



Research Article

# Rhizosphere microbial community structure in the water-level-fluctuation zone under distinct waterlogging stresses

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## Abstract

Rhizosphere microbial communities are believed to be vital in the adaption of dominant plants to strong waterlogging stress in the water-level-fluctuation zone (WLFZ). However, limited knowledge is available on their patterns in the WLFZ under distinct waterlogging stresses. Here, rhizosphere and non-rhizosphere bacterial and fungal communities derived from two typical dominant plants (*Rumex acetosa* L. and *Oxybasis glauca*) in the WLFZ of Three Gorges Reservoir, China were analysed through high-throughput sequencing. A total of 63 phyla, 173 classes, 259 orders, 287 families and 518 genera of bacteria, as well as 15 phyla, 50 classes, 124 orders, 265 families and 652 genera of fungi were detected in soils with different waterlogging stress intensities. The most dominant bacterial and fungal phyla in each sample are Proteobacteria and Ascomycota, respectively. Bacteria and fungi in soil may increase their microbial  $\alpha$  diversity under the intensity of waterlogging stress to cope with this stress. LEfSe analysis showed that the impact of waterlogging stress on fungal community structure in soil is more prominent than that on bacteria. Key fungal biomarkers can be found in each soil sample, but in many samples, key bacterial biomarkers cannot be found. The metabolic pathways

related to aerobic respiration type I and de novo biosynthesis of adenosine ribonucleotides dominate in the microbial community. Redundancy analysis revealed that the structure of rhizosphere microbial communities in different plants is significantly influenced by environmental factors. This study provides a theoretical basis for understanding the relationship between plants and their second genome (rhizosphere microorganisms) in extreme habitats, such as the WLFZ of large reservoirs.

## Keywords

Three Gorges Reservoir; water-level-fluctuation zone; waterlogging stress; rhizosphere microorganisms; biodiversity

## Introduction

Microbes in rhizosphere soils of plants are closely related to the living ecosystem, so that variations in the environment can quickly cause rhizosphere microbial variations (Adeyayo et al. 2022). Changing environment also may force the host plants to re-structure the composition of their rhizosphere microbiota (Liu et al. 2023, Enagbonma et al. 2024). These microbes exhibit high diversity (Benitez et al. 2021, Iannucci et al. 2021, Ling et al. 2022) which can survive in extreme environmental conditions, for example, varying and strong waterlogging stresses in the WLFZ of the reservoirs formed due to the construction of water conservancy projects (Zhang et al. 2021, Li et al. 2021). They are believed to be vital to vegetation restoration in such extreme environment (Chen et al. 2020b, Zhou et al. 2023, Wang et al. 2024b). However, up to now, little is known about their patterns in the WLFZ under varying waterlogging stresses.

Under long-term stress, plants undergo changes in their metabolic activities and transform their rhizosphere secretions (Barra Caracciolo and Terenzi 2021). They can adjust and assemble the structure and function of the rhizosphere microbial community as needed to cope with current stress (Ge et al. 2023). Many studies have found that rhizosphere microorganisms have functions such as promoting plant growth, disease resistance and yield and enhancing plant stress resistance (Liu et al. 2020, Guo et al. 2023). This is because rhizosphere microorganisms can provide plants with available mineral nutrients, plant hormones etc. to promote plant growth (Chamkhi et al. 2022, Dlamini et al. 2022). In addition, the rhizosphere of plants can promote plant growth by attracting beneficial symbiotic microorganisms such as archaea, bacteria and fungi (Chamkhi et al. 2022). In barren tailings areas contaminated with heavy metals/metalloids, rhizosphere microorganisms can adopt a series of survival strategies to adapt to harsh environments and their community structure will undergo corresponding adjustments. Key microbial categories generally have heavy metal/metalloid tolerance, such as *Chlamydomonas*, *Pseudomonas* and *Nocardia* (Geng et al. 2022). Under drought stress, rhizosphere microorganisms can help improve the adaptability of host plants such as sugarcane (Liu et al. 2021). Multiple studies have confirmed that waterlogging stress can cause changes in the structure of plant rhizosphere microbial

communities, such as in sweet cabbage seedlings (Li et al. 2023), soybean (Yu et al. 2022, Lian et al. 2023) and rice (Liu et al. 2023). It is worth mentioning that the influence of plants and rhizosphere microorganisms is mutual. The root phenotype, genotype, developmental stage and species of plants can also affect the rhizosphere microbiota of plants (Zhang et al. 2018, Cotton et al. 2019, Zhang et al. 2021). Although many studies have investigated and analysed the community structure changes of various plant rhizosphere microorganisms under different abiotic stresses (Mukhtar et al. 2019, Khan et al. 2021), there are few reports on the enrichment characteristics of rhizosphere microorganisms of different dominant plants in the WLFZ of Three Gorges Reservoir under different levels of waterlogging stress intensity.

After the operation of the Three Gorges Water Conservancy Project, a water-level-fluctuation zone (WLFZ) with 30 m (145 m-175 m) drop was formed on both sides of the Three Gorges Reservoir due to periodic water storage. Periodic water storage has caused fluctuations in the water level of the Three Gorges Reservoir, resulting in changes in the intensity of waterlogging stress and profound changes in the vegetation structure of the Three Gorges Reservoir's WLFZ. Recent research has reported that the dominant plants in the current WLFZ are mainly herbaceous, where *Rumex acetosa* L. and *Oxybasis glauca* are common dominant plants. Dominant plants in low-altitude areas are inevitably subjected to greater water waterlogging stress and can withstand waterlogging stress for a longer period of time compared to dominant plants in high-altitude areas. Waterlogging stress can affect the level of oxygen in the soil, which in turn, affects soil respiration and the uptake and utilisation of soil nutrients by plants (Yu et al. 2022). The rhizosphere microorganisms of plants are considered as their second genome (Berendsen et al. 2012, Liu et al. 2022), playing an important supporting role in the survival of plants, helping them better utilise nutrients to adapt to waterlogging stress. The dominant plants in the WLFZ of Three Gorges Reservoir may adjust their rhizosphere microorganisms to adapt to this extreme habitat under different levels of waterlogging stress. However, up to now, the characteristics of changes in the rhizosphere microbial community structure of typical dominant plants in the WLFZ of Three Gorges Reservoir under different levels of waterlogging stress are still unclear.

