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**From diversity patterns to assembly processes: plankton
community assembly along a natural salinity gradient in
northern plateau lakes of China**

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Abstract

Global change and anthropogenic activities have accelerated lake salinization in arid and semi-arid regions of northern China, while plankton communities and ecosystem functions are highly sensitive to salinity variation. However, how plankton diversity patterns, community assembly, and functional regulation respond to continuous salinity gradients remains poorly understood. Here, four lakes on the Inner Mongolia Plateau were selected to represent a natural gradient from freshwater to brackish and low-salt conditions. Based on field surveys, taxonomic identification, and integrated analyses including ANOVA, NMDS, SEM, and DNCI, we investigated the effects of salinity on plankton community structure, multidimensional diversity, assembly processes, and ecosystem functioning. Salinity strongly shaped plankton community composition and caused a significant linear decline in taxonomic alpha diversity and functional richness. In contrast, beta diversity showed nonlinear patterns associated with changes in turnover and nestedness contributions. SEM indicated that species richness promoted functional traits, whereas biodiversity and ecosystem functioning were partially decoupled under salinity stress. Community assembly was dominated by deterministic processes across the gradient (DNCI < -2), with stronger environmental filtering in freshwater and low-salt lakes and greater stochasticity in brackish waters. Phytoplankton exhibited stronger declines in taxonomic α -diversity under salinity stress, while zooplankton assembly processes were more sensitive to intermediate brackish conditions. These findings enhance understanding of salinity-driven ecological processes and provide insights for conserving salinizing inland lake ecosystems.

Keywords: Salinity gradient; plankton; community assembly; biodiversity; ecosystem functioning; Inner Mongolia Plateau

Introduction

Global climate change and intensified human activities are driving widespread degradation of inland aquatic ecosystems, among which lake salinization has emerged as a dominant threat in arid and semi-arid regions (Cunillera-Montcusí et al., 2022; Williams, 1999). The Inner Mongolia Plateau, situated in the transitional belt between arid and semi-arid northern China, is characterized by evaporation rates of 1200–3000 mm and annual precipitation of only 50–450 mm (Geng et al., 2024; Yang Zhang, Lan, Mao, Zeng, & Chen, 2018). Such extreme hydrological conditions have produced numerous closed and semi-closed lakes, making this area one of the most lake-dense regions in China. However, these plateau lakes harbor plankton communities that play a central role in material cycling and energy flow. As primary producers, phytoplankton form the base of lake food webs, while zooplankton, as key primary consumers, mediate energy transfer to higher trophic levels; together, they maintain the structural and functional integrity of lake ecosystems (Dehingia, Pankaj, Kakati, Gogoi, & Chakraborty, 2026; Kiørboe, 2011). Because plankton community composition is tightly coupled to water chemistry and responds rapidly to environmental change, plankton are widely used as indicators of lake ecosystem health (Carvalho et al., 2013). Understanding how environmental factors shape plankton diversity and ecological functions is therefore fundamental for predicting the responses of salinizing lakes to ongoing global change (Ma, Yin, Liu, & Song, 2024; Wang et al., 2026).

Among the multiple environmental stressors acting on these lakes, salinity stands out as a master filtering factor (Cunillera-Montcusí et al., 2022; Stenger-Kovács et al., 2023). It imposes direct osmotic stress that eliminates intolerant species and restructures interspecific interactions through cascading effects on resources and predation. Prior research has shown that overall species richness declines with rising salinity, but the response patterns of phytoplankton and zooplankton differ substantially: phytoplankton, with their small cell size and high surface-to-volume ratio, are more sensitive to osmotic fluctuations,

70 whereas zooplankton possess relatively robust osmoregulatory systems and can better withstand
71 moderate salt stress (Cunillera-Montcusí et al., 2022; Dildar, Cui, Ikhwanuddin, & Ma, 2025; Stenger-
72 Kovács et al., 2023). However, most existing studies have focused on taxonomic alpha diversity at a
73 limited number of salinity levels, offering only a static and fragmented perspective. How phytoplankton
74 and zooplankton community composition, taxonomic and functional diversity, and beta diversity change
75 across a continuous freshwater–brackish–low-salt gradient remains poorly resolved (Jeppesen et al.,
76 2007; Ptacnik et al., 2008; Telesh & Khlebovich, 2010). Clarifying these dynamic patterns is the first
77 essential step for understanding the plankton communities in increasingly salinized plateau lakes
78 (Herbert et al., 2015; Hintz & Relyea, 2019).

79 The ecological consequences of such diversity changes cannot be inferred from taxonomic information
80 alone (Cadotte, Carscadden, & Mirotchnick, 2011; Hooper et al., 2005). Biodiversity–ecosystem
81 function theory posits that functional diversity, the range and distribution of functional traits often
82 explains more variance in ecosystem processes than species richness (Chen et al., 2025; Zhu et al., 2026).
83 In lake ecosystems, resource use efficiency (RUE) of phytoplankton and zooplankton serves as a key
84 metric linking community properties to biogeochemical functions (Ptacnik et al., 2008; Striebel, Behl,
85 Diehl, & Stibor, 2009). To date, studies in low-salt lakes have largely been confined to traditional
86 diversity surveys, with the general notion that salinity drives a linear decline in taxonomic alpha diversity
87 (Stenger-Kovács et al., 2023; Wurtsbaugh et al., 2017). Far less attention has been paid to the nonlinear
88 behaviour of functional diversity indices. For instance, some scattered evidence indicates that functional
89 dispersion may peak in brackish transition zones, where remaining species adopt divergent salt-tolerance
90 strategies and maintain complementary resource use (Mouillot, Graham, Villéger, Mason, & Bellwood,
91 2012; Vellend, 2010). Moreover, beta diversity, which captures spatial turnover and nestedness

components, can reveal whether community differentiation under salinity stress is driven by species replacement or species loss, but the relative importance of these components for phytoplankton versus zooplankton remains ambiguous.

Even when diversity patterns are described, how they translate into ecosystem functioning and what mechanisms govern community assembly along the gradient are still open questions. Functional diversity, especially functional beta diversity of zooplankton, is hypothesized to play a critical role in maintaining resource use efficiency and energy transfer, empirical evidence from natural low-salt gradients is scarce (King et al., 2024; Ptacnik et al., 2008; Soininen, Heino, & Wang, 2018). Simultaneously, the theory of community assembly provides the framework for interpreting how deterministic processes (environmental filtering and species interactions) and stochastic processes (dispersal limitation, ecological drift) shape community composition (J. M. Chase & J. A. Myers, 2011; Vellend, 2010). Stress intensity is considered the primary factor tipping the balance between these two types of processes. Along a salinity gradient, stochastic processes are expected to be more influential under benign freshwater conditions, while deterministic filtering intensifies with increasing salt stress (Y. Liu et al., 2026; Zheng & Yin, 2023a). However, empirical testing of this prediction in inland plateau lakes is notably lacking. The phased transitions in assembly mechanisms through freshwater, brackish, and low-salt environments, as well as the differential responses of phytoplankton and zooplankton, have not been quantified (Sun, Zhang, Wang, Huang, & Huang, 2023). In particular, the brackish zone represents a critical transition where deterministic and stochastic forces may both be strong, and the relative dominance remains a subject of debate. Resolving these uncertainties requires a continuous gradient design that captures the full range of salinity stress.

The four lakes selected on the Inner Mongolia Plateau—WLSH (freshwater), JYH(brackish), DH and DLN (low-salt)—naturally form such a gradient while sharing similar geographic and hydrological settings, thus providing an ideal system to address these gaps (C. Liu et al., 2023; C. Liu et al., 2022). According to the international Venice salinity classification, these ecosystems transition clearly from freshwater and brackish water to a convergent low-salt state shared by DH and DLN, which independently evolved highly similar severe salinity constraints. Using field surveys and multiple analytical approaches, we tested the following hypotheses: (1) Salinity acts as a primary environmental filter shaping plankton community structure. (2) Increasing salinity reduces plankton taxonomic diversity and functional diversity while increasing community differentiation. (3) Salinity alters the relationship between plankton biodiversity and ecosystem functioning. (4) Deterministic assembly processes dominate plankton community assembly across the salinity gradient. This study seeks to clarify how a continuous salinity gradient structures plankton communities, alters biodiversity patterns, and affects ecosystem functioning, thereby contributing information relevant to the conservation and restoration of salinizing lakes.

Materials and methods

Study area and sampling sites

The study lakes are located in the Inner Mongolia Autonomous Region, Northern China. This area is situated in the northern part of China, ranging from 97°12' to 126°04' east longitude and 37°24' to 53°23' north latitude (Geng et al., 2024). Due to the longitudinal and conical distribution of this area, the climate changes from semi-arid to arid from east to west, with precipitation decreasing and evaporation increasing accordingly. The average temperature ranges from -3.2°C to 11.5°C. The evaporation in most

areas is between 1,200 and 3,000 mm, and the annual precipitation is approximately 50 to 450 millimeters (Geng et al., 2024).

In July and August 2025, a total of 58 sampling points from 4 lakes were collected along the route from west to east (Figure 1 shows the sampling point map), including Juyan Lake (JYH), Wuliangsu Lake (WLSH), Daihai Lake (DH), and Dalinor Lake (DLN).

