Spatiotemporal variations of bacterial communities and functional genes in the water and sediments of a typical river influenced by reservoir operations

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Introduction: Microorganisms are essential for cycling phosphorus and nitrogen and play a crucial role in maintaining the health and stability of river ecosystems. The reservoir operation changes the river's hydrological processes, forming reservoir inundation areas and influencing the diversity of microorganisms and their environmental functions.

Methods: To study the microbial composition and action mechanism in rivers affected by reservoir operation, Xiangxi River, the closest tributary to the Three Gorges Dam on the Yangtze River, was sampled to examine the spatiotemporal fluctuations of bacterial populations and functional genes in water and sediments. The physicochemical properties, microbial communities and functional genes were analyzed in August 2022 and June 2023.

Results: Spatially, except for conductivity, the chlorophyll (Chl), dissolved oxygen (DO), and pH values in the upper reaches of the basin were higher than those in the mouth (where it joins the Yangtze River). Specific physicochemical gradients created by the reservoir operation drove spatial and temporal shifts in bacterial community structure. In water samples (W), dominant microbial species included *Exiguobacterium* and *Candidatus Fonsibacter*, contributing to organic matter degradation and nutrient transformation. *Nitrospira* indicated their roles as nitrifiers or denitrifiers in sediment samples (S), essential for nitrogen cycling. In the mouth zone, *Methyloceanibacter* dominated in the transition zone, and they were involved in methane or organic metabolism.

Discussion: The dominance of *Microcystis* in the upstream region reflected its prevalence in nutrient-rich, algal-rich environments. *Paralia* in the middle of the river highlighted the favorable conditions of suitable light and moderate flow rates for diatom growth. Reservoir regulation also altered the functional gene composition, making it more similar to that found in lake ecosystems. The most abundant functional genes were those associated with Amino Acid Transport and

Metabolism, while phosphorus-related genes predominantly involved energy production and conversion. The dominance of genes linked to electron transport underscored the pivotal role of microbial respiration and oxidative phosphorylation in energy metabolism, which was fundamental to ecosystem productivity.

1 Introduction

Microorganisms in water and sediment are closely involved in the phosphorus cycle, and their influence is complicated. In water bodies, microorganisms can decompose organic substances containing phosphorus, such as nucleic acids and phospholipids, and convert organic into inorganic phosphorus, further affecting the bioavailability of phosphorus (Caron, 1994; Van Mooy et al., 2009). Microorganisms can absorb dissolved phosphorus and participate in the phosphorus cycle through metabolic activities, thus affecting algae growth and algal blooms (Havens, 2008; Duhamel, 2025). Microorganisms in sediments participate in phosphorus transformation and cycling through various biogeochemical processes (Richardson et al., 2009). Phosphate-solubilizing microorganisms (PSMs) in sediments can dissolve insoluble phosphorus in sediments by secreting organic acids and other metabolites, converting them into forms that plants and other microorganisms can absorb and increasing the available phosphorus content in the water (Rawat et al., 2021; Sadiq et al., 2013).

Environmental factors affect the phosphorus cycle function genes in microorganisms: salinity, pH, and N/P ratio affect the characteristics of microbial communities and phosphorus metabolism processes in sediments (Jalali and Peikam, 2013). These affect the gene expression of phosphorus cycle function and the phosphorus biogeochemical cycle by influencing microbial communities' structure and function (Zeglin, 2015). For example, the coupling mechanism of phosphorus components with bacterial and archaeal community succession in karst lake sediments in plateaus suggests that different active components of inorganic (P_i) and organic (P_o) phosphorus have significant effects on the diversity and composition of microbial communities (Yuan et al., 2024). A study of the Danjiangkou Reservoir found that water temperature (Temp), redox potential, DO, and Chl-a were the main factors affecting the composition of the planktonic bacteria community. These environmental factors were significantly correlated with nitrogen and phosphorus cycle functional genes, resulting in the apparent vertical distribution of these genes in the planktonic bacteria (Chen et al., 2022).

Water conservancy project scheduling affects river habitats and the composition and function of river ecosystems. The construction of reservoirs has altered the natural flow characteristics of rivers, slowed the flow rate, and extended water retention times. These changes result in the enrichment of nutrients, such as nitrogen and phosphorus, which stimulate the rapid growth of algae, thus affecting water quality and the diversity of aquatic organisms (Zhu et al., 2022; Saunders, 2005). Reservoir regulation influences the concentration of nutrients in water bodies and modifies microbial community structure and ecological functions, particularly the release of endogenous phosphorus and its cycling (Dević, 2015). Microorganisms are involved in phosphorus

mineralization, transformation, and absorption through phosphatase genes and phosphate transporter genes, while they also store phosphorus by synthesizing polyphosphates (Janati et al., 2023; Chen et al., 2022). These microorganisms play a critical role in the phosphorus cycle, and the expression of their functional genes is influenced by changes in the reservoir environment, thereby regulating the dynamic processes of phosphorus cycling (Chen et al., 2022; Wang et al., 2017). The response of river microbial communities to environmental changes may be more rapid because the hydrodynamic conditions of rivers are generally more dynamic (Wang et al., 2023). For example, there are significant differences in the composition of planktonic bacterial communities in river regions of the Yangtze River basin, in which Temp is the main influencing factor (Liu et al., 2018). Microbial communities may be more sensitive to long-term environmental changes in relatively static lakes because such environments are relatively stable (Liu et al., 2022). The archaea in lakes often depend on the type of lake, and the dominant microphyla vary significantly with different water bodies, sediments, and lake regions (Zhang et al., 2015). The backwater areas of rivers affected by reservoir operation tend to be lake-type environments (Xu et al., 2024). Studying the composition and functional characteristics of microbial communities in different regions is essential for understanding the characteristics of river-water ecological environments and taking adequate measures to protect ecological functions.

As a tributary significantly influenced by the operation of the Three Gorges Dam, the Xiangxi River faces a pronounced eutrophication issue with annual algal blooms. Analyzing microbial diversity and functional genes related to phosphorus cycling in the Xiangxi River Basin is crucial for elucidating the relationship between microorganisms and nutrient elements in eutrophic regions. This study addresses this issue by 1) investigating the distribution characteristics of physical and chemical parameters from the upper reaches to the mouth of the Xiangxi River Basin; 2) examining the differences and relationships of microbial diversity and phosphorus cycle-related functional genes across various media within the Xiangxi River Basin; 3) comparing the variations in microorganisms and functional genes in sediments from the upper reaches to the mouth of the Xiangxi River and analyzing the underlying causes of differences and the implications for river health.