In order to address the above issues, this study selected two dominant plants in the WLFZ of Three Gorges Reservoir (*R. acetosa* L. and *O. glauca*) and conducted high-throughput sequencing analysis on the microbial community structure of rhizosphere and non-rhizosphere soils from the WLFZ with different waterlogging stress intensities. Their frequency in the sampling area is greater than 20%, so they can be considered as the dominant plants in this area (Jiang et al. 2023). The differences and similarities in the composition, structure and metabolic functions of soil bacteria and fungi under different plant species and waterlogging stress intensities were compared, providing a theoretical basis for elucidating the interaction mechanism between dominant plants and microorganisms in the WLFZ under waterlogging stress. In this study, in order to distinguish different waterlogging stress intensity in the WLFZ of Three Gorges Reservoir, the WLFZ was divided into weak waterlogging stress intensity areas (above 165 m, HL area) and strong waterlogging stress intensity areas (below 165 m, LL area).

## Materials and methods

### Study site

The site of this study is located in the main urban area of Chongqing City, China (Fig. 1). Chongqing City is a municipality directly under the central government of China, consisting of 38 districts and counties and belongs to the subtropical monsoon climate zone. The Jiangbei District, where this research site is located, is one of the core areas of the main urban area of Chongqing City. It is situated in the northern part of Chongqing City and is surrounded by the Yangtze River. The average annual temperature, precipitation, relative humidity and sunshine hours are 18.4°C, 1100.7 mm, 79.4% and 1094.4 hours, respectively. In the WLFZ near Tangjiatuo in Jiangbei District, Chongqing (29.598225°N, 106.649686°E), typical dominant plants include *R. acetosa* L. and *O. glauca*. The WLFZ of Three Gorges Reservoir has often been divided into three areas in previous studies (Zhu et al. 2020, Shen et al. 2022, Chen et al. 2024): area 1 at 145-155 m, area 2 at 155-165 m and area 3 at 165-175 m. In the present study, area 1 and area 2 were combined into an area due to the fact that the water level is higher than 155 m at the sampling time. Thus, the selected sampling sites include high elevation areas (above 165 m) and low elevation areas (below 165 m) in this study, corresponding to weak waterlogging stress areas (HL) and strong waterlogging stress areas (LL), respectively. For each area, there are more than 10 sampling sites which are stochastically determined by the vegetation distribution.

### Rhizosphere soil sampling

Rhizosphere soil refers to the soil directly affected by plant roots, which differs from conventional soil in terms of physical, chemical properties and microbial composition. For each dominant plant, we collected rhizosphere soil from over 20 plant individuals in the HL and LL regions, as well as non-rhizosphere soil from nearby areas and placed them in sterile test tubes and sealed bags in March 2023. Three separate samples were collected for each type. For the rhizosphere and non-rhizosphere samples collected from *R. acetosa* L. at the HL region, they are labelled as RuRHL and RuNHL, respectively, while for the rhizosphere and non-rhizosphere samples collected from the LL region, they are labelled as RuRLL and RuNLL, respectively. Similarly, the rhizosphere and non-rhizosphere samples of *O. glauca* collected from the HL region are referred to as OxRHL and OxNHL, respectively, while the rhizosphere and non-rhizosphere samples of *O. glauca* collected from the LL region are referred to as OxRLL and OxNLL, respectively. The collected samples were put into a portable car refrigerator and brought back to the laboratory. The samples stored in sterile test tubes were sent to Wekemo Company for high-throughput sequencing of 16S and ITS after simple processing. Samples stored in sealed bags are sieved and dried to determine their physicochemical properties.

### Physical and chemical property analysis

A total of 14 indicators were measured for the physicochemical properties of rhizosphere and non-rhizosphere soil samples of dominant plants in the WLFZ, including total

nitrogen, pH, organic carbon (organic matter), alkaline hydrolysable nitrogen, available phosphorus, available potassium, EC, ammonium nitrogen, nitrate nitrogen, urease, catalase, dehydrogenase, alkaline phosphatase and sucrase. The determination methods include Kjeldahl method, glass electrode method, potassium chromate oxidation external heating method, alkaline diffusion method, molybdenum antimony colourimetric method, flame photometry, electrode method, ultraviolet spectrophotometry and kit detection method (Cheng et al. 2022, Wang et al. 2022, Lin et al. 2023). The determination of enzyme activity mainly used commercial reagent kits, such as urease, catalase, alkaline phosphatase and sucrase which were purchased from Nanjing Molfarming Biotechnology Co., Ltd., while the TTC colourimetric method was used for the determination of soil dehydrogenase content.

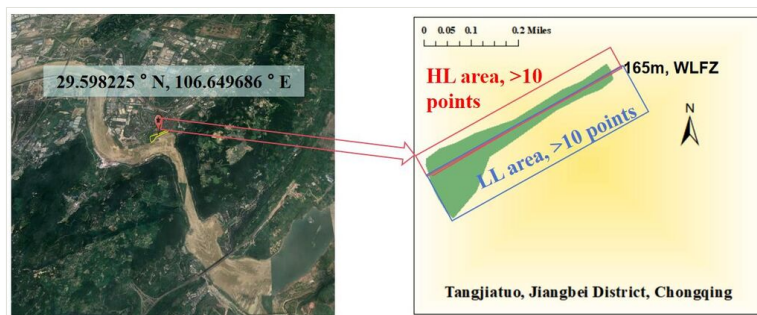


Figure 1.

