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Research Paper

# Response of phytoplankton functional group to spring drought in a large subtropical reservoir*

Yue WU[1, 2], Qi YE[1], Siwen CHEN[1, 2], Kaining CHEN[1, **], Shuzhan MA[3], Yiheng CHANG[1], Xiaoli SHI[1, 2, **]

[1] *State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China*

[2] *University of Chinese Academy of Sciences, Beijing 100049, China*

[3] *State Environmental Protection Key Laboratory of Aquatic Ecosystem Health in the Middle and Lower Reaches of Yangtze River, Jiangsu Provincial Academy of Environmental Science, Nanjing 210036, China*

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**Abstract** Global warming has caused an increase in the frequency and duration of droughts worldwide. Droughts could trigger large changes in physico-chemical conditions and phytoplankton community in waterbodies, resulting in a shift in the phytoplankton community. Spring diatom blooms in reservoirs have been increasingly observed in the past decade in the Taihu Lake basin. The aim of the present study is to elucidate the impacts of droughts on aquatic environment and to determine the driving factors for the succession of the phytoplankton functional groups based on the analysis of data collected during spring from 2009 to 2020 in the Daxi Reservoir. The unimodal relationship between 1-month aggregated precipitation index and phytoplankton species richness indicated the competitive exclusion occurred in extremely drought period. The structural equation modeling indicated that drought-related low water level conditions intensified sediment resuspension, and increased the phosphorus-enriched nonalgal turbidity in the Daxi Reservoir. Concurrently, a steady shift in the Reynolds phytoplankton functional groups from L0, TD, J, X2, and A (phytoplankton taxa preferring low turbidity and nutrient conditions) to TB (pennate diatoms being adapt to turbid and nutrient-rich conditions) was observed. The increased TP and non-algal turbidity in addition to the lowered disturbance contribute to the prevalence of Group TB. Considering the difficulties in nutrient control, timely water replenishment is often a feasible method of controlling the dominance of harmful algae for reservoir management. Finally, alternative water sources are in high demand for ensuring ecological safety and water availability when dealing with drought.

**Keyword**: drought; reservoir; sediments resuspension; phytoplankton functional group; diatom

## 1 INTRODUCTION

In the context of global warming, frequent droughts have been observed and are expected to increase in the coming decades, which will have a profound impact on freshwater ecosystems (Bellinger et al., 2018; Oliveira et al., 2019; Gallouli et al., 2020; Cardoso et al., 2022; Diniz et al., 2023). A reduced water supply leading to shrinking lake area and volume often results in increased nutrient and ion concentrations (Howard and Noble, 2018). Falling water levels can also increase the depth of the mixing layer, the turbidity, and the average temperature of the water column (Brasil et al., 2016; da Costa et al., 2016). Changes in the abiotic conditions inevitably affect the composition of lake biota (Arthaud et al., 2012; Van Loon et al., 2016; Costa et al., 2019; Hall et al., 2022). According to the competitive exclusion principle, phytoplankton competing for the same resource (e.g., phosphorus) cannot coexist at a condition without the variability (Hardin, 1960; Xu et al., 2023). Some harmful algae might outcompete

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** Corresponding authors: knchen@niglas.ac.cn; xlshi@niglas.ac.cn

and trigger bloom episodes during or after droughts (Brasil et al., 2016; Tilahun and Kifle, 2022).

Reservoirs are man-made waterbodies with both lakes and rivers features and their hydraulic characteristics are largely impacted by artificial regulation (Zohary and Ostrovsky, 2011; Bakker and Hilt, 2016). Thus, the ecological effects of droughts on reservoirs might be exacerbated by human activities (Di Baldassarre et al., 2017; Wan et al., 2017; Bellinger et al., 2018). The intensified droughts have been observed in recent decades (Milly et al., 2005; Zhou and Liu, 2018). Concurrently, the frequency and magnitude of diatom blooms have increased in reservoirs and lakes in the past decade (Zhu et al., 2016; Ren et al., 2017). In comparison to shallow lakes, reservoirs are more prone to suffer spring diatom blooms than summer blue-green algae bloom due to their low nutrient levels and high flushing rate (Yatigammana et al., 2011; Ma et al., 2013). Diatom blooms might change the water color and odor, and block filtration systems (Barrett et al., 1996; Halsband-Lenk et al., 2005), thus affecting water supplementation and water safety, which is considered one of the biggest challenges of water source management (Sommer et al., 1986; Horn et al., 2011; Messager et al., 2016; Janssen et al., 2021; Kibuye et al., 2021). However, drought-related diatom blooms in reservoirs are much less studied than cyanobacterial blooms (Huisman et al., 2018). Thus, to understand how phytoplankton community will respond to the enhanced drought and the mechanization of drought-related diatom bloom is meaningful for reservoir management.

Reservoirs are highly disturbed aquatic ecosystems in rainy days (Hardin, 1960; Zohary and Ostrovsky, 2011). Due to the disturbance, competition exclusion seldom be detected among phytoplankton community in reservoirs during rainy days (Xu et al., 2023). The disturbances have profound impacts on ecosystem multifunction of local phytoplankton (Hutchinson, 1961; Reynolds et al., 1993). The Intermediate Disturbance Hypothesis (IDH) note the critical role of disturbance impacts on diversity and productivity. Later, the Dynamic Equilibrium Model (DEM) suggests an extent inter-action of disturbance and productivity that influences species diversity. According to the species predictions by DEM, competitive species will subordinate species in the environment in low disturbance, while medium disturbance would moderate the interspecies competition and allow more species to concurrence (Reynolds et al., 1993; Naselli-Flores et al., 2003; Huston, 2014).

Phytoplankton functional-based approaches can capture the phytoplankton response to all species' specific adaptation and habitat preference (Salmaso et al., 2015). Thereby, it increases the predictability of phytoplankton responses by aggregating information on many species without losing their key traits (Kruk et al., 2021). Phytoplankton classifications include information about species physiology and ecological features such as sensitivities, tolerances, and environmental conditions from individual to ecosystem level (Litchman and Klausmeier, 2008). Evaluating phytoplankton functional response through time contributes to our knowledge about ecosystem dynamics (Reynolds et al., 2002; Devercelli, 2006; Litchman and Klausmeier, 2008).

