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Community assembly mechanism of phytoplankton in drinking water sources of tropical island, China

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Introduction: Phytoplankton, as primary producers in aquatic ecosystems, serves as indicators of the health of water environments. In tropical island regions facing the combined pressures of human activities and climate change, understanding the mechanism underlying the phytoplankton community structure is crucial. This knowledge is essential for safeguarding drinking water sources and for identifying potential ecological risks in aquatic systems.

Methods: This study focused on 22 drinking water sources on Hainan Island, comprising 11 rivers and 11 reservoirs. Phytoplankton samples were collected during December 2023 (dry season) and July 2024 (wet season). We systematically analyzed the α and β diversity, explored the environmental factors influencing community changes, and examined the mechanism underlying the assembly of the phytoplankton community.

Results and discussion: The results revealed a clear seasonal succession in the composition of the dominant phytoplankton community. During the dry season, *Cyanophyta*, *Chlorophyta*, and *Bacillariophyta* were dominant, whereas in the wet season, *Cyanophyta* dominated. Phytoplankton α-diversity was consistently higher in rivers than in reservoirs and β-diversity was predominantly structured by species turnover (>84%). The Mantel test identified water temperature, pH and total phosphorus as key environmental factors influencing changes in the phytoplankton community structure. Co-occurrence network analysis revealed that during the wet season, the phytoplankton community nodes exhibited higher connection density and stronger correlations. The assembly of these community was primarily governed by dispersal mechanism, with niche processes playing a comparatively minor role. This study provides a novel, mechanistic framework for understanding tropical island aquatic ecosystems, offering critical insights for predicting ecological risks and guiding resilience-based water quality management in the tropical aera.

KEYWORDS

community assembly processes, environmental factors, habitat heterogeneity, phytoplankton, tropical islands

1 Introduction

Phytoplankton is microscopic photosynthetic autotrophs with diverse morphologies, from single-celled to multicellular forms, that inhabit aquatic environments (Borics et al., 2012). As the primary producers in aquatic ecosystems, they fix carbon and release oxygen through photosynthesis, thereby supplying the material and energetic foundation for food webs and playing a central role in biogeochemical cycles and ecosystem stability (Borics et al., 2012; Cardinale et al., 2002; Field et al., 1998). Due to its sensitivity to environmental changes, the phytoplankton community serves as a key indicator of the health of aquatic ecosystems, including lakes (Meng et al., 2023; Xiao et al., 2022), rivers (Loick-Wilde et al., 2016), and reservoirs (Alpecho et al., 2024). Understanding the assembly mechanism of the community is crucial for accurately predicting phytoplankton dynamics, thereby supporting aquatic ecological monitoring, evaluation, and scientific management (Cira et al., 2018; Liu et al., 2023; Wu et al., 2023; Yi et al., 2024). Recent studies indicate that the phytoplankton community assembly is shaped by both deterministic and stochastic processes (Liu et al., 2023; Vellend, 2010; Yi et al., 2024). Deterministic processes are primarily driven by environmental filtering, where species suited to particular conditions are selected through mechanisms like resource competition, predation pressure, and environmental selection (Chesson, 2000; Grubb, 1977; Kraft et al., 2015). Conversely, stochastic processes influence community structure through dispersal limitation, ecological drift, and random extinction events, predominating when environmental selection pressure is weak or conditions are homogeneous (Chase, 2003; Isabwe et al., 2018).

Phytoplankton community assembly mechanism vary significantly across different water bodies, primarily influenced by the hydrodynamic characteristics of each system (Xiao et al., 2022; Zhang et al., 2024). In plain rivers, characterized by fast flow velocities and high habitat continuity, deterministic processes like environmental filtering typically prevail (Isabwe et al., 2022). Conversely, in estuarine and lake ecosystems, where hydrodynamic processes are complex or water bodies are relatively still, stochastic processes play a more prominent role (Sun et al., 2023; Xiao et al., 2022). These variations underscore the fundamental impact of hydrodynamic conditions on the assembly processes of the phytoplankton community. Anthropogenic disturbances significantly impact the community assembly mechanism of phytoplankton. In rivers (Isabwe et al., 2018) and estuaries (Zhao et al., 2021) heavily affected by human activities, deterministic processes primarily govern the seasonal dynamics of these communities. Conversely, in plateau floodplains with minimal human interference and pronounced natural hydrological cycles, the assembly mechanism exhibit dynamic transitions. Specifically, deterministic processes dominate during the non-flood season, whereas stochastic processes take precedence during the flood season (Huang et al., 2023a). Recent studies have reinforced the understanding of ecosystem dynamism, showing that diffusion limitation significantly affects community dynamics in summer, whereas niche processes are more influential in spring (Yi et al., 2024). Additionally, environmental changes during spring and autumn exert the most pronounced effects on community structure (Fu et al., 2024; Xu et al., 2023, 2024). Consequently, hydrological changes, such as variations in flow velocity and residence time, along with the cyclical alternation of flood and dry seasons, are crucial in regulating the balance between deterministic and stochastic processes (Huang et al., 2023b; Wu et al., 2018).

The study of the phytoplankton community structure in aquatic systems, including rivers, lakes, and reservoirs, has been a focus of extensive research. For instance, Isabwe et al. (2022) demonstrated that deterministic environmental filtering predominates in shaping the phytoplankton community in urban rivers. In contrast, Xiao et al. (2022) conducted a comprehensive analysis of 81 lakes in the middle and lower reaches of the Yangtze River, revealing that spatial factors have a more significant impact on the phytoplankton community than environmental factors. They concluded that stochastic processes predominantly govern the assembly of the phytoplankton community in these lakes. Jin et al. (2022) demonstrated that in 24 tropical and subtropical reservoirs in China, the dispersal process significantly influenced the assembly of the phytoplankton community more than the niche process. Most current research on the phytoplankton community assembly mechanism primarily targets temperate and subtropical water bodies (Jiao et al., 2020; Zhu et al., 2024). These findings may have limited applicability to tropical water bodies because their ecological drivers differ. Unlike temperate and subtropical systems regulated by four-season thermal cycles, tropical water bodies exhibit persistent thermal stratification (Han et al., 2000) and a hydrological regime dominated by distinct wet and dry seasons (Song et al., 2023). Intense monsoon precipitation can abruptly alter hydraulic retention time and nutrient loading (Travaini-Lima et al., 2016), which may increase the role of stochastic processes (for example, dispersion and drift) relative to deterministic environmental filtering. In addition, the persistently high tropical temperatures accelerate metabolic rates (Latorre et al., 2023), potentially strengthening biological interactions such as competition and predation as primary assembly forces. Consequently, investigating the specific mechanism of the phytoplankton community assembly in these tropical environments is urgent for more accurate predictions of its ecological functions.

This study investigated 22 representative drinking water sources (11 rivers and 11 reservoirs) in Hainan Province to systematically explore the spatio-temporal dynamics of the phytoplankton community through multi-scale comparative observations. The research aims to address several critical knowledge gaps and practical challenges in the current understanding of tropical island aquatic ecology: (1) Foundational ecological patterns: To quantify the distinct divergence of the phytoplankton community between dry and wet seasons, and between riverine and reservoir ecosystems, thereby elucidating the differential impacts of seasonal hydrological pulses and habitat heterogeneity on community assembly; (2) Management and drivers: To identify key environmental drivers governing community turnover, providing precise targets for water quality management; (3) Biotic interaction networks: To analyze the symbiotic and competitive relationships among phytoplankton to evaluate community stability; (4) Core assembly mechanism: To clarify the ecological processes shaping community structure—specifically dispersal limitation versus environmental selection—thereby deepening theoretical insights into biodiversity maintenance in tropical waters. In summary, by employing theoretical frameworks such as the "Dispersal-Niche Continuum" as a lens, this study thoroughly elucidates the assembly mechanism of phytoplankton communities in tropical island water bodies, contributing to the advancement of freshwater ecological theory. Furthermore, it offers a direct scientific basis for ecological risk early warning, water quality optimization, and drinking water security in tropical regions, holding substantial practical value for sustainable water resource management in the context of climate change.