The map of study area.

### High throughput sequencing

After sieving and processing of the sample, DNA was extracted and sequenced at Wekemo Company. The specific steps were as follows: Primer 1 (CCTAYGGGRBGCASCAG and GGACTACNNGGGTATCTAAT) and primer 2 (CTTGGTCATTTAGAGGAAGTAA and GCTGCGTTCCTTCATCGATGC) were used for PCR amplification of 16S V3+V4 variable region and ITS region. Agarose gel of 2% concentration was used for electrophoresis detection of PCR products; Qiagen gel recovery kit for PCR product recovery and purification was used and TruSeq® DNA PCR-Free Sample Preparation Kit was used for library construction. After passing the inspection, sequencing was carried out. The data were processed using QIIME2 to obtain amplicon sequence variants (ASV). The obtained ASV sequences were subjected to taxonomic annotation, species classification and species composition analysis using the UNITE database and GREEGENES database.

### Data analysis

Microbial  $\alpha$  diversity is calculated and analysed to observe or compare the mean species diversity between different samples through QIIME2 software using the Kruskal-Wallis test (a type of non-parametric test) (Bolyen et al. 2019), including chao1 index, faith\_pd, observed\_features, Shannon index and Simpson index:

where 'Observed' is the observed\_features that indicate the number of observed features or species, 'n1' refers to the number of species that appear only once and 'n2' refers to the number of species that appear twice.

$$\text{Shannon index} = - \sum_{i=1}^{\text{Observed}} \frac{n_i}{N} \ln \frac{n_i}{N}$$

where  $n_i$  refers to the number of the  $i^{\text{th}}$  species and  $N$  indicates the total number of sequences.

$$\text{Simpson index} = - \sum_{i=1}^{\text{Observed}} \frac{n_i(n_i - 1)}{N(N - 1)}$$

The faith\_pd refers to the phylogenetic diversity of species that can be calculated by summing all related branch lengths on a rooted tree connecting all taxa in an analysed microbial community (Faith 1992).

These indexes have been extensively adopted to investigate the species richness, abundance and diversity (Zhou et al. 2023, Kumar et al. 2024). Key biomarkers that differentially represented between HL and LL areas were identified by linear discriminant analysis (LDA) effect size (LEfSe) with a LDA score of  $> 4$  (Segata et al. 2011). Redundancy analysis (RDA) was carried out to elucidate the correlations between microbial communities and environmental variables, based on the microbial relative abundances at the phylum level by Wekemo Bioincloud (<https://www.bioincloud.tech>). The MetaCyc metabolic pathways of microbial communities were analysed with PICRUST2 software with default parameters.

## Results and discussion

The results indicate that a total of 38517 bacterial OTUs were found in the rhizosphere and non-rhizosphere soils of dominant plants in the WLFZ of Three Gorges Reservoir, belonging to 63 phyla, 173 classes, 259 orders, 287 families and 518 genera, as well as 8658 fungal OTUs belonging to 15 phyla, 50 classes, 124 orders, 265 families and 652 genera. It can be seen that the number of bacterial OTUs is higher than that of fungal OTUs, which is consistent with the natural forest soil of *Olea cuspidata* (Guo et al. 2023), rhizosphere soil of three endangered plants (*Tetraena mongolica*, *Sarcozygium xanthoxylon* and *Nitraria tangutorum* Bobr) (Xu et al. 2020) and tea garden soil (Zhang et al. 2023). In the soil, the total amount of bacteria often dominates and over 70% of the total soil biomass are often bacteria (Wang et al. 2024a). The identification and analysis of bacteria and fungi in various soil samples in this study were relatively clear at the phylum level, but the proportion of unclassified bacteria at the order and genus classification levels was relatively high (50-72%), while the proportion of unclassified fungi was relatively lower (7-65%).

## Diversity of rhizosphere microbial communities in dominant plants

The diversity of soil microorganisms plays a major role in enhancing community stability under stress (Ding et al. 2021). Similar to our previous work (Zhou et al. 2023), this study used five  $\alpha$  diversity indices (chao1 index, faith\_pd, observed\_features, Shannon index and Simpson index) to explore the diversity of rhizosphere microorganisms under different levels of waterlogging stress. For *R. acetosa* L., the richness and diversity of rhizosphere microorganisms in the LL region are higher than those in the HL region, as shown in Table 1. No matter whether it is bacterial or fungal communities, RuRLL generally has higher chao1 index values, faith\_pd values, observed\_features values, Shannon index values and Simpson index values than RuRHL. It is interesting that this situation also applies to non-rhizosphere soil near the *R. acetosa* L., where various index values of RuNLL are higher than those of RuNHL. For *O. glauca*, its microbial community status is consistent with that of *R. acetosa* L. The chao1 value, faith\_pd value, observed\_features value, Shannon index value and Simpson index value of OxRLL and OxNLL are generally higher than those of OxRHL and OxNHL, respectively. These results indicate that, in order to cope with stronger waterlogging stress, dominant plants in the WLFZ may adopt the ways through the enhancement of rhizosphere microbial diversity to resist stress (Zhou et al. 2023).

Table 1.

Alpha diversity of rhizosphere microbial communities from dominant plants in the Three Gorges Reservoir.

