



# The role of microorganisms in phosphorus cycling at river-lake confluences: Insights from a study on microbial community dynamics

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## ABSTRACT

River-lake confluences are key zones in the river-lake network, essential for managing contaminant transport and transformation. However, the role of biogeochemical transformations, particularly in phosphorus (P) dynamics, has been underexplored. As a result, this study looks into the dynamics of microbial communities and how important microbes are to the cycling of P. It was revealed that microorganisms contribute differently to phosphorus cycling in different hydraulic regions. Regions with higher-velocity and finer sediment showed increased microbial diversity and enhanced capabilities for organic phosphorus (OP) mineralization and inorganic phosphorus (IP) solubilization due to lower bio-available P (bio-P) concentrations. In areas characterized by flow deflection (FD), flow stagnation (FST), and flow separation (FSE), distinct P fraction distributions were observed: Total phosphorus (TP) and bio-P were found to be more abundant in the FST and FD regions, but residual phosphorus (Res-P) and calcium phosphorus (Ca-P) were more prevalent in the FSE region. Sediment characteristics, including P species like aluminum-phosphorus (Al-P), OP, iron-associate phosphorus (BD-P), and sediment mid-diameter ( $D_{50}$ ), significantly influence microbial community composition. These results improve our comprehension of the distribution of microbial community distribution and its role in the phosphorus cycle at river-lake confluence, providing useful provide valuable information for managing river-lake confluences and protecting aquatic ecosystems.

## 1. Introduction

The channel confluence has attracted significant attention in recent years, attributed to its intricate hydraulic characteristics and its impact on downstream reaches, extending to the broader river-lake network (Zhang et al., 2020a). For the interconnection of river-lake systems, confluences are vital structures in that they influence flow velocity and direction, sediment transport, water exchange, and ecological processes (Best, 1987; S. Yuan et al., 2023; Yuan et al., 2018; Riley and Rhoads, 2012). These variables also influence the phosphorus (P) distribution in sediment and water, which is crucial for aquatic ecosystems. Research has shown that river confluences, especially in deep-water regions, can exacerbate P retention on surface sediments, leading to heightened contamination compared to the main river stream (Yuan et al., 2019). External P loading, alongside sediment release and retention, influences water phosphate concentrations (García and de Iorio, 2003). Additionally, microbial activities such as uptake, release by bacteria and algae,

and desorption, precipitation, and dissolution, are crucial for P cycling (Jarvie et al., 2005; House et al., 1995). Sediment characteristics, including organic matter content, particle size, iron and aluminum oxides, and hydrodynamics, also affect P distribution (Ji et al., 2022; Zhu et al., 2022).

Previous research has focused on transport processes, there is a significant gap in understanding the role of biogeochemical transformations within P dynamics, particularly concerning microbial community responses under complex hydrodynamic conditions. Although the impact of nutrient mixing and transport on microbial community structure and functions at confluence zones is acknowledged, the specific ways in which microbial communities adapt to and influence P cycling under these conditions remain underexplored (Li et al., 2020; Chen et al., 2022). The significance of microorganisms in the cycling of P in river ecosystems has been extensively established. They facilitate various processes, including the mineralization of organic phosphorus (OP), the immobilization and release of inorganic

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phosphorus (IP), the synthesis of phosphorus compounds, and the modification of the solubility of phosphorus minerals (Norgbey et al., 2020; Campos et al., 2021). These processes are crucial for phosphorus uptake by aquatic plants, reducing nutrient runoff, and enhancing ecosystem phosphorus pools (Li et al., 2022; Zheng et al., 2019; Hu et al., 2023; Duhamel et al., 2021). However, microbial community responses in sediments under the complex hydrodynamics of river-lake confluences and the subsequent influence on P cycling have not been comprehensively investigated. This knowledge gap hinders a full understanding of nutrient dynamics and the effective management of river confluences and broader river networks. Addressing this gap is essential for improving our grasp of nutrient dynamics in these critical zones and for the effective management of river confluences and broader river networks.

Thus, this study aimed to comprehensively investigate the microbial community responses in sediment under complex hydrodynamics at the river-lake confluence, as well as the influence of microbiota on the process of phosphorus cycling. Specifically, the primary aims of this research were to (1) investigate the features of microbial community composition and distribution at the river-lake confluence under varying hydrodynamic conditions; (2) identify key species and investigate the involvement of microorganisms in the phosphorus cycling process; and (3) explore crucial environmental factors and the confluence impact on the microbial community.

## 2. Materials and methods

### 2.1. Study area and sample collection

The 18 sampling points were established at the confluence of the Yangtze River and Dongting Lake (latitude 29° 27' N, longitude 113° 09' E), where the water of the entire lake system discharge into the Yangtze at Yueyang city. Sediment and water samples were gathered in March 2022. Six sampling sections were created throughout the channels, with three sampling places designated as the right (R), center (C), and left (L) banks of each section, respectively (Fig. 1, Fig. 2A). Using sterilized bottles, samples of water (10~30 cm deep) were taken. For sediment sampling, a grab sampler (XDB0201, Pusen, China) was used to collect samples of the surface sediment (0~5 cm in depth). Aseptic sample bags and ice containers at  $-80\text{ }^{\circ}\text{C}$  were used to store water and sediment samples until the subsequent analysis was conducted within 24 h after sample collection.

### 2.2. Physiochemical analysis

In situ measurements were taken of pH, electrical conductivity (EC), dissolved oxygen (DO), and water temperature (T) (HQ2200, HACH, USA). Concentrations of organic phosphorus (OP), Ammonium The following phosphorus levels in sediments were tested using the appropriate techniques: residual phosphorus (Res-P), calcium bound phosphorus (Ca-P), iron bound phosphorus (BD-P), aluminum bound phosphorus (Al-P), and chloride extractable phosphorus ( $\text{NH}_4\text{Cl-P}$ ) (Text S1). Other parameters, like  $\text{Fe}^{2+}$ ,  $\text{Fe}^{3+}$ , total nitrogen (TN), nitrate