2 Materials and methods

2.1 Sample collection

To systematically investigate the spatio-temporal dynamics of the phytoplankton community in tropical aquatic ecosystems, a comprehensive field survey was conducted across Hainan Province. The study area encompassed 22 representative drinking water sources, comprising 11 reservoirs and 11 rivers. Sampling campaigns were carried out during the dry season (December 2023) and the wet season (July 2024) to capture seasonal variations (Supplementary Figure S1; Supplementary Table S1). For each season, two to three water samples were collected from each source, totaling 128 samples across both seasons (Supplementary Table S2). Sampling was performed at a uniform depth of 0.5 m below the water surface. For qualitative sampling, a No. 25 plankton net (64 µm mesh) was towed slowly in a figure-eight ("∞") pattern underwater for 3–5 min. Samples were fixed immediately after collection by adding 4% formalin. For quantitative sampling, a 5 L standard water sampler was used to collect water; after obtaining 1 L, 15 mL of Lugol's solution was added on-site for fixation. Site information was meticulously recorded and samples were labeled accordingly. All samples were then transported to the laboratory under conditions that maintained low temperatures and protected them from light.

2.2 Identification of phytoplankton samples

A 1L quantitative sample was transferred to a sedimentation cylinder and allowed to stand for 48 hours. After settling, the supernatant was removed with a small siphon, and the remaining concentrate was transferred to a beaker and reduced to a final volume of 50 mL. For taxonomic identification and enumeration, 0.1 mL of the concentrated sample was placed in a phytoplankton counting chamber. Species-level identification was performed with a Nikon E100 microscope using "Atlas of Freshwater Microorganisms" (Zhou and Chen, 2010) and "Descriptions of Freshwater Organisms in China" (Han and Shu, 1995) as the primary references. Three replicates were counted for each sample to ensure accuracy, and the average value was calculated for reliable results.

2.3 Measurement and analysis of environmental factors

In this study, a portable multi-parameter water quality analyzer (ProQuatro YSI, USA) was utilized to measure environmental variables of the surface water at a constant depth of 0.5 m. The on-site measurements included physical indicators such as water temperature (WT), pH, dissolved oxygen (DO), Oxidation-Reduction Potential (ORP) and electrical conductivity (EC). Concurrently, 5 L water samples were collected, promptly stored, and transported to the laboratory for chemical analysis. For preservation, samples designated for chemical oxygen demand (COD), total nitrogen (TN), and total phosphorus (TP) were acidified with sulfuric acid to a pH of 2 or lower. Meanwhile, samples for five-day biochemical oxygen demand (BOD) were kept at 4°C in the dark. All chemical indicator analyses were conducted within 24 hours to ensure accuracy. The analysis methods for environmental variables employed in this study were as follows: COD was determined using the potassium dichromate method; BOD was measured via the dilution and seeding method; TP was detected using the ammonium molybdate spectrophotometric method; and Total Nitrogen (TN) was determined through the alkaline potassium persulfate digestion ultraviolet spectrophotometric method. These parameters were analyzed in strict accordance with the "Environmental Quality Standards for Surface Water" (GB 3838-2002) to ensure data accuracy and comparability (Yang et al., 2023). Supplementary Table S3 provides the seasonal average values of environmental factors for each lake.

2.4 Diversity of α and β in the phytoplankton community

Four indices were employed to assess the biodiversity of phytoplankton in tropical island drinking water sources: Four indices were employed to assess the biodiversity of phytoplankton in tropical island drinking water sources: the Shannon-Wiener diversity index (H′), the Simpson dominance index (DS), the Pielou evenness index (J) and the Margalef richness index (d) (Therriault and Kolasa, 2000; Yi et al., 2024). The corresponding formulas (Equations 1–4) are as follows:

$$H' = -\sum_{i=1}^{s} (P_i \, ln \, P_i) \tag{1}$$

$$D_s = 1 - \sum_{i=1}^{s} (P_i^2) \tag{2}$$

$$J = \frac{H'}{H_{max}} \tag{3}$$

$$d = \frac{S - 1}{lnN} \tag{4}$$

In these formulas, S denotes the total number of phytoplankton species, while Pi indicates the proportion of the i-th species' cell abundance relative to the total abundance. N represents the overall cell abundance of phytoplankton at the sampling sites.

To visualize compositional differences in the phytoplankton community, Principal Coordinates Analysis (PCoA) was performed. PERMANOVA (Anderson, 2017) was then applied to test for significant differences in community composition among habitats and seasons. Finally, β-diversity was quantified using the Jaccard dissimilarity index and decomposed into turnover and nestedness components to elucidate the underlying dynamic processes.

2.5 Co-occurrence network analysis

Spearman rank correlation was used to construct phytoplankton co-occurrence networks for different habitats (rivers and reservoirs) and seasons (dry and wet). Only interspecific associations with strong correlations ($|R| \geq 0.6$) (Barberán et al., 2014) that were statistically significant ($p < 0.05$) (Liang et al., 2023) were retained. In each network, nodes represented phytoplankton species, with node size reflecting species abundance, while edges indicated significant correlations. Networks were visualized in Gephi (Bastian et al., 2009). To describe network topology, the number of nodes, number of edges, modularity index, clustering coefficient, average path length, graph density, and average degree were calculated. Additionally, 1,000 Erdős–Rényi random networks matched to the observed networks by node and edge counts were generated to benchmark these topological metrics.

2.6 Community assembly mechanism

To assess the relative roles of dispersal and niche processes across phases, the Dispersal–Niche Continuum Index (DNCI) framework was applied. Pairwise DNCI values were then compared among phase combinations to identify whether dispersal or niche processes dominated community assembly across hydrological seasons and habitats.

2.7 Statistical analyses

Statistical analyses were performed using R (v.4.4.1) and SPSS (v.27.0). To compare environmental parameters and α-diversity indices among seasons, the Kruskal–Wallis H nonparametric test was applied in SPSS. To detect compositional differences, Principal Coordinates Analysis (PCoA) based on Bray–Curtis distances and Permutational Multivariate Analysis of Variance (PERMANOVA; 999 permutations) were performed using the *vegan* package (v.2.5-6) (Oksanen et al., 2007) in R. Furthermore, β-diversity was decomposed into turnover and nestedness components using the *betapart* package (v.1.5.6) (Baselga and Orme, 2012). For network analysis, networks were constructed and topological parameters computed with the *igraph* package (v.2.1.4) (Csardi and Nepusz, 2005), while empirical and random networks were compared using the Z-test (Zhao et al., 2016). Finally, community assembly mechanism was investigated with the *DNCImper* package (Vilmi et al., 2020) by applying the DNCI_multigroup function to calculate pairwise DNCI values.

3 Results

3.1 Temporal and spatial variations of environmental factors

The physicochemical characteristics of drinking water sources demonstrate distinct dynamic patterns, varying both seasonally (dry vs. wet season) and spatially (river vs. reservoir). Most physical and chemical factors, except salinity (SAL), exhibited significant spatio-temporal variations in drinking water sources during the study period (Kruskal-Wallis H test, $p < 0.05$), as shown in Supplementary Figure S2. In river water, the temperature rose markedly from the dry season (25.38 ± 1.81°C) to the wet season (29.99 ± 2.46°C) ($p < 0.001$). Reservoirs exhibited a similar seasonal warming pattern, with significantly higher water temperatures observed during the wet season compared to the dry season ($p < 0.001$). Nutrient and organic matter analyses revealed that TN (1.24 ± 0.35 mg/L), TP (0.12 ± 0.06 mg/L), and COD (15.03 ± 4.02 mg/L) in rivers during the wet season were significantly higher than those observed in reservoirs during the wet season, as well as in rivers during the dry season ($p < 0.001$). During the wet season, the reservoir's pH (8.65 ± 0.42) and DO (8.17 ± 0.74 mg/L) were significantly higher compared to both the river during the same season and the reservoir in the dry season ($p < 0.001$). Notably, ORP and BOD also exhibited significant differences between the reservoir's dry and wet season ($p < 0.001$).

