

Greater niche overlap and species association of phytoplankton in dry season than in wet season in Wujiang River, Yungui Plateau, China*

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Abstract Phytoplankton plays a crucial role in the energy flow and nutrient cycling of aquatic ecosystems. To understand the spatial and temporal distribution of phytoplankton in the Wujiang River, Yungui Plateau, SW China, samples were collected in 12 locations in wet and dry seasons and analyzed. We hypothesized that phytoplankton assemblages would exhibit significant temporal variability, with niche breadths of dominant species fluctuating seasonally, leading to distinct patterns of species association and community stability. Results show differences in community structure between the two seasons, but such changes did not cause non-significant differences in α -diversity. Diatoms were dominant in the assemblages in terms of biomass, while the numerical abundance of Cyanobacteria was highest in the wet season due to their relatively small cells. Rainfall-driven changes in runoff significantly altered nutrient availability, which in turn strongly affected phytoplankton structure. The more intense water flow contributed to a greater β -diversity in the wet season, driven primarily by species replacement, with stochastic processes played a more important role during the dry season. In the dry season, dominant species exhibited a broader niche breadth and greater niche overlap, along with more positive species associations, suggesting a more stable and resilient community structure. Conversely, in the wet season, species had narrower niche breadth and less niche overlap, leading to a less stable community. Both negative and positive species associations were observed, indicating a complex balance between environmental filtering and competition within the assemblages. These findings provide important insights into how seasonal environmental changes, particularly water flow and nutrient dynamics, shape phytoplankton communities in aquatic ecosystems. Understanding the mechanisms driving changes in community and stability is critical for predicting the impacts of climate change and managing aquatic biodiversity, as fluctuations in water flow and nutrient input may alter ecosystem functioning and productivity.

Keyword: plateau river; dry and wet season; diversity; neutral community model; co-occurrence

1 INTRODUCTION

Phytoplankton, the main primary producer in aquatic ecosystems, can respond quickly to environmental changes and affect other organisms in the food web. Phytoplankton in river ecosystem is a key member because it supplies oxygen and organic carbon to the aquatic food web and regulates the functioning of the local environment. Pollutants

could decrease phytoplankton diversity and change community structure in rivers, affecting the biological integrity of phytoplankton and the service

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function it provides to ecosystems (Hu et al., 2022).

Due to the construction of flow-regulating dams, industrialization and induced inputs from agriculture and domestic activities, river ecosystems have suffered a decline in water quality and biodiversity. Hydrodynamic conditions play a role in the shaping of the phytoplankton community, as several species are prone to thrive in stagnant water conditions (Li et al., 2013). It has been recognized that river flow velocity and retention time are critical factors regulating phytoplankton development in rivers, not least because these factors mediate species dispersal along the river channel (e.g., Stoyneva, 1994; Descy et al., 2017).

Dispersal-related mechanisms are indicated to occur within three processes: (1) the dispersal limitation induced by geographical distribution patterns (Martiny et al., 2006); (2) the mass-effect, which refers to the homogenization effect with the massive supply of species from different locations (Hubbell, 2001; Leibold et al., 2004); and (3) the neutral model, which emphasizes the stochastic balance between immigration, speciation, emigration and extinction of organisms (Hubbell, 2001; Leibold et al., 2004). Phytoplankton communities are the result of both deterministic and stochastic processes. The neutral community model separated the species into neutral and non-neutral partitions, mainly due to the difference in dispersal ability among the species (Chen et al., 2019).

The niche of species reflects their preference in terms of resources, habitat, and functions. Niche overlap indicates the similarity of their function (Marrone et al., 2023). Species with similar niche are expected to develop niche differentiation to decrease competitive exclusion (Pianka, 1974). Species association, defined as the interrelationship between different species, is influenced by environmental conditions (Schluter, 1984). Positive and negative association generally involves the similarity and dissimilarity of species' resource requirements, which induces niche overlap. Accordingly, niche overlap plus species association would provide information on ecological interactions within the community, spatial distribution, and the resource utilization features. Therefore, we hypothesized that (1) there are significant differences of phytoplankton structure between the dry and wet seasons in (sub) tropical rivers (e.g., seasonal effects); (2) the distribution and assembly of the phytoplankton community vary in response to changing environmental conditions (e.g., environmental

effects: water flow, temperature, and precipitation); (3) the differences in niche overlap between the dry and wet seasons lead to distinct patterns of species associations and community stability in (sub) tropical rivers (e.g., resource availability effects). To test these hypotheses, a study was performed to investigate the patterns of phytoplankton structure from 12 locations along the Wujiang River, China. The results revealed the structure, diversity, and assembly rules of phytoplankton community in this plateau river, which can help us understand the distribution and patterns of this fundamental component of aquatic ecosystems. This study provides insights into the factors that regulate phytoplankton diversity in the Yungui Plateau and facilitate future water management as global warming and eutrophication accelerate worldwide.

2 MATERIAL AND METHOD

2.1 Sampling location

Wujiang River, located in the Yungui Plateau with a length of 874 km and a surface catchment of 66 849 km², is the largest southern tributary of the Changjiang (Yangtze) River (Fig.1), and is characterized by a subtropical wet monsoon climate (Kang et al., 2023). Samples were collected from 12 locations along the Wujiang River twice, in the wet (Aug., 2023) and dry season (Dec., 2023). Water temperature (Temp), dissolved oxygen (DO), pH, and electrical conductivity (Cond) were measured on site using an YSI probe (HANNA HI 98194, Italy). Water transparency was estimated using a Secchi disk. Surface water samples were collected at each location from 0.5-m depth using a 5-L water sampler. A sub-sample of 1-L water was used for chemical analyses, and another 1-L water was fixed using Lugol's solution at 1% concentration for phytoplankton identification and counting. All samples were transported back to the lab within 8 h.

2.2 Water chemical analysis

Water chemical variables, including total phosphorus (TP), total nitrogen (TN), total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), phosphate (PO₄³⁻-P), nitrate (NO₃⁻-N), nitrite (NO₂⁻-N), ammonium (NH₄⁺-N), silicate (DSi), total suspended solid (TSS), and chemical oxygen demand (COD_{Mn}) were measured according to standard methods (APHA, 2012). Chlorophyll *a* was estimated according to Lin et al. (2005). Trophic status index (TSI) was calculated according to Li and Zhang (1993).