2 Materials and Methods

2.1 Study area

The Xiangxi River basin is located near Yichang City, Hubei Province, approximately 29 km from the Three Gorges Dam and the first tributary upstream of it. The river originates in the Shennongjia
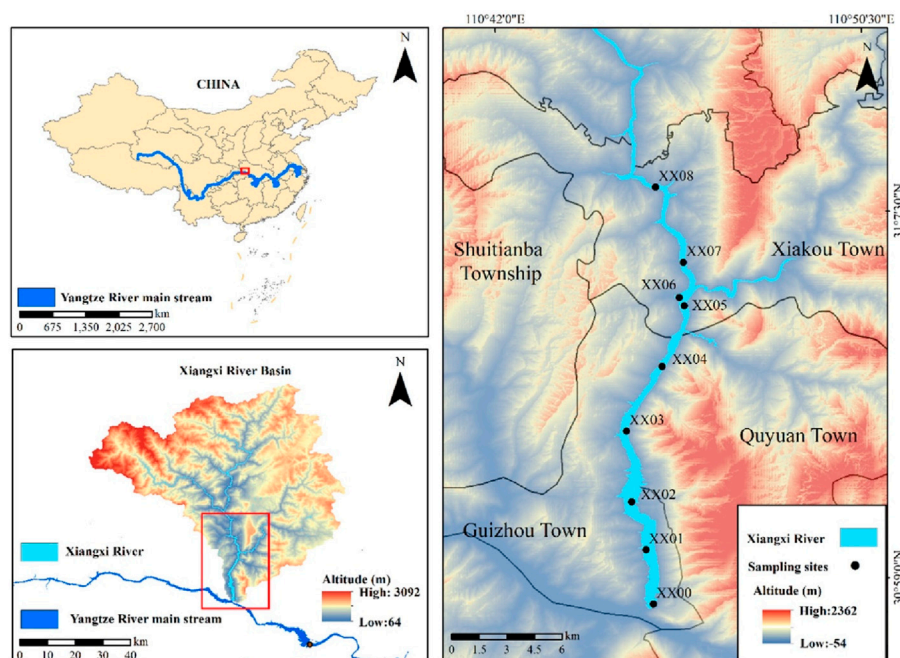
FIGURE 1
Map of the study area including sampling locations.

Forest area in the northwest of Hubei Province. Positioned at the head of the Three Gorges reservoir area, the Xiangxi River basin is affected by the upper support of the main stream of the Yangtze River. The hydraulic interaction reduces flow velocity, resulting in lentic (lake-like) water characteristics. When the reservoir area is at the lowest water level of 145 m, a permanent backwater area of 27.6 km is formed above the mouth of the Xiangxi River, within which two important tributaries, the Gaolan and the Qilixia Rivers, flow into the Xiangxi. Over 70% of the basin's population engages in agriculture, the primary economic activity (Xiang et al., 2022). The upstream Xingshan phosphate rock reserves are approximately 460 million tons and are one of the three major phosphate rock bases in China. The pollution sources of the Xiangxi River primarily are both natural and anthropogenic. Natural pollution arises from the dissolution of local phosphorus-rich strata that release phosphorus into the water (Mainstone and Parr, 2002). Anthropogenic pollution comes from various human activities, including emissions from mining, chemical industries, and other enterprises, as well as agricultural non-point source pollution, which introduces excess nutrients such as nitrogen and phosphorus into the Xiangxi River (Chakraborty, 2021; Xu et al., 2022). These combined pollution sources significantly impact the river's water quality and ecological balance.

2.2 Sample collection

Based on the topography, geomorphology, and extent of the backwater area within the Xiangxi River basin, water samples (W), overlying water samples (O), and sediment samples (S) were collected from key points (river mouth, major tributary confluences, and backwater zone) in August 2022 and June 2023. August and June were chosen because they are the periods when

algal blooms are obvious and severe. The sample points are labeled XX00–XX08 accordingly; the specific sampling points are shown in Figure 1.

2.3 Determination of physicochemical properties

A portable multi-parameter water quality instrument (multi-parameter water quality monitoring system, Xylem (China) Company Limited) was used to measure water Temp, Chl, DO, pH, and conductivity values from surface to bottom at nine sites (Figure 1). W, S, and O were collected from points XX00, XX02, XX03, XX05, XX06, and XX08.

Triplicate W and S were collected at each point and composited to ensure representativeness. W is followed by sampling year and site number (e.g., W1_00 denotes a sample collected in 2022 at site XX00).

A cylindrical sampling device developed by the Institute of Water Ecology and Environment of the China Institute of Water Resources and Hydropower Research (national invention patent No.: ZL200810056757.7) was used to collect S. For each point, S is followed by sample time, site number, and depth (e.g., S1_00_1 denotes the 0–3 cm layer collected in 2022 at XX00; layers 2 and 3 were 3–6 cm and 6–9 cm, respectively). For the XX05 site, where algal blooms occurred at high frequency, samples were conducted every 2 cm from the surface to the bottom.

Disturbed sediment was avoided as far as possible during the sampling process. Overlying water samples were extracted by a negative pressure diversion pipe and stored in sterile glass bottles.

Due to sampling process loss and the quality evaluation of DNA extraction, not all samples obtained from the sampling points met

the requirements of metagenomic analysis. Only the samples that passed quality inspection were considered in this study. All W and O samples were filtered through a 0.22-μm membrane on the same day of sampling; the membrane was stored in a liquid nitrogen environment before microbial diversity and metagenomic detection.

2.4 DNA extraction and metagenome sequencing

DNA extraction was performed using E. Z.N.A.® Soil DNA Kit (Omega Bio-Tek, United States). After genomic DNA extraction, TBS-380 detected DNA concentration, DNA purity was detected by NanoDrop2000, and DNA integrity was detected by 1% agarose gel electrophoresis. DNA was segmented by Covaris M220 (Genetics, China) screening for fragments interrupted by approximately 400 bp. PE libraries were constructed using the NEXTFLEX Rapid DNA-Seq (Bioo Scientific, United States) library building kit. After bridge PCR amplification, metagenomic sequencing was performed using the Illumina NovaSeq/HiSeq Xten (Illumina, United States) sequencing platform.

The raw data were controlled by Fastp software, and contaminated reads with high similarity were removed by BWA software. MEGAHIT, a splicing software based on the succinct de Bruijn graphs principle, assembled the optimized sequences. Contigs ≥300 bp were selected as the final assembly result. MetaGene was used to predict the ORF of the assembled contig, and then CD-HIT software was used to cluster the predicted gene sequences of all samples to construct the non-redundant gene set. Finally, SOAPaligner software was used to align the high-quality reads of each sample with the set of non-redundant genes (95% identity) so that the abundant information of genes in the corresponding sample could be measured.

2.4.1 Taxonomic notes on species

The amino acid sequence of the non-redundant gene set was compared with the NR database (the expected e-value of the BLASTP comparison parameter setting was 1e-5), and species annotation was obtained from the taxonomic information database corresponding to the NR database. The abundance of the species was then calculated using the sum of the corresponding gene abundance of the species to obtain species annotation information at the taxonomic levels of domain, kingdom, phylum, class, order, family, genus, and species.

2.4.2 Functional annotation of COG

The amino acid sequence of the non-redundant gene set was compared with the eggNOG database using BLASTP to obtain the functional information of the COG corresponding to the gene. Then, the COG abundance in the sample was calculated using the sum of the gene abundance corresponding to COG.

2.4.3 KEGG function annotation

The amino acid sequences of the non-redundant gene set were compared with the KEGG (Kyoto Encyclopedia of Genes and Genomes) gene database using BLASTP to obtain the corresponding KEGG function information. The sum of gene abundances corresponding to KO, pathway, EC and module was used to calculate the abundances of corresponding functional categories. Based on the hierarchical annotation of the KEGG function pathway, genes related to the phosphorus cycle were selected, and a set of functional genes related to the phosphorus cycle was established using the P_metabolism gene screening function of Megi Biology.

2.5 Species and functional composition analysis

Based on the annotation results of different databases, the co-occurrence relationship maps were applied to describe the abundance correspondence between the sample and species/functions, thus assisting in understanding of the proportion of species/functions in different groups and showing which microorganisms and functions are in the group and their relative abundance. The similarity of species and functions in various samples was determined using a Venn diagram, and the difference of species or functional components in each sample/group were analyzed using the Kruskal–Wallis H test.

