Research Paper

Climate changes drive phytoplankton community through complementarity and selection effects in a large mesotrophic reservoir*

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Abstract   Understanding the response of the phytoplankton community to climate change is essential for reservoir management. We analyzed a long-term data series (2009–2020) on the phytoplankton community in a large mesotrophic reservoir in the wet season to investigate the impacts of temperature and precipitation increases caused by climate change on the functioning and trait composition of the phytoplankton community. Over the last twelve years, the 3-month accumulative precipitation increased from 291.03 mm to 590.91 mm, and the surface water temperature increased from 25.06 °C to 26.49 °C in wet season, respectively. These changes caused a higher water level, stronger thermal stratification and lower nitrogen concentration in Daxi Reservoir. The dynamic equilibrium model indicated that the increased precipitation and water temperature-related environmental changes would result in a more diverse and productive phytoplankton community. The effects of increasing water temperature and precipitation on the niche complementarity and selection effects within the phytoplankton community were analyzed using structural equation model by means of the functional divergence index and functional evenness index, respectively, elucidating the reasons for the increase in cyanobacteria in the absence of a significant increase in nutrient levels. Based on these results, it is advisable that more stringent phosphorus control standards might be conducted to reduce the risks of cyanobacteria proliferation in the context of global warming.

Keyword: global warming; climate change; reservoir; trait-based phytoplankton functional group; cyanobacteria

1 INTRODUCTION

Global warming and associated climate changes have dramatically modified aquatic ecosystems (Rahmstorf and Coumou, 2011, 2012; Knutti and Rugenstein, 2015; Bacmeister et al., 2018). As a major primary producer, phytoplankton are quite sensitive to these changes, and shifts in their community structure subsequently affect the multifunctionality of aquatic ecosystems (Sadro and Melack, 2012; Kuha et al., 2016a, b; Chang et al., 2020; Costa et al., 2024). As artificial water bodies, reservoirs are highly disturbed ecosystems, as they have a more variable flow rate, a shorter hydraulic residence time, and a higher flushing rate than natural lakes (Soballe and Kimmel, 1987; Elliott,

2010; Hayes et al., 2017). These characteristics might exacerbate the impacts of climate change on their aquatic ecosystems (Piao et al., 2010; Summers and Ryder, 2023). Moreover, reservoirs are often major drinking water resources for local inhabitants, and climate-induced shifts in their state might cause potential risks to ecosystem goods and services (Gámez et al., 2019; Knapp and Milewski, 2020; Abirhire et al., 2023). Thus, understanding long-term phytoplankton succession under climate change and identifying the major impacting factors are imperative for reservoir management.

The most important climate-mediated stress factors affecting phytoplankton include increasing temperatures, changes in precipitation regimes and intensification of extreme weather events (Kasprzak et al., 2017; Absalon et al., 2023). Rising temperatures have directly impacts on phytoplankton community, shifting the dominant species and increasing the phytoplankton productivity (Sommer et al., 2012; Chang et al., 2020). Moreover, an increased water temperature might relate to a stronger thermal stratification favoring the growth of cyanobacteria (Richardson et al., 2018). Precipitation has multiple impacts on aquatic ecosystems (Richardson et al., 2018; Costa et al., 2024). A precipitation event can lead to increased surface runoff from catchment, leading to an increase of nutrient loading (Jennings et al., 2012; Zwart et al., 2017). However, an extremely precipitation events could cause nutrient depletion through flushing or dilution effects (Cobbaert et al., 2014). Meanwhile, the underwater light condition could be rapidly altered by precipitation from the sediment resuspension or turbidity input from catchment (Rip et al., 2007; Cobbaert et al., 2014). The precipitation-induced environmental effects could be a disturbance that significantly shift the community structure of phytoplankton (Meis et al., 2009), play a critical role in determining the relationship between phytoplankton species diversity and productivity (Hutchinson, 1961; Naselli-Flores et al., 2003).

Dynamic Equilibrium Model (DEM) is a useful verbal model that provides a powerful link between phytoplankton community status and disturbance or an environmental gradient (Huston, 1979, 1994). The diversity predictions of DEM provide three distribution patterns of species diversity along productivity and mortality rates (disturbance or environmental gradient), elucidating the productivity-dependent effects of disturbance or environmental factors on species diversity (Huston, 2014).

However, DEMs have a relatively weak predictive ability when phytoplankton communities have mixed functional types (Dodson and Cottingham, 2000; Tonkin and Death, 2012). Phytoplankton trait-based approaches can capture all species-specific responses and adaptations to environmental variability, improving the predictability of phytoplankton responses by aggregating information from many species without losing their key responses and impacts, and can thus be better used to quantify the magnitude of environmental variability and ecosystem function than diversity indices based on traditional taxonomy (Mouillot et al., 2013; Fu et al., 2015). Functional diversity makes up for the shortcomings of the DEM in distinguishing between competitive interactions and species selection by environmental factors in shaping communities (Sonnier et al., 2010; Naeem et al., 2012; Huston, 2014), thus have the potential to reveal the community assembly process (Mason et al., 2008). For example, functional divergence could be a good way to test for increasing niche complementarity (communities with more species comprise and greater trait variation, increasing niche partitioning and/or resource facilitation; with decreasing stress in a wide range of ecological contexts) (Gerisch et al., 2012; Mason et al., 2013). A decrease in functional evenness after a disturbance indicates a strong environmental selection effect (with more species, the inclusion of super performers is more similar) in the local community (Mouillot et al., 2013; Vanderley et al., 2022).