Sample	Microorganism	Chao1	F aith_pd	Observed_features	Shannon	Simpson
RuRHL	Bacteria	3433.82 ± 76.86	228.86 ± 11.22	3400 ± 79.41	10.49 ± 0.10	0.998 ± 0.0003
	Fungi	636 ± 4 3.06	106.24 ± 10.40	636 ± 43.06	5.61 ± 0.02	0.92 ± 0.02
RuRLL	Bacteria	3676.56 ± 601.87	247.10 ± 32.84	3640.33 ± 593.67	10.61 ± 0.69	0.998 ± 0.002
	Fungi	882.33 ± 35.24	149.91 ± 6.34	882.33 ± 35.24	6.94 ± 0.07	0.97 ± 0.001
RuNHL	Bacteria	3557.14 ± 323.97	229.96 ± 5.19	3523.33 ± 314.43	10.46 ± 0.37	0.997 ± 0.0016
	Fungi	654.33 ± 73.62	118.73 ± 8.37	654.33 ± 73.62	5.18 ± 0.60	0.88 ± 0.04
RuNLL	Bacteria	3681.88 ± 430.81	231.45 ± 7.80	3648 ± 421.73	10.75 ± 0.34	0.998 ± 0.0007
	Fungi	916.33 ± 222.85	149.01 ± 29.08	916.33 ± 222.85	6.05 ± 0.38	0.96 ± 0.006
OxRHL	Bacteria	2591.31 ± 882.75	177.58 ± 37.20	2570.67 ± 876.11	9.99 ± 0.67	0.997 ± 0.002
	Fungi	607.33 ± 77.07	101.14 ± 12.37	607.33 ± 77.07	5.01 ± 0.45	0.86 ± 0.07
OxRLL	Bacteria	3549.41 ± 715.35	223.45 ± 27.65	3522 ± 706.09	10.56 ± 0.68	0.998 ± 0.002
	Fungi	721.33 ± 31.90	125.96 ± 5.94	721.33 ± 31.90	5.25 ± 0.10	0.91 ± 0.004
OxNHL	Bacteria	3659.77 ± 107.39	257.81 ± 10.65	3624.67 ± 114.02	10.73 ± 0.18	0.998 ± 0.0005
	Fungi	526.33 ± 41.45	92.75 ± 5.25	526.33 ± 41.45	5.83 ± 0.24	0.95 ± 0.02
OxNLL	Bacteria	3886.62 ± 164.95	278.18 ± 5.09	3854.67 ± 161.30	10.92 ± 0.17	0.999 ± 0.0003
	Fungi	651.33 ± 54.32	105.27 ± 17.03	651.33 ± 54.32	6.34 ± 0.59	0.97 ± 0.009

When comparing the diversity of rhizosphere microbial communities of the two dominant plants mentioned above, it can be found that the diversity of rhizosphere bacteria and fungi in *R. acetosa* L. is generally higher. It is worth noting that there are significant differences in the diversity of rhizosphere bacterial communities between *R. acetosa* L. and *O. glauca* in the HL region. Taking the chao1 index as an example, the chao1 index of *R. acetosa* L. is  $3433.82 \pm 76.86$ , while the chao1 index of *O. glauca* is  $2591.31 \pm 882.75$ , with a large difference between them. However, for the LL region, the diversity of rhizosphere bacterial communities in *R. acetosa* L. and *O. glauca* is comparable with little difference. For example, their chao1 indices are  $3676.56 \pm 601.87$  and  $3549.41 \pm 715.35$ , respectively, with a small difference between them. This indicates that the key factor affecting the diversity of rhizosphere microorganisms in dominant plants in the WLFZ may be the intensity of waterlogging stress, in which the influence of plant species only accounts for a small proportion.

In order to show the differences in the diversity of rhizosphere microbial communities from dominant plants under different microenvironments more clearly, this study used Venn diagrams for analysis (Fig. 2) and found that the unique OTU numbers in the rhizosphere bacterial communities of *R. acetosa* L. at HL and LL were 4536 and 4598, respectively, while those at non-rhizosphere were 4216 and 5399, respectively; For *O. glauca*, OxRHL has the fewest unique OTUs, followed by OxRLL and OxNLL has the most. As for the fungal community, RuNLL has the highest number of unique OTUs in *R. acetosa* L., while XaRLL has the highest number of unique OTUs in *O. glauca* (1114). These results once again confirm that the diversity of rhizosphere microorganisms in dominant plants under high waterlogging stress at low elevations is relatively higher.

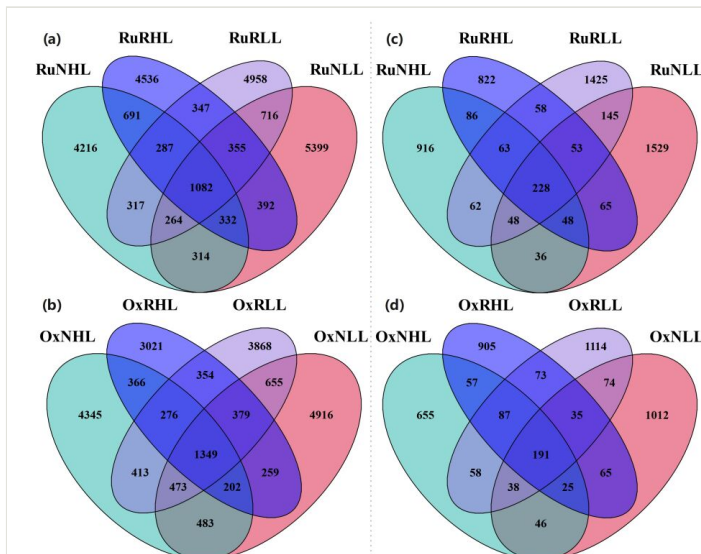


Figure 2.

Venn diagram of bacterial and fungal operational taxonomic units (OTUs) in the rhizosphere and non-rhizosphere soils. (a) Bacteria for *Rumex acetosa* L., (b) bacteria for *Oxybasis glauca*, (c) fungi for *Rumex acetosa* L. and (d) fungi for *Oxybasis glauca*.