3.2 Spatio-temporal patterns of the phytoplankton community and α, β diversity characteristics

A total of 228 phytoplankton taxa (including varieties and forms) were identified through classical morphological analysis. These species distributed across 99 genera within 8 phyla. *Chlorophyta* emerged as the most diverse, comprising 102 species across 41 genera, representing 44.7% of the total species. *Bacillariophyta* followed with 62 species in 26 genera, and *Cyanophyta* with 40 species in 20 genera. In contrast, *Xanthophyta* had the fewest, with just one species in a single genus (Figure 1A). The cell density for each phylum and the overall density were illustrated in Supplementary Figure S3. The overall distribution of

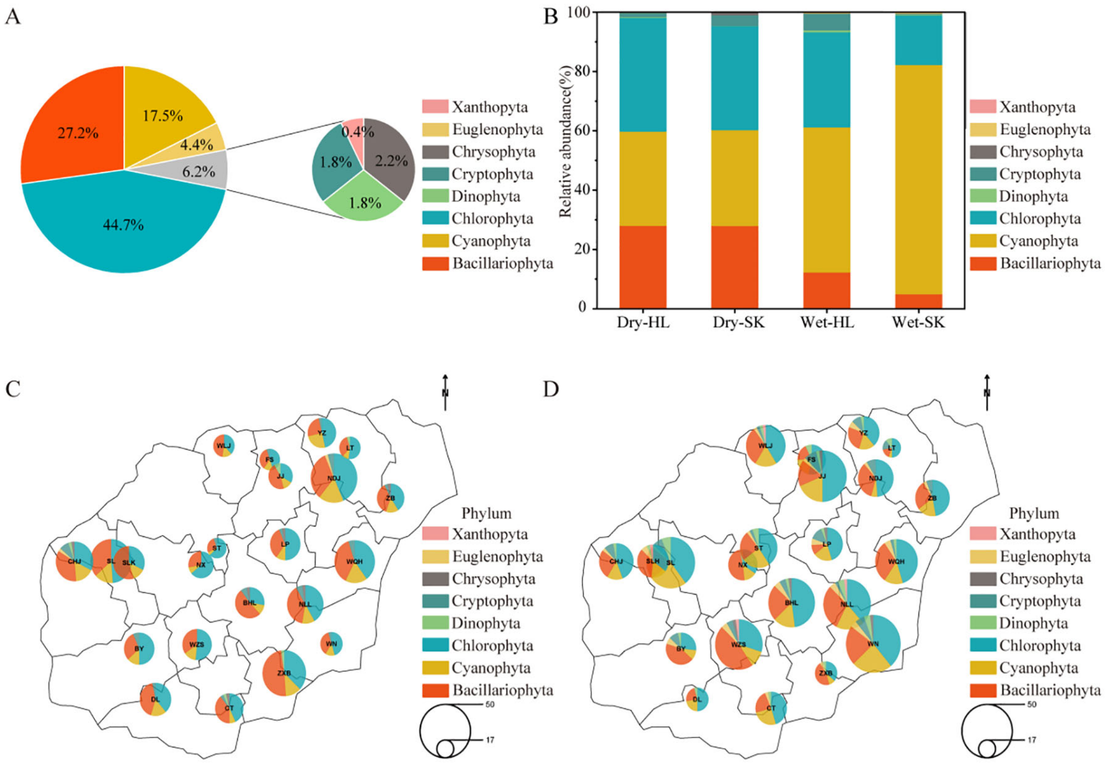

FIGURE 1
Composition of the phytoplankton community in drinking water sources on tropical islands. **(A)** Proportion chart detailing the composition of phytoplankton phyla. **(B)** Changes in relative abundances of the community in rivers and reservoirs comparing dry and wet seasons: "Dry-HL" indicates rivers during the dry season, "Dry-SK" refers to reservoirs in the dry season, "Wet-HL" represents rivers in the wet season, and "Wet-SK" denotes reservoirs in the wet season. **(C)** Distribution map of the phytoplankton community structure during the dry season. **(D)** Distribution map during the wet season. In **(C, D)**, the circle size refers to species richness. For abbreviations of rivers and reservoirs names, see Supplementary Table S2.

phytoplankton density varied from 14.12 to 65.72×10^6 cells/L. Peak density occurred in reservoir samples during the wet season, while the lowest density was recorded in the dry season. Among the different groups, *Cyanophyta* was the most dominant, with density ranging from 4.39 to 44.32×10^6 cells/L. *Chlorophyta* followed, with density varying between 2.81 and 13.73×10^6 cells/L. In contrast, *Xanthophyta* exhibited the lowest density, ranging from 0 to 0.43×10^4 cells/L. The total phytoplankton biomass ranged from 3.51 to 12.38 mg/L (Supplementary Figure S4). Biomass peaked in reservoir samples during the wet season and reached its minimum in the dry season. Among phyla, *Chlorophyta* dominated, with density from 1.54 to 6.49 mg/L. *Bacillariophyta* was the second most abundant group, ranging from 1.57 to 2.67 mg/L.

Analysis of community composition identified 49 phytoplankton species as consistently present across all spatial and temporal conditions. Habitat specificity comparison revealed the greatest overlap of phytoplankton species, totaling 90 species, between rivers and reservoirs during the wet season. Conversely, the overlap was minimal, with only 65 species, between reservoirs in the dry and wet seasons (Supplementary Figure S5). In terms of community dynamics, phytoplankton abundance in rivers and reservoirs was similar during the dry season but differed significantly in the wet season. During the wet season, the relative abundances of *Bacillariophyta* and *Chlorophyta* decreased, while *Cyanophyta* increased significantly, becoming the dominant group (Figure 1B, Supplementary Figure S6). Spatio-temporal analysis of species richness showed that the Nandu River had the highest phytoplankton richness during the dry season, with 46 species, while the Songtao Reservoir recorded the lowest, with 19 species. In the wet season, the Wanning Reservoir exhibited the highest richness, with 54 species, whereas the Longtang River had the lowest, with 18 species (Figures 1C, D).

The analysis of the α-diversity within the phytoplankton community demonstrated distinct spatio-temporal distribution patterns. Spatially, α-diversity was greater in river habitats compared to reservoir habitats (Figures 2A–D). During the dry season, the river exhibited higher Shannon-Wiener and Pielou indices than the reservoir, though these differences were not significant. In contrast, the river showed significantly higher Margalef and Simpson indices. During the wet season, all α-diversity indices were significantly greater in the river than in the reservoir. Temporally, during the wet season, reservoirs exhibited a significantly higher Shannon-Wiener index than during the dry season ($p < 0.01$). Conversely, the Pielou index was significantly elevated in the dry season compared to the wet season ($p < 0.05$). Similarly, the Margalef index in rivers was notably higher during the dry season than in the wet season ($p < 0.001$), while the Simpson