The Daxi Reservoir is a mesotrophic reservoir located in the southwestern part of the Taihu Lake Basin, Changjiang (Yangtze) River Delta (Fig.1). More than 70% of the annually precipitation occurs during the wet season, which could dramatically alter the underwater environment and result in a strong disturbance of the local phytoplankton communities (Yuan et al., 2019; Xu et al., 2023). We observed that the species richness and productivity (represented by chlorophyll a) of phytoplankton increased from 2009 to 2020 in the wet season. In particular, the biomass of cyanobacteria also increased from 0.73 to 4.91 mg/L in monitoring period, despite no significant increase in the nutrient concentration (Fig.2a). We assumed that the rise in precipitation and temperature driven by global warming might cause the succession of the local phytoplankton community. Here, we analyzed a 10-year dataset (from 2009 to 2020, the data of 2010 were not collected due to the project interruption)

including hydrometeorological factors, nutrient concentrations, and the phytoplankton community of the Daxi Reservoir in the wet season (from April to September). We used the diversity prediction of the DEM and trait-based functional diversity indices to analyze the effects of climate change on the local phytoplankton community. The following hypotheses were tested:

1) The increase in precipitation and water temperature promotes species richness and productivity in the Daxi Reservoir.

2) The functional divergence and functional evenness index could predict complementarity and selection effects that drive the long-term variation in the local phytoplankton community in the Daxi Reservoir.

3) Cyanobacteria would benefit more from climate change through the environmental selection effects despite the lack of a significant increase in nutrient concentrations.

2 MATERIAL AND METHOD

2.1 Study area and sampling site

The study was conducted in a large mesotrophic reservoir in Daxi, Jiangsu Province, China. The Daxi Reservoir is in the southwestern part of the Taihu Lake catchment (119.42°E, 31.29°N) (Fig.1).

This reservoir was built in 1960 with a total storage capacity of 170 million m³, a watershed of 92.40 km², and a mean water level of 13.70 m. It currently supplies drinking water to the 790 000 people in the nearby Liyang City. The water from this reservoir eventually flows into Taihu Lake, the third largest freshwater lake in China. Field sampling was conducted in the wet season (April–September) from 2009 to 2020. During the monitoring periods, four sampling points with similar water depths were established to cover the lake zone of the Daxi Reservoir.

2.2 Meteorological data

Meteorological data, including daily records of wind speed (WS, m/s), daily sunshine hours (SSH, h/d), precipitation (mm/d), air temperature (°C) and air humidity (mb), were obtained from the China Meteorological Data Sharing Service System (http://data.cma.cn/). The solar radiation datasets were obtained from the Meteonorm v8.0.2 software. Daily wind speed was averaged from hourly datasets. In view of the lagging effect of precipitation on water bodies, we first applied principal component analysis (PCA) and permutation tests to determine the most robust precipitation indicator from 1-month to 5-month accumulative precipitation (P1M–P5M). The PCA indicated that 3-month accumulative
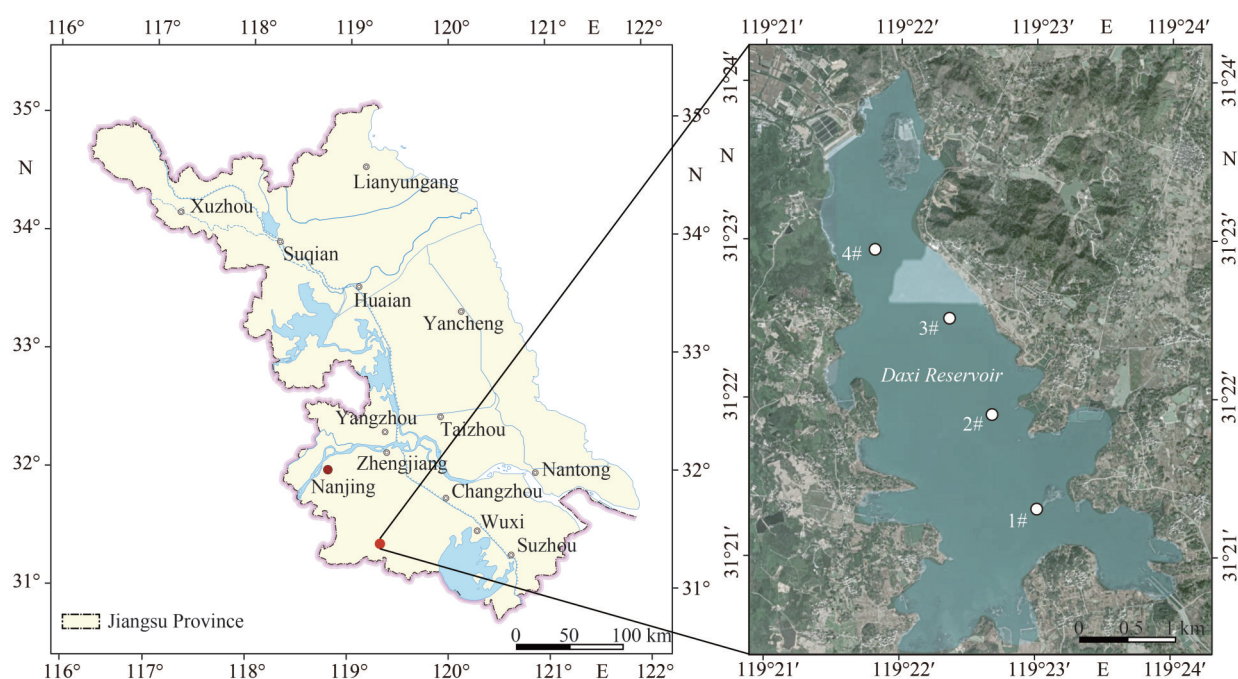

Fig.1 Location and sample sites distribution of Daxi Reservoir
Map review No. GS(2019)3333.

precipitation (P3M) was the most varied environmental gradient in the ten-year dataset and have profound impacts on water environment (Supplementary Fig.S1). Permutation tests showed that the effect of precipitation on the local phytoplankton community reached a maximum at P3M (Supplementary Table S1), suggesting P3M can robustly driving the phytoplankton community in Daxi Reservoir.

