The rhizosphere microbiome reduces the uptake of arsenic and tungsten by *Blechnum orientale* by increasing nutrient cycling in historical tungsten mining area soils

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HIGHLIGHTS

- Soil nutrients inhibited As and W uptake by *Blechnum orientale* in W mining area.
- Soil nutrients shaped rhizosphere bacterial communities and keystone OTUs.
- Rhizosphere keystone taxa enhanced the nutrient cycling in W mining area.

GRAPHICAL ABSTRACT
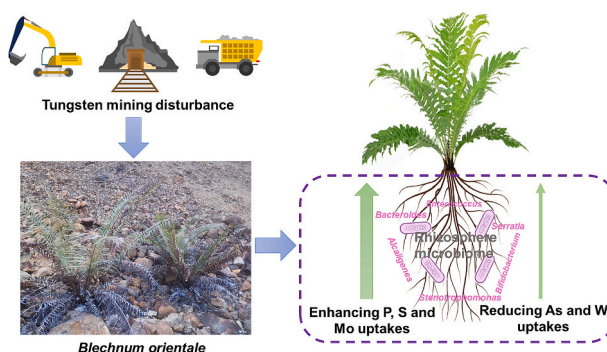
ABSTRACT

The growth of pioneer plants in metal mining area soil is closely related to their minimal uptake of toxic elements. Pioneer plants can inhibit the uptake of toxic elements by increasing nutrient uptake. However, few studies have focused on the mechanisms by which the rhizosphere microbiome affect nutrient cycling and their impact on the uptake of toxic elements by pioneer plants. In this study, we selected *Blechnum orientale* to investigate the potential roles of the rhizosphere microbiome in nutrient cycling and plant growth in a historical tungsten (W) mining area. Our results showed that while the arsenic (As) and W contents in the soil were relatively high, the enrichment levels of As and W in the *B. orientale* were relatively low. Furthermore, we found that the As and W contents in plants were significantly negatively correlated with soil nutrients (S, P and Mo), suggesting that elevated levels of these soil nutrients could inhibit As and W uptake by *B. orientale*. Importantly, we found that these nutrients were also identified as the most important factors shaping rhizosphere microbial attributes, including microbial diversity, ecological clusters, and keystone OTUs. Moreover, the genera, keystone taxa and microbial functional genes enriched in the rhizosphere soils from mining areas played a key role in

nutrient (S, P and Mo) bioavailability, which could further increase the nutrient uptake by *B. orientale*. Taken together, our results suggest that rhizosphere microorganisms can improve pioneer plant growth by inhibiting toxic element accumulation via the increase in nutrient cycling in former W mining areas.

1. Introduction

Pioneer plants can exhibit normal growth in the oligotrophic and highly toxic soils in metal mining areas. The prerequisite for plant growth in mining soils involves developing survival mechanisms to reduce toxic element uptake (Hussain et al., 2023; Qin et al., 2023; Song et al., 2010; Sun et al., 2023). Elevated soil nutrients can not only reduce the mobility of toxic elements in soils but also inhibit their accumulation via complexation with nutrients in plant roots. For example, experimental research has shown that the addition of S and P can form complexes with toxic elements (As and Cd), reducing their mobility and bioavailability (Wisawapipat et al., 2021; Qin et al., 2023). Some studies have further indicated that plants can inhibit the uptake of toxic elements by increasing nutrient (S and P) uptake because plants can synthesize these complexes (Liu et al., 2022c; Song et al., 2010). Subsequently, these complexes are sequestered into plant roots, reducing the translocation of As and Cd to the above-ground parts of the plant (Song et al., 2010; Dai et al., 2018). These studies highlighted the important roles of soil nutrients in the uptake of toxic elements by plants. However, these studies focused primarily on chemically mediated nutrient cycling, and there is limited knowledge regarding microbially mediated nutrient cycling and its role in toxic element uptake by plants.

In fact, rhizosphere microorganisms have been widely reported to be involved in nutrient cycling and thereby reduce the uptake of toxic elements from rhizosphere soils (Li et al., 2016; Sun et al., 2019b; Xiao et al., 2019; Zhang et al., 2022). For example, sulfur-oxidizing bacteria inhabiting rhizosphere soils have been proven to increase soil S bioavailability, subsequently decreasing the uptake of toxic elements by plants (Wu et al., 2021). Sun et al. (2024) reported that members of *Thiobacillus* and *Rhizobium* are the major populations that accelerate the oxidation of As(III) and S^{2-}. Qin et al. (2023) also reported that phosphate-solubilizing bacteria (*Klebsiella* sp. *M2* and *Kluyvera* sp. *M8*) increase the availability of phosphorus in the rhizosphere soil, thereby reducing the uptake of Cd by plants. These findings highlight the potential roles of microbially mediated nutrient cycling in rhizosphere soils in nutrient uptake by plants. However, current knowledge mainly encompasses the roles of specific microorganisms, and there is a limited understanding of the mechanisms by which rhizosphere microbial structures in inhibit on toxic element uptake by pioneer plants.

China is one of the world's largest tungsten (W) producers and consumers (Zhu et al., 2019). In recent decades, extensive W mining has resulted in a large amount of mining waste rock and tailings (Liu et al., 2022b; Xu et al., 2023), which adversely impacts on the surrounding soil ecosystem. Several studies have demonstrated that ecological restoration utilizing pioneer plants is an important pathway for mining (such as Sb, V and Cd) remediation (Fan et al., 2022; Guo et al., 2022; Li et al., 2022b; Zhang et al., 2023; He et al., 2024). Notably, we found that pioneer plant (*Blechnum orientale*) exhibited robust adaptability in the abandoned W mining area, indicating its potential role in mining restoration. Currently, the remediation mechanism of *B. orientale* is still unknown, especially the potential role of the rhizosphere microbiome in the nutrient cycling and plant growth.

