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Deciphering factors influencing planktonic and sedimentary microbial assembly processes in Midwest salinity lakes

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Abstract

The salt lake ecosystem, characterized by extreme environmental gradients, harbors microbes that uniquely adapt to high salt stress through natural selection. However, how abiotic and biotic factors shape the microbial community assembly in Yuncheng Salt Lakes remains unclear. Here, we investigated the assembly processes and meta co-occurrence patterns of microbiota in both water and sediment sampled from 14 distinct wide range of salinity lakes in the Shanxi Yuncheng area, Midwest of China, using 16S rRNA and 18S rRNA gene sequencing technology combined with multivariate ecological and statistical methods. Habitat differentiation led to the differences in microbial diversity, co-occurrence patterns, and community assembly between sedimentary and planktonic communities. Sedimentary prokaryotes were more shaped by deterministic processes than planktonic bacterial communities. Salinity was a major abiotic factor influencing the balance between stochastic and deterministic processes in both sediment and water. Enhanced microbial interactions within sediments exhibited a more prominent impact in shaping community assembly, as indicated by the stronger association between network-inferred species and prokaryotic βNTI. Moreover, we revealed significant differences in how core species concerning βNTI responded to biotic and abiotic factors. Our findings elucidated the ecological process underlying microbial communities in Yuncheng Salt Lakes and shed light on the mechanism of microorganisms to maintain community complexity and diversity in the extreme environment.

Key points

- *Sedimentary prokaryotes were more shaped by deterministic processes than planktonic prokaryotic communities.*
- *Salinity was a major factor influencing the balance between stochastic and deterministic process.*
- *Inter-domain and intra-domain symbiotic interactions within sedimentary communities represent key biotic factors influencing their community assembly.*

Keywords Salinity · Community assembly process · Meta co-occurrence network · Abiotic/biotic factors · Salinity-sensitive species

Introduction

Salt environments are characterized by the high osmotic pressure of salt-forming parent material and are extensively distributed across oceans (Liang et al. 2023), salt lakes, and salt mines (Hintz et al. 2022). Salt lakes, which constitute nearly half of the total inland lake area on Earth, support diverse and active microbial communities that are vitally involved in maintaining ecological balance and driving biogeochemical cycling under extreme conditions (Clauset 2004; Yang et al. 2016; Santini et al. 2022). With the intensification of climate change, increased evapotranspiration, and anthropogenic disturbances, growing attention has been paid to the diversity and assembly patterns of communities

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in saline environments (Otlewska et al. 2020; Haj-Amor et al. 2022; Zhao et al. 2023). The assembly of microbial communities is typically governed by two primary ecological processes: deterministic and stochastic processes (Zhou and Ning 2017). Deterministic processes involve environmental filtering and biotic interactions such as mutualism, predation, competition, and facilitation (Vanwonterghem et al. 2014; Lima-Mendez et al. 2015; Liu et al. 2015). In contrast, stochastic processes encompass random events such as birth, death, immigration speciation, and dispersal limitation (Bahram et al. 2016; Chen et al. 2019). Numerous studies have applied this framework to investigate how abiotic factors shape microbial community heterogeneity. For instance, pH, salinity, and water temperature have been shown to significantly influence microbial biogeography in saline ecosystems (Zhang et al. 2019; Liu et al. 2024a; Han et al. 2024). While some studies of species interactions among salt lakes have been considered (Becker et al. 2012; Zhang et al. 2021a), integrated studies that simultaneously consider both biotic interactions and abiotic factors in shaping microbial community assembly remain scarce. Therefore, disentangling the relative contributions of deterministic processes and stochastic processes continues to be a major challenge in microbial ecology (Ventosa et al. 2015; Shen et al. 2018).

Microbial co-occurrence networks have become a widely used tool to infer potential interspecific relationships (e.g., mutualistic and competitive interactions) between microbial communities (Faust and Raes 2012; Ma et al. 2016; Jing et al. 2024). Recent studies have increasingly used this approach to investigate microbial dynamics in salt lake ecosystems (Chen et al. 2022; Wang et al. 2023). Nevertheless, natural microbial communities exhibit complex assembly mechanisms that transcend domain boundaries, ranging from intra-domain to cross-domain interactions. The status of cross-domain relationships in shaping microbial assembly under salinity stress remains poorly understood (Menéndez-Serra et al. 2023). Prokaryotes and microeukaryotes frequently interact in saline environments (Lin et al. 2019; in ‘t Zandt et al. 2023). However, the extent to which these interactions influence community structure and ecological processes remains largely unexplored. Species that are more sensitive to environmental stressors, such as salinity, may exhibit distinct ecological characters in shaping community assembly (Agler et al. 2016). Microbes that frequently co-occur with other taxa are classified as keystone species and may be important in maintaining community structure and function (Banerjee et al. 2018; Qiao et al. 2024). In addition, microbial taxa that are highly abundant and consistently clustered within the top-ranked module in the co-occurrence network (i.e., module taxa) tend to share similar environmental preferences and engage in closer metabolic cooperation (Hartman et al. 2018). Understanding how these three categories of microbes (salinity-sensitive species, keystone species, and dominant module members) influence microbial community assembly is essential for elucidating ecological mechanisms and informing environmental management strategies.

Sediments and the overlying water column represent two fundamental environments within lake ecosystems, each characterized by unique physicochemical properties and distinct microbial communities (Battin et al. 2009). The water column is frequently subject to environmental disturbances such as surface runoff, precipitation, and evapotranspiration (Zhang et al. 2021c). In contrast, sediments evolve through long-term geological processes such as erosion and deposition, exhibiting greater stability and accumulation characteristics similar to terrestrial soils (Du et al. 2020). Thus, despite the frequent material exchange through the sediment–water interface, the two compartments exhibit substantial differences in physicochemical conditions, microbial community structure, and ecological dynamics (Xia et al. 2014; Cloutier et al. 2015; Nevers et al. 2020). However, critical knowledge gaps remain regarding the distinct microbial assemblages inhabiting each environment and the extent to which these microbes influence or contribute to cross-habitat interactions.

The Yuncheng Salt Lakes (34.91°–35.03°N, 110.78°–111.07°E), located in Shanxi Province, sit in a geographically compact area marked by many pitted saline lakes. These lakes are found within basin depressions formed by mountain faults, which have developed due to substantial tectonic plate movements in recent years. However, unlike the natural saline lakes, the Yuncheng saline lakes have been exploited for more than 2000 years and have developed into an enriched environment with a wide range of salinity levels (Li et al. 2013; Bi et al. 2022). In the present study, based on 16S RNA and 18S RNA amplicon sequencing of 42 sediment samples and 39 water samples collected in the midwestern region of Yuncheng, we investigated the microbial assembly processes to (1) the relative influence of deterministic and stochastic processes on planktonic and sedimentary communities and (2) the driving effects of abiotic and biotic factors on prokaryotic community assembly.

Materials and methods

Sample collection and physiochemical measurement

A total of 81 samples, including 42 sediment samples and 39 water samples, were collected from fourteen midwestern lakes in Yuncheng, Shanxi Province, China (Fig. S1). The sampling sites included YC2, YC3, YC4, YC5, YC14, YC15, YC16, YC18, YC19, YC20, YC21, YC22, YC23, and YC24.