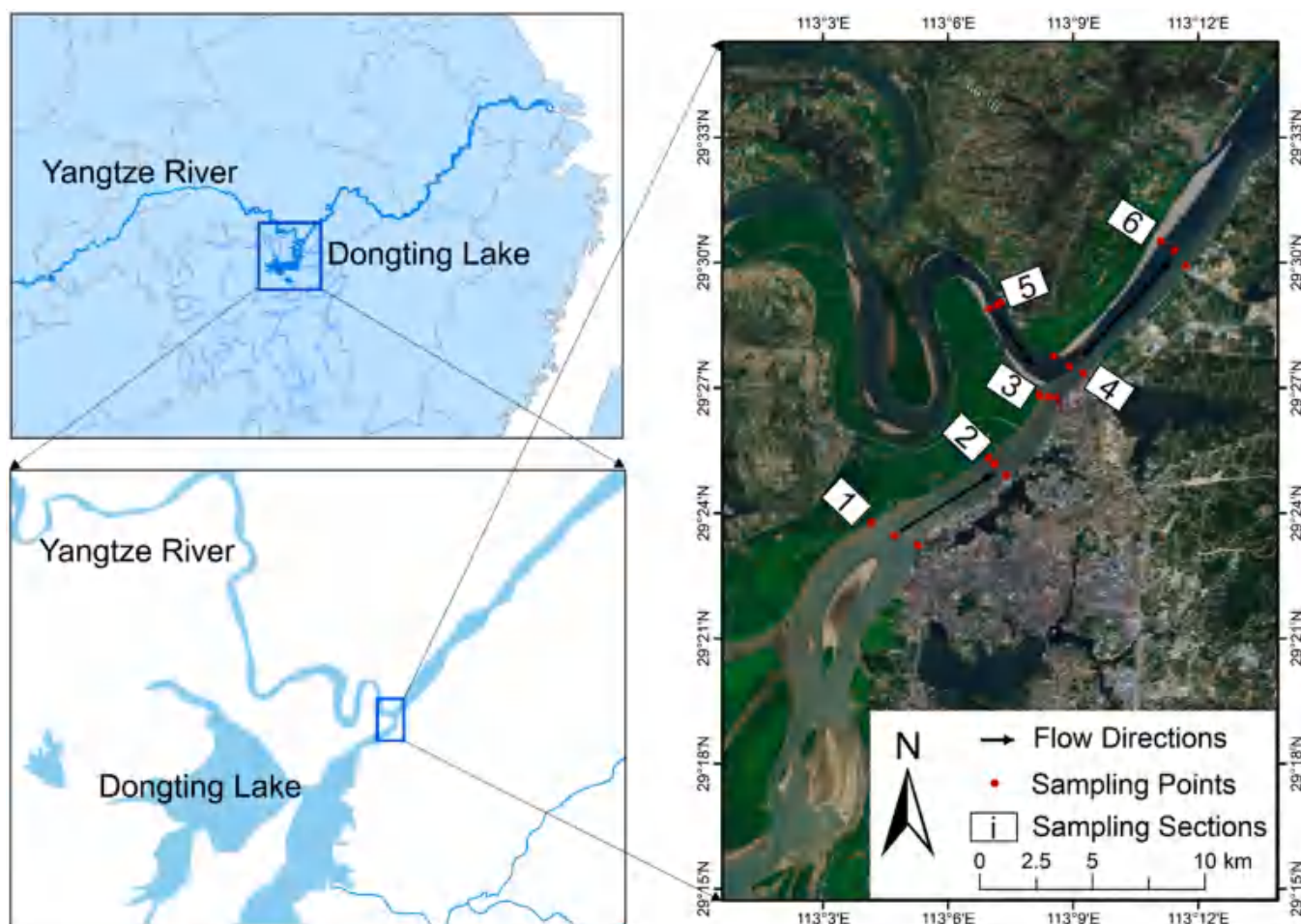
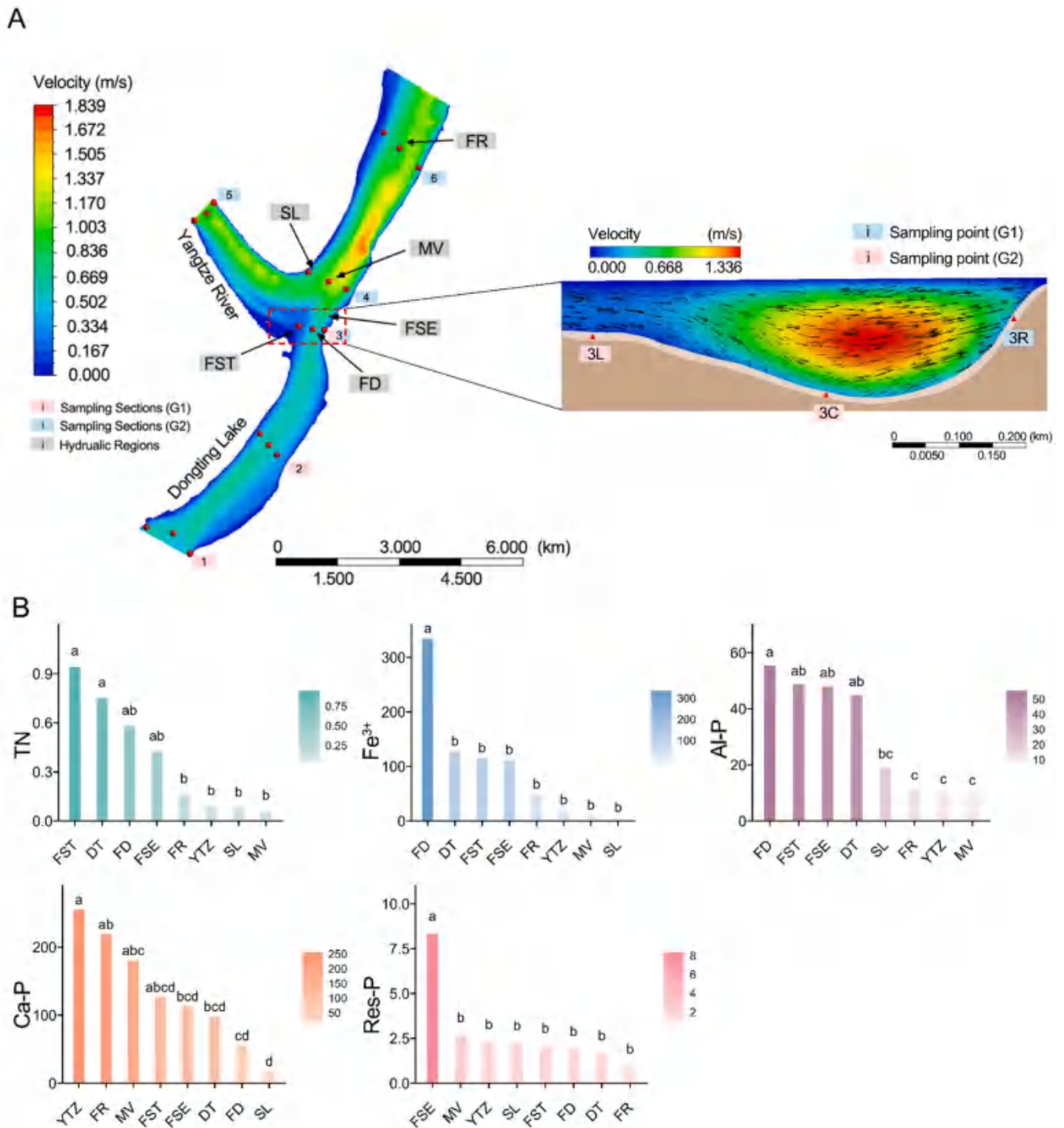


Fig. 1. The diagram map of the study area and setting of sampling points.



**Fig. 2.** (A) Simulated velocity contours in the study area and Section 3: mapping mean velocity magnitudes for regional classification. Velocity values are represented in meters per second ( $m s^{-1}$ ) using a color scale. (B) DMRT of TN,  $Fe^{3+}$ , Al-P, Ca-P and Res-P concentrations at different regions. Different letters indicate significant differences ( $F > 1, p < 0.05$ ).

( $NO_3^-$ -N), ammonia nitrogen ( $NH_4^+$ -N), nitrite ( $NO_2^-$ -N), sulfide ( $S^{2-}$ ), and sulfate ( $SO_4^{2-}$ ) were analyzed following the standard methods (Text S1).

A Teledyne RDI 1200 kHz RiverPro Acoustic Doppler Current Profiler (ADCP, RIV-600, TRDI Ltd., Thousand Oaks, California, USA) with a precision of  $1 mm s^{-1}$  in spatial resolution was used to measure mean three-dimensional (3D) velocity profiles (Text S1). The hydrodynamic situation of the river-lake confluence was modeled by ANSYS FLUENT (version 17.0) (Text S2). The model's accuracy and uncertainty were assessed by coupling it with observed and simulated flow velocity. As

demonstrated in Fig. S1, the average relative error was below than 40 %.

### 2.3. DNA extraction, sequencing, and bioinformatics

Genomic DNA was extracted from homogenized sediment samples using a soil genomic DNA extraction kit (Solarbio, Beijing, China). The DNA was initially evaluated through 1 % agarose gel electrophoresis before being stored at  $-20 ^\circ C$ . PCR amplification and high-throughput sequencing were performed by Majorbio Bio-Pharm Technology Co.,

Ltd. (Shanghai, China), utilizing primers 806R (5'-GGAC-TACHVGGGTWTCTAAT-3') and 338F (5'-ACTCCTACGGGAGGCAG-CAG-3') to amplify the 16S rRNA V3-V4 regions. Functional predictions were made using 16S PICRUST2 (Text S1). All data from the samples are accessible in the Sequence Read Archive (SRA) under project PRJNA1052369 (<http://www.ncbi.nlm.nih.gov/sra/>).

#### 2.4. Statistical analysis

To explore the variation in microbial community structure between groups, principal coordinate analysis (PCoA) and analysis of similarities (ANOSIM) were used. One-way analysis of variance (ANOVA) and Duncan's new multiple range test (DMRT) were employed to explore the difference in chemical content across various hydraulic regions, using package "agricolae" in R version 4.2.1. A Two-tailed Wilcoxon rank-sum test was applied using "ggpubr" in R version 4.2.1 (Gao et al., 2023). Wallis (KW) sum-rank test was combined with linear discriminant analysis (LDA) effect size (LEfSe) analysis. Using Gephi software, co-occurrence network analysis with Spearman correlation ( $p < 0.05$ ,  $r \geq 0.5$ ) revealed community structure and possible ecological functions (Barberán et al., 2012). We computed each node's in-module connectivity ( $Z_i$ ) and among-module connectivity ( $P_i$ ) in order to ascertain its roles within the networks and pinpoint possible keystone species (Text S3). Mantel tests were analyzed using the "vegan" R package in R version 4.2.1 to investigate the connection between environmental elements and the composition of microbial communities (Li et al., 2023a; Wang et al., 2023). To understand the interactions between environmental factors, microbial communities, structural equation model (SEM) was used. Given the sample size, data characteristics, and model complexity, the path model with SEM using the partial least squares (PLS) method was chosen to determine the path coefficients and model fitting parameters by SmartPLS (v. 4.0.9.5). The model performed satisfactorily, suggesting that the PLS-SEM model was well-built and appropriate for more investigation (Table S4-S7).

