

Salinity-driven diversity and assembly of free-living and particle-attached bacterial communities in arid region lakes*

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Abstract Microbial communities in arid region lakes are highly sensitive to salinity fluctuations, yet systematic comparisons of free-living (FL) and particle-attached (PA) bacteria along salinity gradients remain scarce. This study focuses on five lakes in the northwestern China, where salinity ranges from freshwater to brackish (0.17–13.88). Using 16S rRNA high-throughput sequencing, null model analysis, and co-occurrence network approaches, we investigated the diversity and driving mechanisms of FL and PA bacterial communities. Results show that: (1) PA communities exhibited significantly higher α -diversity than FL communities, with PA diversity decreasing as salinity increased, while FL diversity followed a U-shaped trend; (2) beta-dispersion analysis indicated that the spatial heterogeneity of PA communities was stronger compared to FL communities ($P < 0.001$); (3) redundancy analysis (RDA) showed that salinity was the main factor controlling the differentiation of FL communities (35.5% contribution), while water temperature (WT) was the primary driver of PA community variation (37.0%); (4) assembly mechanism analysis suggested that dispersal limitation (DL) was the dominant process shaping FL community assembly (64.2%), whereas homogeneous selection (HoS) governed PA community assembly (58.8%). This study provided novel insights into the response mechanisms and ecological adaptations of microbial communities in arid region lakes to environmental changes, offering critical theoretical support for aquatic microbial ecology in the context of inland lake salinization under climate change.

Keyword: free-living (FL) bacteria; particle-attached (PA) bacteria; salinity; microbial diversity; community assembly mechanism

1 INTRODUCTION

Aquatic ecosystems rely on microorganisms as essential biological components that underpin their functionality and stability. The community composition and metabolic activities of these microorganisms directly influence fundamental ecological processes such as carbon and nitrogen cycling, as well as pollutant degradation (Azam, 1998; Jetten, 2008; Narayanan et al., 2022).

Moreover, microorganisms act as ecological “sentinels”, sensitively reflecting the impacts of climate change and anthropogenic activities (Newton et al., 2011). Because of their rapid responses to environmental disturbances, shifts in

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microbial diversity and functional gene expression can serve as early indicators of fluctuations in physicochemical conditions, such as salinity and temperature (Chen et al., 2015; Ji et al., 2019; Shen et al., 2025). Such changes provide important early warning signals for assessing the cumulative effects of global change on aquatic ecosystems (Allison and Martiny, 2008).

In the arid interior of northwestern China, pronounced climatic warming and drying over the past six decades, superimposed on the effects of human activities, have led to dramatic changes in lake water levels and salinity (Tang et al., 2022). Bosten Lake (BST), which has shifted from a freshwater to a saline system, exemplifies these changes and provides a natural setting for investigating microbial adaptation to salinity stress (Tang et al., 2012). Comparative analyses of microbial communities across natural salinity gradients therefore offer critical insights into the ecological strategies that microorganisms employ to cope with salinity fluctuations.

Bacteria, a fundamental group within the microbial communities, are widely distributed in aquatic environments and play a crucial role in ecosystems (Shoemaker et al., 2017). According to their microhabitats, aquatic bacteria are generally classified as free-living (FL) or particle-attached (PA) types (Crump et al., 1999; Grossart, 2010). Both marine and freshwater studies have demonstrated clear functional and compositional distinctions between these lifestyles (Azam and Malfatti, 2007; Tang et al., 2015). In marine environments, FL bacterial community exhibits higher diversity compared to PA, with structure significantly influenced by factors such as water temperature (WT), salinity, and dissolved oxygen (DO) (Li et al., 2015; Chen et al., 2023; Bezzubova et al., 2024). In contrast to FL bacterial communities, PA bacterial communities are closely linked to the sources and composition of particulate matter and often exhibit higher metabolic activity (Li et al., 2015). In freshwater lakes, FL communities are influenced by factors such as eutrophication and temperature, but their diversity is generally lower than that of PA compartments (Hu et al., 2020).

Currently, studies on FL and PA communities in arid region lakes remain relatively scarce. The extreme environments of these lakes, such as high salinity and intense ultraviolet radiation, may have a profound impact on the diversity and assembly of

bacterial communities (Shen et al., 2025). Community assembly describes how different ecological processes shape microbial community composition and structure. According to niche theory, deterministic processes, including environmental filtering (e.g., pH, temperature, humidity, and salinity) and various biotic interactions (e.g., competition, facilitation, mutualism, and predation), largely control species composition, abundance, and distribution patterns (Chesson, 2000; Chave, 2004). The neutral theory, on the other hand, assumes that all species are ecologically equivalent, with species dynamics primarily controlled by stochastic processes such as birth/death, speciation/extinction, and immigration (Chave, 2004; Hubbell, 2011). However, comprehensive research on these two lifestyles/ecological types of bacteria is still lacking. Addressing this gap is crucial for understanding the ecological functions and adaptive strategies of microbial communities in arid lake ecosystems.

To fill this gap, we investigated bacterial communities in five lakes with contrasting salinity levels in arid Xinjiang, NW China. By comparing the diversity, community structure, and assembly mechanisms of FL and PA bacterial communities in these lakes, the study aims to reveal how different ecological types of bacteria respond to environmental changes, particularly salinity shifts. Specifically, we hypothesize that: (1) FL and PA bacterial communities exhibit distinct diversity patterns and community structures along salinity gradients; and (2) their assembly processes differ, with PA communities being more strongly governed by deterministic mechanisms. This study highlights the contrasting ecological strategies of FL and PA bacteria under salinity stress and expands our understanding of bacterial ecology in inland arid lakes.

