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Variation in rhizosphere microbiota correlates with edaphic factor in an abandoned antimony tailing dump☆

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ABSTRACT

The distribution pattern of root-associated bacteria in native plant growth in tailing dumps with extreme conditions remains poorly understood and largely unexplored. Herein we chose a native plant, *Bidens bipinnata*, growing on both an Sb tailing dump (WKA) and adjacent normal soils (WKC) to in-depth understand the distribution pattern of root-associated bacteria and their responses on environmental factors. We found that the rhizosphere microbial diversity indices in the tailing dump were significantly different from that in the adjacent soil, and that such variation was significantly related with soil nutrients (TC, TOC, TN) and metal(loid) concentrations (Sb and As). Some dominant genera were significant enriched in WKA, suggesting their adaption to harsh environments. Notably, these genera are proposed to be involved in nutrient and metal(liod) cycling, such as nitrogen fixing (*Devosia*, *Cellvibrio*, *Lysobacter*, and *Cohnella*), P solubilizing (*Flavobacterium*), and Sb and As oxidation (*Paenibacillus*, *Bacillus*, *Pseudomonas*, and *Thiobacillus*). Our results suggest that certain root-associated bacteria in tailing dump were governed by soil edaphic factors and play important ecological roles in nutrient amendments and metal cycling for the successful colonization of *Bidens bipinnata* in this tailing dump.

1. Introduction

Mine tailings are the materials remaining after the extraction of economically valuable minerals from ores (Diaby et al., 2007). Mine tailings pose significant risks to the environment and humans due to highly concentrations of toxic metal(loid)s (Dybowska et al., 2006). Over 10 billion tons of mine tailings were discharged worldwide annually (Adiansyah et al., 2015). China is the largest antimony (Sb)- producing country in the world, and most of which the resulting tailings are deposited in tailing dumps without any treatment (Pan et al., 2014). Revegetation, which creates a vegetation cap on a tailing dump, is regarded as the most promising method to relieve the contamination introduced by mine tailings (Lee et al., 2014; Lam et al., 2017). However, plants growth is severely inhibited in tailing dump due to the environmental stress of oligotrophic and elevated contents of metal(liod)s (Mendez and Maier, 2008; Wang et al., 2017).

The interface between microbes and plant roots is considered to greatly influence the growth and survival of plants (Ma et al., 2011). Therefore, alternative phytoremediation methods that exploit rhizosphere bacteria to reduce environmental stress to plants have been investigated. Recent studies showed that root associated bacteria could relieve the adverse impact of nutrients deficiency, metal(liod)s contamination, and facilitate plant growth in soils (Ahkami et al., 2017). For example, rhizosphere bacteria provide essential nutrients for plants, via fixing nitrogen from atmosphere (Ahemad and Kibret, 2014), or solubilizing immobile minerals such as P- and K-feldspar (Oteino et al., 2015). In addition, some root-associated bacteria serve to immobilize metals within the rhizosphere. For example, *Agrobacterium* encoding gene *aioA* rapidly

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oxidize As(III) and Sb(III) to As(V) and Sb(V) (Li et al., 2016), respectively, in plant roots. The generated Sb(V) or As(V) could subsequently sequester Fe/Mn hydroxide/oxyhydroxide precipitates in rhizosphere soil, which reduce Sb/As uptake into plants (He et al., 2018). These studies showed that plants evolve specific survival strategies associated with specialist rhizosphere microbiota to harsh environments in soils. Therefore, exploiting the composition of rhizosphere bacteria inhabiting within native plants is a prerequisite for revegetation of tailing dumps.

However, the existing data on the rhizosphere microbiota associated with tailing dumps is still scarce. Recently, high-throughput sequencing approaches have provided insights into rhizosphere bacteria communities in mine tailings in practical tailing phytostabilization. Namely, Yang et al. (2017) revealed remarkable changes in microbial community composition following tailing phytostabilization. Li et al. (2015b) also found that organotrophic microorganisms were significantly enriched (Li et al., 2015b) and iron- and sulfur-oxidizing bacteria (especially *Leptospirillum* and *Acidithiobacillus*) were less abundant in revegetated tailing compared with bare tailings after 3 years of phytostabilization (Li et al., 2016). These studies have provided a way to understand rhizosphere microbiomes in tailing dumps. However, questions concern how environmental stress affects the root microbial community remain unknown.

Previous studies showed that soil characteristics play vital roles in regulating rhizosphere microbial community (Philippot et al., 2013). In the current study, soil characteristics in tailing dump was significantly different with its adjacent undisturbed soils. It is reasonable hypothesized that native plants growing in tailing dump have evolved distinct rhizosphere microbial community from its adjacent normal soil. To address these questions, we chose a native plant *Bidens bipinnata* growing both in an Sb tailing dump and its adjacent undisturbed soil to uncover their root-associated microbiome by high-throughput sequencing. *Bidens bipinnata* is a native plant that grows in the tailing dumps near Dushan Sb mining areas from southern Guizhou Province, Southwest China, but was not detected four years ago, suggesting that these plants can cope with the environmental stress in tailing dumps and grow there. Through comparative studies of the rhizosphere bacterial composition between the two sampling sites, we provide insights into the environmental stress on the root microbiome in a tailing dump and gain insights into the roles of rhizosphere microorganisms on plant surviving in a tailing dump.

2. Materials and methods

2.1. Site description and sampling

Two sampling sites in the Xiaohe tailing dump (E 105°30′23″, N 25°31′28″), located in Guizhou Province, Southwest China were selected in May 2016. One sampling site (WKA) is located within the tailing dump, which has been receiving tailing deposits from the Banpo Sb mine since June 2006. Another sampling site is from adjacent undisturbed forest soil (WKC), which is less affected by anthropogenic activity. At each site, we employed a randomized field design and chose 20 sampling points where *Bidens bipinnata* had a similar height. After shaking off soil that lightly adhered to root, a total of ~20 g rhizosphere soil samples were collected. At each sampling site, we obtained a composited sample which mixed from 3 pseudoreplicates. After collection, samples were shipped back to laboratory with ice packs (4 °C). Each sample was then divided into two parts: one for microbial analysis and the other for chemical analysis. Notably, the sample for microbial analysis was stored at −40 °C until DNA extraction.

2.2. Chemical analysis

All soil samples for chemical analysis were freezen-dried for 48 h. Prior to grounding the sample, gravel, plant roots, and leaves were removed by passing through a 2-mm sieve. After then, the soils were passed through a 200-mesh sieve after thoroughly ground by using an agate mortar. For soil pH determination, 10 g of ground soils were mixed with 25 ml MQ water in 50 ml Erlenmeyer flask. After then, the soil pH was tested by using a calibrated HACH HQ30d pH meter (HACH, Loveland, USA).

To measure nitrate and sulfate concentration in soil, 10 g of ground soil sample was mixed with 50 ml M. Q water in a 100-ml Erlenmeyer flask, and then the slurry was shaken for 5 min, followed by 4 h of equilibration. After centrifuging at 3500 rpm for 10 min, the supernatants were filtered through a 0.45-μm membrane. Using ion chromatography (DIONEX ICS-40, Sunnyvale, CA, USA), contents of sulfate and nitrate were determined. Nutrient elements including total carbon (TC), total nitrogen (TN), total sulfur (TS), total hydrogen (TH), and soluble sulfur (SS) were directly tested by using an elemental analyzer (vario MACRO cube, Elementar, Hanau, Germany). Prior to analysing total organic carbon (TOC), the inorganic carbon was removed by using 10% HCl. For the determination of trace elements, soil samples were fully digested with HNO_3 and HF (5:1, v/v), after then the trace elements were tested by ICP-MS (Agilent, 7700x, California, USA) (Edgell, 1989). Certified reference of SLRS-5 (National Research Council, Canada) was used for accuracy testing for ICP-MS. The standard soil reference material (GBW07310) was employed for quality control (Xiao et al., 2016b).

