

Article

Microbial Diversity and Community Drivers in Caohai Lake (Guizhou, China) Revealed by 16S rRNA Gene Sequencing

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Abstract

Microorganisms are sensitive indicators of aquatic environmental quality and ecosystem stability. Caohai Wetland, a typical subtropical plateau karst wetland suffering ecological degradation under combined natural-anthropogenic disturbances, is one of the three major plateau freshwater lakes in China and a critical wintering habitat for the Black-necked Crane (*Grus nigricollis*) along the East Asian–Australasian Flyway. Previous research has focused mainly on phytoplankton, aquatic plants, birds, and the water environment, while knowledge of its microbial community, especially the joint controls of multi-factor hydro-environmental conditions and aquatic plants across the whole lake, remains limited. To determine the diversity and seasonal dynamics of the microbial community and the key environmental factors driving it, water samples were collected from 17 sites in Caohai Lake across four seasons during 2022–2023 and analyzed by 16S rRNA gene sequencing, combined with measurements of hydro-physicochemical parameters and aquatic plant biomass and coverage. Among the 1370 ASVs obtained, the top five phyla in descending order of abundance were Pseudomonadota (45.04%), Bacillota (21.75%), Bacteroidota (11.82%), Actinomycetota (11.09%), and Verrucomicrobiota (3.65%). The microbial community exhibited significant seasonal variations, with richness, the Shannon-Wiener index, and Pielou's evenness all significantly higher in autumn than in the other three seasons and lowest in spring. Correlation analysis indicated that water temperature was the primary driver of microbial community structure, while SD, EC, and COD also exerted significant influences; in addition, aquatic plant biomass and coverage were identified as key environmental factors shaping the microbial community composition in Caohai. This study provides fundamental monitoring data to support the assessment of the evolutionary trends of the Caohai wetland ecosystem and its conservation and management.

Keywords: Caohai wetland; microbial community; community structure; seasonal variation; environmental factors



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1. Introduction

Wetland ecosystems play an irreplaceable role in maintaining regional ecological balance, regulating local climate, influencing regional hydrology, and conserving biodiversity [1]. As one of the three major plateau freshwater lakes in China, the Caohai Wetland is a typical representative of subtropical plateau wetland ecosystems in China with rich species resources, and complete system structure and function. Moreover, Caohai Wetland not only lies within the East Asian-Australasian Flyway, providing critical wintering habitat for the Black-necked Cranes (*Grus nigricollis*), a unique high-altitude crane species in China, but also offers important migration routes for other rare birds. Therefore, maintaining the ecological condition and key ecosystem functions of Caohai Wetland is important for regional biodiversity conservation [2,3].

Caohai Lake, situated in the southwest of Weining County and the hinterland of the Wumeng Mountains, is the largest structural karst lake in China. Dominated by a mountainous subtropical southwest monsoon climate, it features distinct vertical climatic zones, abundant sunshine, warm dry winters and cool humid summers. With a catchment area of 120 km², the lake receives water recharge from atmospheric precipitation, surface runoff and groundwater. Located in the upper reaches of the Yangtze River, it serves as the source lake of the Luoze River, a secondary tributary of the Jinsha River via the Hengjiang River (the primary tributary of the Jinsha River), and features a complete plateau karst wetland ecosystem. While maintaining its own balance, the Caohai Wetland also maintains the balance of the regional ecosystem, providing a material basis and an important guarantee for the sustainable development of the regional ecology and economy. In recent years, due to anthropogenic and natural factors, the balance and function of the ecosystem of the Caohai Wetland have been damaged; submerged plants are decreasing, the wetland area is shrinking, and the ecosystem has begun to degrade [2,4]. These changes have attracted close attention from researchers, while earlier research on the Caohai Wetland has predominantly focused on phytoplankton [5], zooplankton [6], aquatic plants [7], birds [8], the water environment [9], and heavy metals [10], studies on its microbial diversity and community drivers remain limited. Recent advances have explored microbial responses to anthropogenic activities in Caohai wetland sediments (2021) [11], and linkages between dissolved organic matter, bacterial communities and anthropogenic disturbances in this plateau lake (2025) [12], as well as the role of lakeshore land use, hydrochemistry and DOM composition in regulating microbial carbon metabolism (2026) [13]. However, comprehensive investigations integrating seasonal dynamics, aquatic plant influences and multi-factor driving mechanisms of microbial communities across the entire Caohai Lake are still lacking.