### 3. Results and discussion

#### 3.1. Hydrodynamic and physiochemical characteristics

The study area was divided into different hydraulic regions using simulated velocity values and directions. The distribution and hydrodynamic characteristics of six separate regions at this confluence are shown in Fig. 2A. Hydraulic junctures of channels typically fall within six distinct regions: flow stagnation zone (FST), flow deflection zone (FD), flow separation zone (FSE), maximum velocity zone (MV), shear layers zone (SL), and flow reestablishment zone (FR) (Best, 1987). Every region has specific hydrodynamic characteristics influencing sediment transport and channel morphology. The results of ANOVA revealed significant differences in TN,  $Fe^{3+}$ , Ca-P, Al-P, and Res-P concentrations across distinct hydraulic regions ( $F > 1$ ,  $p < 0.05$ ), while other chemical materials exhibited homogeneity (Table S2). The homogeneity of most chemical concentrations across diverse regions is rational, given the crucial role of hydrodynamic conditions in the transport process. However, it is noteworthy that, besides transportation processes, transformation processes have been observed to impact the distribution of chemical substances (Yuan et al., 2023a). The F-value of the ANOVA does not offer substantiated evidence of differentiation between any two specific regions. To compare the mean concentrations across each region, DMRT was employed for the five chemical indices (Fig. 2B). It was found that the distribution of chemical levels was inconsistent with the hydraulic region classification. The concentrations of the forementioned five chemical materials at the inflow to confluence zone from Dongting lake (DTI), FST, and FD displayed significant distinctions from those in FSE, SL, MV, FR, and the inflow to confluence zone from Yangtze River (YtZl). Notable variations were observed in Ca-P, Al-P, and Res-P among regions, with Al-P being bio-available and Ca-P associated with P burial

in sediment. Prior studies have indicated heightened phosphorus contamination in confluence areas compared to the mainstream (Yuan et al., 2019). Additionally, sampling points 3L, 3C, and 3R in Section 3, corresponding to the FST, FD, and FSE regions, respectively, exhibited variations in the concentrations of the aforementioned five chemical materials. A prior study revealed variations in nitrogen concentrations and microbial community compositions at a river confluence within the same section (Li et al., 2023b). Thus, the nutrient variation and microbial community within the same section of the river-lake confluence are intriguing.

#### 3.2. Composition and distribution of microbial community

The 8028 bacterial Operational Taxonomic Units (OTUs) were identified across 18 sampling points. The most abundant phylum, *Proteobacteria*, occupied 22.41 % of total bacterial sequences, followed by *Chloroflexi* (13.96 %), *Acidobacteriota* (13.72 %), *Actinobacteriota* (13.37 %), *Firmicutes* (7.81 %), *Bacteroidota* (4.19 %), *Nitrospirota* (2.76 %), *Cyanobacteria* (2.34 %), *Sva0485* (2.19 %), and *Latescibacterota* (1.87 %).

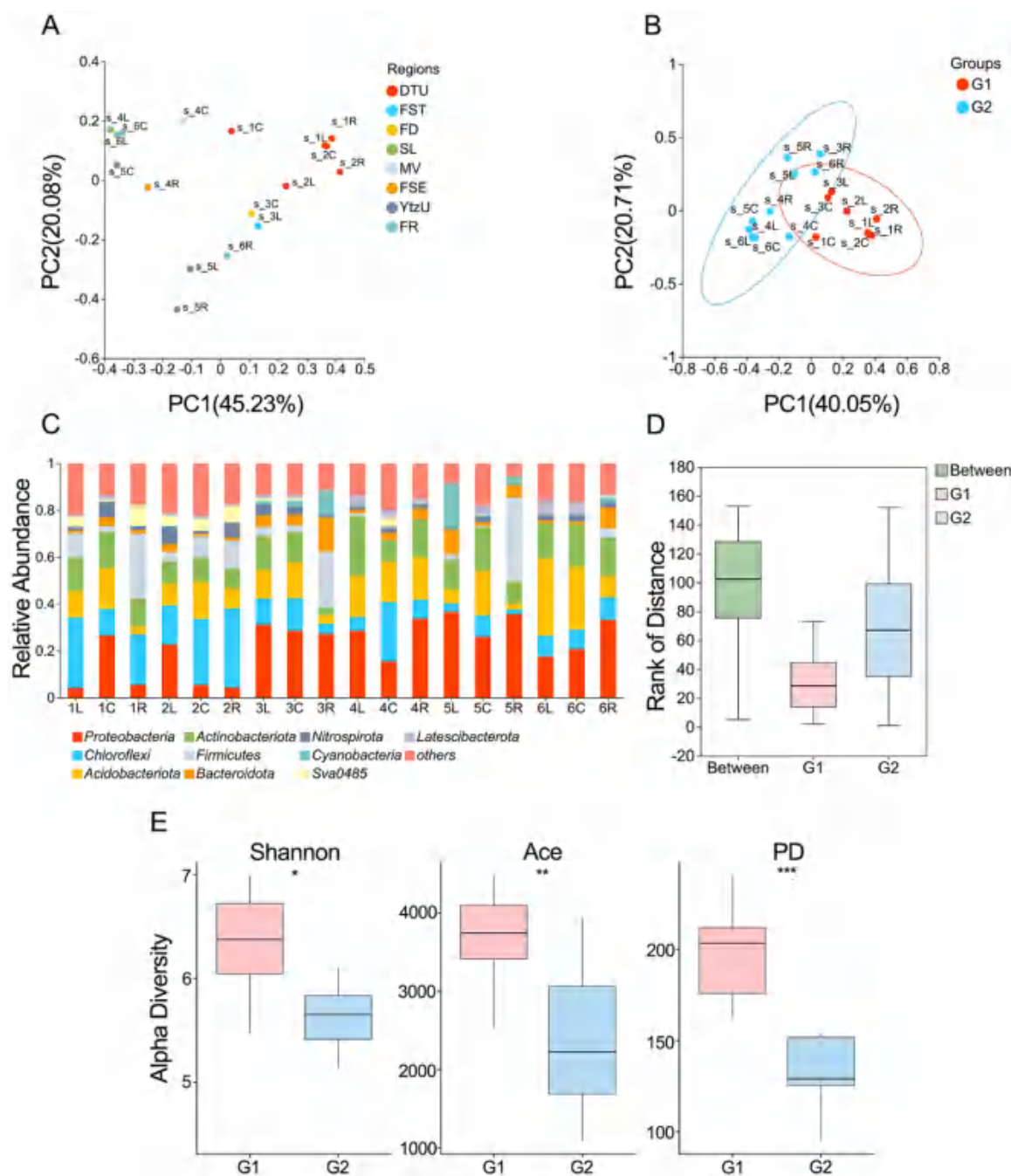
The microbial community compositions within the distinct hydraulic regions, as delineated by their unique hydrodynamic characteristics (Fig. 2A), showed no significant differences. This is attributed to the influence of extrinsic factors, such as nutrient concentrations, which significant influence the microbial community composition. Therefore, based on the results of DMRT, 18 sediment sampling sites could be categorized into two groups (Table S3). Group 1 (G1) encompasses samples from DTI, FST, and FD, while Group 2 (G2) encompasses samples from FSE, SL, MV, FR, and YtZl. G1 and G2 had differences in hydrodynamic characteristics (Fig. S2), indicating that regions contained in G1 have lower velocity and coarser sediment ( $p < 0.05$ , Wilcoxon rank-sum test), which is in line with earlier studies (Yuan et al., 2021). The P content in both sediment and water exhibited variations between G1 and G2. G1's sediment displayed significantly higher concentrations of Al-P, OP, and bio-P, along with lower levels of  $NH_4Cl$ -P and Ca-P ( $p < 0.05$ , Wilcoxon rank-sum test, Fig. S2). In G1's water (Fig. S3), there was a significantly elevated content of total phosphorus (WTP) and particulate phosphorus (PP) ( $p < 0.05$ , Wilcoxon rank-sum test). The results of PCoA (Fig. 3B) and ANOSIM analysis (Fig. 3D) confirmed the significant difference between G1 and G2 (ANOSIM = 0.5702,  $p = 0.001$ ).

The Shannon, Ace, and PD alpha diversity indices were computed and compared in order to look into how the G1 and G2 microbial communities differ in terms of composition. Shannon, Ace, and PD alpha diversity indices in G1 were noticeably greater than in G2, indicating a more diversified and richer microbial community in G1 (Fig. 3E). The outcomes demonstrated that the G1 and G2 microbial communities differed in terms of composition and nutrient contents, which may result in distinct microbiota distribution and functionality within the two groups.

