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JOURNAL OF  
ENVIRONMENTAL  
SCIENCES  
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# Structural and functional variations of phytoplankton communities in the face of multiple disturbances

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## ARTICLE INFO

### Article history:

Received 19 May 2020

Revised 31 July 2020

Accepted 31 July 2020

Available online 14 August 2020

### Keywords:

Algae

Biodiversity

Community ecology

Plankton

Resource use efficiency

Subtropical reservoir

## ABSTRACT

The global decline of freshwater biodiversity caused by climate change and human activities are supposed to disrupt ecosystem services related to water quality and alter the structure and function of aquatic communities across space and time, yet the effects of the combination of these factors on plankton community ecosystem has received relatively little attention. This study aimed to explore the impacts of disturbances (e.g. human activity, temperature, precipitation, and water level) on phytoplankton community structure (i.e. community evenness and community composition) and function (i.e. resource use efficiency) in four subtropical reservoirs over 7 years from 2010 to 2016. Our results showed that community turnover (measured as community dissimilarity) was positively related to disturbance frequency, but no significant correlation was found between phytoplankton biodiversity (i.e. evenness) and disturbance frequency. Phytoplankton resource use efficiency (RUE = phytoplankton biomass/ total phosphorus) was increased with a higher frequency of disturbance with an exception of cyanobacteria. The RUE of Cyanobacteria and diatoms showed significantly negative correlations with their community evenness, while the RUE of Chlorophyta exhibited a positive correlation with their community turnover. We suggest that multiple environmental disturbances may play crucial roles in shaping the structure and functioning of plankton communities in subtropical reservoirs, and mechanism of this process can provide key information for freshwater uses, management and conservation.

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## Introduction

The correlation between biodiversity and ecosystem functioning (BEF) has been a hot topic on ongoing ecological researches in recent years due to increasing biodiversity loss in ecosystems and its impact on ecosystem functioning

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(Loreau et al., 2002; Balvanera et al., 2006; Hooper et al., 2012; Ye et al., 2019; Chai et al., 2020). The maintenance of biological diversity and ecosystem integrity in the face of environmental perturbations has many practical implications, potentially affecting ecosystem goods and services that humans rely upon (Cardinale et al., 2012). However, there is still no general consensus on the underlying drivers of biodiversity effects, especially in man-made aquatic ecosystems (e.g. reservoir) in a changing environment.

Over the past few decades, the combined effects of both the natural and anthropogenic disturbances have severely impacted the ecological communities (Sousa, 1984; Lenihan and Oliver, 1995; Supp and Ernest, 2014). The bulk of previous research on the responses to environmental change normally focused on a single disturbance at a time. However, there is ample evidence showing that the response of natural ecosystems to environmental change is often associated with multiple disturbances (Schindler, 2001; Wilson et al., 2006; Lu et al., 2019). Different kinds of disturbances may have profound impacts on community structure and ecosystem functioning through changes in biodiversity (Vinebrooke et al., 2003; Wilson et al., 2006; Yang et al., 2017; Hodapp et al., 2019). Many BEF studies have focused on narrow topics in biodiversity and ecosystem functions, as well as selections of model communities, yet the combined impacts of climate change and human activities on aquatic ecosystem functioning has received relatively little attention (Hillebrand and Matthiessen, 2009; Filstrup et al., 2014; Pires et al., 2018). Understanding of the combined effects of multiple disturbances on ecosystems is difficult as they cannot be explained by single-stressor studies. Disturbances are synergistic and/or antagonistic when their cumulative impacts are larger and/or less than expected by the calculation of their individual effects, respectively (Folt et al., 1999).

