Catena 248 (2025) 108549

Contents lists available at ScienceDirect

Catena

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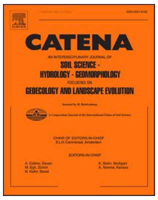

The complex interplay of flooding intensity and land use on soil microbial communities in riparian zones: Insights for ecological restoration

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ARTICLE INFO

Keywords:
Riparian zone
Flooding intensity
Land use
Soil microorganisms
Community assembly

ABSTRACT

The impact of hydrological regimes and land use on soil microorganisms in riparian zones has been well-documented, but their combined effects on the composition and assembly mechanisms of these communities remain unclear. To address this knowledge gap, we conducted a study examining the fungal and bacterial communities in three land use types—artificial mixed forests, natural grasslands, and cornfields—within riparian zones of the China's Three Gorges Reservoir. We also considered how these communities responded to different flooding intensity gradients. Our results show that natural grasslands fostered increased diversity and network complexity of soil microorganisms with stronger flooding at middle and lower elevations. In contrast, artificial mixed forests enhanced microbial diversity and complexity at higher elevations with lower flooding intensity. Notably, land use had a greater influence on shaping soil microbial community structure, while flooding intensity had a greater impact on assembly processes. Dam-triggered flooding led to a convergence of bacterial community assembly processes across land use types, with deterministic processes playing a dominant role. However, this flooding also magnified the influence of stochastic processes on the structure of soil fungal communities. The assembly processes of these communities were primarily influenced by soil pH, SOC, and TK. These findings underscore the importance of developing vegetation restoration strategies based on riparian zone elevations to maintain soil microbial diversity and stability. This approach offers valuable guidance for ecological restoration efforts in similar regions.

1. Introduction

The riparian zone acts as a crucial intermediary between the river's aquatic and terrestrial environments, promoting the general health of the riverine ecosystem (Naiman and Décamps, 1997). Due to influences from hydrological conditions (such as flooding and water level fluctuations) and human activities (such as cultivation or vegetation restoration), the riparian zone has been identified as a possible hotspot for biogeochemical cycling (Wang et al., 2020). Microbes reign supreme in the dynamic soil ecosystem (Sokol et al., 2022), and their growth, activities, and interactions with the environment largely drive the energy flow and material cycling of the riparian zone ecosystem (Crowther et al., 2019). To preserve the well-being and ecological role of the ecosystem, it is crucial to comprehend the composition and assembly mechanisms which drive the reaction of riparian microbial communities to shifts in the external environment (Saleem et al., 2019).

Water level fluctuations (WLFs) is the principal driver behind the functionality of riparian ecosystems (Zhu et al., 2022b), and thus being thought to play a central role in controlling the assembly of soil microbial communities and biogeochemical processes in riparian soils (Ye et al., 2019). Riparian soil microbial communities are influenced by various environmental factors, such as pH, oxygen levels, and nutrient availability, which exert selective pressures on these communities (Tripathi et al., 2018). These selective pressures align with ecological niche-based theories, indicating deterministic processes, like biotic interactions and environmental filtering, control microbial community composition and assembly (Chave, 2004). Additionally, neutral theory believes that stochastic processes also govern the patterns of community

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https://doi.org/10.1016/j.catena.2024.108549
Received 24 February 2024; Received in revised form 19 September 2024; Accepted 8 November 2024

structure (Chen et al., 2019). Null modeling methods have been employed to quantitatively characterize the relative significance of these two ecological processes (Stegen et al., 2013). Despite the extensive literature on the composition and diversity of microbial communities in riparian zones in recent years (Ye et al., 2021; Annala et al., 2022), few studies have been conducted on the assembly processes of microbial communities in reservoir riparian zones, especially under the dual influences of WLFs and anthropogenic disturbances.

The Three Gorges Dam is among the most expansive water conservancy projects globally (Zhang and Lou, 2011). Since its official operation in 2010, the water level of the Three Gorges Reservoir (TGR) has been regulated within a range of 145 m in summer to 175 m in winter (Ye et al., 2019). As a result, there is a water level variance of 30 m, impacting a combined area of 348.9 km^2 in the riparian zone (Zhu et al., 2020). Owing to the dam regulation, the long-term periodic WLFs in the reservoir's riparian zone have caused severe damage to the original habitat and a decline in soil quality, making it a typical ecologically vulnerable and sensitive area (Zhu et al., 2022b). Vegetation restoration is an important strategy for soil remediation in degraded ecosystems, with natural vegetation restoration and artificial planting of flood-tolerant plants (i.e., artificial vegetation restoration) being typical vegetation restoration patterns in riparian zones (Ye et al., 2023a). In addition, during low water level period in summer, the local farmers cultivate crops such as rice and corn on the riparian zone (Zhu et al., 2020). On one hand, the cyclic wet-dry process caused by the periodic WLFs and agricultural activities can suppress the soil microbial development and behavior (Ren et al., 2019), which may affect the microbial community composition and assembly (Ye et al., 2023c). On the other hand, vegetation restoration can increase plant diversity and root exudates, and the decomposition of vegetation after flooding may promote the soil microbial development and behavior (Ren et al., 2018). Both mechanisms may affect the composition and assembly processes of soil microbial communities in the riparian zone. However, current research on soil microbes in riparian zones mainly focuses on the response of bacteria or fungi to single environmental factors (e.g., different land use types or WLFs) (Ye et al., 2023c). There is little research on the joint response of soil bacteria and fungi to multiple factors such as land use (LU) and WLFs, and which factor plays the dominant role when soil composition and assembly processes respond to the combined influences of WLFs and LU. Consequently, it is essential to elucidate the interactive influence of WLFs and LU on the composition and assembly processes of soil microbial communities.

The TGR riparian zone has three main LU strategies: restoration-focused natural grasslands, restoration-focused artificial flood-tolerant vegetation planting, and cultivation of land with a focus on production (Zhu et al., 2022b). In extreme and harsh environments, deterministic processes largely shape the assembly of microbial communities, whereas in relatively mild, less disturbed environments, stochastic processes are more influential (Stegen et al., 2012; Bao et al., 2020). Due to the overwhelming influence of WLFs triggered by the dam on the formation of riparian soil (Hoffmann, 2023), we hypothesize that: (1) soil microbial community structure and assembly processes are more affected by dam-triggered flooding intensity (FI) than by LU, with increasing flooding intensity enhances the effect of deterministic processes; (2) vegetation restoration boosts microbial diversity, network complexity, and the proportion of stochastic processes in community assembly, while decreasing the proportion of deterministic processes. To validate these hypotheses, our study targets to: (1) investigate the compositions and assembly processes of microbial communities in riparian soils under different LU strategies at different water level elevations; (2) quantify the influences of FI and LU on soil community composition and assembly.

2. Materials and methods

2.1. Site description and samples collection

This study was carried out in the Dalangba riparian zone (31°08′30″N, 108°30′50″N) located along the Pengxi River, a tributary of the Yangtze River. Covering an area of around 55.47 km^2, the riparian zone was formed by the WLFs in the Pengxi River, which is a significant tributary of the TGR. The water level in the Pengxi River experiences annual fluctuations between 145 and 175 m ASL, which results from the impact of the Three Gorges Dam regulation (Fig. 1). During winter months, the study area is submerged while the summer brings dry conditions, a contrast to the flooding patterns of rivers affected by monsoon climates (Ye et al., 2019). The area has undergone significant ecological changes as a result of periodic flooding, leading to the disappearance of many native plant communities. The study area experiences a mean yearly temperature of 18.5 °C and receives a mean annual precipitation of 1200 mm, with over 60 % of the total rainfall concentrated in the growing season, extending from April to September. The soil in this area is categorized as purple soil, specifically Eutric Regosols according to FAO soil classification, and it has a loamy sand texture (Zhu et al., 2022b). The primary vegetation types of the natural grassland are *Xanthium sibiricum*, *Paspalum thunbergii*, and *Cynodon dactylon*. Common plant species found in the artificial planting area for ecological restoration of flood-tolerant vegetation include *Taxodium distichum*, *Glyptostrobus pensilis* and *Morus alba*. These trees are able to withstand flooding and riparian, and were planted to provide shoreline protection and ecological buffering function. Both the natural vegetation restoration and the artificial vegetation restoration areas were used as cornfields before the Three Gorges Dam construction (Zhu et al., 2022b).