2.3. Analysis of Sb and As contaminant fractions

The technique used to measure the citric acid-extractable Sb and As redox species (M(III)-C and M(V)-C, M stands Sb or As) was previously reported (Fuentes et al., 2003). Specifically, 0.2 g of ground soil was mixed with 10 ml of 100 mM citric acid (pH: 2.08), and then the slurry was shaken for 60 min, followed by 4 h of equilibration at room temperature. After centrifuging at 3500 rpm for 30 min, the supernatants were filtered through a 0.45-μm membrane. Using HG-AFS (AFS-920, Jitian, Beijing), contents of Sb(III) and As(III) in the soil supernatants were directly tested. Prior to analysing total Sb and As, the sample need to be pre-reduced by 5% ascorbic acid, and 2.5 ml of 5% thiourea. The detailed procedures were reported by our previous study (Xiao et al., 2016b). The contents of Sb(V) and As(V) in soil were calculated from the difference between the total Sb and As and Sb(III) and As(III), respectively. The geochemical fractionations of Sb and As were determined followed a five-stage sequential extraction scheme which reported by Wenzel et al. (2001) and Gault et al. (2003). The reaction conditions, reagents, and reaction time of each fraction are summarized in Table S1. The supernatant was obtained and filtered through a 0.45-μm membrane after each stage of extraction. And then, the contents of Sb and As were analyzed by ICP-MS (Agilent, 7700x, California, USA). In this study, we chose M_{tot}, M_{exe}, M_{srp}, M(III)-C, and M(V)-C to represent the metal(loid) contaminant fractions (Xiao et al., 2016b).

2.4. High-throughput sequencing of the V4 region of 16S rRNA genes

Total genomic DNA was extracted from 0.25 g of well-mixed soil by using the MP FastDNA® spin kit (MP bio, Santa Ana, USA) according to the manufacturer's protocol. After then, the concentration and purity of the extracted DNA were determined by running on a 1% agarose gel. We amplified V4-V5 hypervariable regions of

16S rRNA genes by using the primer pair 515f/907r (515f:5′-GTGYCAGCMGCCGCGGTAA-3′,907r:5′- CYCAATTCMTTTRAGTTT-3′) (Kuczynski et al., 2012). The purified PCR amplicons were then performed on Illumina MiSeq platform (Novogene Bioinformatics Company, Beijing, China). Using FLASH, the paired-end reads were merged together (Magoč and Salzberg, 2011). The merged reads were then assigned samples based on barcodes. The raw reads were filtered by using split_libraries_fastq.py in QIIME (V1.7.0), and the detail criteria were previous reported (Bokulich et al., 2013). Using UCHIME (http://www.drive5.com/usearch/manual/uchime_algo.html), we removed chimeric sequences after comprising with the GOLD database (Haas et al., 2011). Using chimera filtering approach of UPARSE, Operational taxonomic units (OTUs) (97% similarity) were clustered (Edgar et al., 2011). The RDP classifier (Version 2.2, http://sourceforge.net/projects/rdp-classifier/) (Wang et al., 2007) and the Green Genes database (http://greengenes.lbl.gov/cgi-bin/nph-index.cgi) were used to assign phylogenetic taxonomy. The 16S rRNA dataset was deposited into the NCBI Sequence Read Archive under accession number PRJNA549982.

2.5. Statistical analysis

In the current study, we used both weighted and unweighted UniFrac distances to determine the similarity of microbial communities between the two sampling sites (Kuczynski et al., 2012). Principal Coordinate Analysis (PCoA) based on UniFrac distance was used to better visualize the complex multidimensional data (Lozupone et al., 2011). We used statistical two sided T tests to detect the difference of microbial indices between two sampling sites, including alpha diversity (Shannon and Simpson indices), richness (ACE and the Chao1 estimator), and evenness (Ling et al., 2013), with p values < 0.05 considered statistically significant. We used PAST software to perform similarity of percentages analysis (SIMPER) (Li et al., 2018). We then used classification random forest (RF) analysis to identify the main environmental predictors for microbial attributes in soils (Trivedi et al., 2016). In the current study, Sb/As contaminant fractions and nutrient elements were served as predictors to the dominant genera. Percentage increases in the MSE (mean squared error) of variables was then applied to estimate the importance of these microbial attributes (Breiman, 2001).

To further explore their impact on individual OTUs, we used network analysis to reveal the interplay between environmental variables and specific OTUs. In this study, two co-occurrence networks were constructed to visualize the correlation between OTUs and contamination fractions. For the first network, we selected the 100 most abundant OTUs with strong ($|r|>0.6$) and significant ($p < 0.05$) correlations. For the second one, we chose the 1000 most abundant OTUs and 10 contaminant fractions, and only correlations related to the contaminant fractions were chosen. The correlations were visualized when they met the following criteria: (i) the r values between each node were larger than 0.8 and 0.6 for WKC and WKA, respectively, and (ii) the correlations were statistically significant ($p < 0.05$). A modular structure can be explored from a co-occurrence network. Nodes in each module are highly interconnected with each other but less connected to nodes in other modules, which suggest that nodes within a same module may pose similar functions(Sun et al., 2018b). The interactive platform Gephi was applied to visualize the co-occurrence networks (Newman, 2003, 2006).

3. Results

3.1. Variation in soil properties between two sites

Geochemical analysis showed that soil samples from the tailing dump contained a significantly higher concentration of sulfate, total S, and C/N than the adjacent soil, while the adjacent soil contained significantly higher concentrations of total N, total C, and TOC than the tailing dump soil ($n = 40$, $p < 0.05$, *t*-test) (see Fig. S1 and Table S2 for detailed information). There is no significant different between the two soils with respect to pH, Fe_{tot} and Fe(II) (Table S2). Significantly higher concentrations of Sb_{tot} and As_{tot} were observed in tailing dumps than in adjacent soils ($n = 40$, $p < 0.001$, *t*-test, Table S3). Specifically, Sb_{tot} averaged 1021 ± 599 mg/kg in WKA and 34.9 ± 9.8 mg/kg in WKC, and As_{tot} averaged 109.6 ± 7.8 mg/kg in WKA and 4.88 ± 0.49 mg/kg in WKC (Fig. 1 and Table S3). Bioaccessible Sb and As (i.e., the easily