2 MATERIAL AND METHOD

2.1 Study area and sample collection

Five lakes in the arid region of Xinjiang, China, were selected in this study based on their differences in salinity and ecosystem characteristics (Supplementary Table S1). These lakes include BST, Small Bosten Lake (sBST), Sayram Lake (SLM), Ulungur Lake (WLG), and Chaiwopu Lake (CWP). Four to nine sampling sites were established in each lake according to their surface areas (Supplementary Fig.S1). Among them, Bosten Lake is considered as

two distinct lake areas primarily due to significant differences in salinity, ecological environment, and hydrological conditions between the Large and Small Lake areas. The Large Lake area is expansive and strongly influenced by hydrodynamic forces, while the Small Lake area is mainly composed of reed wetlands, with a more diverse and complex ecological environment (Zhang et al., 2020). All samples were collected in July 2023. At each sampling site, 10–20 L of surface water (approximately 0.5 m below the water surface) were collected using a water sampler and placed in pre-cleaned plastic buckets for transportation back to the laboratory, where physicochemical parameters of the water were measured. Additionally, 500–1 000 mL of subsamples was filtered through a filtration device onto a 47-mm diameter, 5- μ m pore size polycarbonate membrane (Millipore, Ireland) for PA samples. The filtered water was then further filtered onto a 47-mm diameter, 0.2- μ m pore size polycarbonate membrane (Millipore, Ireland) for FL samples (Xie et al., 2020). The bacterial-laden filters were placed in sterilized 2-mL centrifuge tubes and stored at -80 °C for DNA extraction.

2.2 Measurement of physicochemical parameters

Physicochemical parameters such as WT, pH, total dissolved solids (TDS), salinity, and DO were measured in situ using a multi-parameter water quality sonde (YSI 6600 v2, Yellow Springs Instruments Inc., USA). Water transparency (Trans) and water depth (WD) were measured using Secchi disk and a water depth gauge, respectively. In the laboratory, the concentrations of total nitrogen (TN), total phosphorus (TP), suspended solids (SS), and dissolved organic carbon (DOC) were determined following standard methods (Jin and Tu, 1990). A summary of the physicochemical parameters for each sampling site in the lakes is presented in Supplementary Table S2.

2.3 DNA extraction, Illumina sequencing, and bioinformatics analysis

DNA extraction from FL and PA bacterial samples was performed using the SPINeasy™ DNA Pro Kit for Siol (MP Biomedicals, USA), following the manufacturer's instructions. The extracted DNA was dissolved in 100 μ L of Tris-HCl buffer, and DNA concentration and purity were assessed using a NanoDrop spectrophotometer. Following quality checks, the bacterial 16S rRNA gene V3–V4 variable region was amplified using primers 338F

(5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') (Fadrosh et al., 2014). The amplicon products were sequenced on the Illumina MiSeq PE300 platform at Guangdong Meige Gene Technology Co., Ltd. to obtain bacterial DNA sequence data from each sample (Wang and Qian, 2009; Bougouffa et al., 2013).

Quality control and processing of the raw sequences from high-throughput sequencing were conducted using QIIME2 (v2023.2). The Demux plugin was used for sample demultiplexing (Bolyen et al., 2019), and the DADA2 plugin was employed for filtering and denoising (Callahan et al., 2016). The phylogeny plugin was utilized to generate a phylogenetic tree using the FastTree method, which is implemented in the QIIME2 phylogeny plugin (Price et al., 2010).

Amplicon sequence variants (ASVs) and representative sequences were annotated based on the bacterial 16S rRNA sequences using the Silva 138 database with the feature-classifier plugin (Bokulich et al., 2018).

2.4 Community assembly mechanism of bacterial community

The β NTI (phylogenetic null model) method, a phylogeny-based randomization approach, was used to assess the community assembly mechanisms of bacterial communities in this study (Stegen et al., 2013). The β NTI method was applied, with calculations performed using the picante and ape packages on the R platform. First, the ASV table and phylogenetic tree were read and aligned with species abundance data. The phylogenetic distance matrix was obtained by calculating the Cophenetic distance (Kembel et al., 2010). Species abundance data were randomized 1 000 times, and the bMNTD (mean nearest taxon distance) values were calculated for each randomization. These values were then compared with the observed bMNTD values. The β NTI value was computed based on these values, where $bMNTD_{obs}$ represents the observed bMNTD value, $bMNTD_{rand}$ represents the randomized bMNTD value, and mean and std are the mean and standard deviation of the randomized results. Deterministic processes were inferred when $|\beta NTI| > 2$, with values greater than 2 ($\beta NTI > 2$) indicating heterogeneous selection (HeS) and values less than -2 ($\beta NTI < -2$) representing homogeneous selection (HoS). Conversely, $|\beta NTI| < 2$ suggested stochastic assembly. Within the stochastic assembly,

dispersal limitation and homogenizing dispersal (HD) were identified when Bray-Curtis-based Raup-Crick metric ($RC_{\text{bray}} > 0.95$ and $RC_{\text{bray}} < -0.95$, respectively). Values of $|RC_{\text{bray}}| < 0.95$ were attributed to drift (Dini-Andreote et al., 2015).

2.5 Co-occurrence network analysis

Co-occurrence patterns of bacterial communities from the five lakes were constructed based on network theory (Gotelli and McCabe, 2002; Deng et al., 2012; Zhou et al., 2014). To simplify the dataset, only ASVs with a relative abundance greater than 0.05% in the five lake samples were retained, and further, ASVs occurring in more than 20% of the samples were selected for network construction (Chase et al., 2011). The co-occurrence network was based on the Spearman correlation coefficient to calculate the correlations between ASVs, and the Benjamini-Hochberg (BH) correction was applied to the correlation P -values. Only significant correlations ($|r| \geq 0.60$, $P \leq 0.01$) were retained to build a weighted undirected network, and isolated nodes with no connections were removed from the network (Zhou et al., 2014). To assess network complexity, several topological parameters were calculated, including the number of nodes, number of edges, the number of positive and negative correlation edges, APL, ND, network density, and clustering coefficient, all of which were computed using the “igraph” package in R (Kraft et al., 2011). All networks were exported in GraphML format and visualized using Gephi 0.10.1.

2.6 Statistical analysis

All statistical analyses were performed in R (version 4.4.2). To evaluate variation in water quality among lakes, one-way ANOVAs were performed on major physicochemical parameters, followed by Fisher’s least significant difference (LSD) post-hoc tests to detect pairwise differences.