In the present study, we selected a pioneer plant (*B. orientale*) to investigate the potential roles of the rhizosphere microbiome in nutrient cycling and plant growth in W mining areas. We investigated (1) the relationship between soil nutrients and toxic element uptake by *B. orientale*; (2) the importance of soil nutrients to rhizosphere microbial attributes, including microbial diversity, ecological clusters, and keystone OTUs; and (3) the potential roles of the rhizosphere microbiome in toxic element uptake by pioneer plants. Our study provides new insights into the role of rhizosphere microorganisms in plant growth in metal mining areas. Furthermore, this study provides both theoretical and technical support for the ecological restoration of historical W mining areas.

2. Materials and methods

2.1. Site description and sampling

The selected sampling area in this study was the Lianhuashan tungsten mine in Guangdong Province, southern China, as sampling area (23°38′5″ N, 116°50′22″ E). This mine operational from 1958 to 1999. Two sampling sites were selected: one was located in an abandoned mining area and the other was located in an undisturbed non-mining area. The undisturbed area was located in non-mining areas. The undisturbed areas are mainly covered by forests, which are approximately 1–2 km away from the mining area. We used a random field sampling method to collect pioneer plants (*Blechnum orientale*) with similar heights during sample collection. A total of 14 plant samples, 14 rhizosphere soil samples, and 14 bulk soil samples were collected in the mining area, and 6 plant samples, 6 rhizosphere soil samples, and 6 bulk soil samples were collected in the undisturbed areas. The plant samples were divided into aboveground and belowground parts. During the collection of rhizosphere soil, the roots were first pulled up and then gently shaken to remove loose soil. The remaining rhizosphere soil was then placed in a self-sealing bag. Bulk soils were collected from mixed soils around pioneer plants, with an average weight of approximately 2 kg. The soil samples were also divided into two parts, one for physicochemical parameter analysis and the other for microbial analysis. All samples were carefully collected and put in self-sealing bags, immediately stored in a mobile freezer (4 °C) and were brought back to the laboratory for further processing when they were carefully collected and put in self-sealing bags. Soil samples for microbial DNA extraction were transferred to an ultralow temperature freezer (−40 °C) for storage.

2.2. Chemical analysis

The plant samples were washed with deionized water and then dried at 50 °C. The soil samples were air-dried and then ground (200 mesh) using a ceramic mortar and pestle. Ten grams of soil sample was added to 25 ml of MQ water, shaken, and allowed to settle, and the soil pH was measured using a pH meter (PHS–3C, China). The total organic matter (TOC), total sulfur (TS) and total nitrogen (TN) contents in the soils were determined using an element analyzer following the procedure described by Xiao et al. (2017). For the soil samples, 100 mg of soil samples was digested with mixed concentrated acid (HCl + HF + HNO₃ + HClO₄). For the plant samples, 200 mg samples were completely digested with HCl + HNO₃. The major and trace element concentrations in the soils and plants were determined by inductively coupled plasma mass spectrometry (ICP-MS) (Agilent, 7900, California, USA). During the digestion experiment, standards (GBM908-10 and MRGeo08), blanks and replicates were used to ensure the quality and accuracy of the experiment. In addition, standard solutions from the Analysis and Testing Center of National Nonferrous Metal and Electronic Materials, China, were also inserted during the test process to ensure the reliability of the test process.

2.3. High-throughput sequencing of the V4 region of the 16S rRNA gene

Soil genomic DNA was extracted from 0.25 g of sample using an MP fastDNA® Spin Kit (MP bio, Santa Ana, USA) according to the manufacturer's protocol. The concentration and purity of the extracted DNA were determined by electrophoresis on a 1 % agarose gel. The extracted DNA samples were stored at −80 °C prior to analysis. The V4-V5 hypervariable region of the 16S rRNA gene was amplified using the primer pair 515f/907r (515f: 5′-GTGYCAGCMGCCGCGGTAA-3′, 907r: 5′-CYCAATTCMTTTRAGTTT-3′) (Kuczynski et al., 2011). The purified PCR amplicons were sequenced on an Illumina MiSeq platform. Paired-end reads were merged using FLASH and filtered by QIIME 2 (Quantitative Insights into Microbial Ecology) (Bokulich et al., 2013; Magoč and Salzberg, 2011). Chimeric sequences were removed using UCHIME (http://www.drive5.com/usearch/manual/uchime_algo.html). Operational taxonomic units (OTUs) (97 % similarity) were clustered using the chimera filtering approach with UPARSE (Edgar et al., 2011). The phylogenetic taxonomy of each OTU was assigned using the RDP classifier (version 2.2, http://sourceforge.net/projects/rdp-classifier/) and the Greengenes database (http://greengenes.lbl.gov/cgi-bin/nphindex.cgi). PICRUSt was used to investigate the metabolic potential of the microbiota. The OTU table was input into PICRUSt on the imageGP web platform for metagenome prediction using the Kyoto Encyclopedia of Genes and Genomes (KEGG) database (Langille et al., 2013).

2.4. Statistical analysis

We compared the differences in environmental parameters and microbial diversity using the one-way analysis of variance (ANOVA). Principal coordinate analysis (PCoA) analysis based on weighted UniFrac distances was used to analyze the intergroup microbial composition differences. The most important environmental factors that affected the microbial diversity, community structure and keystone OTUs were determined by using random forest (RF) analysis based on the rfPermute package (R statistical software, version 3.0.2). The OTUs with significant differences in abundance between sample groups were determined using the tidyverse and DESeq2 packages (R statistical software, version 3.0.2). Co-occurrence network analysis was used to determine the microbial community structure of the rhizosphere soil samples. We selected the top 1000 OTUs in terms of abundance and calculated their Spearman correlation coefficients (ρ). In this study, we considered only those meeting the criteria of $|\rho| > 0.6$ and $p < 0.05$ to construct the network diagram (Li et al., 2022a). The co-occurrence network diagram was visualized using the Gephi software platform. The average Z score was calculated for each ecological module. Differences in predicted microbial metabolic function between groups were compared using the Stamp software platform.