In June 2020, soil samples were collected from ten study sites in the TGR riparian area, according to different water level elevations and LU types (**Fig. S1**). These sites consist of 173 m within a mixed forest of mulberry and metasequoia (173 M), 168 m within a mixed forest of mulberry and metasequoia (168 M), 173 m of grassland (173G), 168 m of grassland (168G), and 163 m of grassland (163G). Additionally, there were areas of 173 m, 168 m, 163 m, and 178 m of corn fields (173C, 168C, 163C, 178C) as well as 178 m of secondary forest (178F). Among these, 173 M and 168 M were chosen as representative study sites for restoration-focused artificial flood-tolerant vegetation planting, while 173G, 168G, and 163G were selected as study sites for restoration-focused natural grasslands; 178F, 178C, 173C, 168C and 163C were selected as controls. Cornfields in the riparian zone (173C, 168C and 163C) were affected by both periodic flooding and agricultural activities, 178C was only affected by agricultural activities, and 178F was unaffected by periodic flooding and agricultural activities. The detailed information on cornfield management practices were described in our previous study, please refer to Zhu et al. (2020). Different elevations experience different flooding times and flood intensities under the process of regulating the Three Gorges Dam. Sites at high elevation experience shorter flooding times and slighter dam-triggered flood intensity, while sites at low elevation suffer longer flooding times and stronger FI (**Table S1**). The FI index at different water level elevations was reckoned by dividing the average flooding days at each elevation from the start of the dam's operation until the end of 2019 by 365 days. For detailed calculation procedures, please refer to Zhu et al. (2022b).

At each site, six soil samples, each weighing approximately 500 g and taken from a depth of 0–20 cm, were randomly collected using a soil corer. Soil samples were obtained using sterile tubes, ensuring that there was no contact with the soil corer, and all personnel wore medical masks and sterile gloves during the process. The samples were transported to the laboratory on dry ice for microbial DNA extraction and high-throughput sequencing. The remaining soil samples were also brought to the laboratory for further examination. To ensure homogenization, all samples were passed through a 4 mm sieve, with stones, debris, and

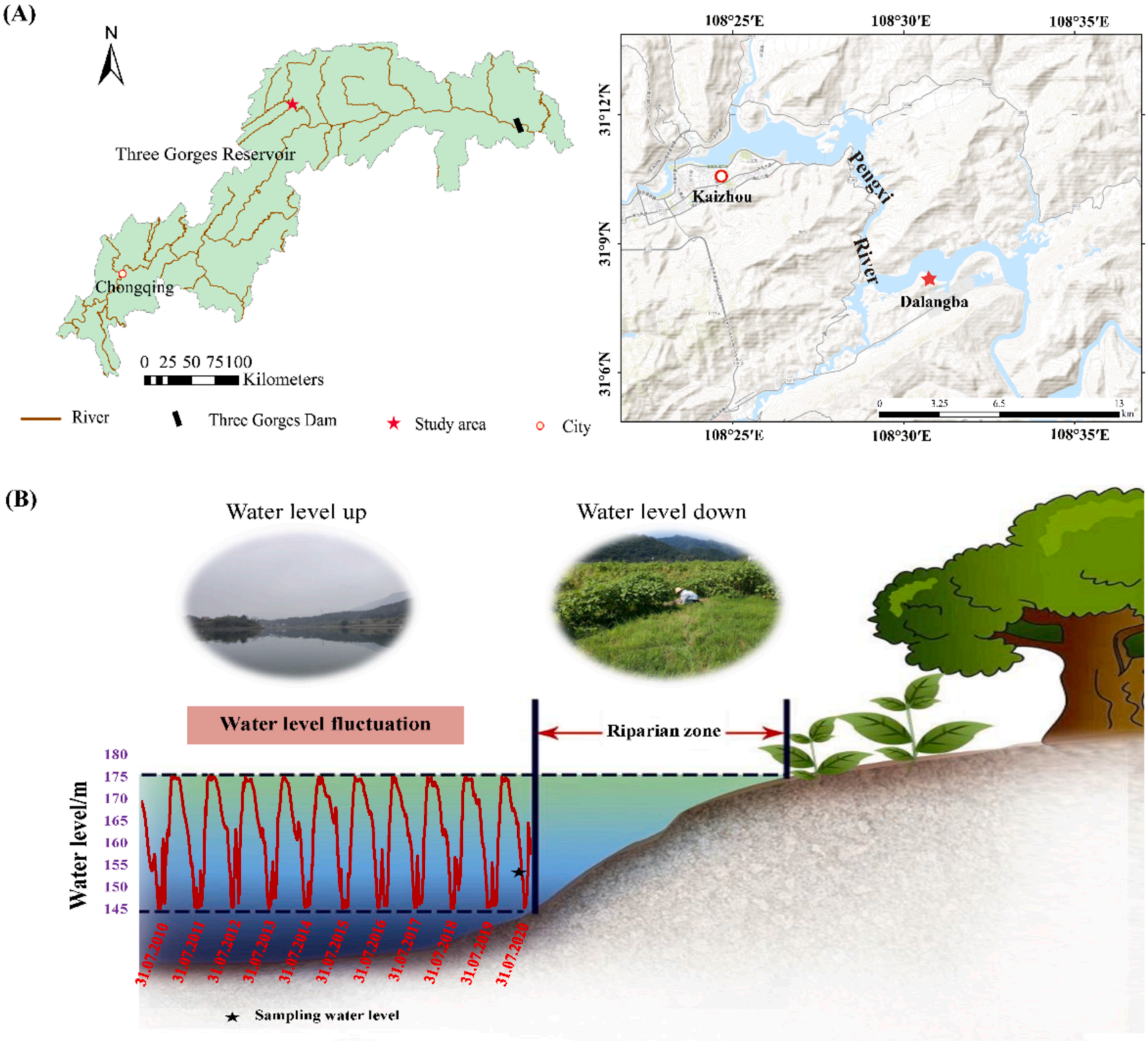

Fig. 1. Location of study area (A) and water level fluctuations in the riparian zone of the TGR (B).

plant roots being removed in the process. Edaphic physical and chemical properties were evaluated after the samples were naturally air-dried.

2.2. Analytical methods

An element analyzer (vario TOC, elementar, Germany) was used to test soil total nitrogen (TN) and total carbon (TC). Carbon to nitrogen (C:N) ratio was determined based on the TC and TN results. Soil pH was extracted in a 1:2.5 soil-to-water ratio, and subsequently measured using a potentiometer (FE20, Mettler Toledo, USA). We measured soil organic carbon (SOC) via TOC/TNb Analyzer (Multi N/C 3100, Analytik Jena, Germany). We used the ring knife method to determine soil bulk density (SBD) (VanRemortel and Shields, 1993). We used wet sieving technique to measure the mean weight diameter (MWD) representing the soil aggregate stability (Haynes, 1993). Soil total potassium (TK) and phosphorus (TP) content were measured using the flame photometry and molybdenum-antimony resistance colorimetric, respectively (Zhu et al., 2022a). Soil texture (i.e., Sand, Silt, Clay) was determined by a laser particle size analyzer (Mastersizer 3000, Malvern Co., UK). These edaphic physicochemical properties were shown in **Table S2**.

2.3. Extracting DNA and utilizing high-throughput sequencing

The DNeasy PowerSoil Kit (Qiagen, Hilden, Germany) was used to extract total DNA from 0.25 g of soil. The V4 regions of bacterial 16 S rRNA gene was amplified using primers pairs 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) (Ye et al., 2021). The fungal ITS gene was amplified using primers pairs ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCTGCGTTCTTCATCGATGC-3′) (Bell et al., 2020). The PCR products were mixed and purified before being sequenced on the Illumina NovaSeq 6000. This process was conducted by Novogene Biotechnology Co., Ltd. (Beijing, China).

Raw fastq files of fungal ITS gene and bacterial 16S rRNA gene were quality-filtered and analyzed using QIIME2 (v. 2020.11), following the official guidelines (Ye et al., 2021). Quality-filtered sequences were subsequently conducted with DADA2 for the detection, correction, and phylogenetic tree construction (Zhou and Ning, 2017). Taxonomic assignments for the ITS and 16S rRNA genes were conducted employing the Naive Bayes classifier trained with the UNITE 7.2 database and Silva 132 database, respectively (Ye et al., 2021). To enhance taxonomic annotation and comparability across studies, the QIIME2 pipeline was utilized to generate Amplicon Sequence Variants (ASVs). For more details, please refer to a previous publication (Gao et al., 2021b). Microbial sequencing data for this study were deposited in the NCBI Sequence Read Archive (SRA) database with entry number PRJNA1042948.

2.4. Exploring microbial community assembly processes and network properties

The changes in the soil microbial community phylogenetic diversity were evaluated employing the beta nearest taxon index (βNTI) which represents the microbial community assembly processes. The βNTI values were calculated from a null model created by 999 randomizations based on phylogenetic tree and ASV table using the *picante* package in R v. 4.1.3 software (Huo et al., 2023). βNTI values > 2 or < -2 manifest heterogeneous selection and homogeneous selection, respectively, suggesting a dominant deterministic processes. βNTI values range from -2 to 2 indicating a dominant stochastic process. The community-based Raup-Crick matrix (RCbray) was reckoned employing the *vegan* package in R v. 4.1.3 software. RCbray values > 0.95 is dispersal limitations; RCbray values < -0.95 indicate homogenizing dispersal, and $|\mathrm{RCbray}|$ less than 0.95 is an undominated process (Ye et al., 2023b).