### Structural characteristics of rhizosphere microbial communities in dominant plants

As shown in (Fig. 3), the dominant bacterial phylum in rhizosphere and non-rhizosphere bacterial communities of *R. acetosa* L. is Proteobacteria, but its relative abundance in rhizosphere soil is higher than that in non-rhizosphere soil (> 46% vs. < 43%). This is similar to the soil conditions in the rhizosphere of *Cynodon dactylon* and *Hemarthria altissima* in the Three Gorges Reservoir area, where Proteobacteria has also been found to be their dominant phylum (Tan et al. 2023). In addition, Proteobacteria is also one of the dominant bacterial phyla in the rhizosphere of *Cynodon dactylon*, *Metasequoia glyptostroboides* and *Chrysopogon zizanioides* in the WLFZ of Danjiangkou Reservoir (Chen et al. 2020a). Li et al. also showed that no significant differences were observed in the rhizosphere and non-rhizosphere soil microbial communities of plants (such as *Taxodium distichum*, *Salix matsudana*, *Cynodon dactylon* and *Hemarthria altissima*) in the WLFZ of Three Gorges Reservoir (Li et al. 2020). Proteobacteria is composed of diverse microorganisms, covering a very complex phenotype and physiological characteristics. For example, many phototrophic, chemotrophic and heterotrophic microorganisms belong to Proteobacteria (Gupta 2000). The intensity of waterlogging stress did not change the dominant bacterial phylum in the rhizosphere and non-rhizosphere bacterial communities of *R. acetosa* L. However, overall, the soil dominant bacterial phylum Proteobacteria in areas with stronger waterlogging stress had a higher relative abundance. The suboptimal bacterial phyla are somewhat different, with Acidobacteria and Firmicutes being the dominant phyla in RuNHL and RuNLL and Bacteroidetes are the dominant phyla in RuRHL and RuRLL.

Ascomycota is at the highest relative abundance in the rhizosphere and non-rhizosphere soils of *R. acetosa* L., with relative abundance close to or greater than 80% in RuRHL, RuNHL and RuNLL (Fig. 4). Ascomycota consists of three subphyla, namely Pezizomycotina (13 classes, 124 orders and 507 families), Saccharomycotina (1 class, 1 order and 13 families) and Taphrinomycotina (5 classes, 5 orders and 6 families) (Wijayawardene et al. 2018), widely present in soils around the world and some ascomycetes dominate fungal communities (Egidi et al. 2019). However, the relative abundance of Ascomycota in RuRLL is only 53.8%, which is significantly different from the first three. This is because RuRLL has a higher proportion of Chytridiomycota, Glomeromycota and Rozellomycota compared to other samples, with these three fungal phyla accounting for nearly 28%. The increase in waterlogging stress intensity did not change the dominant pattern of Ascomycota in fungal communities in the rhizosphere and non-rhizosphere soils of *R. acetosa* L.

At the taxonomic level of order, the proportion of various bacterial orders in the rhizosphere and non-rhizosphere soil samples of *R. acetosa* L. is relatively low. The highest relative abundance is Clostridiales in RuNLL, accounting for 12.22%, with few exceeding 10%. Zhang et al. also found that Clostridiales are dominant bacteria in greenhouse grape rhizosphere soil and are affected by water stress (Zhang et al. 2019). The situation of fungi is different, with relative abundance exceeding 10% for Pleosporales, Hypocreales, Glomerellales, Capnodiales, Helotiales, Sordariales and Venturiales. At the taxonomic level of genus, the dominant bacterial genera in the

rhizosphere and non-rhizosphere soil samples of *R. acetosa* L. are *Kaistobacter*, *Flavobacterium* etc., accounting for less than 20%. *Kaistobacter* and *Flavobacterium* were also found to be dominant bacteria in the soil of the Shizishan mining area in Tongling, Anhui Province (Huang et al. 2019). In addition, *Kaistobacter* and *Flavobacterium* have been reported as potential degradation microorganisms of the chloroacetamide herbicide acetochlor in soil (Han et al. 2021). It can be seen that the impact of waterlogging stress intensity on the bacterial communities in the rhizosphere and non-rhizosphere soils of *R. acetosa* L. mainly occurs at lower taxonomic levels (such as order and genus levels). In areas with strong waterlogging stress, the relative abundance of the top 10 bacterial orders in the rhizosphere and non-rhizosphere soils of *R. acetosa* L. decreased by 10% and 13%, respectively, compared to areas with low waterlogging stress; the total number of bacterial genera in the top 10 rhizosphere and non-rhizosphere soils of *R. acetosa* L. in areas with strong waterlogging stress decreased by 16% and 13%, respectively, compared to areas with low waterlogging stress (Fig. 3). Under strong waterlogging stress, the total abundance of the top 10 fungal orders and genera in the fungal communities of rhizosphere and non-rhizosphere soil from *R. acetosa* L. decreased to a certain extent (Fig. 4).

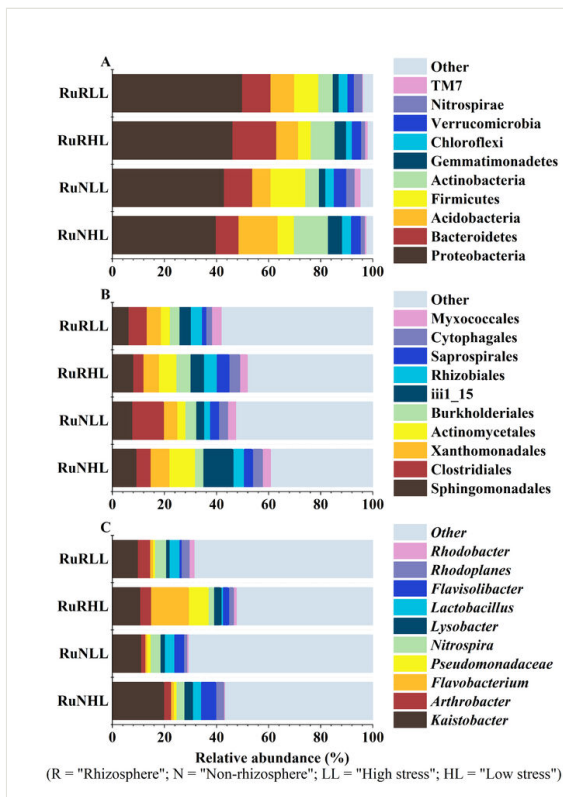


Figure 3. Relative abundance of bacteria in rhizosphere and non-rhizosphere soils of *Rumex acetosa* L. at the phylum (A), order (B) and genus (C) levels.