Detailed geographic and sampling information are available in Table S1. At each lake, three replicate samples were randomly collected, with two sampling sites located 100 m apart. At each site, sediments were collected in triplicate from 3 depths (0–5 cm, 5–10 cm, 10–15 cm) of a 1 m^2 area using a sterile spatula, and then thoroughly homogenized to form a composite sample. Each composite was divided into two parts: approximately 5 g sediment sample was transferred to a 2-mL microcentrifuge tube, and about 100 g was collected in sealed bags for physiochemical measurements. Surface water (0–50 cm depth) was simultaneously collected in borosilicate glass containers (5 L) and subsequently aliquoted into three 1.67-L subsamples for sequential filtration through 3-μm (pre-filtration), 0.45-μm, and 0.22-μm polyether sulfone (PES) membranes (Millipore, Billerica, MA, USA). The filtrate from the final 0.22-μm membrane was collected and stored in 50-mL centrifuge tubes for subsequent physicochemical analysis. The remaining filter membranes were cryopulverized to recover particulates and then transferred to RNase/DNase-free microcentrifuge tubes. All samples stored in microcentrifuge tubes were immediately frozen at − 80 °C for DNA extraction, while the remaining water and sediment samples were preserved at − 20 °C.

The salinity and pH of water samples were measured in situ using a Hydrolab DS5 multiparameter water quality meter (Hach Company, Loveland, CO, USA). For sediment analysis, 2 g of sediment was suspended in 20 mL of distilled water in a 50-mL centrifuge tube. The suspension was thoroughly mixed and centrifuged at 5000 × g for 5 min. The mixture was well mixed and then centrifuged at 5000 g for 5 min. The supernatant was collected for subsequent physicochemical determination. Water samples were directly used in 50-mL tubes after filtration of 0.22-μm membranes. Concentrations of lithium (Li^+), sodium (Na^+), ammonium (NH_4^+), potassium (K^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), fluoride (F^-), chloride (Cl^-), nitrite (NO_2^-), nitrate (NO_3^-), Bromine (Br^-), and sulfate (SO_4^{2-}) were measured with ion chromatograph (CIC-D120, Qingdao Shenghan Chromatograph Technology Co., Ltd). Total organic carbon (TOC) was analyzed with an Elementar Vario TOC (Isoprime, Germany). Total phosphorus (TP) was determined using the antimony-molybdenum blue colorimetric method following the standard protocol (GB9837-1988).

DNA extraction and processing

Total genomic DNA was extracted from sediment samples (0.5 g) and water samples (filtered membranes) using the DNeasy PowerSoil Pro Kit (QIAGEN, Hilden, Germany). The V4 region of the 16S ribosomal RNA (rRNA) gene was amplified using 515-F (GTGCCAGCMGCCGCG GTAA) and 806-R (GGACTACHVGGGTWTCTAAT) primer pairs to characterize prokaryotic communities. For microeukaryotes, the V4 region of the 18S ribosomal RNA (rRNA) gene was amplified using 528-F (GCGGTAATT CCAGCTCCAA) and 706-R (AATCCRAGAATTTCACCT CT) primer pairs. PCR reactions for the amplified 16S rRNA gene and 18S rRNA gene were carried out with 15 μL of Phusion® High-Fidelity PCR Master Mix (New England Biolabs), 0.2 μM of forward and reverse primers, and ~ 10 ng template DNA. The thermal cycling protocol involved an initial denaturation step at 98 °C for 1 min, followed by 30 cycles of denaturation at 98 °C for 10 s, annealing at 50 °C for 30 s, and elongation at 72 °C for 30 s. PCR products were mixed in equidensity ratios and then purified with Qiagen Gel Extraction Kit (Qiagen, Germany). Finally, sequencing was conducted on an Illumina NovaSeq platform, and 250 bp paired-end reads were generated.

Raw sequence data were demultiplexed through barcode identification. The reads were trimmed and merged by FLASH (VI.2.7, http://ccb.jhu.edu/software/FLASH/). Stringent quality filtering criteria were implemented to obtain sequences that met the standard of an average quality score > 20. All chimera sequences were removed using the UCHIME algorithm (http://www.drive5.com/usearch/manual/uchime_algo.html). Deblur was used to cluster partial corresponding regions into amplicon sequence variants (ASVs). The ASVs with more than two sequences were classified as prokaryotes or microeukaryotes based on the SILVA Release 132 database. The ASVs with confidence < 0.85 were removed, and all sequences were rarefied to an even number of sequences to ensure consistency and comparability in downstream analyses.

Community assembly analysis

To determine the relative contribution of deterministic and stochastic processes to community assembly, we used Stegen et al.'s null model (Stegen et al. 2013) to calculate the phylogenetic diversity (β-nearest taxon index, βNTI) and taxonomic diversity (Bray–Curtis-based Raup-Crick, RC_{bray}) of microbial communities. |βNTI|> 2 signified the prevalence of deterministic processes, with βNTI < − 2 indicating homogeneous selection and βNTI > 2 implying heterogeneous selection. |βNTI < 2| should integrate with the value of $|RC_{bray}|$ to estimate community assembly process. $RC_{bray} < -0.95$ and $RC_{bray} > 0.95$ indicated homogenous dispersal and dispersal limitation, respectively. $|RC_{bray}| < 0.95$ represented undominated processes including weak selection, weak dispersal, diversification, and drift processes.

Construction of co-occurrence networks

Co-occurrence networks of planktonic and sedimentary prokaryotes and microeukaryotes were constructed to characterize the interconnectedness and potential associations among microbial taxa. Species present in at least 25% of all prokaryotic samples and 12.5% of all microeukaryotic samples were selected for network construction. We calculated Spearman rank correlations between species and visualized the positive and significant correlations ($r > 0.7$ and $p < 0.001$) using the Fruchterman-Reingold algorithm in the "igraph" R package, which has been extensively used in the literature and is comparable across studies (Delgado-Baquerizo et al. 2020). Several fundamental topological network properties were estimated, including node numbers, edge numbers, network degree, and modularity. Network modularity indicates the extent to which a network can be partitioned into distinct modules, thereby revealing the underlying patterns of interconnections among nodes (Clauset 2004). Microbial taxa that frequently co-occurred with others were considered as keystone species (Layeghifard et al. 2017). Highly abundant microbes from the top three modules, ssOTUs, and keystone species in the meta-network were constructed random forest model to identify how these species contribute to overall βNTI. Finally, we identified 243 and 102 core species in the sedimentary and planktonic communities, respectively, which showed significant correlations with pairwise βNTI in meta co-occurrence networks. Random forest analysis was performed using the "rfPermute" R package to assess how factors of core species contributed to the overall planktonic community assembly process.