To analyze the potential associations of interspecies within a microbial community, a co-occurrence network for both bacterial and fungal community was constructed with the Molecular Ecological Network Analyses pipeline developed by Deng et al. (2016). Spearman's correlation analysis was used to investigate the abundance tables of both bacteria and fungi to determine correlation coefficients (R) and P values, following the approach outlined in Barberán et al. (2012). We created thresholds for the network using random matrix theory (RMT), and used these to construct a proximity matrix that we then used to identify nodes and connecting edges within a co-occurrence network. Finally, we utilized Gephi v 0.9.2 to visualize the co-occurrence network. The positioning of a node (ASV) in a network can be determined by its 'within module connectivity' (Zi) and 'among module connectivity' (Pi). Based on these values, nodes can be classified into four categories: connectors (Zi less than 2.5, Pi greater than 0.62), module hubs (Zi greater than 2.5, Pi less than 0.62), network hubs (Zi greater than 2.5, Pi greater than 0.62), and peripherals (Zi less than 2.5, Pi less than 0.62). Network hubs, module hubs, and connectors are considered to be keystone taxa that build communities and play a vital role in maintaining community structure. Removing these taxa may cause modules and networks to break down (Ye et al., 2021).

2.5. Data analysis and graphic plotting

R v. 4.1.3 software was used for all calculations and statistical analyses. Prior to analysis, the Kolmogorov-Smirnov test was conducted for normality check and Levene's test was performed for homogeneity of variances. The data was transformed when the assumptions were not met (Zhu et al., 2023). The differences in edaphic microbial, richness βNTI and physicochemical properties among diverse land-use types were identified by analysis of variance (ANOVA) using *agricolae* package. To analysis the variations in the fungal and bacterial community structures under different LU types, Principal Coordinates Analysis (PCoA), ADONIS, ANOSIM and MRPP were conducted using the *vegan* package. Further, variation partitioning (*vegan* package) analysis quantified the impacts of LU and FI on soil microbial structure. Mantel test (*ggcor* package) was conducted to explore environmental drivers of microbial communities. Further, the individual impacts of various edaphic physicochemical properties on fungal and bacterial community structure were calculated by hierarchical partitioning (*rdacca.hp* package). The relative importance of LU and FI to the impact on edaphic microbial community assembly were quantified using variation partitioning and hierarchical partitioning (*hier.part* package), respectively. The main soil predictors (i.e., intrinsic driving factors) affecting microbial community assembly were analyzed using random forest regression (*rfPermute* package). Graphs were plotted utilizing the *ggplot2* package.

3. Results

3.1. Soil microbial diversity and community composition

A total of 27,352 bacterial ASVs and 9,750 fungal ASVs were obtained in this study. The microbial communities showed distinct variations in composition based on LU and water level elevations (**Fig. S2**). The species with the top three relative abundances in all 10 sites were the dominant species (Delgado-Baquerizo et al., 2018). The dominant bacterial at the phylum level across all study sites were Actinobacteriota, Chloroflexi, Acidobacteriota. Generally, the relative abundance of Proteobacteria increased with elevation in the same LU types. Specifically, the relative abundance of Proteobacteria in cornfields was higher than that of the other LU types at the same elevation. No significant difference in the relative abundance of Acidobacteriota was found among all LU types. The relative abundance of fungi at the phylum level varied significantly, with dominant taxa being Ascomycota, Basidiomycota, Mortierellomycota. The relative abundance of Ascomycota increased with elevation in the same LU types. Natural grasslands had the highest abundance of Ascomycota at the same elevation. The relative abundance of Mortierellomycota was higher in soils at elevations of 173 m and 178 m compared to elevations of 168 m and 163 m across different LU types.

Within the same LU type, there was no significant difference in bacterial richness among different elevations in the cornfield, while the fungal richness at 168C was the highest. In the grassland, bacterial richness decreased with increasing elevation, while the trend of fungal richness was opposite. No significant difference in bacterial and fungal richness was found among different elevations in the artificial forest (Fig. 2). At the same elevation, both bacterial and fungal richness in the artificial forests were significantly higher than those in the cornfields. Within the riparian zone (i.e., lower than 175 m elevation), there was no significant difference in bacterial and fungal richness among the natural grasslands and the artificial forests (Fig. 2).

PCoA analysis revealed that microbial community compositions were distinct among the LU types with three different statistical approaches (Fig. 3, Table 1). Bacterial community structure was more sensitive to changes in LU type than fungal community structure. The first two principal coordinates explained 41.65 % and 41.44 % of the variation in soil bacterial and fungal community composition, respectively. Furthermore, variation partitioning analysis quantified the impact of LU type and FI on bacterial and fungal community structure in the riparian zone of the TGR (**Fig. S3**). Results showed that microbial community structure was more affected by LU type (8.34 % for bacteria and 7.68 % for fungi) than by FI (7.11 % for bacteria and 5.29 % for fungi).

3.2. Soil properties affecting microbial community

The Mantel test indicated a correlation between soil properties (Sand, Silt, Clay, TK, SOC, MWD, TN, TC, pH, and SBD) and the structure of bacterial communities. Similarly, fungal community structure was found to be affected by TK, SOC, TN, TC, C:N, pH, SBD, Clay, Silt, and Sand (Fig. 4A). Hierarchical partitioning analysis further quantified the individual contribution of different soil physiochemical factors to microbial community changes, indicating that soil pH, Sand, Silt, and Clay were the primary drivers for bacterial community structure (Fig. 4B), while fungal community structure was primarily drove by TK, C:N ratio and pH (Fig. 4C).

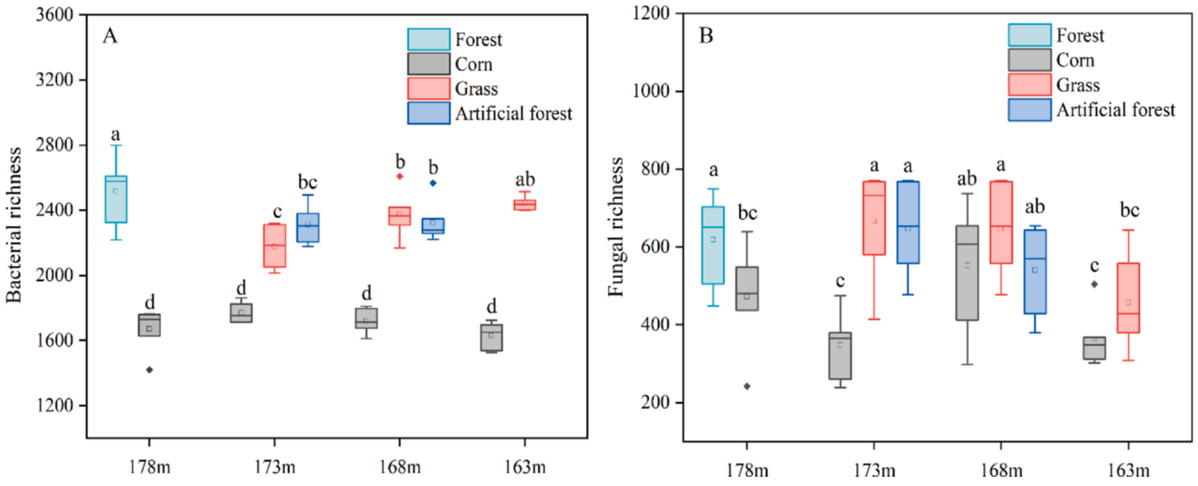

Fig. 2. Soil bacterial and fungal community Alpha diversity under natural forests, corn fields, grasslands and artificial mixed forests at four different elevations. Distinguishing lowercase letters signify significant variations in soil microbial alpha diversity across various LU types ($p < 0.05$).