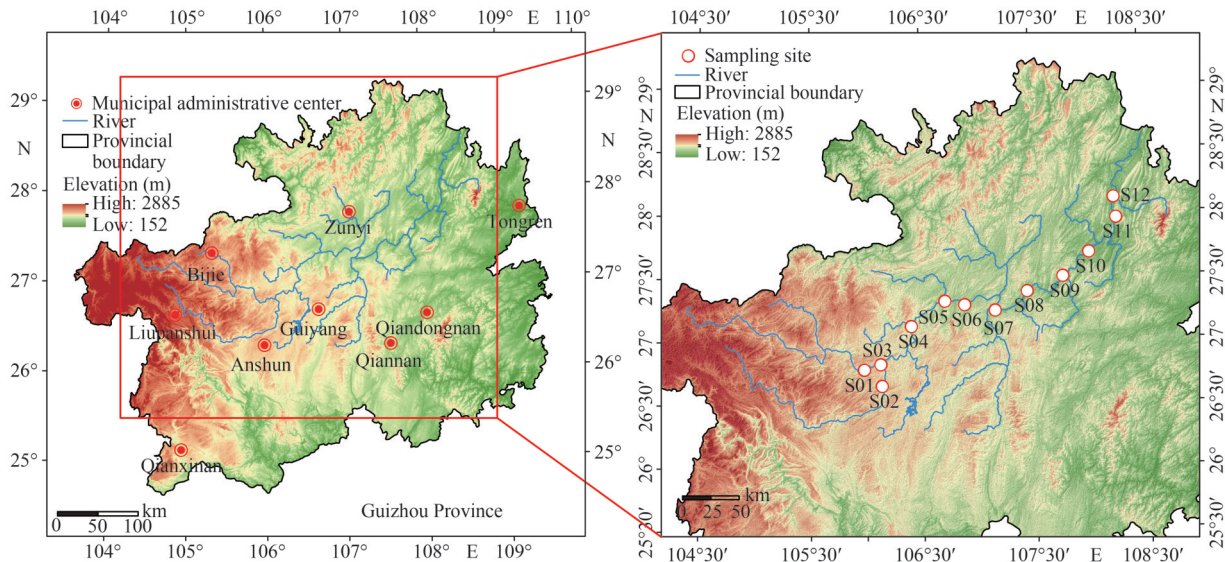


Fig.1 Map of the 12 sampling locations (S01–S12) along the Wujiang River in the Yungui Plateau

Map review No. GS(2024)0650.

2.3 Phytoplankton enumeration

Phytoplankton samples, after Lugol's fixation were kept at 4 °C until analysis. Species were identified and counted under an inverted microscope with 10×40 optical magnification according to Utermöhl method (Utermohl, 1958). At least 400 units (cells or colonies) were counted for each sample. Biomass of species was estimated by biovolume calculation (mm^3/L) using a geometric approximation and assuming the unit fresh weight as $\text{mass } 1 \text{ mm}^3/\text{L}=1 \text{ mg/L}$ (Hillebrand et al., 1999).

2.4 Statistical analysis

Species richness and diversity indexes, including Simpson, Shannon, and Pielou's evenness index were calculated using "vegan" package in R (Oksanen et al., 2024). Bray-Curtis dissimilarity was applied to measure β -diversity. Besides, Jaccard similarity (Jac) was used for β -diversity partitioning into species turnover (Jtu) and nestedness (Jne) using "betapart" package. Analysis of variance (ANOVA) was applied to test whether there was significant difference between the wet and dry seasons. The correlation between phytoplankton community dissimilarity (Bray-Curtis index), and geographical and environmental distance was analyzed using Mantel tests. Redundancy analysis (RDA) was performed to analyze the relationship between environmental factors and phytoplankton assemblages. Permutational multivariate analysis of variance (PerMANOVA) is a non-parametric

multivariate statistical permutation test and used to compare whether there is significant on phytoplankton composition between two seasons. Mantel's test was performed to evaluate the correlation between two distance matrices (environmental distance and phytoplankton community dissimilarity, geographic distance and community dissimilarity) using the Mantel correlogram.

Relative importance index (RII) is a parameter assessing the relative importance of one species within a community or an ecosystem. This index is based on abundance, frequency, and biomass of species as $\text{RII}=(N+W)\times F\times 10\ 000$ (N represents the abundance of species; W refers to the relative biomass of species; F is the frequency of occurrence) (Pinkas et al., 1971). Niche overlap, ranging from 0 to 1, refers to organisms with no niche similarity to organisms that share the same niche (Pastore et al., 2021). Species association indicates the co-occurrence of species in the community, reflecting the interactions among species (Schluter, 1984). The overall species association between species pairs was measured by the variation ratio (VR), and the significance was tested using χ^2 -test (Perelman et al., 2001). Species association coefficient (AC) between pairs was calculated to show the degree of species association (Gu et al., 2017).

Neutral community model (NCM) assumes that the composition of communities can be explained by dispersal of species from the surroundings and by ecological drift within the community (Hubbell,

2005; Sloan et al., 2006). This model estimates a major part of the community variation referring to the stochastic balance between the species loss and gain. N_m is a central parameter reflects the balance between speciation and drift. A high N_m indicates greater diversity and a strong influence of the metacommunity on local community composition. R^2 measures the goodness-of-fit for the neutral model to observed community data. An R^2 close to 1 suggests that the community might align closely with neutral assumptions. Modified stochastic ratio (MST) is a special form of normalized stochasticity ratio, with values ranging between 0 and 1. The value less than 0.5 refers to the dominance of deterministic processes, while values above 0.5 implies the dominance of stochastic processes, such as colonization by chance, demographic randomness and ecological drift (Ning et al., 2019).

3 RESULT

3.1 Environmental variable in Wujiang River in dry and wet season

PCA revealed a temporal pattern in environmental factors, with elevated levels of temperature, pH, total suspended solids, and nitrite observed during the wet season, and higher conductivity, Secchi depth, and chemical oxygen demand recorded in the dry season (Fig.2a). Spatially, an altitudinal gradient was present across the 12 sampling sites, ranging from 900–1 000 m above sea level in upstream regions to 300–400 m downstream (Fig.2b). The TSI was lower in the dry season than in the wet season, while TP showed similar mean values across seasons. In contrast, TN was higher in the dry season, and chlorophyll-*a* concentrations were lower during this season compared to the wet season