Identification of salinity-sensitive ASVs

Since the Yuncheng Salt Lakes were characterized by varying salinity gradients, we calculated the point-biserial correlation coefficient for species that showed a positive association with low-, medium-, and high-salinity levels using the "indicspecies" R package. In addition, we assessed differential ASVs abundance within microbial communities in sediment and water environments using the likelihood ratio test (LRT) in the "edgeR" R package. ASVs, which exhibited significantly varied abundance across different salinity levels with a false discovery rate (FDR) corrected *p*-values < 0.05, were considered responsive to salinity. Then, we defined ASVs confirmed by both indicator species analysis and LRT as salinity-sensitive ASVs (ssOTUs) (Hartman et al. 2018).

Microbial source tracker

Source tracker is a widely-used method for identifying the origins of communities and populations (Huang et al. 2019). Fast expectation–maximization microbial source tracking (FEAST) analysis with an expectation–maximization algorithm helps distinguish different source types while reporting the proportion contributed by unknown sources (Shenhav et al. 2019). This study investigated the bidirectional cross-medium interactions between sediment and water by quantifying species-specific contributions to habitat heterogeneity.

Statistical analysis

Geographic variables were determined using the principal coordinates of neighbor matrices (PCNM) analysis, which can deconvolute total spatial variation into a discrete set of explanatory spatial scales (Shi et al. 2018). Specifically, we performed Mantel tests (permutations = 9999) to evaluate correlations between microbial community dissimilarity matrix (Bray–Curtis distance) and abiotic factors (Euclidean Matrix). To determine the relative importance of geographic and environmental variables, we conducted multiple regression analysis using the multiple regression on matrices (MRM) approach. We used variable clustering of assessing redundant variables before MRM in the "Hmisc" R package to delineate huge collinearity influence and removed the variables with a Spearman's correlation coefficient > 0.7. Retained variables were then standardized using the "ecodist" R package. We used the MRM function with 9999 permutations to obtain the relationship between retained variables and βNTI. Canonical correspondence analysis (CCA) was also applied to estimate the influence of environmental factors on microbial communities (Dixon 2003). Distance-decay relationship (DDR) analyses were performed by first quantifying the compositional similarity of microeukaryotes (1-Bray–Curtis dissimilarity) and then calculating the distance between pairs of samples using the "geosphere" R package. PICRUSt2 was adopted to predict the functional potential of the microbial community based on the relative abundance of marker gene sequences in samples (Douglas et al. 2020).

Structural equation modeling (SEM) analysis was employed to measure the direct or indirect effect of selected abiotic and biotic factors on microbial community construction using the "piecewiseSEM" R package. We assessed the goodness-of-fit of the model using Shipley's test of directed separation ensuring that no missing relationships among unconnected variables, as supported by a non-significant Fisher's C value ($p > 0.05$). Subsequently, we interpreted the path coefficients and *p*-values of the model, which described the strength and direction of relationships among different variables.

Results

Microbial source tracking, diversity, and composition in water and sediment

The FEAST source tracker analysis showed weak cross-interaction between water and sediments. Approximately

10% of the sediment microbial community originated from the water column, and a comparable proportion of the water community was derived from the sediment. A significant proportion of the community in both environments was attributed to unknown sources (Fig. 1a).

A total of 19,239 ASVs of 16S rRNA sequences spanned across 8 archaea phyla and 65 bacteria phyla. Sedimentary prokaryotes harbored significantly higher diverse and extensive communities than planktonic prokaryotes, as evidenced by their higher Shannon and Simpson indexes (Fig. S2). The number of archaeal ASVs varied widely across sedimentary and planktonic samples. Specifically, archaea occupied 0.02–12.96% of the ASVs in sediment samples, while the proportion of archaeal ASVs ranged from 0.09 to 80.10% in water samples, dominated by *Euryarchaeota*, *Nanoarchaeota*, and *Thaumarchaeota* (Fig. S3). A total of 11 dominant bacterial phyla (relative abundance of more than 1% in at least one sample) accounted for 74.81–99.76% of the total ASVs. Overall, *Gammaproteobacteria*, *Euryarchaeota*, *Tenericutes*, and *Verrucomicrobia* prevailed in planktonic communities, whereas the relative abundance of *Firmicutes*, *Deltaproteobacteria*, *Chloroflexi*, *Acidobacteria*, and *Gemmatimonadetes* was more than twice as much in sedimentary communities than in planktonic communities (Fig. 1).

Assembly mechanisms of sedimentary and planktonic microbial communities

For an effective determination of the assembly processes of prokaryotic communities, null model-based analyses were employed to explore the relative contribution of deterministic and stochastic processes to planktonic and sedimentary communities. The observed microbial β-diversity in water and sediments was significantly distinct from the null expectation (PERMDISP $p < 0.001$, Table 1). The large proportion of determinism in sediment communities (53.31%) suggested that deterministic processes exerted greater influence on sedimentary communities than on planktonic communities. Stochastic processes exhibited a greater contribution to planktonic communities (62.35%), among which dispersal limitation occupied the largest proportion in the planktonic community assembly mechanism (Fig. 2). Homogeneous selection accounted for a similar proportion of community assembly processes in both water and sediment environments (water, 19.84%; sediment, 18.35%). Meanwhile, dispersal limitation was identified as the dominant stochastic process shaping microbial communities in both habitats.