Richness, Faith’s phylogenetic diversity (Faith pd), and the Shannon index were calculated with the vegan package, after normalizing all samples to the minimum sequencing depth (15 148 reads). Community compositional dissimilarity was quantified using Bray-Curtis distances computed with the “vegdist()” function (“vegan” package) for each sampling site. Principal coordinates analysis (PCoA) was used to visualize β -diversity patterns across FL and PA bacterial communities in five lakes. The analysis was performed using the ASV

table, with Bray-Curtis dissimilarity used to quantify community composition differences. No prior data preprocessing or transformation was applied, and the Bray-Curtis distance matrix was directly calculated from the raw ASV data. Group differences were evaluated using PERMANOVA with the “adonis()” function from the “vegan” package, with 999 permutations to assess group differences (Geng et al., 2022). The percentage of variance explained by the first two principal coordinates (PCoA1 and PCoA2) was calculated based on eigenvalues. Results were visualized using the “ggplot2” package. Geographical distance between sampling locations was also considered in the analysis to assess its influence on community composition. The correlation between geographical distance and Bray-Curtis dissimilarity was analyzed using distance-decay analysis, where we tested the relationship between geographical distance and community dissimilarity. Beta-dispersion analysis was performed using the “betadisper()” function from the “vegan” package, with Bray-Curtis dissimilarity calculated using the “vegdist()” function. The taxonomic composition of bacterial communities at the phylum level across the studied lakes was visualized using the “ggplot2” package, showing the relative abundance of the top 9 phyla, with each sample’s contribution represented as a proportion of the total abundance. To identify differentially abundant taxa between FL and PA communities across taxonomic levels (phylum to genus), we applied linear discriminant analysis (LDA) effect size (LEfSe) (Segata et al., 2011). This analysis was restricted to ASVs with relative abundance $> 0.1\%$.

To assess how physicochemical parameters influenced bacterial community composition, we first examined correlations between environmental variables and community structure using Spearman correlation analysis with the “corr.test()” function in the “psych” package (Huber et al., 2020). To reduce multicollinearity, variance inflation factor (VIF) analysis was applied, and the environmental parameters with VIF values greater than 10, such as WD, Trans, EC, salinity, SS, Chl a , TN, and TP, were excluded. Redundancy analysis (RDA) was then performed to quantify the contributions of key environmental drivers to community variation, including salinity, WT, pH, and DO (Lepš and Šmilauer, 2003; Tang et al., 2021).

3 RESULT

3.1 Comparison of environmental characteristics among different lakes

The main five water physicochemical parameters of the five lakes are presented in Table 1. All parameters exhibited significant differences among the lakes. Specifically, CWP had significantly higher TDS than the other lakes. SLM was characterized by a lower WT and a higher DO concentration. Based on the salinity classification, CWP (11.16) is classified as a saline lake; SLM (1.84) and WL (2.02) is classified as brackish lakes; while BST and sBST have relatively low salinity, with values of 0.68 and 0.17, respectively, both of which are classified as freshwater lakes. The pH values of the five lakes ranged from 8.0 to 9.04, with the highest chlorophyll concentration observed in WL, ranging from 5.23 to 6.98 $\mu\text{g/L}$ (Supplementary Table S2).

3.2 Diversity and geographical distribution of FL and PA bacteria along salinity gradients

Overall, PA bacterial communities generally exhibited higher richness, Shannon, and Faith's phylogenetic diversity indices than FL communities across the studied lakes (Fig.1a). The only exception was observed in CWP, where the Shannon index of PA communities was lower than that of FL communities. Along the salinity gradient, PA diversity declined from freshwater to saline conditions, whereas FL diversity followed a U-shaped pattern.

PCoA revealed significant compositional separation among lakes for both the FL and PA bacterial communities (Fig.1b). Examining within-group variation, FL communities from different lakes clustered more tightly in the ordination space, indicating lower β -diversity. In contrast, PA communities exhibited greater dispersion, reflecting higher β -diversity (Supplementary Fig.S2a). This

differential in-group variation was quantitatively confirmed by beta-dispersion analysis, which showed PA samples to be significantly more dispersed than FL samples (Supplementary Fig.S2b). Consequently, the overall community distance (beta-diversity) between FL and PA groups was also statistically significant. Correlation analyses with environmental variables revealed distinct drivers of diversity for FL and PA communities (Fig.1c). For FL communities, diversity indices were positively correlated with WD, Trans, pH, and DO. In contrast, PA diversity was more strongly associated with pH, TDS, Salinity and TN.

Finally, distance-decay analysis indicated that Bray-Curtis dissimilarity was significantly correlated with geographical distance ($P < 0.001$), confirming the influence of spatial separation on both FL and PA communities (Supplementary Fig.S3). However, the explanatory power for FL communities was relatively low ($R^2 = 0.29$), implying that other environmental factors, such as salinity, DO, and WT, also played important roles in shaping their community composition.

3.3 Species composition of FL and PA communities

The taxonomic composition of FL and PA communities exhibited notable differences across the studied lakes (Fig.2). In FL communities, Verrucomicrobiota was most abundant at intermediate salinity, while Actinobacteriota dominated in sBST, BST, WL, and CWP. The taxonomic composition of PA communities exhibits different trends. In PA communities, the relative abundance of Cyanobacteria and Chloroflexi is higher than that in FL communities, and in PA communities, Cyanobacteria dominate in the brackish lake WL and saline lake CWP. In SLM, Proteobacteria dominate, and the proportion of Bacteroidota is higher than in the other lakes.

LEfSe analysis further clarified the specialized bacterial lineages of FL and PA communities

Table 1 Mean values of the main physicochemical parameters for the studied lakes

Lake	WT (°C)	pH	TDS (mg/L)	DO (mg/L)	Salinity
Small Bosten Lake (sBST)	24.16±0.77 ^a	8.00±0.23 ^d	235±10 ^c	6.69±1.01 ^c	0.17±0.004 ^c
Bosten Lake (BST)	24.16±0.48 ^a	8.64±0.05 ^c	871±60 ^c	7.66±0.19 ^b	0.68±0.033 ^c
Sayram Lake (SLM)	18.09±0.95 ^b	8.96±0.04 ^a	2270±5 ^b	8.28±0.52 ^a	1.84 ±0.020 ^b
Ulungur Lake (WL)	24.89±0.74 ^a	8.79±0.01 ^b	2488±52 ^b	7.83±0.18 ^{ab}	2.02±0.042 ^b
Chaiwopu Lake (CWP)	24.58±1.04 ^a	8.85±0.11 ^{ab}	12221±1910 ^a	6.86±0.17 ^c	11.16±1.894 ^a

Different lowercase letters indicate significant differences ($P < 0.05$). WT: water temperature; TDS: total dissolved solids; DO: dissolved oxygen.