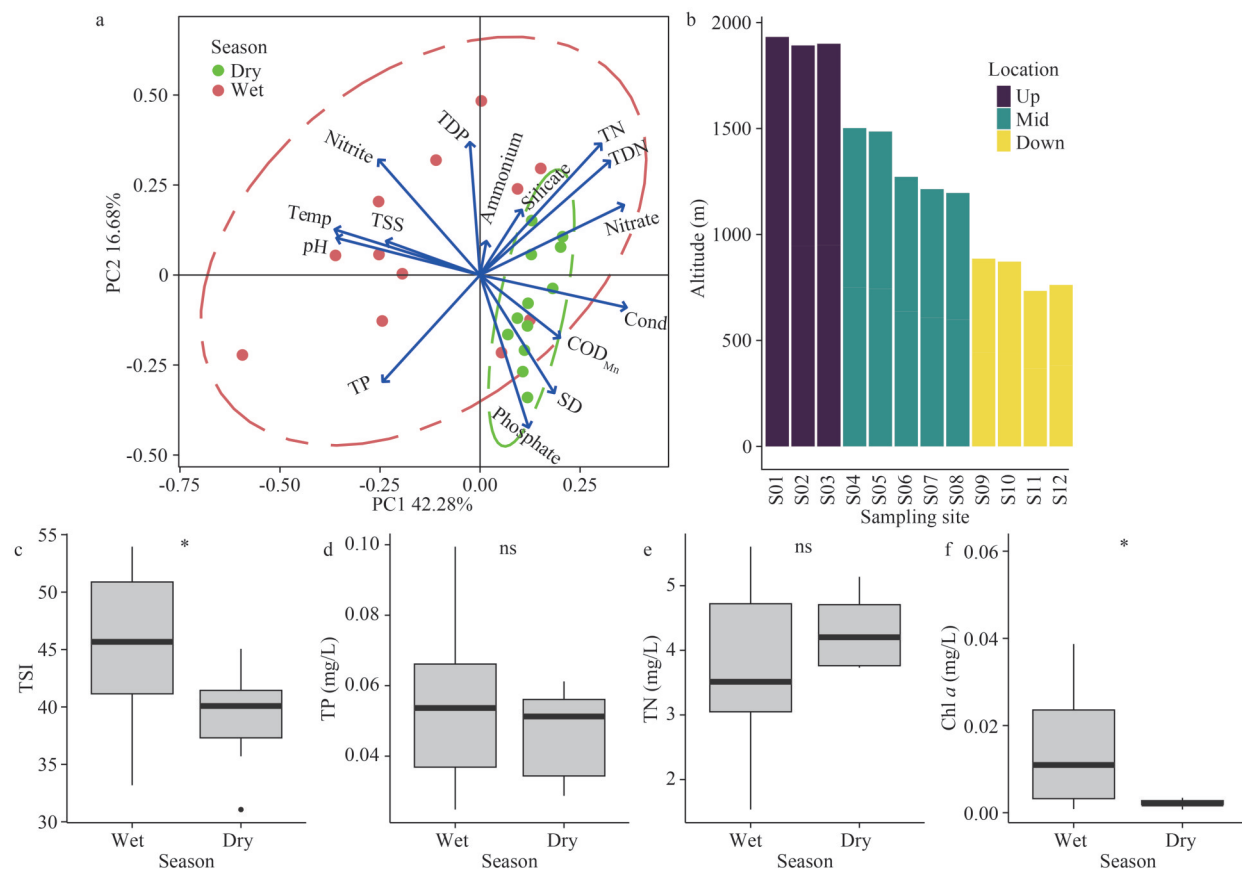


Fig.2 PCA biplot of all environmental factors (a); the altitude of 12 sampling locations (b) and main environmental variables (c: trophic status index (TSI); d: total phosphorus (TP); e: total nitrogen (TN); f: chlorophyll *a*) in Wujiang River in the dry and wet seasons

TP: total phosphorus; TN: total nitrogen; TDP: total dissolved phosphorus; TDN: total dissolved nitrogen; TSS: total suspended solids; SD: Secchi depth; Cond: conductivity; COD_{Mn}: chemical oxygen demand; Chl *a*: chlorophyll *a*. * indicates significant difference between two seasons with $P < 0.05$; ns: non-significant.

(Fig.2c–f). ANOVA tests indicated significant seasonal differences on TSI, SD, pH, Cond, water temperature, nitrite concentration and chlorophyll *a* ($P < 0.001$).

3.2 Phytoplankton composition and diversity in dry and wet season

In this study, a total of 66 phytoplankton species were identified in the Wujiang River during the wet season, representing 6 phyla, 12 class, 26 order, 36 families, and 50 genera. During the dry season, 57 species were documented, belonging to 5 phyla, 12 class, 30 order, 37 family, and 44 genera in the dry season. In the wet season, 22.73% of the species were distributed across phyla, including 22.73% in Bacillariophyta (15 species), 46.97% from Chlorophyta (31 species), 16.67% in Cyanobacteria (11 species), 6.06% in Pyrrophyta (4 species), and Cryptophyta (4 species), and 1.52% in Euglenophyta (1 species). In the dry season, species distribution shifted, with Bacillariophyta accounting for 23 species (40.35%), Chlorophyta for 21 species (36.84%), Cyanobacteria for 7 species (12.28%), Cryptophyta for 4 species (7.02%), and Pyrrophyta for 2 species (3.51%).

Figure 3 presents the absolute and relative biomass and abundance at the phylum level across sites for both wet and dry seasons. Biomass and abundance were higher in the wet season compared to the dry season. In terms of biomass, Bacillariophyta was the dominant phylum during the wet season, followed by Cyanobacteria and Chlorophyta. In contrast, Cyanobacteria exhibited the highest numerical abundance, dominating the community composition in the wet season.

Significant seasonal differences were observed in the biomass of Cyanobacteria, Chlorophyta, and Bacillariophyta between the dry and wet seasons ($P < 0.01$). Bacillariophyta emerged as the dominant phylum in the Wujiang River, exhibiting a higher relative biomass in the dry season compared to the wet season. Significant differences were found in the relative biomass of Cyanobacteria and Bacillariophyta between the two seasons ($P < 0.01$). Specifically, the relative biomass of Bacillariophyta decreased in the wet season, coinciding with an increase in Cyanobacteria biomass (Fig.3c). Spatially, greater variability in phytoplankton distribution during the wet season than in the dry season, with some locations dominated by Cyanobacteria and Chlorophyta. Additionally, the abundance of

Chlorophyta and Bacillariophyta varied significantly between the seasons ($P < 0.05$). During the dry season, Bacillariophyta were the dominant group, followed by Chlorophyta. In contrast, during the wet season, Cyanobacteria became the dominant group, followed by Chlorophyta and Bacillariophyta in abundance (Fig.3d). Significant differences in the relative abundance of both Cyanobacteria and Bacillariophyta were observed ($P < 0.01$). Additionally, during the dry season, some locations exhibited a relative increase in the abundance of Cryptophyta.