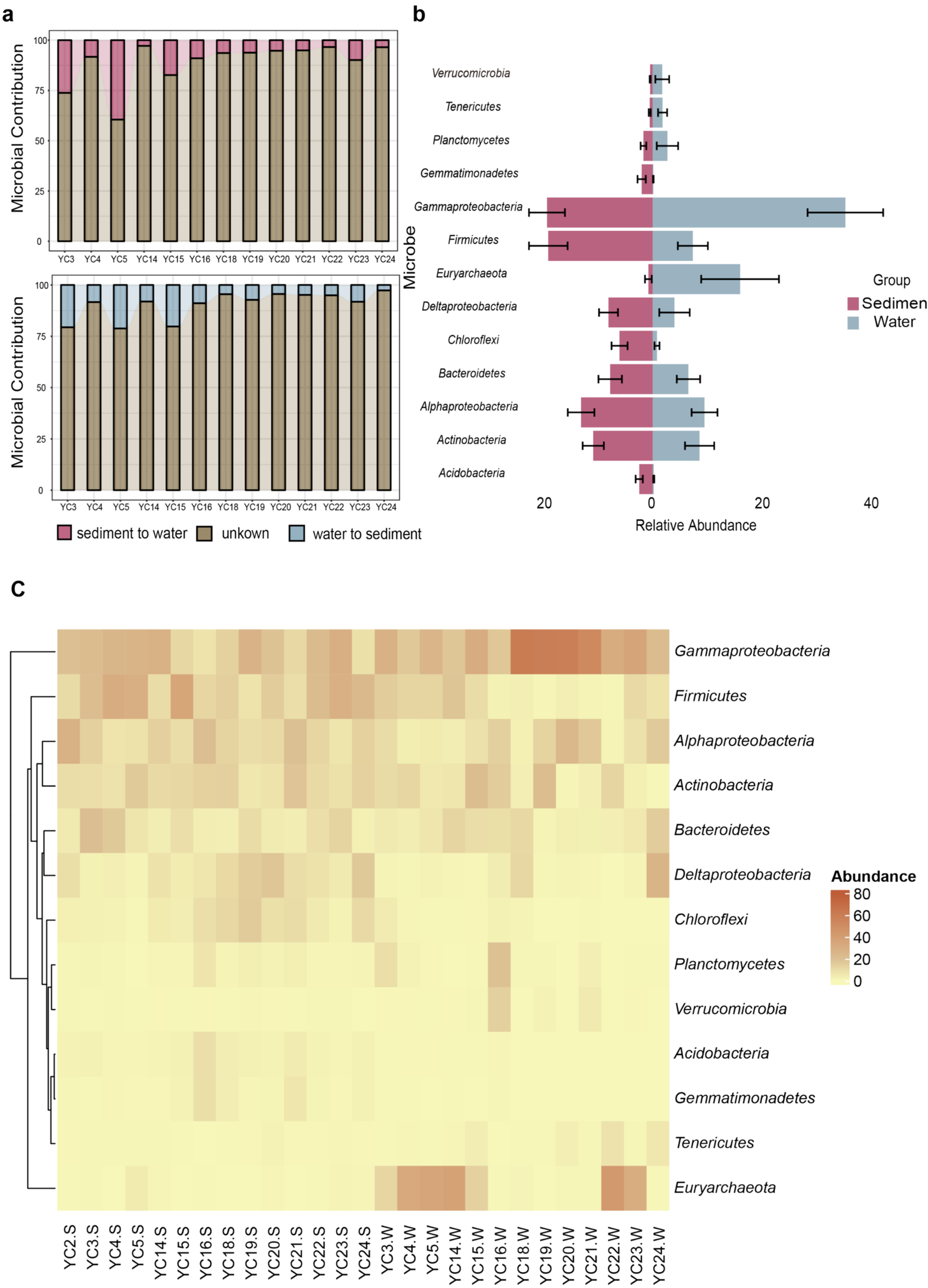
Abiotic and biotic drivers of microbial community assembly

We further analyzed the ecological factors that drove the different community assembly processes in water and sediment environments. According to multiple covariance examination and forward selection, the environmental factors and geographical factors of pH, salinity, NH_4^+, Mg^{2+}, Ca^{2+}, SO_4^{2-}, PCNM1, PCNM3, PCNM6 in sediment and salinity, Mg^{2+}, and PCNM6 in water showed significant and high correlation with community heterogeneity on the two explanatory axes of CCA (Fig. 3a, Table S2). More factors of physiochemical parameters showed a significant correlation with community variation in sedimentary communities than in planktonic communities. βNTI was also correlated with geographic and environmental factors through MRM analysis (Table S3). In sediments, βNTI showed a significantly stronger correlation with salinity than with geographical distance, as evidenced by the correlation values for various ions in both matrices which were higher than those associated with geographical factors (Fig. S5). Both sediment and water βNTI values were remarkably correlated with salinity changes (Δ-salinity, $p < 0.001$; Fig. S5). In sediments, βNTI shifted from values greater than the null expectation to values lower than expected. Conversely, the water environment exhibited the opposite trend, with βNTI values shifting from lower-than-expected to a trend that had higher-than-expected turnover (Fig. 3b).

Interactions between microeukaryotes and prokaryotes are common across various habitats and may play a great part in ecological processes. Although no significant differences were observed in microeukaryotic alpha diversity between sediment and water (Fig. S2), the prokaryotic assembly process still showed correlations with the microeukaryotic community (Fig. 4).

Co-occurrence network of microeukaryotes and prokaryotes

Based on the influence of salinity on community assembly mechanisms, we identified 166 and 57 prokaryotic ssOTUs in sediment and water, respectively, using likelihood ratio tests (edgeR) and correlation analysis (indicator species). Interestingly, a larger proportion of microeukaryotic OTUs of sediment and water means microeukaryotes were more sensitive to prokaryotes (Fig. S6). To further evaluate the co-occurrence patterns of these ssOTUs, we constructed prokaryote-microeukaryote co-occurrence networks for both sediment and water environments. Compared to the water environment, the sedimentary network exhibited a more compact structure and a greater number of interactions, as evidenced by a significantly higher number of sediment-specific nodes (Fig. S7). ssOTUs were well represented in the co-occurrence networks, with over 80% of them clustered within the top three network modules in both habitats, especially sediment Module 3, occupied 22.41% of ssOTUs, which suggested that salinity was of considerable importance in shaping sedimentary meta co-occurrence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Alphaproteobacteria
Actinobacteria
Bacteroidetes
Deltaproteobacteria
Chloroflexi
Planctomycetes
Verrucomicrobia
Acidobacteria
Gemmatimonadetes
Tenericutes
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◂**Fig. 1** Prokaryotic communities in water and sediment. **a** FEAST source tracker analysis showing the contribution of water to sediment and vice versa **b** Relative abundance of dominant phyla in water and sediment samples **c** Heatmaps illstrating major microbial compositions across samples

network (Fig. 5, Fig. S8). Moreover, network-level node analysis revealed that non-salinity-sensitive species exhibited a greater potential for cross-domain interactions than ssOTUs in sediment, with stronger cross-domain interactions observed in the sediment environment (24.5% vs. 1.5%). Furthermore, we explored the relationship between species in co-occurrence networks and prokaryotic community assembly processes. Mantel tests revealed that both salinity-sensitive and non-salinity-sensitive species significantly influenced community assembly (Table S4). Notably, non-salinity-sensitive species showed the strongest correlation with prokaryotic βNTI (Mantel's $r = 0.5354$, $p < 0.001$, permutations = 999). In contrast, within the water community, only non-salinity-sensitive species in the co-occurrence network exhibited a remarkable association with community assembly (Mantel's $r = 0.4692$, $p < 0.001$, permutations = 999) (Agler et al. 2016; Banerjee et al. 2016).

Given the significant correlation of network-associated species for βNTI, we combined ssOTUs, keystone species, and species from the top three ranked network modules and applied a random forest model to identify those with the most significant influence on βNTI. Based on the criterion of IncMSE% > 0, we identified 243 species in sediment and 102 species in water (Fig. 6a). Notably, the maximum IncMSE% reached 369% in sediment and 124% in water. Furthermore, species from the top three network modules exhibited a greater explanation power for community assembly in sediment compared to water (74% vs. 60%) (Table S5). To identify the key drivers influencing the abundance of these species, we constructed a random forest model incorporating four abiotic variables (pH, salinity, PCNM, and all_env_PC1) along with four biotic network properties ("all_nodes," "all_edges," "all_transitivity," and "all_average_density") based on prior multivariate regression analysis. Our results indicated that in both sediment and water environments, geographic factors and salinity emerged as the most significant abiotic determinants of microbial abundance patterns. Moreover, abiotic factors had a significantly stronger influence on prokaryotic species compared to microeukaryotic species (Fig. 6b). In contrast, in the sediment environment, microeukaryotic species were more strongly influenced by biotic factors than prokaryotes.