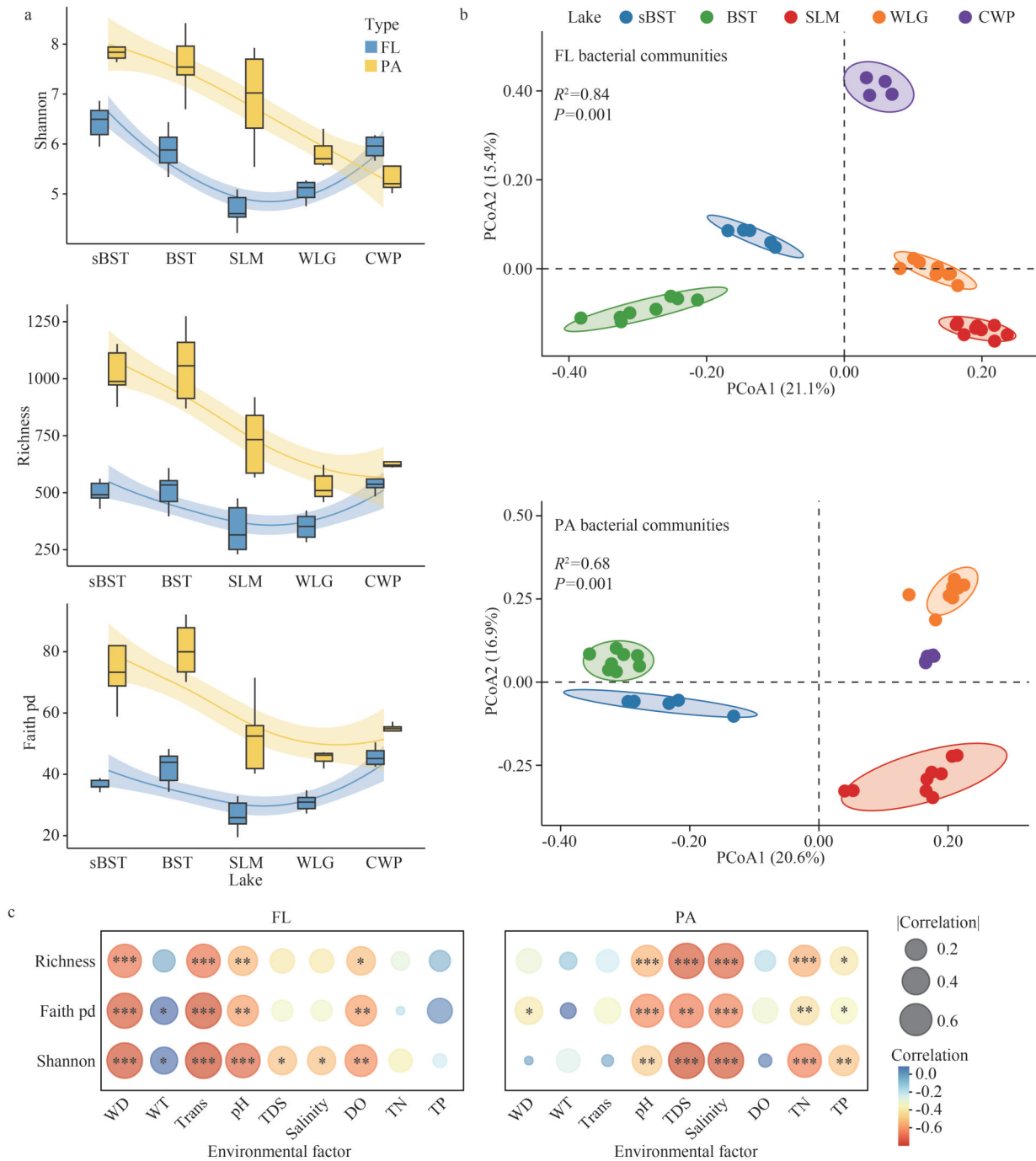


Fig.1 Diversity patterns (a) and community structures (b) of free-living (FL) and particle-attached (PA) bacteria in the five lakes; correlation heatmap of the alpha-diversity indices in FL and PA bacteria with main environmental factors (c)

sBST: Small Bosten Lake; BST: Bosten Lake; SLM: Sayram Lake; WLG: Ulungur Lake; CWP: Chaiwopu Lake; WD: water depth; WT: water temperature; Trans: transparency; TDS: total dissolved solids; DO: dissolved oxygen; TN: total nitrogen; TP: total phosphorus. In (c), *, **, and *** denote statistically significant correlations at $P<0.05$, $P<0.01$, and $P<0.001$, respectively.

in the lakes (Fig.3). Overall, Actinobacteriota and Bacteroidota had significantly higher average proportions in FL communities, while Alphaproteobacteria, Chloroflexi, Cyanobacteria, and

Firmicutes were significantly more abundant in PA communities. Notably, within the Actinobacteriota phylum, the Corynebacteriales order was enriched in the PA communities.