Species richness and Simpson index were similar in both seasons. ANOVA results showed a non-significant difference in richness and diversity indices between the dry and wet seasons ($P > 0.10$) (Table 1).

3.3 Correlation between environmental factors and phytoplankton assemblages

Species turnover was the major contributor for β -diversity in both seasons, with higher values in the wet season than in the dry season (Fig.4a–b). The PerMANOVA test showed a significant difference in phytoplankton community structure between the dry and wet seasons ($P < 0.001$). Mantel's test showed that the correlation between dissimilarity of phytoplankton assemblages and geographic distance along the Wujiang River is non-significant ($P > 0.05$) (Fig.4c). A significant correlation was detected between phytoplankton and environmental dissimilarity only in the wet season ($P = 0.007$) (Fig.4d).

RDA showed that nitrate, nitrite, phosphate and TSS were significant environmental variables for phytoplankton community development in Wujiang River, with nitrite and TSS negatively correlated with RDA 1st axis, and nitrate and phosphate positively correlated. Altogether phosphorus and nitrogen availability explained more than 30% of total variation (Fig.5a). Nitrate, ammonium, and silicate were the most significant variables for phytoplankton in the wet season, accounting for 72.36% of the total variance (Fig.5b). Nitrate and silicate were the most significant variables for phytoplankton in the dry season (Fig.5c).

3.4 Neutral community model in dry and wet season

Neutral community model (NCM) depicts the relationship between occurrence frequency and relative abundance of species. R^2 in the dry season was higher than that in the wet season, indicating

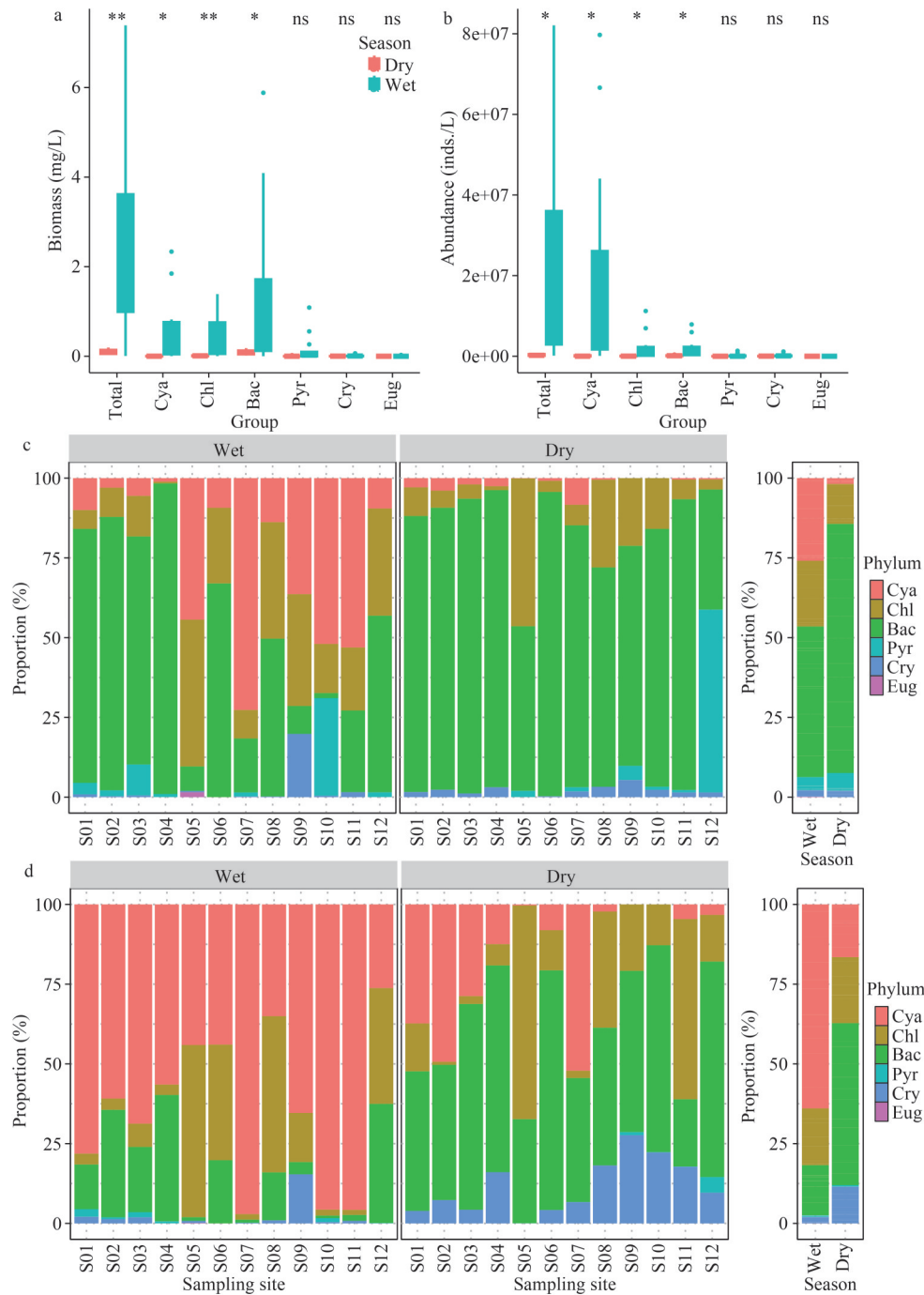


Fig.3 Biomass (a) and abundance (b) of phytoplankton at phylum level in the dry and wet seasons; relative biomass (c) and relative abundance (d) of phytoplankton assemblages at phylum level, in the dry and wet seasons

Cya: Cyanobacteria; Chl: Chlorophyta; Bac: Bacillariophyta; Pyr: Pyrrophyta; Cry: Cryptophyta; Eug: Euglenophyta; ** indicates significant difference between two seasons with $P < 0.01$; * indicates significant difference between two seasons with $P < 0.05$; ns: non-significant.

the likelihood of neutral model (Fig.6a–c). The community assembly processes were more affected by stochastic processes rather than by deterministic ones. Nm value was 3 in dry season and 2 in the wet season, implying decreasing species dispersal in the

wet season.