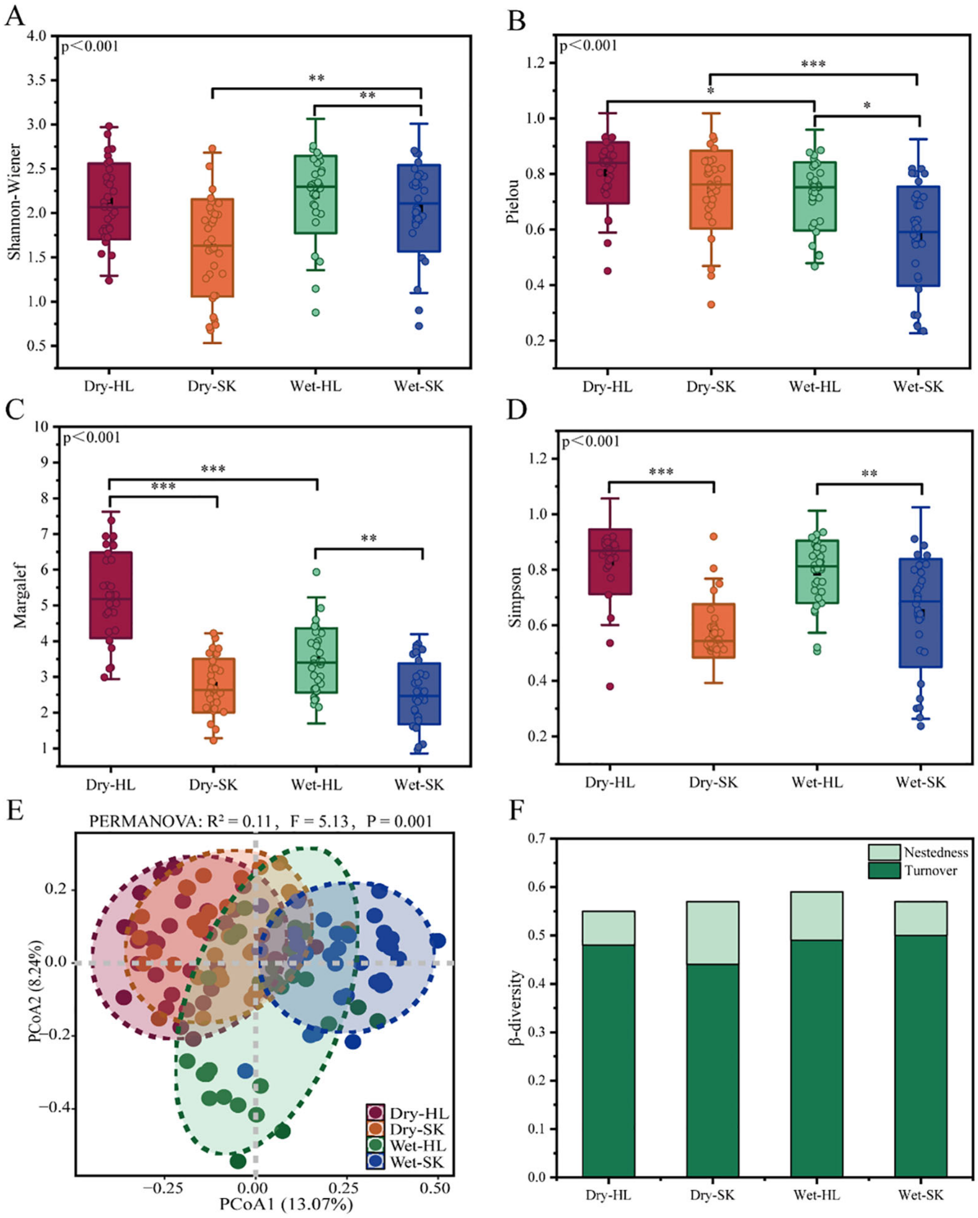

FIGURE 2

Temporal and spatial patterns of the phytoplankton community diversity in drinking water sources on tropical islands. **(A)** Variations in the Shannon-Wiener diversity index over time and space. **(B)** Differences in the Pielou evenness index across these dimensions. **(C)** Changes in the Margalef richness index at various sampling locations. **(D)** Seasonal variations in the Simpson dominance index, with significance levels denoted by * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. **(E)** Principal Coordinates Analysis (PCoA) of the phytoplankton community structure in rivers and reservoirs, comparing dry and wet seasons, assessed using a PERMANOVA test. **(F)** Spatio-temporal changes in the phytoplankton β-diversity index, along with its components of turnover and nestedness. Dry-HL, rivers during the dry season; Dry-SK, reservoirs during the dry season; Wet-HL, rivers during the wet season; Wet-SK, reservoirs during the wet season.

index showed no significant temporal variation (Figures 2A–D). Further analysis using PCoA (Figure 2E) and PERMANOVA (Supplementary Table S4) confirmed significant differences in the phytoplankton community composition across various spatio-temporal conditions ($R^2 = 0.11$, $F = 5.13$, $P = 0.001$).The phytoplankton community showed consistently moderate β-diversity across environments and seasons, with values of 0.55 for rivers in the dry season, 0.57 for reservoirs in the dry season, 0.59 for rivers in the wet season, and 0.57 for reservoirs in the wet season. This narrow range (0.55–0.59) indicates that species turnover remained relatively stable across the examined spatial and temporal scales. A closer examination of the β-diversity components indicated that the turnover processes played a significantly larger role in community differences than the nestedness process, contributing 86.4%, 76.4%, 84.0%, and 87.9%, respectively (Figure 2F; Supplementary Figure S7).

3.3 Relationship between the phytoplankton community and the surrounding environment

The Mantel test's statistical analysis revealed notable differences in how the phytoplankton community structure and diversity relate to environmental factors across seasons and habitats. In the dry season, river environments showed a significant negative correlation between TN and community structure ($r< 0.25$, $p < 0.05$). Conversely, in reservoirs, pH demonstrated a strong positive correlation ($0.25< r< 0.05$, $p < 0.01$), while ORP and latitude (Lat) exhibited weak positive correlations. During the wet season, DO in rivers was positively correlated with the community structure, whereas ORP, TP, and TN showed negative correlations. In reservoirs, temperature was positively correlated with BOD, and ORP was negatively correlated (Figure 3A). Phytoplankton α-