As an important component of freshwater systems, microorganisms are numerous and complex in composition, and this diversity makes microorganisms sensitive to changes in the aquatic environment in which they are located; microbial communities respond rapidly to changes in physicochemical and habitat conditions and can therefore provide information on ecosystem condition and functioning. In this study, we do not treat ecological stability as a static or invariant property. Rather, wetland condition is interpreted in a dynamic sense, in which key ecosystem functions are maintained despite natural seasonal environmental variability, while changes in the structure and metabolic function of the microbial community will, in turn, have an impact on the functioning of aquatic ecosystems [14]. Therefore, it is of great significance to explore the microbial diversity and community drivers of Caohai Lake to understand the evolutionary trend of the ecosystem and to guide the protection and management of the Caohai Wetland.

We used 16S rRNA gene amplicon sequencing because it is a culture-independent, high-throughput approach that is well suited to comparing bacterial community compo-

sition across many sites and sampling periods and to detecting broad temporal shifts in freshwater microbial assemblages [15,16]. The study had three objectives: (1) to characterize bacterial taxonomic diversity and seasonal variation across Caohai Lake and its inlet tributaries; (2) to identify the hydro-physicochemical and aquatic-plant variables associated with microbial community structure; and (3) to evaluate whether the observed relationships are consistent with patterns reported from other plateau, shallow-lake, and wetland systems. We note, however, that 16S rRNA amplicon data are based on relative sequence abundance and are subject to primer/PCR and database biases, have limited species- or strain-level resolution for some taxa, and do not directly measure microbial activity or functional potential [16].

2. Materials and Methods

2.1. Study Area and Sample Collection

The study area is located in the Caohai Lakes (Figure 1, 104°12' E–104°18' E, 26°49' N–26°53' N) within the Caohai National Nature Reserve, in Guizhou Province, southwestern China. This area belongs to a region that has a subtropical humid monsoon climate, with an average annual temperature of 10.5 degrees Celsius, precipitation of 1000 mm, and an elevation of 2172–2234 m, with water depths ranging from 1 to 3 m. There were 17 sample collection sites (Figure 1), including 13 lake sites (S01–S13) and 4 inlet tributary sites (Z01–Z04). Sample collection was conducted in April, July, and October 2022 and January 2023, respectively. Survey indicators include environmental DNA samples, water, aquatic plant biomass and cover. A few sites were not sampled because the water level was too low for boats to arrive. Finally, a total of 60 samples were collected.

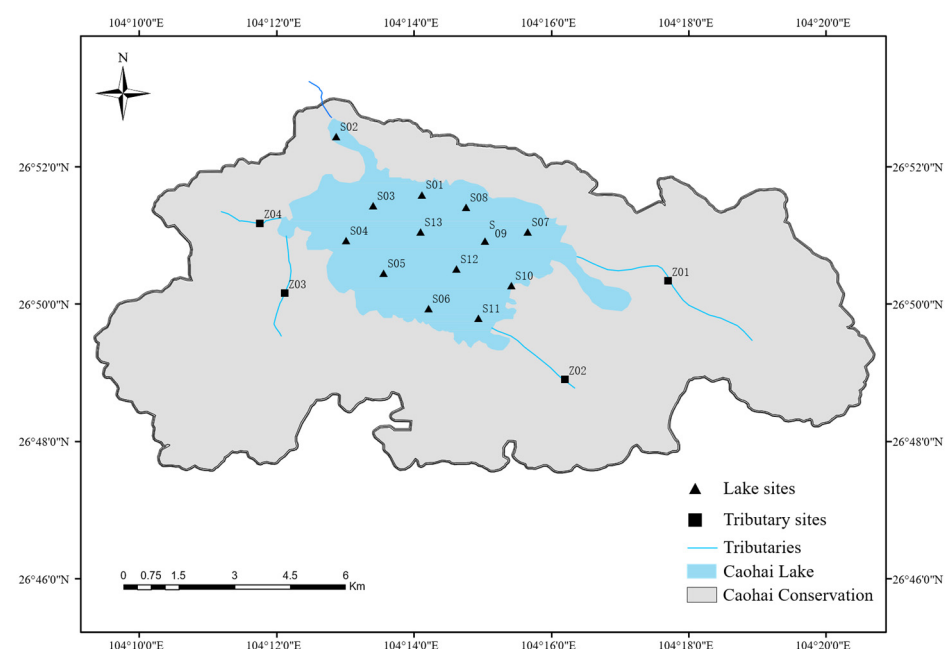


Figure 1. Study area and sampling sites in Caohai Lake.

2.2. Physical and Chemical Indicator Measurement Methods

The pH, WT, DO, and EC of the overlying water were measured by a portable multi-parameter meter (SX751, SANXIN, Shanghai, China). TU was measured by a turbidimeter (WGZ-200B, Sapeen, Shanghai, China). A Secchi disk was used to test SD. Standard methods in China for assessing surface water were used to quantify CODMn, COD, TSS, TN, TP, $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$.