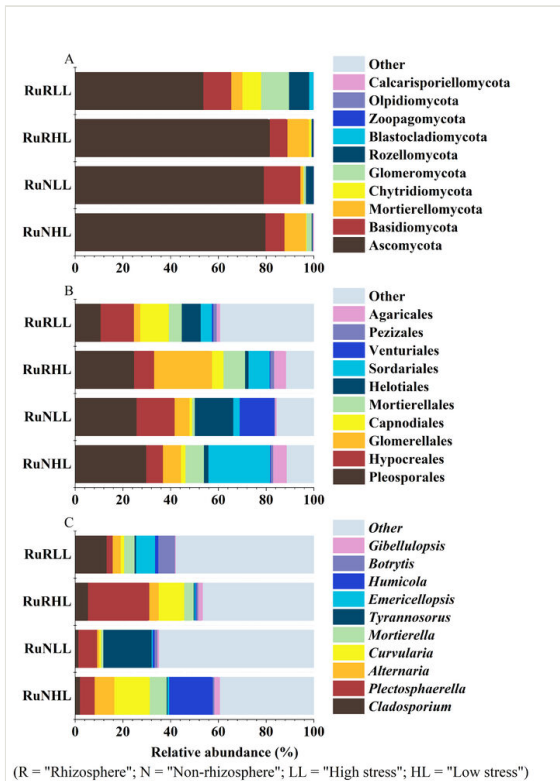


Figure 4.

Relative abundance of fungi in rhizosphere and non-rhizosphere soils of *Rumex acetosa* L. at the phylum (A), order (B) and genus (C) levels.

The relative abundance of bacterial and fungal communities in the rhizosphere and non-rhizosphere soils of *O. glauca* in the WLFZ of Three Gorges Reservoir are shown in Figs 5, 6, respectively. Similar to *R. acetosa* L., Proteobacteria is the most dominant bacterial phylum amongst all samples of *O. glauca* (46.82-58.40%). These results, along with previous studies (Tan et al. 2023), show that, after years of periodic waterlogging stress, the soil in the WLFZ of Three Gorges Reservoir has formed a microecological pattern dominated by Proteobacteria as the main dominant bacteria. Many studies have found that, in addition to the WLFZ of the Three Gorges Reservoir, Proteobacteria can adapt to diverse habitats and they are also commonly found in the rhizosphere soil of species, such as *Eichhornia crassipes* (Sharma et al. 2021), Chinese medicinal herb *Dendrobium* (Zuo et al. 2021) and Peanut (Dai et al. 2019). The other major dominant bacterial phyla include Bacteroidetes, Acidobacteria, Firmicutes and Actinobacteria, which account for over 5% of the majority of the samples. For fungi, the most dominant phylum is Ascomycota, with a relative abundance generally above 80%. However, in OxRHL, the relative abundance is about 60%. The relative abundance of Mortierellomycota and Chytridiomycota significantly increased, reaching 16.14% and 17.00%, respectively.

Ascomycota is one of the most common fungi in the rhizosphere soil of plants, such as *Camellia yuhsienensis* Hu (Li et al. 2020), *Stipa purpurea* (Liu et al. 2022) and banana (Shen et al. 2015). Clostridiales is the only bacterial order that accounts for over 10% in the soil samples of *O. glauca* and was found in OxNLL samples with a relative abundance of 14%. Sphingomonadales is the bacterial order with the highest relative abundance amongst other three samples, with a relative abundance of less than 8%. The situation of fungi is different, with Pleosporales (18.59-31.22%) being the most dominant fungal order amongst the four groups of samples. *Kaistobacter* is a relatively dominant bacterial genus in the soil samples of *O. glauca*, but its relative abundance is not high (5.33-10.9%). It is worth noting that the fungal community structure of different soil samples of *O. glauca* varies greatly at the genus level. *Cladosporium* and *Gibellulopsis* are dominant fungal genera in OxNHL, *Plectosphaerella* and *Tyrannosorus* are dominant fungal genera in OxNLL, *Mortierella* and *Curvularia* are dominant fungal genera in OxRHL and *Cladosporium* and *Alternaria* are dominant fungal genera in OxRLL. These results indicate that an increase in waterlogging stress intensity does not change the absolute dominant position of Proteobacteria and Ascomycota in the microbial community in the rhizosphere and non-rhizosphere soils of *O. glauca*, but has a relatively significant impact on other microorganisms.