3 Results

3.1 Physicochemical properties

Figure 2 shows the water Temp, Chl, DO, pH, and conductivity values. In August 2022, the water Temp was 7–8°C higher than in June 2023, and the DO, pH, and conductivity values were also elevated in August compared to June. Spatially, the Chl, DO, and pH values in the upper reaches of the basin were higher than those in the mouth, while conductivity values were higher in the mouth than in the upper reaches. Surface water Temp, Chl, DO, pH, and conductivity were generally high and decreased with increasing water depth.

Surface Temp was highest in August 2022, the highest Temp was 31.39°C, and the bottom Temp was the lowest. The minimum Temp was 25.22°C (Figure 2A). In June 2023, the highest surface Temp was 24.08°C, and the lowest bottom Temp was 17.63°C (Figure 2B). In the horizontal direction, from the mouth to the upstream, the overall change of water Temp was not noticeable. In the vertical direction, in August 2022 the vertical water Temp decreased significantly in the mouth and upstream sections. In June 2023, the vertical water Temp of the upstream section decreased significantly.

In 2022, the Chl value in the middle reaches of the study area was higher than that in the river's mouth and upper reaches, ranging from 0.29 ug/L to 15.62 ug/L (Figure 2C). In 2023, the upstream value was higher than in other regions. The highest value was in the XX05 section, which reached 120.36ug/L (Figure 2D).

The DO value in the study area varied greatly. In 2022, the highest DO value was located at XX07 and XX09 upstream, with a value of 15.83 mg/L. The value in the water layer below 5 m was below 6.6 mg/L (Figure 2E) (Figure 2E). In 2023, the distribution of DO values at each point was relatively concentrated, the upstream DO value was relatively high, and the surface DO value of XX09 was the highest at 12.36 mg/L (Figure 2F).

The pH values in the study area varied greatly, ranging from 7.73 to 9.7. In 2022, the values of each point were significantly
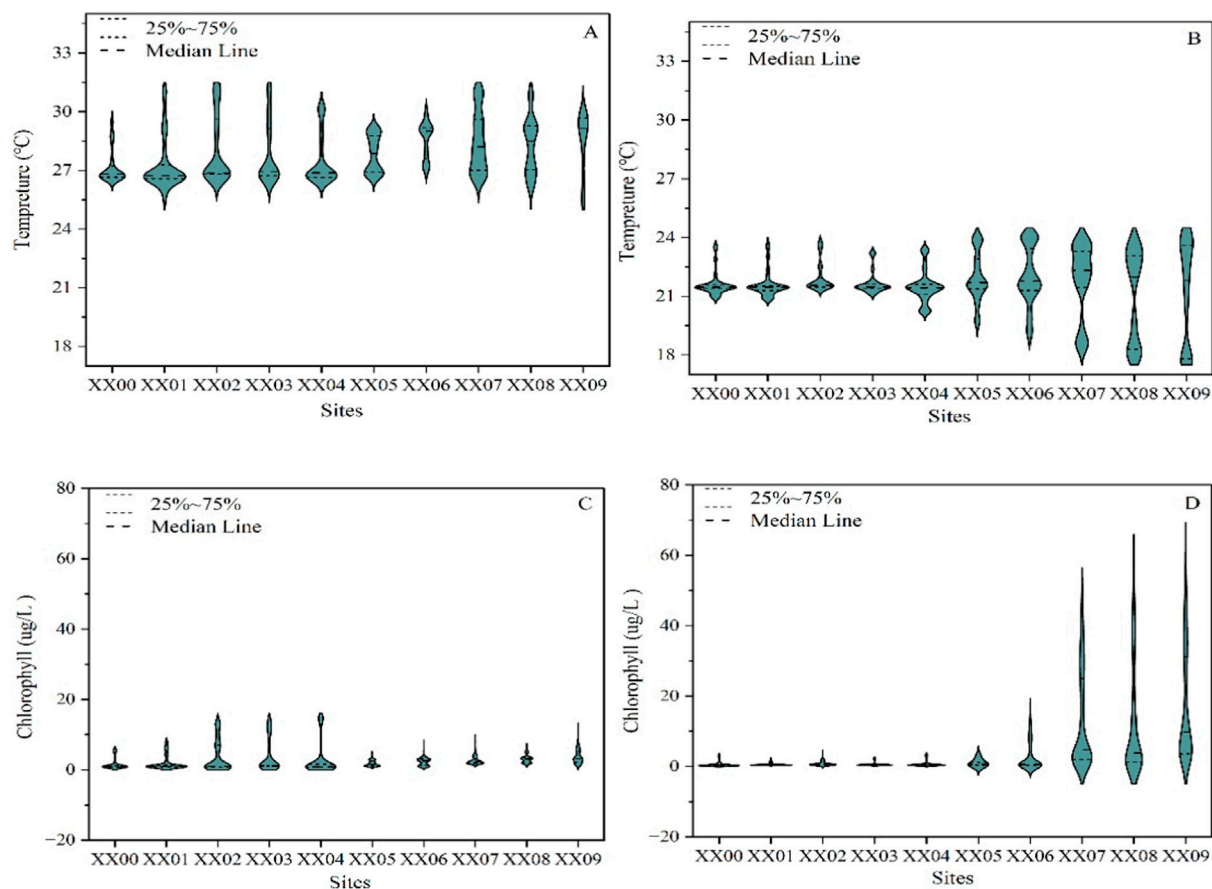
FIGURE 2
(Continued).

different, with the highest value at XX08 and the lowest at XX01 (Figure 2G). In 2023, the pH values were relatively concentrated, all above 8.5. The surface layer was 5 m. The pH value was large. The maximum value was 9.55, located in the upstream XX09 point, and the minimum value was 8.5 at XX03 (Figure 2H).

The conductivity values of the mouth zone in 2022 and 2023 had an extensive fluctuation range. In 2022, from the mouth zone to site XX04, the conductivity value was concentrated at 450 us/cm, and the upstream was relatively low, mainly concentrated at 380 us/cm (Figure 2I). In 2023, at position XX00–XX04 near the mouth zone, the conductivity value was mainly concentrated at 450 us/cm, and the upstream fluctuated greatly, ranging 266.3–455 us/cm (Figure 2J).

3.2 Microbial community

The microbial composition of the study area was quite rich. According to the results of species and abundance information of different taxonomic levels in the NR database, the most abundant species were *Betaproteobacteria, Actinomycetia*, and *Alphaproteobacteria,* followed by *Gammaproteobacteria* and *Deltaproteobacteria.* Lu et al. (2020) analyzed spatial variation in bacterial biomass in the Xiangxi River and found that *Flavobacteriia, Betaproteobacteria*, and *Acidobacteria* were abundant in the river.

Figure 3 compares the similarity of microbial populations classified by genes in samples of different groups. Compared with 2023, microbial populations in 2022 had 77.35% identical genes, 5.49% unique genes in 2022, and 17.16% unique genes in 2023. The results of microbial gene level richness in W, O, and S showed that all samples shared 49.94% of the genes, 1.42% of the samples were unique to W, 4.39% were unique to O, and 17.08% were unique to S. The differences in microbial genes in different sampling points from mouth to upstream were compared. Among them, 39.39% of microbial genes were standard to all sites. It was found that S_05 had the highest proportion, accounting for 9.59%, followed by S_02, accounting for 1.95%, and S_00, accounting for 0.79%. Comparing the proportion of microbial gene diversity from surface to bottom S at site XX05, the common genes accounted for 32.37%, the relatively high genes were in the surface layer and S_05_06, accounting for 4.37% and 6.45%, respectively, and the proportion of genes in other layers was similar.