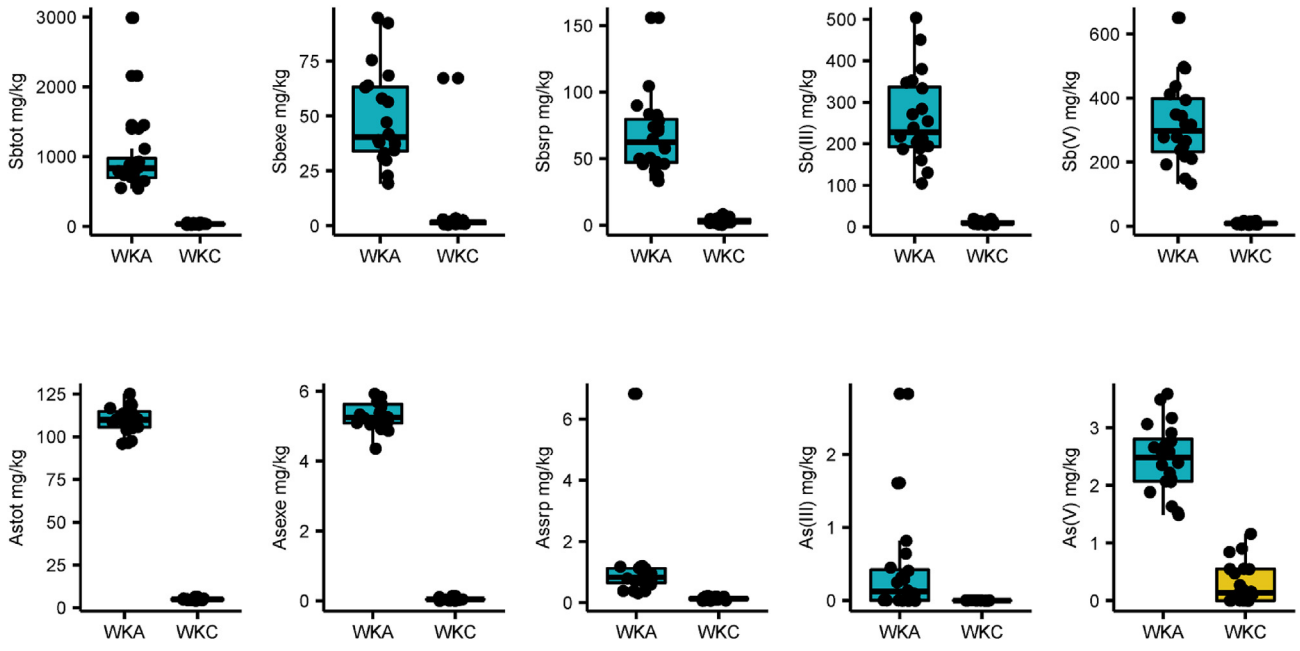

Fig. 1. Distribution of metal(loid)s and their bioavailable fractions between tailing dump (WKA) and adjacent soil (WKC).

exchangeable fraction (M_{exe}) and specifically sorbed surface-bound fraction (M_{srp})) together accounted for less than 40% and 15% of Sb_{tot} and As_{tot} in all samples, respectively. In this study, citric acid-extractable Sb (Sb(III)-C and Sb(V)-C) and As (As(III)-C and As(V)-C) fractions were also regarded as bioaccessible fractions and accounted for a small portion of M_{tot} in the current study (Table S4). It is notable that all Sb/As contaminant fractions were significantly higher in WKA than in WKC (Table S3, *t*-test, $p < 0.05$), whereas nutrient elements in WKA were significantly lower than those in WKC, indicating oligotrophic and high metal(loid) geochemical conditions in this tailings.

3.2. Changes in microbial diversity

A total of 11,439,522 high-quality sequences were obtained for 40 soil samples from two sampling sites, and they were analyzed with a mean of 285,988 reads per sample (ranging from 123,746 in sample WKC08-2 to 513,440 in sample WKA05-1) (Table S5). After quality filtering and target extraction, a mean of 103,518 and 92,412 valid sequences for WKA and WKC remained for community analysis, respectively. These reads were clustered into 398,244 OTUs (Table S6). The alpha diversity indices, including observed species, Shannon, and Simpson, and the richness estimators (ACE and the Chao1 estimator) demonstrated a significant site-specific pattern in which alpha diversity in undisturbed soil is much higher than that in the tailing dump (Table S7, $p < 0.05$). A distinctly different pattern between the tailing dump and its adjacent undisturbed soil was observed by PCoA (Fig. 2B). Within a single habitat (tailing dump or adjacent undisturbed soil), the close clustering of samples indicated that there was similar community composition, whereas strong compositional variability was found between sampling sites. This result was further confirmed by the unweighted pair group method with arithmetic mean (UPGMA) (Fig. 2A), which showed that the bacterial community structures between sampling sites were significantly different.

3.3. Comparison between two groups

A Venn diagram indicated that a small proportion (19%) of bacteria was uniquely identified in WKC, whereas 48% were uniquely identified in WKC. Another relatively large proportion of OTUs (33%) were shared by both study sites (Fig. 3A). The relative abundances of the top 30 abundant OTUs in WKA and WKC were significantly different (Fig. S2). The average relative abundance of the ten most abundant microbial species exhibited different relative abundances between two sampling sites (Fig. 4). For example, at the phylum level, *Proteobacteria* and *Firmicutes* were significantly enriched in soil samples from the tailing dump, whereas *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Verrucomicrobia*, *Planctomycetes*, *Gemmatimonadetes*, and *Nitrospirae* were enriched in the adjacent undisturbed soils ($p < 0.05$, *t*-test). No significant difference was found for *Bacteroidetes* between two soils. At the genus level, the

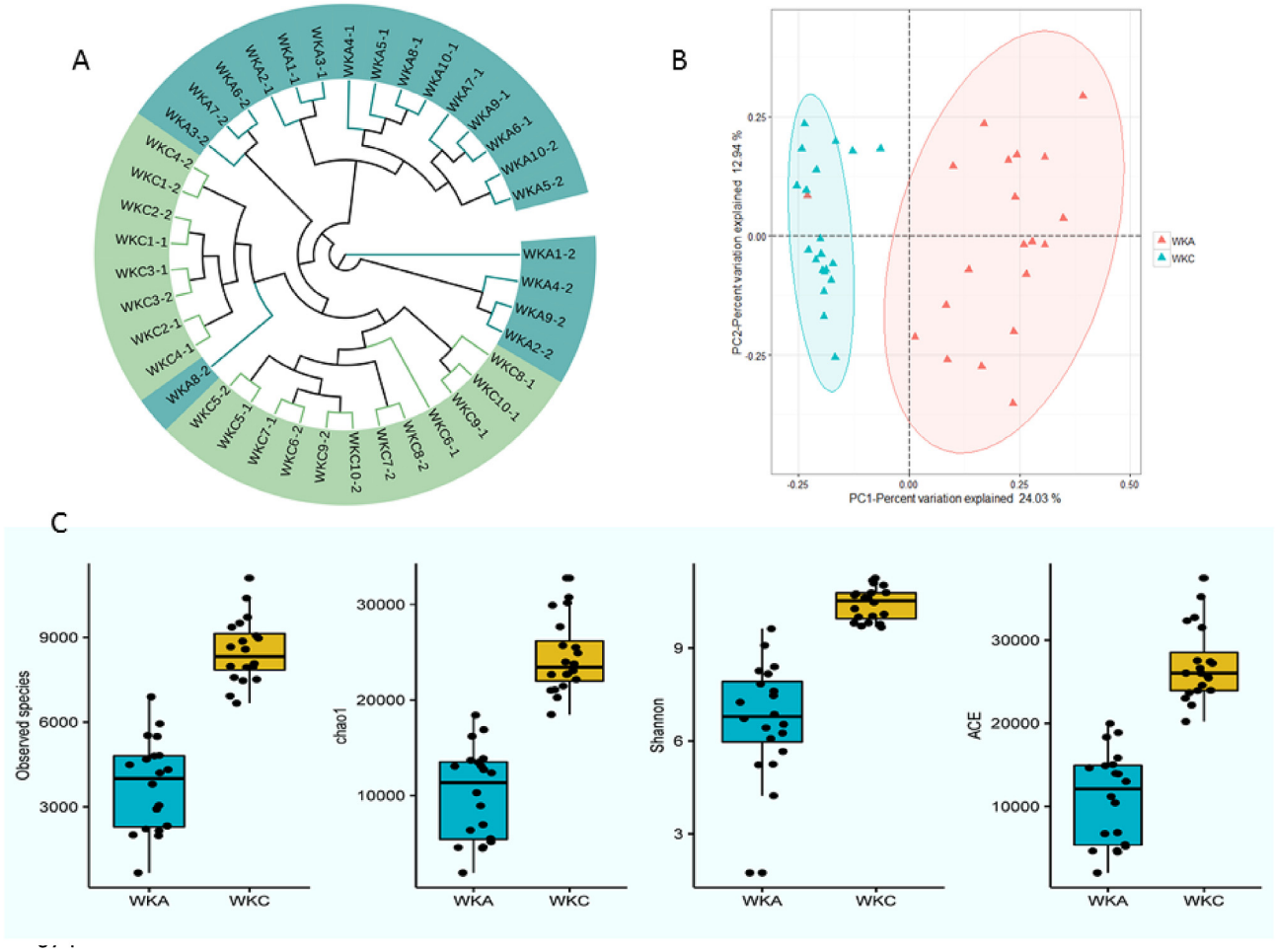

Fig. 2. Overall microbial community composition in WKA and WKC were revealed by (A) UPGMA; (B) ordination plots of PCoA results; (C) barplot of alpha diversity indices (including Observed species, Chao1, Shannon, and ACE) between WKA and WKC.