Globally, freshwater biodiversity is experiencing greater declines than those in terrestrial ecosystems due to the combined effects of human activities and climate change in their watersheds (Schindler, 2001; Rigos et al., 2014). For example, reservoir and lake ecosystems are highly susceptible to variations in the surrounding environmental features influenced by both local human activities (e.g. land use and artificial water transfer) and regional climate changes (e.g. temperature and precipitation) (Paillisson and Marion, 2011; Jeppesen et al., 2015; Yang et al., 2017; Isabwe et al., 2018). Shifts in ecosystem state may cause ecological degradation and alter the integrity of whole reservoir ecosystems (Johnson et al., 2001). Therefore, reservoirs have been presented as a classic example for illustrating the response of plankton composition and ecosystem processes to multiple disturbances (Yang et al., 2017). However, there are still large gaps in the understanding of ecological feedbacks that occur in subtropical reservoirs under multiple disturbance conditions (Evtimova and Donohue, 2014).

Phytoplankton communities are a crucial function component in maintaining ecosystem stability, and they clearly support a positive BEF relationship in lakes and reservoirs (Ptacnik et al., 2008; Filstrup et al., 2014). Elser et al. (2000) showed that aquatic biodiversity is closely related to the resources use efficiency (RUE) of organisms. The definition and quantification of RUE vary considerably

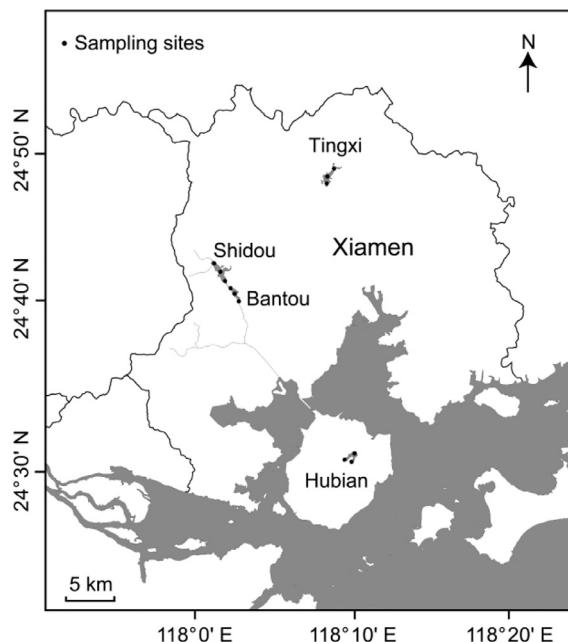
across different types of ecosystems (Hodapp et al., 2019). For example, in freshwater and marine ecosystems, the RUE was measured as standing stock (i.e. biomass or biovolume) standardized by the limiting nutrient (i.e. nitrogen or phosphorus) for the community (Ptacnik et al., 2008; Hillebrand and Matthiessen, 2009). Recently, Hodapp et al. (2019) unified the concept of RUE and quantified it as the ratio of biomass per unit of available resource. Likewise, phytoplankton functioning can be estimated as the ratio of phytoplankton biomass per unit limiting nutrient (Ptacnik et al., 2008). Many phytoplankton species can coexist despite the limited number of resources for which they compete each other (i.e. the Paradox of Plankton; Hutchinson, 1961). For example, based on a dataset from Fennoscandian lakes and Baltic Sea, Ptacnik et al. (2008) quantified phytoplankton RUE from phytoplankton biomass and demonstrated that phytoplankton RUE was increased with taxonomic richness. Further, there is evidence showing that phytoplankton RUE varied with different trophic levels along the food chain (Duffy et al., 2007). Cross-correlations between producer community richness and fertilization can be positive or negative according to the type of ecosystem, but higher nutrient availability consistently leads to lower species evenness (higher dominance) (Hillebrand et al., 2007). In highly productive ecosystems, evenness may be a better indicator of biodiversity metrics than species richness to describe BEF relationships, as species richness tends to over-emphasize the importance of rare species (Filstrup et al., 2014). Recently, the use of turnover metrics has been strongly encouraged, as biodiversity metrics such as evenness or species richness may underestimate the extent of compositional change (Hillebrand et al., 2017). Previous studies have found that communities and ecosystems with high species diversity may also exhibit higher stability and show less turnover with time (Ptacnik et al., 2008).