3.3 Functional gene abundance

Compared to the Clusters of Orthologous Groups (COG) database, the highest proportions of functional genes in all samples collected from the basin were classified under categories
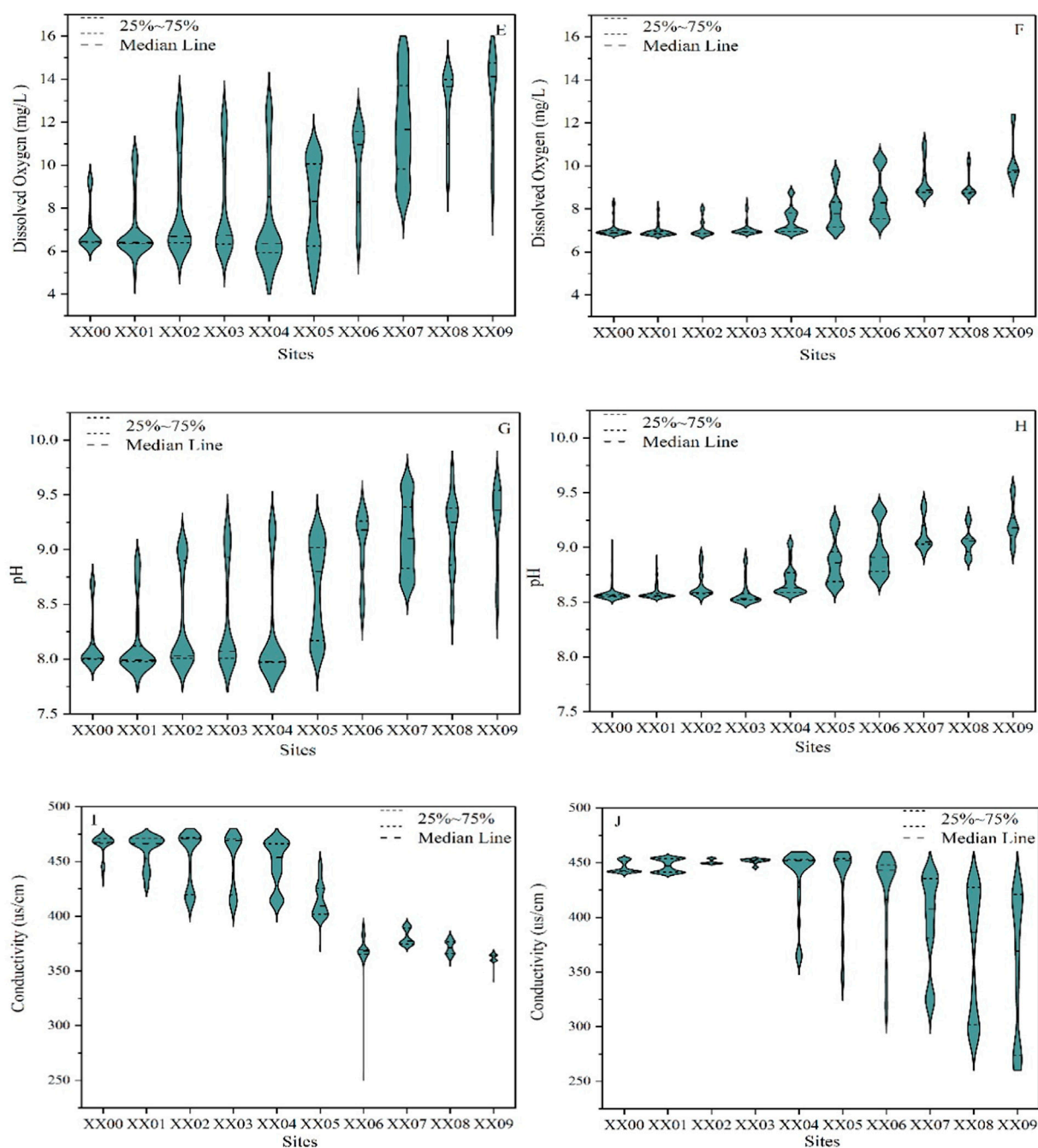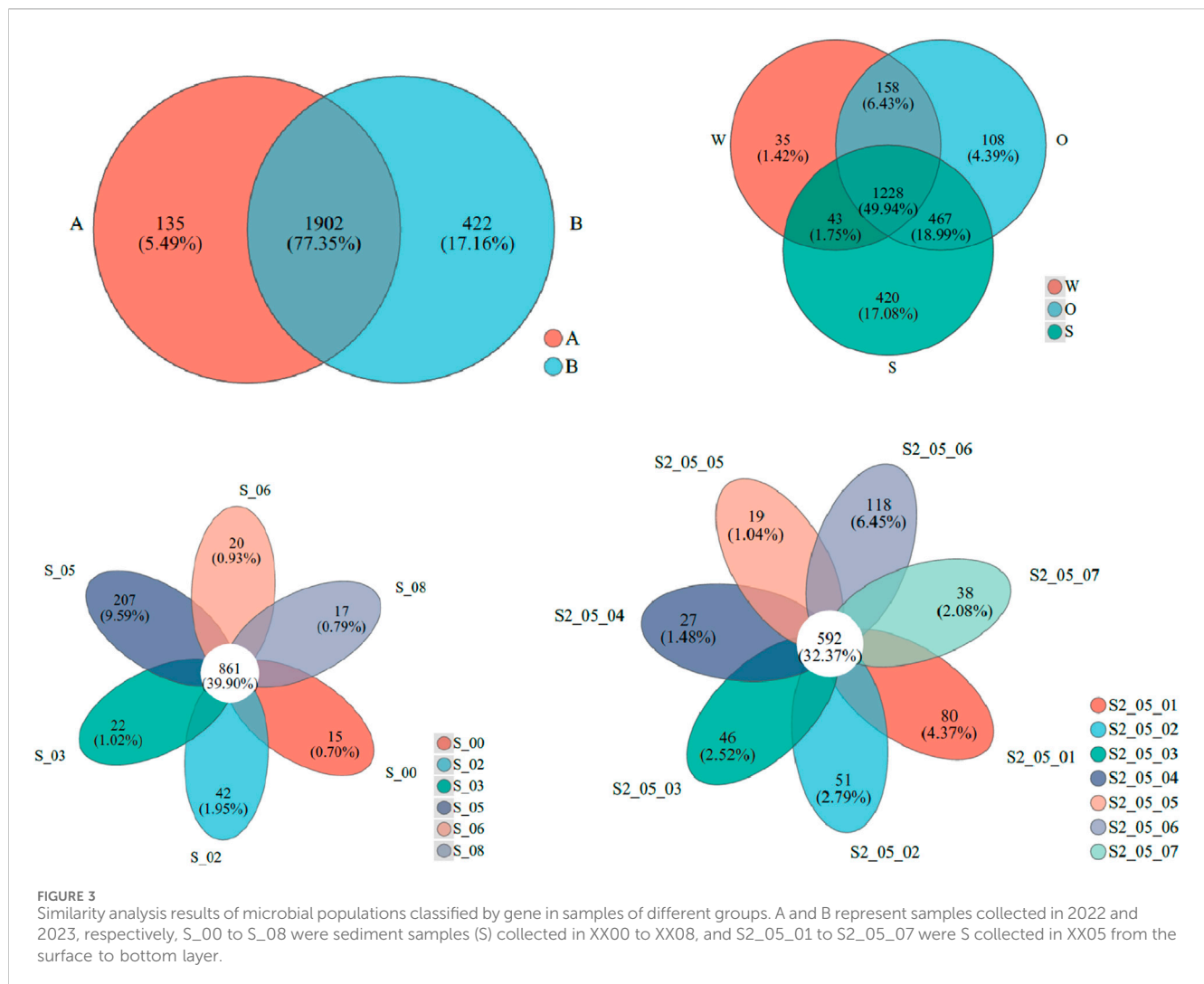
FIGURE 2
(Continued). Physicochemical properties, including Temp, Chl, DO, pH, and conductivity, in the Xiangxi River. Figures to the left are samples collected in 2022 and to the right in 2023.