The Daxi Reservoir is in the southwest of the Taihu Lake basin and experienced a heavy diatom bloom (triggered by *Achnanthidium* and *Synedra*, belong to the functional group TB) in the spring (March, April, and May) of 2020 with the chlorophyll *a* (Chl *a*) reached 60.02 μg/L when a drought occurred. This bloom lasted for approximately two months and was terminated with heavy precipitation and a rising water level. The biomass of group TB peaked three times during the monitoring period with the low water levels caused by low precipitation. However, the driving factors of drought-triggered diatom blooms in reservoirs are still unclear. This study aims to understand how droughts impact the local phytoplankton community through diversity prediction in DEM and phytoplankton functional group-based analysis, and trying to elucidate the critical driving mechanism of drought-related diatom blooms. Data on multiple parameters from 2008 to 2020 were analyzed, including hydrometeorological parameters, underwater light conditions, nutrient concentrations, and phytoplankton functional groups, with the following objectives:

1) to elucidate the effects of precipitation-induced disturbance on the assembly process of phytoplankton community;

2) to elucidate the impacts of droughts on the alternation of underwater environment in Daxi Reservoir;

3) to assess the response of phytoplankton functional group to drought condition;

4) to find out the mechanism of drought-triggered spring diatom bloom in Daxi Reservoir.

# 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. Daxi Reservoir is located 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 $m^3$, a watershed of 92.40 $km^2$, a mean water level of 13.70 m, a mean depth of 5.70 m, and a maximum depth of 9.00 m. It currently supplies drinking water for 790 000 people in the nearby city of Liyang. The water from this reservoir eventually flows into Taihu Lake, the third largest freshwater lake in China. Field sampling was conducted in spring (March, April, and May) from 2008 to 2020. Unfortunately, samples from 2010 were not collected due to the project interruption. During the monitoring periods, four sampling points were established to cover the entire reservoir (Fig.1).

## 2.2 Meteorological data

The meteorological data, including daily records of wind speed (WS, m/s), sunshine duration (SSH, h/d), and daily precipitation (PRE, mm/d), were obtained from the China Meteorological Data Sharing Service System (http://data.cma.cn/). Daily WS was averaged from hourly datasets, while daily SSH was averaged from 1 month before sample date. The precipitation index was calculated by summing up the daily rainfall of the whole month before sampling day (P1M). All obtained meteorological data are shown in Supplementary Fig.S1.

## 2.3 Water parameter

Integrated water samples were collected using a 5-L plastic tube at each sampling site. The water level (WL, m) was acquired from a water level gauge. The transparency of water was measured by Secchi depth (SD, m). A multiparameter sonde (6600V2, YSI, Inc.; http://www.ysi.com) was used for dissolved oxygen (DO, mg/L), pH, and water temperature (WT, °C) measurements in situ. Nutrient concentrations, including total nitrogen (TN, mg/L), nitrate nitrogen ($NO_3^-$-N, mg/L), nitrite 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 Standard Methods for the Examination of Water and Wastewater (E W Rice et al., 2012). Chlorophyll-*a* (mg/L) concentration was calculated from spectrophotometric measurements after extraction in 90% hot ethanol. Chemical oxygen demand ($COD_{Mn}$, mg/L) of water was determined by titration after oxidation of the organic compounds and reduced materials by potassium permanganate solution. All measured water parameters are shown in Supplementary Fig.S1.

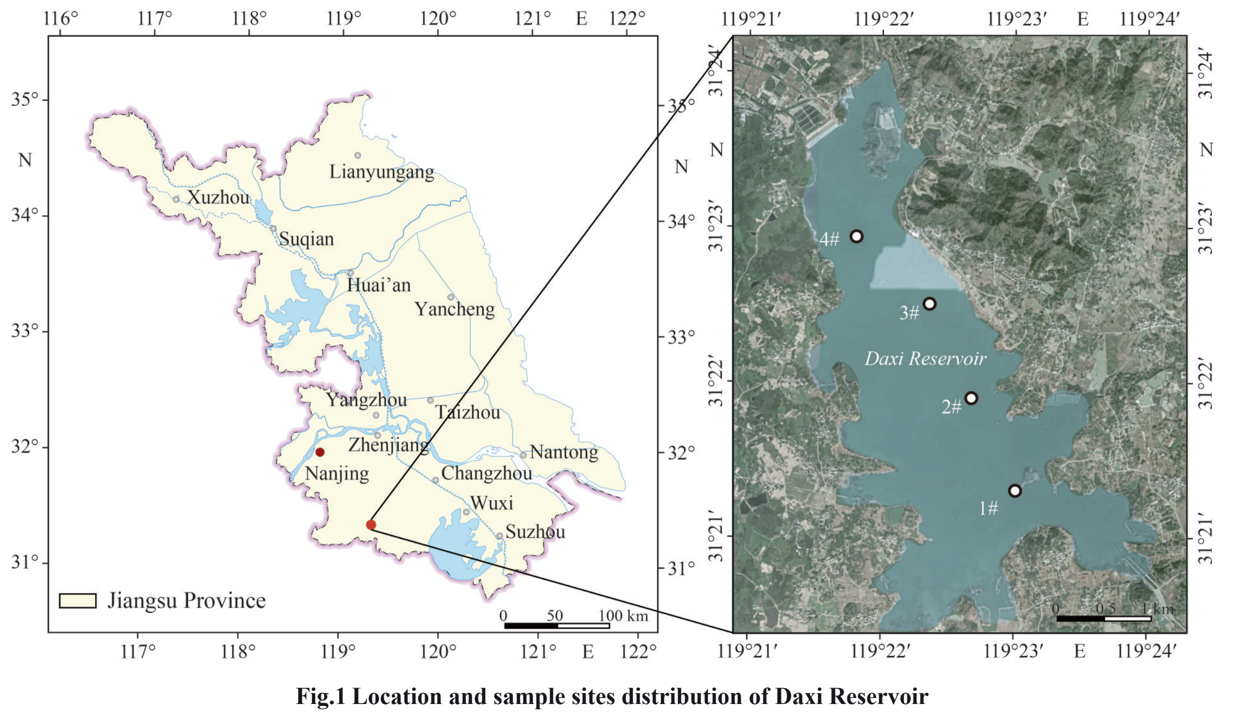


**Fig.1 Location and sample sites distribution of Daxi Reservoir**

Map review No. GS(2019)3333.

### 2.4 Phytoplankton parameter

One liter of surface layer water (0.30–1.00 m below the surface) was collected and fixed with 10-mL Lugol's solution. The fixed sample was concentrated to 50 mL for cell counting and biomass estimation of phytoplankton. Phytoplankton were identified and enumerated using an upright microscope (Olympus BX53, Japan). Phytoplankton species were grouped into classic taxonomic approach and Reynolds functional groups (RFG) (Reynolds et al., 2002; Abonyi et al., 2018; Kruk et al., 2021) for further analysis.

### 2.5 Nonalgal turbidity assessment

To assess the light attenuation caused by nonalgal turbidity, total attenuation was divided into attenuations caused by algal and nonalgal optically absorbed matter (Portielje and Van der Molen, 1999). The relation between SD and Chl *a* can be formulated as follows:

$$\frac{1}{\mathrm{SD}} = \frac{1}{\mathrm{SD}_0} + \left(\frac{\alpha}{\mathrm{PA}}\right) \cdot \mathrm{Chl}\ a,$$

where $\alpha$ is the specific extinction coefficient of Chl *a*, PA is the Poole-Atkins coefficient, and $\mathrm{SD}_0$ is the Secchi-disk transparency without algae (Jupp et al., 1994). Therefore, 1/SD represents the total turbidity indicator, and $1/\mathrm{SD}_0$ represents the nonalgal turbidity indicator.