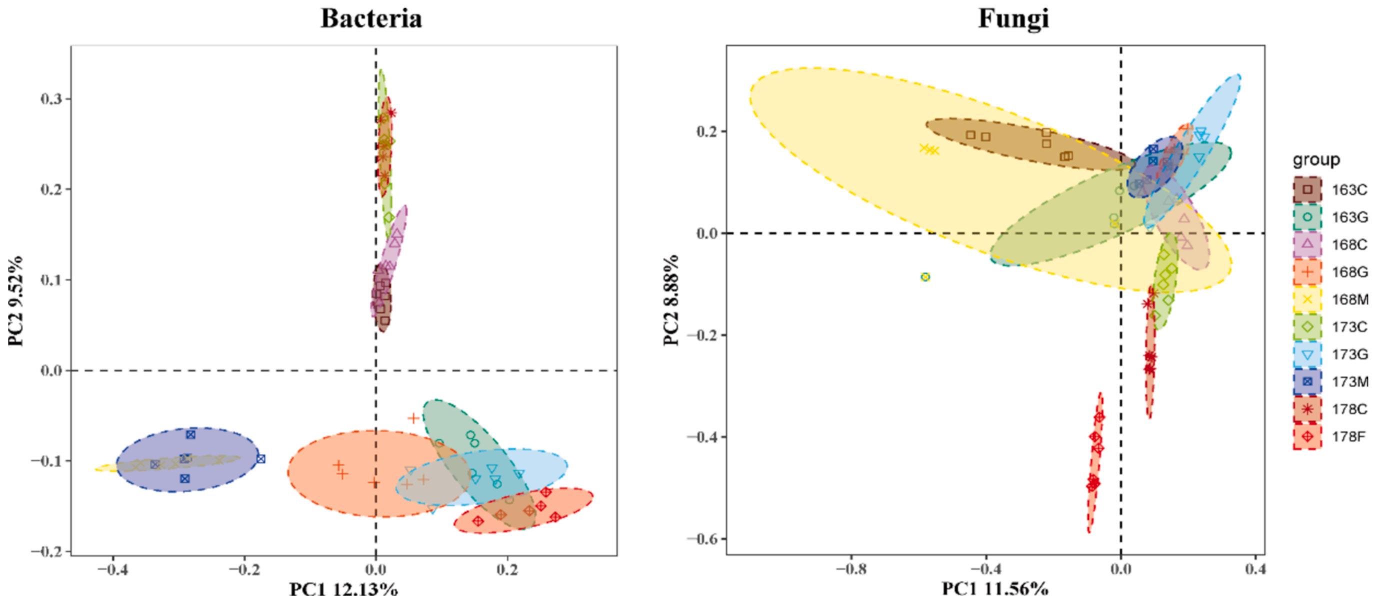

Fig. 3. Principal coordinate analyses (PCOA) of weighted uniFrac distances of soil bacterial and fungal communities in various LU types. 163C, 163 m corn field; 163G, 163 m grassland; 168C, 168 m corn field; 168G, 168 m grassland; 168 M, 168 m mulberry and metasequoia mixed forest; 173C, 173 m corn field; 173G, 173 m grassland; 173 M, 173 m mulberry and metasequoia mixed forest; 178C, 178 m corn field; 178F, 178 m natural forest.

Table 1
Effects of land use types on bacterial and fungal community compositions.

Microbes	Treatments	ADONIS		ANOSIM		MRPP	
		R^2	*p*	R	*p*	A	*p*
Bacteria	10 LU types	0.463	0.001**	0.883	0.001**	0.207	0.001**
Fungi		0.364	0.001**	0.575	0.001**	0.152	0.001**

Note: Significance tests were conducted with three different statistical approaches (ADONIS, ANOSIM and MRPP). "**" indicates a significant difference at $p < 0.01$ among different land use types (10 LU types: 163C, 163G, 168C, 168G, 168 M, 173C, 173G, 173 M, 178C, 178F).

3.3. Microbial co-occurrence networks

At the ASV level, both bacterial and fungal co-occurrence networks were created for each treatment (Fig. 5). Meanwhile, we calculated the bacterial and fungal topological properties of networks (Table 2). Results revealed that, at the same elevation, except for the fungi at 168 M, the natural grasslands had the highest modularity, average degree, and average path length. The artificial forests were intermediate, and the cornfields had the lowest values. Generally, 178F and 178C had the highest and lowest values of the modularity, average degree, and average path length, respectively. In all treatments, the proportions of negative links in both fungal and bacterial networks were dominant. However, natural grasslands and artificial forests increased the positive links of the microbial networks.

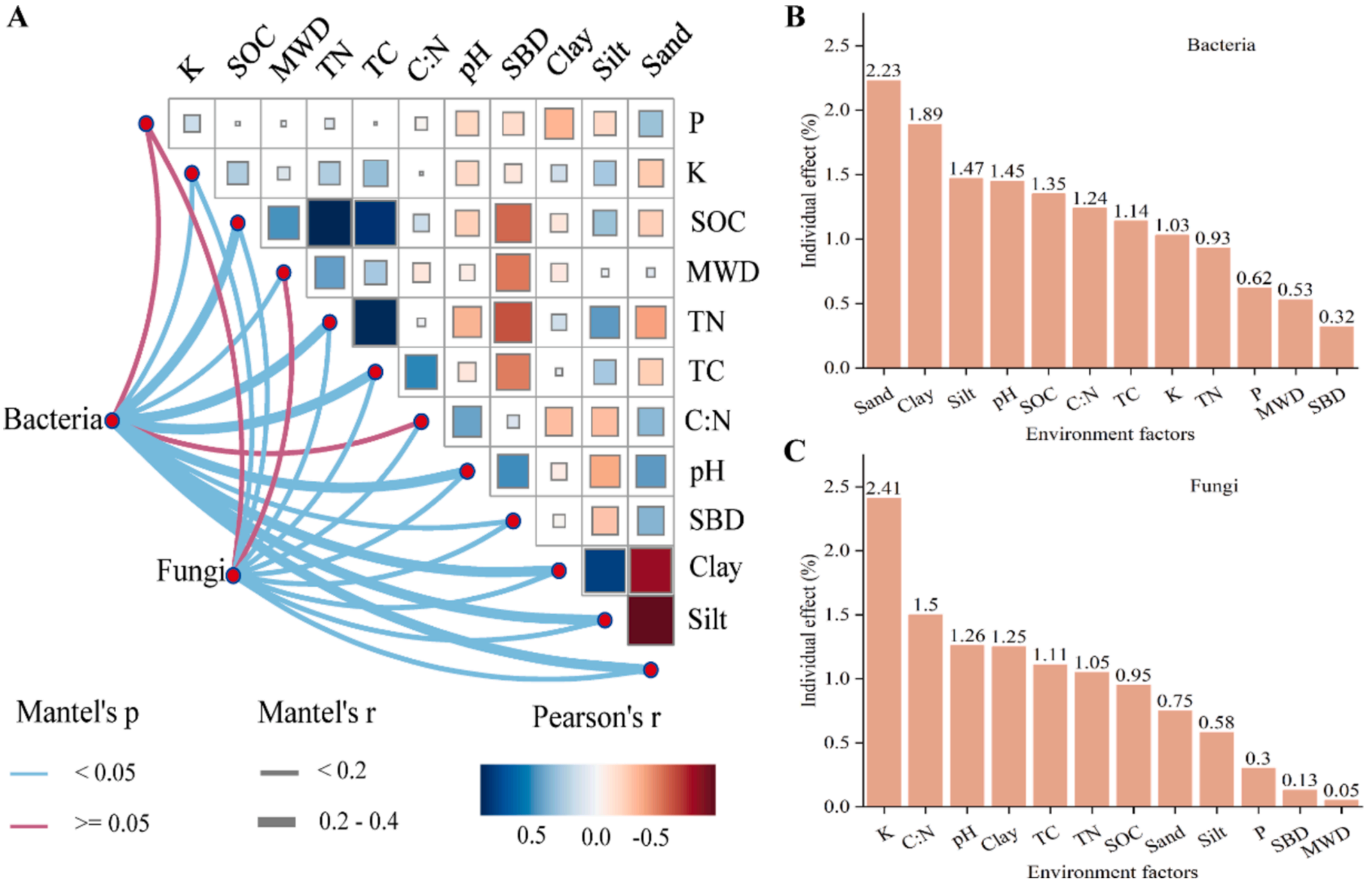

Fig. 4. The correlation between soil physicochemical properties and the structure of soil microbial communities analyzed by Mantel Test (A). Individual effects of soil physicochemical properties on soil bacterial (B) and fungal (C) community structure revealed by Hierarchical Partitioning. P: Soil total phosphorous, SOC: Soil organic carbon, K: Soil total potassium, MWD: Mean weight diameter, SBD: Soil bulk density, TN: Soil total nitrogen, TC: Soil total carbon, C:N: Carbon-to-nitrogen ratio.

As is illustrated in the Zi-Pi plot, 1 bacterial node from 163G sank into connectors and 28 nodes from the other study sites sank into module hubs (Fig. 6A). The keystone bacterial taxa were Acidobacteriota, Proteobacteria, Gemmatimonadota, Firmicutes, Methylomirabilota, Chloroflexi (**Table S4**). For fungal networks, 17 nodes sank into module hubs, 8 nodes sank into connectors and 1 node sank into network hubs (Fig. 6B). Members from Basidiomycota, Ascomycota, and Kickxellomycota were identified as keystone taxa (**Table S5**).

3.4. *Assembly process of microbial communities*

The null models using βNTI and RCbray indicated that deterministic processes primarily droved the bacterial community assembly, while the fungal community assembly were the primarily governed by stochastic processes across all study sites (Fig. 7). For bacteria, the community assembly was influenced by homogeneous selection, which accounted for 100 % in the 163C, 168C, 168G, 173C, 173G, and 173 M. In the 163G and 168 M, homogeneous selection accounted for 60 % and heterogeneous selection for 40 %. Notably, in the never-flooded area (i.e., 178C and 178F), bacterial communities in a certain proportion of study sites were driven by stochastic processes, with both dispersal limitation and homogeneous dispersal contributed 20 % of the variation in 178F, and 20 % contributions of dispersal limitation in 178C (Fig. 7A, C). Both deterministic and stochastic processes influenced fungal community assembly in the never-flooded zone. Except for the 163G, stochastic processes predominantly drove fungal community assembly in the riparian zone (Fig. 7B, D).