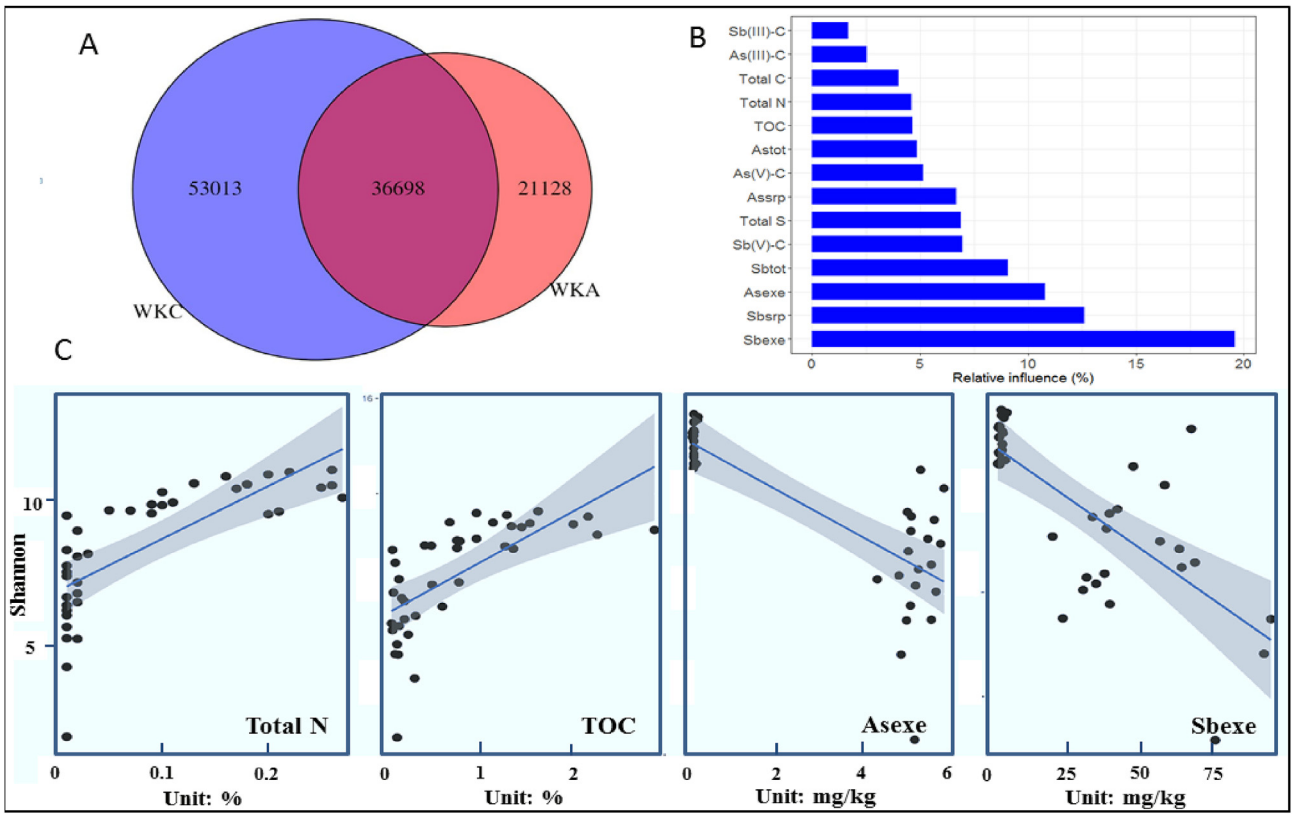

Fig. 3. Overall microbial community distribution response to environment variables (A) Venn diagram for the OTUs in WKA and WKC; (B) random forest analysis of environmental parameters for samples from WKA; (C) Correlation between shannon indices and typical environmental variables (including Total N, TOC, As_{exe}, and Sb_{exe}).

abundant genera also demonstrated differences between the two sites. For instance, *Pseudomonas* and *Sphingobium* were significantly enriched in the tailing dump, while *Janthinobacterium* and *Rhodoplanes* were significantly enriched in the adjacent soils. Interestingly, *Bacilli*, *Lysobacter*, *Sphigomonas*, *Flavobacterium*, *Cellvibrio*, and *Paenisporosarcina* were not significantly different between the two sites (Fig. 4).

3.4. Interactions between bacterial community composition and environmental parameters

Using regression analysis, we found that sulfate, total S, C/N, and C/H were negatively correlated with alpha diversities and richness (as quantified by parameters including the Chao1, observed species, Shannon index, ACE, Simpson index, and PD whole tree) ($p < 0.05$). In contrast, total N, total C, TOC, and total H were positively correlated with alpha diversities and richness (Fig. 3C and Table S8). Remarkably, all ten Sb and As contaminant fractions were negatively correlated with alpha diversity indices and richness estimators (Fig. 3C and Table S9). Random forest analysis was employed to further quantify the relative influence of each environment variable (Fig. 3B). The analysis showed that Sb_{exe}, Sb_{srp}, As_{exe}, Sb_{tot}, and Sb(III)-C were classified as the top five environmental factors that most influenced the microbial community in WKA.

3.5. The dominant genera shared between two sampling sites

The abundant OTUs and genera from rhizosphere soil in WKA were also detected in WKC but with different relative abundances (Figs. 3A and 4). Hence, taxa shared within the microbial communities of either WKA or WKC were determined. Dominant shared genera were defined at more or >1% mean relative abundance (Gobet et al., 2010). The dominant shared genera among the WKA sampling points were *Agrobacterium*, *Bacillus*, *Cellvibrio*, *Cohnella*, *Corynebacterium*, *Devosia*, *Flavobacterium*, *Lysobacter*, *Methylotenera*, *Mycoplana*, *Paenibacillus*, *Paenisporosarcina*, *Pedobacter*, *Pseudomonas*, *Sphingobium*, *Yonghaparkia*, and *Janthinobacterium* (Fig. 5). It is notable that all dominant shared genera in WKA were rarely shared in WKC. Five rare shared genera in WKA were dominantly shared among the WKC sampling points, namely *DA101*, *Janthinobacterium*, *Kaistobacter*, *Rhodoplanes*, and *Variovorax* (Fig. 5).