We used minimal quantile regression (1%) to estimate the lowest boundary relationship between Chl *a* (equal to algal biomass) and 1/SD, and the Chl-*a* concentration imposes a minimum on the reciprocal of Secchi-disk transparency. This minimum (black solid line in Supplementary Fig. S2a) can be described according to the following equation:

$$\frac{1}{\mathrm{SD}} = 0.02 \times \mathrm{Chl}\ a + 0.30.$$

Thus, the nonalgal turbidity indicator $1/\mathrm{SD}_0$ could be back-calculated using the given Chl-*a* content and SD value via:

$$\frac{1}{\mathrm{SD}_0} = \frac{1}{\mathrm{SD}} - 0.02 \times \mathrm{Chl}\ a - 0.30.$$

### 2.6 Redundancy analysis (RDA)

RDA was applied to determine the correlation between environmental factors and the Reynolds' functional group of phytoplankton. Detrended correspondence analysis (DCA) was first performed. The length of the first DCA axis was 2.4 in the present study. Hence, redundancy analysis (RDA) was used for the subsequent constrained ordination. To select the variables that were closely related to the phytoplankton community dynamics, a Monte Carlo permutation test was applied before RDA, and only significant variables ($P$<0.05) were retained for further analysis. Redundancy analysis, detrended correspondence analysis and Monte Carlo permutation tests were carried out using the "vegan" package of R software.

### 2.7 Structural equation modeling (SEM)

Structure equation modelling was established to explain the casual-relationship between environmental variables and the biomass of bloom-trigger diatom groups (TB). SEM is an extension of general linear models in which a set of linear regressions is solved simultaneously to find out whether an entire covariance matrix is consistent with a hypothesized set of causal pathways (Arhonditsis et al., 2006). We started with initial models that included all plausible pathways between Monte Carlo permutation-selected physical, chemical, climate, and biomass of TB group. Then, most of non-significant pathways were eliminated to optimize the model. We used a Chi-square ($\chi^2$) test (models were reliable when the Chi-square test's $P$ values >0.05) and comparison fit index (CFI, models have strong prediction ability when CFI>0.95) to select the best fit of the models. The standardized path coefficient between two variables represents the relative strength of a relationship. All data were ln transformed before the SEM analysis. SEMs were performed in R using "Lavaan" package (Oberski, 2014).

### 2.8 Statistical method

The quadratic regressions were applied to test the relationship between species richness, productivity (Chl *a*), and precipitation, respectively. The regression model was performed using "ggtrendline" R package. Correlations between environmental factors and biomass of phytoplankton functional groups were assessed using Spearman and Mantel tests via "ggcor" R package.

## 3 RESULT

### 3.1 Phytoplankton taxa and functional group

A total of 7 phyla and 74 genera of phytoplankton were observed in the spring in the Daxi Reservoir, which were mainly Cyanophytes (20 genera), Diatoms (22 genera) and Chlorophytes (23 genera). Other detected phyla included Cryptophyta (3 genera), Pyrrophyta (3 genera), Euglenophyta (2 genera), and

Chrysophyta (1 genus). Diatoms were the largest contributor, accounting for approximately 77.31% of the total phytoplankton biomass, followed by Chlorophyta (18.61%) and Cyanophyta (3.82%) (Fig.2a).

The identified taxa were clustered into 18 functional groups according to Reynolds et al. (2002) and Abonyi et al. (2018) (Fig.2b), their habitat preferences are shown in Supplementary Table S1. The group TB, composed mainly of pennate diatoms, had the highest biomass fraction among all groups (55.31%), followed by group TD (majorly composted by Chlorophyta, 14.11%), group J (majorly composted by Chlorophyta, 8%), and group A (composted by centric diatom, 7%). Group TB peaked at May 2011 and May 2014, and trigger a bloom in March 2020 with the biomass of 101.43 mg/L (Fig.2b).

### 3.2 Environmental factor

As shown in Fig.3b, P1M was positively correlated with WT (Spearman's $R$=0.37, $P$<0.001), $NO_3^-$-N ($R$=0.22, $P$<0.05), $NO_2^-$-N ($R$=0.23, $P$<0.05), SD ($R$=0.21, $P$<0.05), and WL ($R$=0.23, $P$<0.01), and strong negatively correlated with $COD_{Mn}$ ($R$=-0.40, $P$<0.001), and pH ($R$=-0.52, $P$<0.001). The maximum $COD_{Mn}$ and Chl *a* were observed during a diatom bloom events in March 2020 with a value of 12.35 mg/L and 60.02 μg/L (Supplementary Fig.S1). The non-algal turbidity indicator $1/SD_0$ was negatively correlated with $NO_3^-$-N and $NO_2^-$-N ($R$=-0.39 and -0.34, respectively, $P$<0.001) and reached its peak value (1.57) in May 2011, at the same time we observed a deterioration in underwater light conditions (SD=0.51 m).

### 3.3 The dynamics of phytoplankton

Redundancy analysis was performed to elucidate the variations of phytoplankton functional groups along environmental factors (Fig.3a). $1/SD_0$, WT, WL, WS, TN, TP, and P1M, were significant factors revealed by the Monte Carlo permutation test ($P$<0.05). RDA 1 and RDA 2 explained 12.09% and 7.40% of the variation in the functional groups, respectively. RDA 2 was mostly explained by WT, while RDA 1 was positively oriented with WL, P1M and TN, and was negatively correlated with WS, $1/SD_0$, and TP. Groups L0, TD, J, X2, and A were positively correlated with RDA 1, preferring calm and low turbidity condition. In contrast, Group TB was strongly negatively correlated with RDA 1, showing different habitat preference. The group TC, H1, P, and D were explained by RDA 2, mainly relating to water temperature-related factors (Fig.3a).