For aquatic plant sample collection, four 0.2 m² quadrats were randomly established within a 5 m radius around each sampling site, following the standard vegetation survey protocol for plateau wetlands [17]. The total coverage of aquatic plants in each quadrat was determined by visual estimation. The whole plant containing shoots and roots was collected from each plot and washed to remove sediment and surface residues, drained of floating water, and biomass measurements were taken immediately thereafter.

2.3. Environmental DNA Collection, Extraction, Sequencing and Processing Methods

1.5 L of water was collected from each sampling site using clean PET bottles. The collected water samples were promptly transported to a nearby laboratory and stored at a temperature between 0 and −4 °C. Subsequently, 0.22 µm polycarbonate membranes (Whatman, Cytiva, Maidstone, UK) were employed to filter the water samples. These filtered membranes were then stored in a frozen state at −80 °C until DNA extraction.

Genomic DNA extraction was performed using the Sodium Dodecyl Sulfate (SDS) method. The target regions (16S V3-V4) of the 16S rRNA genes were amplified using specific primers (341F: CCTAYGGGRBGCASCAG, 806R: GGACTACNNGGGTATCTAAT) [18]. Each PCR mixture consisted of 15 µL of Phusion[®] High-Fidelity PCR Master Mix (Thermo Fisher Scientific, Waltham, MA, USA), 0.2 µM of each primer, and 10 ng of the target DNA. The PCR cycling conditions comprised an initial denaturation step at 98 °C for 1 min, followed by 30 cycles at 98 °C (10 s), 50 °C (30 s), and 72 °C (30 s), concluding with a final extension at 72 °C for 5 min.

The amplicons were extracted from 2% agarose gels and then purified using the Qiagen Gel Extraction Kit (QIAGEN GmbH, Hilden, Germany) following the manufacturer's instructions. Subsequently, the purified amplicons were sequenced on a NovaSeq platform (Illumina, Inc., San Diego, CA, USA), generating 250 bp paired-end reads.

FLASH (Version 1.2.11) was employed to merge paired-end reads [19] and quality filtering on the raw tags was performed using fastp (Version 0.20.0) to obtain high-quality Clean Tags. Clean Tags were compared to the Silva reference database (Release 138, <https://www.arb-silva.de>) using Vsearch (Version 2.15.0) to detect and remove chimera sequences, resulting in effective tags [20]. Denoising of effective tags was carried out using the deblur module in QIIME2 (Version 202006) to produce initial Amplicon Sequence Variants (ASVs). Taxonomic annotations were performed using QIIME2 and the Silva Database for 16S. Only ASVs with a total abundance greater than 0.005% were retained [21]. Then the ASV table was resampled to the minimum number of sequences (20,476) from each sample.

2.4. Data Analysis

For phylogenetic analysis, matrices were aligned using MAFFT 7.3 [22] and ambiguously aligned regions were removed using Trimal 1.2 [23]. Phylogenetic analysis was conducted using the maximum likelihood (ML) method implemented in IQ-TREE (v1.6.12) [24]. The best-fit substitution model (TVMe+I+G4) was selected based on the Bayesian Information Criterion (BIC). Richness, the Shannon–Wiener index, and Pielou's evenness for each sample were calculated using the vegan (2.7-6) package for R [25] at the ASV level. Sample clustering analysis (based on Bray–Curtis distance) and species stacking analyses based on the top 10 phyla with the highest abundance were implemented through the vegan and ggtree (4.3.0) packages for R. PCA and RDA analyses were completed using the online analysis tool Clustvis (<https://biit.cs.ut.ee/clustvis> accessed on 2 September 2026) and the online analysis platform TUTU (<https://www.cloudtutu.com>). Generalized Additive Models (GAM) were fitted using the mgcv package (v1.9-0) for R, with smoothing

parameters (k) set to 5 for all predictors to avoid overfitting, and the optimal k value was selected via generalized cross-validation (GCV).

3. Results

3.1. α -Diversity

A total of 1370 ASVs were obtained, covering 17 phyla (Figure 2). The top 5 phyla with the highest percentage of ASV numbers were Pseudomonadota (45.04%), Bacillota (21.75%), Bacteroidota (11.82%), Actinomycetota (11.09%) and Verrucomicrobiota (3.65%). In terms of number of reads, the top five phyla with the highest percentage were Pseudomonadota (54.75%), Actinomycetota (15.09%), Bacillota (11.68%), Cyanobacteriota (9.87%), and Bacteroidota (5.00%).