Sampling and laboratory analysis

At each sampling point, surface water was collected using a 1.5-liter acrylic sampler, which was then stored in two 500-ml polyethylene bottles and sealed well for transportation to the laboratory for testing and analysis. All samples were measured using the same detection methods and instruments (Yan et al., 2023). The pH value, total dissolved solids (TDS), conductivity, salinity (Sal) and dissolved oxygen (DO) were measured on-site using the German WTW 3630 multi-parameter water quality rapid analyzer. Transparency (SD) was measured on-site by a Secchi disk. Total phosphorus (TP) was determined by ammonium molybdate spectrophotometry (UV-2600 PC; Shimadzu, Kyoto, Japan), and total nitrogen (TN) was determined by alkaline potassium persulfate digestion ultraviolet spectrophotometry. Chemical oxygen demand (CODMn) was determined by potassium permanganate titration. The content of chlorophyll a (Chl-a) was filtered through a Whatman GF/C (0.45 microns) filter membrane in water samples and determined by acetone extraction spectrophotometry with an error of $\leq 2\%$. Total suspended solids were determined by membrane filtration (GF/F, 0.7 microns) with an error of no more than 2%.

At each sampling site, a 1 L surface water sample (0.5 m depth) was collected using a 5 L acrylic water sampler for quantitative plankton analysis. These 1 L whole-water samples were immediately fixed with 1.5% Lugol's iodine solution on-site and allowed to sediment undisturbed for 48 h in the laboratory. The

supernatant was carefully siphoned off using a small-diameter silicone tube to concentrate the sample to a final volume of 100ml for comprehensive taxonomic identification and cell counting. Crucially, to ensure that the entire size-spectrum of the phytoplankton community (including micro-, nano-, and pico-phytoplankton) was captured without size-bias, all subsequent phytoplankton quantitative metrics, biomass estimations, and functional trait allocations—particularly those for cell sizes $<20\ \mu\text{m}$ were conducted exclusively based on these unconcentrated, sedimented whole-water samples. Additionally, a phytoplankton net with a $64\ \mu\text{m}$ mesh size was towed through the water column solely for qualitative auxiliary observation and morphological verification of rare or colonial taxa (e.g., *Microcystis* colonies). For zooplankton, a total of 50 L of surface water was filtered through a $64\ \mu\text{m}$ mesh net at each site, and the concentrated residue was preserved in 50 mL bottles with 4% formalin for quantitative counting and identification.

Calculation of plankton indices

To systematically reveal the changing patterns of the community structure, diversity characteristics and ecological functions of plankton under salinity gradients, this study quantitatively characterized the phytoplankton and zooplankton communities from both taxonomic and functional dimensions. Meanwhile, by calculating Resource Use Efficiency (RUE), the utilization and transformation capabilities of plankton communities for nutrient resources under different salinity environments were evaluated (Ye et al., 2019; Yongxin Zhang et al., 2024).

1. Taxonomic diversity

The dominance index (Y) is used to identify the dominant species in phytoplankton and zooplankton communities, and its calculation formula is:

$$Y = \left(\frac{n_i}{N} \right) \times f_i$$

Here, n_i represents the number of individuals of the i -th species, N is the total number of individuals in the community, and f_i is the frequency of occurrence of this species in all samples. When $Y > 0.02$, this species is defined as the dominant species

Taxonomic α -diversity is characterized by Species Richness (species Richness, SR) and Shannon-Wiener diversity index (H').

Species richness (SR) is defined as the total number of species recorded in each sample.

The calculation formula of the Shannon-Wiener diversity index is as follows:

$$H' = - \sum_{i=1}^S p_i \ln(p_i)$$

In the formula: S represents the number of phytoplankton species in the sample, n_i is the number of individuals of the i -th phytoplankton species, and N is the total number of individuals of all species.

The Bray-Curtis dissimilarity coefficient was used to calculate the taxonomic β -diversity, quantitatively characterizing the turnover differences in the species composition of the plankton community among different sampling points, and reflecting the spatial differentiation characteristics of the community species composition under the salinity gradient.

$$BC_{jk} = \frac{\sum_{i=1}^S |n_{ij} - n_{ik}|}{\sum_{i=1}^S (n_{ij} + n_{ik})}$$

2. Functional diversity

Functional diversity was quantified using species-level functional trait matrices of phytoplankton and zooplankton based on a multidimensional trait-space approach. Functional traits were selected according

to their ecological relevance to resource acquisition, life-history strategies, environmental adaptation, and tolerance to salinity stress, which are widely recognized as key determinants of plankton responses to environmental gradients (Morim, Henriques, Vasconcelos, & Dolbeth, 2023; Pulina & Satta, 2023). For phytoplankton, functional traits included cell size, morphology, colony formation ability, silica content, habitat preference, motility, and reproductive mode (Table 1). These traits are closely associated with nutrient uptake efficiency, competitive ability, dispersal capacity, resistance to grazing pressure, and adaptation to osmotic stress (Kruk et al., 2010; Litchman, de Tezanos Pinto, Klausmeier, Thomas, & Yoshiyama, 2010; Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002). Cell size influences nutrient acquisition and metabolic rates, while motility and colony formation contribute to habitat selection and environmental tolerance under fluctuating salinity conditions .

For zooplankton, functional traits included body size, feeding guild, reproductive type, life cycle, and locomotion mode (Table 2). These traits are strongly linked to trophic interactions, energy transfer efficiency, dispersal ability, and environmental adaptability ((Barnett, Finlay, & Beisner, 2013; Litchman, Ohman, & Kiørboe, 2013). In particular, body size and feeding strategy determine resource utilization patterns and trophic position, whereas reproductive traits and life-history characteristics influence population persistence under environmental stress (Kiørboe, 2011).

Functional α -diversity was characterized using two complementary indices: Functional Richness (FRic) and Functional Dispersion (FDis). FRic quantifies the volume of multidimensional functional niche space occupied by species within a community and reflects the extent of potential niche utilization . Higher FRic values indicate a broader range of functional strategies and greater occupation of ecological niche space. FDis measures the abundance-weighted mean distance of species to the centroid of the functional trait space and reflects the degree of functional trait dispersion within a community. Higher

FD_{is} values indicate stronger functional differentiation among species and greater potential for niche complementarity and resource partitioning.

Functional β -diversity was calculated based on species-level functional trait distance matrices. Principal Coordinates Analysis (PCoA) was first applied to construct multidimensional functional trait space, after which pairwise distances among communities were calculated to quantify differences in functional composition across sampling sites. Functional β -diversity was further partitioned into turnover and nestedness components to distinguish trait replacement from trait loss along the salinity gradient.

All classification diversity and functional diversity indicators were calculated in the R 4.2.1 platform, and mainly analyzed using vegan, FD and betapart software packages.

3. Plankton resource use efficiency

To evaluate the utilization capacity of plankton communities for water nutrient resources and the functional level of the ecosystem, in this study, the Phytoplankton Resource Use Efficiency (PRUE) and Zooplankton Resource Use Efficiency (ZRUE) were calculated respectively (Jiang et al., 2024).

Phytoplankton resource utilization efficiency (PRUE) is defined as the biomass of phytoplankton supported by a unit of nutrient resources, and the calculation formula is as follows:

$$RUE = \frac{Chl-a (\mu g/L)}{TN(mg/L) \text{ .or. } TP(mg/L)}$$

Zooplankton resource utilization efficiency (ZRUE) is defined as the amount of zooplankton biomass supported by a unit of phytoplankton biomass, and its calculation formula is:

$$RUE_{zp} = \log_{10} \left(\frac{Biomass(zooplankton)}{Biomass(phytoplankton)} + 1 \right)$$

Statistical analysis

237 All statistical analyses were conducted in R version 4.3.2 (R Core Team, Vienna, Austria).
238 Environmental variables were log-transformed [$\log(x + 1)$] when necessary and standardized using Z-
239 score transformation prior to analysis.

240 One-way analysis of variance (ANOVA) followed by Tukey's HSD test was used to examine differences
241 in environmental variables, plankton diversity indices, ecosystem function indicators, and community
242 assembly metrics among freshwater, brackish, and low-salinity lakes. Statistical significance was set at
243 $P < 0.05$.

244 Non-metric Multidimensional Scaling (NMDS) based on Bray–Curtis dissimilarity matrices was
245 performed using the vegan package to evaluate differences in phytoplankton and zooplankton community
246 composition across salinity gradients. Community differences among lake types were further tested
247 using Permutational Multivariate Analysis of Variance (PERMANOVA) with 999 permutations
248 (Kruskal, 1964).

249 Ecosystem functioning was assessed using phytoplankton resource use efficiency (PRUE), zooplankton
250 resource use efficiency (ZRUE), and ecosystem multifunctionality (EMF). EMF was calculated as the
251 average of the Z-score standardized values of chlorophyll-a concentration (Chl-a), PRUE, and ZRUE.

252 Structural Equation Modeling (SEM) was used to evaluate the direct and indirect effects of salinity on
253 ecosystem multifunctionality through plankton diversity. Separate SEMs were constructed for
254 phytoplankton and zooplankton communities using the lavaan package. Model performance was assessed
255 using the Comparative Fit Index (CFI), Goodness-of-Fit Index (GFI), Root Mean Square Error of
256 Approximation (RMSEA), and coefficient of determination (R^2).