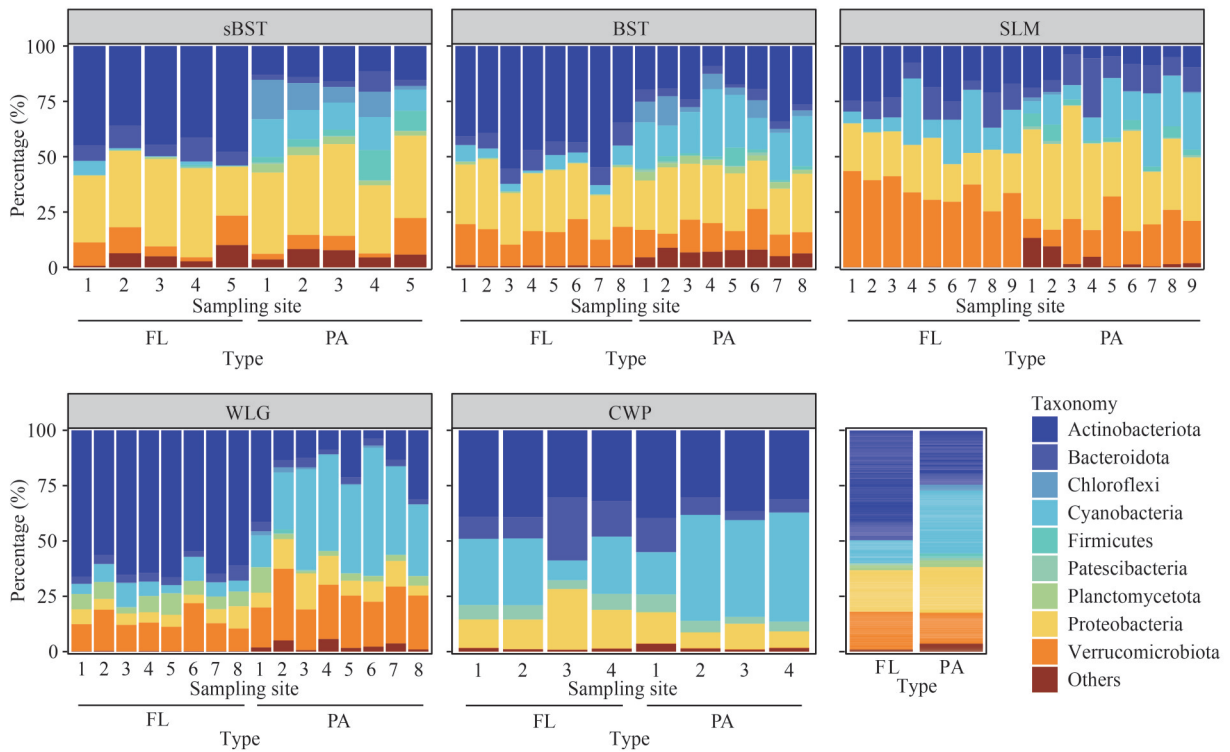


Fig.2 The phylum-level taxonomic composition of bacterial communities across the studied lakes

sBST: Small Bosten Lake; BST: Bosten Lake; SLM: Sayram Lake; WLG: Ulungur Lake; CWP: Chaiwopu Lake. FL: free-living; PA: particle-attached.

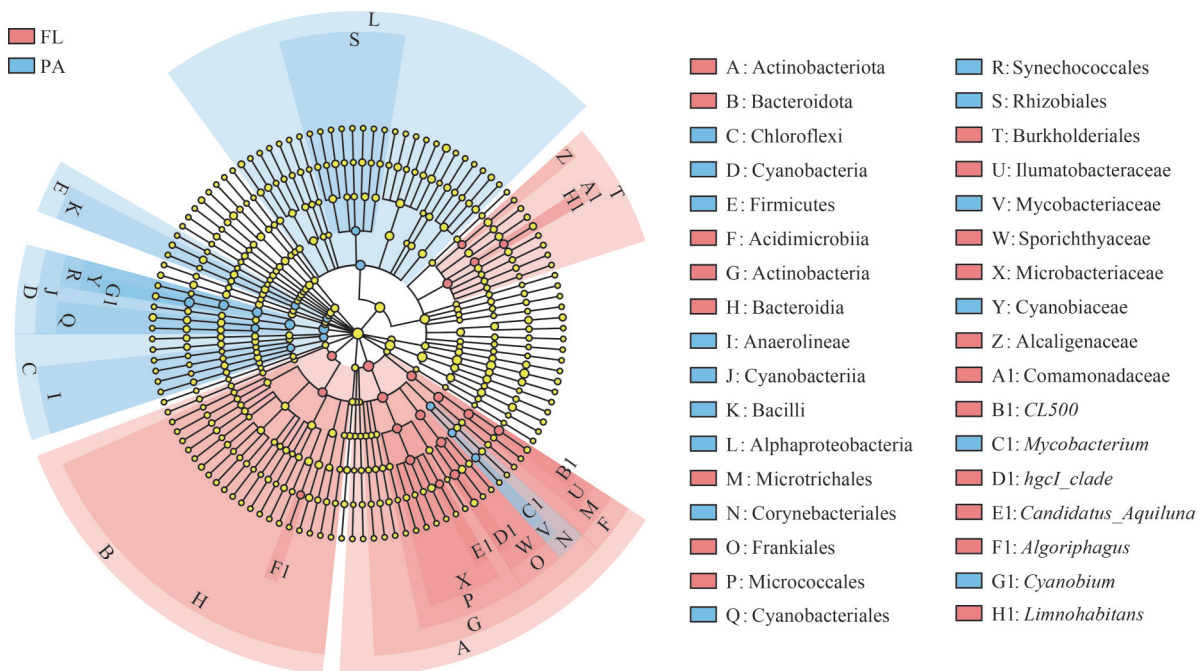


Fig.3 The LefSe results showing the taxonomic differences between free-living (FL) and particle-attached (PA) bacterial communities

Red circles represent bacteria significantly enriched in FL communities, while blue circles indicate those enriched in PA communities. Yellow circles denote taxa with no significant differences between the two community types. The analysis employed log linear discriminant analysis (LDA) with a threshold of $LDA > 4$ and $P < 0.05$, corrected using the Benjamini and Hochberg false discovery rate (FDR) test. The diameters of the circles are proportional to the relative abundance of the corresponding taxa.

3.4 Environmental driver of FL and PA bacterial community structures

RDA identified salinity, WT, pH, and DO as the major environmental factors shaping both FL and PA bacterial communities (Fig.4). For FL communities, salinity and pH emerged as the dominant drivers, explaining 35.5% and 34.8% of the structural variation, respectively. In contrast, PA communities were primarily influenced by WT and pH, which accounted for 37.0% and 31.9% of the variation, respectively.

3.5 Analysis of differences in community assembly mechanisms

The assembly of FL and PA bacterial communities was predominantly influenced by dispersal limitation

(DL) and HoS, respectively (Fig.5). DL accounted for 64.2% of FL community assembly, while HoS contributed 26.6%. In contrast, HoS was the primary driver of PA community assembly, contributing 58.8%, with DL accounting for 30.3%. HeS and HD had minimal impacts on both communities. These findings highlight the contrasting assembly mechanisms, where FL communities are more constrained by spatial processes, whereas PA communities are more influenced by environmental selection.