#### 3.3. P cycling potential and microbial community characteristics

The genes responsible for IP solubilization and regulation of P were the most prevalent among all genes observed (Fig. 4). More specifically, the G2 group exhibited elevated levels of IP solubilization genes, with a notably significant increase (33.58 %) in the proportion of the *ppa* gene in G2. The majority of OP mineralization genes exhibited low relative abundance in both G1 and G2; however, G2 showed a notable increase, especially in the cases of *phoD* (55.54 %), *phoX* (50.75 %), *ugpQ* (9.78 %) and *phnFGHIJKLMN* (87.53 %–236.36 %). The majority of P transportation genes displayed high expression in both G1 and G2, with *pstABC* (11.46 %–11.59 %) significantly more prevalent in G1, while *phnE* (89.10 %) and *ugpBC* (32.90 %–56.71 %) were more pronounced in G2. Of these genes involved in P regulation, no significant difference was observed.

In G1 and G2, higher expression of OP mineralization genes and IP



**Fig. 3.** Characteristics of the microbial community at the confluence. (A, B) PCoA analysis based on Abund-Jaccard distance, with 95 % ellipse confidence, illustrated bacterial community composition at different sampling points. (C) Microbial community bar plot at the phylum level. (D) ANOSIM analysis at the phylum level. (E) Microbiota diversity as measured by Shannon, Ace, and PD index was observed in G1 and G2. P values were from a two-tailed Wilcoxon rank-sum test. The significance levels are denoted by asterisks (\*), where \* indicates  $p < 0.05$ , \*\* indicates  $p < 0.01$ , and \*\*\* indicates  $p < 0.001$ .

solubilization genes were observed in G2. The results indicated that the sediment concentrations of TP, OP ( $p < 0.05$ , Wilcoxon rank-sum), Al-P ( $p < 0.05$ , Wilcoxon rank-sum), and bio-P ( $p < 0.05$ , Wilcoxon rank-sum) were lower in G2 than in G1 (Fig. S2). Microorganisms can enhance the available P content by solubilizing inert IP and mineralizing OP compounds in low-P conditions (Zeng et al., 2022). The pivotal genes linked to IP solubilization encompass *gcd*, *ppx*, and *ppa*, responsible for encoding glucose dehydrogenase, exopolyphosphatase, and inorganic pyrophosphatase, respectively. The *ppa* gene, specifically encoding inorganic pyrophosphatase, plays a crucial role in hydrolyzing polyphosphate compounds, thereby enhancing the solubilization of IP. Previous studies have documented that in low-P condition environments,

microorganisms respond by increasing the production of phosphatases encoded by OP mineralization genes (Wei et al., 2019). *PhoD* and *phoX* are the principal genes responsible for encoding alkaline phosphatases. These enzymes facilitate the mineralization of OP, which is synthesized by bacteria in response to P starvation. They serve as vital indicators of OP cycling and are closely associated with P bioavailability in aquatic ecosystems (Wang and Pant, 2010). This adaptive response helps alleviate P limitation through the mineralization of OP compounds and solubilization of IP.

As for P transportation, the high affinity of the phosphate transport system (*pstSCAB*) was higher in G1 than G2 (11.58 %–11.60 %), and the sn-glycerol 3-phosphate transport system (*ugpABCE*) was lower in G1

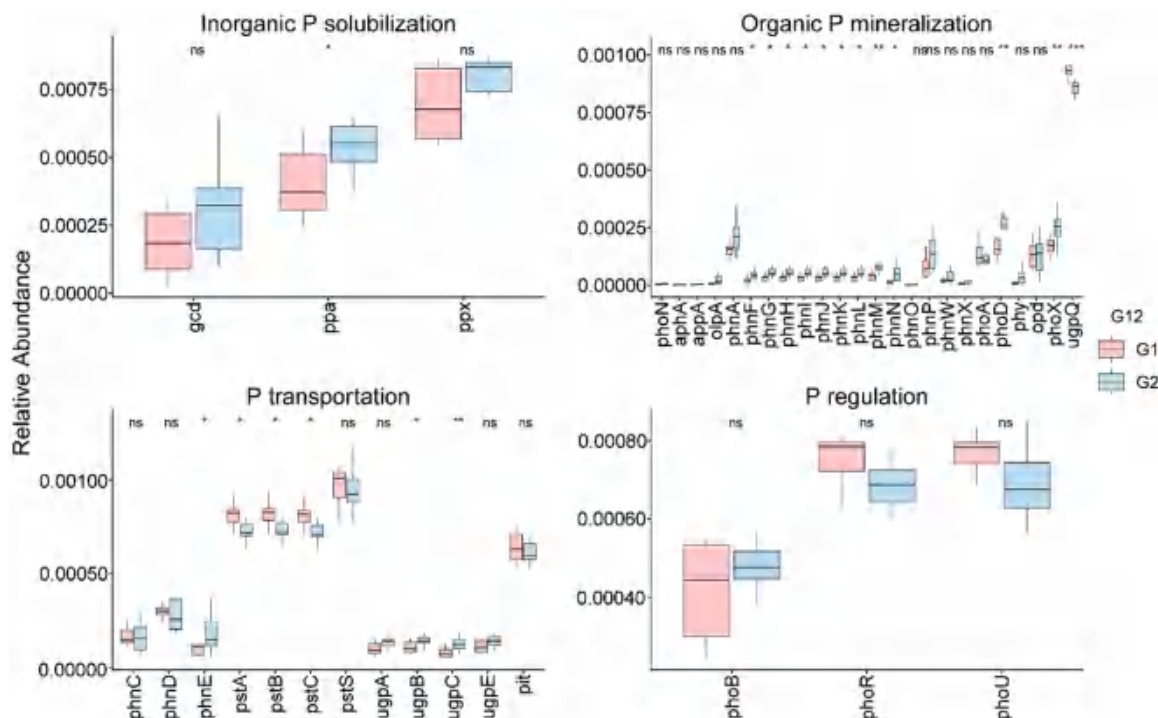


Fig. 4. The results of the Wilcoxon rank-sum test for differential significance analysis of the relative abundance of phosphorus cycling genes. The significance levels are denoted by asterisks (\*), where \* indicates  $p < 0.05$ , \*\* indicates  $p < 0.01$ , and \*\*\* indicates  $p < 0.001$ .

than G2 (26.79%–56.96%). The elevated presence of bio-P may lead to increased expression of *pstSABC* in G1 (Fig. S2) in that *pstSCAB* serves as the primary P transporter when P is high (Dai et al., 2020). In order to efficiently employ alternate P sources, the *pho* two-component system regulates the expression of phosphate transporters (*pstSCAB* and *pit*), showed no significant difference in G1 and G2 (Nishino et al., 2005; Wanner, 1993). The results suggested that microorganisms in sediment at G1 might have a greater P-assimilating capacity (Hsieh and Wanner, 2010).

Using 16S PICRUSt2, the analysis of the functional roles of microorganisms in P cycling showed that microorganisms in G1 have an enhanced capacity for P assimilation, whereas those in G2 are more inclined towards IP solubilization and OP mineralization.

Furthermore, the co-occurrence network analysis reveals that the microbial community in G1 had a more connected and interactive network, characterized by higher mean degree, graph density, modularity, and mean clustering coefficient (Fig. 5C). Typically, module hubs, network hubs, and connectors are deemed essential species in microbial networks. In G1, *Cytophaga* (within *Bacteroidota*) and *Symbiobacteraceae* (within *Firmicutes*) were recognized as module hubs. *Bacteroidota* and *Firmicutes* were reported to be phosphate-solubilizing microbes (Wu et al., 2022). *Firmicutes* and *phoD* were found to be negatively correlated in a prior investigation (Cui et al., 2023). This result aligned with the lower relative abundance of the OP mineralization genes in G1.

In G2, *Neisseriaceae* (within the *Betaproteobacteria* class), *Polycyclovorans* (within the *Gammaproteobacteria* class), and *Pedosphaeraceae* (within the *Gammaproteobacteria* class) were identified as module hubs. The *Proteobacteria* phylum, a key group of *phoD*-containing bacteria, plays a leading role in oxidative phosphorylation (Lang et al., 2022). The result corresponded with the alkaline phosphatase genes' higher relative abundance in G2 (*phoD* and *phoX*).

The microbial community in G1 exhibits a more interconnected network and is characterized by species with a higher P assimilation capacity, while G2 shows a network with key species associated with OP mineralization and a higher abundance of related genes.