3. Results

3.1. Geochemical distributions of soils in mining and undisturbed areas

The rhizosphere and bulk soils from the mining area (MRS and MBS) exhibited extreme acidity (pH ranging from 3.64 to 4.63), low nutrient levels (with TOC ranging from 0.15 to 0.77 % and TN ranging from 0.02 to 0.07 %, respectively) and high levels of toxic element levels (with total W contents ranging from 161 to 3960 mg kg^{-1} and total As contents ranging from 997 to 6690 mg kg^{-1}) (Fig. 1 and Table S1). The rhizosphere and bulk soils of the undisturbed area (URS and UBS) also displayed moderate acidity (pH ranging from 3.86 to 5.39) and low nutrient levels (with TOC ranging from 0.15 to 0.77 % and TN ranging from 0.09 to 0.24 %), and low level of toxic element levels (with As ranging from 7.3 to 565 mg kg^{-1}, with W ranging from 2.0 to 385 mg kg^{-1}) (Fig. 1 and Table S1). In addition, the soil pH and total K and Na contents in the MRS samples were significantly lower than those in the URS samples ($p < 0.05$). In contrast, the contents of TN, TOC, TP, TS, Fe,
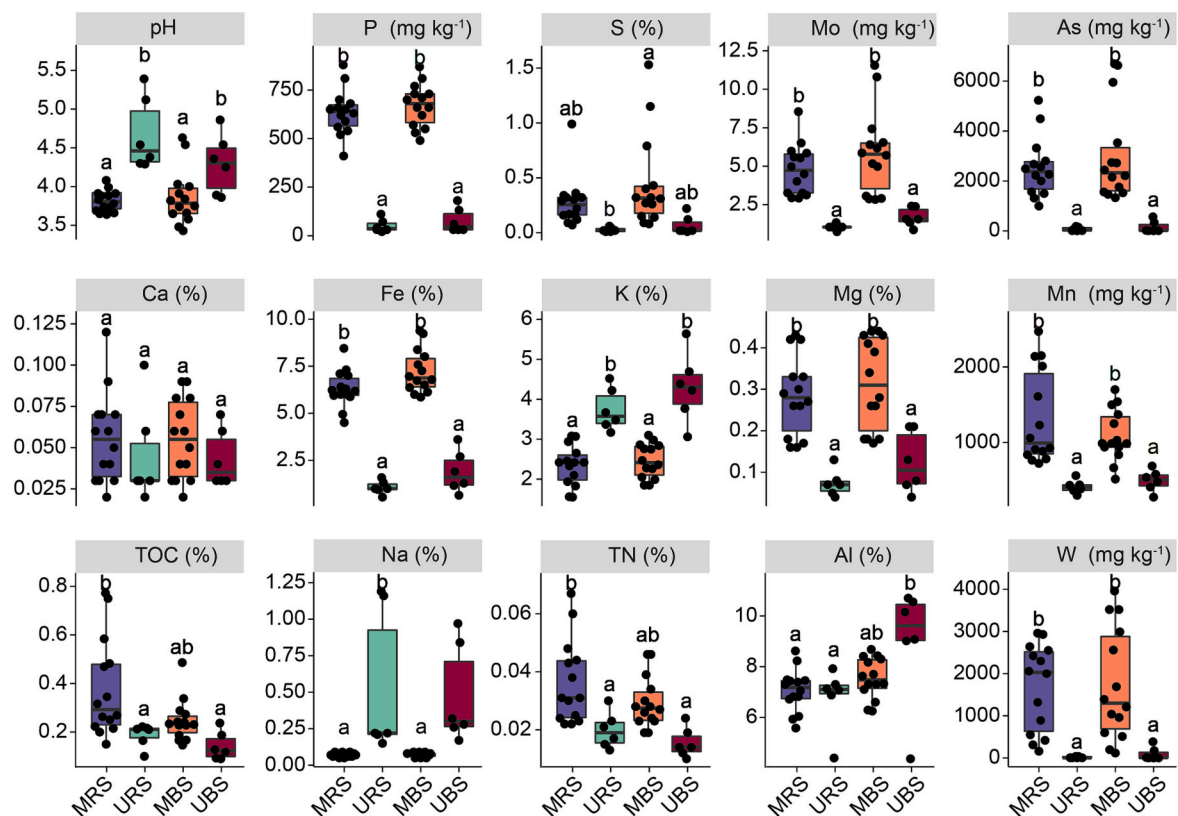

Fig. 1. Geochemical profiles of rhizosphere soils in the mining area (MRS) and undisturbed area (URS), bulk soils in the mining area (MBS), and bulk soils in the undisturbed area (UBS).

Mn, As, W and Mo in the MRS samples were significantly higher than those in the URS samples ($p < 0.05$). Notably, there were no differences in any of the geochemical parameters between the rhizosphere soil and associated bulk soil in either the mining or undisturbed areas. Correlation analysis further showed that pH was generally negatively correlated with most metals (such as Fe, Mn, As, and W) and nutrients (TOC, TS, TP, and TN). (Fig. S1). The exposed sulfides in abandoned mining areas generated high levels of acidity and large amounts of heavy metals, resulting in extremely low pH and high heavy metal levels in soils.

3.2. Element uptake by Blechnum orientale growth in mining and undisturbed areas

The biomass of the aboveground (AG) parts of *B. orientale* ranged from 8.38 to 67.58 g (in dry weight); and the biomass of the belowground (UG) parts of *B. orientale* (in dry weight) ranged from 0.27 to 53.14 g (in dry weight). The distributions of the Al, As, Fe, K, Mg, Mn, Mo, Na, P, S and W contents in the AG and UG parts of the pioneer plants (*B. orientale*) are shown in Fig. 2 and Table S2. The results revealed a significant variation in element distribution between the two parts of the plants. For instance, essential elements for plants, such as S, K, Mg, Mn, Mo, Na, and P, were predominantly enriched in the aboveground parts of the plants, while toxic elements, such as As and W, were mainly enriched in the belowground parts of the plants (Fig. S2). Additionally, the As and W contents of plants collected from mining areas were significantly greater than those in plants collected from undisturbed areas (Table S2). Bioaccumulation factors (BCFs, the ratios of element concentrations in the plants and soils) are usually used to evaluate the enrichment of harmful elements in plants (Jiang et al., 2022). The BCF results of As and W in *B. orientale* are shown in Table S2. The average BCF values of W in the AG and UG of plants in the mining area were 0.01 and 0.06, respectively, and the average BCF values of As in the AG and UG of plants in the mining area were 0.01 and 0.05, respectively. Although the contents of As and W in *B. orientale* were greater in the MRS samples than those in the URS samples, the BCFs of As and W in the MRS samples were significantly lower than those the in URS samples ($p < 0.05$). Notably, the soil nutrients (P, Mo and S) showed a substantial negative correlation with the BCFs of As and W in the UG of plants ($p < 0.05$) (Fig. 2). Moreover, significantly positive correlations between nutrients (P, Mo and S) and As and W were found in both parts of the plants (Fig. S3).