The relative contributions of deterministic and stochastic processes to community assembly were quantified using the Dispersal–Niche Continuum Index (DNCI) (Vilmi et al., 2020). DNCI analyses were conducted using 1,000 bootstrap iterations and 999 random permutations. DNCI values lower than -2 indicate deterministic dominance; values greater than $+2$ indicate stochastic dominance, and values between -2 and $+2$ suggest a balanced contribution of both processes.

All figures were generated using the ggplot2 package.

Results

Spatial Variations in Water Hydrochemical Parameters

Water physicochemical parameters differed significantly among lakes ($p < 0.05$) (Figure S1). Salinity-related variables, including EC and TDS, increased markedly from WLSH to DH and DLN, confirming the existence of a natural salinity gradient. Nutrient variables (TN, TP, $\text{NH}_3\text{-N}$) and organic matter indicators (CODMn, COD, Chla, SS) also showed significant spatial variation among lakes. In particular, DLN exhibited relatively high nutrient concentrations, whereas WLSH generally showed lower ionic concentrations and conductivity. These results indicate substantial environmental heterogeneity among lakes and provide the environmental context for subsequent analyses of plankton diversity and community assembly.

The community structure characteristics of plankton

Phytoplankton community composition varied markedly among lakes along the salinity gradient. A total of seven major phytoplankton groups were recorded, including Cyanophyta, Cryptophyta, Xanthophyta, Bacillariophyta, Dinophyta, Euglenophyta, and Chlorophyta. Freshwater lake WLSH exhibited the highest taxonomic richness, whereas species richness decreased substantially in JYH, DH, and DLN.

Chlorophyta and Xanthophyta contributed most to the phytoplankton assemblages across all lakes, while several minor groups, including Dinophyta and Euglenophyta, were mainly restricted to WLSH. The dominant taxa also shifted along the salinity gradient, with *Cyclotella meneghiniana* and *Microcystis* spp. showing relatively high abundances in low-salt lakes, whereas taxa such as *Ankistrodesmus* and *Cryptomonas* were more common in freshwater and brackish environments. The taxonomic richness of major phytoplankton and zooplankton groups across lakes is shown in (Figure S2).

Zooplankton community composition also showed clear differences among lakes. Rotifera represented the dominant group in all lakes and accounted for the majority of recorded species. Freshwater WLSH supported substantially higher zooplankton richness than the other lakes. Protozoa were only detected in WLSH, whereas copepod-related taxa increased in relative importance under higher salinity conditions. Heatmap analysis further revealed distinct distribution patterns of dominant zooplankton taxa among lakes (Figure 3). Nauplius larvae and copepodites were particularly abundant in DH and DLN, whereas several rotifer species, including *Keratella valga* and *Brachionus angularis*, were mainly associated with WLSH and JYH.

NMDS ordination revealed significant spatial separation of plankton communities among lakes. For phytoplankton, samples from WLSH formed a distinct cluster separated from those of low-salt lakes, while JYH occupied an intermediate position along the gradient. A similar pattern was observed for zooplankton communities, with clear differentiation among freshwater, brackish, and low-salt lake assemblages. These results indicate pronounced turnover in plankton community composition along the salinity gradient (Figure 4).

Characteristics of plankton species abundance and biomass

Phytoplankton biomass and density exhibited marked variation among lakes along the salinity gradient. Community composition shifted substantially across lakes. In WLSH, Cryptophyta constituted the largest proportion of phytoplankton biomass, together with Cyanophyta, Chlorophyta, and Bacillariophyta. Cyanophyta dominated biomass in JYH, whereas Bacillariophyta became the predominant group in DH. In DLN, Chlorophyta and Cryptophyta increased in relative importance. Overall phytoplankton biomass was highest in DH and lower in WLSH, JYH, and DLN. (Figure 2)

Patterns of phytoplankton density differed from those of biomass. Cryptophyta dominated cell density in WLSH, whereas Bacillariophyta became explicitly dominant in DH. In DLN, Cryptophyta became completely dominant, accounting for nearly all recorded cells in DLN. In contrast, JYH was characterized by relatively high proportions of Cyanophyta and the lowest total phytoplankton density across the salinity gradient (Figure 3) .

Zooplankton communities were consistently dominated by Copepoda, which accounted for the majority of total biomass and density in all lakes. Cladocera were recorded in JYH, DH, and DLN, whereas Rotifera were mainly restricted to WLSH and JYH. Zooplankton biomass reached its maximum in DH, while density was also highest in DH (and lowest in JYH). Heatmap analyses further revealed clear shifts in dominant phytoplankton and zooplankton taxa among lakes, indicating pronounced community differentiation along the salinity gradient .

Plankton taxonomic diversity across salinity gradient

Taxonomic α -diversity of both phytoplankton and zooplankton declined significantly along the salinity gradient. Freshwater lake WLSH exhibited the highest species richness (SR) and Shannon diversity (H), whereas diversity decreased progressively in JYH, DH, and DLN. The decline was more pronounced for

phytoplankton than for zooplankton, indicating stronger compositional changes in phytoplankton communities across the salinity gradient. In contrast, zooplankton diversity showed a relatively moderate reduction, although both diversity indices remained consistently lower in low-salt lakes than in freshwater environments.

Patterns of taxonomic β -diversity differed markedly between phytoplankton and zooplankton. Phytoplankton communities maintained relatively high β -diversity throughout the gradient, particularly in freshwater and brackish lakes, indicating substantial spatial variation in species composition among sampling sites. Decomposition of β -diversity revealed that species turnover contributed more strongly than nestedness, suggesting that community differentiation was primarily driven by species replacement among habitats.

In contrast, zooplankton β -diversity exhibited a different pattern. Although total β -diversity remained relatively high in freshwater and brackish lakes, the contribution of nestedness increased in low-salt lakes. This pattern indicates that differences among zooplankton communities were increasingly associated with species loss and reduced community complexity. Consequently, phytoplankton communities were mainly characterized by species replacement along the salinity gradient, whereas zooplankton communities showed stronger nestedness associated with progressive reductions in species richness. The partitioning of taxonomic β -diversity into turnover and nestedness components is presented in (Figure S3).

Plankton functional diversity across salinity gradient

Functional diversity of both phytoplankton and zooplankton showed pronounced variation along the salinity gradient. For phytoplankton, functional richness (FRic) declined progressively from freshwater

to low-salt lakes, with the highest values observed in WLSH and the lowest values in DH and DLN. In contrast, functional dispersion (FDis) remained relatively high in WLSH and JYH but decreased in the low-salt lakes, indicating reduced functional trait variability under higher salinity conditions.

Patterns of phytoplankton functional β -diversity further revealed substantial differentiation among lakes. Total functional β -diversity was generally higher in JYH and DLN than in WLSH. Decomposition analyses showed that turnover contributed more strongly than nestedness to overall functional β -diversity, suggesting that functional differences among phytoplankton communities were primarily associated with trait replacement rather than the loss of functional strategies.

Zooplankton functional α -diversity exhibited a pattern similar to that of phytoplankton. Functional richness decreased markedly along the salinity gradient, with the highest values occurring in WLSH and substantially lower values in DH and DLN. However, zooplankton functional dispersion remained relatively stable across lakes, indicating that the remaining taxa maintained comparable levels of functional trait dispersion despite reductions in richness.

In contrast to phytoplankton, zooplankton functional β -diversity was characterized by a stronger contribution of nestedness. Total functional β -diversity was highest in WLSH and JYH and declined in the low-salt lakes. Nestedness accounted for a considerable proportion of community differentiation, whereas turnover contributed less to functional dissimilarity. These results indicate distinct functional diversity responses of phytoplankton and zooplankton to increasing salinity (Figure 5). The partitioning of functional β -diversity is shown in (Figure S4).

Diversity changes and ecosystem functions

For the zooplankton SEM , the model showed a satisfactory fit ($GOF = 0.60$). Salinity exerted significant negative effects on both functional β -diversity ($\beta = -0.74$, $P < 0.001$) and species richness ($\beta = -0.83$, $P < 0.001$). Species richness was positively associated with functional β -diversity ($\beta = 0.60$, $P < 0.001$). In contrast, neither functional β -diversity ($\beta = -0.07$) nor species richness ($\beta = -0.12$) had significant direct effects on ecosystem function. Salinity, however, had a significant positive direct effect on ecosystem function ($\beta = 0.54$, $P < 0.05$). The model explained 85% of the variation in species richness, 7% of the variation in functional β -diversity, and 30% of the variation in ecosystem function ($R^2 = 0.85, 0.07$, and 0.30 , respectively).

For the phytoplankton SEM , the model also showed an acceptable fit ($GOF = 0.40$). Salinity significantly reduced functional richness ($\beta = -0.43$, $P < 0.01$) and species richness ($\beta = -0.64$, $P < 0.001$). Species richness positively affected functional richness ($\beta = 0.60$, $P < 0.001$). Functional richness showed a relatively strong negative effect on ecosystem function ($\beta = -0.27$), whereas the direct effect of species richness on ecosystem function was weak ($\beta = 0.04$). Salinity also exhibited a negative direct effect on ecosystem function ($\beta = -0.34$). The model explained 79% of the variation in species richness, 19% of the variation in functional richness, and 17% of the variation in ecosystem function ($R^2 = 0.79, 0.19$, and 0.17 , respectively). (Figure 6)

Shift in Community Assembly Mechanisms Along the Salinity Gradient

The dispersal-niche continuum index (DNCI) revealed consistent patterns in the assembly mechanisms of phytoplankton and zooplankton communities across the salinity gradient . DNCI values for both groups remained below the threshold value of -2 in all lake types, indicating that deterministic processes dominated community assembly throughout the study system.