Additionally, significant disparities in the microbiota were detected

between the 2 groups. With an LDA threshold of 3.5, eight bacterial clades show statistically significant differences (Fig. 6). The results unveiled that bacterial lineage with increased abundance in G1 were mainly *Chloroflexi* (primarily of orders *Anaerolineae* and *Dehalococcoidia*), *Firmicutes* (mainly of families *Bacillaceae* and *Clostridiaceae*), *Sva0485*, *Spirochaete* (genus), *Armatimonadota*, and *Patensibacteria*. G2 exhibited enrichment in *Veillonellales-Selenomonadales* (from class to order, within *Firmicutes*), *Pseudomonas* (from order to genus), and *GAL15*.

More species, identified as dominant phyla in the P cycle, were enriched in G1. Despite fewer species being enriched in G2, they played a crucial role in the phosphorus biogeochemical process. *Chloroflexi*, *Firmicutes*, and *Sva0485* were prevalent phyla in the microbial community (Fig. 3C) and essential in phosphorus biogeochemical cycling. It has been reported that *Firmicutes* contribute to substrate phosphorylation and drive the link between aerobic C fixation and phytase (Ma et al., 2021) which could lead to the release of P. P is released from organic substances by the metabolic alteration of organic materials by *chloroflexi*, particularly *Dehalococcoides* (Rao et al., 2022). *Sva0485* was assumed to be capable of sulfate reduction which could indirectly induce the release of phosphates and inhibit the binding of Fe and phosphates in hypoxic sediments (Lukkari et al., 2009; Caraco et al., 1989). At the genus level, *Pseudomonas*, which was reported to have capabilities in P solubilization and mineralization, was enriched in G2 (Jin et al., 2023).

The results indicate that G1 is characterized by bacterial communities with a higher overall involvement in P cycling, whereas G2 is enriched with different bacterial taxa that also play significant roles in P biogeochemical processes.

#### 3.4. The difference between hydrodynamic and P fractions content in Section 3

The 3 distinct sampling points, each characterized by different hydrodynamics (Fig. 2A), exhibited significant variations in the concentrations of TN,  $\text{Fe}^{3+}$ , Al-P, Ca-P, and Res-P (Fig. 2B). Furthermore, the microbial communities in these sections were categorized into two

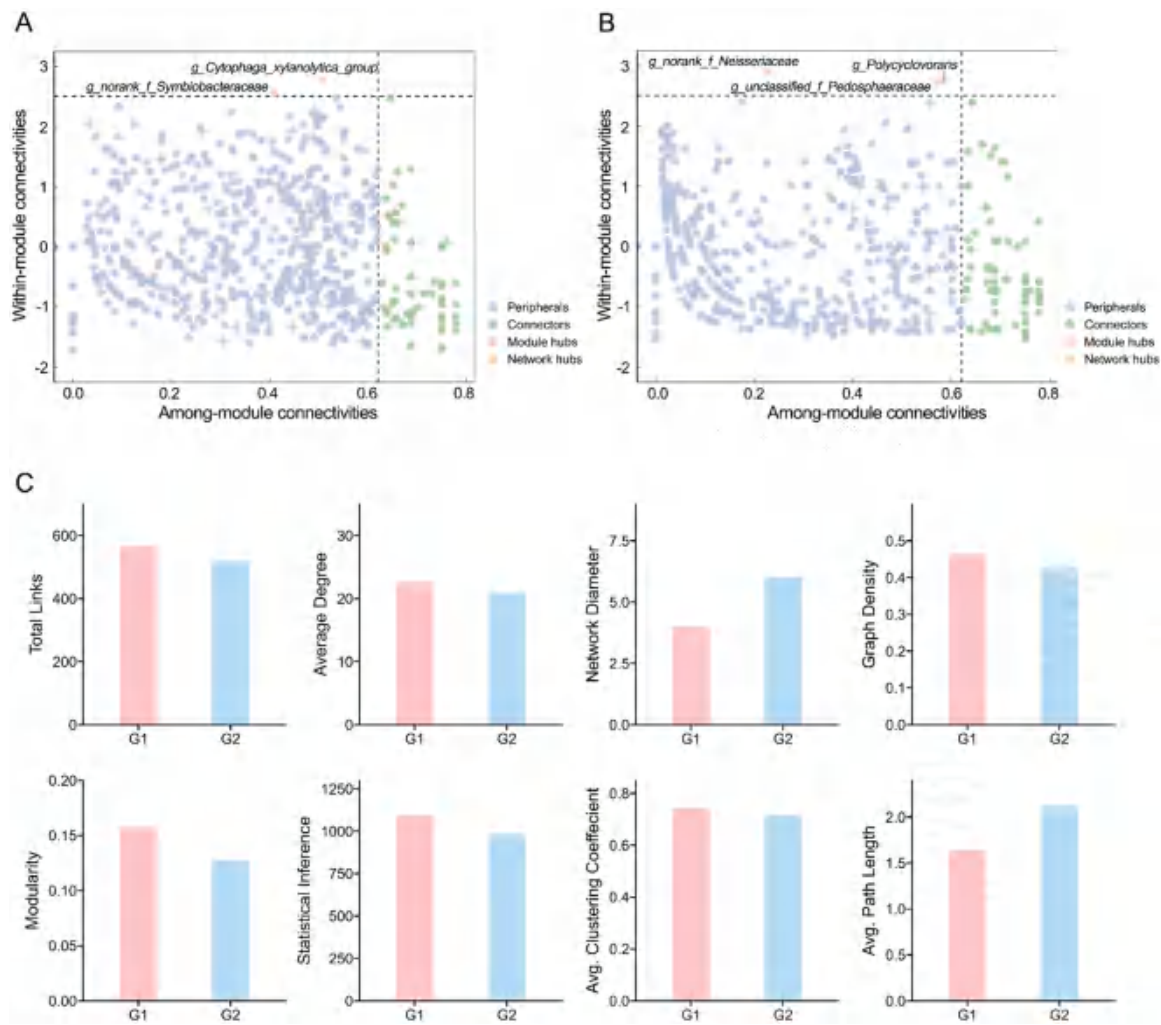


Fig. 5. (A, B) Zi-Pi analysis result of microbial community within G1 and G2, respectively. (C) Parameters of microbial community network within G1 and G2.

groups, in line with earlier research (Li et al., 2020). Though 3 L, 3C, and 3R are situated in the same sampling section, they belong to the flow stagnation zone (FST), flow deflection zone (FD), and flow separation zone (FSE), respectively. FST features significant flow stagnation and high sedimentation rates at the junction apex (Bilal et al., 2020). The FD region experiences changes in flow direction and velocity, leading to sediment deposition and erosion (Balouchi et al., 2022). FSE is where lake flow separates from the river, creating recirculation and low pressure that can cause sedimentation and scouring (Leite Ribeiro et al., 2012). Due to the unique characteristics of different flow regions,  $D_{50}$  and the concentration of different P fractions were distinct, potentially contributing to variations in microbial community composition. As illustrated in Fig. 7, the finer sediment in the FSE region than in FD and FST is consistent with a prior study that documented helical flow and finer sediment in that area (Yuan et al., 2021).

The P species' distribution in Section 3 in sediment roughly resembles that of groups G1 and G2 (Fig. S2). Content of P fractions varied in Site 3 L (FST), 3C (FD), and 3R (FSE). Specifically, concentrations of TP, BD-P, and OP were higher in Site 3 L (FST) and 3C (FD), while Ca-P, Res-P, and loosely sorbed P ( $\text{NH}_4\text{Cl-P}$ ) were more in Site 3R (FSE). Al-P was not much different among the three regions. The concentration of TP was also lower in Site 3R ( $397.4 \text{ mg kg}^{-1}$ , FSE) than Site 3 L ( $642.9 \text{ mg kg}^{-1}$ , FST) and Site 3C ( $480.6 \text{ mg kg}^{-1}$ , FD), but the  $D_{50}$  of Site 3R (2.17 mm, FSE) was finer than Site 3 L (6.32 mm, FST) and Site 3C (6.08 mm, FD), which could be the result of the high content of silt in FST and FD (Fig. 7). Elevated levels of  $\text{Fe}^{3+}$  and  $\text{Fe}^{2+}$  in Site 3 L and Site 3C are

responsible for the increased concentration of BD-P in these areas. The distribution of TOC and DOC in Section 3 diverged from that of OP, likely because of the impact of a microbial population that is more numerous and diversified at Sites 3 L and 3C (Table S7). The lower relative abundance of OP mineralization genes in G1 provides additional support for this observation (Fig. 4).  $\text{NH}_4\text{Cl-P}$ , loosely sorbed, is easy to release into the overlying water. The higher concentration of  $\text{NH}_4\text{Cl-P}$  in FSE may suggest the possibility of phosphorus actively releasing from sediment into the water (Ma et al., 2023). Ca-P was a fairly stable P fraction in river sediment, which is related to the P bury in sediment (Yuan et al., 2019). Sampling points of FSE and FST were near the riverbank, which could lead to a higher content of Ca-P in the two regions than the FD region (Kozyrev et al., 2023). BD-P, Al-P,  $\text{NH}_4\text{Cl-P}$ , and OP were bio-P. The content of bio-P was higher in Site 3 L ( $108.4 \text{ mg kg}^{-1}$ , FST) and 3C ( $123.12 \text{ mg kg}^{-1}$ , FD) than in Site 3R ( $103.3 \text{ mg kg}^{-1}$ , FSE), which is consistent with the forementioned result. Those microorganisms in FSE (G2), with a lower P-condition, could be more conducive to IP solubilization and OP mineralization. In water, WTP, total dissolved phosphorus (TDP), and PP in Site 3 L (FST) were higher than Site 3C (FD) and Site 3R (FSE) (Fig. S4). That could be due to the FST region's higher TP and coarser sediment.