Structural equation modeling

Salinity exhibited a negative effect on the number of microeukaryotic and prokaryotic nodes in sediment, but no noticeable effect was observed in water. βNTI showed a stronger response to spatial variables in water supporting the predominance of stochastic processes in aquatic environments. The SEM models exhibited satisfactory fits to the data, with goodness-of-fit statistics as follows: sediment ($p = 0.418$, Fisher's $C = 1.744$, AIC = 29.744) and water ($p = 0.769$, Fisher's $C = 0.526$, AIC = 28.256). Although the SEM model showed a better statistical fit for the water environment, it should be noted that the dimensionality reduction of βNTI may have led to an overestimation of model performance in this case.

Discussion

The mechanisms underlying ecological community assembly have received increasing attention in recent years (Dini-Andreote et al. 2015; Zhang et al. 2019; Ning et al. 2019). A growing number of researches have demonstrated that both abiotic and biotic factors act as key drivers of microbial community assembly and subsequently influence microbial diversity (He et al. 2021; Goberna and Verdú 2022; Li et al. 2022). Here, based on amplicon sequencing approaches in Yuncheng Salt Lakes across a broad salinity gradient, we systematically investigated the microbial assembly mechanisms and meta co-occurrence pattern between microeukaryotes and prokaryotes in Yuncheng Salt Lakes. Our results demonstrated the following: (i) limited contribution of community's interaction between water and sediment. (ii) Deterministic processes predominated in the sedimentary community, while stochastic processes exerted a leading effect on the planktonic community. (iii) Salinity was the major abiotic factor in determining microbial deterministic assembly in both water and sediment. (iv) Inter-domain and intra-domain interaction was an important biotic factor shaping sedimentary community assembly mechanism.

Material exchange across the sediment–water interface displayed a limited contribution in facilitating microbial species dispersal between these habitats. FEAST analysis confirmed that only a small proportion of species in the water originated from the sediment and vice versa, supporting the hypothesis that habitat heterogeneity, rather than cross-habitat dispersal, was the primary driver of distinct microbial community assembly patterns in these environments (Allen et al. 2020; Lv et al. 2022). Water environments were characterized by higher fluidity and a greater degree of mineral diffusion, while sedimentary environments were relatively stable with minerals closely bound (Ward et al. 2020). Notably, sampling sites with smaller salinity differences between water and sediment such as YC2 and YC5 exhibited a relatively higher proportion of shared species, accounting for approximately 25% of water–sediment exchange on average (Fig. 1a). Additionally, the dominant phyla in both water and

Table 1 Identification of ecological mechanisms shaping microbial communities in water and sediments via taxonomic and phylogenetic perspectives. Taxonomic community assembly was calculated by the deviation of the observed differences of communities from random expectation by permutational analysis of multivariate dispersion (PERMDISP), represented by stochasticity ratio. Phylogenetic community assembly was calculated using βNTI and RC_{bray} ratio values based on weighted Bray–Curtis distance. Major ecological processes are presented

	Median average distance	Chi-squared	*p*	Stochastic ratio	βNTI	RC_{bray}
Water	0.644	29.39	0.003447	62.35%	– 0.1473	0.8996
Sediment	0.6476	22.81	0.04338	46.69%	1.4384	0.8651

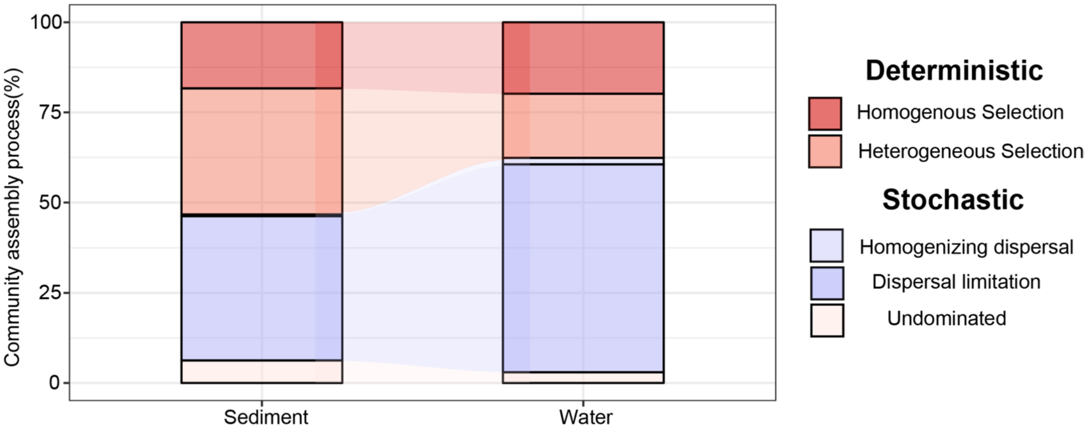

Fig. 2 Relative influences of deterministic and stochastic processes on Yuncheng Salinity Lake community assembly in water and sediments

sediment were significantly correlated with environmental factors such as pH, ion concentrations, and cation levels (Fig. S4). These results suggested that environmental conditions were an important factor in both constraining microbial colonization from water to sediment and facilitating bidirectional microbial migration between the two habitats.

In this study, planktonic and sedimentary microbial communities were found to exhibit distinct structural patterns. Although abiotic factors are known to influence microbial diversity and community composition in saline environments, their functions of shaping microbial assembly processes within salt lakes remain insufficiently understood. Heterogenous selection was the main ecological deterministic process in both water and sediment. The significant correlation between salinity levels and βNTI indicated that salinity was the primary abiotic factor mediating the deterministic assembly in sediment and water. In addition to salinity, βNTI was significantly correlated with geographic distance (Fig. S5), indicating that dispersal limitation, a key stochastic process, also played a critical role in shaping planktonic microbial communities (Chave and Leigh 2002). Based on these findings, we inferred the community assembly mechanisms in both water and sediment of Yuncheng Salt Lakes by integrating the effects of salinity and geographic structure. With increasing salinity, sedimentary and planktonic communities exhibited contrasting shifts in their assembly processes: sediments shifted from deterministic to stochastic processes, whereas water communities showed the opposite trend (Fig. 2B). Such phenomenon may be due to strong selection for non-salt-tolerant species in low-salinity conditions, where resources were abundant and competition for ecological niches promoted both abundant and rare taxa (Mo et al. 2021; Wu et al. 2024). However, the upper limit of salinity tolerance of the sedimentary and planktonic microorganisms varied. In planktonic communities, a balance between environmental selection and geographic isolation appeared to be maintained under low-salinity conditions (0–4%). Under extreme high-salinity conditions (8–10.5%), microorganisms could allocate significant energy to regulate osmotic pressure and synthesize compatible solutes to survive in these harsh environments (Oren 1999; Ionescu et al. 2024). For instance, members of the phylum *Euryarchaeota* dominate planktonic communities at the highest salinity levels, correlating with decreased microbial diversity and a shift towards more deterministic community assembly processes (Wagg et al. 2019).