To disentangle the main factors driving community construction, intrinsic soil properties and external environmental factors affecting βNTI were analyzed (Fig. 8, Fig. 9). Variation partitioning analysis revealed that microbial community construction was more affected by FI (14.3 % for bacteria and 6.9 % for fungi) than by LU type (4.3 % for bacteria and 0.7 % for fungi). Hierarchical partitioning analysis further verified that the impact of FI on microbial community assembly exceeded that of LU (Fig. 8B, D). Furthermore, random forest regression analysis was performed to investigate the intrinsic factors (i.e., soil properties) driving community construction. The findings indicated that pH, SOC, and TK were important predictors for bacterial community assembly processes (Fig. 9A), while fungal community assembly processes were the most influentially affected by TK, SOC, and fungal composition (Fig. 9B).

4. Discussion

4.1. *Microbial community composition and assembly processes in response to FI*

WLFs are a primary force controlling the functionality of riparian ecosystems (Zhu et al., 2020). Soil environment alterations due to WLFs can impact microbial growth and reproduction, consequently affecting microbial community composition and distribution patterns (Ye et al., 2023c). Results showed that the relative abundance of bacterial Proteobacteria and fungal Ascomycota increased with elevation within the same LU types, indicating that these two gangs were sensitive to WLFs (**Fig. S2**). Proteobacteria and Ascomycota are considered to be fast-growing copiotrophic groups (r-strategies) that are able to survive in

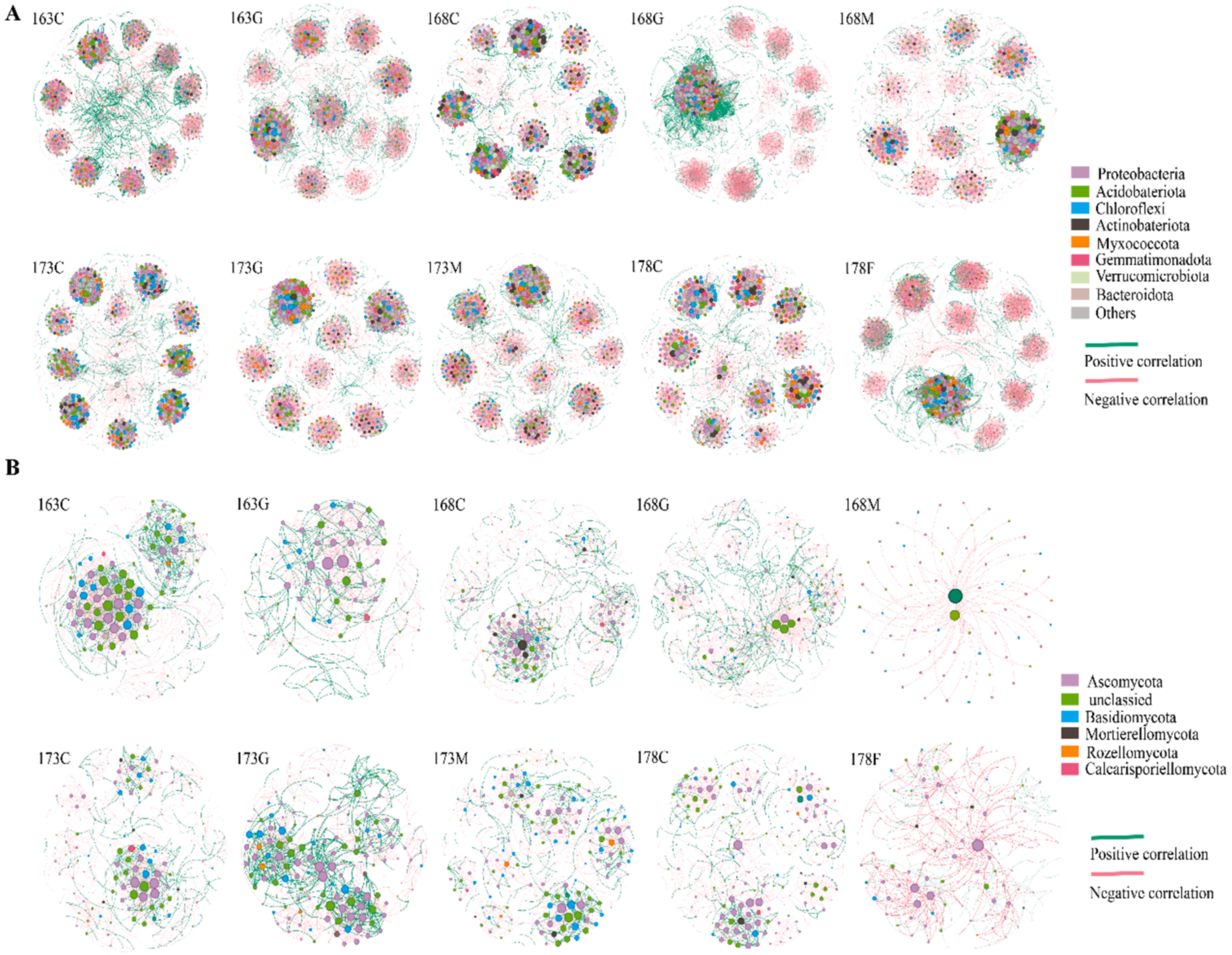

Fig. 5. Co-occurrence networks of soil bacterial (A) and fungal (B) communities in various land-use types in the riparian zone of the TGR.

Table 2
Network topology of soil bacterial and fungal communities.

Category	Treatments	Nodes	Links	Average degree	Betweenness centralization	Modularity	Average Path Length	P/N of the network
Bacteria	163C	923	6041	13.090	1681.546	0.811	3.691	0.106
	163G	953	11188	23.480	2564.331	0.879	3.974	0.189
	168C	917	6566	14.321	1840.208	0.801	3.517	0.143
	168G	970	26855	55.371	625.247	0.880	3.728	0.151
	168 M	849	6851	16.139	845.759	0.803	3.516	0.108
	173C	1013	8355	16.496	1973.697	0.835	3.563	0.126
	173G	816	8252	20.225	857.059	0.892	3.517	0.145
	173 M	896	8157	18.208	1726.936	0.857	3.531	0.146
	178C	813	6297	15.491	1314.111	0.640	3.560	0.101
	178F	1016	15752	31.008	3799.158	0.883	3.826	0.228
Fungi	163C	183	987	8.787	154.732	0.437	3.792	0.498
	163G	95	388	10.168	102.937	0.513	4.345	0.687
	168C	303	937	5.185	172.719	0.730	3.597	0.487
	168G	320	940	6.875	620.443	0.750	3.860	0.435
	168 M	68	80	2.353	51.088	0.134	2.313	0
	173C	222	711	6.405	565.252	0.624	3.889	0.448
	173G	204	1422	6.971	249.693	0.721	4.235	0.895
	173 M	255	875	6.863	531.267	0.807	3.848	0.501
	178C	222	711	6.405	715.878	0.733	3.587	0.337
	178F	146	400	6.479	258.586	0.817	3.884	0.905

unstable environments (Wang et al., 2021). Higher elevations correspond to less environmental disturbance triggered by flooding (Zhu et al., 2022b), resulting in a rise in the relative abundance of Ascomycota and Proteobacteria. Bacterial richness decreased with increasing elevation in the natural grasslands, while the trend of fungal richness was opposite (Fig. 2). The rise in soil bacterial diversity with increased disturbance from wet-dry cycles caused by WLFs may stem from bacteria's capacity to swiftly adapt to shifting environmental conditions and

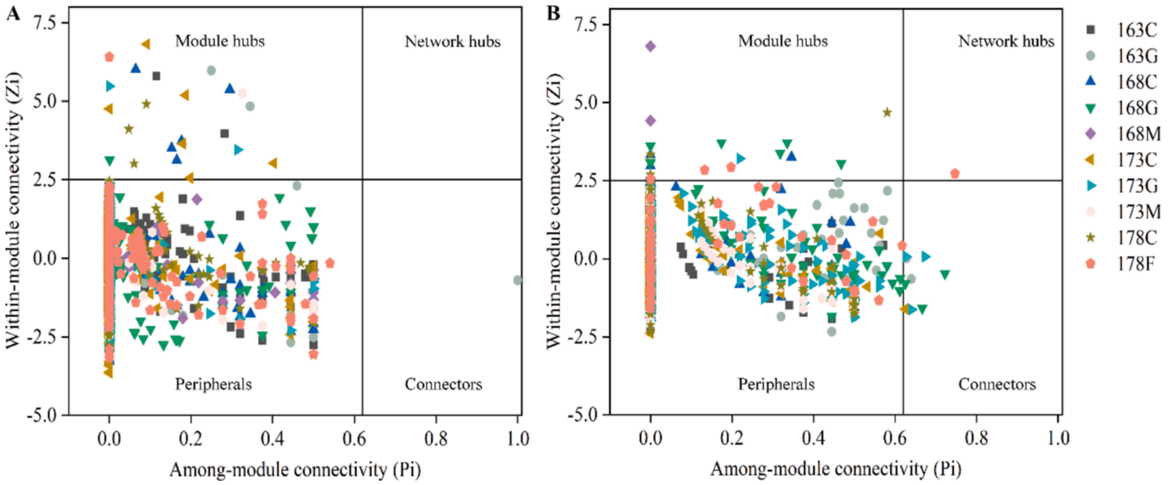

Fig. 6. Keystone taxa analysis of the soil bacterial (A) and fungal (B) community in various land-use types in the riparian zone.