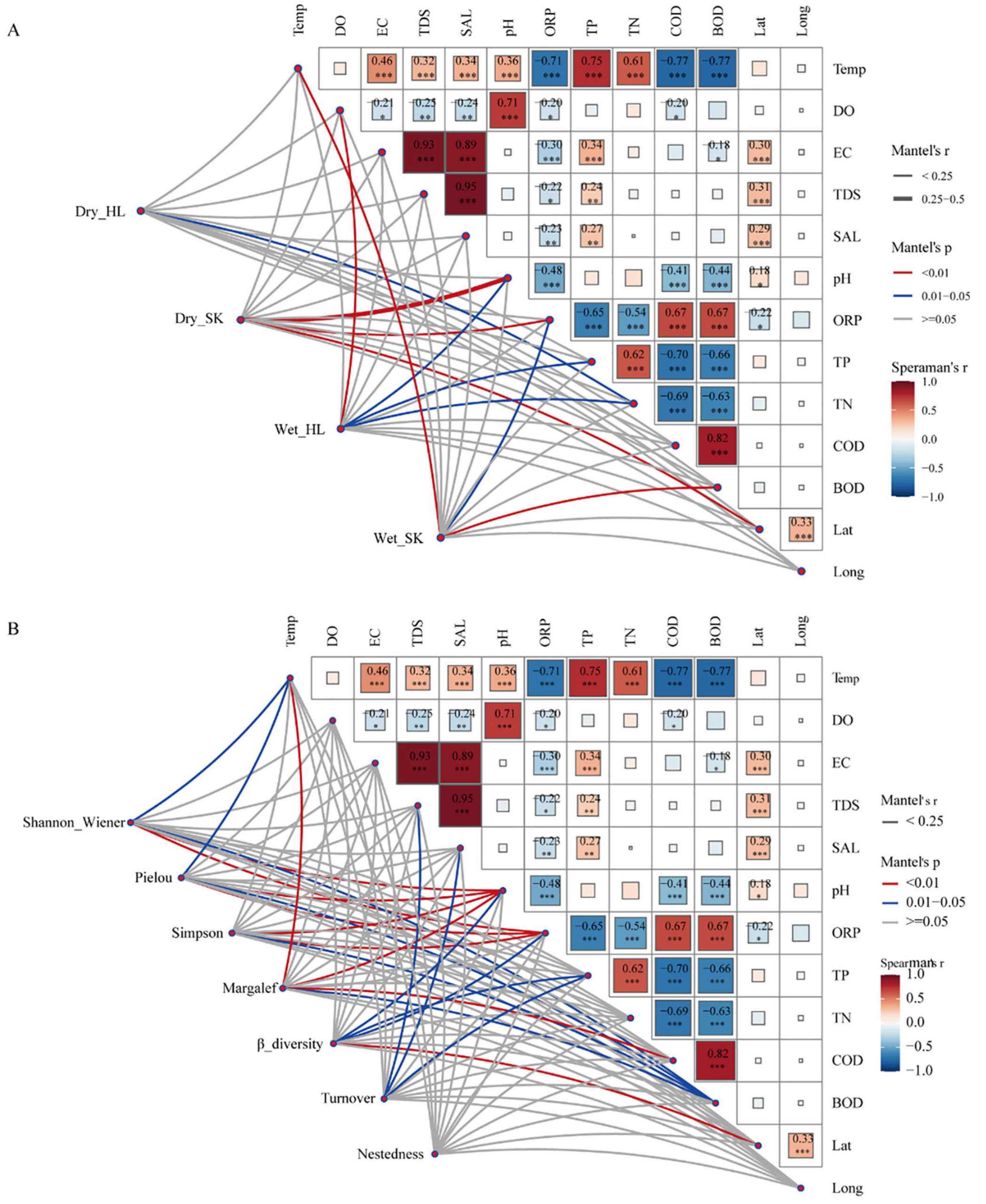

FIGURE 3
Correlation analysis between the phytoplankton community, its diversity, and various environmental factors. **(A)** The Mantel test results for the relationship between phytoplankton abundance and water environmental factors. **(B)** The Mantel test results for the correlation between phytoplankton α/β diversity and water environmental factors. The study distinguishes between different conditions: Dry-HL refers to a river in the dry season, Dry-SK to a reservoir in the dry season, Wet-HL to a river in the wet season, and Wet-SK to a reservoir in the wet season. Statistical significance is indicated by asterisks: * denotes p < 0.05, ** denotes p < 0.01, and *** denotes p < 0.001.

diversity generally demonstrated a negative correlation with temperature and BOD, while showing a positive correlation with pH and ORP. Notably, the Margalef richness index uniquely responded to temperature and COD. Overall, β-diversity exhibited negative correlations with ORP, TP, and pH, but was positively correlated with Lat. A significant negative correlation was observed between the turnover component of β-diversity and TDS, SAL and TP. In contrast, the nestedness component showed no significant association with any water quality parameters (Figure 3B).

3.4 Analysis of the co-occurrence network and the community assembly mechanism

The phytoplankton co-occurrence networks constructed for four distinct habitat conditions exhibited entirely positive connections and highly modular structures (Figures 4A–D). The analysis of the network's topological structure revealed that the river ecosystem's complexity, including average degree and graph density, was lower compared to the reservoir ecosystem. Notably, the reservoir network during the wet season demonstrated the greatest stability, characterized by a clustering coefficient of 0.701 and a modularity of 0.810, whereas its stability in the dry season was comparatively weaker (Supplementary Table S5). In terms of habitat connectivity, node-sharing analysis revealed that the river and reservoir shared the most nodes (49 species) during the wet season, but shared the fewest (only 23 species) during the dry season (Supplementary Figure S8B). Regarding species composition, the dominant nodes were primarily composed of *Chlorophyta*, *Bacillariophyta* and *Cyanophyta*. Seasonal variations significantly impacted this composition: during the wet season, the proportion of *Chlorophyta* nodes was substantially higher compared to the dry season, whereas *Bacillariophyta* exhibited an inverse pattern. Interestingly, *Cyanophyta* represented the smallest proportion in the river network during the wet season (Supplementary Figure S8A).

Most notably, although *Euglenophyta*, *Chrysophyta* and *Cryptophyta* occupied a relatively small proportion of network nodes—reflecting lower species richness—they exhibited

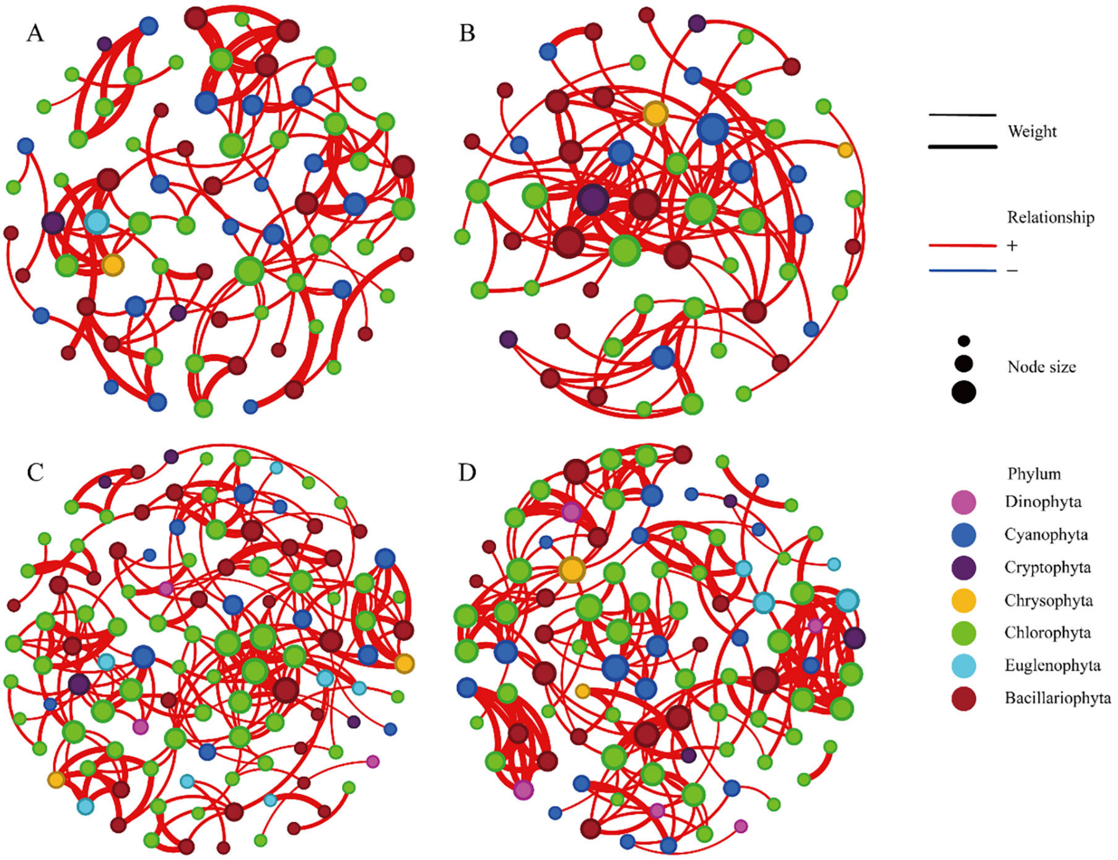

FIGURE 4
The co-occurrence network structures of the phytoplankton community in drinking water sources on tropical islands. **(A)** Rivers in the dry season, **(B)** Reservoirs in the dry season, **(C)** Rivers in the wet season, and **(D)** Reservoirs in the wet season. The networks are visualized using a phylum-based attribute layout. In these networks, each node signifies a phytoplankton species, and each edge indicates a relationship, with red lines for positive and blue lines for negative interactions. The species are color-coded according to their respective phyla. Additionally, the node size reflects the number of connections it has. The connections between nodes indicate statistically significant ($p \leq 0.05$) and strong correlations, as determined by Spearman's correlation coefficient, with $|R| \geq 0.60$.

exceptionally high average connectivity within specific habitats. This topological feature implies that they may function as "keystone taxa," playing a crucial role in maintaining community stability (Supplementary Table S6). Specifically, *Euglenophyta* demonstrated the strongest connectivity in the dry season river (Dry-HL) network (average degree: 6.00). Conversely, *Cryptophyta* were most active in the dry season reservoir (Dry-SK) network (average degree: 4.33). Furthermore, *Chrysophyta* maintained high connectivity across both habitats during the wet season (Wet-HL: 5.00; Wet-SK: 5.50). These findings suggest that these rare or low-abundance groups exert a disproportionate influence on community assembly and succession through intense interspecific interactions, particularly in response to complex environmental fluctuations.