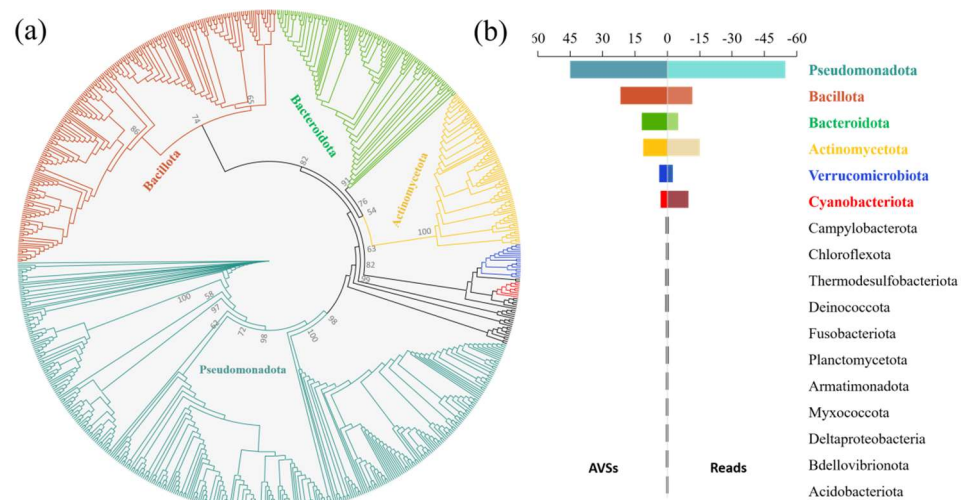


Figure 2. Sample clustering analysis (based on Bray–Curtis distance) and species stacking analyses (a) radial phylogenetic tree; (b) species stacking analysis based on abundance.

Comparisons of α -diversity between different regions (lake and tributaries) and between seasons were made based on Richness, Shannon–Wiener index, and Pielou’s evenness (Figure 3). The results showed that Richness was not significantly different between the lake area and tributaries (Figure 3a), but both the Shannon–Wiener index and Pielou’s evenness were significantly higher in tributaries than in the lake area (Figure 3b,c). Between seasons, species diversity showed autumn > summer > spring > winter (Figure 3d); the Shannon–Wiener index was lowest in spring, roughly equal in summer and winter, and highest in autumn (Figure 3e), while evenness indices were higher in autumn and winter than in spring and summer (Figure 3f). Richness, the Shannon–Wiener index, and Pielou’s evenness were significantly higher in autumn than in the other three seasons. In spring, all three indices were lower than in the other three seasons. In summer, all three indices had wider variations and were more different among sampling sites.

3.2. β -Diversity

The results of the sample clustering analysis (Figure 4a upper) whose reliability was assessed via PERMANOVA, and species stacking analysis (Figure 4a lower) based on Bray–Curtis distances are shown in Figure 4. Most of the samples in spring clustered into a single branch (red), with the highest abundance of Cyanobacteriota, followed by Pseudomonadota and Actinomycetota. Most of the samples in summer clustered into a single branch (blue), with the dominant taxa being mainly Pseudomonadota and Bacillota. Whereas autumn (purple) and winter (green) samples were not clearly differentiated and clustered into one

branch, with Pseudomonadota as the main dominant taxon and a relatively high abundance of Actinomycetota in some samples.

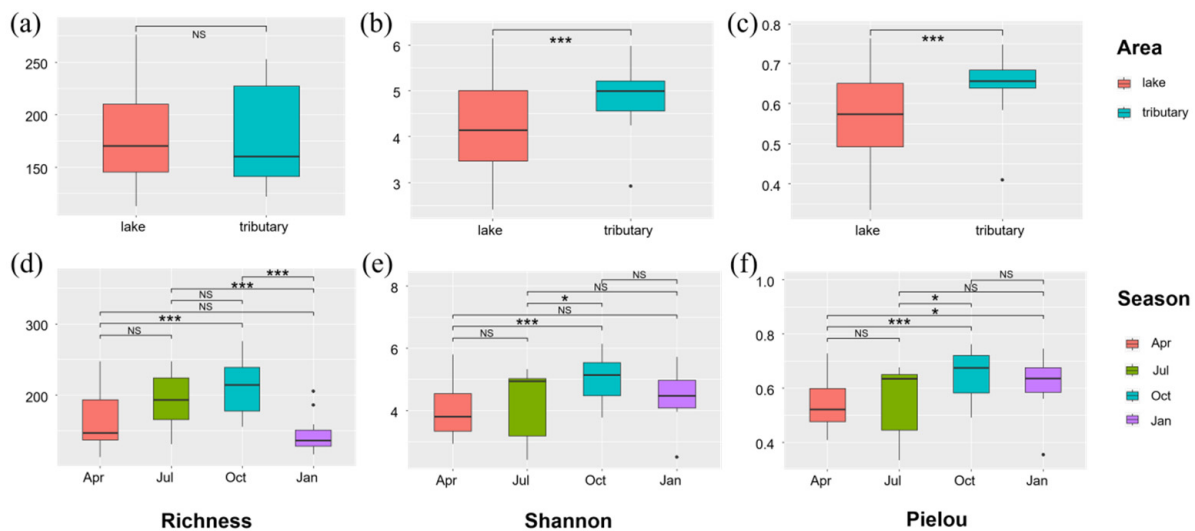


Figure 3. α -diversity based on Richness, Shannon–Wiener index and Pielou's evenness. (a) Comparison of species Richness between lake and tributaries; (b) comparison of species Shannon–Wiener index between lake and tributaries; (c) comparison of species Pielou's evenness index between lake and tributaries; (d) comparison of species Richness among different seasons; (e) comparison of species Shannon–Wiener index among different seasons; (f) comparison of species Pielou's evenness index among different seasons. Dots represent outliers. * $p < 0.05$, *** $p < 0.001$; NS indicates no significant difference.