Significant difference on MST values was observed between the dry and the wet seasons ($P < 0.001$), with MST values above 0.5 in the dry season, and a relative balanced distribution of values

Table 1 α -diversity indices ([minimum, maximum] values) of phytoplankton communities in the dry and wet seasons

Season	Richness	Simpson	Shannon	Evenness
Dry	[13, 25]	[0.34, 0.85]	[0.83, 2.15]	[0.32, 0.76]
Wet	[6, 26]	[0.48, 0.87]	[1.33, 2.28]	[0.36, 0.92]

around 0.5 in the wet season (Fig.6d). C-score observation value in wet season was 3.300 2 with significant difference with the simulated value 3.232 9 standard effect size (SES)=2.395 1. C-score observation value was 3.238 1 with in-significant difference with the simulated value was 3.233 6 (SES=0.17) (Fig.6e–f).

3.5 Dominant species niche width, overlap, and species association

Top 10 dominant species were identified using the RII values (Supplementary Table S1). The niche width of dominant species is listed in Table 2. The niche width was broader in the dry season than the wet season. The proportion of niche overlap above 0.6 was 75% in the dry season and 17.8% in the wet season (Fig.7a–b). The overall species association in the dry season VR was 3.13 ($W=37.61, N=12, S=8$), while in the wet season VR was 1.74 ($W=20.91, N=12, S=10$). S refers to the total number of species, and N means the number of samples. W value was used to test the significance of association. Positive

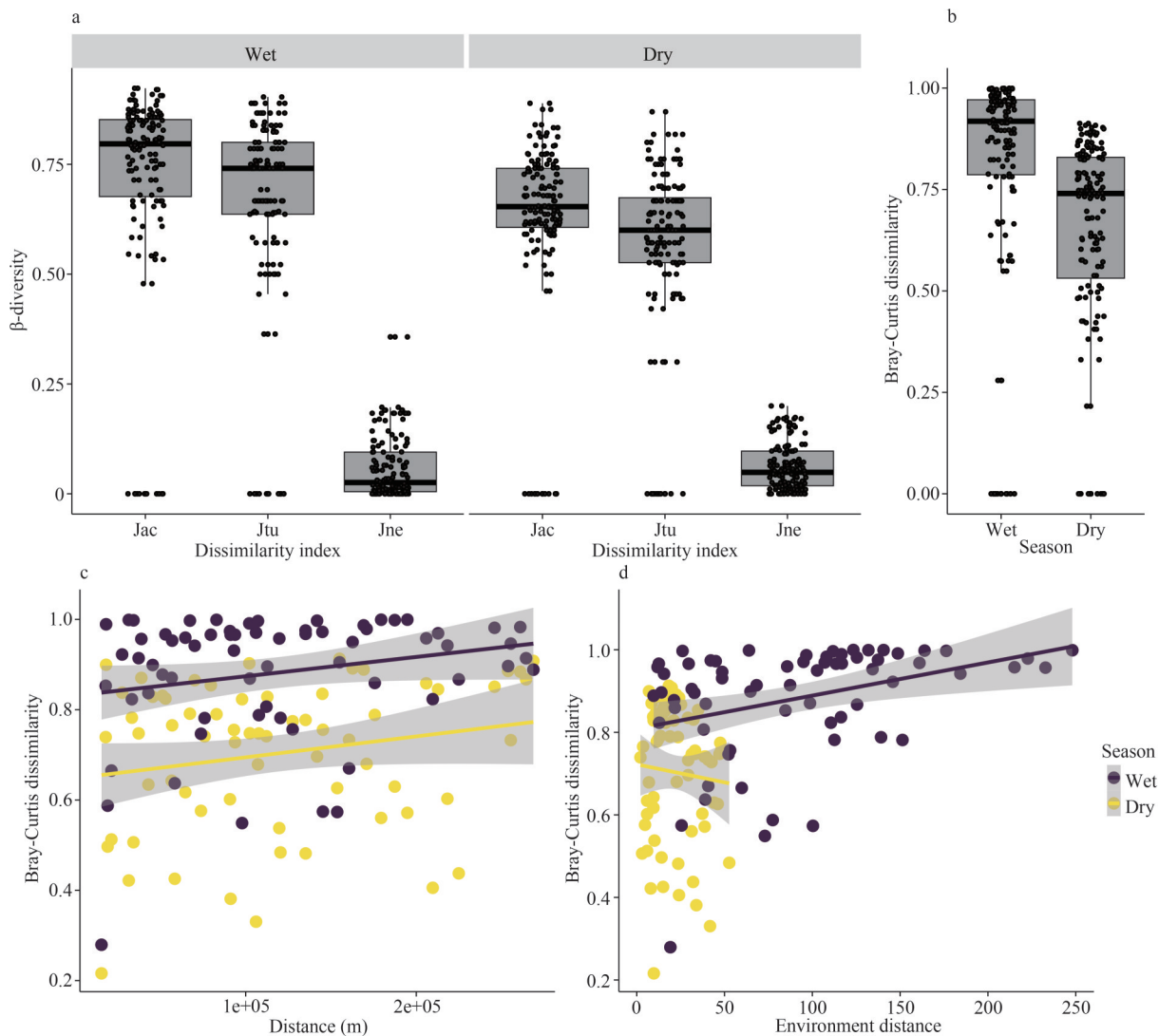


Fig.4 Partitioning of Jaccard dissimilarity (Jac) into species turnover (Jtu) and nestedness (Jne) (a); and Bray-Curtis dissimilarity in the dry and in the wet season (b); Mantel’s test on phytoplankton community dissimilarity and geographic distance (c) and environmental distance (d)