However, the relative importance of deterministic and stochastic processes varied among salinity regimes. In freshwater lakes, both phytoplankton and zooplankton exhibited the lowest DNCI values, with median values below -5 , indicating strong deterministic assembly. DNCI values increased markedly in the brackish lake JYH, reaching approximately -3.5 for phytoplankton and -3.0 for zooplankton. This pattern suggests a reduced dominance of deterministic processes and a greater contribution of stochastic processes in the intermediate salinity environment. In contrast, DNCI values declined again in the low-salt lakes DH and DLN, approaching levels observed in freshwater lakes.

Differences between phytoplankton and zooplankton were most evident in the brackish lake. Zooplankton exhibited consistently higher DNCI values than phytoplankton, indicating a stronger shift toward stochastic assembly under intermediate salinity conditions. In contrast, DNCI values of the two groups converged in freshwater and low-salt lakes, where deterministic processes remained strongly dominant.

Overall, community assembly followed a similar pattern for both phytoplankton and zooplankton, characterized by strong deterministic assembly in freshwater lakes, increased stochasticity in the brackish lake, and a return to stronger deterministic assembly in low-salt lakes. (Figure 7)

Discussion

1. Salinity Filtering

Salinity is widely recognized as one of the most influential environmental gradients in inland aquatic ecosystems because it simultaneously affects physiological performance, nutrient cycling, species interactions, and food-web organization (Stenger-Kovács et al., 2023). Consistent with this view, both phytoplankton and zooplankton communities differed markedly among freshwater, brackish, and low-

salinity lakes in the present study. Ordination analyses revealed clear separation among lake types, indicating that salinity strongly constrained community composition. Similar patterns have been reported from low-salt lakes on the Tibetan Plateau (Gao, Chen, Govaert, Wang, & Yang, 2019; Gu et al., 2024) and in Inner Mongolian lakes (Deng et al., 2024; Gong et al., 2022), suggesting that salinity-driven community differentiation is a widespread feature of inland lake ecosystems rather than a site-specific phenomenon. These findings further support the view that salinity functions as a major ecological filter governing species distribution and community assembly (C. Liu et al., 2023; Tang et al., 2021).

The observed community differentiation is likely driven by several complementary mechanisms. Elevated salinity increases osmotic stress (Stenger-Kovács et al., 2023; von Weissenberg, Mottola, Uurasmaa, Anttila, & Engström-Öst, 2022), forcing organisms to allocate additional energy to ion regulation and cellular homeostasis at the expense of growth and reproduction. As environmental stress intensifies, salt-sensitive taxa are progressively excluded, whereas species possessing effective osmoregulatory strategies or broader physiological tolerance become dominant. Such environmental selection strengthens habitat filtering and reduces the pool of species capable of persisting under low-salt conditions. The responses of phytoplankton and zooplankton may also differ because phytoplankton are more likely to adapt through physiological plasticity, whereas zooplankton often rely on life-history strategies such as resting eggs and broader salinity tolerance to persist under osmotic stress.

In addition to these direct physiological effects, salinity indirectly influences community structure by modifying nutrient availability and trophic interactions. Increasing salinity can alter phosphorus release from sediments and nitrogen transformation processes (Gardolinski, Worsfold, & McKelvie, 2004; van Diggelen et al., 2014), thereby changing resource availability for primary producers. The hydrochemical

characteristics of our study lakes (Figure S1) indicate that this process is closely linked to evaporation, which simultaneously concentrates dissolved salts and nutrients. Total phosphorus and total nitrogen increased markedly in the low-salinity lakes (DH and DLN) compared with WLSH Lake (Figure S1), creating nutrient-rich conditions that favor opportunistic and stress-tolerant phytoplankton capable of rapidly exploiting available resources despite strong osmotic stress. Changes in salinity may also restructure trophic interactions. Previous studies in Tibetan lakes have shown that increasing salinity is frequently accompanied by the loss of fish populations, altering grazing pressure and promoting shifts in zooplankton communities. The community patterns observed in this study therefore likely result from the combined effects of physiological selection, nutrient enrichment, and trophic regulation rather than from salinity alone.

Overall, our results demonstrate that salinity regulates plankton communities through multiple interacting pathways. Direct physiological filtering, evaporation-driven changes in water chemistry, and shifts in trophic interactions collectively shape community composition across the salinity gradient. The corresponding changes in both taxonomic and functional diversity further indicate that salinity influences not only which species persist but also how ecological functions are distributed within plankton communities, emphasizing its central role in structuring inland lake ecosystems.

2. Multidimensional responses of biodiversity to salinity

A central objective of this study was to evaluate how different dimensions of biodiversity respond to natural salinity gradients. Our results demonstrated contrasting responses of taxonomic and functional diversity (Mammola, P. Carmona, Guillaume, & Cardoso, 2021; Villéger, Mason, & Mouillot, 2008), indicating that biodiversity changes under salinization cannot be adequately described by species

richness alone. Taxonomic α -diversity declined consistently with increasing salinity, supporting the predictions of niche theory and environmental filtering (J. Chase & J. Myers, 2011; Mo et al., 2021). Freshwater lakes maintained the highest species richness, whereas salt-sensitive species were progressively excluded as salinity increased, resulting in marked reductions in species richness and Shannon diversity. Similar responses have been widely reported in inland low-salt lakes (C. Liu et al., 2022), suggesting that declining taxonomic diversity is a predictable consequence of salinization. In contrast, functional diversity showed a more complex response. Although functional richness decreased under high salinity, other functional indices remained relatively stable or exhibited nonlinear variation, indicating that taxonomic loss was not accompanied by proportional functional loss. Such patterns are consistent with functional redundancy (Loreau, 2004), whereby different species perform similar ecological roles. Consequently, ecosystem functions can be maintained despite substantial species turnover, particularly in plankton communities where many taxa share comparable feeding strategies, body sizes, and reproductive characteristics.

Brackish lakes exhibited relatively high functional heterogeneity despite only intermediate taxonomic richness. As ecological transition zones, these habitats often function as ecotones (Basset et al., 2013), allowing the coexistence of freshwater and salt-tolerant taxa with contrasting ecological strategies. This coexistence expands functional trait space and helps maintain functional diversity even under increasing environmental stress. The β -diversity analyses further support this interpretation (Baselga, 2010). Taxonomic β -diversity was dominated by turnover rather than nestedness, indicating that community differentiation resulted primarily from species replacement instead of simple species loss. Along the salinity gradient, salt-sensitive taxa were replaced by salt-tolerant species with different ecological traits, leading to substantial reorganization of community composition. These results suggest that salinization

promotes the assembly of ecologically distinct communities through strong environmental sorting rather than merely reducing biodiversity.

Taken together, our results show that salinity reshapes biodiversity across multiple dimensions. Taxonomic diversity primarily reflects species loss and replacement, whereas functional diversity captures the reorganization of ecological strategies during community succession. Considering both dimensions therefore provides a more comprehensive understanding of plankton responses to salinization than species richness alone and highlights the importance of incorporating functional traits into biodiversity assessment and conservation of salinizing lake ecosystems.

3. Biodiversity–ecosystem functioning relationships under salinity stress

Understanding how biodiversity influences ecosystem functioning remains a central challenge in ecology, particularly under increasing environmental stress (Loreau et al., 2001). Classical biodiversity–ecosystem functioning (BEF) theory predicts that greater biodiversity enhances ecosystem processes through niche complementarity and more efficient resource utilization (Tilman, Wedin, & Knops, 1996). However, our SEM results revealed a different pattern along the natural salinity gradient. Although salinity significantly reduced both taxonomic and functional diversity of phytoplankton and zooplankton, neither species richness nor functional diversity exerted significant direct effects on ecosystem functioning. Instead, salinity maintained strong direct pathways, particularly in the zooplankton model, indicating that ecosystem functioning became increasingly regulated by environmental conditions rather than biodiversity itself. These results suggest that salinization not only restructures plankton communities but also shifts the dominant controls of ecosystem functioning from biological diversity toward abiotic environmental filtering.

One explanation for this decoupling is the functional redundancy within plankton communities (WALKER, 1992). As salinity increased, salt-sensitive species were progressively excluded, whereas stress-tolerant taxa with similar ecological functions persisted. Consequently, essential ecosystem processes could be maintained despite considerable species loss because overlapping functional roles continued to be performed by the remaining taxa (Biggs et al., 2020). This interpretation is also supported by the contrasting responses of functional diversity observed in this study. Functional richness declined significantly with increasing salinity, whereas functional dispersion remained comparatively stable, indicating that although the occupied trait space became smaller, the remaining species still represented the core functional characteristics of the community. Such redundancy likely buffered ecosystem functioning against taxonomic erosion. At the same time, salinity acts not only as a biological filter but also as a direct regulator of ecosystem processes (Du, Tong, Meng, & Jiao, 2026). Elevated salinity can modify nutrient solubility, microbial metabolism, sediment–water nutrient exchange, and trophic transfer efficiency (Søndergaard et al., 2007), thereby influencing ecosystem functioning independently of biodiversity. This mechanism explains why salinity retained strong direct effects in the SEM while diversity-mediated pathways remained weak. The stronger direct effect observed in the zooplankton model further suggests that higher trophic levels may be more sensitive to physicochemical stress because zooplankton are regulated simultaneously by environmental conditions and trophic interactions. Meanwhile, the positive relationships between functional diversity and species richness indicate that broader functional trait space still promotes species coexistence through niche differentiation, even though its contribution to ecosystem functioning is indirect. Similar buffering effects of functional redundancy have also been reported in northern Chinese river fish assemblages experiencing severe nutrient enrichment (J. Zhang, Liu, Chen, & Yin, 2025).