The results of PCA analyses (Figure 4b,c) showed that, among different regions, there was no clear distinction between lake and tributary sites (Figure 4b). In contrast, between seasons (Figure 4c), the results of PCA analyses were consistent with the results of cluster analyses, with the majority of samples clustered together in the spring (red), clearly differentiating them from the other samples. The majority of samples in summer (blue) were clustered together, while samples in autumn and winter were clustered together with no clear distinction.

3.3. Correlation Analyses

The RDA analyses revealed that water depth, WT, EC, SD, COD, TSS, aquatic plant biomass and coverage were the top eight environmental factors influencing microbial community structure (Figure 5). To further elucidate the impact of key environmental factors on microbial communities, we employed the GAM method to model the effects of COD, EC, SD and WT—identified as the top four influential factors. The results showed that microbial species richness was weakly and negatively correlated with COD at 25–40 mg/L COD (Figure 6a), and the Shannon Wiener index and Pielou evenness index first increased and then decreased with increasing COD (Figure 6b,c). Under EC conditions of 250–500 $\mu\text{S}/\text{cm}$, species richness, Shannon–Wiener index and Pielou evenness index were negatively correlated with EC, decreasing with increasing EC (Figure 6d–f). Under SD conditions from 30 to 120 cm, species richness was negatively correlated with SD (Figure 6g), and the Shannon Wiener index and Pielou evenness index were positively correlated with SD and increased with increasing SD (Figure 6h,i). Under WT conditions from 5 to 25 $^{\circ}\text{C}$, species richness first increased and then decreased with increasing WT (Figure 6j), and the Shannon Wiener index and Pielou evenness index were negatively correlated with WT and decreased with increasing WT (Figure 6k,l).

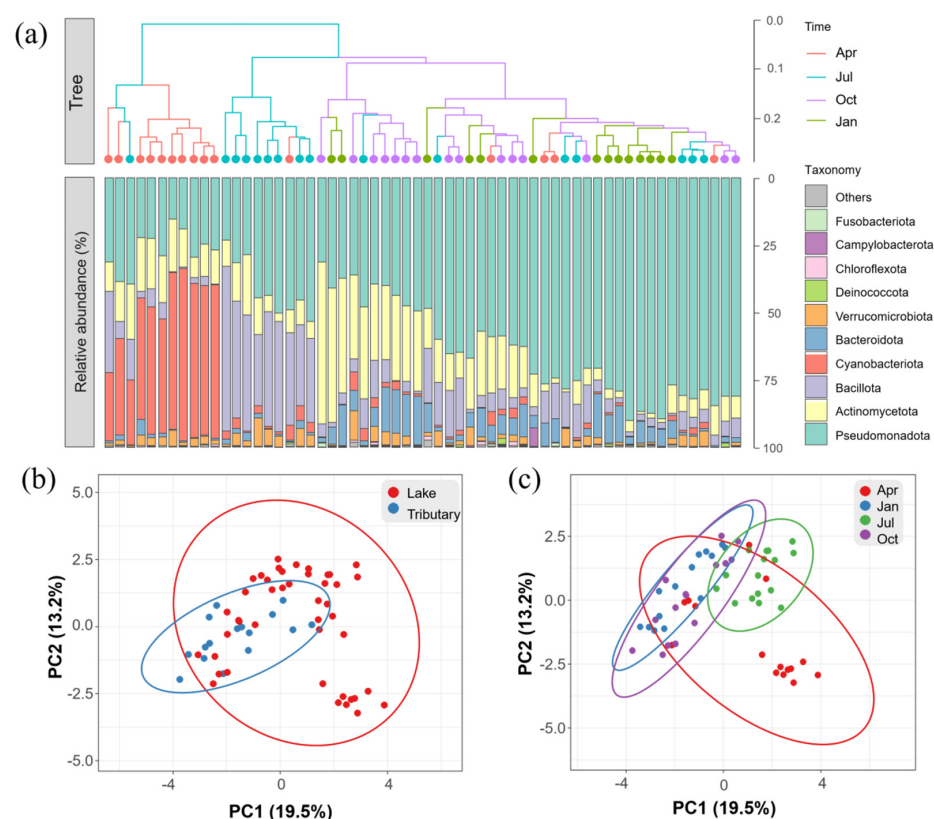


Figure 4. The results of the sample clustering analysis. (a) (upper) Sample clustering analysis, (a) (lower) species stacking analysis, (b,c) the results of PCA analyses.