2.3 Water parameter

Integrated water samples were collected using a 5-L plastic tube at each sampling site in the wet season (April–September). The water depth was measured in-situ at sample points using a Sonar bathymeter and then averaged into a mean water depth (MD, m). The transparency of the water was measured by Secchi depth (SD, m). A multiparameter sonde (6600V2, YSI) was used for dissolved oxygen (DO, mg/L), pH, and surface and bottom water temperature (SWT and BWT, respectively, °C) measurements. Nutrient concentrations, including total nitrogen (TN, mg/L), nitrate nitrogen (NO_3^--N, mg/L), ammonia (NH_4^+-N, mg/L), total phosphorus (TP, mg/L), and orthophosphate (SRP, μg/L), were analyzed following the Standard Methods for the Examination of Water and Wastewater (EW Rice, 2012). Chlorophyll-*a* concentration (μg/L) was calculated from spectrophotometric measurements after extraction in 90% hot ethanol (Chen et al., 2003). COD_{Mn} (mg/L) of the water was determined by titration after oxidation of the organic compounds and the materials reduced by potassium permanganate solution.

2.4 Relative water column stability (RWCS)

In this study, the intensity of thermal stratification was estimated by RWCS (Becker et al., 2009). The RWCS was calculated as follows:

$$RWCS=(\rho_b-\rho_w)/(\rho_4-\rho_5),$$

where ρ_b and ρ_w represent the bottom water density (g/cm³) and surface water density (g/cm³), respectively. ρ_4 and ρ_5 represent the pure water density (g/cm³) at 4 °C and 5 °C, respectively. The water density is a function of water temperature (°C) and can be calculated from the empirical formula (Lawson and Anderson, 2007).

The BWT was measured in situ from only 2019 to 2020 year-round. For the remainder of the time, the BWT was calculated using a freshwater lake model (the Flake). The Flake is a one-dimensional model that is based on a two-layer parametric representation of the evolving temperature profile and on the integral budgets of heat and kinetic energy for the layers in question (Mironov et al., 2010; Woolway and Merchant, 2019). The Flake has been shown to accurately reproduce bottom water temperatures as well as thermocline in a range of lake contexts (Kirillin et al., 2013; Shatwell et al., 2016; Woolway and Merchant, 2019).

The measured BWT values from 2019 to 2020 were randomly divided into two parts: 60% of the dataset was used to adjust the output values, and the other 40% part was used to test the accuracy of the predicted values. The determination coefficient (R^2) and mean absolute percentage error (MAPE) of this method were 0.91 and 0.06, respectively, indicating that the calculated BWT has good predictive ability (Supplementary Fig.S2). Then, the adjusted BWT on the corresponding sampling date and the in situ measured mean surface water temperature index were used to calculate the RWCS.

2.5 Phytoplankton analysis and functional approach

One liter of surface layer water (0.30–1.00 m below the surface) was collected and fixed with 10 mL of Lugol's solution. The fixed sample was concentrated to 50 mL for cell counting and biomass estimation of phytoplankton. Phytoplankton were identified to the species or genus level and counted under upright microscope (Olympus BX53, Japan).

The phytoplankton functional trait identification was based on the principles from Weithoff (2003) and Abonyi et al. (2018). The traits possessed by the most of algal cells in each genus or species were summarized in a presence-absence data frame (Table 1 and Supplementary Table S2), and then were used to calculate the functional diversity indices. Most published indices are highly correlated (e.g., quadratic entropy is positive correlated with functional richness), and some have poor efficiency in detecting assembly rules (Mouchet et al., 2010; Mason et al., 2013). In view of this, we selected functional evenness (FEve) and functional divergence (FDiv) for further study. FEve and FDiv are mutually independent and can predict the community assembly processes efficiently (Mouchet et al., 2010; Mason et al., 2013). FEve represents the regularity of the abundance distribution in a filled niche space (Arthaud et al., 2012), is maximized when all traits have similar

abundances, and reduced when certain traits are heavily selected or filtered out (Mason et al., 2013). FDiv representing the abundance-weighted variance of trait values across component species (Liu et al., 2023). High functional divergence values are linked to a high level of niche differentiation among species in communities, implicating that the species are markedly dissimilar and exhibit strong complementary effects (Mouchet et al., 2010). The functional diversity metrics were calculated based on cell number datasets of phytoplankton using the "FD" package in R (Laliberté and Legendre, 2010).

2.6 Structural equation modeling (SEM)

Structure equation modeling was established to explain the relationship between the environmental variables, phytoplankton community assembly process (represented by FEve and FDiv) and the cyanobacterial biomass. SEM is an extension of general linear models in which a set of linear regressions is solved simultaneously to determine whether an entire covariance matrix is consistent with a hypothesized set of causal pathways (Arhonditsis et al., 2006).

We assumed the changes in environmental factors shifted the contribution of selection (represented by FEve) and niche complementary effects (FDiv) on assembly of phytoplankton community in Daxi reservoir. We first used permutation tests to select the environmental factors that significantly drive the trait composition of the phytoplankton community, and then used these factors in addition to functional diversity indices to construct a full model that included all possible pathways. Then, most of the nonsignificant pathways were eliminated to optimize the model. We used a chi-square (χ^2) test (models were reliable when the chi-square test P values were >0.05) and a comparison fit index (CFI, models have strong prediction ability when CFI >0.95) to select the best fit of the models. The standardized path coefficients between two variables represented the relative strength of a relationship. All data were log transformed before the SEM analysis. SEMs were performed in R using the "Lavaan" package (Oberski, 2014).