E (amino acid transport and metabolism), C (energy production and conversion), and R (general function prediction) in the original data. After screening, the functional gene categories most related to the phosphorus cycle were C (energy production and conversion), G (carbohydrate transport and metabolism), and I (lipid transport and metabolism) (Figure 4). The results revealed that the highest microbial abundance in W and S was associated with amino acid transport, protein decomposition, and synthesis. At the same time, the primary function involved in phosphorus metabolism was energy production and conversion.

To further analyze the distribution characteristics of phosphorus cycle functional genes, their proportion related to the phosphorus cycle in the study area was compared with the KEGG database. The results showed that the most abundant functional genes were K00341, K00342, and K02274 followed by K00335, K02111, and K02112. The most abundant gene names were nuoL, nuoM, and coxA, followed by ctaD, nuoF, and ATPF1A. K00341 (nuoL), K00342 (nuoM), and K02274 (coxA) are essential genes in the oxidative phosphorylation pathway. K00341 and K00342 encode subunits of nicotinamide adenine dinucleotide (reduced form, NADH):

FIGURE 3
Similarity analysis results of microbial populations classified by gene in samples of different groups. A and B represent samples collected in 2022 and 2023, respectively, S_00 to S_08 were sediment samples (S) collected in XX00 to XX08, and S2_05_01 to S2_05_07 were S collected in XX05 from the surface to bottom layer.

ubiquinone oxidoreductase (Complex I). *K02274* encodes a subunit of cytochrome c oxidase (Complex IV). These proteins are critical for generating a proton gradient across the inner mitochondrial membrane through electron transport which drives adenosine triphosphate (ATP) synthesis. *K02112* (ATP5A) directly catalyzes the phosphorylation of ADP (adenosine diphosphate) to ATP, forming high-energy phosphate bonds, and represents a central component of ATP synthase (Complex V) in the oxidative phosphorylation process (Chadwick et al., 2018).
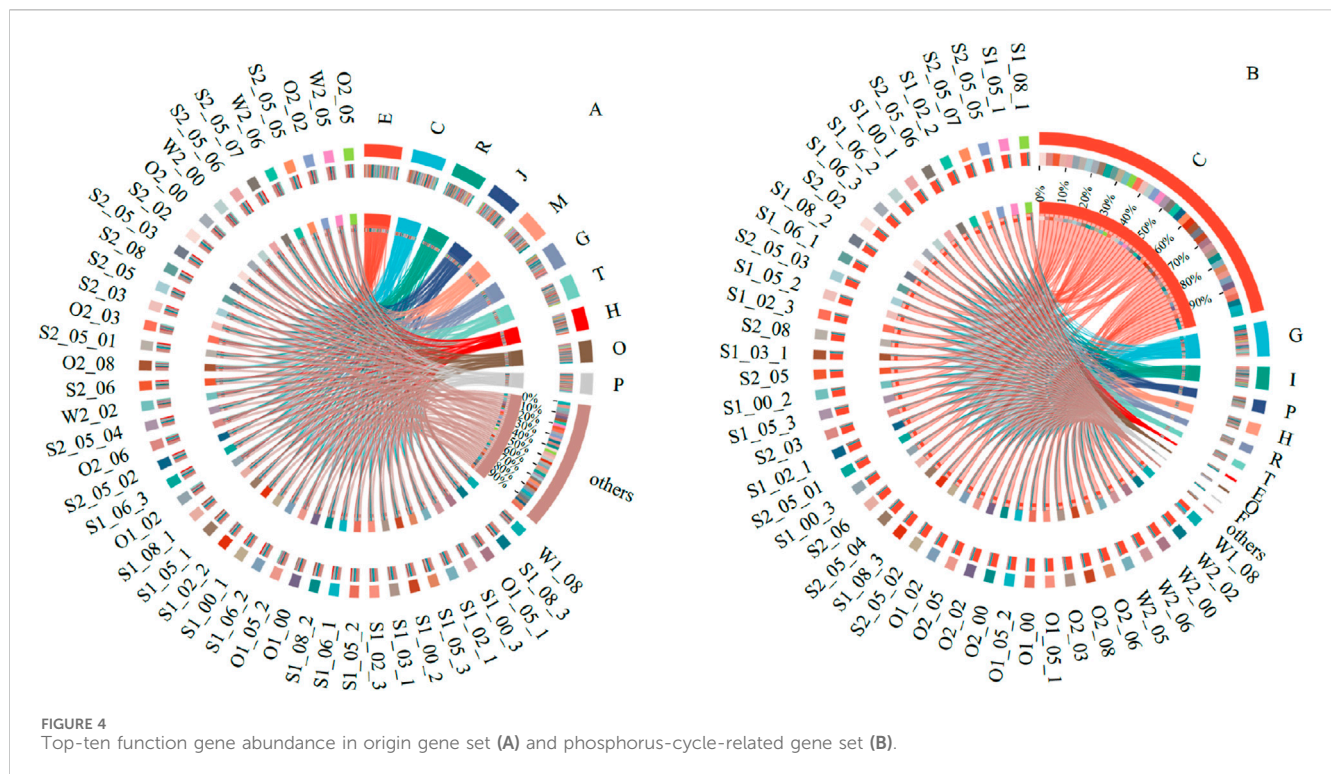
Comparing functional gene similarity in 2023 and 2022, 88.45% of the functional genes were identical, 2.82% of the particular genes were in 2022, and 8.73% were in 2023. The results of functional gene richness in W, O, and S showed that all samples shared 85.63% of functional genes, 1.41% were unique to W, 0.85% were unique to O, and 2.25% were unique to S. The differences of functional genes in different sampling points from the mouth to upstream were compared. Of functional genes, 69.49% were common to all sites. It was found that the proportion of unique genes in S_05 was the highest, accounting for 4.23%, followed by S_02 and S_03, accounting for 1.81%, and S_00 being relatively low. The proportion of microbial functional gene diversity was compared across the surface to bottom S at site XX05, where the common

genes accounted for 62.67%. In S_05_01 and S_05_02, the unique genes accounted for 4.45% and 1.71%, respectively, and the proportion was similar in other layers.

3.4 Spatial distribution of microbial community and functional genes

The distribution of microorganisms in different media environments was significantly different. The most abundant microorganisms included *Exiguobacterium*, *Candidatus Fonsibacter*, and *Clavibacter*, which were mainly distributed in water samples, followed by overlying water samples, and they were less distributed in sediment samples (Figure 5A). In addition to the three microorganisms mentioned above, *Limnohabitans* and *Macrococcus* occupied a high proportion of O. *Nitrospira*, *Rubrivivax*, and *Nocardioides* had many microorganisms in S.

The spatial distribution of microbial communities in S of the Xiangxi River, from the mouth zone to upstream regions, revealed distinct ecological patterns and reflected the underlying mechanisms driving these changes. The microbial species composition showed

FIGURE 4
Top-ten function gene abundance in origin gene set **(A)** and phosphorus-cycle-related gene set **(B)**.

significant variations across different locations (Figure 5B), with *Nitrospira*, *Methyloceanibacter*, and *Microcystis* being the most abundant species in S. *Nitrospira* was the dominant species in the mouth zone S but decreased in abundance upstream. At the same time, *Microcystis*, *Nocardioides*, and *Methyloceanibacter* were more prevalent in the upstream region. The middle of the river was characterized by a higher diversity of species, including *Paralia*, *Methanoregula*, and *Coscinodiscus*. These shifts in microbial community structure from the mouth to upstream S were driven by environmental gradients and ecological functions that reflected the distinct conditions and processes in each area.