3.3. Microbial diversities and taxa enrichments in the rhizosphere and bulk soils

A total of 2,570,592 high-quality sequences were obtained from all the samples through Illumina MiSeq sequencing. After completing quality screening and extraction, 9215 OTUs were identified based on 97 % sequence similarity. A total of 50 phyla, 67 classes, 160 orders, 312 families, and 831 genera were identified in all the samples, respectively. PCoA indicated that there was a clear discrepancy in microbial diversity between rhizosphere and bulk soils under mining and undisturbed conditions (Fig. 3). Although the alpha diversity indices (observed species, Chao1, ACE, Shannon and Simpson indices) did not significantly differ among the sample groups, the number of observed species in the rhizosphere soils was greater than that in the bulk soils (Fig. S4).

RF was conducted to determine the relative importance of edaphic factors on alpha diversity indices in rhizosphere soils. The results showed that phosphorus (P) was the most critical predictor of the observed species and Chao1 index in rhizosphere soils, while sulfur (S), pH and molybdenum (Mo) were the most important predictors of the ACE, Shannon and Simpson indices, respectively (Fig. 3). Correlation analysis revealed that S and Mo were positively correlated with the ACE and Chao1 indices, except Mo with the Chao1 index (Fig. S5). Correlation analysis also demonstrated that pH was negatively correlated with *Gammaproteobacteria* and *Bacilli*; S and Mo were positively correlated with *Gammaproteobacteria*, *Bacteroidia*, and *Bacilli* but negatively correlated with *Ktedonobacteria*, *Acidobacteriia* and *Thermoleophilia* (Fig. S3). Furthermore, we conducted linear model analysis to quantify the OTUs enriched in each group (Fig. 4). The enriched OTUs from MRS mainly consisted of *Chloroflexi*, *Proteobacteria*, *Actinobacteria* and *Acidobacteria*.

3.4. Characterization of the microbiota ecological clusters in rhizosphere soils

Co-occurrence network analysis was used to unveil ecological clusters of the microbiota in rhizosphere soils (Fei et al., 2023; Wang et al., 2023; Geng et al., 2024). The results indicated the presence of three major ecological clusters (M0, M1, and M2) in the rhizosphere soils (Fig. 5A). In M0 and M1, the Z score of MRS samples did not differ from that of URS samples (Fig. 5D). However, the Z score of MRS samples was significantly greater than that of URS samples in M2 (Fig. 5D). RF analysis indicated that Mo was the most important predictor of M0, S was the most important predictor of M1, and pH was the most important predictor of M2 (Fig. 5C). Additionally, the taxonomic assignments at the class level for each ecological cluster were distinct. For example, M0 was dominated by *Gammaproteobacteria*, M1 was mainly composed of *Ktedonobacteria*, and M2 was dominated by *Alphaproteobacteria* and *Acidobacteria* (Fig. 5B).

Furthermore, 11 keystone OTUs were identified based on the criteria of the nodes with low betweenness centralities and high degrees in the
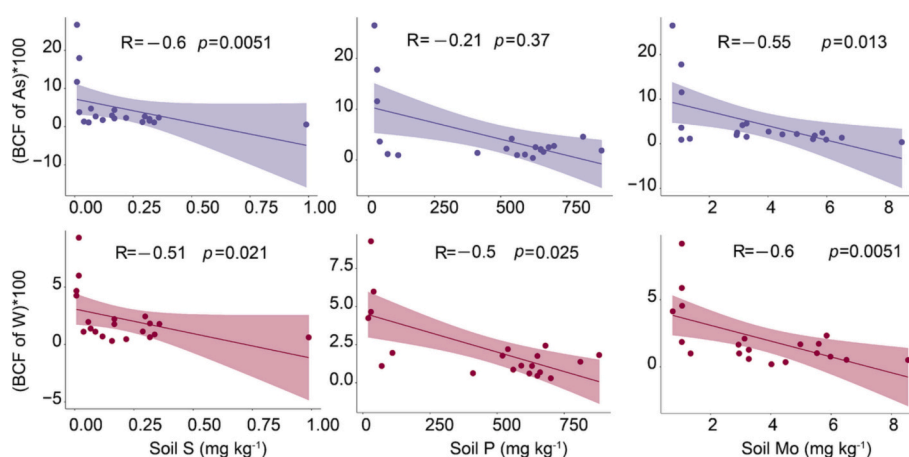