The weakened biodiversity–ecosystem functioning relationship observed here has broader ecological implications. Combined with the DNCI results, which showed that deterministic processes dominated plankton community assembly under increasing salinity, our findings indicate that environmental filtering not only determines which species persist but also increasingly governs ecosystem functioning. As physicochemical constraints intensify, the contribution of biodiversity to ecosystem processes becomes progressively weaker, a pattern consistent with the Stress Gradient Hypothesis and previous studies demonstrating that environmental stress can override biodiversity effects in extreme habitats. Nevertheless, the weak diversity–function relationship should not be interpreted as evidence that biodiversity is unimportant. Instead, it suggests that functional redundancy temporarily buffers ecosystem functioning against species loss. Continued salinization may gradually eliminate functionally unique taxa and erode this buffering capacity, eventually causing abrupt declines in ecosystem functioning once critical functional thresholds are exceeded. Therefore, maintaining functional diversity is essential not only for preserving present ecosystem functions but also for sustaining the long-term resilience of salinizing lake ecosystems.

4. Community assembly along the salinity gradient

Understanding the mechanisms governing community assembly is a fundamental objective of ecological research. Community assembly theory proposes that ecological communities are jointly regulated by deterministic processes, including environmental filtering and species interactions, and stochastic processes such as dispersal limitation, ecological drift, and random colonization (J. M. Chase & J. A. Myers, 2011; Zhou & Ning, 2017). Along environmental gradients, the relative importance of these mechanisms is expected to shift with increasing environmental stress. Our DNCI results showed that deterministic processes dominated the assembly of both phytoplankton and zooplankton communities

532 across the entire salinity gradient (Stegen et al., 2013). All DNCI values remained well below the
533 threshold of -2 , indicating that community composition was primarily structured by environmental
534 selection rather than random ecological processes. These results suggest that plankton communities in
535 the Inner Mongolian lakes are assembled mainly through habitat filtering, whereby only species
536 possessing suitable physiological and ecological traits can persist under local environmental conditions.

537 The predominance of deterministic assembly is consistent with the strong environmental constraints
538 imposed by salinity (Zheng & Yin, 2023b). Increasing salinity acts as a powerful ecological filter by
539 excluding salt-sensitive species and favoring taxa with greater physiological tolerance, thereby
540 strengthening trait–environment matching during community assembly. However, deterministic
541 processes also remained dominant in freshwater lakes, indicating that salinity is not the only factor
542 regulating community assembly. Other environmental variables, including nutrient availability, dissolved
543 oxygen, hydrological conditions, and habitat heterogeneity, are also likely to contribute to niche selection
544 (Keddy, 1992). These findings suggest that plankton communities are assembled through the combined
545 effects of multiple environmental gradients, with salinity representing one of the dominant, rather than
546 the sole, ecological filters operating in this lake system.

547 Although deterministic processes dominated overall, the relative contribution of stochasticity
548 increased in the brackish lakes. This transition is particularly noteworthy because brackish lakes
549 represent intermediate habitats where freshwater and salt-tolerant species coexist. Such transitional
550 environments are generally characterized by greater environmental heterogeneity and overlapping
551 regional species pools, increasing opportunities for dispersal, priority effects, and ecological drift
552 (Tews et al., 2004). Consequently, deterministic and stochastic processes interact more strongly in

these lakes, resulting in greater variability in community assembly. This interpretation is consistent with our diversity analyses, which showed relatively high functional heterogeneity and pronounced species turnover in the brackish lakes, suggesting that ecological transition zones are particularly dynamic stages of community reorganization. Zooplankton also exhibited larger DNCI fluctuations than phytoplankton, probably because their longer generation times, stronger dispersal limitation, and greater dependence on trophic interactions make them more responsive to environmental fluctuations. In contrast, the rapid reproduction and high dispersal capacity of phytoplankton may buffer stochastic influences even though environmental filtering remains the dominant assembly mechanism.

Overall, our assembly analyses demonstrate that salinity influences not only which species occur in lake ecosystems but also the mechanisms through which communities are assembled (Chase, 2007; Olli, Tamminen, & Ptacnik, 2022). Combined with the diversity and structural equation modeling results, these findings indicate that salinization simultaneously reshapes biodiversity patterns, modifies biodiversity–ecosystem functioning relationships, and strengthens deterministic assembly through environmental filtering. This integrated response highlights salinity as a key ecological driver regulating both the structure and functioning of plankton communities across natural salinity gradients.

5. Study Limitations

Several limitations in our sampling design should be noted. First, our field survey was restricted to a single seasonal window in mid-summer (July and August). Because plankton communities in plateau lakes exhibit strong seasonal successions across spring, summer, and autumn, this single-season snapshot cannot capture annual temporal dynamics or variations driven by ecological drift.

Second, our reliance on surface water sampling (0.5 m depth) may overlook potential vertical micro-stratification or diel vertical migration of certain plankton taxa. Nevertheless, this spatial survey was intentionally timed to leverage a continuous natural salinity gradient during the period of maximum environmental stress. Mid-summer represents a critical physiological window where high evaporation maximizes salinity concentrations and high temperatures drive biological metabolic rates to their annual peaks. By applying DNCI and SEM frameworks, we successfully decoupled the multi-dimensional taxonomic and functional responses along this ambient gradient. The strong environmental filtering captured in this peak-stress snapshot provides essential baseline data for understanding plankton community structuring under severe salinity constraints.

Conclusions

Our study demonstrates that natural salinity gradients drive multidimensional changes in plankton biodiversity, community assembly, and ecosystem functioning in Inner Mongolian lakes. Taxonomic α -diversity and functional richness declined consistently with increasing salinity, whereas functional dispersion and β -diversity exhibited nonlinear responses, indicating that plankton communities adapt to salinity stress through species replacement and functional trait reorganization rather than through a simple loss of diversity. Community assembly was dominated by deterministic processes across the entire salinity gradient, although the relative contribution of stochastic processes increased in brackish lakes before deterministic assembly became dominant again under higher salinity. Structural equation modeling further showed that salinity reduced both taxonomic and functional diversity, while exerting stronger direct effects on resource use efficiency than biodiversity itself. Together, these findings indicate that intense seasonal salinity constraints simultaneously reshape biodiversity, alter community assembly mechanisms, and strengthen abiotic

control over ecosystem functioning. This study successfully clarifies the multi-dimensional plankton responses under acute mid-summer salinity stress, providing foundational baseline information regarding the environmental filtering thresholds within these specific plateau lake systems.

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Author contributions

Y.Z., W.L., J.Z., Z.W., P.H., Y.T., X.Z., L.H., J.Q., R.W. and X.Y. conceived the study. Y.Z., W.L., P.H., Z.W. analyzed the data. X.Y., Y.T. and J.Z. designed the statistical framework and extended the analysis. W.L., J.Z., Z.W., P.H. and Y.Z. wrote the original draft. All authors contributed to manuscript editing.

Competing interests

The authors declare no conflicts of interest.

Ethical Approval

This is not applicable.

Consent to Participate

This is not applicable.

Consent to Publish

This is not applicable.

Data Availability Statement

Data will be available on reasonable request.

Graphs and Figures:

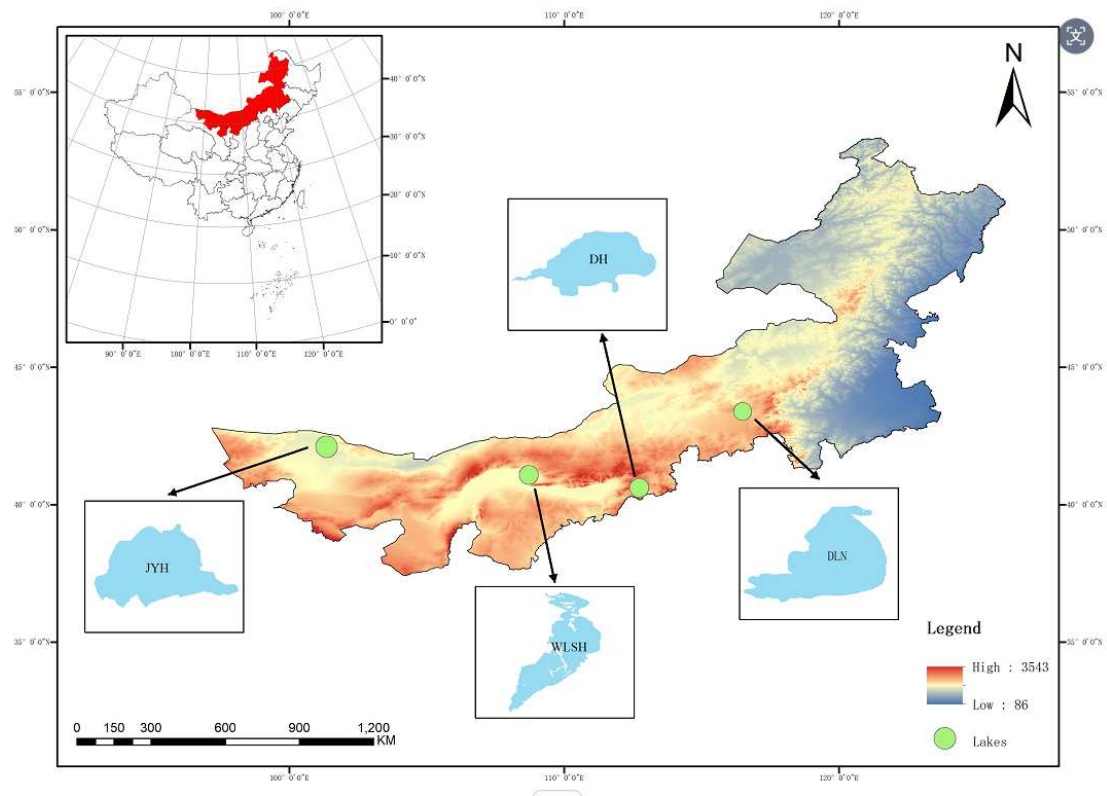
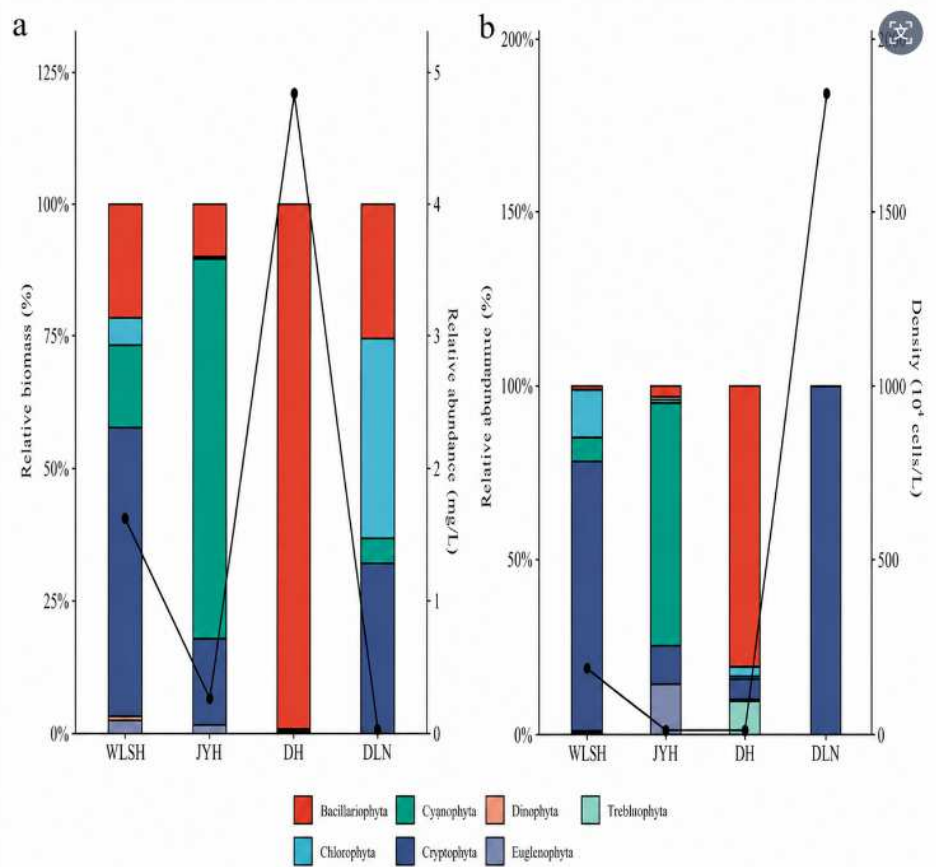


Figure 1 Geographic distribution of four study lakes and sampling sites on the Inner Mongolia Plateau(WLSH-Fresh water,JYH-brackish,DH,DLN-low-salt)



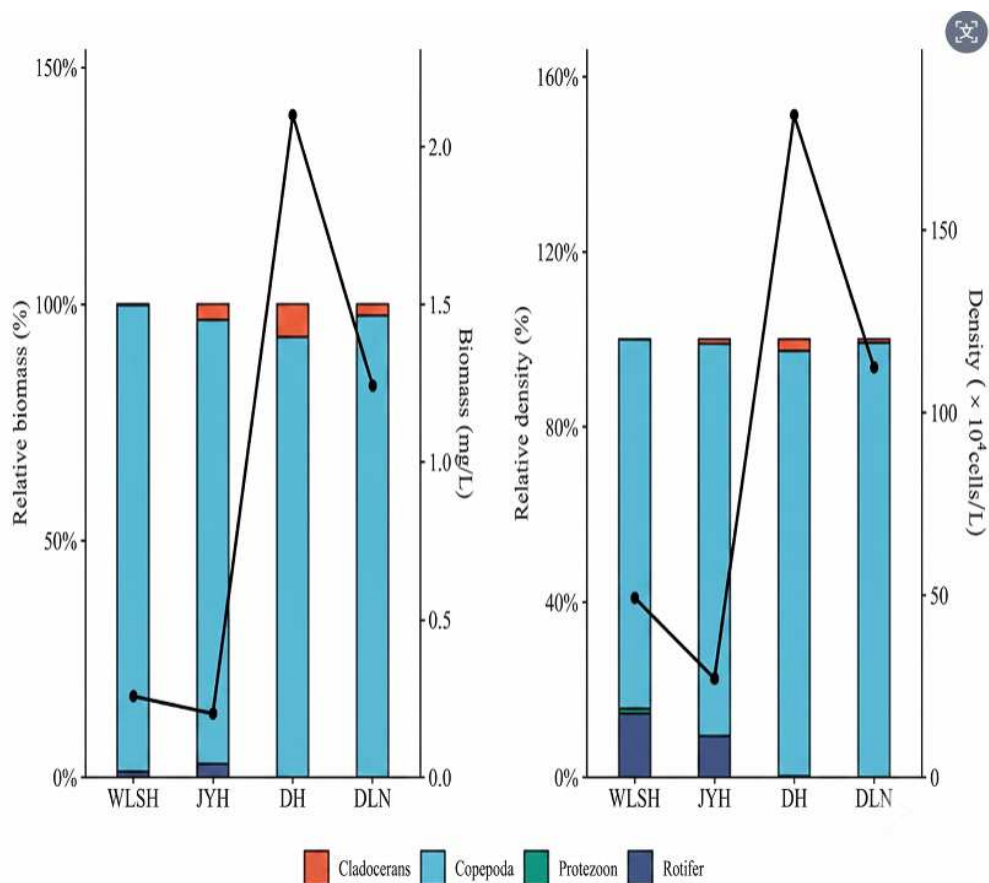


Figure 2 Taxonomic composition of phytoplankton and zooplankton across four lakes, presented as stacked relative biomass and density bar charts.

(a) Relative biomass proportion of phytoplankton groups; (b) cell density of phytoplankton (unit: 10^4 cells L^{-1});

(c) relative biomass proportion of zooplankton groups; (d) individual density of zooplankton (unit: 10^4 ind L^{-1}).

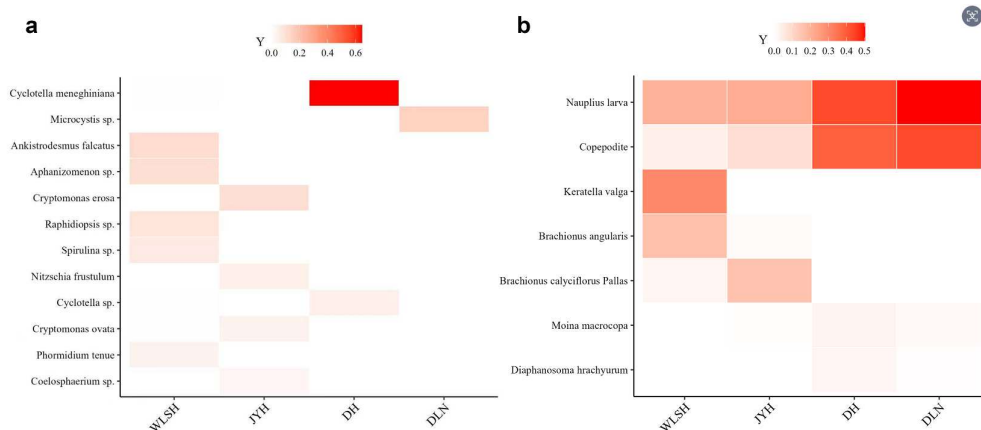


Figure 3 Heatmaps illustrating the dominance index (Y) of dominant plankton taxa across WLSH, JYH, DH and DLN. Color gradient represents the magnitude of the dominance index (0–0.6 for phytoplankton, 0–0.5 for zooplankton), with warmer colors indicating higher dominance. (a) Dominant phytoplankton species; (b) dominant zooplankton species.