The Dispersal-Niche Continuum Index (DNCI) analysis revealed significant spatio-temporal heterogeneity in community assembly mechanism. All pairwise comparisons exhibited significantly negative DNCI values (Table 1), indicating the predominance of dispersal-driven stochastic processes in shaping tropical island phytoplankton community. Specifically, intense hydrological connectivity during the wet season facilitated the highest level of passive dispersal between the reservoir and river (DNCI = -28.81). In contrast, reduced water levels during the dry season significantly attenuated this dispersal effect (-13.42), leading to a relative resurgence in the influence of environmental filtering. These findings were further corroborated by null model simulations, where the "Niche + Dispersal" model yielded the lowest E-values and provided the optimal fit to the empirical data, outperforming the pure niche model (Figure 5). Collectively, these results confirm the dominant role of dispersal processes in this ecosystem, with environmental selection playing a subsidiary role under specific hydrological conditions.

4 Discussion

4.1 Spatio-temporal variations and diversity of the phytoplankton community structure

Our results showed that phytoplankton species in the studied tropical island drinking water sources were diverse, predominantly comprising *Chlorophyta* and *Bacillariophyta* (Figure 1A). This aligned with observations by Kumar et al. (2020) and Wagaw et al. (2021) regarding tropical lakes and reservoirs. During the dry season, the abundance of phytoplankton in rivers and reservoirs of tropical island water sources was similar, with *Bacillariophyta*, *Cyanophyta*, and *Chlorophyta* being dominant (Figure 1B). Similar phytoplankton abundance composition have been reported in studies by Mohammed et al. (2023) and Moura et al. (2013). During the wet season, characterized by higher temperature, *Cyanophyta's* abundance proportion increased, contrasting with the declining trend of *Bacillariophyta* (Figure 1B, Supplementary Figure S6). This seasonal succession pattern aligns closely with previous studies. In long-term monitoring of Prashar Lake and Hongmen Reservoir, Jindal et al. (2014) and Liu et al. (2021a) reported that high temperatures and abundant nutrients (such as phosphate) during the wet season (or summer) drove *Cyanophyta* outbreaks and dominance, whereas low temperatures limited their growth. Meanwhile, rainfall-induced turbidity reduces light penetration, inhibiting diatom growth and diminishing their abundance (Duong et al., 2019; Lin et al., 2011).

TABLE 1 The DNCI values for the phytoplankton community across various spatio-temporal contexts.

Group1	Group2	DNCI	CI.DNCI	S.DNCI
Dry-HL	Dry-SK	-13.42	1.71	0.86
Dry-HL	Wet-HL	-23.17	1.66	0.83
Wet-SK	Dry-SK	-25.81	1.96	0.98
Wet-SK	Wet-HL	-28.81	1.93	0.97

Positive DNCI values suggest that niche differentiation predominates in community assembly, whereas negative values indicate that dispersal is the primary process. CI.DNCI denotes the confidence interval of DNCI, and S.DNCI represents the standard deviation of DNCI. Dry-HL, rivers during the dry season; Dry-SK, reservoirs during the dry season; Wet-HL, rivers during the wet season; Wet-SK, reservoirs during the wet season.

Spatially, rivers consistently exhibited higher α-diversity than reservoirs, regardless of the season. This disparity is likely attributed to differences in habitat heterogeneity and hydrological dynamics. Rivers are characterized by high spatial heterogeneity—including velocity gradients, substrate diversity, and fluctuating nutrient inputs—which create varied niches that support a wide range of generalist species (Sriswasdi et al., 2017). In contrast, the relatively static and homogeneous environment of reservoirs tends to promote competitive exclusion, resulting in the dominance of a few specialist species and a consequent reduction in overall diversity (Clavel et al., 2011; Therriault and Kolasa, 2000). Temporally, divergent patterns were observed between species diversity and evenness. The Shannon-Wiener diversity index peaked during the wet season, likely due to rainfall-induced nutrient influxes (N and P) that compromise water quality but stimulate the proliferation of tolerant taxa, such as *Chlorophyta* and *Cyanophyta* (Barçante et al., 2020). Conversely, Pielou's evenness exhibited a significantly declining trend during the wet season ($p < 0.05$). This suggests that while nutrient enrichment increases species richness, the concurrent rise in water temperatures favors the rapid expansion of specific dominant species. These dominant taxa outcompete others, thereby reducing community evenness despite the higher overall richness (Vallina et al., 2017; Yang et al., 2021). The spatio-temporal pattern of α-diversity is fundamentally shaped by the tropical monsoon marine climate of the study area. Characterized by distinct dry and wet seasons, this climate features concentrated precipitation during the summer, resulting in significant fluctuations in water levels and temperatures. Such environmental variability directly drives the seasonal succession of the phytoplankton community (Wentzky et al., 2020). Although specific rainfall data were not collected in this study, prior research has established that precipitation regimes exert a strong regulatory effect on phytoplankton distribution. Notably, heavy rainfall events typically promote habitat homogenization and accelerate the physical dispersion of plankton in tropical water