3.6 Co-occurrence network pattern of FL and PA bacterial communities

In both FL and PA networks, Proteobacteria and Actinobacteriota dominated the phylum-level

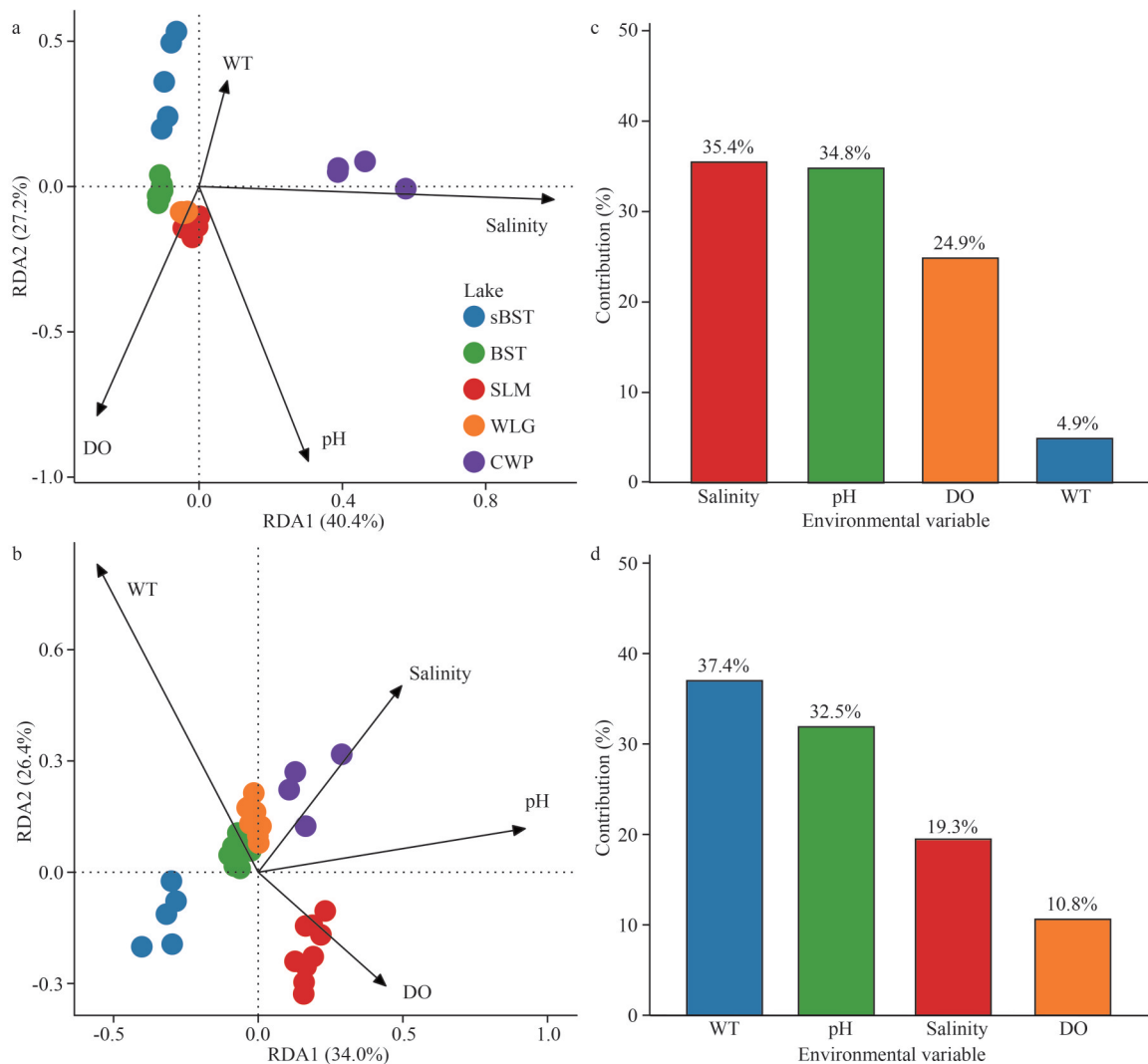


Fig.4 Redundancy analysis (RDA) of free-living (FL) (a) and particle-attached (PA) (b) bacterial communities, as well as the contribution of environmental variables to variation in community composition in FL (c) and PA (d) communities

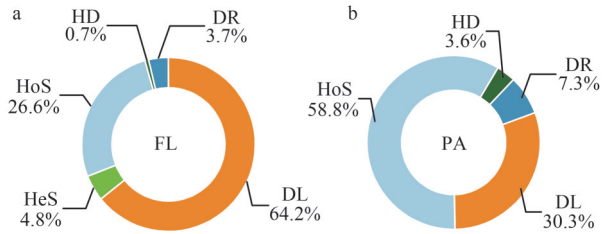


Fig.5 Proportion of deterministic and stochastic processes influencing free-living (FL) (a) and particle-attached (PA) (b) bacterial communities

DL: dispersal limitation; DR: drift; HoS: homogeneous selection; HeS: heterogeneous selection; HD: homogenizing dispersal.

composition (Fig.6). However, the FL network contained a greater abundance of nodes affiliated with Verrucomicrobiota, whereas Cyanobacteria nodes were more prevalent in the PA network. Structural characteristics of the two networks further illustrated their distinct ecological interactions

(Table 2). Although both networks exhibited similar average path length (APL), the PA network displayed larger network diameter (ND) and higher average degree (AD), indicating a more dispersed yet densely interconnected structure with more frequent node interactions. These differences suggest contrasting ecological strategies and interaction patterns between FL and PA bacterial communities.