Mantel and Spearman's test was conducted to assess the correlation between environmental factors and the four most abundant phytoplankton functional groups (Fig.3b). The group TB was majorly driven by water level (Mantel's $R$=0.29, $P$<0.001), underwater light condition (SD and $1/SD_0$, $R$=0.28 and 0.15, respectively, $P$<0.001), and TP ($R$=0.13, $P$<0.001), and highly contribute to the Chl *a* and $COD_{Mn}$ ($R$=0.37 and 0.36, $P$<0.001). The group TD

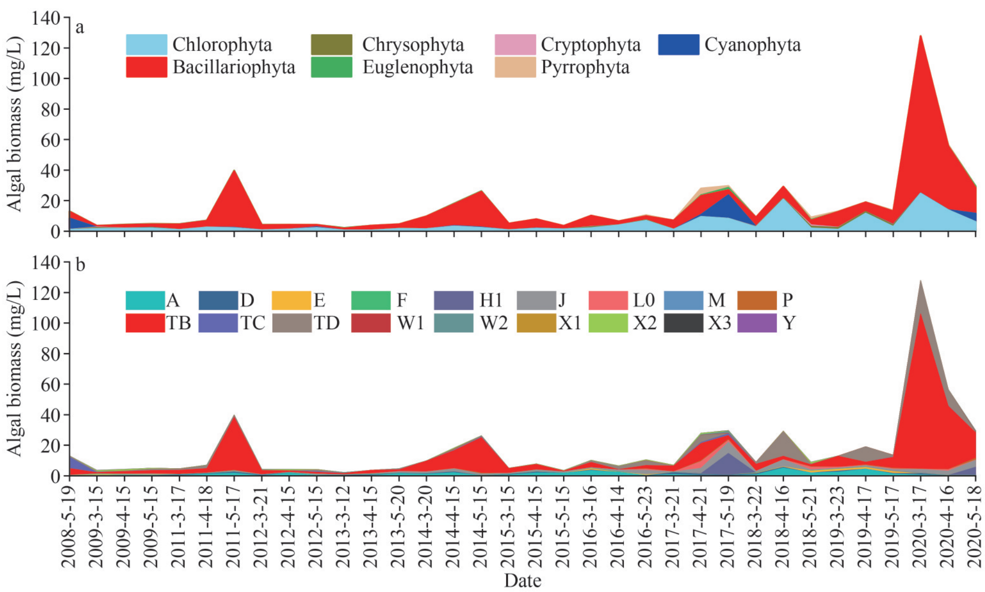


**Fig.2 The composition of phytoplankton community groups throughout the study period**

a. phylum composition; b. functional group composition.

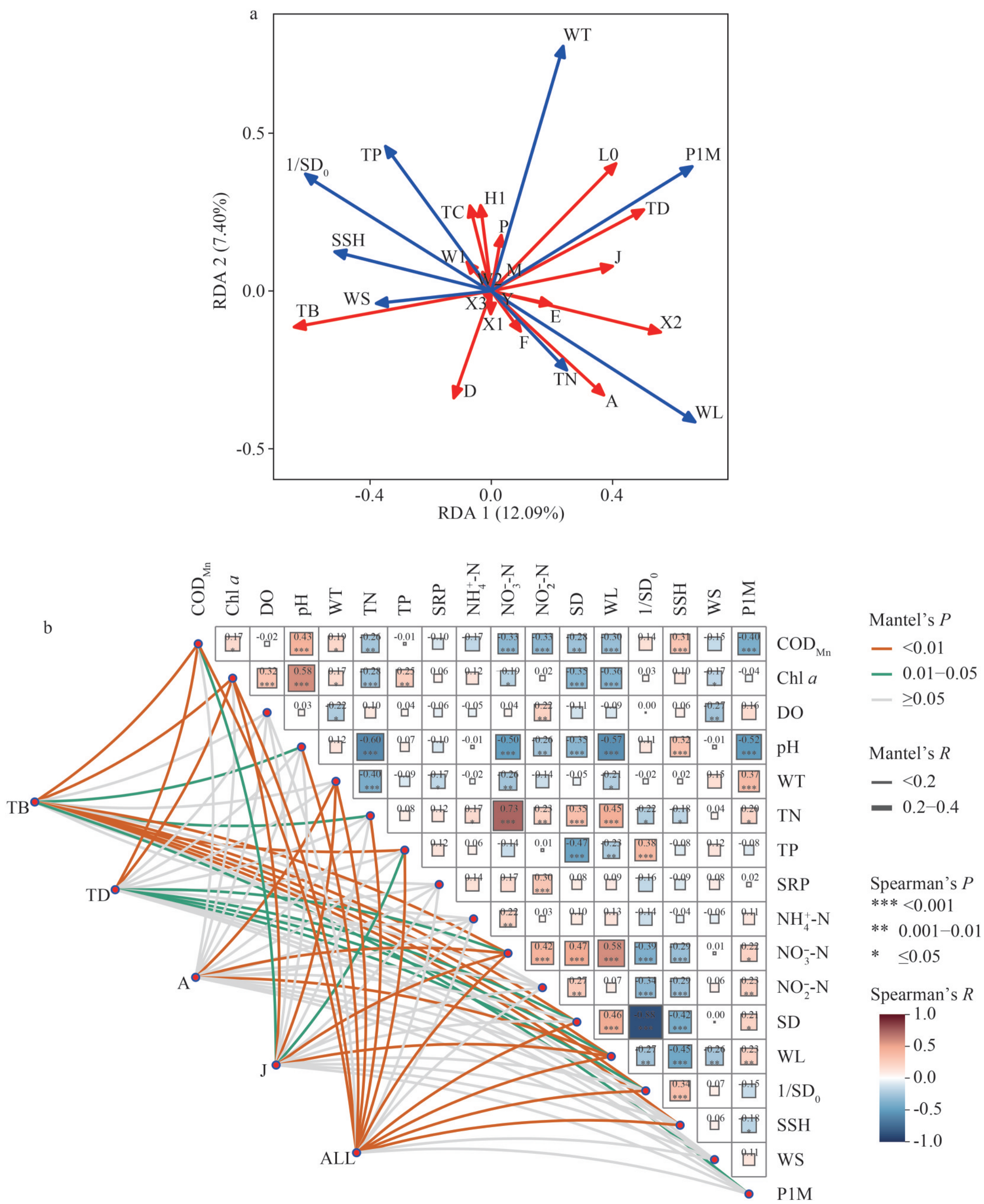


**Fig.3 Environmental factors driving phytoplankton community**

a. RDA ordination of the phytoplankton functional group with environmental variables. Blue vectors point to the direction of the increase for a given environmental variable, red vectors point to the direction of the increase for a phytoplankton functional group; b. relationships between environmental variables and composition of the phytoplankton functional community. Pairwise comparisons of environmental factors are displayed with a color gradient denoting Spearman's correlation coefficient. Phytoplankton functional groups were related to each environmental factors by Mantel's test.

was driven by $NO_3^-$-N ($R$=0.16, $P$<0.05), light condition ($R$=0.09, $P$<0.05 for SD and $R$=0.11, $P$< 0.05) and P1M ($R$=0.09, $P$<0.05). The group A was highly correlated with $NO_3^-$-N ($R$=0.13, $P$<0.001), WL ($R$=0.10, $P$<0.001), and WT ($R$=0.08, $P$<0.001). The group J was highly correlated with WL ($R$=0.15, $P$<0.001) and $NO_3^-$-N ($R$=0.11, $P$<0.001) (Fig.3b).