Fig. 2. The relationships between soil nutrients (S, P and Mo) and bioaccumulation factor (BCF) values (*100) of As and W in the underground parts of *Blechnum orientale* plants.
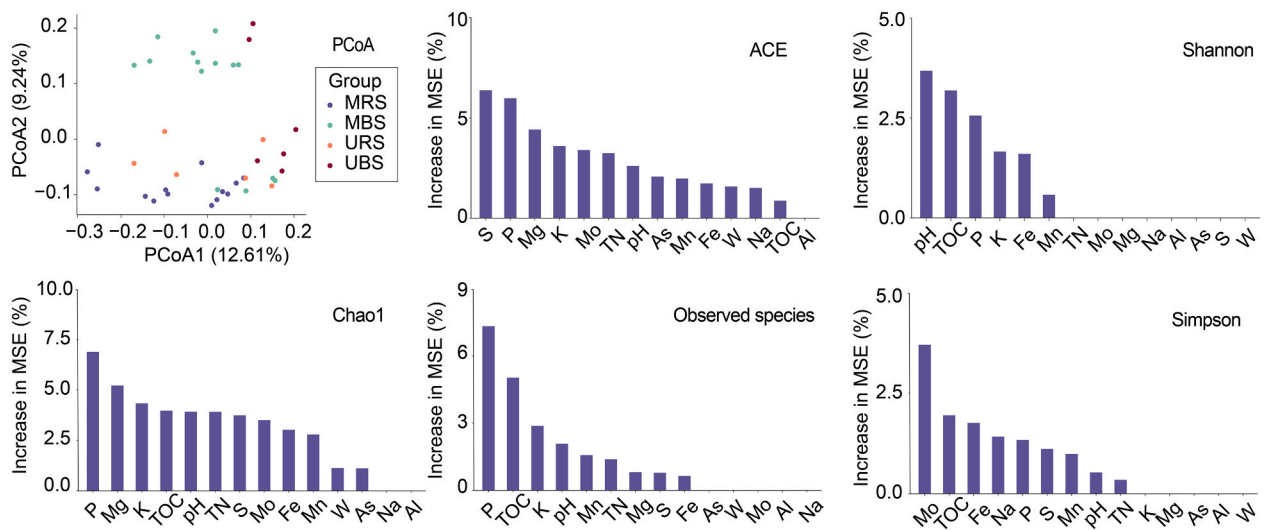
Fig. 3. PCoA plot illustrating the Bray_Curtis distance of community beta diversity; random forest analysis was employed to predict the microbial α-diversity indices (observed species, Chao1, ACE, Shannon and Simpson indices) based on edaphic factors in rhizosphere soils. In the figures of the random forest analysis results, MSE means "mean squared error".
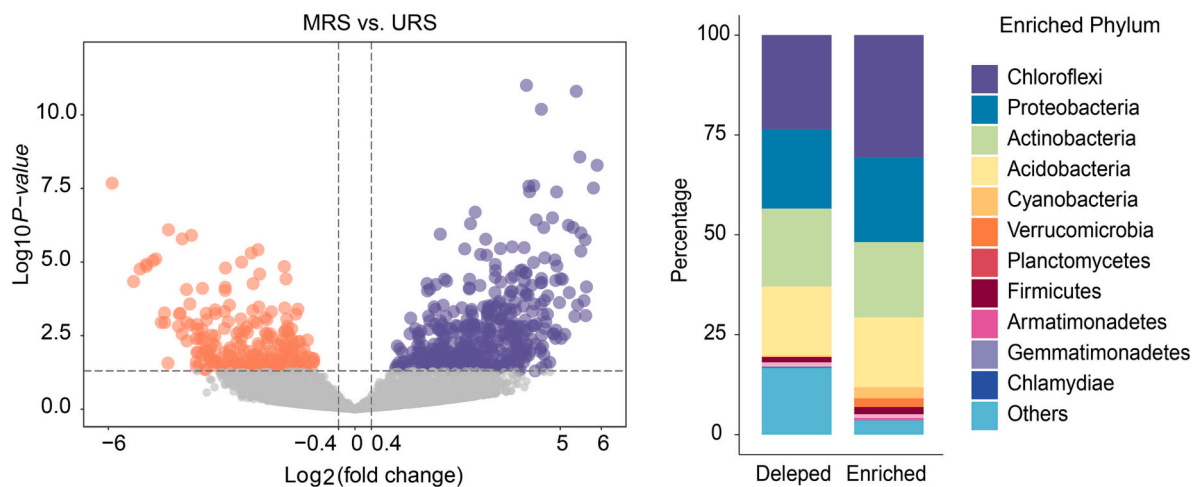

Fig. 4. Volcanic plots illustrating significantly enriched (purple circles) and depleted (orange circles) OTUs, along with the distributions of enriched species (at the phylum level) in the MRS and URS.

co-occurrence network in rhizosphere soils (Li et al., 2022b). We also utilized RF analysis to revealed the key factors influencing these keystone OTUs (Fig. S6). The results showed that Mo was the most important predictor for OTU_95 (g_*Enterococcus*), OTU_108 (f_*Muribaculaceae*), OTU_233 (g_*Stenotrophomonas*) and OTU_482 (f_*Ruminococcaceae*); P was the most important predictor for OTU_142 (g_*Bacteroides*) and OTU_401 (g_*Massilia*); and S was the most important predictor for OTU_166 (g_*Bifidobacterium*) and OTU_227 (g_*Serratia*). Interestingly, keystone OTUs, including OTU_95, OTU_233, OTU_227, OTU_185, OTU_166, OTU_142 and OTU_108, were notably enriched in the rhizosphere soils of the mining area (Fig. 5E).

3.5. Interactions between the enriched genera and edaphic factors in rhizosphere soils

As depicted in Fig. 6, the genera *Pseudomonas*, *Alcaligenes*, *Serratia*, *Vibrio*, *Bacteroides*, *Mycobacterium*, *Lacunisphaera*, *Rhodopila* and *Candidatus_Koribacter* exhibited enrichment in rhizosphere soils in mining areas. Furthermore, we employed RF analysis to further analyze the factors controlling the enriched genera (Fig. 7). The results showed that

S was the most influential factor affecting *Serratia* and *Bacteroides*, while Mo was the most influential factor affecting *Alcaligenes*.

3.6. Predicted metabolic functions

Potential microbial metabolic functions were predicted using PICRUSt based on the 16S rRNA gene sequences. The results indicated that the abundance of metabolic genes related to P, S and Mo cycling in the rhizosphere soils of the mining area was greater than that in the undisturbed area (Fig. S7).