Variation in environmental conditions could dramatically shift the BEF relationships within an ecosystem (Wardle and Zackrisson, 2005; Steudel et al., 2012; Isbell et al., 2015; Verbeek et al., 2018). However, only a few studies have focused on the processes underlying observed disturbance-induced alterations in BEF relationships (Hodapp et al., 2016). Given the fact that the variety of environmental disturbances are likely to be more severely impacted by climate change and human activities, there is a pressing need to better understand how freshwater ecosystems are influenced by multiple disturbances for better predicting their performance under a changing environment in future. For these reasons, in this study, we did not just focus on a single disturbance. Here, our main goal was to explore how does increasing environmental disturbance frequency alter the relationships among phytoplankton biodiversity, community turnover and resource use efficiency in four subtropical reservoirs over a seven-year period.

We hypothesized that: (1) phytoplankton communities will show different responses to disturbance frequency in terms of biodiversity and compositional turnover. Phytoplankton biodiversity has a positive correlation with the frequency of disturbance (H1a), whereas phytoplankton turnover exhibits a positive correlation with the frequency of disturbance (H1b); (2) phytoplankton functional change (phytoplankton RUE) increases with increasing frequency of disturbance (H2).

**Table 1 – General characteristics of the four reservoirs in this study.**

	Tingxi (n = 84)	Shidou (n = 84)	Bantou (n = 81)	Hubian (n = 72)
Watershed land use	Forest	Forest	Forest	Urban
Reservoir surface area (km <sup>2</sup> )	1.95	3.96	0.55	1.03
Depth (m)	20.90 ± 7.31	13.57 ± 5.58	7.17 ± 2.35	5.45 ± 2.06
Transparency (m)	1.65 ± 0.63	1.55 ± 0.61	1.15 ± 0.38	1.02 ± 0.30
Water temperature (°C)	23.45 ± 5.45	24.04 ± 5.58	23.73 ± 5.22	23.08 ± 6.22
Total nitrogen (mg/L)	1.87 ± 1.34	2.00 ± 1.53	2.08 ± 1.58	2.70 ± 1.81
Total phosphorus (µg/L)	38.49 ± 27.53	23.94 ± 11.70	29.81 ± 14.29	42.73 ± 28.21
Total phytoplankton biomass (mg/L)	14.51 ± 18.68	294.35 ± 828.67	25.12 ± 36.69	47.68 ± 82.06

**Fig. 1 – Location of the four reservoirs and twelve sampling sites from Xiamen city in Fujian province, southeast China.**

## 1. Materials and methods

### 1.1. Study sites and sampling

The study was conducted in four subtropical reservoirs: Tingxi (24°48' N, 118°08' E), Shidou (24°42' N, 118°00' E), Bantou (24°40' N, 118°01' E), and Hubian (24°30' N, 118°10' E) (Fig. 1). They are all located along a gradient from urban to remote rural regions and are important drinking water sources for millions of local inhabitants (Yang et al., 2016). Both Tingxi and Shidou reservoirs have deeper water depths than Bantou and Hubian reservoirs (Table 1). Shidou (370 days) and Bantou (340 days) reservoirs have longer average water residence time than Tingxi (98 days) and Hubian (18 days) reservoirs (Yang et al., 2016). Both Shidou and Bantou reservoirs have a very well protect forested catchment, but are experiencing numerous natural and external disturbances (e.g. agriculture and deforestation). Tingxi Reservoir has a more pristine watershed with nearly 100% of primary forest coverage. These reservoirs