### 3.4 The relationship between precipitation, productivity and species richness

Two regression models were all shown a unimodal pattern (Fig.4a & b). According to the DEM's species predictions (Reynolds et al., 1993; Naselli-Flores et al., 2003; Huston, 2014), the unimodal relationship between phytoplankton

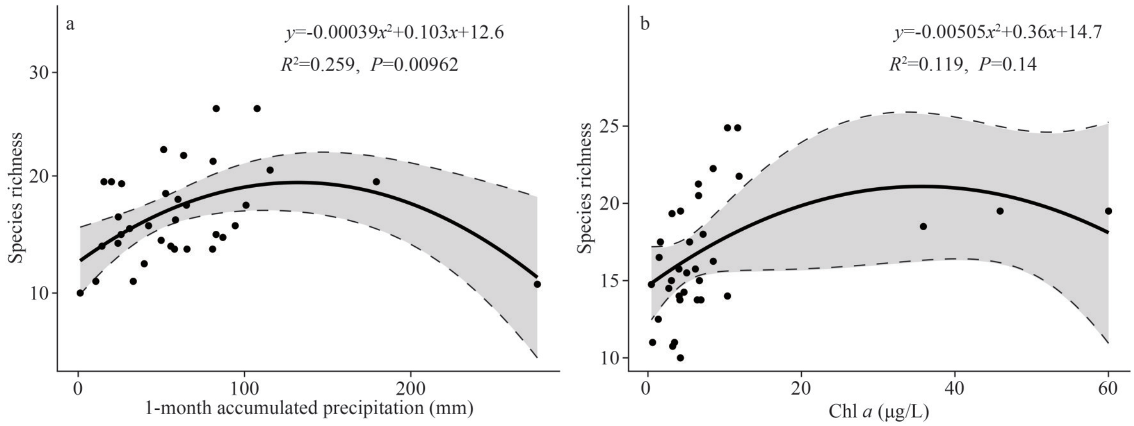


**Fig.4 Species diversity prediction in DEM**

a. the unimodal relationship between species richness and P1M; b. the unimodal relationship between species richness and productivity.

productivity (Chl *a*) and species diversity indicated that local phytoplankton community have a moderate productivity and was easily to be disturbed by P1M. While the unimodal relationships between precipitation-induced disturbance and species diversity illustrated that the phytoplankton community was shaped by inter-species competition and high mortality rate (flushing rate) during extremely drought and rainy periods, respectively.

### 3.5 The principal factor affecting the biomass of bloom forming group TB

The results of the SEM model showed the relationships among climate variables, water level, non-algal turbidity indicator 1/SD$_0$, TP, and the biomass of TB (Fig.5). The Chi-square test' *P*, CFI,

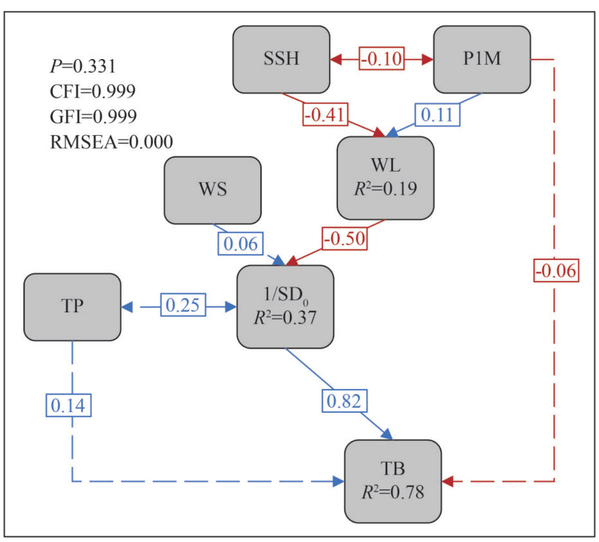


**Fig.5 SEM model showed the relationships among climate variables, water level, non-algal turbidity indicator 1/SD$_0$, TP, and the biomass of TB**

GFI and RMSEA were 0.31, 0.999, 0.999, and 0.000, respectively, indicating that our model fit the data well. The unidirectional arrows represent the casual relationships between two variables, the double arrows represent the covariance between two variables. The solid line and dash line noted that the correlation ships were significant ($P<0.05$) or insignificant ($P>0.05$). The SSH and P1M significantly contribute to the WL (path effects= -0.41 and 0.11, respectively). Then, the decreased WL strongly cause the increasements of 1/SD$_0$ (path effect=-0.50), probably due to low water levels lead to a stronger disturbance in water column thus enhanced the sediments resuspension. The rising non-algal turbidity was highly correlated with TP (path effect=0.25). Finally, the increased TP, 1/SD$_0$ and decreased precipitation-related disturbance promoted the competitiveness of TB (path effect= 0.14, 0.82, and -0.06, respectively).

The unidirectional arrows represent the casual relationships between two variables, the double arrows represent the covariance between two factors.

## 4 DISCUSSION

### 4.1 Effect of drought on the environmental parameters of Daxi Reservoir

According to the Spearman's test and SEM, water level was significantly determined by P1M and SSH (Spearman's $R$=0.23 and -0.45, $P<0.01$ and 0.05, path effect=-0.41 and 0.11, respectively), implying that precipitation induced water load and drought-related surface evaporation together determined the volume and depth (equal to water level) of Daxi Reservoir. The WL was highly correlated with the water column stability in addition to wind fetch and wind velocity further decided the magnitude of sediments resuspension (Abirhire et al., 2020; Janatian et al., 2020). We observe WL was significantly correlated to $1/SD_0$ and TP (Spearman's $R$=-0.27 and -0.23, $P$<0.01 and $P$<0.01, respectively), probably due to the lower water level result in a stronger resuspension process thus entrainment suspension solid to water column thus deteriorate the underwater light condition (da Costa et al., 2016). Moreover, a strong correlation ship was detected between $1/SD_0$ and TP ($R$=0.38, $P$<0.001 in Spearman's test, covariance=0.25 in SEM), and the peaks of TP occurred with high $1/SD_0$ despite lack of precipitation induced nutrient load. Thus, we suggest that the drought-induced low water level caused a strong wind-induced disturbance in the water column, thereby enhancing the resuspension of high phosphorus content sediments.

## 4.2 Effect of drought on phytoplankton community

Reservoirs are river-lake hybrids, and their physical-chemical and biological features are extremely sensitive to climate change. The more the reservoir water inflow increase, the more it will act as a river. We found a significant correlation ship between water level and 1-month accumulated precipitation in Daxi Reservoir (Spearman's $R$=0.23, $P$<0.01), implicate that the precipitation regime robustly driven the water inflow of Daxi Reservoir.