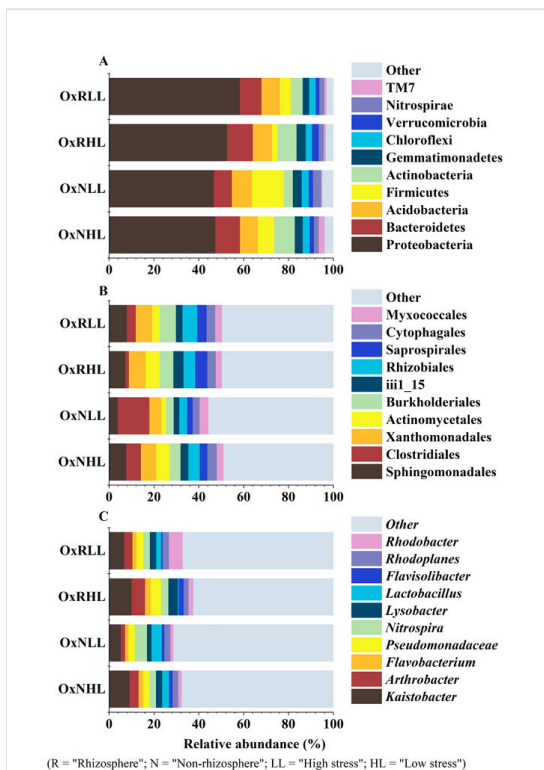


Figure 5.

Relative abundance of bacteria in rhizosphere and non-rhizosphere soils of *Oxybasis glauca* at the phylum (A), order (B) and genus (C) levels.

## Analysis of Key Biomarkers and Potential Metabolic Functions

Waterlogging stress alters the composition and diversity of soil microbial communities, which may lead to the formation of key biomarkers in different samples and affect their metabolic functions. The LEfSe method was used to analyse the differences in microbial community between rhizosphere and non-rhizosphere soil samples of *R. acetosa* L. and *O. glauca*, respectively. The LDA threshold is consistent with previous study (Zhou et al. 2023), set to > 4 with a p-value < 0.05 (Suppl. material 1). This study first analysed the key biomarkers in the bacterial community of soil samples. The results showed that for *R. acetosa* L., no key biomarkers of bacterial community were found in RuNHL, while the key biomarkers in RuRLL were Rhizobiales, Hyphomicrobiaceae and *Novosphingobium*, the key biomarkers in RuRHL were Bacteroidetes, Gammaproteobacteria and *Ramlibacter* and the key biomarkers in RuNLL were Lachnospiraceae and *Ruminococcus*. For *O. glauca*, no key bacterial community markers were found in the samples from the HL region. Only one key biomarker (Proteobacteria) was found in OxRLL, while up to nine biomarkers were found in OxNLL including *Ruminococcus*, Firmicutes, Clostridiales, Clostridia, Lachnospiraceae, Lactobacillales, Deltaproteobacteria and *Oscillospira*. The results of this study indicate that areas with strong waterlogging stress tend to have more key bacterial biomarkers.

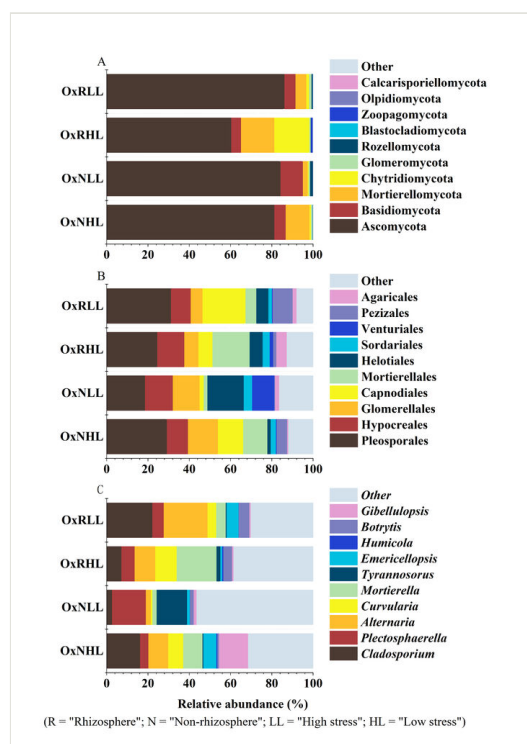


Figure 6.

Relative abundance of fungi in the rhizosphere and non-rhizosphere soils of *Oxybasis glauca* at the phylum (A), order (B) and genus (C) levels.

This study continued to analyse key biomarkers in fungal communities in soil samples, which were significantly different from bacteria. Key fungal biomarkers were found in soil samples from areas with strong and low waterlogging stresses. For *R. acetosa* L., RuRHL has the least number of key biomarkers with a total of three, all of which appear at the genus level, including *Pseudopithomyces*, *Schizothecium* and *Gibberella*. There are a total of seven key biomarkers in RuNHL, mainly at the genus and family levels (6/7). It is worth noting that, compared to these samples with high elevation and low stresses, the number of key biomarkers in the samples from the LL area is significantly higher, with 13 and 10 key biomarkers in RuNLL and RuRLL, respectively. This may be the result of soil microorganisms adjusting their microbial community structure to adapt to strong waterlogging stress. For *O. glauca*, OxRLL contains three key biomarkers at the order, family and genus levels, including *Cladosporium*, Capnodiales and Cladosporiaceae. Interestingly, *Mortierella* in OxRHL exhibits significant differences at the genus, family, order, class and phylum levels compared to other samples. There are five key biomarkers in OxNHL, including Orbiliaceae, Orbiliomycetes, Orbiliales, *Curreya* and *Gibellulopsis*. Ten key biomarkers were identified in OxNLL, of which six were at the genus level and no significant differences were found at the phylum level.