In conclusion, Section 3 is pivotal at the river-lake confluence due to its intricate hydrodynamics, significantly influencing phosphorus distribution. The observed severity of phosphorus contamination in the FST region is noteworthy. The composition and phosphorus-cycling abilities of the microbial communities in FST, FD, and FSE may then be impacted

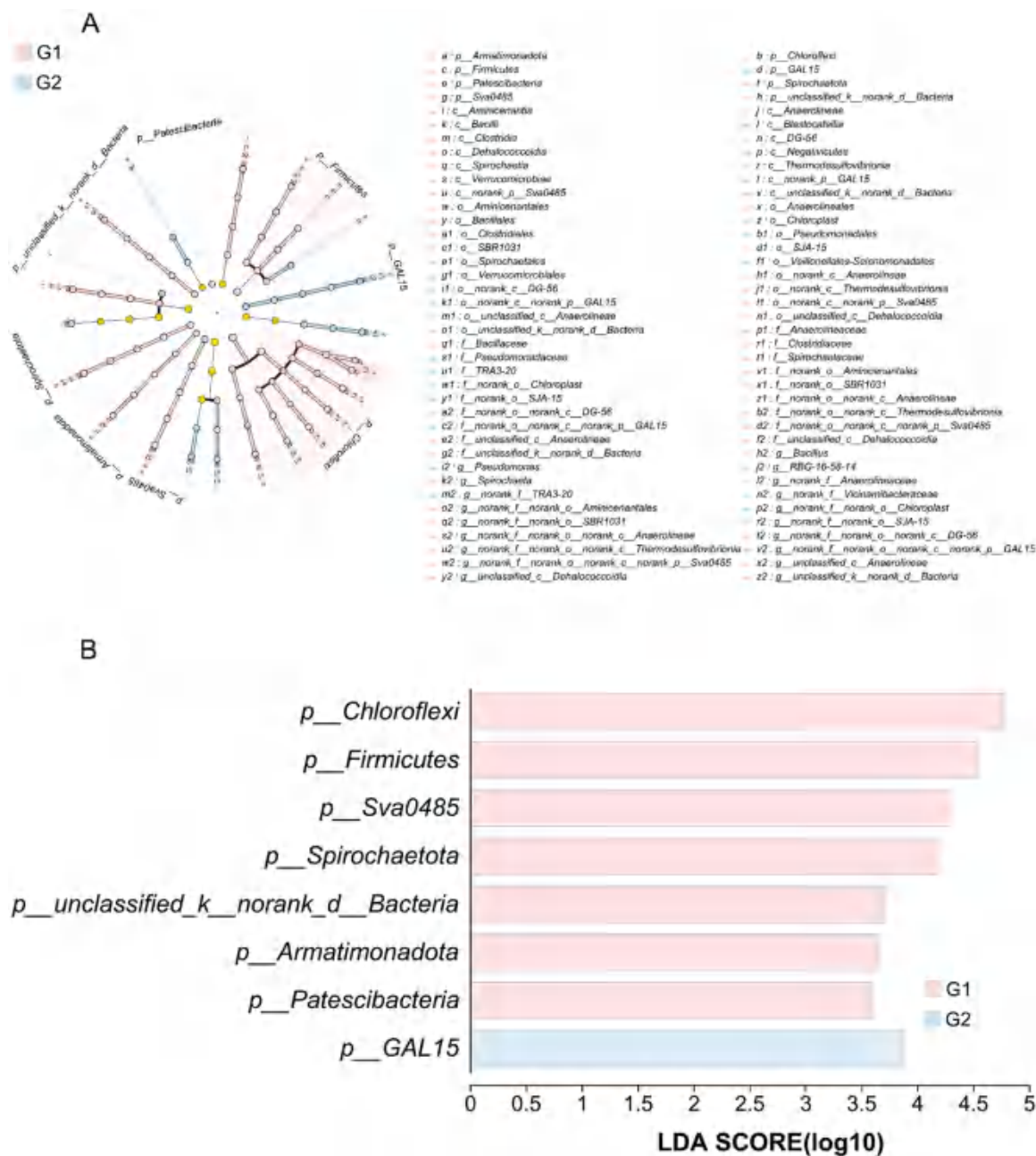


Fig. 6. LDA and LEfSe analysis (LDA > 3.5,  $p < 0.05$ ) to uncover discriminative taxonomic differences between microbial communities in G1 and G2. (A) Cladogram showing the phylogenetic distribution of microbial lineages in G1 (pink) and G2 (blue). The points extending from the center to the outer sphere symbolize the level of phylum, class, order, family, and genus level. (B) Indicator microbial groups with LDA values >3.5.

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### 3.5. Environmental factors related to microbial community composition

To separate plausible environmental drivers of the microbial community in sediments, the Mantel test and Spearman heatmap were employed. The results showed that TOC, TN, DOC, pH, Al-P, OP, Within the sediment,  $\text{NH}_4^+$ , BD-P, and D50 were the primary environmental elements affecting the ecosystem of microorganisms (Fig. 8A) (Zhu et al., 2023; Liang et al., 2023a). The Pearson correlation coefficient indicated a positive correlation among all factors except pH. BD-P, Al-P, and OP are important fractions of P in the river and lake sediment. pH conditions can affect the stability, availability, and release of these fractions, influencing the overall phosphorus dynamics in river ecosystems (Bao et al., 2020). This study's findings about pH's negative link

with Al-P, BD-P, and OP are consistent with other research suggesting that high pH promotes the release of Al-P and BD-P (Zhao et al., 2022).

All of the above factors were positively correlated (Mantel's  $p < 0.05$ ) with the microbial community. Specifically, TOC was the primary factor, with TN, DOC, Al-P, and OP following. These factors were reported to be positively linked with microbial biomass and could impact the relative abundance of microbial taxa because of their importance in microbial growth and reproduction as well as other metabolism processes (Da Costa et al., 2023; Jorgensen et al., 2012). Al-P and OP, both indicative of bio-P, consistently demonstrate a positive association with the microbial community, in line with the previously discussed findings (Kreiling et al., 2023). D50 of the sediment was a key factor affecting the microbial community and was indicated as the main elements contributing to the varied microbial community structures (Zhang et al., 2020b). Sediment pH significantly impacts microbial communities,