At the whole-lake scale, co-occurrence networks were consistently dominated by Proteobacteria and Actinobacteriota, yet lake-specific features were evident (Supplementary Fig.S4). For instance, the saline lake was characterized by the presence of Patescibacteria and a relatively high ND (12.7) (Supplementary Table S3, reflecting a dispersed network structure with sparse interactions (density=0.07). In contrast, the freshwater lake exhibited a markedly higher AD (65.0), indicative of a highly connected and compact network. The mesotrophic

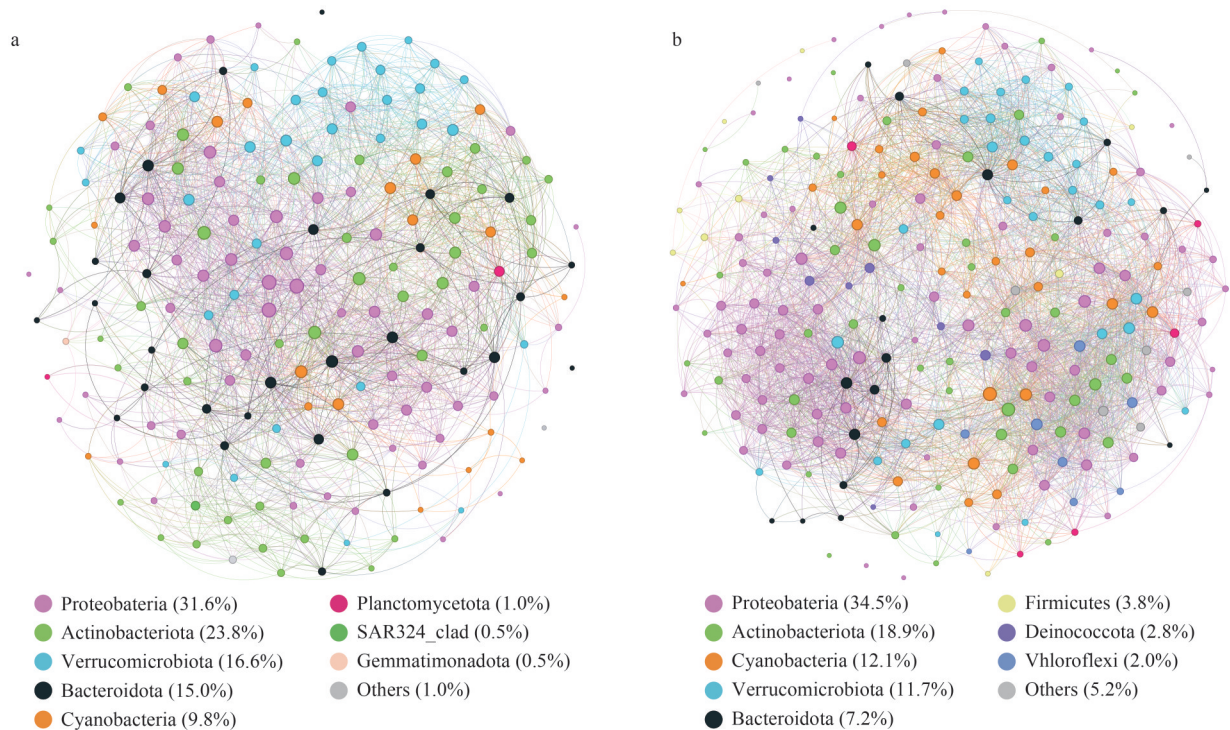


Fig.6 Co-occurrence network analysis of free-living (FL) (a) and particle-attached (PA) (b) bacterial communities

Table 2 Network properties between free-living (FL) and particle-attached (PA) bacterial communities

Type	N	E		avgCC	APL	ND	AD	Density
		Positive	Negative					
FL	193	1 847 (79.6%)	473 (20.4%)	0.534	1.51	3.19	24.04	0.125
PA	249	3 055 (82.3%)	659 (17.7%)	0.538	1.51	4.39	29.83	0.120

N: No. of nodes; E: No. of edges; avgCC: average clustering coefficient; APL: average path length; ND: network diameter; AD: average degree; density: network density.

lake WLG showed a notable enrichment of Cyanobacteria. Collectively, these results highlight that microbial co-occurrence networks vary substantially among lakes, reflecting diverse ecological adaptations to distinct environmental conditions.

4 DISCUSSION

4.1 Effect of salinity on the α -diversity of FL and PA bacterial communities

Our results revealed that salinity had distinct effects on the α -diversity of FL and PA communities in the studied lakes (Fig.1). Overall, FL communities exhibited higher diversity in both freshwater and saline environments, while diversity decreased in brackish environments, showing a U-shaped trend. First, in FL communities, we observed higher diversity in both low-salinity and high-salinity environments. This phenomenon aligns with previous studies, likely because these environments provide more suitable ecological niches (Wang et al., 2011; Ji et al., 2019). In freshwater environments, nutrient availability is abundant, and factors such as temperature and light conditions are relatively stable, providing an ideal foundation for bacterial survival and reproduction (Newton et al., 2011). In contrast, in saline environments, despite the higher salinity, bacteria have adapted to these unique conditions through long-term evolution, leading to the formation of distinct ecological niches (Zhu et al., 2025). Secondly, trophic status is also an important factor to consider. SLM has the lowest trophic status among the studied lakes (Supplementary Table S1), and its FL community exhibits lower α -diversity (Fig.1a). This phenomenon is consistent with previous studies, which indicate that at low TSI values, FL communities show lower richness and Chao 1 indices (Shen et al., 2024). Low trophic status typically limits microbial growth and reproduction, especially in nutrient-poor environments (Xie et al., 2024), where the functionality and diversity of planktonic bacterial communities may be further constrained (Shen et al., 2024). Therefore, trophic status may interact with salinity to jointly drive the U-shaped diversity trend in FL communities.

Further correlation analysis revealed a strong negative correlation between salinity and diversity indices in PA communities (Fig.1c). As the salinity gradient increased, the Shannon index of PA

communities showed a decreasing trend. The increase in salinity may alter the composition of phytoplankton communities and organic aggregates (OA) (Muylaert et al., 2009), limiting the resources available to PA bacteria. As resources become scarcer, PA community diversity declines. Moreover, increasing salinity imposes physiological stress on certain PA bacterial groups, inhibiting their growth and reproduction, and further reducing species richness (Yan et al., 2024).

It is worth noting that other environmental factors can also influence the α -diversity of communities. For FL communities, correlation analysis showed a negative correlation between Trans and DO (Fig.1c). For PA communities, factors such as the abundance of OA in the lake and their characteristics, such as composition, size, shape, and surface roughness, may affect bacterial attachment and colonization (Siebers et al., 2024). Future studies could integrate these environmental factors to further analyze the changes in diversity under the dominance of salinity.