As predicted by DEM, we found a unimodal relationship between phytoplankton productivity (Chl $a$) and species diversity (Fig.4b). This condition was also observed in sub-trophic reservoirs with a large catchment area/reservoir area (Xu et al., 2023), implying that local phytoplankton community have a moderate productivity and was easily to be disturbed by precipitation. The relationships between precipitation induced disturbance (P1M) and species diversity also present a unimodal pattern (Fig.4a), implying that the phytoplankton community was regulated by inter-species competition and high mortality rate (flushing rate) during very drought and rainy periods, respectively (Connell and Orias, 1964; Reynolds et al., 1993; Barone and Naselli Flores, 1994). Our RDA analysis also revealed that the group TB out competed other phytoplankton species in well mixing, high turbidity, and nutrient (TP) enriched condition (left end of RDA 1, Fig.2a). The environmental disturbances could moderate the interspecies competition, preventing the establishment of a competitive equilibrium (Connell and Orias, 1964; Xu et al., 2023). However, an extremely disturbance might filter out almost species, and retain some species via trait filtering (Mouchet et al., 2010). Our results show that the P1M was positively correlated with SD and WL, implying the raised P1M enhanced the underwater light condition and might calm the water column. Accordingly, we observed that the groups L0 (prefer calm water column), TD (tolerant to high flushing), J (prefer clear water body), X2 (prefer stable water column), and A (prefer clear water column) dominated the right end of RDA 1.

## 4.3 Drought contributed to the bloom of group TB

According to the unimodal relationship between P1M and species richness (Fig.4a), we suggest that the drought caused a low renewal of the water body, enhanced the competitive exclusion process, and thus provided a prerequisite for TB to outcompete. Moreover, spring diatom blooms are recognized as being highly related to nutrients and light condition (Kiss and Genkal, 1993; Ferris and Lehman, 2007; Lehman et al., 2007; Edwards et al., 2016). Three peaks of biomass of TB were observed in May 2011, May 2014, and March 2020 at 34.53, 23.15, and 101.43 mg/L, respectively (Fig.2b). During these periods, the P1M was 26.1, 52.6, and 30 mm, the WL was 15.38, 14.96, and 15.12 m, which was lower than their mean value (64.57 mm and 16.53 m, respectively) in spring. Non-algae turbidity indicator $1/SD_0$ values were 1.57, 0.68, and 0.72, TP concentrations increased to 0.03, 0.03, and 0.05 mg/L, which were significantly higher than their spring mean values of 0.44 and 0.02 mg/L, respectively. In fact, TB group was composed of planktonic pennate diatoms that were able to tolerate light deficiency and preferred nutrient-enriched environments (Ferris and Lehman, 2007; Kong et al., 2021). Thus, we noted the drought-related increase in $1/SD_0$ and TP was the major driven factors for TB blooms.

## 4.4 Implication for reservoir management

The critical question for reservoir managers is how to keep the biomass of bloom-forming algae at safe levels to reduce the potential threat to water supplies. Nutrient reduction could significantly reduce the risk of algal bloom events and is a widely accepted bottom-up measurement that could thoroughly control algal biomass (Schindler, 1974; Istvánovics et al., 2002; Strom, 2002; Liang et al., 2020). However, this process might take a long time and is quite costly. Our results suggest that the nutrient load is not only from surface runoff in the catchment, but also from endogenous sediment release, which increases the difficulty of reduction. In addition, it may be quite difficult for nutrient management to achieve this goal because phytoplankton blooms can occur in water ecosystems with wide nutrient ranges due to the presence of multiple species with different optimal nutrient niches (Eppley, 1972; McCarthy and Eppley, 1972). For example, our RDA analysis also showed that an increase in TN does not cause an increase in TB biomass (Fig.3a).

Our findings together with the species predictions made by the DEM, indicate that a prolonged period of drought could lead to the emergence of certain species that outcompete others, thereby increasing the risk of blooms in springtime. In view of this, we suggest a timely water replenishment is crucial for maintain high phytoplankton diversity and reduces the bloom risks during spring droughts. In addition, a timely replenish could rapidly rise the water level and moderate the resuspension process (Coops and Hosper, 2002; Naselli-Flores and Barone, 2005), further reduce the endogenous nutrients load and the risks of algal bloom.

## 5 CONCLUSION

The drought-related environmental changes and affected the local phytoplankton community in the Daxi Reservoir. Low water level conditions resulted in mixing and sediment resuspension in high frequency and intensity, thus leading to the changes in nutrients and light availability for phytoplankton groups. RFG's group TB would form blooms under high TP, low light and low disturbance conditions in spring. Thus, It is critical to store a sufficient water source or prepare alternative water sources to cope with severe drought in spring to ensure ecological safety and water availability.

## 6 DATA AVAILABILITY STATEMENT

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

### References

Abirhire O, Davies J M, Guo X L et al. 2020. Understanding the factors associated with long-term reconstructed turbidity in Lake Diefenbaker from Landsat-imagery. *Science of the Total Environment*, **724**: 138222, https://doi.org/10.1016/j.scitotenv.2020.138222.

Abonyi A, Ács É, Hidas A et al. 2018. Functional diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the Danube River due to global warming, human impacts and oligotrophication. *Freshwater Biology*, **63**(5): 456-472, https://doi.org/10.1111/fwb.13084.

Arhonditsis G B, Stow C A, Steinberg L J et al. 2006. Exploring ecological patterns with structural equation modeling and Bayesian analysis. *Ecological Modelling*, **192**(3-4): 385-409, https://doi.org/10.1016/j.ecolmodel.2005.07.028.

Arthaud F, Vallod D, Robin J et al. 2012. Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes. *Aquatic Sciences*, **74**(3): 471-481, https://doi.org/10.1007/s00027-011-0241-4.

Bakker E S, Hilt S. 2016. Impact of water-level fluctuations on cyanobacterial blooms: options for management. *Aquatic Ecology*, **50**(3): 485-498, https://doi.org/10.1007/s10452-015-9556-x.

Barone R, Naselli Flores L. 1994. Phytoplankton dynamics in a shallow, hypertrophic reservoir (Lake Arancio, Sicily). *Hydrobiologia*, **289**(1-3): 199-214, https://doi.org/10.1007/BF00007421.

Barrett P R F, Curnow J C, Littlejohn J W. 1996. The control of diatom and cyanobacterial blooms in reservoirs using barley straw. *Hydrobiologia*, **340**(1-3): 307-311, https://doi.org/10.1007/BF00012773.

Bellinger B J, Richter A, Porras A et al. 2018. Drought and management effects on biophysicochemistry in a rapidly-flushed reservoir. *Lake and Reservoir Management*, **34**(2): 182-198, https://doi.org/10.1080/10402381.2017.1384770.

Brasil J, Attayde J L, Vasconcelos F R et al. 2016. Drought-induced water-level reduction favors cyanobacteria blooms in tropical shallow lakes. *Hydrobiologia*, **770**(1): 145-164, https://doi.org/10.1007/s10750-015-2578-5.