2.7 Statistical method

Mann-Kendall tests were used to test the trends of time-series datasets using the "Kendall" package in R. Tau indicates the trends and scope of the change in a variable, and variables with $P<0.05$

Table 1 Morphological, physiological, and behavioral traits of phytoplankton according to Weithoff (2003) and Abonyi et al. (2018)

	Trait	Category	Group
Morphological trait	Biovolume	<100 μm³	S
		100–1 000 μm³	M
		1 000–10 000 μm³	L
		>10 000 μm³	XL
	Greatest axial linear dimension (GALD)	<35 μm or >35 μm	GAL
	Organization	Single-celled	SIN
		Colonial	COL
		Filamentous	FIL
Physiological trait	N₂-fixation		N2F
	Si requirement		SIR
	Pigment composition	Chlorophyll *b*	CHB
		Chlorophyll *c*	CHC
		Phycobiliprotein	PYC
Behavioral trait	Motility	Presence/absence of flagella	FLA
	Vacuolated		VAC
	Life form		
	Benthic		BEN
	Planktonic		PLA

were considered significant. Quadratic regressions were applied to test the relationship between the species richness, functional diversity indices, and environmental factors. The regression model was performed using the "ggtrendline" package in R. PCA, RDA and permutation tests were performed using the "vegan" package in R. Correlations between the functional diversity indices and trait abundance were assessed using Pearson's tests via the "ggcor" package in R.

3 RESULT

3.1 Long-term trend in environmental variables

All measured environmental variables are shown in Supplementary Fig.S3. Mann-Kendall tests showed that the 3-month accumulated precipitation ($P<0.001$, Tau=0.55) and surface water temperature ($P<0.001$, Tau=0.52) were the most increased variables during the monitoring period (Fig.2a). The year-average values of the P3M in 2020 (26.49 °C) was 1.43 °C higher than in 2009 (25.06 °C), while the P3M in 2020 (590.91 mm) was about double from 2009 (291.03 mm). The MD and RWCS

increased slightly ($P<0.05$, Tau=0.17 and 0.13, respectively), implying that higher water depth enhanced thermal stratification in Daxi Reservoir when temperatures were simultaneously rising. Chlorophyll a and COD_{Mn} levels significantly increased in 2009 from 2.25 μg/L and 4.62 mg/L to 31.78 μg/L and 6.40 mg/L in 2020, respectively ($P<0.01$, Tau=0.28 for chlorophyll a and $P<0.01$, Tau=0.25 for COD_{Mn}). Together we observed the Secchi depth decreased from 1.32 m in 2009 to 0.74 in 2020. These are likely due to the rise in phytoplankton biomass. The concentration of NO_3^--N ($P<0.001$, Tau=-0.44) declined from 0.37 to 0.18 mg/L.

3.2 Variation in phytoplankton functional traits and functional diversity indices

A total of 7 phyla and 62 genera of phytoplankton were observed during the monitoring periods in the Daxi Reservoir, which were mainly Cyanophyta (10 genera), Bacillariophyta (11 genera) and Chlorophyta (28 genera). Other detected phyla included Cryptophyta (2 genera), Pyrrophyta (6 genera), Euglenophyta (4 genera), and Chrysophyta
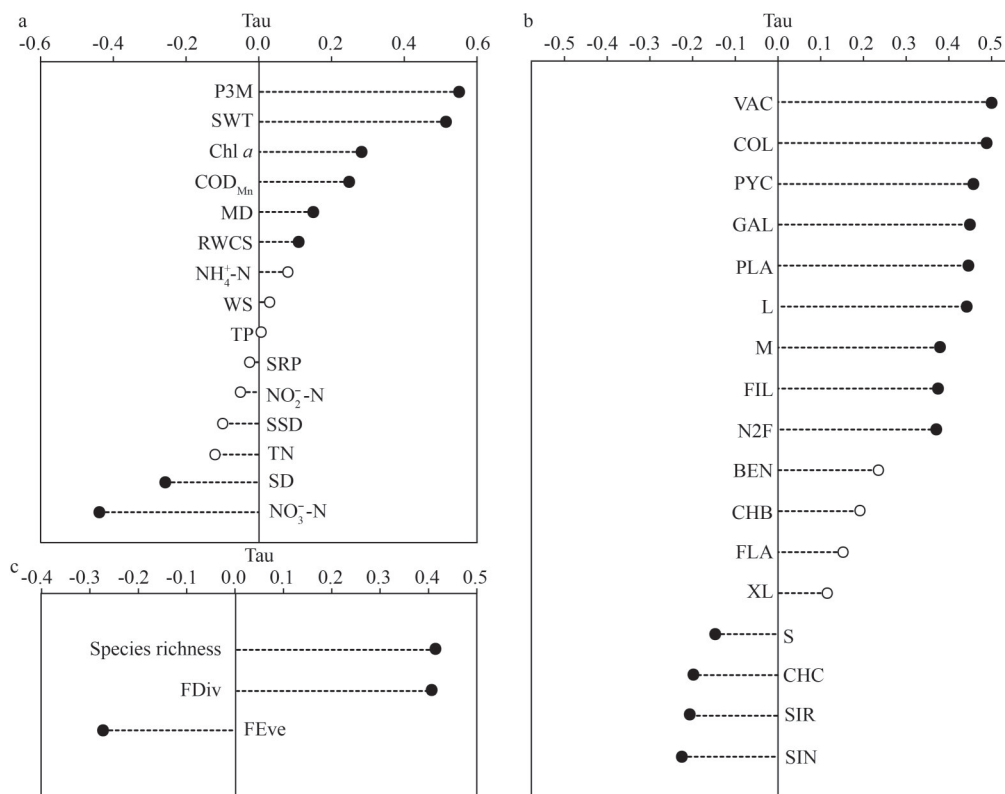

Fig.2 Tau values of Mann-Kendall trend tests for each environmental variables (a), each phytoplankton trait-based group (b), and the relative abundance of species richness and functional indices (c)

Significant (solid dots, $P≤0.05$) and non-significant (empty dots, $P>0.05$) trends are summarized.

(1 genera). Bacillariophyta account for 47.06% of total phytoplankton biomass and was the most dominant phyla, followed by Chlorophyta (23.83%) and Cyanophyta (16.25%) The biomass fractions of phytoplankton were shown in Supplementary Fig.S4.