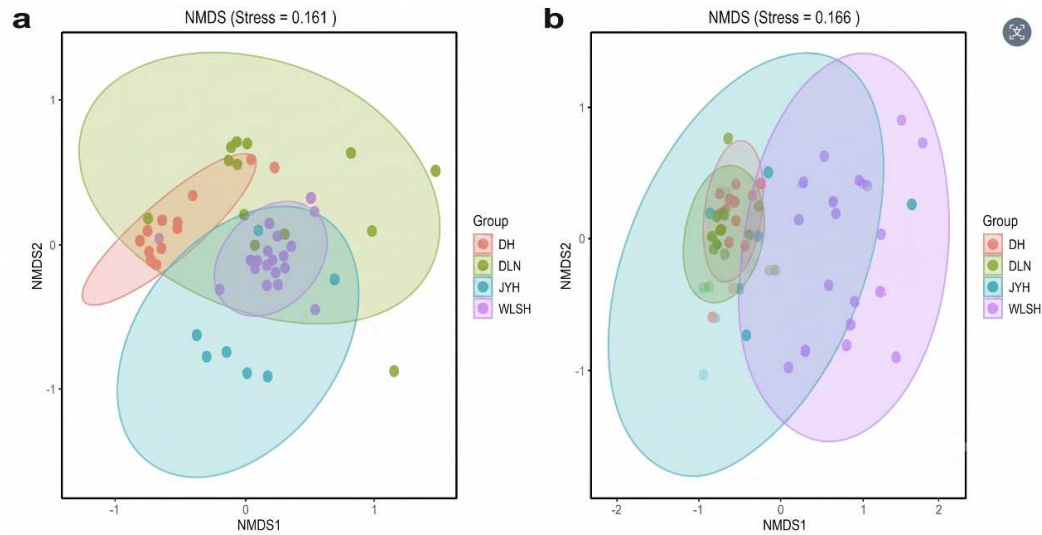


Figure 4 Non-metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis community dissimilarity, showing plankton compositional differentiation among the four lake groups (Stress values labeled at the top left of each panel). Colored ellipses denote 95% confidence intervals for each lake cluster: red = DH, green = DLN, cyan = JYH, purple = WLSH. (a) Phytoplankton community ordination; (b) zooplankton community ordination.

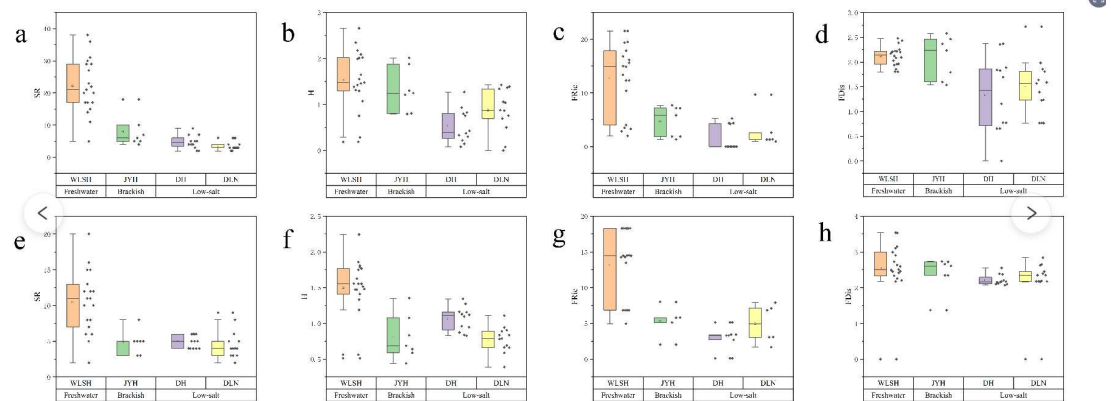


Figure 5 Taxonomic and functional alpha-diversity of phytoplankton and zooplankton along salinity gradients. Panels a–d (top) and e–h (bottom) show diversity metrics of phytoplankton and zooplankton, respectively: Species Richness (SR; a, e), Shannon-Wiener index (H; b, f), Functional Richness (FRic; c, g), and Functional Dispersion (FDis; d, h). X-axis denotes sampling sites grouped by salinity: WLSH (freshwater), JYH (brackish), DH and DLN (low-salt). In boxplots, central lines

show medians, box edges the 25th/75th percentiles, whiskers cover non-outlier data range, and jitter dots stand for individual samples.

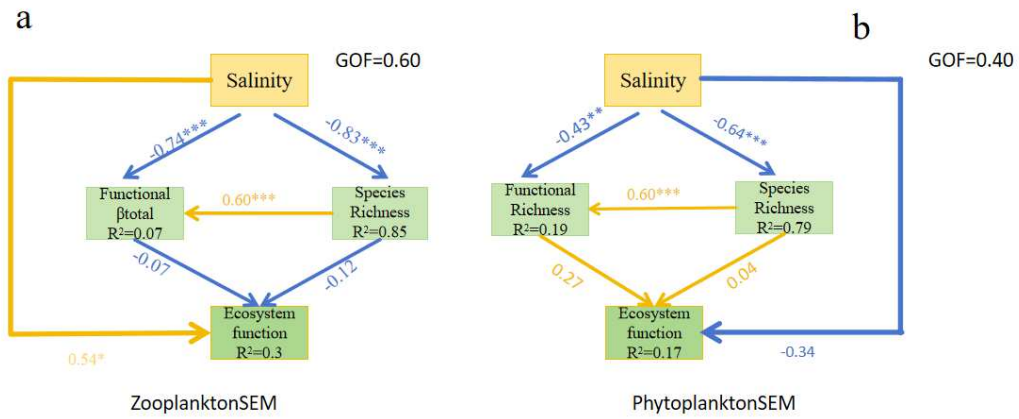


Figure 6 Structural equation modeling (SEM) pathways of salinity, plankton biodiversity, and ecosystem multifunctionality

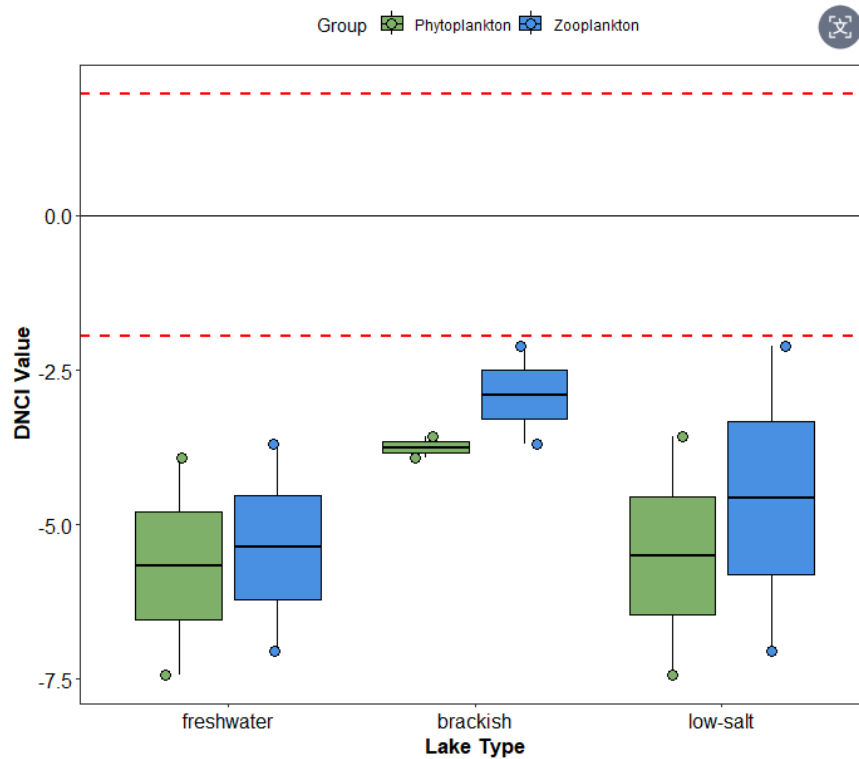


Figure 7 DNCI index distribution of phytoplankton and zooplankton across freshwater, brackish, and low-salt lake types

Table 1 Key Functional Traits and Coding Standards for Phytoplankton

character		category	coding
Form	Size	<20µm	Size1
		20-200µm	Size2
		>200µm	Size3
	Algae morphology	monoplast	Form1
		Chain-like or filamentous	Form2
		Colonial	Form3
	Colloid	Exist	Col1
		Without	Col2
	Silica	Present	Sil1
		Absent	Sil2
Behavior	Motility	Mesotrophic	Hab1
		Medium nutrition	Hab2
		Eutrophic	Hab3
		Has flagella	Fla1
Life history	Mode of reproduction	Without flagella	Fla2
		Sexual reproduction	Rep1
		Asexual reproduction	Rep2

Table 2 Key Functional Traits and Coding Standards for Zooplankton

character	category	coding
Size	<100µm	Size1
	150-300µm	Size2
	300-700µm	Size3
	700-1500µm	Size4
	>1500µm	Size5
Food source	Fungivore	F
	Phytophage	P
	Carnivore	C
	Omnivore	O
Breeding type	Sexual	1
	Asexual	2
Life cycle	Long	S
	Short	L
Motor pattern	Pelagic	P
	Adherent	A
	Facultative planktonic	F