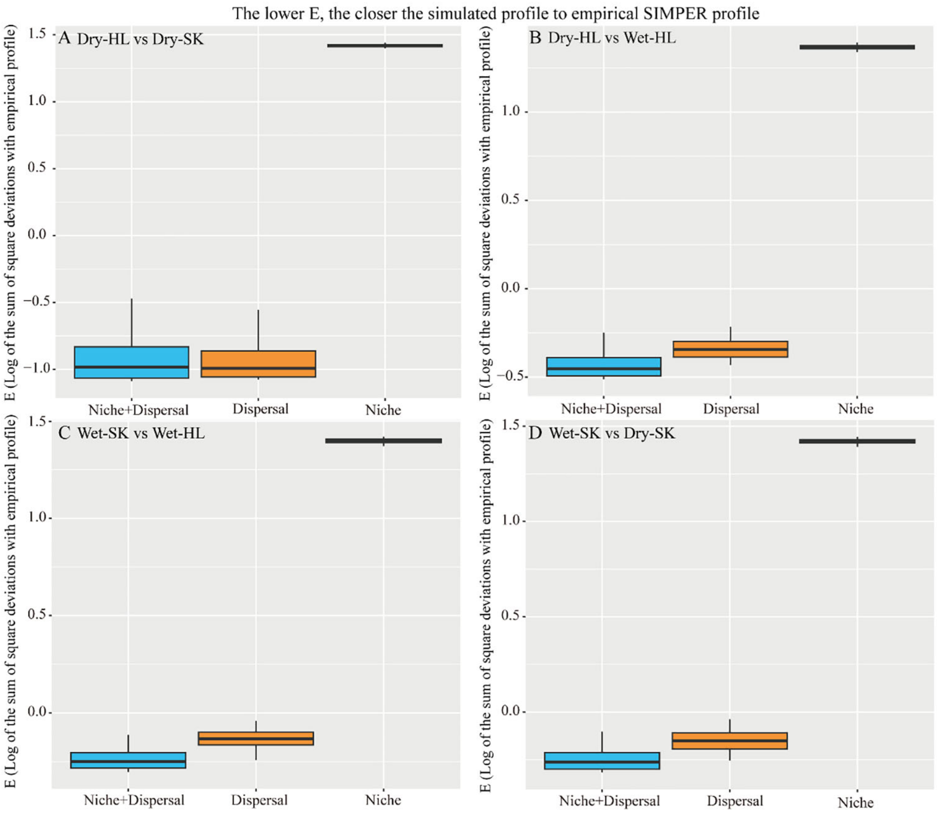

FIGURE 5
PER-SIMPER analysis assessing the relative significance of dispersal and niche processes in the assembly of the phytoplankton community across various spatial and temporal scales. The comparisons are made between: **(A)** Dry-HL and Dry-SK; **(B)** Dry-HL and Wet-HL; **(C)** Wet-SK and Wet-HL; and **(D)** Wet-SK and Dry-SK. In this analysis, the ordinate E denotes the logarithm of the sum of squared deviations between the empirical and simulated distributions. A lower E value suggests a greater likelihood that the corresponding process predominates in community assembly. Dry-HL, rivers during the dry season; Dry-SK, reservoirs during the dry season; Wet-HL, rivers during the wet season; Wet-SK, reservoirs during the wet season.

bodies (Brasil et al., 2016). Collectively, these climatic and hydrological factors elucidate the pronounced spatio-temporal differences observed in the phytoplankton community structure.

In examining the β-diversity of drinking water sources on tropical islands across various spatio-temporal scales, the turnover component predominates over the nestedness component. This indicates that differences in species composition are primarily due to spatial replacements, a pattern consistent with previous findings in studies of β-diversity among phytoplankton communities in different biological groups and regions (Bottero et al., 2020; Maloufi et al., 2016). The prominence of the turnover component in this study area may result from factors such as habitat loss, geographical isolation, dispersal limitations, environmental filtering, and competition (Gutiérrez-Cánovas et al., 2013). The fragmented distribution of drinking water sources on tropical islands has resulted in considerable geographical isolation between rivers and reservoirs (Supplementary Figure S1). This isolation fosters a distinct microhabitat pattern by enhancing habitat condition heterogeneity, including variations in hydrological conditions and localized anthropogenic disturbances, while simultaneously restricting biological diffusion (Li et al., 2018, 2024).

4.2 Response mechanism of the phytoplankton community structure to water quality indicators

Water temperature, nutrients and pH significantly impact the structure of the phytoplankton community. Among these factors, water temperature is crucial for influencing community structure and succession (Angeler, 2013; Legendre, 2014; Su et al., 2017). It directly affects phytoplankton metabolism, growth, and reproduction by regulating enzyme activity (Pulsifer and Laws, 2021), particularly impacting the succession of cyanobacteria and diatoms. In tropical island environments, this study highlights that seasonal water temperature variations are a key driver of the phytoplankton community succession, notably the alternating dominance between cyanobacteria and diatoms. During the wet season, favorable water temperatures promote cyanobacteria growth, leading to a marked increase in their abundance. Previous studies indicate that cyanobacteria exhibit enhanced competitiveness and reproductive ability when water temperatures exceed 20°C, achieving optimal growth between 25°C and 35°C, thus becoming the dominant group (Li et al., 2019; Rhee and Gotham, 1981). During the dry season, river water temperatures are relatively low. There is a significant negative correlation between *Bacillariophyta* cell density and water temperature ($p < 0.05$), aligning with diatoms' cold-stenothermal ecological characteristics (Abirhire et al., 2015). In tropical regions, although the dry season's lower water temperatures are still higher than temperate winters, they sufficiently inhibit thermophilic *Cyanophyta* and *Chlorophyta*, thereby giving diatoms a competitive advantage. Diatoms thrive in low-temperature, well-mixed water environments (Firsova et al., 2023), making them more likely to proliferate in rivers during the dry season.

Nitrogen input increased the nitrogen content in the water body but did not affect the α-diversity of phytoplankton. This could be because, although nitrogen input boosted phytoplankton quantity to some extent, it did not significantly alter community composition (Kafouris et al., 2019). Nitrogen input can influence the growth rate and competitiveness of phytoplankton (Nwankwegu et al., 2020). While some phytoplankton may grow faster due to nitrogen input, their competitive relationships with other species might remain stable.

Nutrient concentrations in water bodies are crucial for phytoplankton growth and reproduction, with their spatial and temporal variations greatly affecting phytoplankton density and community structure evolution (Szymczak-Żyła et al., 2017). During the wet season, total phosphorus concentrations in reservoirs and rivers increase significantly, coinciding with marked rises in the abundance and density of *Cyanophyta* and *Chlorophyta*. This spatio-temporal model underscores the critical role of phosphorus in the dynamics of cyanobacterial populations. As noted by Carvalho et al. (2013), phosphorus concentration is a determining factor for the potential environmental capacity to support cyanobacterial growth. The elevated phosphorus levels during the wet season likely alleviate nutrient limitations experienced in the dry season, thereby enhancing the carrying capacity of aquatic systems for cyanobacteria. This shift strengthens the competitive advantage and dominant position of cyanobacteria within the phytoplankton community. Additional research indicates that, under certain conditions, the stimulatory effect of nutrients—particularly phosphorus—on cyanobacterial growth may surpass the impact of rising water temperatures (Rigosi et al., 2014). These findings underscore phosphorus as a crucial regulator of the phytoplankton community composition and dynamics. During the wet season, elevated phosphorus levels not only boost phytoplankton density but also facilitate the dominance of *Cyanophyta* in community succession. In tropical island inland freshwater wetlands, where phosphorus is a limiting factor, increased dissolved phosphorus significantly enhances the absorption and utilization efficiency of various algae, especially *Cyanophyta* and *Chlorophyta* (Brookes and Carey, 2011; Wu et al., 2020). While some research indicates that phosphorus input can enhance phytoplankton species diversity (Jiang and Nakano, 2022; Xu et al., 2022), our study revealed no significant correlation between elevated phosphorus levels in water and the α-diversity index of the phytoplankton community. This lack of correlation can be attributed to phosphorus input not altering the community's composition and structure. Further analysis suggests several mechanisms behind this phenomenon. Firstly, the phytoplankton community possesses adaptability that allows it to thrive in high-phosphorus environments. It achieve this by adjusting its metabolic pathways and growth patterns in response to increased phosphorus input (Stephens et al., 2024). In environments with elevated phosphorus levels, organisms can enhance phosphorus absorption and utilization to sustain normal growth and reproduction. This phenomenon is partly due to phosphorus's role in stimulating the robust growth of submerged macrophytes, which indirectly modulate the phytoplankton community (Muylaert et al., 2010). Submerged macrophytes impact phytoplankton in two primary ways. Firstly, they release chemical substances that inhibit phytoplankton growth and development (Pakdel et al., 2013). Secondly, they offer habitats for zooplankton, thereby intensifying predation pressure on phytoplankton (Vilas et al., 2018).