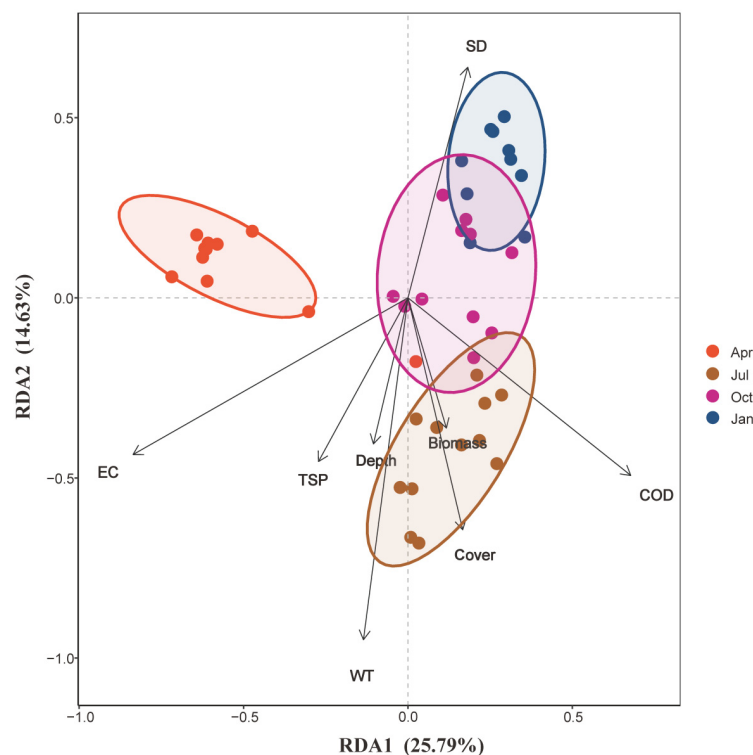


Figure 5. The results of RDA analyses between different seasons and environmental factors influencing microbial community structure. Forward selection based on the Akaike Information Criterion (AIC) was applied to retain significant explanatory variables, and variance inflation factors (VIF) were calculated to assess multicollinearity among predictors. All retained variables had VIF values < 5, indicating no severe multicollinearity issues.