The main functional genes in W, O, and S were functions *C, G,* and *1*: lipid transport and metabolism, followed by *P*: inorganic ion transport and metabolism and *H*: coenzyme transport and metabolism. In the three mediators, the difference in functional genes reached a very significant level. The dominant functions in W and S were functions *G* and *C,* respectively (Figure 5C).

The main functional genes collected from different spatial locations were functions *G*, *1*: lipid transport and metabolism, *P*: inorganic ion transport and metabolism, followed by *R*: general function prediction, *T*: signal transduction mechanism, and *E* (*Amino acid transport and metabolism*). The differences in functional genes in different spatial locations were significant, and the differences in functional genes in the top four reached a significant level (Figure 5D).

The high richness of general function prediction genes in the middle of the river introduced an aspect of functional plasticity within microbial communities in these areas (Figure 5E). According to the KEGG database, the most abundant functional genes were *nuoL* (NADH-quinone oxidoreductase subunit L), *nuoM* (NADH-

quinone oxidoreductase subunit M), and *coxA ctaD* (cytochrome c oxidase subunit I). The primary function was oxidative phosphorylation. Other abundant functional genes were *ATPF1A atpA* (F-type H⁺/Na⁺-transporting ATPase subunit alpha), *ppk1* (polyphosphate kinase, RNA degradation; oxidative phosphorylation), and *sdhA frdA* (succinate dehydrogenase flavoprotein subunit, metabolic pathways). For *nuoL, nuoM, coxA ctaD* (cytochrome c oxidase subunit I), *ATPF1A atpA*, and *sdhA frdA*, abundance in S was richer than in O and W samples. For the functional gene *ppk1*, the abundance was higher in W and O than in S.

In the mouth zone environment, reservoir operations had a greater influence, and the higher availability of organic matter and oxygen supported more active aerobic respiration. This process was facilitated by the electron transport chain (ETS), with key genes such as *nuoL*, *coxA*, *ctaD*, *ATPF1B*, and *atpD* involved in ATP production and energy conversion (Figure 5F). These genes were part of the NADH: ubiquinone oxidoreductase complex (complex I), which was critical for energy production in aerobic conditions (Brandt, 2006). The high abundance of these functional genes in the mouth zone indicated that microorganisms in these areas relied heavily on aerobic processes to metabolize organic matter and convert organic phosphorus into inorganic forms—a key step in phosphorus cycling. Thus, mouth zone microbial communities played an active role in phosphorus mineralization, transforming organic phosphorus into the bioavailable inorganic phosphate essential to primary productivity (Lin et al., 2024).

Figure 6A shows the richness of functional genes in different microorganisms. Function C accounted for the highest proportion of functional genes among the top ten microorganisms. Unlike other microorganisms, the highest functional genes in *Bacilli* were

FIGURE 5
Kruskal–Wallis H test bar plots. **(A)** Comparison of significant differences in microbial distribution among W, O, and S samples. **(B)** Comparison of microbial distribution in S from different locations of mouth zone. **(C)** Comparison of microbial function among W, O, and S samples. **(D)** Comparison of microbial function in S from different locations of mouth zone. **(E)** Comparison of functional genes in W, O, and S samples. **(F)** Comparison of functional gene differences in S from different locations of mouth zone.
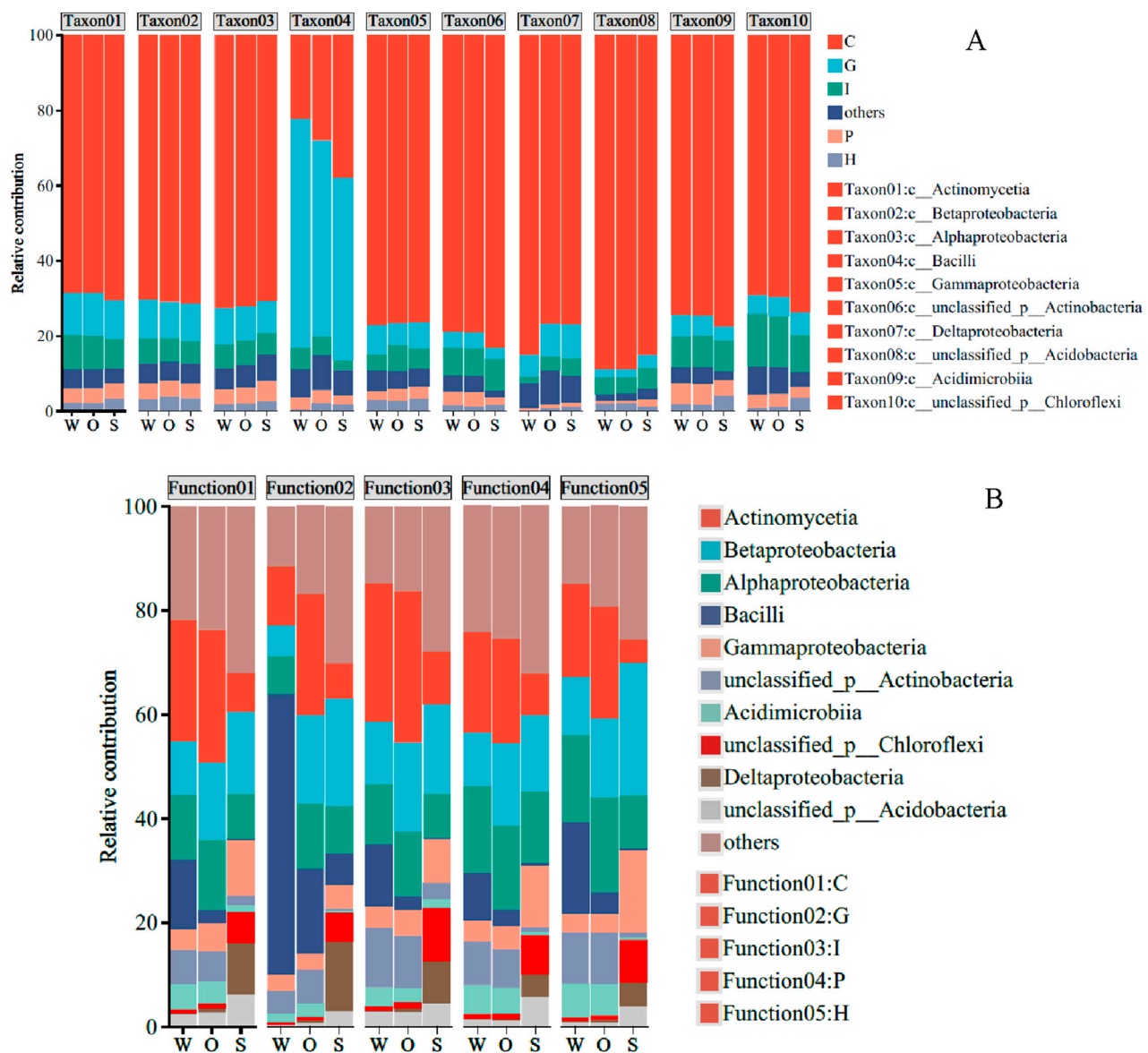
FIGURE 6
Functional distributions for specific microorganisms in W, O, and S samples **(A)**, and comparison of differences in microbial abundance corresponding to specific functions in W, O, and S samples **(B)**.

function *G*. Among them, carbohydrate transport and metabolism function in W and O was higher than in S.