A total of 17 traits were detected among the identified phytoplankton. The algal composition of each trait is shown in Fig.3. The PLA was the most diverse trait, incorporating all identified phytoplankton phyla. It displayed an increase during the monitoring period (Tau=0.44, $P<0.05$; Fig.2b). The SIN, BEN, CHC, and SIR traits were mostly contributed by Bacillariophyta. They were decreased overtime ($P<0.05$, Tau=-0.20 for CHC; $P<0.05$, Tau= -0.22 for SIR, and $P<0.001$, Tau=-0.25 for SIN). Phytoplankton with vacuolated (VAC, $P<0.001$, Tau= 0.51) and colonial (COL, $P<0.001$, Tau=0.50) traits experienced the greatest increases (Fig.2b). The

variation of the calculated species richness and functional diversity indices are shown in Supplementary Fig.S5. Species richness ($P<0.001$, Tau=0.42) and functional divergence ($P<0.01$, Tau=0.41) increased with time, while functional evenness ($P<0.001$, Tau= -0.27) presented the opposite trend (Fig.2c).

3.3 Relationships between the phytoplankton community and climate variables

We used quadratic regression models to test the relationships between species richness, chlorophyll a and the surface water temperature. As described by DEM diversity prediction, the species richness increased approximately linearly with productivity (chlorophyll a), 3-month accumulative precipitation and the surface water temperature, and all regressions were statistically significant ($P<0.05$) (Fig.4).
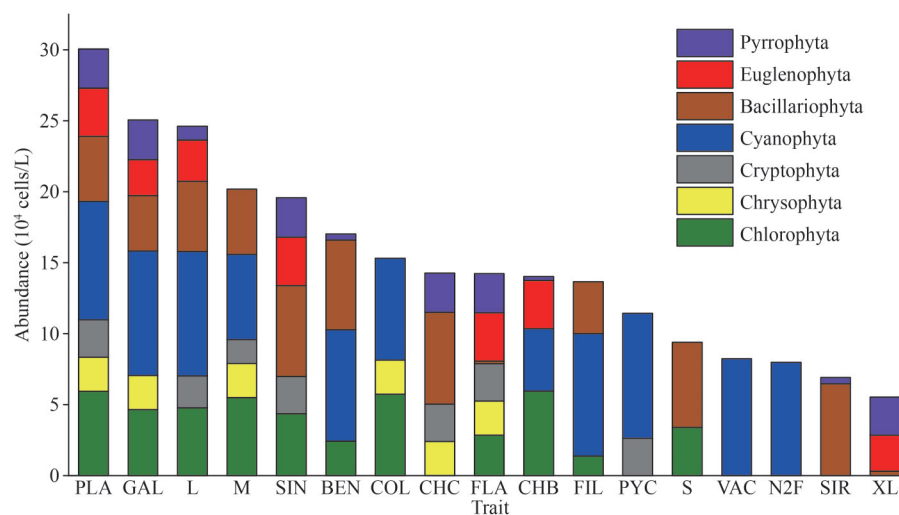
For the relationships between the functional

Fig.3 The algal phyla component of each trait-based phytoplankton group and the mean value of all samples
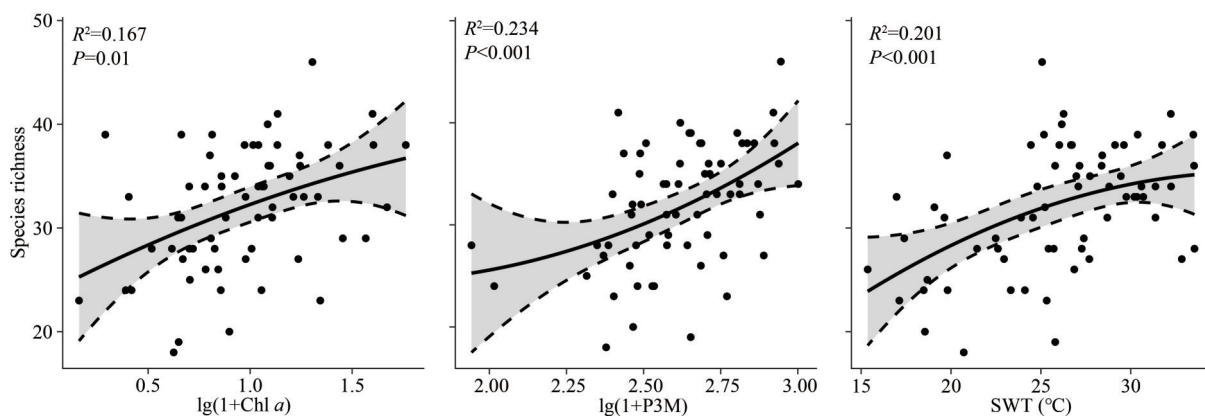

Fig.4 Regression models of species richness of phytoplankton against productivity (represented by chlorophyll-*a* concentration), three months aggregated precipitation, and surface water temperature for Daxi Reservoir in wet periods, determined by quadratic regression equation

diversity indices and environmental variables, all regressions were determined to be significant. The functional evenness was better correlated with 3-month accumulative precipitation (R^2=0.22, P< 0.001), while the functional divergence was better correlated with surface water temperature (R^2=0.36, P<0.001) (Fig.5).

3.4 The driver of the functional trait composition of phytoplankton

Redundancy analysis was performed to assess the relationships between various environmental factors and different phytoplankton traits. Two axes of the RDA explained 43.43% of the variation in traits (Fig.6a). Monte Carlo permutation tests determined that the SWT, P3M, SD, NO_3^--N, RWCS, and MD were the significant variables that drove the trait components of the phytoplankton community. RDA 1 was mostly correlated with surface water temperature and 3-month accumulative precipitation, while RDA 2 was mostly correlated with the Secchi depth. Phytoplankton with GAL, L, N2F, and FIL traits robustly increased with increasing surface water temperature and 3-month accumulative precipitation (represented by RDA 1), while those with the SIN, CHC and SIR traits presented the opposite relationship with RDA 1 (Fig.6). The findings demonstrate that changes in climate and alterations in underwater environments have caused

a shift in the dominant phytoplankton community. This shift has resulted in smaller, single-cell algae being replaced by larger, linear-shaped and colonial algae.