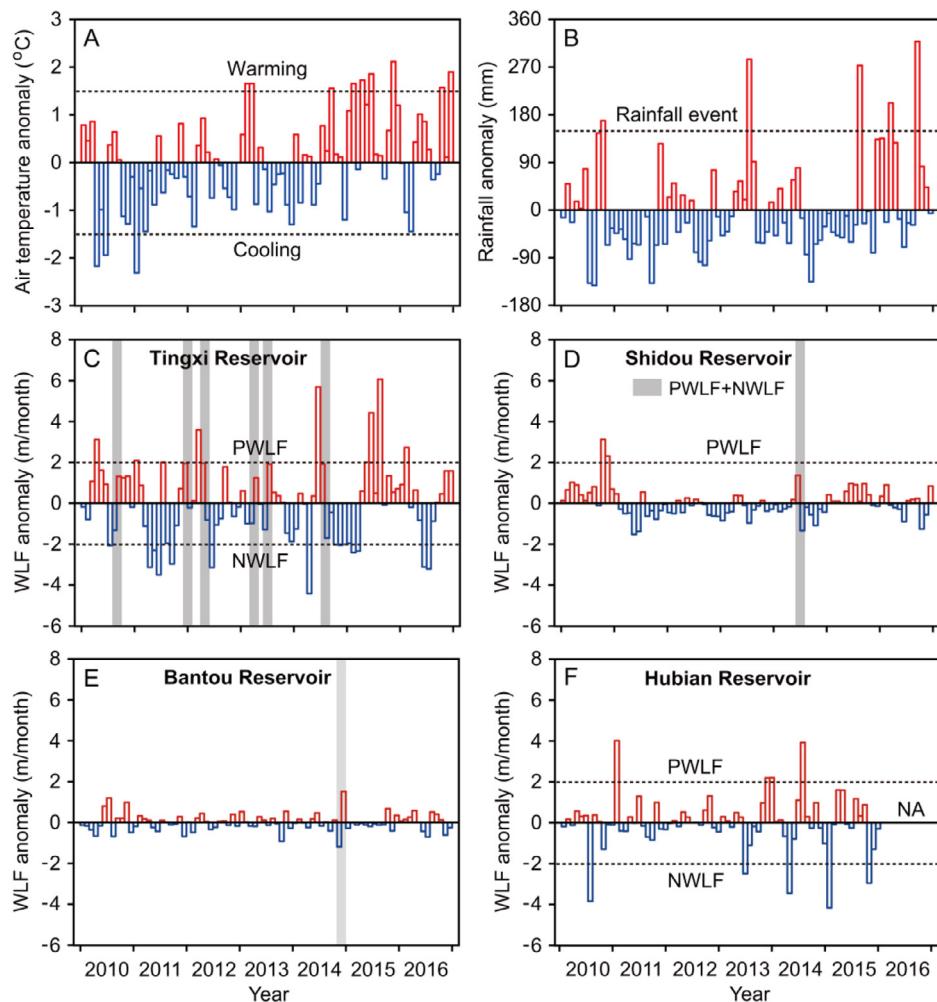
covered a wide range of nutrient concentrations, which resulted in various mean phytoplankton biomasses from 14.51 to 294.35 mg/L (Table 1). Despite high total phosphorus (TP) concentrations in the four reservoirs, preliminary investigations showed that phytoplankton biomass has a stronger relationship with TP than with total nitrogen (TN), and therefore TP was a much better predictor of phytoplankton biomass (Yang et al., 2016). In early 2010, both Shidou and Bantou reservoirs experienced a harmful cyanobacterial bloom which posed a serious threat to drinking water supplies in Xiamen. In order to protect the water quality of the watershed, a village that located in the upstream of Shidou and Bantou reservoirs was relocated, livestock breeding was prohibited, and the agriculture was restricted in and after the 2010 (Yang et al., 2017). The trophic states of the four reservoirs were classified from oligo-mesotrophic to eutrophic levels (Yang et al., 2012; 2016).

Sampling campaigns were carried out from January 2010 to October 2016 in four studied reservoirs. Sampling frequency was quarterly coinciding with the four seasons. We did not take water samples in Hubian Reservoir in 2016. We collected surface water samples from the riverine, transitional, and lacustrine zones, each of which corresponding to the upper, middle, and lower sections of the reservoir (Lv et al., 2014). Water transparency was estimated by using a Secchi disk. Water temperature, electrical conductivity, pH, and dissolved oxygen of the surface water were measured with a Water Quality Monitoring System (Hydrolab DS5, Hach Company, USA). Three liters of integrated water samples from the epilimnion (surface waters) were collected in each sampling site. Samples for nutrient analyses were preserved in a pre-cleaned plastic bottle and subsequently sent to the laboratory for further analysis. Phytoplankton samples were fixed in the field with 1.5% neutral Lugol's iodine solution for later species identification and individual counting (Yang et al., 2017).