4. Discussion

4.1. Soil nutrients inhibit As and W uptake by pioneer plants

Mining waste rocks and soils typically contain exceptionally high concentrations of toxic elements, posing formidable challenges for ecological restoration efforts in abandoned mining areas (Sun et al., 2019b; Xiao et al., 2019; Xu et al., 2023). In this study, soils from abandoned W mining areas were characterized by low nutrient levels
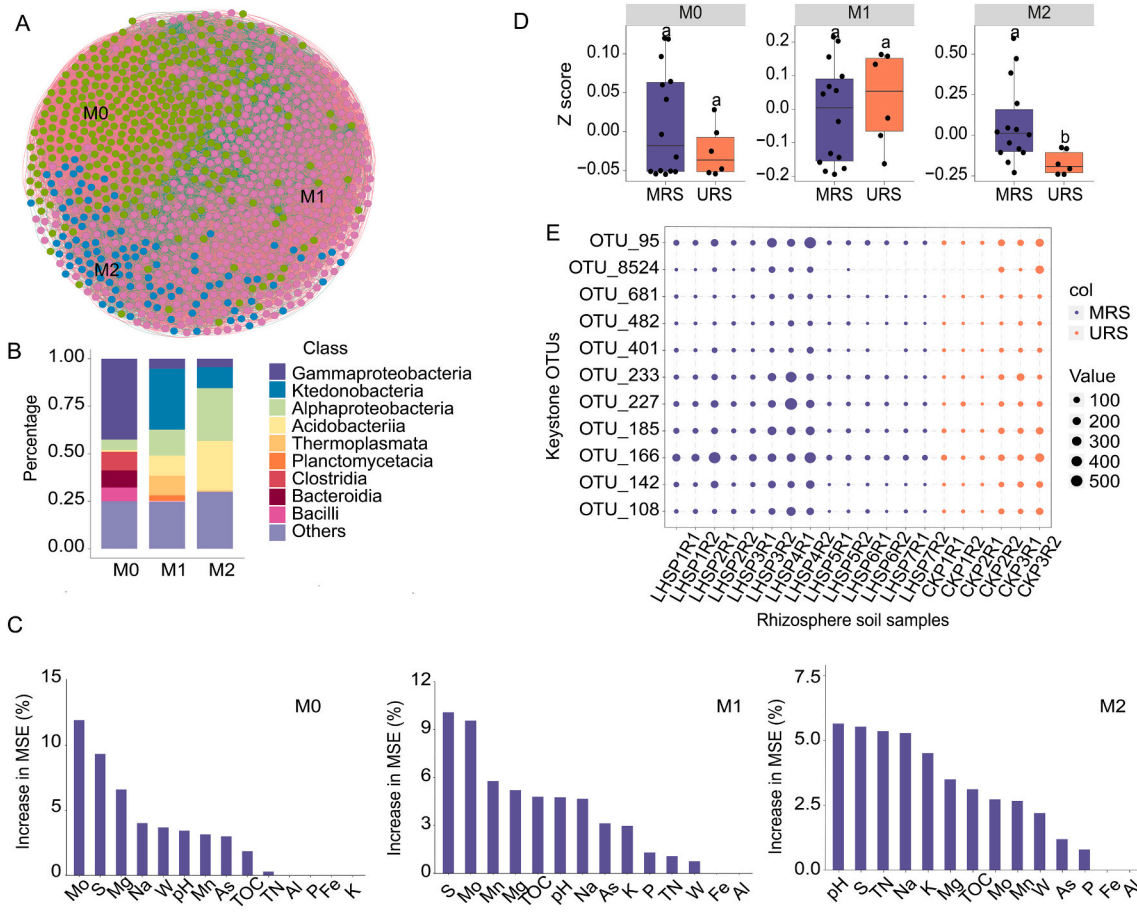
Fig. 5. A) Microbial co-occurrence network colored by the major ecological clusters (M0, M1 and M2) with the top 1000 OTUs; B) microbial distributions (at the class level) in each module (M0, M1 and M2); C) random forest analysis of module clusters predicted by edaphic factors; D) distributions of Z scores in the MRS and URS; E) bubble diagram showing the distributions of keystone OTUs in the rhizosphere soils of mining and undisturbed areas.
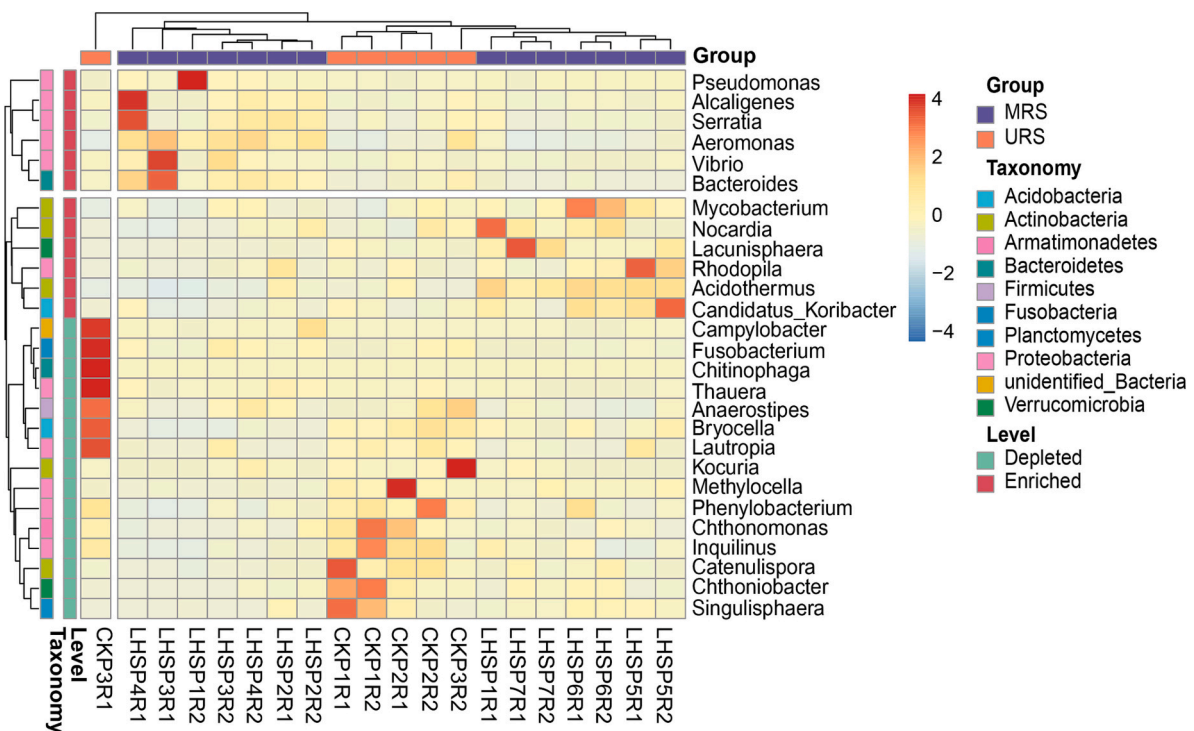