Microorganisms in natural environments display a high diversity and engage in various types of interactions between prokaryotes and microeukaryotes, including mutualism, competition, and predation (Carpenter and

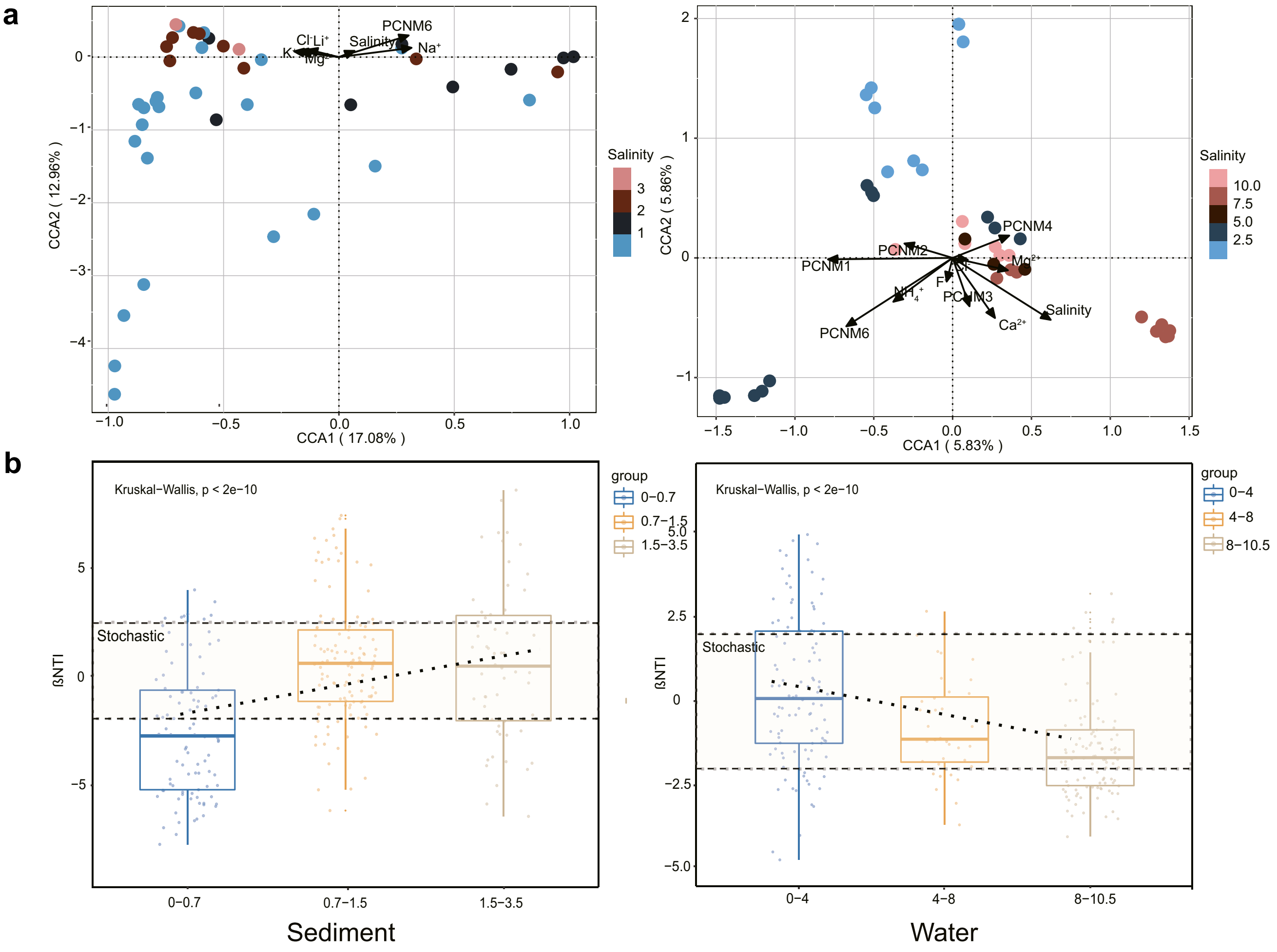

Fig. 3 Plots of factors influencing community structure. **a** Major environmental variables in shaping water and sediment community based on Bray–Curtis dissimilarity identified by CCA. **b** Patterns of βNTI across different categories in salinity for water and sediment sub-community. Boxplots within the panels showed the variation in βNTI across low, medium, and high categories of water and sediment

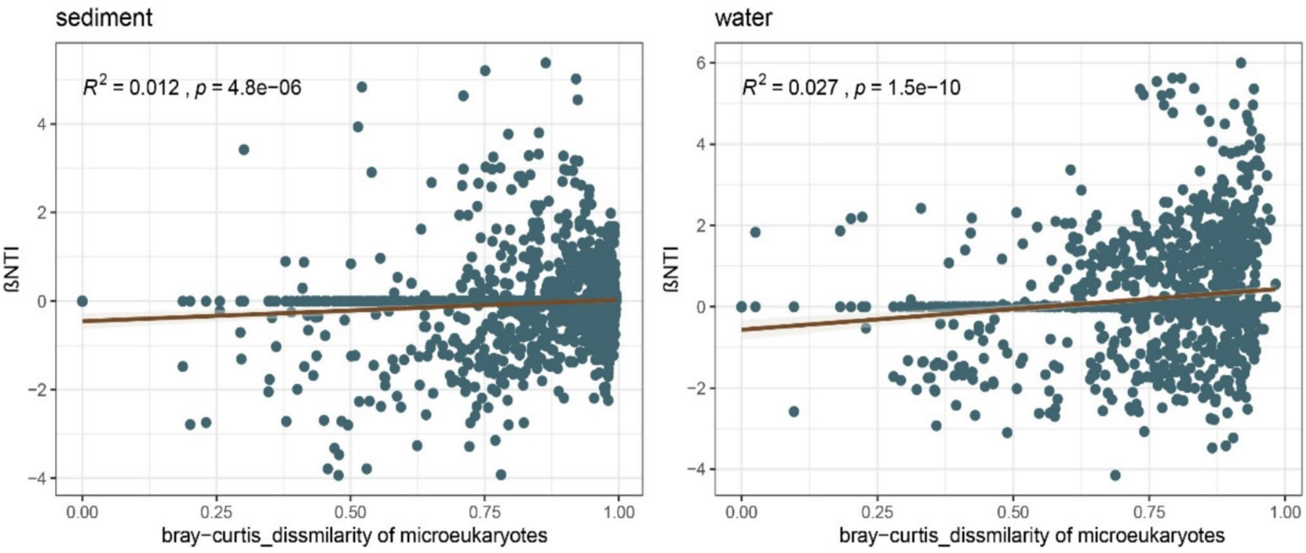

Fig. 4 Patterns of βNTI across different media in the microeukaryotes community for planktonic and sedimentary communities