The Spearman correlation coefficient matrix (Fig.6b) showed that the increase in species richness was contributed by the large, linear shape algae (R^2= 0.39, P<0.01 for L and R^2=0.73, P<0.001 for GAL) and cyanobacteria (R^2=0.42, P<0.001 for VAC, R^2= 0.39, P<0.001 for N2F and R^2=0.69, P<0.001 for PYC). The enhanced selection effects (reduction in FEve) were mostly related to the enhanced nitrogen-fixation cyanobacteria (N2F, R^2=-0.41, P<0.001). The increase in FDiv was highly related to the GAL (R^2=0.82, P<0.001), FIL (R^2=0.77, P<0.001), N2F (R^2=0.39, P<0.001), PYC (R^2=0.86, P<0.001), and VAC (R^2=0.42, P<0.001).

3.5 Factor that boost the establishment of cyanobacteria

Our results showed that the cyanobacteria (trait VAC and N2F, mainly composed of the nitrogen-fixing and buoyant-positive cyanobacteria, *Aphanizomenon*) increased in the past ten years (Fig.2b). The SEM results illustrated that the χ^2 test's P, CFI, GFI, and RMSEA values were 0.488, 0.999, 0.999, and 0.00, respectively, indicating that our model fit the data well (Fig.7). We suggest that the increased 3-month precipitation (increased water depth) and surface
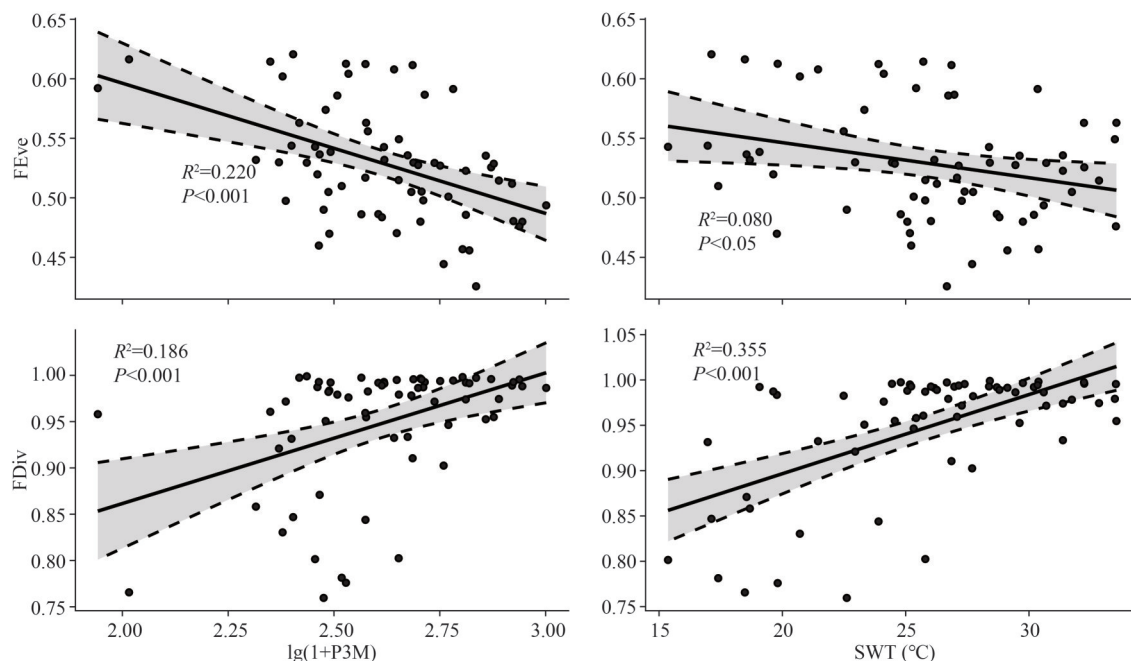

Fig.5 Regression models of trait-based functional diversity indices of phytoplankton community against three months aggregated precipitation and surface water temperature for Daxi Reservoir in wet periods
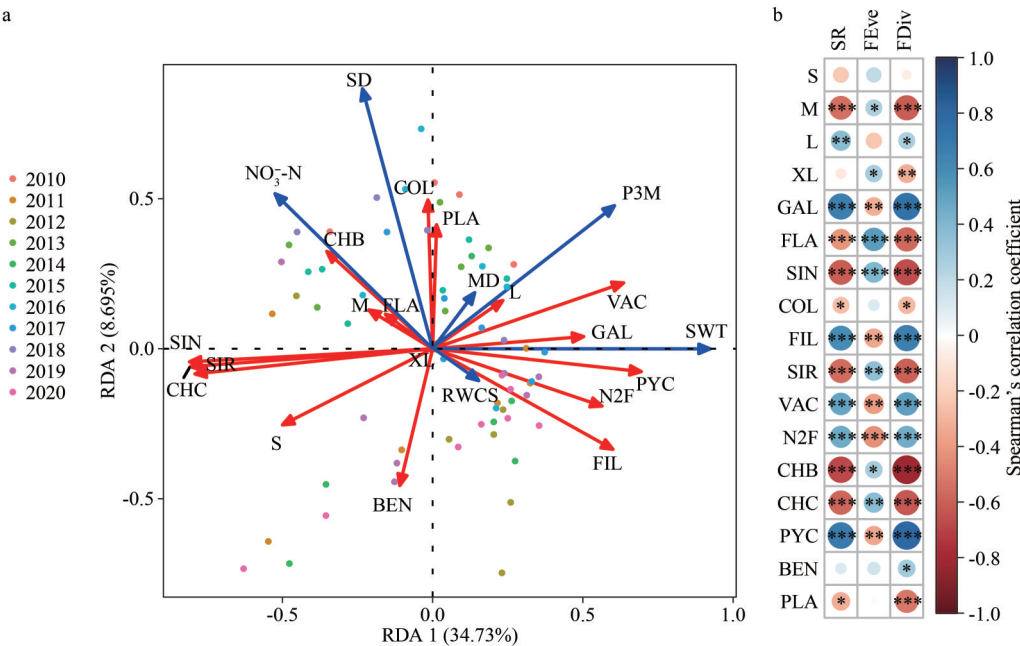
Fig.6 The impacts of environmental variables on phytoplankton traits component in Daxi Reservoir revealed by RDA (a) and the trait component driving variation of functional diversity indices and species richness (SR) determined by Pearson correlation coefficient (b)