For the specific functional gene, the microbial composition in W, O, and S was significantly different (Figure 6B). For functional gene *C*, *Gammaproteobacteria* and *Betaproteobacteria* occupied the highest proportion in S, while *Actinomycetia* and *Betaproteobacteria* occupied the highest proportion in W and O. *Bacilli* had the highest proportion in W for gene function G, followed by *Alphaproteobacteria*. The microorganisms with the highest proportion in O were *Actinomycetia*, *Betaproteobacteria*, and *Alphaproteobacteria*. *Gammaproteobacteria* and *Betaproteobacteria* occupied the highest proportion in S. For functional genes *1*, *P*, and *H*, *Gammaproteobacteria* and *Betaproteobacteria* occupied the highest proportion in S and *Gammaproteobacteria* and *Actinomycetia* occupied the highest proportion in W and O.

4 Discussion

4.1 Spatial differentiation of microbial communities and their responses to environmental gradients

The predominance of *Exiguobacterium*, *Candidatus Fonsibacter*, and *Clavibacter* in W underscores the importance of these microorganisms in environments rich in organic matter and nutrients. *Exiguobacterium*, known for thriving in nutrient-rich, low-oxygen conditions (García et al., 2025), shares functional significance with *Candidatus Fonsibacter* and *Clavibacter*. These latter genera exhibit metabolic versatility and degrade complex organic compounds, suggesting crucial roles in organic matter processing within these systems (Kumari and Das, 2023).

The high proportions of *Limnohabitans*, *Macrococcus*, and *Methylobacterium* in O reflect this zone's dynamic nature. *Limnohabitans*, associated with freshwater organic matter degradation, likely responds to organic inputs from algal blooms or other sources (Ren et al., 2023). *Macrococcus* and *Methylobacterium*, key players in carbon and nitrogen cycling (Li et al., 2018), further highlight the importance of heterotrophic metabolism. The enrichment of these microorganisms suggests that O acts as a transitional zone for active organic matter processing before transport to S.

Nitrospira, *Rubrivivax*, and *Nocardioides* dominated sedimentary environments. *Nitrospira*, a key nitrifier, thrives in the low-oxygen conditions typical of sediments (Daims et al., 2011). *Rubrivivax* utilizes diverse organic and inorganic compounds, contributing to organic matter decomposition, while *Nocardioides* participates in denitrification and aromatic compound degradation (Yi et al., 2022). This microbial dominance reflects specialized metabolic strategies essential for survival in nutrient-rich, low-oxygen sediments.

Nitrospira was the most abundant genus within the mouth zone, emphasizing its critical role in the nitrogen cycle via nitrite oxidation (Daims et al., 2015). Its prevalence indicates that sediment samples in the mouth zone significantly influence nitrogen cycling, nutrient dynamics, and ecosystem function. *Methyloceanibacter*, abundant here and adapted to the nutrient-rich mouth zone, utilizes diverse carbon substrates (Walker, 2022; Pandey and Pande, 2023). The predominance of these species underscores the importance of nutrient availability and hydrodynamic conditions in creating a favorable environment for microbial growth and transformation.

In contrast, upstream sediment samples were dominated by *Microcystis*, *Nocardioides*, and *Methyloceanibacter*. The high abundance of the cyanobacterium *Microcystis* signals potential productivity, likely linked to increased nutrient inputs from land use or pollution that fuel algal blooms (Wurtsbaugh et al., 2019). The prevalence of *Nocardioides* (involved in organic matter degradation) and *Methyloceanibacter* reflects a shift in ecological functions as communities transition from the dynamic mouth to more stable upstream regions. This suggests that upstream sediment communities focus more on organic matter breakdown and are less influenced by tidal and salinity fluctuations (Morrissey et al., 2014).

Mid-river S exhibited notably higher microbial diversity, with *Paralia*, *Methanoregula*, and *Coscinodiscus* being abundant. The diatom *Paralia*, essential in siliceous phytoplankton communities, contributes to primary productivity and nutrient cycling; its abundance suggests favorable light and moderate flow conditions. *Methanoregula*, a methanogenic archaeon (Lyu et al., 2018), indicates active anaerobic processes like methane production. The presence of the diatom *Coscinodiscus* further emphasizes the role of diatoms in nutrient cycling and productivity at S, driven by specific hydrological and organic inputs.

Overall, the composition of these microbial communities reflects distinct ecological functions and environmental conditions at each spatial scale. The transition from the nutrient-rich mouth to the stable upstream regions involves microbial composition and functionality shifts: mouth zone communities focus on nitrogen cycling and carbon metabolism, upstream communities on organic matter degradation, and mid-river communities support diverse processes, including anaerobic metabolism and primary productivity. This diversity mirrors the hydrological and ecological variability across the river's regions.

4.2 Spatial differentiation of functional genes and their responses to environmental gradients

Functional patterns aligned with expectations, as heterotrophic bacteria rapidly utilize dissolved organic matter for energy in aquatic environments (Wetzel, 2003). The higher proportion of genes dedicated to carbohydrate metabolism in W indicates enhanced metabolic potential and nutrient regeneration, supporting aquatic ecosystem productivity (Reddy et al., 2019).

Sediment samples exhibited the highest proportion of energy production and conversion genes, reflecting their role as microbial reservoirs where anaerobic processes (e.g., fermentation and sulfate reduction) predominate (Mallik et al., 2024). This elevated energy production potential likely stems from accumulated organic matter, which fosters diverse microbial activity that utilizes available substrates (Arndt et al., 2013).

Genes for lipid transport/metabolism (*I*), inorganic ion transport/metabolism (*P*), and coenzyme transport/metabolism (*H*) were high in proportion in both W and S. This dual prevalence underscores the importance of lipids as energy stores and membrane components—critical for growth under nutrient limitation (Rajpurohit and Eiteman, 2022)—and highlights the role of ion exchange in maintaining cellular homeostasis across habitats (Adhikary et al., 2024).

In upstream S, the high expression of carbohydrate transport/metabolism genes (*G*) suggests abundant organic carbon sources, facilitating robust microbial growth and diversity (Yu et al., 2023). This aligns with freshwater sediments being organic matter hotspots that promote carbohydrate degradation (Raza et al., 2023). Concurrently, the prevalence of genes *P* emphasizes nutrient cycling's importance in these high-nutrient environments (Xu et al., 2018).

Mouth zone S showed a predominance of lipid transport/metabolism (*I*) and signal transduction (*T*) genes, indicating microbial adaptation to fluctuating salinity and nutrients. Lipids serve dual structural and energy-storage roles vital in dynamic environments (Beney and Gervais, 2001), while signal transduction mechanisms enable responsive regulation to environmental changes and resource competition (Crump and Bowen, 2024).

The dominance of oxidative phosphorylation genes (e.g., *nuoL* and *coxA*) reflects adaptation to anaerobic/microaerophilic sediment conditions, where electrons from NADH drive ATP synthesis (Yang and Chen, 2021). This is particularly advantageous given sediment oxygen fluctuations (Lasaga and Ohmoto, 2002). The higher abundance of these genes in S than W underscores the enhanced metabolic capacity of sedimentary microbes.

Elevated *ATPF1A* (encoding an ATP synthase subunit) indicates reliance on chemiosmotic gradients for ATP production, consistent with ATP synthase's role in variable energy landscapes (Nirody

et al., 2020). High *sdhA* (succinate dehydrogenase) expression further reveals complex metabolic networks that process carbon substrates via pathways like the citrate cycle (Pan et al., 2023).