Fig. 6. Enrichment heatmaps displaying the enriched and depleted genera in the MRS and URS samples, respectively.
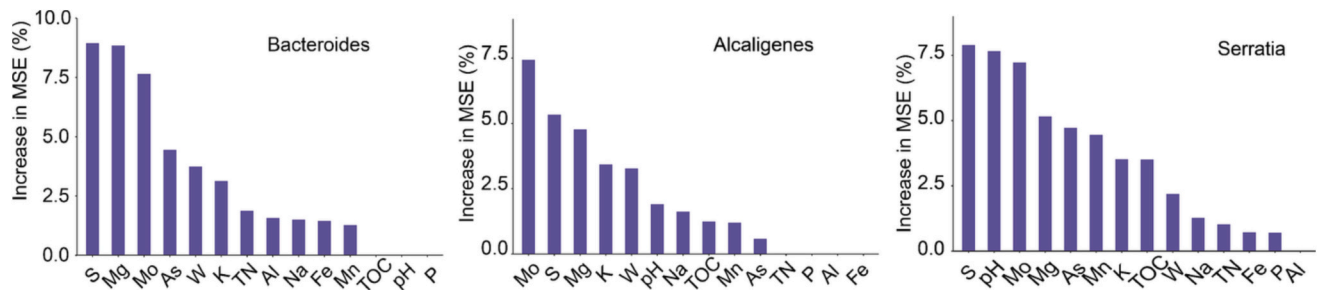
Fig. 7. Random forest analysis of genera enriched in the rhizosphere soils of mining areas.

and high As and W concentrations. Interestingly, a pioneer plant (*Blechnum orientale*) was found in this abandoned W mining area. Our findings revealed that the adaptability of *B. orientale* to such an extreme environments is closely linked to its reduced uptake of As and W. This result aligns with the observation that pioneer plants in metal mining areas exhibit limited uptake of toxic elements (Li et al., 2022b; Qian et al., 2022). Furthermore, we found that the lower uptake and translocation of As and W were closely associated with the elevated levels of nutrients (S, P and Mo) in rhizosphere soils. Current evidence suggests that the nutrients, such as S, P and Mo, may compete with As and W for uptake in cellular ion channels or reduce their phytotoxic effects by forming chelates (Koutsospyros et al., 2006; Shi et al., 2022; Zhuang et al., 2023). Our results are consistent with those of previous studies showing that plants growing in soils contaminated with toxic elements can inhibit the uptake of toxic elements through the competitive adsorption of nutrients (Liu et al., 2022c; Song et al., 2010; Wisawapipat et al., 2021). For example, As can compete with P adsorption in P transport channels in plant root cells (Shi et al., 2022; Zhuang et al., 2023). Additionally, studies have suggested that both As and W can easily complex with sulfhydryl and P-organic compounds to block toxic elements within plant roots (Koutsospyros et al., 2006; Zhuang et al., 2023). Notably, Mo serves as a crucial substance for cofactors in living organisms (Koutsospyros et al., 2006). However, when W enters an organism's cell, it can easily replace Mo during the synthesis of enzymes, thereby decreasing their activity (Koutsospyros et al., 2006). These studies suggest that the soil nutrients may play a key role in the uptake of As and W by plants. Importantly, extensive research has confirmed the crucial role of microorganisms in the biogeochemical cycling of nutrients and toxic elements in rhizosphere soils (Fan et al., 2022; Sun et al., 2019b; Sun et al., 2021; Xiao et al., 2019; Xu et al., 2022). Therefore, we hypothesized that *B. orientale* growing in W mining areas is likely to facilitate the biogeochemical cycling of nutrients by influencing the rhizosphere microbiome, thereby regulating the As and W uptake.

4.2. Effects of mining disturbance on rhizosphere microbial community distributions

In the present study, PCoA revealed distinct patterns in rhizosphere microbial community between mining and undisturbed areas through PCoA analysis (Fig. 3). This observation is consistent with prior studies indicating mining disturbance has a sustainable impact on rhizosphere microbial communities (Qian et al., 2022; Xiao et al., 2019). Moreover, we found that a majority of rhizosphere keystone OTUs were significantly enriched in mining areas compared to undisturbed areas. This suggested that mining disturbance serves as a selective force in shaping the assembly of the rhizosphere microbiome in the soil of *B. orientale* (Fig. 5E). Previous studies have suggested that plants release specific physiological root exudates into the soil to alleviate environmental stresses (Qian et al., 2022). We found that the enriched taxa in the rhizosphere soils from mining areas predominantly belonged to the phyla *Chloroflexi*, *Proteobacteria*, *Actinobacteria* and *Acidobacteria* (Fig. 4). These phyla been frequently identified in rhizosphere soils from

various mining sites, including Pb/Zn mines (Zhang et al., 2022), Sb mines (Xie et al., 2022), and Cu mines (Jiang et al., 2021). For example, *Acidobacteria* has been reported to be a versatile heterotroph with an oligotrophic (more *K*-selected) lifestyle (Chen et al., 2020; Li et al., 2021; Xiao et al., 2019), whereas *Proteobacteria* is known for its fast growth and ability to utilize a variety of carbon sources, representative of copiotrophs (Xiao et al., 2021a). The enrichment of *Acidobacteria* and *Proteobacteria* in the rhizosphere soils from mining areas is consistent with their capacity to colonize nutrient-limited soils, where phyla contribute to increasing soil nutrient contents. Therefore, mining disturbance significantly altered the rhizosphere microbiome, facilitating *B. orientale* growth in W mining areas.