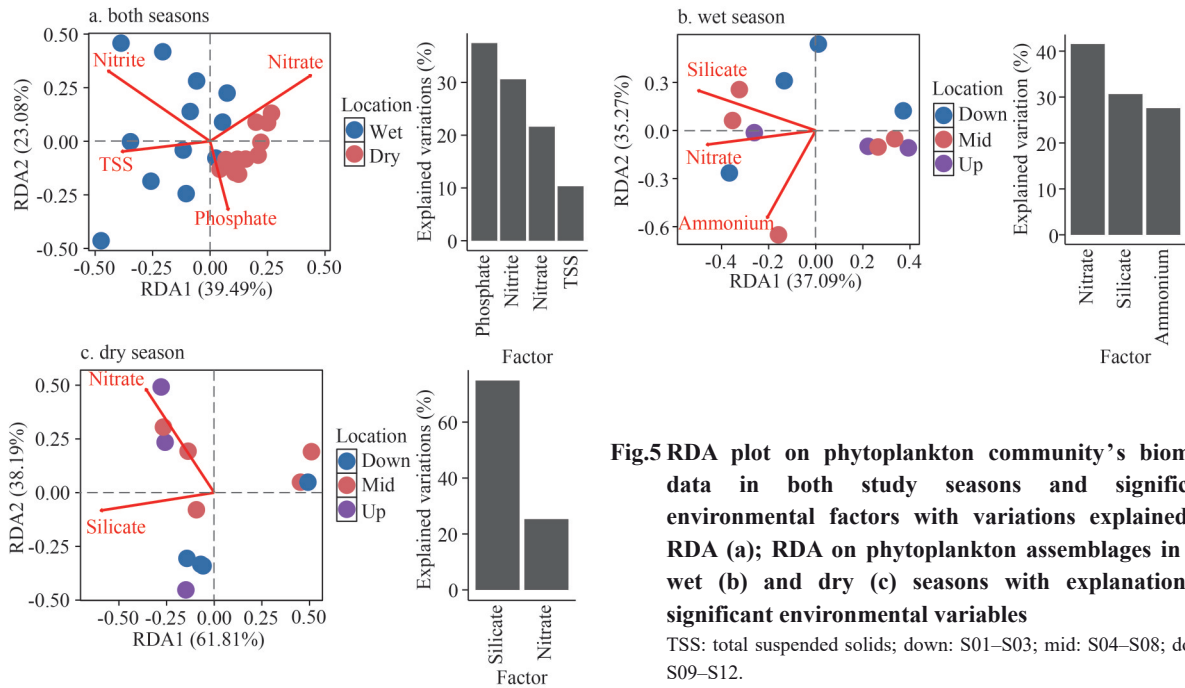


Fig.5 RDA plot on phytoplankton community's biomass data in both study seasons and significant environmental factors with variations explained in RDA (a); RDA on phytoplankton assemblages in the wet (b) and dry (c) seasons with explanation of significant environmental variables

TSS: total suspended solids; down: S01–S03; mid: S04–S08; up: S09–S12.

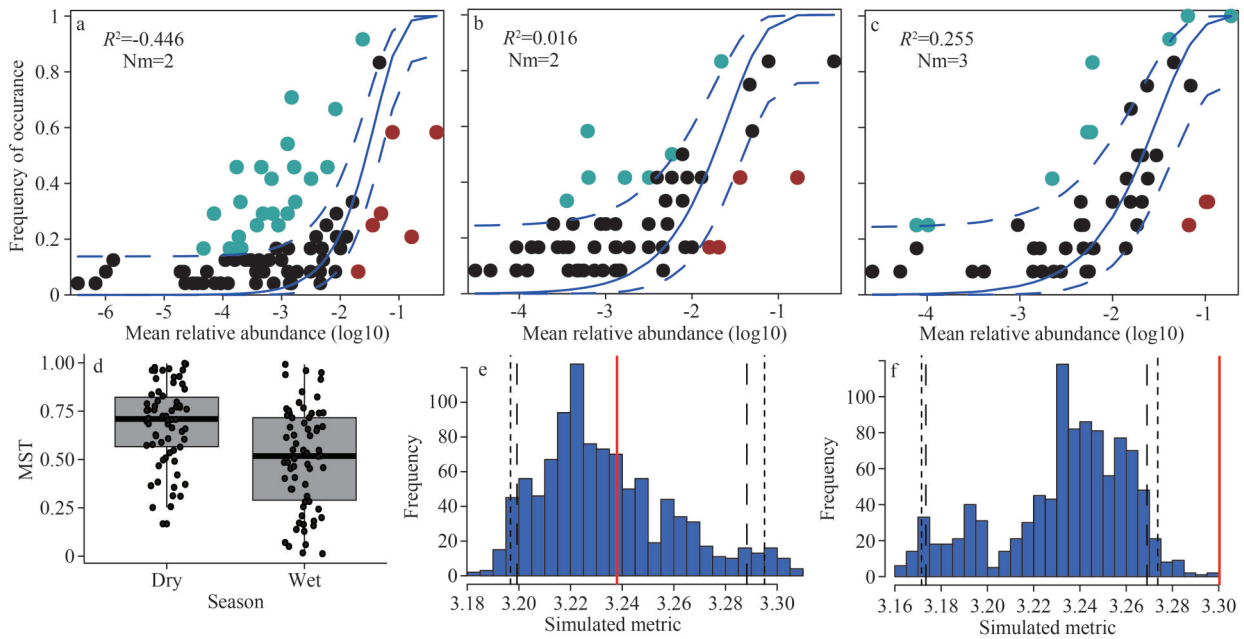


Fig.6 Neutral community model (NCM) of phytoplankton communities in both (a), wet (b), and dry (c) season; modified stochasticity ratio (MST) in dry and wet season (d); and species co-occurrence patterns by C-score in wet (e) and dry (f) season

Solid blue line represents the best fit to the Sloan neutral community model, and dashed blue line represents 95% confidence intervals around the neutral community model predictions. Nm indicates the movement of phytoplankton between different communities; R^2 is the goodness of fit to the model, with a higher value denoting a better fit. The red solid line represents observed values of C-score; the dotted dark line represents the simulated C-score values at the lower and upper 95% confidence interval (1-tail test); the dashed dark line represents simulated C-score values at the lower and upper 95% confidence interval (2-tail test).

species associations were found in the dry and wet seasons, as indicated by the VR and W values for the

dominant species. *Cyclotella* sp., *Fragilaria* sp., and *Limnithrix* sp. showed overlap with the other

dominant species in the dry season. In the wet season, *Limnothrix* sp. showed a great overlap with *Pseudanabaena* sp., *Cylindrospermopsis* sp., and *Cryptomonas ovata*, *Aulacoseira varians* had a great overlap with *Navicula* sp. (Fig.7a). Pairwise dominant species association (AC) were shown in Fig.7c–d. An AC value equals to 1 indicated the dominant species in the dry season were all positively associated.