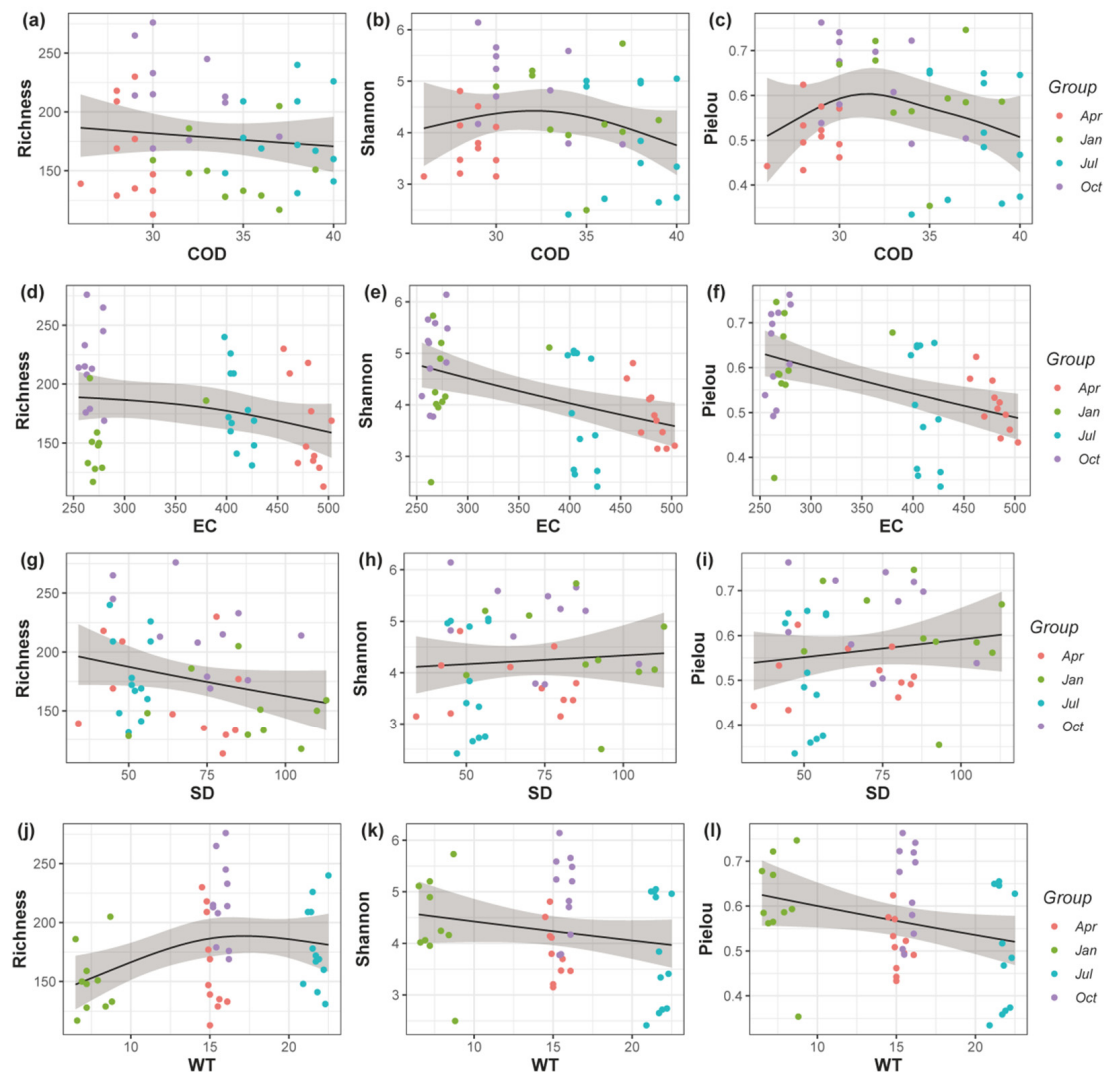


Figure 6. Correlation analysis between the top eight environmental factors and Richness, Shannon–Wiener index and Pielou’s evenness index. The grey shaded areas indicate the 95% confidence intervals. (a) Correlation between COD and Richness; (b) Correlation between COD and Shannon Wiener index; (c) Correlation between COD and Pielou’s evenness index; (d) Correlation between EC and Richness; (e) Correlation between EC and Shannon Wiener index; (f) Correlation between EC and Pielou’s evenness index; (g) Correlation between SD and Richness; (h) Correlation between SD and Shannon Wiener index; (i) Correlation between SD and Pielou’s evenness index; (j) Correlation between SD and Richness; (k) Correlation between SD and Shannon Wiener index; (l) Correlation between SD and Pielou’s evenness index.

4. Discussion

Microbial community dynamics in the Caohai exhibit pronounced seasonality, with water temperature identified as a key driver. Previous studies have established that temperature can directly or indirectly influence microbial community dynamics in aquatic ecosystems [26,27]. On the southeastern Tibetan Plateau, Liu et al. [28] also demonstrated that climate predictors—particularly mean annual temperature—outweighed local factors in shaping stream bacterial and fungal communities along a 990–4600 m elevation gradient. The environmental associations observed in Caohai also have parallels in freshwater systems outside China, while highlighting the context dependence of individual drivers. Lake Lanier (USA) [16], where 16S rRNA amplicon data captured temporal microbial shifts and seasonal mixing was an important driver; Lake Garda (Italy) [29], where repeated annual cycles of bacterioplankton succession were associated with temperature, strati-

fication, nutrients, and phytoplankton; a seven-year study of a large shallow eutrophic lake in Estonia [30], where temperature and nutrients were important within years but interannual variability associated with water level, mixing, and dissolved humic matter was even greater; and shallow lakes in the Pannonian Basin (Hungary) [31], where pH, dissolved oxygen, conductivity, primary production, hydrological setting, and site-specific conditions influenced bacterioplankton and macrophyte effects were context dependent. The four seasonal surveys in the present study captured marked within-year temperature variation, which likely contributed to the observed seasonal community pattern. The temporal scope of this study should be interpreted as a one-year seasonal survey rather than a characterization of the full long-term hydroclimatic envelope of Caohai. Sampling in April, July, October 2022 and January 2023 was sufficient to compare the four sampled seasonal conditions and to test associations between microbial communities and the environmental gradients observed during that period, but it cannot establish whether the magnitude of those gradients was representative of interannual variability. We have therefore restricted our interpretation to seasonal patterns observed in 2022–2023 and regard multi-year monitoring as necessary to test the long-term generality of these relationships in Caohai. As a shallow lake with an average water depth of less than 2 m, Caohai is susceptible to the impact of factors like wind and wave disturbances, significantly influencing SD and consequently affecting microbial community structure. The positive relationship between SD and microbial evenness highlights the importance of light penetration for phototrophic and mixotrophic microbes, as well as the role of reduced sediment resuspension in maintaining stable microhabitats. Moreover, the notable impact of EC and COD on the microbial community aligns with findings from studies on the effects of environmental factors on aquatic organisms in the Caohai Lake, which have confirmed that aquatic environmental parameters were key factors affecting microbial communities [5,7]. The negative correlation between EC and microbial diversity suggests that elevated ion concentrations may impose osmotic stress on sensitive taxa, selecting for halotolerant groups such as Actinomycetota, which were more abundant in high-EC samples. The notable impacts of EC and COD further align with regional comparative studies: Qiu, M. et al. [7] showed that trophic status and hydrochemistry (including conductivity and organic load proxies) were closely linked to planktonic microbiota across Yun-Gui Plateau lakes.