The *ppk1* gene (involved in polyphosphate metabolism and RNA degradation) was more abundant in W and O than S. This suggests roles in nutrient cycling and organic matter breakdown in dynamic environments, potentially facilitating polyphosphate accumulation and energy recycling (Tully and Ryals, 2017; Duhamel, 2025).

Upstream, decreased electron transport system (ETS) gene abundance implies a metabolic shift toward less oxygen-dependent pathways (e.g., fermentation and denitrification) suited to low-oxygen, organic-poor conditions (Hollingham, 2014). Such anaerobic adaptations in nutrient-scarce sediments can affect phosphorus cycling: denitrification may trigger internal phosphorus release from sediments, exacerbating eutrophication (Sun et al., 2022).

Functional gene distribution illustrates microbial adaptation to reservoir-induced environmental gradients. Mouth zone S with higher oxygen and nutrients supports communities optimized for aerobic respiration and efficient phosphorus cycling. Conversely, oxygen/nutrient-limited upstream S hosts anaerobically adapted communities that alter phosphorus dynamics through sediment release (Parsons et al., 2017).

This study highlights the central role of electron transport chain genes in aerobic microbial phosphorus cycling and demonstrates the metabolic flexibility of microbial communities in responding to reservoir-induced changes. Such adaptability is crucial for understanding phosphorus cycle regulation in impacted river ecosystems (Duhamel, 2025).

4.3 Interaction characteristics of microbial species and gene functional composition

The results highlight the fundamental role of energy metabolism across diverse microbial communities, which is essential for maintaining ecological balance and supporting biomass production in varying environments (Alvarenga et al., 2013). The prominence of energy metabolism genes across microorganisms suggests that these energy acquisition strategies are critical drivers of microbial diversity and community structure.

For bacilli, carbohydrate transport and metabolism genes were the most abundant functional category. This prevalence likely reflects their adaptation to organic-rich environments like sediments or water bodies (Trabucho Alexandre, 2015), suggesting a pivotal role in complex organic matter degradation and nutrient cycling.

G genes were more pronounced in W and O than in S. This aligns with the understanding that dissolved organic matter in aquatic environments is readily bioavailable (Dittmar et al., 2021). The rapid turnover of organic materials in these environments creates an enriched substrate pool, catalyzing higher metabolic activity. Consequently, this pattern indicates functional specialization within microbial communities for efficient resource utilization and dynamic ecosystem processes (Louca et al., 2018).

The disparity in functional gene abundance between S and W emphasizes the importance of habitat-specific adaptations. Sediments often serve as nutrient sinks with complex carbon sources requiring specialized degradation pathways (Leithold et al., 2016), while microorganisms in water access more readily bioavailable carbon, enhancing carbohydrate metabolism functions. This dynamic interaction underscores the importance of understanding spatial variations in microbial functional potential to predict ecosystem responses to environmental changes.

The distinct microbial compositions associated with specific functional genes across W, O, and S samples reflect nuanced community–environment interactions. This reveals significant differences in microbial diversity and functional gene representation, highlighting the importance of habitat-specific adaptations in shaping metabolic capabilities.

Regarding functional gene *C*, *Gammaproteobacteria* and *Betaproteobacteria* predominated in S. These groups are typically associated with anaerobic/microaerophilic sediment conditions, facilitating diverse energy utilization through processes like sulfate reduction and denitrification (Qian et al., 2019; Zhang et al., 2022). Their ability to occupy low-oxygen niches enhances their significance in sediment biogeochemistry.

In contrast, *Actinomycetia* and *Betaproteobacteria* were more represented in W and O, suggesting a functional shift influenced by physicochemical properties. *Actinomycetia*, known for degrading complex organic compounds, may be critical to nutrient cycling within the water column (Mallik et al., 2024). Their presence alongside *Betaproteobacteria*—involved in organic matter degradation and ammonia oxidation—emphasizes that microbial interactions regulate aquatic nutrient dynamics (Hui et al., 2022).

Bacilli showed the highest proportion of functional gene *G* in water samples, highlighting their role in processing readily available organic substrates. *Alphaproteobacteria*, the second most abundant group, further indicates specialization in carbohydrate metabolism within aquatic nutrient cycles. The higher representation of *Actinomycetia*, *Betaproteobacteria*, and *Alphaproteobacteria* in overlying water samples underscores the importance of functional diversity and their potentially facilitating efficient organic matter turnover (Bergauer et al., 2018).

For functional genes *I*, *P*, and *H*, the dominance of *Gammaproteobacteria* and *Betaproteobacteria* in sediment samples highlights their diverse metabolic potentials. These groups exhibit adaptability in sediment biogeochemistry processes like lipid metabolism and ion transport (Huettel et al., 2014). Conversely, a higher abundance of *Gammaproteobacteria* and *Actinomycetia* in W/O suggests a shift toward dynamic nutrient availability interactions.

Overall, the significant differences in microbial community composition across various habitats reveals a complex interplay of environmental factors driving the functional capacities of these microorganisms. Understanding these dynamics is critical for predicting ecosystem responses to changes in nutrient inputs and environmental conditions. Further research should focus on the specific ecological roles of these microbial communities and their functional genes in various aquatic systems, which might provide deeper insights into their contributions to biogeochemical cycling.

5 Conclusion

Dominant microbial species, including *Exiguobacterium* and *Candidatus Fonsibacter*, were found to contribute to organic matter degradation and nutrient transformation, while *Nitrospira* played a key role in nitrogen cycling as nitrifiers or denitrifiers. The mouth zone, enriched in nutrients, supported *Methyloceanibacter*, which was involved in methane or organic-matter metabolism. *Microcystis* dominated in the upstream region, indicative of nutrient-rich, algal-rich conditions. In the middle of the river, *Paralia* thrived due to favorable light and flow conditions.

Reservoir regulation altered functional gene composition, making it more like that of lake ecosystems. Genes related to amino acid transport and metabolism were most abundant. Phosphorus-related genes are primarily involved in energy production and conversion, highlighting the crucial role of microbial respiration and oxidative phosphorylation in supporting ecosystem productivity.

This study has demonstrated the effects of reservoir-induced changes on microbial diversity, suggesting impacts on microbial processes and nutrient cycling in river systems downstream from a large dam. In terms of limitations, temporal sampling during only 2 months may not fully capture the annual variability in microbial dynamics, and more frequent and extended sampling would provide a better understanding of seasonal changes. Secondly, the functional roles of microbial species, particularly in phosphorus cycling and their interactions within the community, were not fully explored. A deeper analysis of gene–environmental correlations would enhance the understanding of microbial functions and the implications for protecting river water quality and ecological conditions below dams.

Data availability statement

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

Author contributions

JW: Data curation, funding acquisition, methodology, software, writing – original draft, and writing – review and editing. SsL: Data curation, formal analysis, investigation, methodology, supervision, and writing – original draft. YW: Conceptualization, funding acquisition, resources, and writing – original draft. MK: Supervision, validation, and writing – review and editing. XZ: Data curation, investigation, software, and writing – original draft. SzL: Software, supervision, validation, and writing – original draft. YB: Project administration, supervision, and writing – original draft. XC: Supervision, validation, and writing – original draft. ZH: Supervision, validation, and writing – original draft. MS: Data curation, investigation, and writing – original draft. HH: Data curation, investigation, and writing – original draft.

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Conflict of interest

Authors JW, YW, SL, and YB were employed by China Three Gorges Corporation.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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