Current research on rhizosphere soil microorganisms in the WLFZ of reservoirs in the upper reaches of the Yangtze River often only involves the metabolic functions of bacteria, with little involvement of fungi. This study analysed the potential metabolic functions of rhizosphere bacteria and fungal communities of dominant plants in the WLFZ of the Reservoir using PICRUSt2 (Douglas et al. 2020) and MetaCyc database (Caspi et al. 2020). The results showed that the proportion of various metabolic pathways in both rhizosphere and non-rhizosphere soil samples was relatively low, regardless of whether it was *R. acetosa* L. or *O. glauca*. PWY-3781 [Aerobic respiration I (cytochrome c)] is a relatively dominant metabolic pathway (~ 1.5%) and strong waterlogging stress hardly changes the relative abundance of the top 10 metabolic pathways in soil bacterial communities (Fig. 7a and c). PWY-3781 and PWY-7279 [Aerobic respiration II (cytochrome c) (yeast)] is the dominant fungal metabolic pathway in all tested soil samples, accounting for more than 6%, while the relative abundance of other metabolic pathways is less than 4% (Fig. 7b and d). PWY-3781 is a common metabolic pathway in soil microbial communities, such as in sorghum soil treated with nitrogen fertiliser (Fei et al. 2022) and rhizosphere soils of *Brachystegia boehmii* (Maquia et al. 2021) and *B. spiciformis* (António et al. 2022). Liu et al. found that PWY-3781 and PWY-7279 are highly abundant precursor metabolites in lake samples from the Yunnan Plateau (Liu et al. 2023).

### Redundancy analysis

Through microbial  $\alpha$  diversity analysis, community structure composition analysis and metabolic pathway analysis, it was found that there are differences in the bacterial and fungal communities in the rhizosphere soil of dominant plants in the WLFZ of Three Gorges Reservoir under different waterlogging stress intensities, which may be related to their soil physicochemical properties and enzyme activities. Therefore, this study

elucidated the correlation between these properties and the rhizosphere microbial community of dominant plants in the WLFZ through redundancy analysis (RDA).

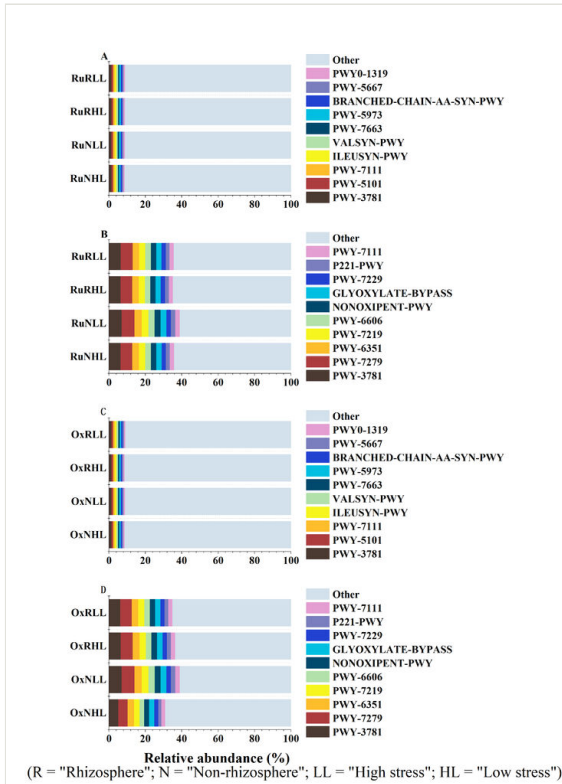


Figure 7.

The bacterial (A for *Rumex acetosa* L. and C for *Oxybasis glauca*) and fungal (B for *Rumex acetosa* L. and D for *Oxybasis glauca*) metabolic pathway analyses in the rhizosphere and non-rhizosphere soils.

Fig. 8 shows the RDA results between dominant plant rhizosphere soil bacterial/fungal communities, soil physicochemical properties and soil enzyme activity in the Tangjiatuo section of the Three Gorges Reservoir under different waterlogging stress intensities. The length of the arrow reflects the strength of the association between influencing factors and microbial communities, with longer arrows indicating stronger associations and shorter arrows indicating weaker associations (Li et al. 2022). For *R. acetosa* L., the first and second principal axes explained 34.25% and 16.58% of the variance in relative abundance of bacterial communities, respectively, accounting for a total of 50.83% of the variance change. EC and pH are two significant factors affecting the community of *R. acetosa* L. bacteria ( $p < 0.01$ ). The physicochemical properties and soil enzyme activity explain 57.75% of the variance in relative abundance of fungal communities. Consistent with the bacterial community, amongst numerous factors, EC and pH significantly affect the fungal community structure in the rhizosphere and non-rhizosphere soils of





bacterial and fungal communities of typical dominant plants (*R. acetosa* L. and *O. glauca*) in the WLFZ of Three Gorges Reservoir (Tangjiatuo section) by sampling rhizosphere and non-rhizosphere soils under different waterlogging stress intensities for physical and chemical property analysis, enzyme activity determination and high-throughput sequencing. The intensity of waterlogging stress can affect the assembly of microbial community structure in soil and stronger waterlogging stress may lead to an increase in microbial diversity in soil to cope with enhanced stress. The fungal community structure is more susceptible to changes in waterlogging stress than the bacterial community structure, as evidenced by the widespread presence of key fungal biomarkers in the soil. However, only some soil samples were found to contain key bacterial biomarkers and these samples lacked bacterial communities that differed significantly from other soil samples. Compared with waterlogging stress, the influence of plant species on the composition of rhizosphere microbial community structure is relatively small. The impact of environmental factors on the soil microbial communities in the rhizosphere and non-rhizosphere of different plants varies greatly. Soil microbial communities in *R. acetosa* L. are mainly affected by pH and EC, while those in *O. glauca* are mainly affected by nitrogen indicators and soil enzyme activity.

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## Author contributions

LZ: Conceptualisation, Methodology, Data curation, Writing-original draft preparation, Writing-reviewing and editing. SW: Supervision, Project administration, Writing-reviewing and editing. MM: Validation, Writing-reviewing and editing. HZ: Validation, Writing-reviewing and editing. JH: Validation, Writing-reviewing and editing. JY: Validation, Writing-reviewing and editing.

## Conflicts of interest

The authors have declared that no competing interests exist.

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## Supplementary material

### Suppl. material 1: Supplementary file

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