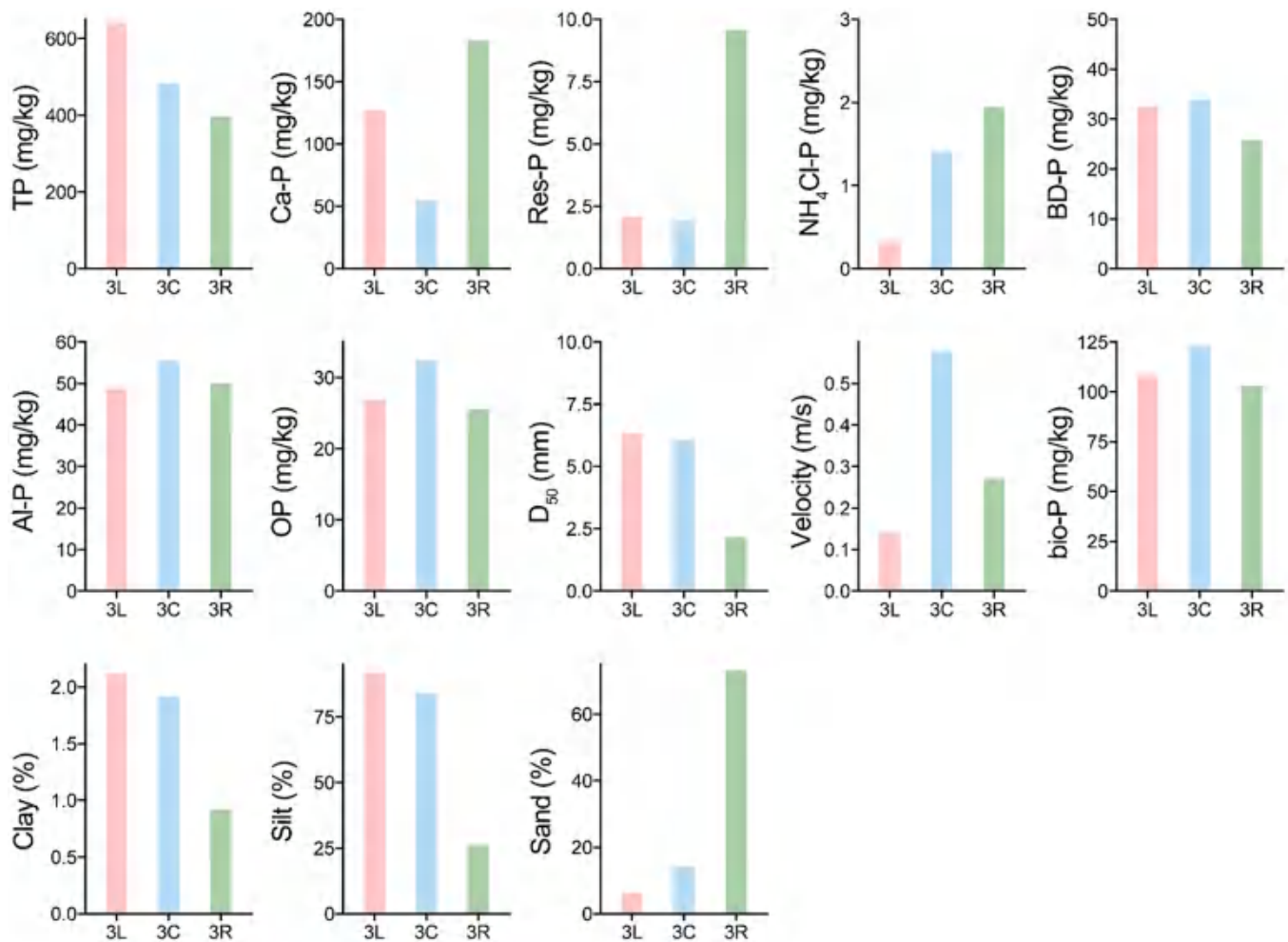


Fig. 7. The distribution of phosphorus species, median sediment size, and sediment component in sampling Section 3.

influencing differences in bacterial community diversity and beta diversity (Bertolet et al., 2022) (Pu et al., 2023). Additionally, pH-related variations in microbial community composition have been linked to changes in sediment functioning (Bertolet et al., 2022).

*Chloroflexi* and *Firmicutes* were positively linked to OP, TOC, and TN but negatively associated with pH (Kou et al., 2020). Notable positive associations were discovered between *Spirochaetota* and TN, TOC, and DOC, indicating that *Spirochaetota* plays a role in carbon and nitrogen cycling in sediment but has a negative correlation with pH (Liu et al., 2023). *Patescibacteria* showed a substantial inverse correlation with pH, whilst *Firmicutes* and *Patescibacteria* showed a considerably positive link with TN, TOC, DOC, and Al-P (Ivanova et al., 2020). *Armatimonadota* was significantly and positively related to OP, S<sup>2-</sup>, Al-P, TN, and TOC, but negatively related to Ca-P, NH<sub>4</sub>Cl-P, and pH. The phyla mentioned above were the differential taxonomies between G1 and G2. The results indicated that those microbial species may be essential to P release and absorption in sediment, influencing P cycling in river-lake confluence, following the above results. *Proteobacteria* were negatively correlated with OP and S<sup>2-</sup>, and positively related to Res-P. A previous study found that *Proteobacteria* was one of the dominant phyla of *phoD*-harboring bacteria (Lang et al., 2022). *Cyanobacteria*, which is significantly negatively related to OP and S<sup>2-</sup> but positively related to Ca-P, NH<sub>4</sub>Cl-P, and pH, can absorb and store P (Gu et al., 2020; Cottingham et al., 2015) and release P into the water column, influencing the activity of other microorganisms involved in P cycling, such as phosphate-solubilizing bacteria (Jentsch et al., 2023).

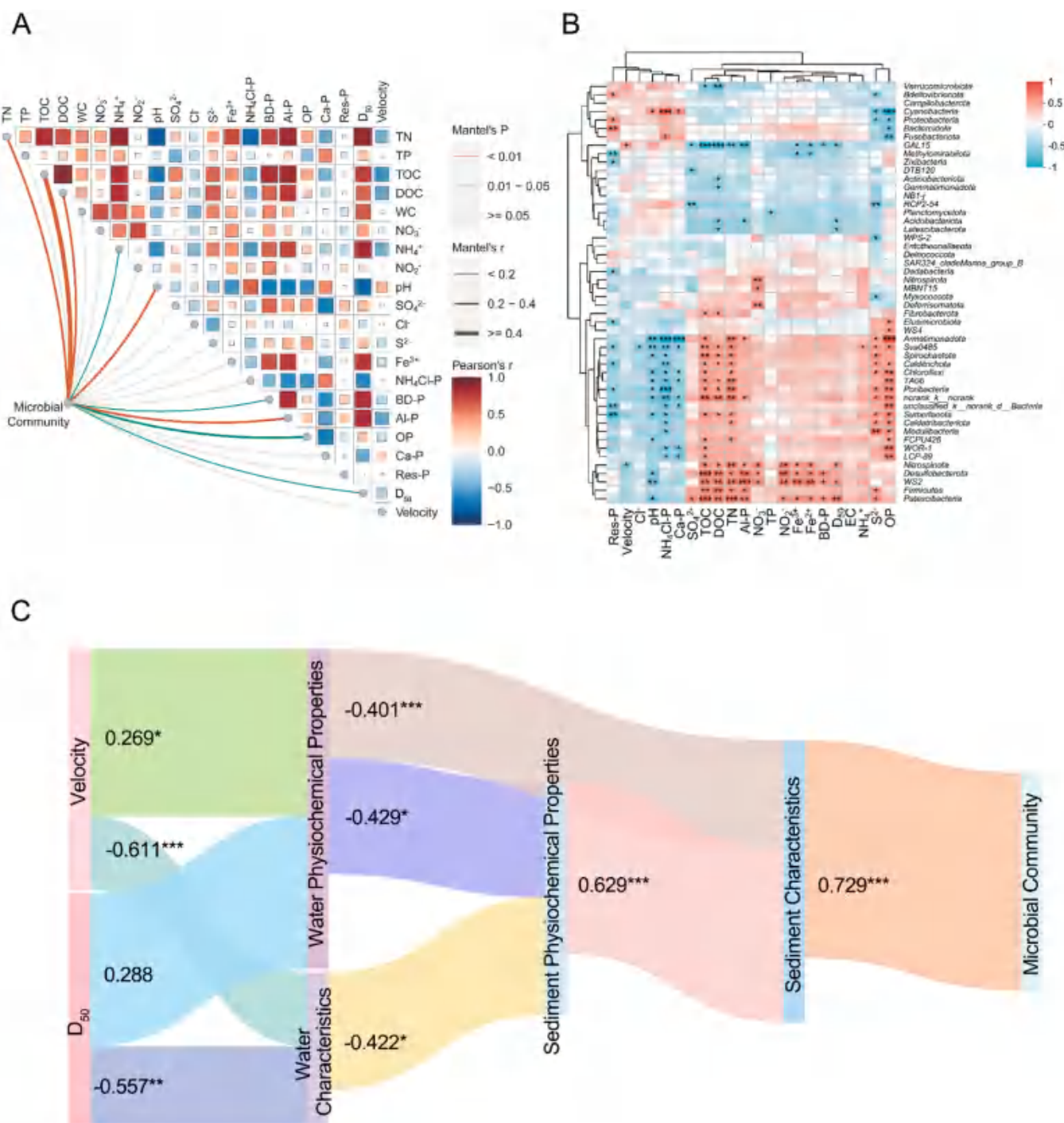
Overview of the whole heatmap, the species that linked negatively

with Ca-P, NH<sub>4</sub>Cl-P, and Res-P were positively connected with OP, Al-P, and BD-P. While BD-P was strongly correlated with oxidation-reduction potential. Alkaline phosphatase in sediment and microbial community activities are acknowledged as pivotal elements driving the transformation between various phosphorus fractions (Tian et al., 2022). The findings were consistent with prior research, which documented that microorganisms play a key role in phosphorus recycling in river sediment, with part of the TP in river sediment being recycled by bacterial activities (Campos et al., 2021). The findings reported here suggested that microbial communities contribute to the cycling and availability of P in the river-lake system sediment, which could influence P contamination in the downstream reaches.