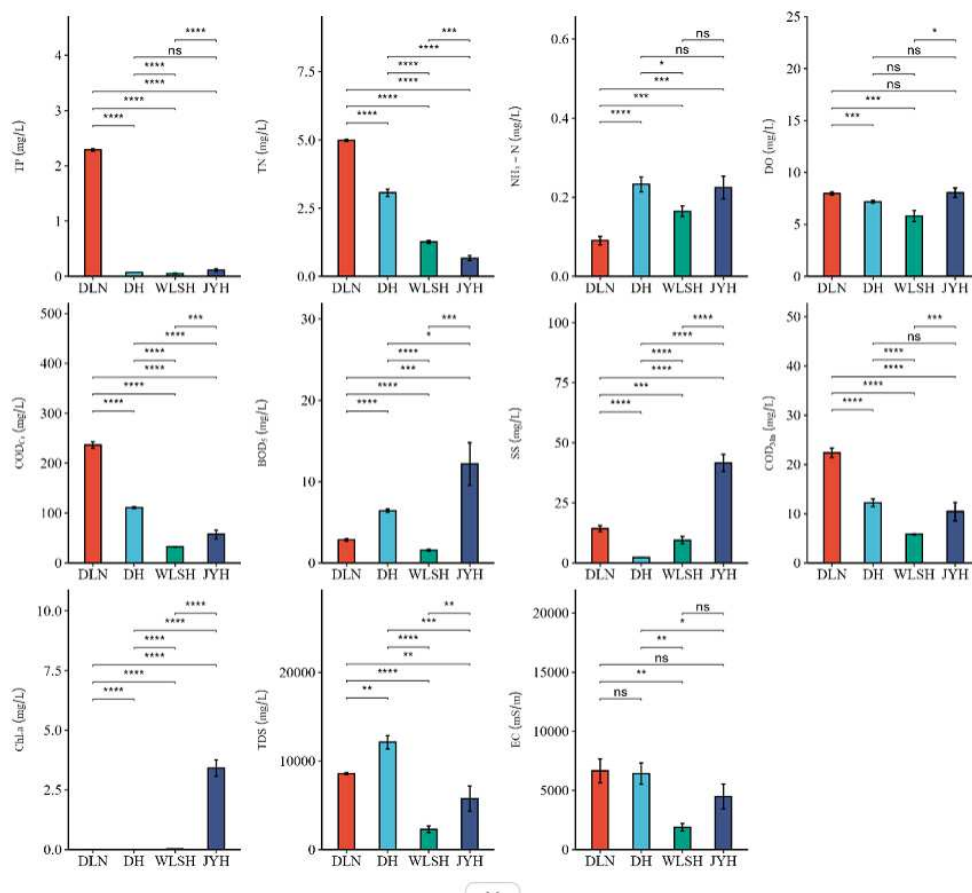


Figure S1 Inter-lake spatial variation of key hydrochemical parameters

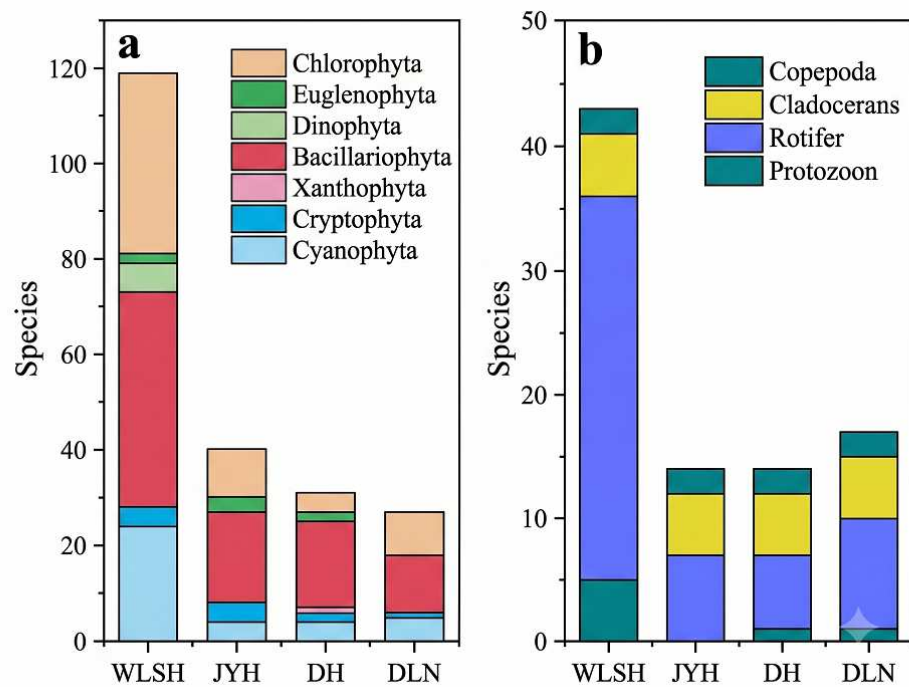


Figure S2 Stacked bar charts showing total species richness of major taxonomic groups for phytoplankton (a) and zooplankton (b) across WLSH, JYH, DH and DLN. Each color segment corresponds to one algal/faunal taxonomic group, and the y-axis represents total species number per lake.

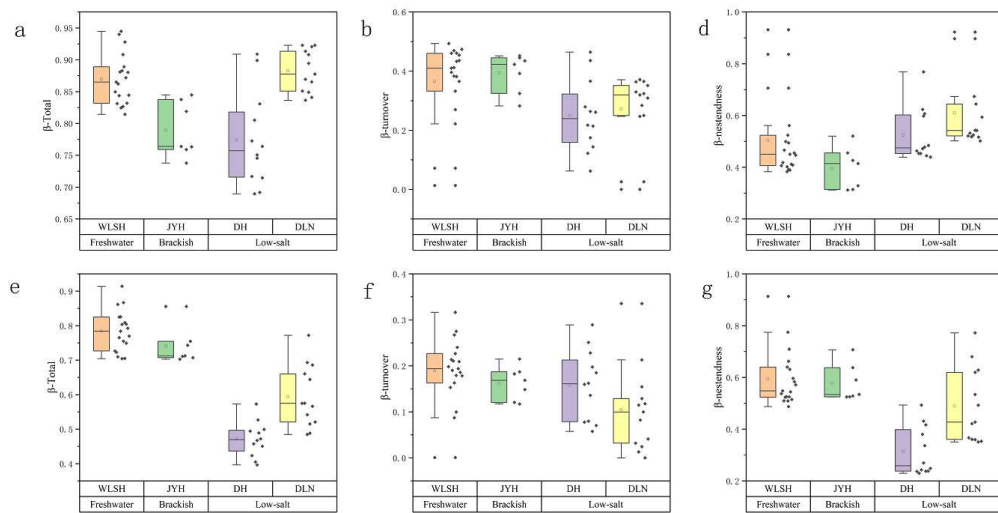


Figure S3 Distributions of total β -diversity, turnover and nestedness components for phytoplankton and zooplankton across lakes with different salinity levels
Upper row (a–d): phytoplankton communities; Lower row (e–g): zooplankton communities.
a,e: total β -diversity (β Total); b,f: β -diversity turnover (β turnover); d, g: β -diversity nestedness (β nestedness).
Four lake groups: WLSH (freshwater), JYH (brackish), DH and DLN (low salinity).

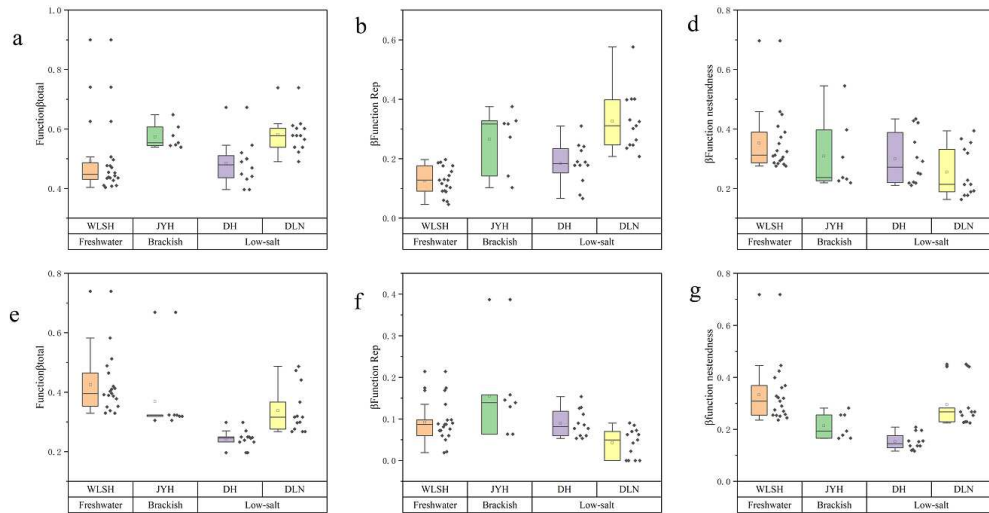


Figure S4 Distributions of total functional β -diversity, functional replacement and functional nestedness for phytoplankton and zooplankton across lakes with distinct salinity levels
Upper row (a–d): phytoplankton functional β -diversity; Lower row (e–g): zooplankton functional β -diversity.
a, e: total functional β -diversity (Function β total); b, f: functional replacement (β Function Rep); d, g: functional nestedness (β Function nestedness).
Four lake groups: WLSH (freshwater), JYH (brackish), DH and DLN (low salinity).

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