Similarity of percentages analysis (SIMPER) based on average Bray-Curtis dissimilarity was used to determine the relative contribution of an individual genus to the dissimilarity between communities between tailing dump and its adjacent soils. The top 30 genera were responsible over 50% cumulative dissimilarity for the microbial community shift (Fig. 6A). Among them, *Pseudomonas* had the largest dissimilarity contribution (6.25%), followed by *Sphingobium* (5.76%), *Bacillus* (5.39%), *Lysobacter* (4.26%), *Cellvibrio* (3.14%), *Sphingomonas* (3.08%), *Flavobacterium* (2.97%), and *Janthinobacterium* (2.94%) (Table S10). Notably, all these genera were significantly enriched in WKA (Fig. 6B).

To disentangle the potential environmental drivers for dominant genera in rhizosphere soils in tailing dump, we used Random Forest modelling to identify the nutrient and metal(liod) drivers for the distribution of 5 dominant genera (including *Cellvibrio*, *Flavobacterium*, *Cohnella*, *Devosia*, and *Lysobacter*) (Fig. 7). Evidently, different kind of edaphic variables contributed differently to the various microbial genera. For example, C/N was the most important variable for predicting many genera, including *Cellvibrio*, *Flavobacterium*, and *Lysobacter*; Sulfate was the important variables for

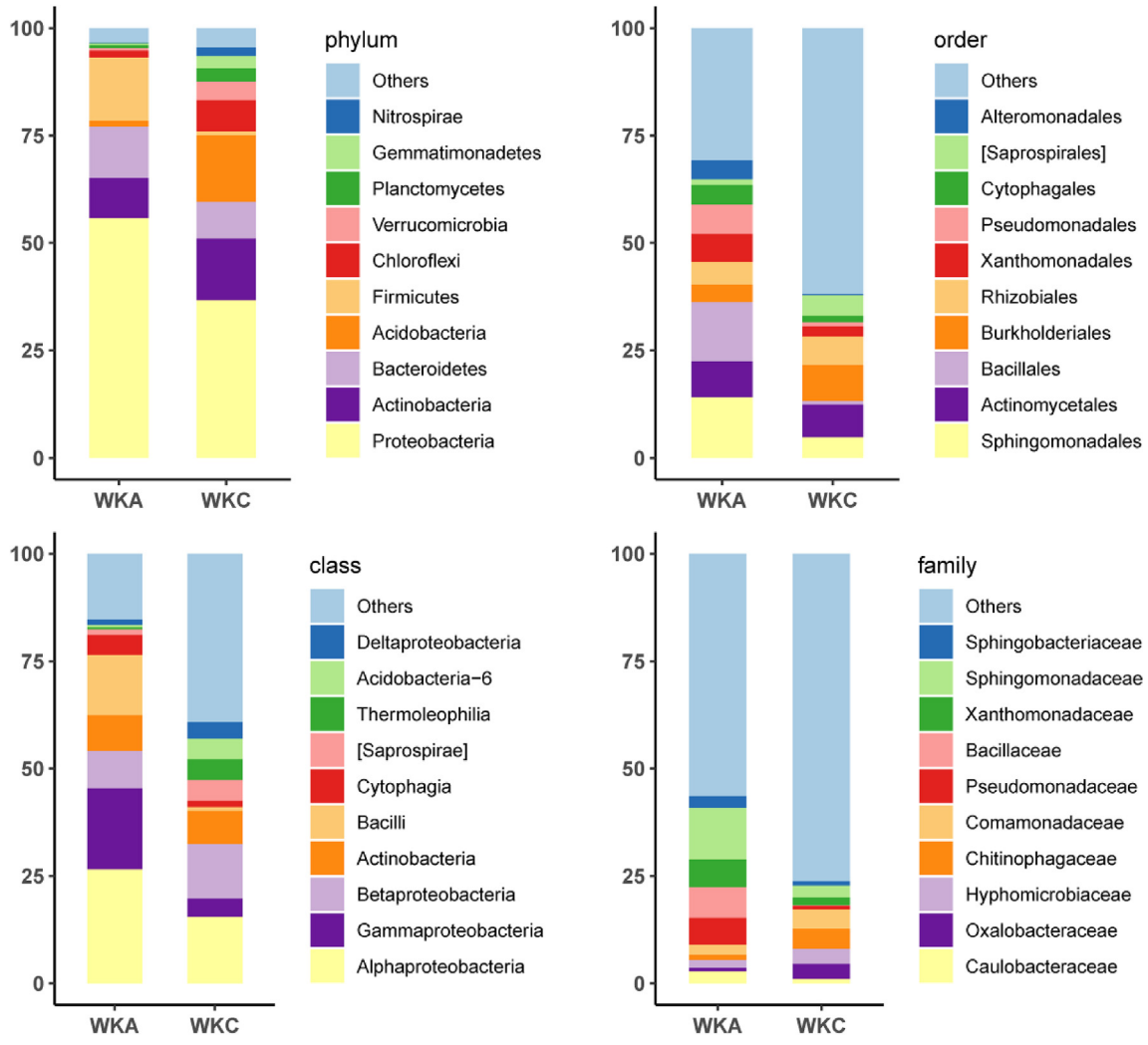

Fig. 4. Taxonomic distribution of ten most abundant bacterial taxa (from phylum to family level) between WKA and WKC.

Lysobacter; TOC, for *Flavobacterium*; Sb and As contaminant fractions for predicting dominant genera were As_{srp}, for *Flavobacterium* and *Cellvibrio*; and Sb(V), for *Flavobacterium*.

3.6. Biotic interactions revealed by co-occurrence network

In the current study, an environment-microbe network was constructed to reveal the interactions between the Sb or As contaminant fractions and the 1000 most abundant OTUs (accounting for >50% of the total valid reads, Table S11 for the phylogenetic information). Only strong ($r > 0.6$) and significant ($p < 0.05$) correlations between contaminant fractions and OTUs were included in the network. Interestingly, all eight "hubs" (the largest node in each module) originate from contaminant fractions. Among these hubs, As_{srp}, Sb_{tot}, and Sb(V)-C formed the largest nodes, suggesting their impact on the microbial assemblages (Fig. 8A). Notably, OTUs affiliated with genera of including *Pseudomonas*, *Bacillus*, *Paenibacillus*, and *Thiobacillus* were strongly connected with these "hubs".

In addition, we used the top 100 OTUs to construct a network (see Table S12 for the phylogenetic information) to elucidate the interactions between microorganisms in tailing dump. The resulting network consists of 97 nodes and 854 edges (Fig. 8B). Four major modules which consisting of most nodes were obtained. Module II is the largest module, with 27 nodes, followed by modules I and III, which contained 25 and 18 nodes, respectively.

4. Discussion

4.1. Influence of metalloids and nutrients on rhizosphere bacterial community

In the current study, the bacterial diversity within the tailing dump (WKA) was significantly lower than that in adjacent soils (WKC). This finding is consistent with that of Lewis et al. (2012) who observed similar bacterial community trends in mined bauxite soils, where the bacterial diversity was significantly lower in mined soils than in unmined soils after even more than 20 years of reclamation. Similarly, another study reported significantly lower bacterial community diversity in reclaimed coal mine soils than in its adjacent undisturbed soils (Quadros et al., 2016). Using RF analysis, we found that various Sb and As fractions and nutrient parameters were the main determinants influencing rhizosphere bacterial community in WKA. Given that tailing dumps are characterized by low nutrient levels and extremely high concentrations of Sb compared with adjacent soils, it is reasonable to propose that nutrients and metal(loid)s were the main causes for the low bacterial diversity in tailing dump. This also accords with previous