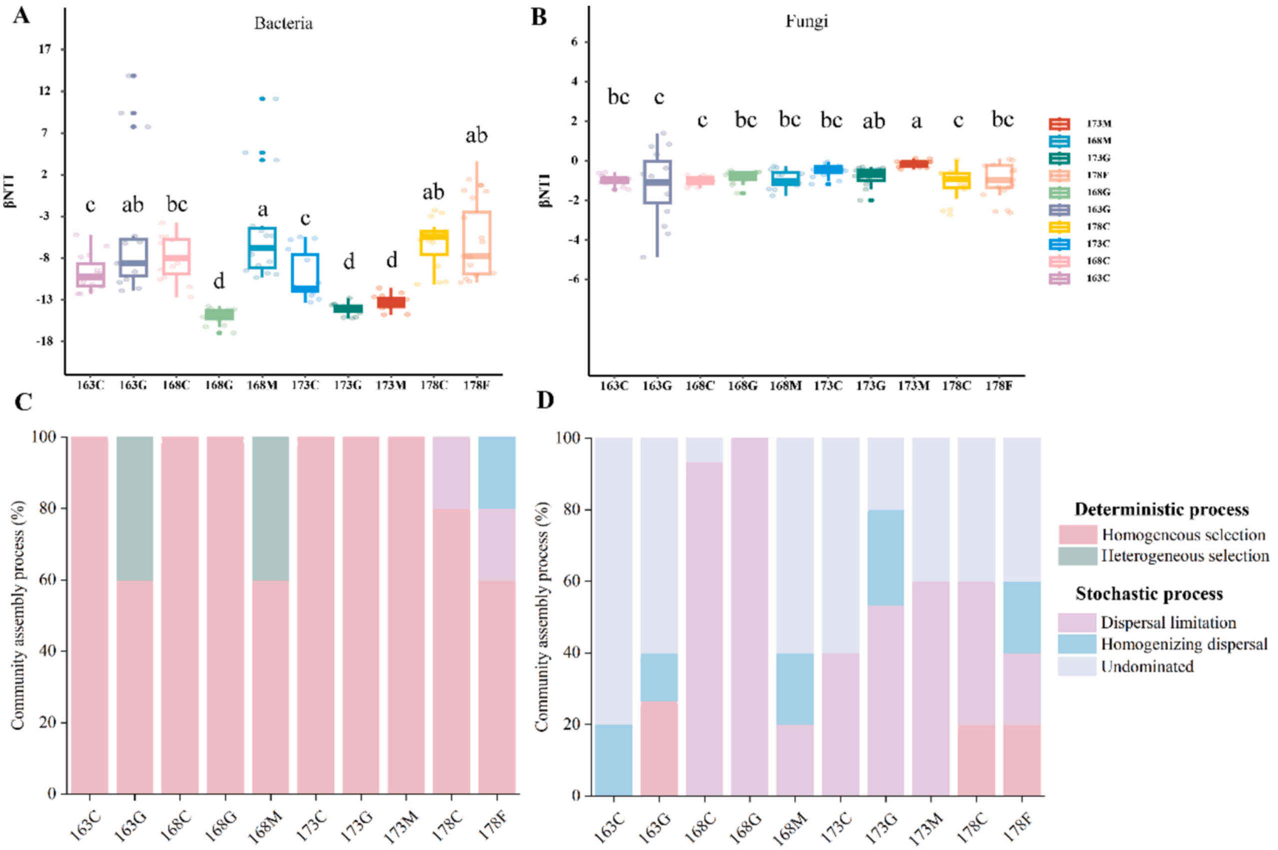

Fig. 7. Assembly process of soil bacterial (A) and fungal (B) communities in various land-use types in the riparian zone of the TGR. Contributions of different ecological processes in assembling the soil bacterial (C) and fungal (D) communities. Significantly different βNTI values at various LU types ($p < 0.05$).

utilize diverse resources (Van Elsas et al., 2019). In contrast, fungi might exhibit greater specialization in resource utilization and lesser adaptability to rapid moisture level changes (Tedersoo et al., 2014). Specifically, owing to prolonged and frequent flooding, material and energy exchange is frequent in the subaqueous zone at low elevation, allowing for the coexistence of anaerobic and aerobic bacteria, resulting in higher bacterial richness (Wang et al., 2019). However, the high elevation zone, which is closer to the land, is less affected by WLFs and maintains an aerobic environment over time, resulting in a decline in both the quantity and variety of anaerobic bacteria and a decrease in bacterial richness in the soil (Ye et al., 2023c).

Microbial co-occurrence patterns are one of the important driving factors in community construction (Yang et al., 2023). In this research, within the same LU type, the average degree, modularity degree, and average path length generally increased with decreasing elevation, except for the cornfields (Table 2). This indicates that soil microbial network complexity in the riparian zone decreases with increasing flooding intensity (Zheng et al., 2022). The reduction in network complexity could be due to amplified environmental disruption and resource constraints (**Table S2**; Banerjee et al., 2019). These results align with prior observations that the network complexity of soil microbes increases with resource availability, for instance, diminishing

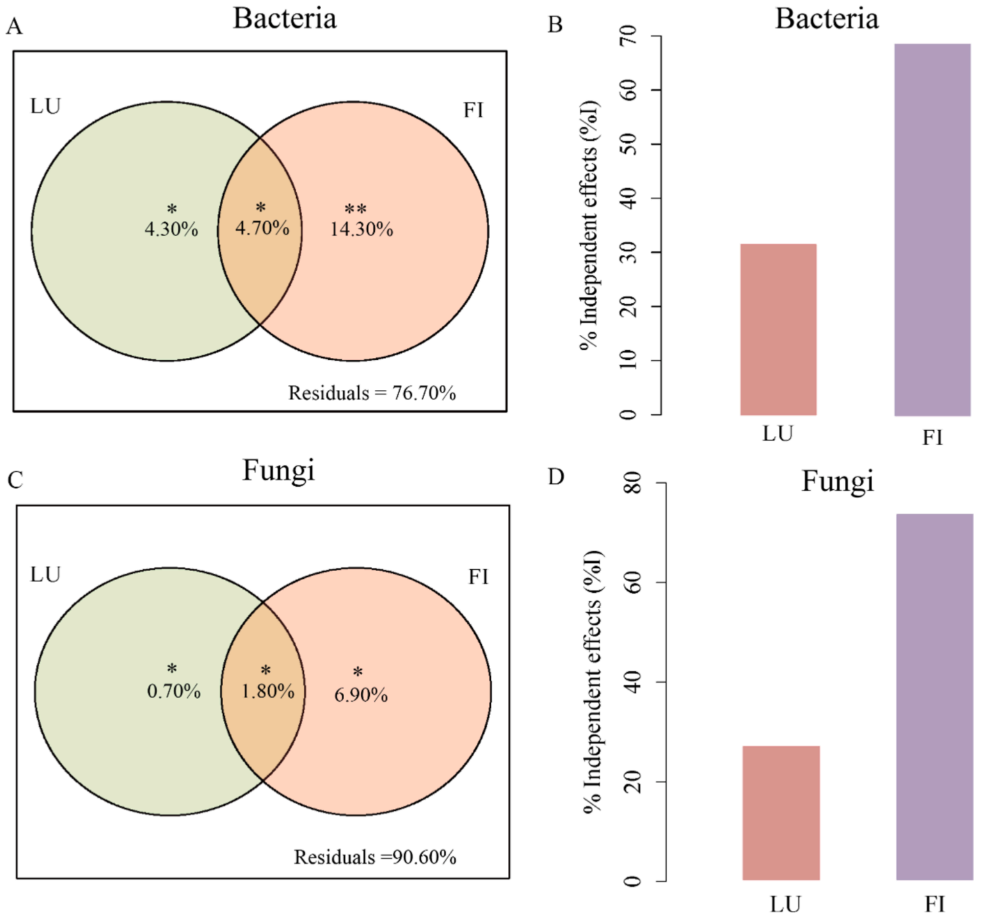

Fig. 8. The influence of LU (LU) and FI (FI) on the soil bacterial (A&B) and fungal (C&D) community assembly. * * $p < 0.01$, * $p < 0.05$.

with soil richness and water accessibility (Qiu et al., 2021). The proportions of negative links in fungal and bacterial networks were dominant across all treatments. The negative interactions observed among microorganisms may indicate intense competition for nutritional resources in response to periodic WLFs (Zheng et al., 2022). Additionally, it has been demonstrated by previous research that negative interactions minimize co-oscillation of disturbed communities (Zhong et al., 2022), thereby enhancing the microbial networks stability and enabling coexistence of microbial communities in disturbed environments (de Vries et al., 2018). Keystone species are essential for maintaining the stability of the microbial network, and their removal can lead to significant changes in the structure and function of the community (Banerjee et al., 2018). In this study, the keystone species were recognized as Acidobacteriota, Proteobacteria, Gemmatimonadota, Firmicutes, Methylomirabilota, Chloroflexi, Ascomycota, Basidiomycota, and Kickxellomycota (Fig. 6). These keystone taxa exhibit strong resistance and profoundly influence the maintenance of stability in riparian ecosystems (Ma et al., 2022; Tedersoo et al., 2014).