### 1.2. Data collection and sample analysis

The hydro-meteorological data, including monthly averaged air temperature, water level, water retention time, and precipitation, were taken from Xiamen Meteorological Bureau and Xiamen Water Resources Bureau.

The chemical and biological characteristics of the water samples were analyzed following the standard methods. Nutrient parameters were measured following the method described by Greenberg et al. (1992). Phytoplankton samples were



**Fig. 2 – Weather and hydrological disturbance events recorded over the full time series in the four reservoirs. PWLF, positive water level fluctuation; NWLF, negative water level fluctuation. The shaded zones represent combined disturbances of PWLF and NWLF. Note that no data were collected for the Hubian Reservoir in 2016.**

counted using Utermöhl counting chambers under a Motic AE31 inverted microscope (Motic Corporation, China). Phytoplankton species was identified following John et al. (2002) and Hu and Wei (2006). For each sample, at least 500 individuals were counted (Yang et al., 2016). Species cell size was estimated based on 30 cells or individuals, and converted to species biovolume according to standard geometric formulae presented in Hillebrand et al. (1999). The biomass of each species was calculated from biovolume assuming a density of 1 mg/mm<sup>3</sup> (Wetzel and Likens, 2000).

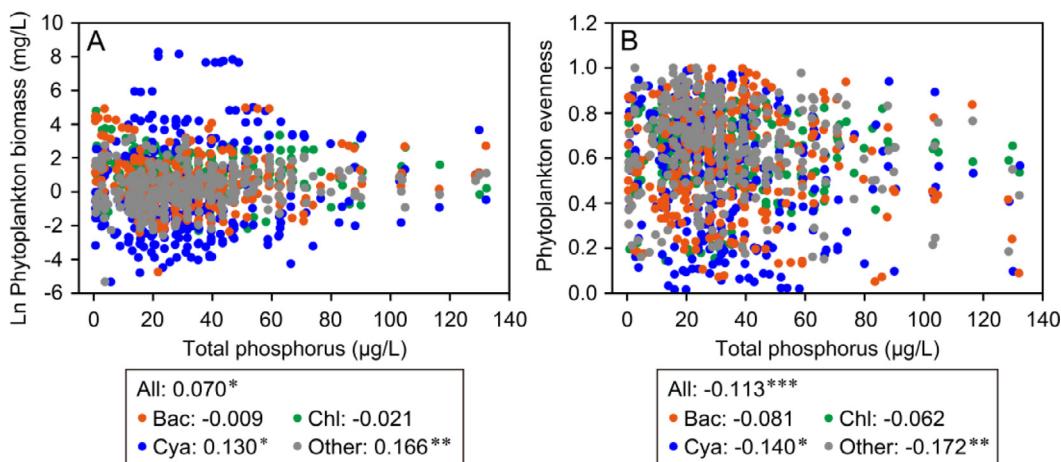
### 1.3. Definition of disturbance event

We defined a disturbance as a variable that exceeds its critical and normal threshold and can significantly affects individual physiology or population performance (Yang et al., 2017). Extreme temperature events such as warming and cooling were characterized by temperature anomalies  $> +1.5^{\circ}\text{C}$  and  $< -1.5^{\circ}\text{C}$  based on the historical data, respectively (Fisher et al., 2015). Precipitation events indicated the monthly precipitation anomalies higher than 150 mm based on the histori-

cal data (Kelner et al., 2014). Extreme water level fluctuations (WLF) were described as WLF anomalies above +2 m/month (positive WLF, PWLF) or below -2 m/month (negative WLF; NWLF) for two consecutive months (Yang et al., 2016). The frequency of the disturbance was characterized based on monthly resolution data in this study. Over the 7-year time span of the observations, one human-resettlement, 11 temperature (three cooling and eight warming events), 5 precipitation, and 28 WLF disturbances were identified in these four reservoirs (Fig. 2; Appendix A Table S1).