In the reservoir during the dry season, phytoplankton abundance correlated strongly and positively with pH, a pattern observed in other tropical reservoirs. Silva et al. (2014) reported that pH is a primary regulator of tropical reservoir phytoplankton, and multiple regression analysis identified pH as one of the most important parameters explaining variation in phytoplankton abundance (Mostafa et al., 2023). By contrast, in the river habitat during the wet season, phytoplankton abundance correlated significantly and negatively with pH, consistent with Chakraborty (2009). One plausible mechanism is that pH alters the bioavailability of nutrients and trace metals, thereby constraining phytoplankton physiology (Parthasarathi et al., 2011). During the wet season, strong river flow amplifies environmental fluctuations (for example, acidification or rapid pH shifts), which can stress species that lack tolerance to such changes. The phytoplankton α-diversity indices (Shannon, Pielou, Simpson, Margalef) in this study all correlated significantly and positively with pH, whereas β-diversity correlated significantly and negatively with pH. Thus, higher pH—particularly in the reservoir during the wet season—appears to increase local species richness and evenness while concurrently increasing compositional similarity among sampling sites. Mechanistically, elevated pH likely improves the carbonate chemistry of the water and enhances silicate dissolution (Koester et al., 2016), thereby creating more favorable growth conditions for groups such as *Chlorophyta* and *Bacillariophyta* (Lv et al., 2024; Zhang et al., 2019) and supporting higher α-diversity. At the same time, this pH-driven improvement in habitat suitability may partly homogenize community composition across habitats, reduce species turnover, and lower β-diversity. These findings align with previous studies that identified pH as a key driver of phytoplankton diversity (Lin et al., 2023; Sun et al., 2022) and reported that high pH often coincides with high diversity (Lv et al., 2024).

4.3 Analysis of the phytoplankton co-occurrence network and community assembly mechanism

Ecological network analysis reveals that positive interactions dominate among phytoplankton, aligning with previous findings on the phytoplankton community in China's drinking water (Zhang et al., 2023). These co-occurrence networks exhibit notable differences across various spatial and temporal scales, primarily due to the heterogeneity of nutrient supply environments. Research indicates that nutrient supply conditions significantly influence the topological structure and scale of these networks (Hillebrand and Lehmpfuhl, 2011; Hu et al., 2017). In reservoir drinking water source areas, the unique geographical isolation coupled with oligotrophic conditions imposes dual constraints on the phytoplankton community: it limits both species growth and reproduction rates while significantly reducing species migration between habitats (Hayes et al., 2015). River ecosystems, characterized by significant flow fluctuations and high water velocities, enhance water connectivity, facilitating the migration and diffusion of phytoplankton. In these dynamic systems, the formation of the phytoplankton community primarily relies on spatial diffusion rather than local species interactions. This results in weaker interspecies associations and a simpler network structure (Chen et al., 2019). In contrast, reservoirs provide a stable environment where the phytoplankton community forms mainly through interactions among local species, leading to a more complex network structure. During the wet season, reservoir water temperatures are significantly higher than in the dry season ($p< 0.05$), which can substantially increase the metabolic efficiency of the phytoplankton community. This, in turn, accelerates the consumption rate of water nutrients. Under such environmental pressures, significant niche differentiation may occur between sensitive taxa with high nutrient requirements and generalist taxa (Sam, 2020). As niche separation increases, species repulsion within the network rises, leading to reduced clustering and modularity. This phenomenon elucidates the weakening of species interaction intensity and the decline in stability of the co-occurrence network during the dry season. Key taxa are crucial in regulating the phytoplankton community interaction networks, playing a fundamental role in sustaining community structure and function (Liu et al., 2022). Notably, global phytoplankton network analysis reveals that most key species are rare taxa with low abundance and infrequent occurrence. Research findings demonstrate that in the four co-occurrence networks, taxa with the highest average connectivity are *Euglenophyta*, *Cryptophyta*, and *Dinophyta*, rather than the more common *Chlorophyta*, *Cyanophyta*, and *Bacillariophyta*. This finding reinforces the notion that rare species play crucial, irreplaceable roles in sustaining the stability of the microbial community (Barabási, 2009). Research on eukaryotic plankton in reservoirs suggests that the interaction between rare and abundant taxa enhances the plankton community's resilience to environmental changes. This cooperation acts as a buffer, protecting the plankton network from disturbances and thereby supporting the ecosystem's overall function and stability (Xue et al., 2018).

The assembly of the phytoplankton community in drinking water sources on tropical islands is primarily influenced by dispersal, particularly between reservoirs and rivers during the wet season. Consistent with previous research indicating that random processes predominantly influence the assembly of the phytoplankton community (Yi et al., 2021; Zhao et al., 2021), this phenomenon can be elucidated through two primary mechanisms. First, the river, serving as the main water source for the reservoir, continuously introduces terrestrial and upstream phytoplankton propagules due to its relatively swift flow. This process results in a sustained exogenous inoculation of the reservoir community, which underpins the observed similarity between the two communities (Lu et al., 2020). Second, heavy rainfall and other events during the study period can significantly increase river runoff, potentially leading to reservoir overflow or active flood discharge. Such occurrences establish a rapid and efficient hydrological connection (Song et al., 2020). Although a reservoir typically functions as a relatively hydrodynamic closed system under normal conditions, the combination of continuous inoculation and intermittent high-intensity exchanges effectively facilitates the cross-water propagation of phytoplankton propagules. Consequently, this interaction demonstrates a high degree of diffusion homogeneity at the community level (Liu et al., 2021b). Furthermore, prior studies highlight that both stochastic and deterministic processes in ecological community construction exhibit significant scale dependence. At the local scale, deterministic processes, particularly homogeneous selection, typically dominate community assembly (Gu et al., 2021; Pearman et al., 2022). In contrast, as spatial scale increases, dispersal limitation intensifies, and stochastic processes gain prominence (Niño-García et al., 2016). Consequently, in the drinking-water source rivers and reservoirs of tropical islands, the phytoplankton community assembly is primarily influenced by stochastic processes. This is likely due to the expansive spatial scale of the study area, which amplifies dispersal limitation and diminishes the influence of deterministic processes.

5 Conclusions

This study systematically examined the structural characteristics, diversity evolution and community assembly mechanism of the phytoplankton community in tropical island drinking water sources across dry and wet seasons. The findings revealed that: (1) There were significant seasonal and habitat-specific differences in the phytoplankton community structures. (2) Environmental factors, including water temperature, pH, and nutrients, significantly influenced the community structure across both seasonal and habitat dimensions. (3) Co-occurrence network analysis showed that phytoplankton in various habitats developed distinct interaction patterns, with the reservoir network during the wet season exhibiting increased complexity and stability. (4) Predominantly, the community assembly mechanism was driven by the dispersal process, which is further intensified by the enhanced water connectivity characteristic of the wet season.

Based on the results, we advocate for the implementation of seasonally differentiated management strategies. In reservoirs, management should prioritize hydrological dispatching and internal nutrient control, specifically water level and optimized outflow during the rainy season. Conversely, for rivers, strategies should emphasize watershed-scale source control of external nutrients and the maintenance of ecological connectivity to facilitate species dispersal and sustain high biodiversity, thereby enhancing ecosystem resilience. Additionally, we recommend real-time monitoring of key environmental drivers to serve as an early-warning system for proactive pollution control.

Overall, this study offers valuable insights and guidance for the protection of aquatic ecosystems and biodiversity in drinking water sources on tropical islands, particularly regarding the management of the phytoplankton community across various seasons and habitats. Such research is essential for enhancing our understanding of the mechanism driving phytoplankton diversity and for supplying scientific evidence to support the conservation of freshwater ecosystems on tropical islands.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

XL: Writing – original draft, Investigation, Visualization, Writing – review & editing. QL: Visualization, Methodology, Investigation, Writing – original draft. BC: Investigation, Conceptualization, Writing – review & editing. XJ: Funding acquisition, Investigation, Writing – review & editing, Conceptualization. SA: Writing – review & editing. EY: Writing – review & editing. QF: Methodology, Writing – review & editing. WZ: Writing – review & editing, Investigation, Resources, Visualization. ZG: Funding acquisition, Conceptualization, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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