4 DISCUSSION

4.1 Environmental factor in wet and dry season

According to the TSI values, the waters of the Wujiang River can be classified as mesotrophic in the dry season, and slightly eutrophic in the wet season. Chlorophyll *a*, a proxy for primary productivity, was greater in wet season than in the dry season. Results from PCA indicate nitrate,

Table 2 Niche width index of dominant species in dry and wet season

Species	Wet	Dry
<i>Cyclotella</i> sp.	3.60	5.79
<i>Fragilaria</i> sp.	3.11	5.99
<i>Limnothrix</i> sp.	4.10	3.95
<i>Aulacoseira varians</i>	1.14	3.48
<i>Nitzschia</i> sp.	3.49	8.38
<i>Pseudanabarna</i> sp.	3.95	2.68
<i>Navicular</i> sp.	2.74	5.28
<i>Cryptomonas ovata</i>	3.02	6.15
<i>Dactylococcopsis</i> sp.	1.20	–
<i>Cylindrospermopsis</i> sp.	1.98	–

–: no presence of this species.

conductivity, and COD_{Mn} as the main factors controlling primary productivity in the wet season,

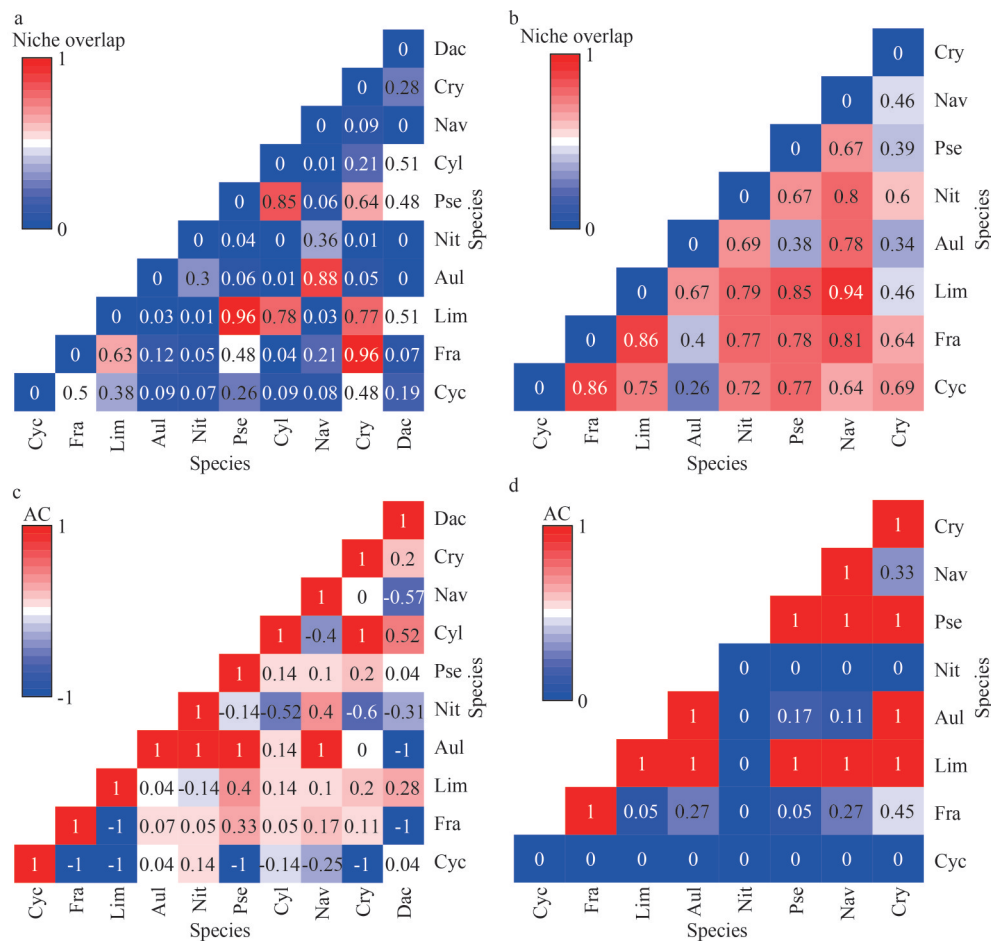


Fig.7 The dominant species niche overlap in the wet (a) and dry (b) season; species association (AC) between dominant species in the wet (c) and dry (d) season

Dac: *Dactylococcopsis* sp.; Cry: *Cryptomonas* sp.; Nav: *Navicula* sp.; Cyl: *Cylindrospermopsis* sp.; Pse: *Pseudanabaena* sp.; Nit: *Nitzschia* sp.; Aul: *Aulacoseira varians*; Lim: *Limnothrix* sp.; Fra: *Fragilaria* sp.; Cyc: *Cyclotella* sp.

while temperature, pH, TDP and TSS are the most important factors in the dry season. The anthropogenic activities, including industrial and domestic wastewater, fertilizer application, and tourism, have contributed to the increasing trophic state by runoffs in the wet season. High summer rainfall may have increased nutrient availability via surface runoff events and promoted algal proliferation (Zhang et al., 2012). Conversely, during the dry season, low temperature and reduced light levels reduce immediate eutrophication symptoms. They contribute to nutrient build-up, which can lead to a rapid eutrophication response when temperature and light increase in the spring, driving explosive algal growth.

4.2 Phytoplankton community structure and diversity

Phytoplankton assemblages of the Wujiang River were composed of both limnoplanktic (e.g., Cyanobacteria) and potamoplanktic (e.g., Bacillariophyta) species, with the latter adapted to unidirectional water flow. Higher biomass/abundance values were recorded during the wet season, driven by various taxonomic phyla. The discrepancy between biomass and abundance is attributable to cell size (e.g., diatoms with relatively large cells vs. cyanobacteria with small cells). Therefore, the high abundance of cyanobacterial cells contributed only a small proportion to the total biomass. In terms of biomass, phytoplankton assemblages in the wet season were dominated by diatoms, including *Cyclotella* sp., *Aulacoseira varians*, *Fragilaria* sp., and *Nitzschia* sp. However, diatoms remained dominant in the dry season, likely due to lower temperatures and light intensities, which provided them with a competitive advantage over other species (Reynolds, 2006). Enhanced temperature and light intensity in the wet season facilitated higher phytoplankton growth rates, resulting in greater overall biomass and abundance, primarily driven by Bacillariophyta, Cyanobacteria, and Chlorophyta.

Diatoms, due to their silicified and heavy frustules, experience reduced buoyancy, making them sensitive to water column stability (Naselli-Flores and Padisak, 2024). Precipitation events increase runoff and subsequently elevate water discharge rates in river watersheds (Kundzewicz et al., 2015). Turbulence and mixing within the water column favors the retention of diatoms in the photic layers, where light availability supports their

photosynthetic activity (Yang et al., 2016). This dynamic explains the observed diatom dominance during the wet season, when increased rainfall and faster water flow disrupt water column stability and promote diatom proliferation. Furthermore, studies indicate that water temperature and silicon availability were key factors shaping phytoplankton community composition in river systems. Elevated temperatures in the wet season may expedite the conversion of organic to inorganic nutrients, fostering cyanobacteria growth through the synergistic effects of nutrient availability and temperature (Reinl et al., 2023).