Cardoso M M L, Sousa W, Brasil J et al. 2022. Prolonged drought increases environmental heterogeneity and plankton dissimilarity between and within two semiarid shallow lakes over time. *Hydrobiologia*, **849**(17-18): 3995-4014, https://doi.org/10.1007/s10750-022-04882-0.

Connell J H, Orias E. 1964. The ecological regulation of species diversity. *The American Naturalist*, **98**(903): 399-414, https://doi.org/10.1086/282335.

Coops H, Hosper S H. 2002. Water-level management as a tool for the restoration of shallow lakes in the Netherlands. *Lake and Reservoir Management*, **18**(4): 293-298, https://doi.org/10.1080/07438140209353935.

Costa M R A, Menezes R F, Sarmento H et al. 2019. Extreme drought favors potential mixotrophic organisms in tropical semi-arid reservoirs. *Hydrobiologia*, **831**(1): 43-54, https://doi.org/10.1007/s10750-018-3583-2.

da Costa M R A, Attayde J L, Becker V. 2016. Effects of water level reduction on the dynamics of phytoplankton functional groups in tropical semi-arid shallow lakes. *Hydrobiologia*, **778**(1): 75-89, https://doi.org/10.1007/s10750-015-2593-6.

Devercelli M. 2006. Phytoplankton of the middle Paraná River during an anomalous hydrological period: a morphological and functional approach. *Hydrobiologia*, **563**(1): 465-478, https://doi.org/10.1007/s10750-006-0036-0.

Di Baldassarre G, Martinez F, Kalantari Z et al. 2017. Drought and flood in the Anthropocene: feedback mechanisms in reservoir operation. *Earth System Dynamics*, **8**(1): 225-233, https://doi.org/10.5194/esd-8-225-2017.

Diniz L P, Petsch D K, Mantovano T et al. 2023. A prolonged drought period reduced temporal β diversity of zooplankton, phytoplankton, and fish metacommunities in a Neotropical floodplain. *Hydrobiologia*, **850**(5): 1073-1089, https://doi.org/10.1007/s10750-023-05140-7.

Edwards K F, Thomas M K, Klausmeier C A et al. 2016. Phytoplankton growth and the interaction of light and temperature: a synthesis at the species and community level. *Limnology and Oceanography*, **61**(4): 1232-1244, https://doi.org/10.1002/lno.10282.

Eppley R W. 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin*, **70**(4): 1063-1085.

E W Rice, APHA. 2012. Standard Methods for the Examination of Water and Wastewater. 22nd edn. American Public Health Association, American Water Works Association, Water Environment Federation. Washington, DC.

Ferris J A, Lehman J T. 2007. Interannual variation in diatom bloom dynamics: roles of hydrology, nutrient limitation, sinking, and whole lake manipulation. *Water Research*, **41**(12): 2551-2562, https://doi.org/10.1016/j.watres.2007.03.027.

Gallouli E, Ali H O, Aamiri A. 2020. Impact of climate change on the phytoplankton community of the Aglou-Sidi Ifni coastline (Moroccan Atlantic coast). *E3S Web of Conferences*, **183**: 01004, https://doi.org/10.1051/e3sconf/202018301004.

Hall J W, Hannaford J, Hegerl G. 2022. Drought risk in the anthropocene. *Philosophical Transactions of the Royal Society A*: *Mathematical*, *Physical and Engineering Sciences*, **380**(2238): 20210297, https://doi.org/10.1098/rsta.2021.0297

Halsband-Lenk C, Pierson J J, Leising A W. 2005. Reproduction of *Pseudocalanus newmani* (Copepoda: Calanoida) is deleteriously affected by diatom blooms—a field study. *Progress in Oceanography*, **67**(3-4): 332-348, https://doi.org/10.1016/j.pocean.2005.09.003.

Hardin G. 1960. The competitive exclusion principle. *Science*, **131**(3409): 1292-1297, https://doi.org/10.1126/science.131.3409.1292.

Horn H, Paul L, Horn W et al. 2011. Long-term trends in the diatom composition of the spring bloom of a German reservoir: is *Aulacoseira subarctica* favoured by warm winters? *Freshwater Biology*, **56**(12): 2483-2499, https://doi.org/10.1111/j.1365-2427.2011.02674.x.

Howard K, Noble P. 2018. Hydrological perturbations drive rapid shifts in phytoplankton biodiversity and population dynamics in Butte Lake (Lassen Volcanic National Park, California). *Lake and Reservoir Management*, **34**(1): 21-41, https://doi.org/10.1080/10402381.2017.1360418.

Huisman J, Codd G A, Paerl H W et al. 2018. Cyanobacterial blooms. *Nature Reviews Microbiology*, **16**(8): 471-483, https://doi.org/10.1038/s41579-018-0040-1.

Huston M A. 2014. Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology*, **95**(9): 2382-2396, https://doi.org/10.1890/13-1397.1.

Hutchinson G E. 1961. The paradox of the plankton. *The American Naturalist*, **95**(882): 137-145, https://doi.org/10.1086/282171.

Istvánovics V, Somlyódy L, Clement A. 2002. Cyanobacteria-mediated internal eutrophication in shallow Lake Balaton after load reduction. *Water Research*, **36**(13): 3314-3322, https://doi.org/10.1016/S0043-1354(02)00036-2.

Janatian N, Olli K, Cremona F et al. 2020. Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. *Limnology and Oceanography*, **65**(4): 717-731, https://doi.org/10.1002/lno.11342.

Janssen A B G, Droppers B, Kong X Z et al. 2021. Characterizing 19 thousand Chinese lakes, ponds and reservoirs by morphometric, climate and sediment characteristics. *Water Research*, **202**: 117427, https://doi.org/10.1016/j.watres.2021.117427.

Jupp D L B, Kirk J T O, Harris G P. 1994. Detection, identification and mapping of cyanobacteria-using remote sensing to measure the optical quality of turbid inland waters. *Australian Journal of Marine and Freshwater Research*, **45**(5): 801-828, https://doi.org/10.1071/MF9940801.

Kibuye F A, Zamyadi A, Wert E C. 2021. A critical review on operation and performance of source water control strategies for cyanobacterial blooms: Part I-chemical control methods. *Harmful Algae*, **109**: 102099, https://doi.org/10.1016/j.hal.2021.102099.

Kiss K T, Genkal S I. 1993. Winter blooms of centric diatoms in the River Danube and in its side-arms near Budapest (Hungary). *Hydrobiologia*, **269**(1): 317-325, https://doi.org/10.1007/BF00028030.

Kong X Z, Seewald M, Dadi T et al. 2021. Unravelling winter diatom blooms in temperate lakes using high frequency data and ecological modeling. *Water Research*, **190**: 116681, https://doi.org/10.1016/j.watres.2020.116681.