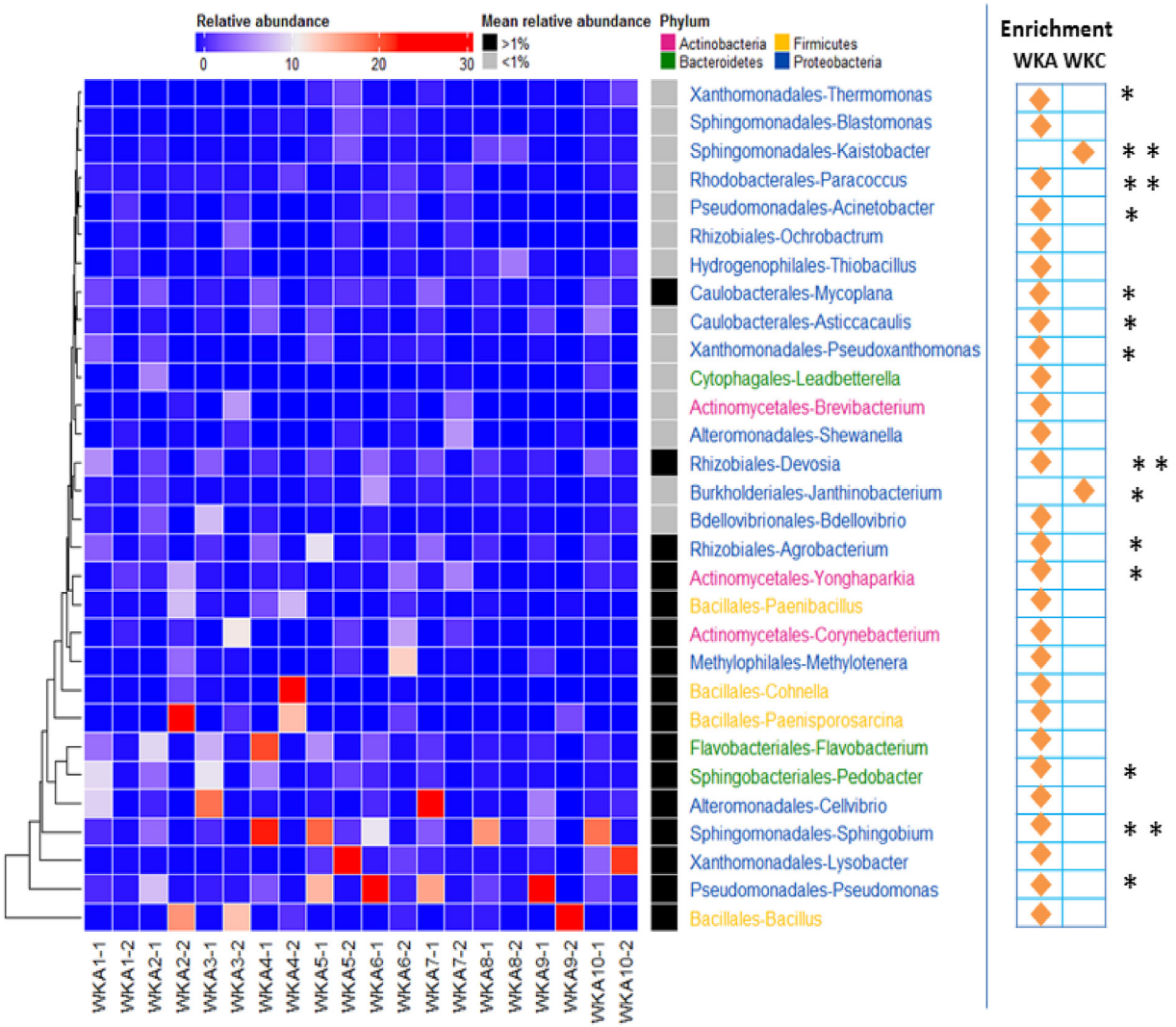

Fig. 5. Heatmap of the top 30 shared genera in WKA. Relative abundances were log transformed and colored from blue to red to indicate high-to-low relative abundances. Shared genera were identified as dominant (>1% relative abundance) or rare (<1% relative abundance). The name of each genus is colored by phylum class (pink: *Actinobacteria*; dark yellow: *Firmicutes*; green: *Bacteroidetes*; blue: *Proteobacteria*). The enrichment and significance (* represents $p < 0.05$; ** represents $p < 0.01$) of each genus in WKA or WKC are also indicated.

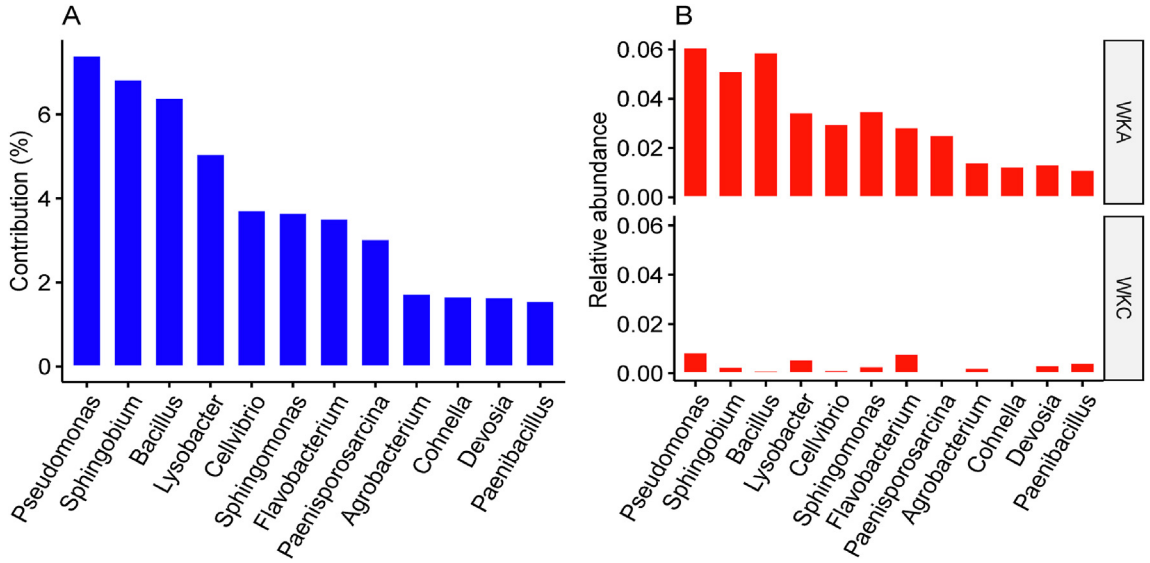

Fig. 6. Similarity of percentages analysis (SIMPER) based on average Bray-Curtis dissimilarity: (A) The relative contribution of top 12 genera to the dissimilarity between communities of tailing dump and adjacent soils. (B) The relative abundance of top 12 genera which pose top dissimilarity contributions (from left to right as descending order).