4.2 Dominant environmental driver shaping FL and PA bacterial communities

Our results show that salinity is the first and third most important environmental factor for variations in FL and PA bacteria communities, respectively (Fig.4). The differences in community structure may be closely related to the taxonomic composition of the two bacterial types. In FL communities, Actinobacteriota dominate in freshwater lakes, and Verrucomicrobiota also have a certain proportion in both freshwater and brackish lakes. However, in the saline lake CWP, the abundance of Verrucomicrobiota is extremely low, which may be due to environmental filtering that hinders the effective colonization and persistence of species with low tolerance to salinity in saline lakes (Triadó-Margarit et al., 2019). In contrast, Cyanobacteria make up a large proportion of PA bacteria community. Interestingly, while previous studies have shown that Cyanobacteria are typically a dominant group in eutrophic freshwater environments within PA bacterial communities (Shen et al., 2022), in our study, they were more abundant in the saline lake CWP. This may be because CWP, as a middle-eutrophic lake, has a high nutrient supply that mitigates the limitations of salinity on Cyanobacteria, and the increase in nutrients helps enhance the abundance of

Cyanobacteria in the saline lake (Yue et al., 2019).

WT is one of the key environmental factors influencing bacterial community structure, with a significant impact on the PA community. Temperature fluctuations can directly affect community composition and distribution by regulating microbial metabolic activity, autotrophic productivity, and adaptability (Shen et al., 2021; Goyal et al., 2022). In SLM lake, the water temperature remains consistently low, and these cooler conditions may promote the proliferation of Proteobacteria in the PA community while inhibiting the growth of Actinobacteriota. Previous studies have confirmed this trend, as Proteobacteria, particularly Alpha- and Gamma-proteobacteria, were found to be highly abundant in the microbial communities of Antarctic ecosystems, suggesting that low-temperature conditions facilitate the growth of cold-adapted groups (Doytchinov and Dimov, 2022). The proportion of Verrucomicrobiota was also relatively high (Fig.2). This group of bacteria may be better adapted to cold environments, which is consistent with the idea that low temperatures can favor the growth of certain cold-adapted groups (Liu et al., 2024).

In this study, despite significant differences in the ecological niches of FL and PA bacterial communities, the contribution of pH to driving changes in both communities was remarkably similar. This observation aligns with patterns identified by Xiong et al. (2012) in alkaline lake sediments on the Qinghai-Xizang Plateau, forming a cross-ecosystem response: whether in water bodies (as in this study) or sediments, pH is a core environmental factor that regulates the spatial differentiation of microbial communities. Specifically, fluctuations in pH reshape community structure through three complementary effects: changes in pH directly disrupt bacterial metabolic activities (Madigan et al., 2021); extreme pH conditions destabilize the charge balance of enzyme proteins, leading to the destabilization of active site conformations of enzymes such as ATPase and dehydrogenase, forcing microorganisms to shift metabolic pathways (Baker-Austin and Dopson, 2007); abnormal H⁺ concentration gradients weaken the stability of the lipid bilayer in cell membranes, affecting the transmembrane proton motive force and hindering the active transport of nutrients (Alberts et al., 2022). These cellular-level effects regulate microbial growth conditions and competitive advantages, influencing the growth rates

and survival abilities of different bacterial groups, ultimately manifesting as changes in community composition. Notably, while spatial heterogeneity differs between aquatic and sediment environments, pH remains the dominant environmental factor driving changes in community structure, emphasizing its universal role in regulating microbial community composition.

4.3 Difference in community assembly mechanisms between FL and PA communities

The results showed that FL communities were mainly assembled via DL, while PA communities were primarily shaped by HoS (Fig.5). This difference can be explained as follows:

Firstly, geographical isolation significantly impacts bacterial community distribution. Lakes WLG, SLM, and CWP are situated in separate watersheds, and the lack of hydrological connectivity between BST and sBST limits bacterial dispersal between them. Because FL bacteria are smaller and exhibit lower carbohydrate metabolic activity than PA bacteria (Nemergut et al., 2013; Zhou and Ning, 2017; Ren et al., 2022), they are more affected by DL.

Secondly, the α -diversity of PA bacterial communities decreased with increasing salinity, indicating that high-salinity environments select for more adaptable species. This aligns with environmental selection theory (Vellend, 2016), where specific environmental factors drive community structure toward stability and determinism (Zhang et al., 2021). As PA bacteria associate with organic particles, their community structure is influenced by particle composition, which varies across lakes but has consistent elemental composition (Li et al., 2015). This reinforces the HoS effect driven by substrate composition (Ma et al., 2020).

Thirdly, species interactions play a key role in deterministic processes (Barton and Northup, 2011). The network properties of FL and PA bacterial communities reflect these differences (Yang et al., 2017). The PA bacteria co-occurrence network has a larger diameter and higher average degree (Table 2), indicating stronger interactions and higher sensitivity to environmental changes (Xia et al., 2020). The PA communities also exhibited a higher proportion of positive correlations, suggesting more synergistic relationships. These differences highlight that PA communities are more influenced by environmental

selection.

Although HoS strongly impacts PA communities (Fig.5), DL is not entirely absent, especially in open ecosystems where PA communities are also influenced by stochastic processes (Dang and Lovell, 2016). This indicates that in lake ecosystems, stochastic processes and environmental selection are interconnected rather than independent (Aguilar and Sommaruga, 2020). The study results support this view, revealing differences in the community assembly mechanisms between FL and PA communities and emphasizing the complexity of community assembly.

5 CONCLUSION

This study examined FL and PA bacterial communities across five lakes in arid northwest China, revealing clear lifestyle-dependent responses to salinity. PA diversity declined with increasing salinity, whereas FL diversity exhibited a U-shaped pattern. Both communities were shaped by salinity and other physicochemical factors. Assembly processes also diverged: PA communities were mainly structured by deterministic HoS, while FL communities were governed primarily by stochastic DL. By comparing FL and PA bacterial communities, this study reveals how bacteria with different lifestyles respond differently to salinity and its interaction with other environmental factors. These findings provide valuable data and theoretical insights for future research on bacterial communities under salinity variation, enhancing our understanding of microbial community assembly mechanisms.

6 DATA AVAILABILITY STATEMENT

Raw sequence data have been deposited in the Genome Sequence Archive of the BIG Data Center (<https://www.ngdc.cn/cn/gsa>) under accession number CRA024273.

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Electronic supplementary material

Supplementary material (Supplementary Tables S1–S3 and Figs.S1–S4) is available in the online version of this article at <https://doi.org/10.1007/s00343-026-5200-y>.