The symbols *, **, and *** mean $P<0.05$, <0.01, and <0.001, respectively.
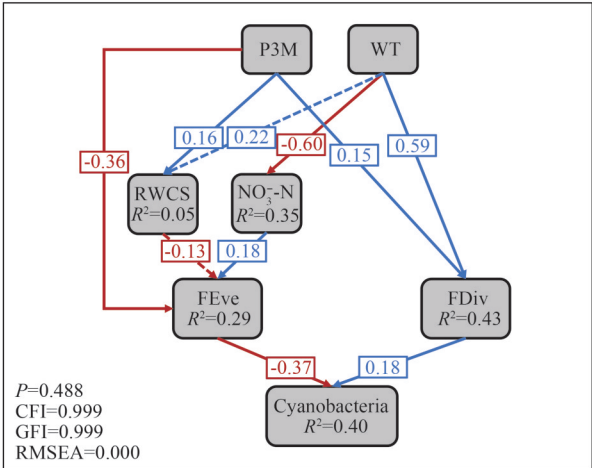

Fig.7 The casual effects between environmental factors, phytoplankton community assembly process, and biomass of cyanobacteria

The blue lines represent positive relationships and the red lines represent negative relationships. The solid and dash lines represent the significant and insignificant relationships, respectively.

water temperature leads to a robust thermal stratification, cause a higher relative water column stability (path effect=0.16 and 0.22, respectively), and the surface water temperature contributes to the reduction in NO_3^--N (path effect=-0.60). The shifted environmental variables (RWCS, NO_3^--N) and the direct impacts of P3M (e.g., nutrient input) together

contribute to the selection effects (represented by FEve). Precipitation-related disturbances and rising temperatures directly impact the niche complementarity effects (represented by FDiv). As a result, the selection effects and niche complementarity indicators together drove the biomass of cyanobacteria (path effect=-0.37 and 0.18, respectively). However, the selection effects (FEve) had a higher contribution on cyanobacteria than niche complementarity (FDiv), implying that the environmental selection effects have a greater contribution than the niche complementarity effects to cyanobacteria biomass.

4 DISCUSSION

4.1 Climate changes drive the functional divergence in the phytoplankton community

As predicted by the DEM, we detected an approximately linear increase pattern in phytoplankton species richness along with productivity, and surface water temperature (Fig.4), as the rising temperature related to the increasing nutrients utilization efficiency and boosting physiological activity of local species (Magnuson et al., 1997; Sommer et al., 2012; Chang et al., 2022; Xu et al., 2023).

We observed that functional divergence was more likely to be explained by rising surface water

temperature (R^2=0.36, P<0.001) (Fig.4). An increased FDiv can be indicative for higher degree of niche differentiation and therefore higher complementary (Mason et al., 2013; Fu et al., 2015). For example, nitrogen-fixation cyanobacteria commonly prefer high temperature (Carey et al., 2012). The promoted nitrogen-fixing cyanobacteria (N2F, Fig.6a) was significantly correlated with FDiv (Fig.6b) can reduce the phytoplankton competition for nitrogen (Tanvir et al., 2021). The increased traits of PYC along with increased temperature could enhance the availability of long wavelength light to the phytoplankton community (Li et al., 2023) (Fig.6a), which was also positively correlated with FDiv. This temperature-diversity relationships were also observed in subtropical oceanic and reservoir ecosystems, as the local species might have relatively high temperature preferences (Winder and Sommer, 2012; Righetti et al., 2019; Zhang et al., 2022).

We also detected a linear increasing relationship between species diversity and the disturbance regime (3-month accumulative precipitation) (Fig.4). This diversity-disturbance relationship was commonly observed in resource-rich conditions where niche overlap was low and complementary effects were high. The growth rate of phytoplankton is high enough to counteract the disturbance (mortality) caused by precipitation during the wet season (Cardinale et al., 2005; Huston, 2014). In the context, strong precipitation-related disturbance allows the coexistence of both well-suited and poorly-suited taxa by regulating the birth rate and mortality of local species, preventing some species from out-competing and excluding others, and therefore promoting the niche differentiation in community (Hutchinson, 1961; Reynolds et al., 1993; Naselli-Flores et al., 2003). We observed the superiority of small algae (trait S) was reduced by increasing precipitation (Fig.6a), probably due to the water inflow-related dilution and flushing effects. Together, an increasing trend in functional divergence along with the 3-month accumulative precipitation was detected. In addition, heavy rainfall leads to a huge water loading from watershed, resulting in a rapid increase in the volume of the water body in the reservoir. Some motile species can adjust their position in water column (e.g., cyanobacteria with trait VAC) to obtain more nutrient and outcompete non-motile species, which was considered to acquire additional niches (Lindenschmidt and Chorus, 1998;

Sengupta et al., 2017) and positively correlated with FDiv (Fig.6b). In addition, water flow among waterbodies might be responsible for assembling taxa with diverse origin and habitats (Mihaljević and Stević, 2011; Stević et al., 2013). For instance, riverine Pyrrophyta with the trait GAL is capable of proliferation autotrophically and heterotrophically (Jacobson and Anderson, 1996; Faithfull et al., 2011). Such mechanism could also lead to increase in the occurrence of alien species, which consequently increased the functional divergence of phytoplankton communities.