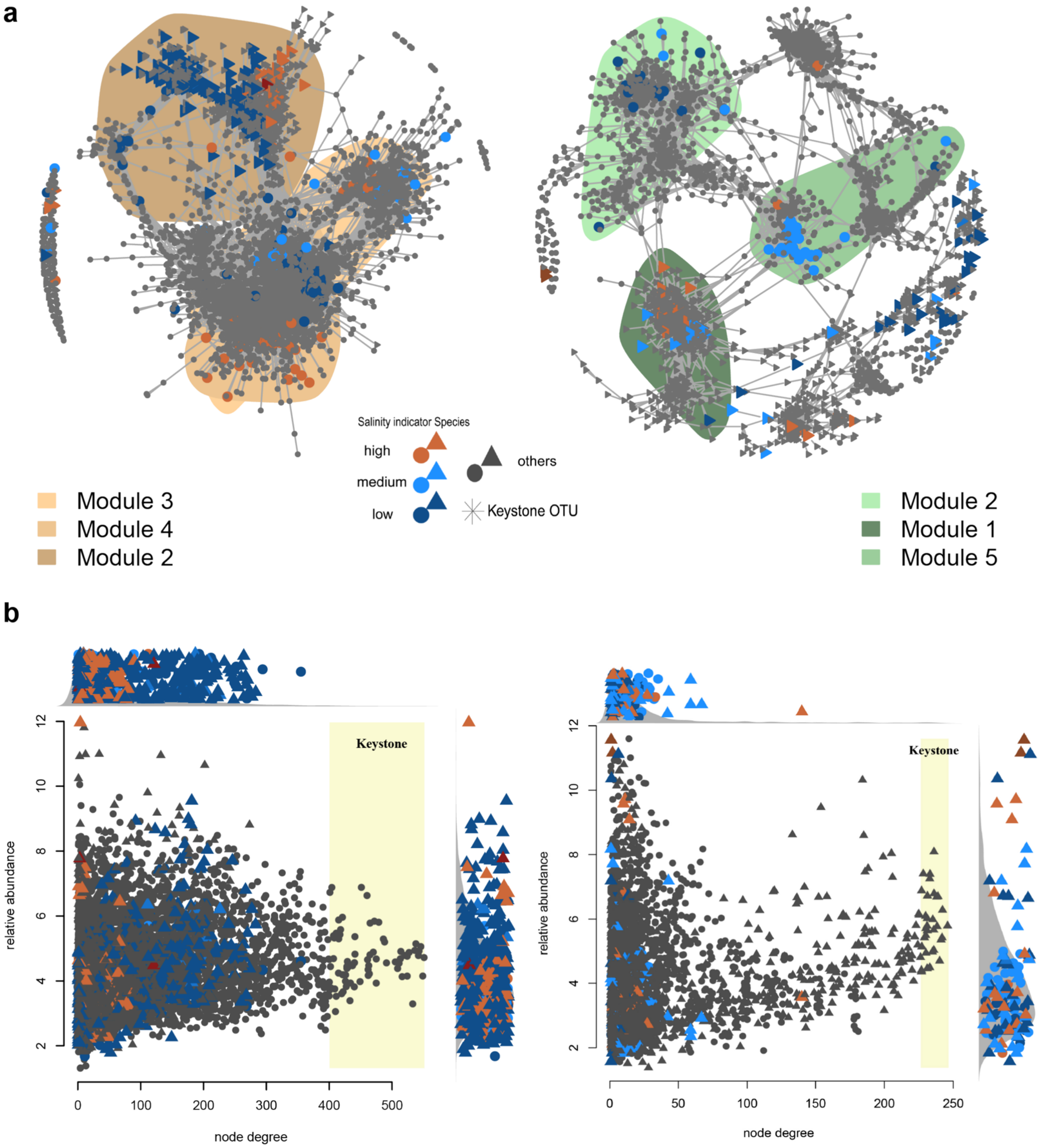

Fig. 5 Co-occurrence patterns of OTUs in water and sediment. **a** Co-occurrence networks visualizing significant correlations ($\rho > 0.7$, $p < 0.001$) indicated gray lines between prokaryotes and microeukaryotes in water and soil communities. Circles indicate prokaryotes, triangles indicate microeukaryotes, and keystone species are represented with asterisks. Species are colored by their association with different salinity responsive; gray ASVs are insensitive to salinity. The shaded area represents the top three network modules **b** Degree of co-occurrence and abundance of ssOTUs. Relative abundance (as counts per million, CPM) of all ASVs from the water and sediment microbiome co-occurrence networks was plotted as a function of their degree of co-occurrence. Circles and triangles refer to prokaryotes and microeukaryotes, respectively. ASVs were colored by their association with the different environmental media (water and sediment) and keystone species (top 1% degree of co-occurrence) have yellow backgrounds. Side panels recapitulate the distributions of co-occurrence degrees and abundance for the ssOTUs (shapes colored by association with salinity)