A non-significant difference in phytoplankton diversity was observed between the two study seasons, implying similar patterns of species diversity over time. The significant difference in community composition indicates temporal turnover of species in this river. Furthermore, β -diversity partitioning suggested that species replacement, rather than nestedness, was the major contributor to β -diversity in Wujiang River in both seasons. Along sampling locations, environmental heterogeneity typically changes, leading to variations in species richness and turnover. The non-significant distance-decay patterns could be due to the relatively small spatial scales of the present study, and the mass-effect of the river ecosystem.

4.3 Phytoplankton community assembly

NCM posits that all species within a community are ecological equivalent. Therefore, differences in species abundance and diversity arise from stochastic processes (random fluctuations). The low overall goodness of fit in NCM implied the greater relative importance of deterministic processes in the Wujiang River phytoplankton assemblages. R^2 represents the overall goodness-of-fit of the neutral community model. A higher R^2 indicates the closer alignment with the neutral model, suggesting that the community structure is more influenced by stochastic processes and less by deterministic processes. MST introduced varying degrees to which randomness influences community dynamics. The dry season showed MST values above 0.5, indicating the relative importance of stochastic processes in shaping phytoplankton assemblages. In the dry season, the dominance of algal abundance was Bacillariophyta>Chlorophyta>Cyanobacteria>Cryptophyta. Green algae had the highest dispersal ability in phytoplankton due to their resting stages that facilitate dispersion and ensure desiccation

tolerance (Rodríguez-Flores and Carmona-Jiménez, 2018). A higher MST indicates that chance events play relative more important roles in determining which species are abundant or rare. Compared to the dry season, deterministic and stochastic processes contributed more equally to shaping phytoplankton assemblages in the wet season. Deterministic processes, particularly environmental selection, contributed more to phytoplankton assemblage structure in the wet season than in the dry season. This is supported by the C-score model, which revealed a stronger influence of deterministic processes in the wet season, as shown by segregation in co-occurrence patterns, whereas low standard effect sizes in the dry season indicate a more random pattern. The increased rainfall and flow rates create a more homogeneous environment, and environmental filtering selects for species adapted to such conditions. In the dry season, reducing flow increases habitat fragmentation. Relatively-slow-moving river create diverse habitats where dispersal can lead to variable community structures. Furthermore, the fluctuations of local environment increase the likelihood of rare species present in the community.

4.4 Niche and species association of dominant species

When the niche overlap between two species is greater than 0.6, the species can be considered to show significant similarities in resource use (Wathne et al., 2000). Species with similar traits that utilize similar resources in similar habitats are generally considered to show significant niche overlap (Mouillot et al., 2005). In the dry season, *Pseudanabaena* sp. showed the greatest overlap with *Cyclotella* sp., *Fragilaria* sp., and *Nitzschia* sp., indicating that they share similar resources (e.g., nutrients availability) or habitat preference. Our data show that the niche overlap value of the dominant species pair varied in the different study seasons, which could be due to the sorting of species with different competitive advantages. Reduced niche overlap in the wet season implies that increased water flow facilitated resource accessibility and diminished intraspecific competition among dominant species. Negative species associations correlate with reduced niche overlap because species are adapting to minimize competition and avoid direct resource use overlap. Species coexistence is regulated by niche partitioning to reduce direct competition.

Compensatory effects ensure that when one species shift, other species can adjust in response to fluctuating environment. Compared to the dry season that supports broader niches, the wet season's narrower niches underscore the selective pressures of environmental filtering on specific traits.

In the dry season, dominant species exhibited greater niche overlap and increased VR compared to the wet season, suggesting a stable successional pattern within the phytoplankton community in the Wujiang River (Ma et al., 2022). First, environmental filtering appears to selectively sort species with varying fitness levels but similar ecological niches, in line with the habitat-optimum hypothesis (Mouillot et al., 2007). Lower water flow conditions provide sufficient time for optimally adapted species to overcome environmental filters. Dominant groups with similar adaptive traits exhibit similar niche preferences, resulting in greater overlap and dominant species broader niche width. Secondly, the heightened niche overlap points to intensified competition among these species. Highly specialized species with less direct competition alongside stronger positive associations that signal relative stability within the assemblage. Enhanced resource use and cooperative interactions facilitate coexistence. A higher degree of independence among dominant species (positive association) supports the influence of stochastic processes, potentially due to reduced water flow, which enhances locational independence along the river (Fig.8).

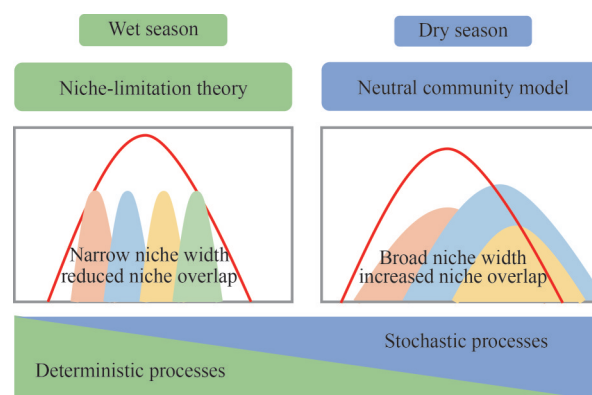


Fig.8 Schematic illustration of species niche overlap and community assembly mechanisms of phytoplankton communities in the wet and dry season

Wet season: environmental filtering selected well-adapted species in the community, and these selected species having narrower niche width with reduced niche overlap; dry season: increased niche overlap by species having broader niche width, and the reduced water flow causes dispersal limitation, and variable local environmental with fluctuation lead to more stochastic pattern.

5 CONCLUSION

This study provided ecological information on the temporal variations of the phytoplankton community along the Wujiang River, China. It revealed the dominant species with their niche overlap and species association in both wet and dry seasons, which could help us understand the dynamics of community assembly and stability in plateau rivers. In fact, communities are generally composed of species characterized by different ecological niches. However, in the case of phytoplankton, the main niche axes for all species are relatively few and determined by the availability of nutrients and light. The modulation of phytoplankton access to these resources is generally mediated by the hydrology of the environment. It could therefore be assumed that phytoplanktonic species share a similar fundamental niche but occupy different realized niches (partly overlapping, but always within the fundamental niche), whose extent depends on environmental filters and biological interactions (Naselli-Flores et al., 2021; Marrone et al., 2023). Water flow induced variations were key factors determining the phytoplankton community structure and species interactions in Wujiang River. Hydrology therefore represents fundamental environmental variables that cannot be disregarded and must be included in all the monitoring programs aimed at analyzing phytoplankton dynamics and structure, especially in the scenario of climate change and eutrophication.

6 DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Table S1) is available in the online version of this article at <https://doi.org/10.1007/s00343-025-4200-7>.