4.2 Climate changes drive the Function evenness in the phytoplankton community

Functional evenness could reflect selection effects associated with environmental changes in a local community (Mouillot et al., 2013; Otero et al., 2020; Smith et al., 2022; Liu et al., 2023). We observed that the linearly decreasing functional evenness was robustly explained by the increasing 3-month accumulated precipitation and surface water temperature (Fig.5; R^2=0.22, P<0.001), indicating that the environmental alternation promoted phytoplankton with the same traits. With RDA 1 (Fig.6a), the traits S, CHC, and SIR decreased and the traits L, GAL, FIL, and VAC increased, indicating that the increased 3-month accumulative precipitation and surface water temperature resulted in smaller, single-cell diatom being replaced by larger, linear-shaped and motile algae. During wet and warm seasons, the water column experiences greater stability and transparency, which favor the growth of motile phytoplankton (Reynolds et al., 2002). The high relative water column stability also provides ideal conditions for zooplankton groups, as they can maintain their populations in the upper epilimnion (Becker et al., 2009; Olli et al., 2015; Wei et al., 2023). The reduction in small single-celled diatom and the increase in large, colonial green or blue-green algae (e.g., *Coelastrum* spp. and *Aphanizomenon* spp.) showed an enhanced grazing pressure during monitoring period (Reynolds, 2006; Sommer et al., 2012). Species of larger and linear shapes (Groups L and GAL) are considered more tolerant to grazing pressure than smaller diatoms to be preyed (Groups S and CHC) (Litchman and Klausmeier, 2008). The joint effect of the high surface water temperature and 3-month accumulative precipitation on the Daxi Reservoir boosted the impacts of the trait-based selection effects on the

phytoplankton community, potentially causing species to become more clustered in functional space, thus reducing functional evenness (Fig.5).

4.3 Driving factor of cyanobacteria

Cyanobacteria (with the N2F and VAC traits; Fig.3) significantly increased in the Daxi Reservoir during the past ten years (Fig.2), which potentially threatens the water resource safety. Cyanobacteria can occur in a wide range of environmental conditions and habitats, and some groups can become prevalent in the phytoplankton community (Paerl and Paul, 2012; Paerl and Otten, 2013; Huisman et al., 2018). Our results suggest that climate change could affect niche complementarity and selection effects in the phytoplankton community and further promote cyanobacteria in the Daxi Reservoir.

As mentioned in context, the impacts of climate-related environmental changes on phytoplankton could be represented by functional divergence index (complementarity effects) and functional evenness index (selection effects). We conducted a SEM to elucidate the causal relationships between environmental variables, the phytoplankton community assembly process (functional divergence and functional evenness) and cyanobacterial biomass. The contribution of FEve to Cyanobacteria (-0.37) was larger than the path effect of FDiv to Cyanobacteria (0.18). This result indicate that the increased cyanobacterial biomass was primarily contributed from the climate changes-related selection effects. Functional evenness was robustly correlated with the GAL, VAC, N2F, and FIL traits (Fig.6b), indicating that the climate filtering process of climate change-related alterations in the functional components of phytoplankton was associated with an increase in species with traits related to cyanobacteria. The 3-month accumulated precipitation had the highest load on FEve (path effect=-0.36), probably because it driven the light condition, carried nutrients and trace metal elements to the waterbody from the catchment. The NO_3^--N value also had a considerable load on FEve (path effect= 0.18), indicating that the enhanced denitrification process under high-temperature conditions caused decreasing NO_3^--N concentrations to serve as a selection pressure that favored nitrogen-fixing cyanobacteria (N2F) (Finden et al., 1984). The high relative water column stability in the wet season in the Daxi Reservoir provides ideal conditions for cyanobacteria groups, as they can maintain their

populations in the upper epilimnion through the VAC trait (O'Neil et al., 2012; Huisman et al., 2018). Moreover, linear shape (GAL trait) cyanobacteria can tolerant enhanced grazing pressure in surface water layer (Reynolds, 2006). As a result, cyanobacteria would outcompete other species in high temperature, low nitrogen, and high grazing pressure water column.

5 IMPLICATION FOR RESERVOIR MANAGEMENT

We observed a significant increase in precipitation and surface water temperature in the Daxi Reservoir from 2009 to 2020 (Fig.2a). Our analysis showed that these changes had a profound impact on local phytoplankton and resulted in a more productive and diverse community.

We compiled evidence on the functional structure of phytoplankton communities by analyzing their functional traits and diversity indices. As a result, trait-based functional divergence and functional evenness successfully demonstrated the promoted niche complementarity and trait-based selection effects driven by climate change. Moreover, the results showed that the climate change-related trait-based filtering process (functional evenness) directly or indirectly promote the VAC, N2F, and GAL traits, therefore boosting the growth of cyanobacteria. We suggest that the analysis of functional space can estimate the importance of different ecological processes in shaping phytoplankton communities in the context of environmental change. A model describing the quantitative relationship between phytoplankton trait group and environmental factor is highly suggested to develop to better predict the function shift of aquatic ecosystem.

In current study, the relationships between cyanobacteria and environmental variables were elucidated. We suggest that cyanobacteria would be promoted due to climate change-related selection effects. Increasing precipitation results in a higher nutrient load in the reservoir, increasing the total nutrient content of the water body if the hydraulic residence time was long enough. This condition might favor some motile cyanobacteria (e.g., *Aphanizomenon* and *Microcystis*) as they could adjust their position in water column to obtain nutrients. In addition, the nitrogen fixation cyanobacteria might be promoted by the rising temperature and reducing NO_3^--N. However, phosphorus is widely proven to be a key factor in

promoting the growth of blue-green algae, it is advisable that more stringent phosphorus control standards should be conducted to reduce the risks of cyanobacteria bloom in the context of global warming.

6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are available from the corresponding author upon reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Tables S1–S2 and Figs.S1–S5) is available in the online version of this article at https://doi.org/10.1007/s00343-024-3260-4.