In summary, the results showed that TOC, TN, DOC, pH, Al-P, OP, NH<sub>4</sub><sup>+</sup>, BD-P, and D<sub>50</sub> are key factors shaping microbial communities in sediments, with TOC being the most influential. Microbial taxa linked to P cycling were negatively affected by pH. Microbial communities positively correlated with bioavailable P fractions and negatively with less bioavailable forms, emphasizing their role in P cycling. These results highlight the significant impact of microbial communities on P availability and dynamics in confluence.

### 3.6. Direct and indirect effects of the confluence on microbial community

The PLS-SEM analysis revealed that 62.5 % of the variance in microbial community composition could be accounted for (Fig. 8C). The results indicated that sediment characteristics influenced the microbial community ( $r = 0.790$ ,  $p < 0.001$ ). Water physiochemical properties ( $r$



**Fig. 8.** Associations between environmental factors and microbial community. (A) Mantel test between environmental factors and microbial community. (B) Spearman correlations between the relative abundance of microbial species and environmental factors. (C) PLS-SEM image of the relationships among the microbial community, hydrodynamic parameters, water properties, and sediment properties. The significance levels are denoted by asterisks (\*), where \* indicates  $p < 0.05$ , \*\* indicates  $p < 0.01$ , and \*\*\* indicates  $p < 0.001$ .

= -0.319,  $p < 0.1$ ) and water characteristics ( $r = -0.618$ ,  $p < 0.05$ ) were key factors influencing sediment characteristics, both negatively related to sediment properties and then negatively affecting the microbial community directly and indirectly.

Velocity and  $D_{50}$  were parameters related to hydrodynamics that indirectly affect microbial communities by influencing water and sediment properties.  $D_{50}$  was notably lower ( $p < 0.1$ , Wilcoxon rank-sum) in G2 than in G1, and flow velocity in G2 was higher than in G1 (Fig. S2). Velocity positively influenced water characteristics ( $r = 0.269$ ,  $p < 0.1$ )

and water physiochemical properties ( $r = 0.288$ ,  $p = 0.139$ ). Reduced velocity enhances nutrient retention, leading to higher TP and WTP concentrations in G1, especially in the FST region (Bukaveckas, 2007). Fast-moving water showed higher dissolved oxygen, alkalinity, and conductivity, influencing microorganisms. Complex hydrodynamic at the river-lake sediment confluence cause the variation of material concentration across hydraulic regions.  $D_{50}$  negatively influenced water characteristics ( $r = -0.611$ ,  $p < 0.001$ ) and water physiochemical properties ( $r = -0.557$ ,  $p < 0.05$ ) (Ji et al., 2022). Phosphorus contents

in water were affected by suspended particles and sediments, with WTP and PP concentrations were considerably greater in G1 than in G2, while TDP did not differ significantly, although it was slightly higher in G2. PP was identified as the major component of TP in water. Finer sediment could maintain more P, thereby influencing the microbial community dynamics. This aligns with the observed negative relationship between  $D_{50}$  and the microbial community.

The concentrations of nutrients in water directly affected the nutrient content of the sediment. Nutrients in the water interact with the sediment through processes such as adsorption, desorption, and precipitation. Sediments acted as sinks or sources of nutrients, depending on the prevailing conditions. Nutrients were retained in the river system were influenced by nutrients that were either reintroduced into the water column or restored in sediment (Liang et al., 2023b). River water discharge influences sediment and water column nutrient concentrations, with changes in flow affecting sediment transport and deposition, thereby affecting nutrient content (Dalu et al., 2019).

Sediment had a direct and significant influence on microbial communities. Sediment characteristics, especially TOC, TN, DOC, pH, Al-P, OP,  $\text{NH}_4^+$ , and BD-P, affected microbial community structure and certain species (Fig. 8B). BD-P, Al-P, and OP were critical for microbial growth and the structure and activity of microbes (Tee et al., 2021). TOC and DOC, the measures of organic carbon content in sediment, served as an energy and nutrients source for microbial communities, supporting a more diverse and abundant microbial community (Li et al., 2019). TN and  $\text{NH}_4^+$  were nitrogen sources for microbial communities that could promote the growth of nitrogen-utilizing microbial populations (Ren et al., 2019). The microbiological communities' composition was affected by pH because different microbial taxa have varying pH preferences, and changes in pH can favor certain microbial populations over others (Liu et al., 2015). Sediment microorganisms have critical roles in regulating major biogeochemical and eco-environmental processes, including biogeochemical cycles and the dynamics of nutrients (Zhang et al., 2020c). Combined with the results of the previous studies, it was found that phosphorus in sediments is closely linked to microbial communities, which interact with each other in the river-lake confluence area.

These findings highlight the importance of sediment and water interactions in nutrient cycling and microbial dynamics, suggesting that managing sediment and flow conditions could improve phosphorus control in river-lake systems.

### 3.7. Integrative analysis of hydrodynamic and environmental influences on microbial composition

Previous discussions indicated that hydrodynamics impact microbial communities by influencing flow velocity and sediment characteristics, which affect microbial distribution. Additionally, it was noted that environmental factors such as TOC, TN, DOC, pH, and various P fractions (Al-P, OP, BD-P) have a substantial impact on microbial communities' composition. A comprehensive analysis of these findings suggests that both hydrodynamic and environmental factors jointly influence microbial community composition, with certain factors playing more dominant roles.

Hydrodynamic conditions, such as reduced flow velocity and coarser sediment in G1, create a distinct environment that affects nutrient availability and microbial habitat, which in turn alters microbial diversity and abundance. Environmental factors like TOC and TN are critical for microbial growth and metabolism, while pH and P fractions directly influence the stability and cycling of key nutrients.

Comparative analyses indicate that while both hydrodynamics and environmental factors are important, environmental factors, Al-P and OP, exert a pronounced influence on microbial community composition due to their direct impact on microbial metabolism and nutrient dynamics. The Mantel test and Spearman heatmap revealed that TOC is the most dominant factor, followed by TN, DOC, and specific P fractions,

suggesting that nutrient availability is a primary driver of microbial community structure. Nevertheless, hydrodynamic factors indirectly affect microbial communities by shaping the sediment environment, thus modulating the influence of these key environmental drivers. While environmental factors primarily determine the composition of microbial community, their effects are moderated by the underlying hydrodynamic conditions.

## 4. Conclusion

This study investigated how complex hydrodynamics at river-lake confluences influence sediment microbial communities and phosphorus (P) dynamics. River confluences play a crucial role due to their unique environmental conditions. The study revealed that microorganisms contribute differently to P cycling depending on the hydrodynamic characteristics of their environment. Flow velocity and  $D_{50}$  positively influenced microbial community through water and sediment properties. Microorganisms enriched in different confluence regions played key roles in P cycling in aquatic systems. The involvement of microorganisms in P biogeochemical processes is influenced by microbial communities composition. Regions with higher velocity and finer sediment exhibit enhanced OP mineralization and IP solubilization. Within Section 3, the complex hydrodynamics of the FST, FD, and FSE regions, along with variations in  $D_{50}$  and P fractions, contributed to separate of microbial communities into two distinct groups (G1 and G2). This segregation underscores the significant role of confluences in influencing microbial functions and P transformations. The findings highlight the importance of considering these dynamics for effective aquatic ecosystem management and protection, especially in similarly complex river network settings.

### CRedit authorship contribution statement

**Jie Liang:** Writing – review & editing, Funding acquisition, Conceptualization. **Min Yan:** Writing – original draft, Methodology, Formal analysis, Data curation. **Ziqian Zhu:** Writing – review & editing, Validation, Data curation. **Lan Lu:** Methodology, Data curation. **Junjie Ding:** Data curation. **Qinxue Zhou:** Data curation. **Xiang Gao:** Data curation. **Ning Tang:** Data curation. **Shuai Li:** Data curation. **Xiaodong Li:** Data curation. **Guangming Zeng:** Data curation.

### Declaration of competing interest

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

### Data availability

Data will be made available on request.

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### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.watres.2024.122556](https://doi.org/10.1016/j.watres.2024.122556).

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