Meanwhile, this study provides initial insights into the impact of aquatic plant biomass and coverage on the microbial community composition in Caohai. Given the noticeable changes, such as the reduction in wetland area and degradation of aquatic plant communities in recent years within the Caohai wetland ecosystem [2], the interactions between aquatic plants and microbial communities have become a crucial area of research. Notably, Yan et al. (2019) [32] delved into the community structure and functional diversity of epiphytic and bacterioplanktonic bacteria associated with aquatic plants, while Xia et al. (2023) [5] investigated co-occurrence patterns between algae and bacteria in epiphytic biofilms of submerged macrophytes. Additionally, Qiu et al. (2023) [7] unveiled the effects of plant communities on the structure of bacteria and fungi. These studies collectively underscore the pivotal role of aquatic plant communities in shaping microbial community dynamics in the Caohai, emphasizing their broader significance for the wetland ecosystem in this region.

Beyond describing community patterns, our findings carry direct implications for the protection and management of Caohai Wetland. As water temperature was identified as the primary driver of microbial community variation, seasonal thermal regimes should be regarded as a key management parameter: maintaining natural hydrological seasonality, protecting cool-water refugia, and preventing thermal or wastewater discharges are essential to preserve microbial diversity. The low alpha diversity observed in spring identifies

a period that merits continued surveillance, although low diversity alone should not be interpreted as evidence of ecological instability. The strong effects of transparency (SD), electrical conductivity (EC) and chemical oxygen demand (COD) indicate that reducing organic and ionic loading—through stricter control of agricultural and domestic inputs, restoration of submerged vegetation to limit sediment resuspension, and reduction in external nutrient loads—would directly improve the habitat conditions that sustain a more even and diverse microbial community. Notably, the significant influence of aquatic plant biomass and coverage suggests that restoring submerged macrophyte communities can serve as an active management lever; microbial responses could be incorporated into evaluations of submerged-macrophyte restoration, alongside physicochemical and plant-community metrics, directly addressing the degradation of aquatic plant communities observed in Caohai in recent years. The seasonal baseline established here (2022–2023) also provides the reference conditions required to convert microbial diversity and composition into routine bioindicators for long-term ecological monitoring and early warning of further wetland degradation. Such applications are well supported by comparable systems: a review of freshwater biomonitoring has shown that microbial community structure, diversity and functional genes respond sensitively to eutrophication and to organic and ionic pollution and can be integrated into biotic indices that improve the resolution of routine water-quality assessment [33]; and in the shallow Baiyangdian Lake (China), a bacteria-based index of biotic integrity derived from 16S rRNA data was demonstrated to track the trajectory of ecosystem restoration under intensive ecological interventions [34]. Adopting an analogous microbial-indicator framework for Caohai would allow managers to evaluate the effectiveness of restoration measures and to detect deviations from reference conditions earlier than conventional physicochemical monitoring alone.

This study preliminarily revealed the microbial community changes and driving factors in the Caohai from 2022 to 2023, which enriched the ecological monitoring data of the Caohai water during the ecosystem recovery period (or reconstruction period) and is of some significance in guiding the management and restoration of the Caohai in the future. However, ecosystem recovery and development are the result of interactions between the environment and organisms and between different biological groups. For example, algae and bacteria have a complex relationship with specific interactions [32,35] that influence each other's waxing and waning [35]. Similarly, microhabitats of aquatic plant-attached biofilms are strong drivers of epiphytic bacteria and algae [36]. It further affects other aquatic organisms such as zooplankton, benthos, and fish. Therefore, in order to study the evolutionary trend of the wetland ecosystem in Caohai Lake, it is essential to record in detail the changes in individual aquatic communities such as microorganisms, and, of course, more comprehensive and systematic aquatic ecological monitoring would be of greater reference value and guidance. Therefore, more researchers and scholars are needed to devote more attention to the study of the ecosystem of Caohai to provide theoretical support for the protection and management of Caohai.

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Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

ASVs	Amplicon Sequence Variants
16S rRNA	16S ribosomal deoxyribonucleic acid
PCR	Polymerase Chain Reaction
PCA	Principal Component Analysis
RDA	Redundancy Analysis
GAM	Generalized Additive Model

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