The assembly of soil microbial communities was significantly impacted by WLFs in the riparian zone of the TGR. In the never-flooded zone, the assembly of bacterial and fungal communities is influenced by both deterministic and stochastic processes. In the periodically flooded zone, bacterial community assembly is solely driven by deterministic processes (i.e., homogeneous selection), while fungal community assembly is entirely driven by stochastic processes (predominant for dispersal limitation and undominated processes) (Fig. 7). These results indicate that flooding alters the assembly processes of microbial communities. Moreover, variation partitioning analysis revealed that soil microbial community assembly was more affected by FI (14.3 % for bacteria and 6.9 % for fungi) than by LU type (4.3 % for bacteria and 0.7 % for fungi) (Fig. 8). This finding was in line with our first hypothesis, which further verified that WLFs were the predominant external environmental factors driving soil microbial community assembly processes. As powerful environmental filter, WLFs changed the availability of resources and environmental conditions for microbes (Ye et al., 2023c; Zhu et al., 2023). Moreover, river water, characterized by high mobility and connectivity, leads to a high degree of homogenization in the water-land transition zone habitat (Grill et al., 2019). Consequently, homogenous selection and homogenous dispersal significantly contribute to the soil bacterial and fungal community assembly in the riparian zone, respectively (Chen et al., 2019; Zhang et al., 2022).

This study revealed distinct variations in the community assembly mechanisms of soil bacteria and fungi. Specifically, while bacterial communities were primarily affected by deterministic processes, fungal communities were more affected by stochastic processes (Fig. 7), which aligned with prior reports conducted by Chen et al. (2020) and Zhang et al. (2022). As possible explanations for the results: firstly, the size of fungal cells is typically larger than that of bacteria, and some fungi can even form multicellular structures and attach to environmental media (Heaton et al., 2020; Zhang et al., 2022). As a result, fungi generally have weaker dispersal ability compared to bacteria, resulting in a stronger role of dispersal limitation in fungal community assembly. Moreover, fungi tend to exhibit stronger adaptability and resistance to environmental changes than bacteria (Wu et al., 2021). Therefore, the contribution of selection to bacterial community assembly is higher than that to fungal community assembly.

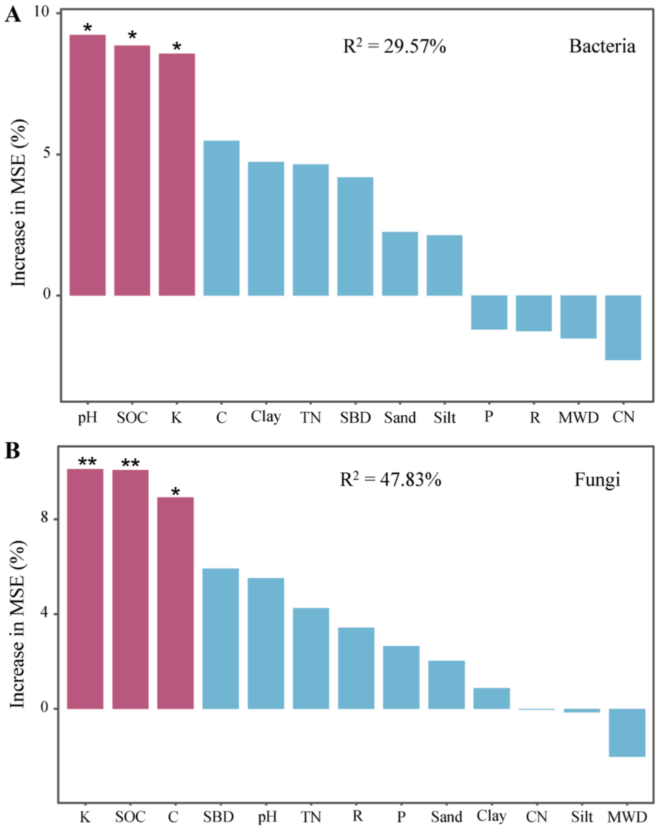

Fig. 9. Random Forest regression analysis of the influence of soil properties and microbial structure on bacterial (A) and fungal (B) community assembly. P: Soil total phosphorus, K: Soil total potassium, SOC: Soil organic carbon, C: Microbial bray-curtis dissimilarity, R: Alpha diversity of soil microbes, MWD: Mean weight diameter, TN: Soil total nitrogen, C:N: Carbon-to-nitrogen ratio, SBD: Soil bulk density.

4.2. *Effects of LU strategies on microbial community composition and assembly processes*

The differences in LU strategies can cause the variations in surface conditions and edaphic properties, which significantly impact microbial communities (Peters et al., 2019; Cornell et al., 2023). At the same elevation, Proteobacteria were found to be more abundant in cornfields compared to other LU types, while natural grasslands exhibited the highest abundance of Ascomycota (**Fig. S2**). One possible explanation for these findings is that cornfields, due to intensive agricultural practices like tillage, fertilization, and pesticide application, may favor the growth of Proteobacteria (Moreno-Espíndola et al., 2018). Conversely, natural grasslands provide a suitable habitat for Ascomycota, benefiting from factors such as open canopies, high light availability, and nutrient cycling dynamics (Egidi et al., 2019). There was no significant difference in bacterial and fungal richness between the grassland and the artificial forest at elevations below 175 m. Furthermore, both bacterial and fungal richness in the artificial forests and natural grasslands were higher than those in the cornfields (Fig. 2). The results were in line with our second hypothesis that vegetation restoration enhanced microbial richness in the riparian zone, which can be attributed to several factors. Both artificial vegetation restoration and natural vegetation restoration have been shown to increase vegetation diversity in riparian zones, promoting the amount of organic material and improving nutrient accessibility (**Table S2**), thus providing a more diverse and favorable environment for microbial communities (Lu et al., 2022). Additionally, vegetation restoration helps stabilize soil structure, reduce erosion, improve soil moisture, and create conditions conducive to microbial growth and diversity (Zhu et al., 2022b).

Variation partitioning analysis showed that microbial community composition was more influenced by LU type (8.34 % for bacteria and 7.68 % for fungi) than by FI (7.11 % for bacteria and 5.29 % for fungi) (**Fig. S3**), which contradicted with our first hypothesis. Moreover, the result was inconsistent with the relative importance of LU and FI affecting microbial community assembly processes (Fig. 8; **Fig. S3**). The reasons are speculated as follows: firstly, vegetation restoration can to some extent offset the impact of factors such as WLFs on the riparian zone ecosystem (Zhu et al., 2020), thereby promoting the sustainable development of the entire ecosystem. Secondly, soil microbial community assembly is a dynamic process (Zhou and Ning, 2017), while the data results of community composition show the static characteristics of soil microbes at the time of sampling (Nemergut et al., 2014). Therefore, the impact of external environment (e.g., LU and WLFs) on microbial community structure has a certain lag compared to its impact on community assembly processes. Nevertheless, further verification is needed for this interesting result. Hierarchical partitioning analysis revealed that soil texture and pH were the primary drivers for bacterial community structure (Fig. 4B), while fungal community structure was primarily drove by TK, C:N ratio and pH (Fig. 4C). These results aligned with prior studies, reveling that the soil microbial communities were shaped by TK (Rosenstock et al., 2016), pH (Malik et al., 2018), soil texture (Xia et al., 2020), and C:N ratio (Liu et al., 2020). Texture can regulate hydraulic connectivity of pore size, thereby regulating microhabitat heterogeneity, providing different ecological niches for bacteria, and promoting coexistence of bacterial species (Xia et al., 2020). Soil fungal root growth and mycelial expansion can be influenced by the solubility and availability of potassium in the riparian zone (Shen et al., 2022), thereby affecting the growth and reproduction of fungi. Some studies have suggested that the soil C:N ratio, as a vital indicator of nutrient availability, has complex effects on the soil microbial community structure (Ou et al., 2019; Liu et al., 2020). The suitable pH environment in soil provides favorable conditions for microbial growth and reproduction (Malik et al., 2018). However, owing to the diverse range of microbial species, the optimal pH values and suitable ranges required for growth vary among different microorganisms. In the riparian zone, periodic flooding can lead to a neutral pH in the soil, which alters the availability and distribution of soil nutrients and subsequently affects the composition of microbial communities (Ou et al., 2019).