Kruk C, Piccini C, Devercelli M et al. 2021. A trait-based approach predicting community assembly and dominance of microbial invasive species. *Oikos*, **130**(4): 571-586, https://doi.org/10.1111/oik.07694.

Lehman J T, Platte R A, Ferris J A. 2007. Role of hydrology in development of a vernal clear water phase in an urban impoundment. *Freshwater Biology*, **52**(9): 1773-1781, https://doi.org/10.1111/j.1365-2427.2007.01808.x.

Liang Z Y, Soranno P A, Wagner T. 2020. The role of phosphorus and nitrogen on chlorophyll *a*: evidence from hundreds of lakes. *Water Research*, **185**: 116236, https://doi.org/10.1016/j.watres.2020.116236.

Litchman E, Klausmeier C A. 2008. Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution, and Systematics*, **39**: 615-639, https://doi.org/10.1146/annurev.ecolsys.39.110707.173549.

Ma P M, Shi L D, Zhao X F et al. 2013. A bloom-forming freshwater diatom: *Achnanthidium catenatum*. *Journal of Lake Sciences*, **25**(1): 156-162, https://doi.org/10.18307/2013.0120. (in Chinese with English abstract)

McCarthy J J, Eppley R W. 1972. A comparison of chemical, isotopic, and enzymatic methods for measuring nitrogen assimilation of marine phytoplankton. *Limnology and Oceanography*, **17**(3): 371-382, https://doi.org/10.4319/lo.1972.17.3.0371.

Messager M L, Lehner B, Grill G et al. 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications*, **7**: 13603, https://doi.org/10.1038/ncomms13603.

Milly P C D, Dunne K A, Vecchia A V. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, **438**(7066): 347-350, https://doi.org/10.1038/nature04312.

Mouchet M A, Villéger S, Mason N W H et al. 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**(4): 867-876, https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Naselli-Flores L, Barone R. 2005. Water-level fluctuations in mediterranean reservoirs: setting a dewatering threshold as a management tool to improve water quality. *Hydrobiologia*, **548**(1): 85-99, https://doi.org/10.1007/s10750-005-1149-6.

Naselli-Flores L, Padisák J, Dokulil M T et al. 2003. Equilibrium/steady-state concept in phytoplankton ecology. *Hydrobiologia*, **502**(1-3): 395-403, https://doi.org/10.1023/B:HYDR.0000004297.52645.59.

Oberski D. 2014. lavaan. survey: an R package for complex survey analysis of structural equation models. *Journal of Statistical Software*, **57**(1): 1-27, https://doi.org/10.18637/jss.v057.i01.

Oliveira C Y B, Oliveira C D L, Almeida A J G et al. 2019. Phytoplankton responses to an extreme drought season: a case study at two reservoirs from a semiarid region, Northeastern Brazil. *Journal of Limnology*, **78**(2): 176-184, https://doi.org/10.4081/jlimnol.2019.1869.

Portielje R, Van der Molen D T. 1999. Relationships between eutrophication variables: from nutrient loading to transparency. *Hydrobiologia*, **408-409**: 375-387, https://doi.org/10.1023/A:1017090931476.

Ren J, Zhu G W, Jin Y W et al. 2017. Combined effects of water exchange rate and nutrient on diatom proliferation in Hengshan Reservoir, Taihu Basin. *Journal of Lake Sciences*, **29**(3): 604-616, https://doi.org/10.18307/2017.0309. (in Chinese with English abstract)

Reynolds C S, Huszar V, Kruk C et al. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, **24**(5): 417-428, https://doi.org/10.1093/plankt/24.5.417.

Reynolds C S, Padisák J, Sommer U. 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. *Hydrobiologia*, **249**(1-3): 183-188, https://doi.org/10.1007/BF00008853.

Salmaso N, Naselli-Flores L, Padisák J. 2015. Functional classifications and their application in phytoplankton ecology. *Freshwater Biology*, **60**(4): 603-619, https://doi.org/10.1111/fwb.12520.

Schindler D W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. *Science*, **184**(4139): 897-899, https://doi.org/10.1126/science.184.4139.897.

Sommer U, Gliwicz Z M, Lampert W et al. 1986. The peg-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie*, **106**(4): 433-471, https://doi.org/10.1127/archiv-hydrobiol/106/1986/433.

Strom S. 2002. Novel interactions between phytoplankton and microzooplankton: their influence on the coupling between growth and grazing rates in the sea. *Hydrobiologia*, **480**(1-3): 41-54, https://doi.org/10.1023/A:1021224832646.

Tilahun S, Kifle D. 2022. Limnological responses of a shallow tropical reservoir to recent incidence of hydro-climatic anomaly suggest potential challenges of future restoration efforts. *Environmental Science and Pollution Research*, **29**(7): 10729-10739, https://doi.org/10.1007/s11356-021-16433-6.

Van Loon A F, Gleeson T, Clark J et al. 2016. Drought in the anthropocene. *Nature Geoscience*, **9**(2): 89-91, https://doi.org/10.1038/ngeo2646.

Wan W H, Zhao J S, Li H Y et al. 2017. Hydrological drought in the anthropocene: impacts of local water extraction and reservoir regulation in the U.S. *Journal of Geophysical Research*: *Atmospheres*, **122**(21): 11313-11328, https://doi.org/10.1002/2017JD026899.

Xu Y P, Wang L, Tang Q H et al. 2023. The relationship between phytoplankton diversity and ecosystem functioning changes with disturbance regimes in tropical reservoirs. *Ecosystems*, **26**(4): 752-767, https://doi.org/10.1007/s10021-022-00791-4.

Yatigammana S K, Ileperuma O A, Perera M B U. 2011. Water pollution due to a harmful algal bloom: a preliminary study from two drinking water reservoirs in Kandy, Sri Lanka. *Journal of the National Science Foundation of Sri Lanka*, **39**(1): 91-94, https://doi.org/10.4038/jnsfsr.v39i1.2930.

Zhou H, Liu Y B. 2018. Spatio-temporal pattern of meteorological droughts and its possible linkage with climate variability. *International Journal of Climatology*, **38**(4): 2082-2096, https://doi.org/10.1002/joc.5319.

Zhu G W, Jin Y W, Ren J et al. 2016. Characteristics of diatom blooms in a reservoir-water supply area and the countermeasures in Taihu Basin, China. *Journal of Lake Sciences*, **28**(1): 9-21, https://doi.org/10.18307/2016.0102. (in Chinese with English abstract)

Zohary T, Ostrovsky I. 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters*, **1**(1): 47-59, https://doi.org/10.5268/IW-1.1.406.

## Electronic supplementary material

Supplementary material (Supplementary Figs.S1–S2 and Table S1) is available in the online version of this article at https://doi.org/10.1007/s00343-024-3190-1.