RF analysis revealed that soil nutrients, such as P, S and Mo, were the most important predictors of most microbial diversity indices in rhizosphere soils (Fig. 3). This finding is consistent with prior studies indicating that soil nutrients are the most important factors shaping rhizosphere microbial diversity in metal mining areas (Dai et al., 2018; Sun et al., 2019b; Xiao et al., 2021b). Furthermore, we identified soil P, Mo and S as the most important predictors of ecological clusters and 8 keystone OTUs (Figs. 5C and S6). These findings indicate that soil nutrients are the most important factors shaping rhizosphere microbial communities and structures in *B. orientale* in W mining areas. Consistently, existing evidence has also revealed the robust effects of soil nutrients on the rhizosphere microbiome. For example, S is an important factor that regulates soil microbial distribution and metabolism in Cd-contaminated paddy soils (Liu et al., 2022a); P is one of the main factors affecting the structure and assembly of microbial communities in As/Sb-contaminated rhizosphere soil (Yu et al., 2021). Mo has been identified as the key substance for the biosynthesis of metalloenzyme cofactors for microbial metabolism, especially for N fixation (Moussa et al., 2022; Wang et al., 2022). Importantly, we observed that soil Mo, P and S were significantly different between the mining and undisturbed areas (Fig. 1). Taken together, our findings indicate that changes in soil Mo, P, and S induced by mining disturbance lead to alterations in the microbial attributes of rhizosphere microbial communities.

4.3. Keystone OTUs and genera enriched in the rhizosphere soils involved nutrient cycling

Microbial keystone taxa identified through co-occurrence network analysis are acknowledged to play a crucial role in preserving the stability of microbial ecological networks (Herren and McMahon, 2018; Xiong et al., 2021). Thus, removing any single keystone taxon may lead to substantial changes in the distribution patterns of microbial community structures (Deng et al., 2022). The keystone OTUs enriched in the rhizosphere soils of mining areas belonged to the genera *Enterococcus*, *Stenotrophomonas*, *Serratia* and *Bifidobacterium*, which have been verified to play important roles in detoxifying toxic elements and enhancing nutrient availability (Han et al., 2018; Rathi and Nandabalan, 2017; Rau et al., 2009; Yao et al., 2022). For instance, *Enterococcus* and *Stenotrophomonas* are known as Cu-resistant rhizobacteria that enhance plant growth by promoting P solubilization (Abbaszadeh-Dahaji et al.,

2019; Rathi and Nandabalan, 2017). Members of *Serratia* (*Serratia marcescens* PRE01) possess vanadium resistance traits and facilitate plant nutrient intake of P by activating the nonavailable P in rhizosphere soil (Wang et al., 2020). *Bifidobacterium*, a gram-positive bacterium, binds and absorbs more metals through synthesized hydroxyl, phosphate and carboxyl ligand molecules (Arun et al., 2021). These results suggested that keystone taxa enriched in rhizosphere soil improve nutrient bioavailability, not only by immobilizing toxic elements through chelation but also by increasing nutrient uptake by pioneer plants in W mining areas.

Importantly, we found that the rhizosphere genera of *Serratia*, *Bacteroides*, and *Alcaligenes* were significantly enriched in the mining areas. *Serratia* and *Bacteroides* are commonly found in the S-enriched environments and play important roles in S biotransformation (Chen et al., 2020; Sun et al., 2019a). Consistently, S metabolism genes were enriched in the rhizosphere soils of mining areas (Fig. S7), and soil S was the most important predictor of *Serratia* and *Bacteroides* (Fig. 7). Current evidence shows that microbially mediated S cycling can improve plant growth and immobilize As and W in rhizosphere soils (Chen et al., 2022; Mohajerin et al., 2014). Members of *Alcaligenes*, such as *Alcaligenes faecalis SRR-11* and *aoxS*, possess arsenite-oxidizing genes (such as *aoxS*, *aoxR*, *aoxA*, *aoxB*, *aoxC*, and *aoxD*) in highly As-contaminated drinking water (Chang, 2015). This arsenite oxidase involved in the detoxification of As from *Alcaligenes faecalis* is a Mo/Fe-based protein (Santini Joanne and vanden Hoven Rachel, 2004). Thus, the enrichment of genera and predicted genes related to Mo metabolism in the rhizosphere soils of the mining area could be explained by the As and W detoxifying effects exerted by the rhizosphere microbiome in *B. orientale* in the W mine (Fig. S7). Furthermore, soil Mo is considered as the most important factor shaping *Alcaligenes* distributions (Fig. 7). Taken together, our results indicate that the keystone OTUs and genera enriched in the rhizosphere soils of mining areas play a crucial role in inhibiting the uptake of As and W by *B. orientale* by enhancing P, Mo and S cycling. This further facilitates the adaptation and growth of the plant in abandoned W mining areas.

5. Conclusion

In this study, we revealed that a pioneer plant (Blechnum orientale) growing in W mining areas exhibited a low uptake of As and W. The increase in soil Mo, P, and S induced by mining disturbance led to the inhibition of As and W uptake by *B. orientale* and an alteration in the rhizosphere microbial diversity, ecological clustering, and keystone taxa. The enrichment of keystone taxa and genera in rhizosphere soils mediated by nutrient (P, S and Mo) cycling can increase nutrient bioavailability, which may promote the inhibition of As and W uptake by *B. orientale*. In this study, the potential roles of the rhizosphere microbiome in regulating As and W uptake by *B. orientale* were explored, which provided important theoretical and experimental evidence for the effective implementation of phytoremediation in abandoned W mining areas.

CRediT authorship contribution statement

Xiaolong Lan: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Funding acquisition, Writing – original draft. **Zengping Ning:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Conceptualization. **Yanlong Jia:** Writing – review & editing, Visualization, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wenjie Lin:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Enzong Xiao:** Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Qianyun Cheng:** Writing – review & editing, Visualization, Funding

acquisition, Formal analysis. **Qiaoxue Cai:** Methodology, Investigation. **Tangfu Xiao:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171429.

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