LU strategies altered the soil microbial community coexistent networks in the riparian zone. The results of this study indicated that, within the riparian zone, the ranking of network complexity is as follows: natural grasslands > artificial forests > cornfields, with the exception of the fungi at 168 M. Additionally, the network complexity was found to be the highest in 178F and the lowest in 178C (Fig. 5; Table 2). These results aligned with our second hypothesis that vegetation restoration enhanced network complexity. The speculated reasons are as follows: compared to monoculture cornfields, vegetation restoration with diverse plant species improved the edaphic quality (Hou et al., 2019). This is evidenced by the improvement of soil texture, a moderate pH value, and an increase in nutrient content such as TK (Fig. 4; **Table S2**). Consequently, a more diverse range of microhabitats is created for different microbial species, resulting in the formation of more complex microbial communities (Harris, 2009). Compared to the unflooded cornfields (i.e., 178C), the cornfields in the riparian zone exhibited a more intricate network of microbial communities, suggesting that continuous tillage reduced network complexity (Fig. 4; **Table S2**). In contrast, the cornfields in the riparian zone of TGR remained fallow for about 6 months during the flooding period, potentially promoting nutrient storage in the cornfields (Zhu et al., 2020). In addition, 178F had the higher network complexity than 178C, indicating that conversion from forest to cropland could decrease the connection of soil networks (Xue, 2022). Grasslands and artificial forests increased positive links in microbial networks (Table 2), indicating that vegetation restoration eased the competition between microorganisms. These results were in line with a higher proportion of stochastic processes in bacterial community assembly in forest compared to cornfield (Fig. 7). Therefore, the rise in stochastic processes results in an augmentation of symbiotic relationships among microbial populations (Huo et al., 2023).

In the never-flooded area, a particularly higher proportion of stochastic processes, especially homogeneous dispersal, in forest land compared to cornfields indicated that converting forests into farmland will reduce the proportion of stochastic processes in microbial community assembly (Fig. 7). In general, stochastic processes play a dominant role in habitats with lower environmental pressures. The lower decomposition rate of organic matter and the connectivity of water bodies result in slower internal material turnover, thereby mitigating the impact of microbial disturbances from the external environment (Stegen et al., 2012). In this study, frequent agricultural activities in cornfields, such as plowing and fertilization, significantly alter soil physical and chemical factors. The intense external environmental disturbances create certain ecological niche patterns, where environmental filtering selects certain microorganisms to survive (Liu et al., 2021). Consequently, the deterministic processes in community assembly are higher in cornfields compared to forests.

Soil physicochemical properties acted as a stringent environmental filter and leads to phylogenetic clustering in microbial assembly (Jiao and Lu, 2020). In the riparian zone of the TGR, the periodic flooding and discharge caused the homogeneous abiotic environment, thereby leading soil microbial communities into more similar structures (Li et al., 2019). The random forest regression reveled that soil microbial community assembly was significantly affected by pH, SOC and TK (Fig. 9A), while TK, SOC, and fungal composition significantly influenced fungal community assembly (Fig. 9B). In this study, the soil pH ranged between 6.75 and 7.64 (**Table S2**). The increased influence of determinacy in riparian soils suggests that adaptive lineages of diverse taxa may tend to accumulate in neutral environments (Barnett et al., 2020). However, a prior study contradicts this, indicating that pH conditions close to neutral led to more stochasticity in bacterial communities (Tripathi et al., 2018). Differences in research outcomes may be a consequence of the contrasting features of LU patterns (Jiao and Lu, 2020). Prior studies verified that land-use changed SOC and TK that impose homogeneous selection in bacterial community assembly and dispersal limitation in fungal community assembly (Barnett et al., 2020). Additionally, the fungus was characterized by a strong regional presence and has a limited range of distribution (Huo et al., 2023). Thus, fungal composition affected the fungal community assembly primarily governed by stochastic processes.

4.3. Insights into ecological restoration of riparian zones

Periodic flooding and LU can shape soil characteristics, and riparian soils are often influenced by the coupling of these two external environmental factors (Ye et al., 2019). Unreasonable LU may lead to soil functional degradation, resulting in reduced microbial community diversity and functional loss (Gao et al., 2014). Therefore, improving LU management is crucial for maintaining microbial ecological functions and restoring fragile riparian ecosystems (Long and Qu, 2018).

To restore soil microbial community function and improve the health of riparian ecosystems, agricultural activities were supposed to be prohibited (Fig. 2; Gao et al., 2014). A recent study revealed that plant diversity also had a significant influence on community assembly (Huo et al., 2023). Therefore, it was necessary to increase the diversity of microbial available resources through vegetation restoration to maintain microbial ecological functions (Calderón et al., 2017). However, due to long-term, periodic flooding, microbial community assembly was regulated by environmental filtering and dispersal limitation, posing significant challenges for the riparian zone of the TGR (Zheng et al., 2021). It was recommended to replace cultivated land in the riparian zone with LU practices that involved planting flood-tolerant vegetation and natural vegetation regeneration (Zhu et al., 2022b). Our results indicated that in high-elevation areas, artificial restoration sites had the highest network complexity and microbial diversity, while in low-elevation areas, natural vegetation restoration sites had the highest network complexity and microbial diversity (Figs. 2, 5; Table 2). In artificial vegetation restoration sites at high water levels, the impact of water level fluctuations is minimal, resulting in a greater variety of plant types. This environment offers more habitat and nutrient sources for microorganisms compared to other LU types, thereby supporting higher microbial diversity and complexity (Zhu et al., 2022b). In contrast, natural vegetation restoration sites in the riparian zone exhibit a diverse range of plant types and coverage due to their inherent resilience at lower elevations. The prolonged and frequent flooding stress enhances the exchange of materials and energy, creating a variety of ecological niches for different microbial communities, which leads to increased diversity and complexity among these communities (Gao et al., 2021a; Jia et al., 2024). Therefore, considering the differences in flood intensity, different vegetation restoration strategies should be adopted in different flood intensity areas to achieve the best restoration results (Zhu et al., 2022b). In high elevation areas, flood-tolerant vegetation could be appropriately planted to increase plant diversity and soil microbial diversity, offsetting the weakened ecological functions caused by flooding (Ren et al., 2018). In low elevation areas, human interference should be minimized to promote natural vegetation restoration. Vegetation restoration took time and further research was needed to clarify its impact on community structure and assembly mechanisms of the soil microbes (Zhou and Ning, 2017).

5. Conclusions

This study examined how the composition and assembly processes of soil bacterial and fungal communities respond to the dual impacts of FI and LU in the riparian zone of the TGR. Microbial diversity and network complexity were lowest in cornfields at same flooding intensity. Natural grasslands enhanced soil microbial diversity and network complexity in riparian zones with stronger flooding intensity at middle and low elevations. Conversely, artificial mixed forests enhanced soil microbial diversity and network complexity in riparian zones with lower flooding intensity at high elevations. Both natural grasslands and artificial mixed forests increased the positive links in the microbial network compared to cornfields. Flooding intensity and LU had distinct impacts on soil microbial community composition and assembly processes; specifically, land use had a greater impact on composition, while flooding intensity affected the assembly processes. Dam-triggered flooding leads to convergence of soil bacterial communities' assembly processes across different LU types in riparian zones, dominated by deterministic processes, leading to increased stochasticity in soil fungal community assembly. Soil pH, SOC, and TK are dominant soil physicochemical factors influencing microbial community assembly. These findings promote our comprehension of microbial diversity and community stability, offering valuable insights for the scientific management of LU in reservoir riparian zones.

Based on the findings of this study, we recommend the following sustainable management strategies to maintain the ecological balance of the TGR area: prioritize the protection and restoration of artificial mixed forests at high elevations and natural grasslands at low elevations to promote soil microbial diversity and community stability. These practices can enhance microbial diversity and improve ecosystem stability. Future research should focus on long-term monitoring of microbial communities in response to changing environmental conditions and LU practices, as well as exploring the role of specific plant–microbe interactions in promoting ecosystem resilience in riparian zones.

CRediT authorship contribution statement

Kai Zhu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Fei Ye:** Supervision, Methodology, Formal analysis. **Yu Mei:** Methodology, Investigation, Data curation. **Weitao Jia:** Investigation, Formal analysis, Data curation. **Xiai Zhu:** Supervision, Methodology, Formal analysis. **Shuzhen Li:** Software, Formal analysis. **Shengjun Wu:** Supervision, Funding acquisition, Conceptualization. **Songlin Zhang:** Investigation, Formal analysis. **Ping Huang:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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.

Acknowledgements

This study was sponsored by the National Natural Science Foundation of China (42407417, 42377320, 32101380), the Three Gorges' follow-up scientific research project from Chongqing Municipal Bureau of Water Resources (No. 5000002021BF40001), Natural Science Foundation of Guangdong Province (2022A1515010828), and Yunnan Fundamental Research Projects (202301AT070354).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2024.108549.

Data availability

Data will be made available on request.

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