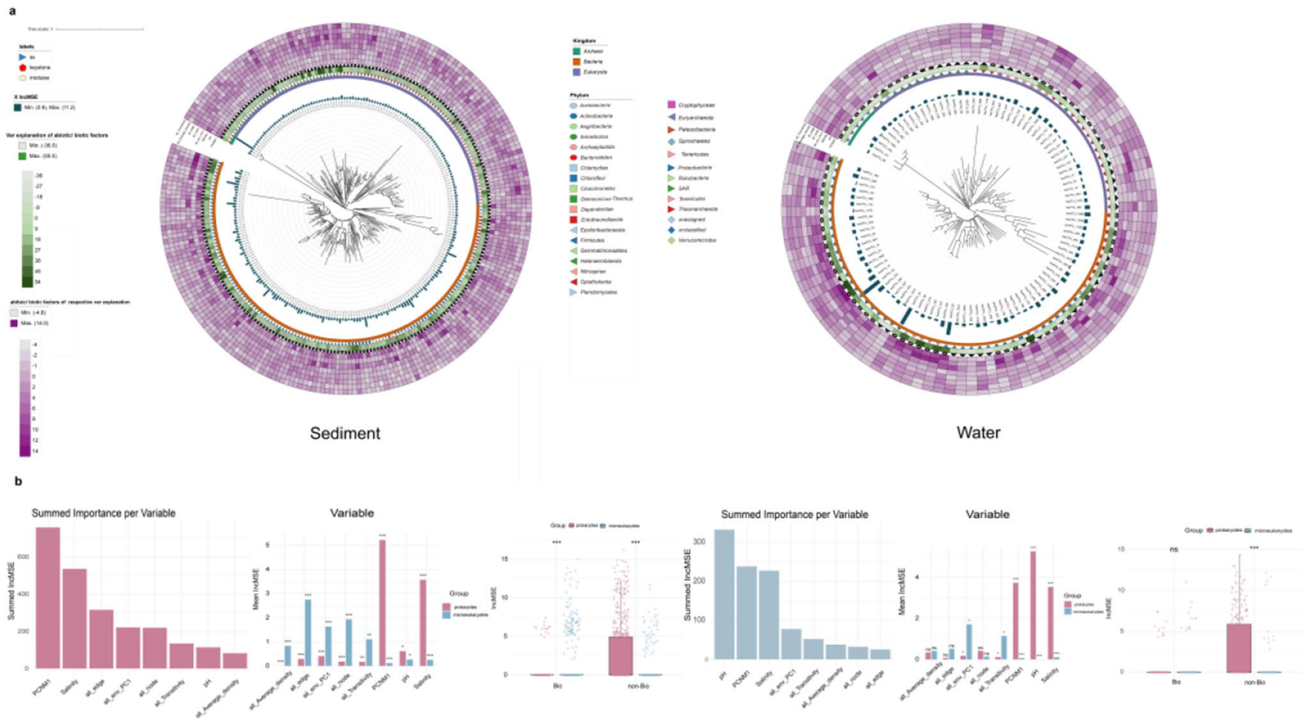

Fig. 6 Phylogenetic distribution for the random forest (IncMSE% > 0) analysis with βNTI and relative abundance of ASVs in prokaryotes-microeukaryotes meta-network. **a** The phylogenetic tree was constructed using the maximum likelihood method. The heatmap with the green color shows the relative importance of the relative abundance of selected dominant taxa (module, keystone, ssOTUs) explaining the abiotic and biotic factors. The heatmap with purple color shows the relative importance of abiotic and biotic factors in explaining the select dominant taxa, estimated via multiple regression modeling and variance decompositions analysis. The barplot with a dark green color shows each selected dominant taxa explanation towards βNTI **b** The bar chart illustrates the relative importance of key variables and highlights the differences in influencing factors between prokaryotes and microeukaryotes. The boxplot compared the effects of biotic and abiotic factors on microbial communities

Foster 2003; Carini et al. 2014; Manirakiza et al. 2022). Our study revealed a significant correlation between microeukaryotic diversity and prokaryotic community assembly (Fig. 3). However, diversity alone was not a direct indicator of microbial interactions (Hou et al. 2024). Through examining interspecific associations across and within domains, network analysis provided insights into the complexity of microbial communities that transcend conventional diversity metrics and taxonomic profiling (Hou et al. 2024). Our findings indicated that interactions between microeukaryotes and prokaryotes were more than ten times greater than interdomain interactions among microeukaryotes, accounting for one-sixth of prokaryote-prokaryote links (Table 2). Furthermore, all identified keystone species in the water were microeukaryotes, which may play a more significant role than prokaryotes in sustaining planktonic lake ecosystems and their multifunctionality (Adl et al. 2019). For instance, *Bacillariophyta*, a highly abundant diatom phylum within the *SAR* supergroup, demonstrated the capacity for carbon fixation even under hypersaline conditions (Liu et al. 2024b). This finding underscored the ecological importance of cross-domain interactions in salt lake environments.

Despite recent advances in microbial network analysis, limited studies have elucidated how microbial interactions influenced community assembly processes. Most investigations have focused on assessing correlations between network topological features and assembly mechanisms (Lin et al. 2023; Wang et al. 2023), or on linking species within modular clusters to specific environmental factors (Zhang et al. 2021c). However, a more rigorous identification of environmentally sensitive species, combined with an analysis of their co-occurrence patterns, may offer deeper insights into the mechanisms underlying prokaryotic community assembly. In our study, we combined the edgeR and indicator species algorithms to identify species sensitive to changes in salinity. We found that salinity-sensitive species comprised up to 22.4% of the total abundance in the M2 module of the sediment. The significant correlation between βNTI and salinity-sensitive prokaryotes, microeukaryotes, and non-salinity-sensitive species in sediment microbial communities suggested that salinity directly influenced the assembly processes of prokaryotes, as well as symbiotic relationships, both within and across domains, that shape microbial community structure (Song et al. 2022). Combining the contrast

Table 2 Properties of water and sediment meta co-occurrence networks

Community	OTUs[a]		Connections[b]			Keystone[c]		ssOTUs[d]	
	Prokaryotes	Microeukaryotes	Prokaryotes-prokaryotes	Prokaryotes-microeukaryotes	Microeukaryotes-microeukaryotes	Prokaryotes	Microeukaryotes	Prokaryotes	Microeukaryotes
Sediment	5228	2039	443,052	67,117	3660	72	0	166 (0.76%)	382 (21.49%)
Water	1539	1335	231,134	41,077	898	0	28	57 (0.25%)	83 (39.14%)

[a] The number of network nodes

[b] The number *r* of edges

[c] The number of keystone OTUs

[d] The number of ssOTUs and its relative abundance versus all microbiota

microbial assembly mechanism revealed by SEM, salinity exerted significant effects on both prokaryotic and microeukaryotic co-occurrence networks and indirectly influenced βNTI through enhanced cross-domain associations in sediments, suggesting that deterministic processes, particularly those mediated by interdomain cooperation and environmental filtering, played a central role in shaping prokaryotic community assembly (Fig. S9).

By tracking the abundance variation of ssOTUs along the salinity gradient, we observed a general decrease in prokaryotes abundance with increasing salinity, while microeukaryotic communities, specifically *Opisthokonta* and *Archaeplastida*, showed an increasing abundance with ascending salinity levels (Fig. S10). This observation suggests that microeukaryotes may exhibit greater salinity tolerance within microbial communities and supports that prokaryotic community assembly is primarily driven by environmental selection, consistent with the size-dispersal hypothesis (Zhang et al. 2021b). Furthermore, the phyla associated with prokaryotic keystone taxa in sediments (e.g., *Firmicutes*, *Bacteroidetes*, *Actinobacteria*, and *Euryarchaeota*) and those associated with microeukaryotic keystone taxa in water both exhibited increasing abundance trends with rising salinity, indicating that the salinity tolerance of keystone species contributes significantly to their ecological roles within microbial networks (Fig. S11).

According to the pivotal engagement of core species in shaping the microbial assembly process (Hu et al. 2017; Yan et al. 2021; Sun et al. 2023), ssOTUs, keystone species, and module taxa influencing βNTI were selected as core species. We found that core microeukaryotes contributed substantially less to prokaryotic community assembly than core prokaryotes. In both sediment and water, the core prokaryotic community was more strongly influenced by environmental factors, whereas core microeukaryotes were more susceptible to network-related parameters (Fig. 6b), filling the gaps between how factors affect core species abundance and further influence the community assembly process. In general, core microeukaryotes possess more complex cellular structures, and some occupy higher trophic levels in food webs than bacteria, which results in varying responses to other trophic levels (Euringer and Lueders 2008). However, our study did not quantify the absolute abundance of prokaryotes and microeukaryotes to accurately reflect the differences in microorganisms at each salinity level, which necessitates further in-depth investigation in the future.

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Author contribution J.C.H. designed this research, finished data analysis, and wrote this manuscript. T.Y.C. revised this manuscript. C.A.L. supported expert guidance in data analysis for this research. L.W. contributed ideas and revised the manuscript. J.C.H., C.A.L., L.W., and W.Q.Z participated and supported sampling for this work together. K.Y. contributed conceptualization, funding acquisition, project administration, resources, supervision, review, and editing.

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Data availability All raw sequence data have been submitted to the NCBI Sequence Read Archive (SRA) database (accession number: PRJNA1111396). The authors declare that all other data supporting the findings of this study are available within the article and its supplementary information files or from the corresponding author on request.

Declarations

Ethics approval and consent to participate This research does not involve human participants or animal subjects and therefore does not require ethics committee approval.

Competing interests The authors declare no competing interests.

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