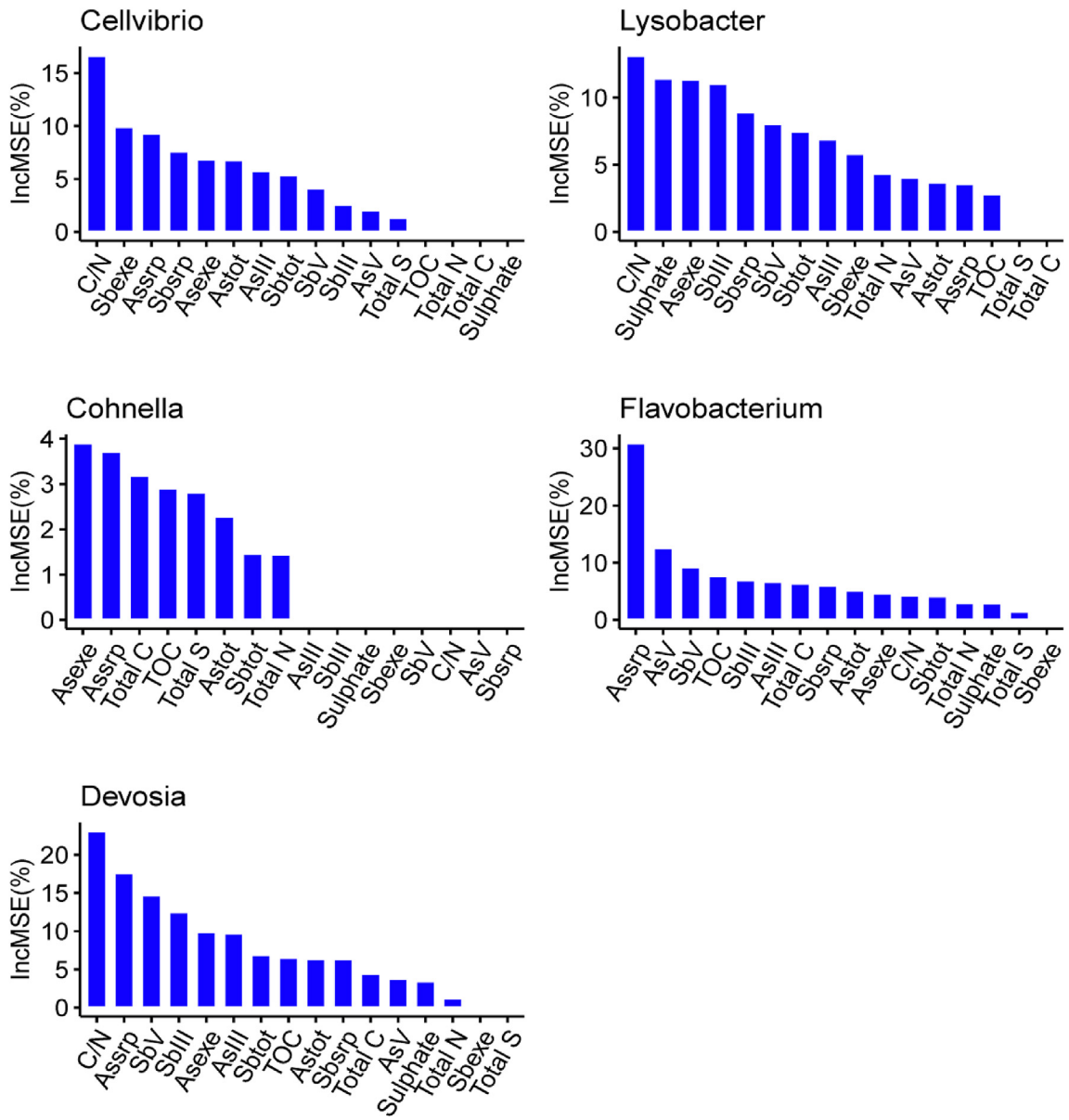

Fig. 7. The potential Sb/As and other environment drivers of dominant genera distribution in rhizosphere soils in tailing dump by random forest (RF) analysis.

studies which showing that nutrient elements facilitate the basic metabolism of bacteria (Wang et al., 2017), whereas heavy metals reduce or even remove the metabolic capability of carbon and nitrogen (Li et al., 2015a). Consistently, our results showed that bacterial alpha diversity and richness was positively correlated with all nutrient parameters and negatively correlated with all Sb and As contaminant fractions in this study ($p < 0.05$, Fig. 3 and Tables S8–S9).

4.2. The dominant genera involved in nutrient cycling

In the current study, we have identified several dominant shared genera in WKA. Given that *Devosia*, *Cellvibrio*, *Lysobacter*, and *Cohnella* were identified as the top contributors to the dissimilarity between microbial communities of tailing dump and adjacent soils, it is reasonable proposed that they may play an important role in the plant root in tailing dump (Fig. 6B). Among these genera, *Devosia*, *Cellvibrio*, *Lysobacter*, and *Cohnella* have frequently been detected in the rhizosphere soils of several plants, such as *Neptunia natans* (*Devosia*) (Rivas et al., 2002), *Hordeum secalinum* (*Cellvibrio*) (Suarez et al., 2014), *Arabidopsis halleri* (*Lysobacter*) (Muehe et al., 2015), and *Capsicum annuum* (*Cohnella*) (Wang et al., 2012a), and identified as nitrogen-fixing bacteria, which catalyzes the conversion of N_2 gas to ammonia (Suarez et al., 2014). The abundance of nitrogen-fixing bacteria in rhizosphere soils has important environmental implications for plant surviving in low-N tailing dumps (<0.01%). Consistently, we found that Total N and C/N, in general, are significant predictors of the distribution patterns of these four genera (Fig. 7).

Flavobacterium has been isolated from rhizosphere soils of different plants such as cotton (Kämpfer et al., 2017), maize (Gao et al., 2015), tomato (Kim et al., 2006), and *Suaeda corniculata* (Sun et al., 2016). The genus *Flavobacterium* contains species that have been reported as plant growth-promoting rhizobacteria (PGPR) (Etesami and Maheshwari, 2018). Previous studies found that *Flavobacterium* can provide essential nutrients for plant