### 1.4. Statistical analysis

We applied linear mixed-effects models to quantify the linear relationships between the response and predictor variables. The composition of phytoplankton community was derived from species abundance data. Pielou's evenness was used as a measure of phytoplankton evenness which is one of robust measurements for species diversity (Pielou, 1969). Phytoplankton community turnover between the two sampling events was quantified using the Bray-Curtis dissimilarity met-



**Fig. 3 – Relationships between phytoplankton biomass or evenness and total phosphorus in the four subtropical reservoirs.** Pearson correlation coefficients ( $r$ ) are provided for regressions of all phytoplankton groups. All, all phytoplankton groups; Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Other, other phytoplankton groups. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

ric, which takes relative abundance into account within the ‘vegan’ package in R environment (Oksanen et al., 2013). Additionally, phytoplankton functional change was estimated from the change in RUE. Phytoplankton RUE was quantified as phytoplankton biomass per unit total phosphorus according to previous publication (Ptacnik et al., 2008).

To test our hypotheses, we measure the frequency of disturbance, the phytoplankton community biodiversity (i.e. evenness), community turnover (i.e. Bray-Curtis dissimilarity), and functioning (i.e. resource use efficiency) for all phytoplankton and four major groups. A positive correlation between phytoplankton evenness and disturbance frequency would support H1a, whereas a positive correlation between phytoplankton community turnover and disturbance frequency could confirm H1b. Likewise, we tested for significant correlations between the frequency of disturbance and measures of functional change (i.e. phytoplankton RUE) for hypothesis 2.

All statistical analyses were performed by using R software version 3.5.0 (R Development Core Team, 2018).

## 2. Results

### 2.1. The frequency of disturbances related to phytoplankton community

We found that precipitation, temperature and total phosphorus (TP) were the main factors that influenced phytoplankton community composition, while water level and total nitrogen (TN) had less effect (Appendix A Fig. S1). Both phytoplankton biomass ( $r = 0.070$ ,  $P < 0.05$ ) and evenness ( $r = -0.113$ ,  $P < 0.001$ ) were significantly related to TP across all phytoplankton groups (Fig. 3). When only considering the individual groups, phytoplankton biomass and evenness displayed significant relationships in Cyanobacteria and other phytoplankton groups (Fig. 3B). Relationships between seasonal changes in phytoplankton biomass and disturbance fre-

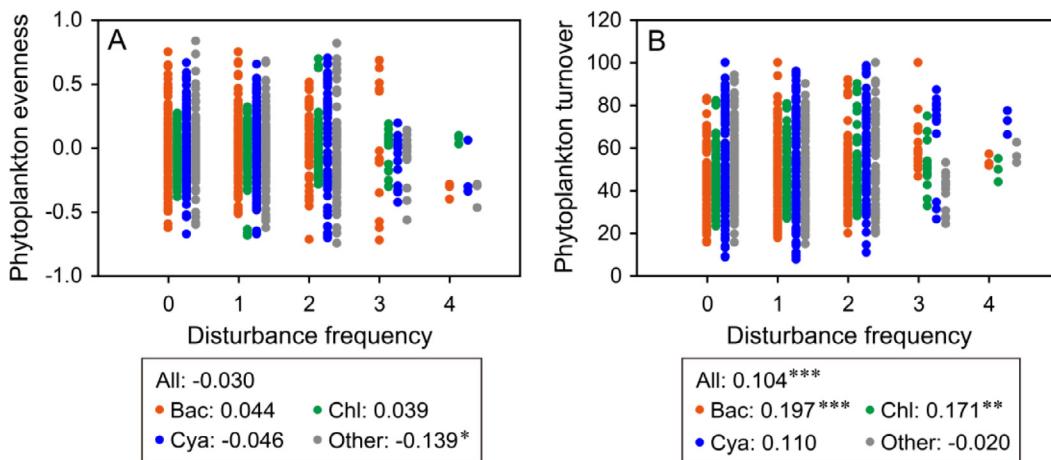
quency can be varied with different nutrient conditions (Appendix A Fig. S2). In an oligo-mesotrophic environment, phytoplankton biomass was significantly related to the frequency of disturbance across all phytoplankton groups, but not for eutrophic waters.

