B., 2016. Microbial regulation of the soil carbon cycle: evidence from gene-enzyme relationships. *ISME J* 10, 2593–2604.
- van der Heijden, M., Hartmann, M., 2016. Networking in the plant microbiome. *PLoS Biol.* 14 (2), e1002378.
- Wang, Q., Garrity, G., Tiedje, J., Cole, J., 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl. Environ. Microbiol.* 73 (16), 5261–5267.
- Wang, Z., Zhang, B., He, C., Shi, J., Guo, J., 2020. Sulfur-based mixotrophic vanadium (v) bio-reduction towards lower organic requirement and sulfate accumulation. *Water Res.* 189, 116655.
- Wei, G., Li, M., Shi, W., Tian, R., Chang, C., Wang, Z., Wang, N., Zhao, G., Gao, Z., 2020. Similar drivers but different effects lead to distinct ecological patterns of soil bacterial and archaeal communities. *Soil Biol. Biochem.* 144, 107759.
- Xiao, E., Krumins, V., Xiao, T., Dong, Y., Tang, S., Ning, Z., Huang, Z., Sun, W., 2016. Depth-resolved microbial community analyses in two contrasting soil cores contaminated by antimony and arsenic. *Environ. Pollut.* 221, 244–255.
- Xiao, E., Ning, Z., Xiao, T., Sun, W., Qiu, Y., Zhang, Y., Chen, J., Gou, Z., Chen, Y., 2019. Variation in rhizosphere microbiota correlates with edaphic factor in an abandoned antimony tailing dump. *Environ. Pollut.* 253, 141–151.
- Xiao, E.Z., Ning, Z.P., Sun, W.M., Jiang, S.M., Fan, W.J., Ma, L., Xiao, T.F., 2021. Thallium shifts the bacterial and fungal community structures in thallium mine waste rocks. *Environ. Pollut.* 268, 115834.
- Xue, L., Ren, H.D., Li, S., Leng, X.H., Yao, X.H., 2017. Soil bacterial community structure and co-occurrence pattern during vegetation restoration in Karst rocky desertification area. *Front Microbiol* 8, 2377.
- Yao, F., Yang, S., Wang, Z., Wang, X., Ye, J., Wang, X., DeBruyn, J., Feng, X., Jiang, Y., Li, H., 2017. Microbial taxa distribution is associated with ecological trophic cascades along an elevation gradient. *Front. Microbiol.* 8, 2071.
- Ye, J., An, N., Chen, H., Ying, Z., Zhang, S., Zhao, J., 2020. Performance and mechanism of carbon dioxide fixation by a newly isolated chemoautotrophic strain *Paracoccus denitrificans* PJ-1. *Chemosphere* 252, 126473.
- Zhang, B., Wang, S., Diao, M., Fu, J., Xie, M., Shi, J., Liu, Z.Q., Jiang, Y.F., Cao, X.L., Borthwick, A.G.L., 2019. Microbial community responses to vanadium distributions in mining geological environments and bioremediation assessment. *J. Geophys. Res. Biogeosci.* 124, 601–615.
- Zhang, D., Cui, R., Fu, B., Yang, Y., Wang, P., Mao, Y., Chen, A., Lei, B., 2020a. Shallow groundwater table fluctuations affect bacterial communities and nitrogen functional genes along the soil profile in a vegetable field. *Appl. Soil Ecol.* 146, 103368.
- Zhang, H., Li, S., Ma, B., Huang, T., Qiu, H., Zhao, Z., Huang, X., Liu, K., 2020b. Nitrate removal characteristics and ¹³C metabolic pathways of aerobic denitrifying bacterium *Paracoccus denitrificans* Z195. *Bioresour. Technol.* 307, 123230.
- Zhao, X., Huang, J., Lu, J., Sun, Y., 2019. Study on the influence of soil microbial community on the long-term heavy metal pollution of different land use types and depth layers in mine. *Ecotox. Environ. Safe* 170, 218–226.