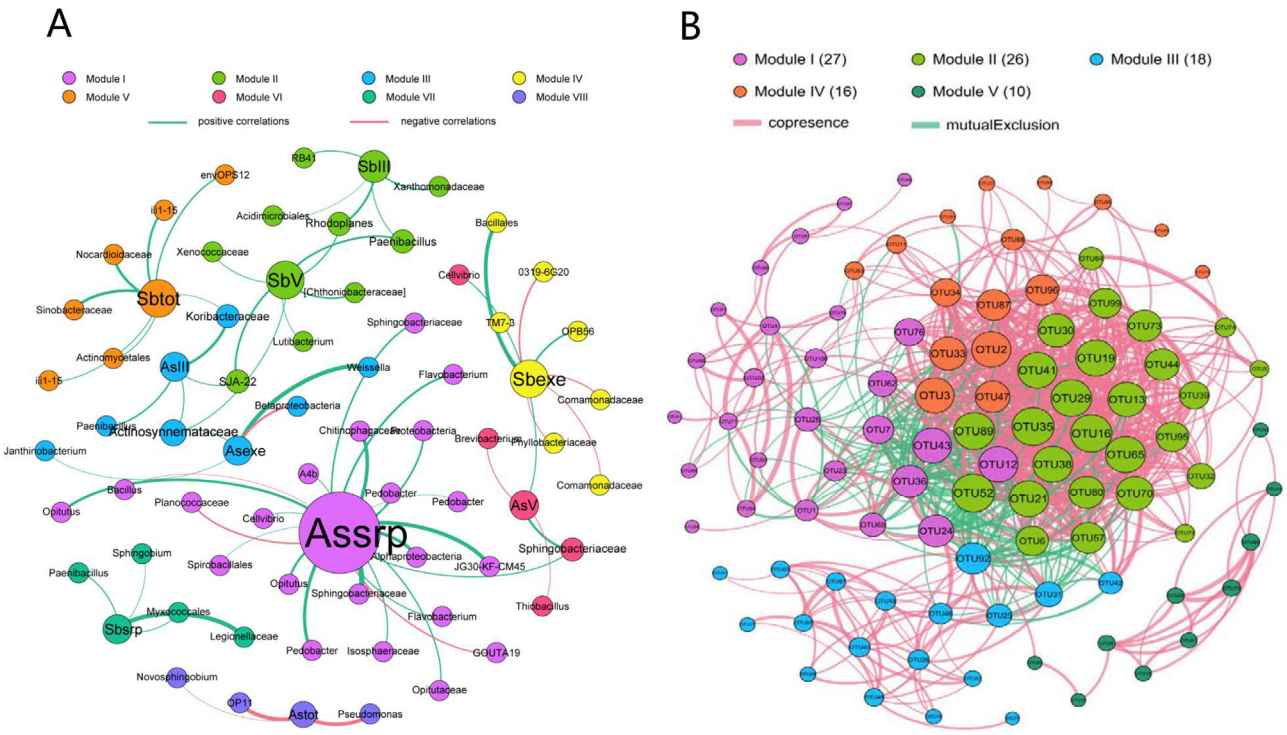

Fig. 8. Co-occurrence networks showing the correlation between environmental parameters and either the (A) top 100 bacterial OTUs or the (B) top 1000 OTUs at the tailing dump. Edges shown for only strong (|r|>0.6) and significant ($p < 0.05$) Spearman correlations. The size of each node is proportional to its number of connections (i.e., degree); the thickness of each connection between two nodes (i.e., edge) is proportional to the value of the corresponding Spearman's correlation coefficients, which ranged from |0.6| to |1|. The co-occurrence network is colored by modularity class. (For an interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

growth by mechanisms such as solubilizing inorganic phosphorus from immobile minerals in the soil or fixing nitrogen from the atmosphere (Oteino et al., 2015). Such observations were partly consistent with our result that the relative abundance of *Flavobacterium* was significantly correlated with TC, TN, and TOC ($p < 0.05$). Given that tailing dumps are dominated by low-N and low-P environments (<0.01%), it is not surprising to see the proliferation of *Flavobacterium* within rhizosphere soils. Collectively, these data indicate dynamic microbial nutrients cycling in the plant rhizosphere, which may play a beneficial role for *Bidens pilosa* survival in tailing dumps with low contents of nutrients.

4.3. Interactions between soil microbiota and Sb and As

It is notable that metal(loid)s could explain over 80% of the variation in microbial diversity in WKA, suggesting that metal(liod)s were the main determinants influencing rhizosphere bacterial community in WKA. Thus, changes in contents of Sb and As contaminant fractions led to drastic changes in soil bacterial communities. Consistent with RF result, we found that all eight hubs (the largest nodes) from co-occurrence network were Sb or As contaminant fractions, suggesting that the microbial assemblages were substantially affected by Sb and As fractions. Taken together, these results suggest that Sb and As contaminant fractions play crucial roles in maintaining the stability of microbial structure. Such observations accord with our earlier observations, which showed that Sb and As contaminant fractions were the important environmental variables to shape microbial community (Xiao et al., 2016a, 2016b; 2016c; Sun et al., 2018b).

Notably, we found that OTUs affiliated within the genera of *Pseudomonas*, *Bacillus*, *Thiobacillus*, and *Paenibacillu* demonstrated extensive strong and significant correlations with Sb and As contaminant fractions. Given that *Pseudomonas* and *Bacillus* were identified as the two most abundant genera in WKA and considered as the two largest contributors to the dissimilarity of microbial communities between tailing dump and its adjacent soils (Fig. 6A), it is reasonable to propose that these two genera play an important role in metabolic activity in the plant root in tailing dump. *Pseudomonas* and *Bacillus* have been frequently reported in Sb contaminated environmental compartments, such as river sediments, soils (Xiao et al., 2016b; Sun et al., 2017), and tailing dump (Xiao et al., 2016a). Additionally, both *Pseudomonas* and *Bacillus* have been positively correlated with contents of As and Sb contaminant fractions in Sb contaminated soils (Xiao et al., 2016b) and river sediments (Xiao et al., 2016c). Of particular interest, *Pseudomonas* and *Bacillus* were identified possessing gene of *anoA* which could rapidly oxidize As(III) and Sb(III) to As(V) (Li et al., 2016) and Sb(V) (Wang et al., 2012b; Jia et al., 2014), respectively. Currently, *Pseudomonas* and *Bacillus* have been widely reported in various plant roots growing in As-polluted soils, such as As hyperaccumulator *Pteris vittata* (PV) (Wang et al., 2012b; Han et al., 2015), rice (Jia et al., 2014), and *Cirsium arvense* (L.) (Das et al., 2014). Microbial oxidation of Sb(III)/As(III) to Sb(V)/Sb(V) could decrease Sb/As uptake into plant due to plant roots (such as those of *Lolium perenne*) prefer uptake of Sb(III) over Sb(V) in soils (He et al., 2018). Collectively, these results suggested that *Pseudomonas* and *Bacillus* have a high tolerance of Sb and As contamination in soils and may play a role in decreasing Sb or As transfer from soils to plants. In the current study, *Thiobacillus* was dominant enriched in tailing dump and positively correlated with As(V) and Sb(V) (Fig. 8A). *Thiobacillus* is moderately thermophilic acidophiles and widely reported as sulfur-oxidizing bacteria (SOB). Of particular interest was a study by Mandl and Vyškovský (1994) which reported that arsenic(III) is catalytically oxidized by iron(III) in the presence of *Thiobacillus*

ferrooxidans. More recently, Sun et al. (2018a) found the presence of arsenate reductase and oxidase in the *Thiobacillus*-affiliated bin by using metagenomic-binning. These suggest the potential role of *Thiobacillus* in As cycling. Moreover, *Thiobacillus* spp. have been detected in Sb tailings as reported by our group previously (Xiao et al., 2016a; Sun et al., 2018a). Previous studies showed that *Thiobacillus ferrooxidans* could oxidize trivalent antimony bearing minerals, such as antimony-bearing sulphide minerals (Karavaiko, 1970), low-grade stibnite (Rossi, 1971), and synthetic antimony sulphides (Silver and Torma, 1974). Evidence has been presented that *Thiobacillus ferrooxidans* could autotrophic grows by only using the energy released from oxidation of trivalent antimony (Lyalikova, 1971). Moreover, using Random Forest analysis, we identified that As(V) and Sb(V) are significant predictors of the distribution patterns of *Thiobacillus*. This suggests that *Thiobacillus* may play an important role in Sb and As cycling in the plant root in tailing dump. At the current study, *Paenibacillus* in relative abundances in WKA were significant higher than WKC. Moreover, the OTUs related to the genus *Paenibacillus* were positively correlated with Sb(III), Sb(V), Sb_{srp}, and As(V) in the co-occurrence network (Fig. 5B). Random Forest analysis showed similar result which *Paenibacillus* was mainly driven by Sb_{tot}, Sb(V), As_{exe}, and As(III). Such observation partly consistent with previous studies that *Paenibacillus* spp. have been isolated from As polluted soils and identified as having resistance to high concentrations of both As(III) and As(V) (Shagol et al., 2014). However, none has reported that members of *Paenibacillu* are responsible for Sb cycling.

5. Conclusion

In the current study, we identified the rhizospheric microbiome of *Bidens bipinnata* and their responses on environmental stress in both an abandoned Sb tailing dump and its adjacent soil. Our results showed that the microbial diversity and compositions were significant different between tailing dump and its adjacent undisturbed soils and such differences could be explained by nutrients parameters (TC, TOC, TS, and Total N) and metal(loid) concentration (As_{tot}, As_{exe}, As(V), Sb_{exe}, and Sb(V)) changes. Importantly, the dominant genera identified in WKA were mainly involved in nutrient cycling (nitrogen fixing, P solubilizing) and Sb and As cycling, which may play a beneficial role for *Bidens pilosa* survival in Sb tailing dumps. Through this study, we could gain insights into the ecological roles of rhizosphere microorganisms on native plants surviving in a tailing dump.

Conflicts of interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2019.06.097.

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