Phytoplankton evenness was not significantly ( $r = -0.030$ ,  $P = 0.29$ ; Fig. 4A) related to the frequency of disturbance across all phytoplankton groups, but was significant for the compositional turnover of phytoplankton ( $r = 0.104$ ,  $P < 0.001$ ; Fig. 4B). Phytoplankton evenness only displayed a significant and negative relationship with disturbance frequency in other phytoplankton groups (Fig. 4A), whereas phytoplankton turnover significantly and positively correlated with disturbance frequency in both Bacillariophyta and Chlorophyta (Fig. 4B). The frequency with which species occurred in phytoplankton communities was well described by the neutral model (Fig. 5). The majority of species fell above the neutral prediction, but Cyanobacteria species were found to mainly occur below the predicted neutral curve.

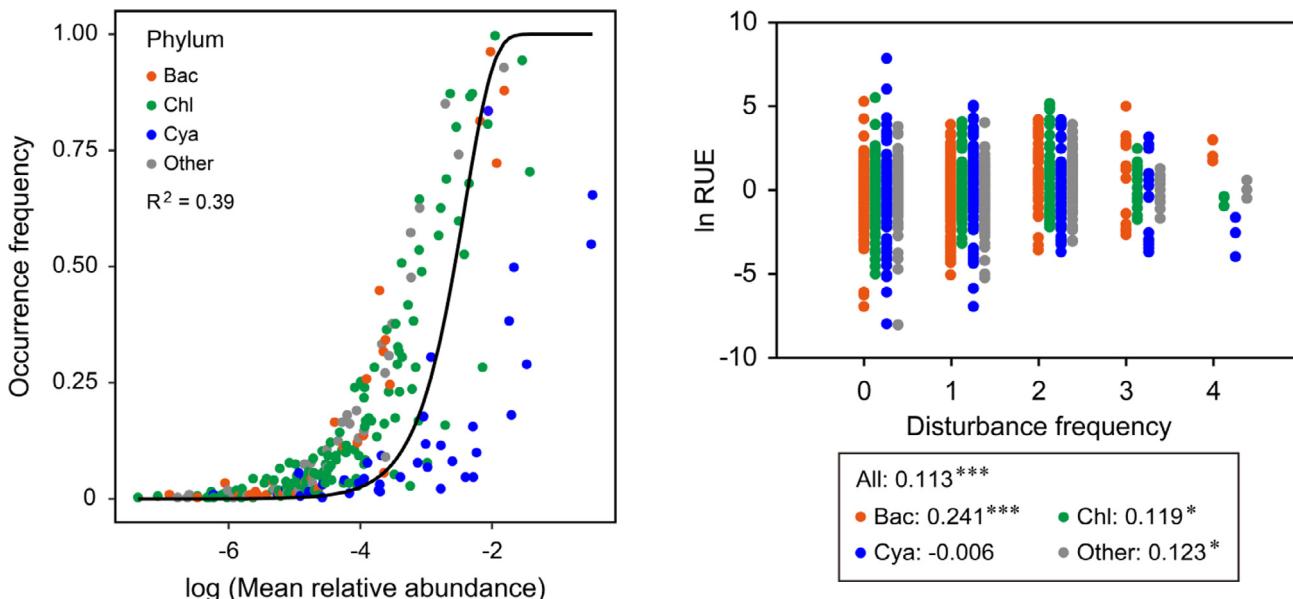
The relationship between phytoplankton evenness and phytoplankton turnover was significant across all phytoplankton groups ( $r = 0.082$ ,  $P < 0.01$ ; Appendix A Fig. S3), and this positive correlation was also seen in Bacillariophyta and other phytoplankton groups (Appendix A Fig. S3).

### 2.2. Relationships between disturbance frequency and phytoplankton RUE

Variation in phytoplankton RUE was significantly and positively correlated to the frequency of disturbance across all phytoplankton groups ( $r = 0.113$ ,  $P < 0.001$ ), and this significant correlation was also seen in Bacillariophyta, Chlorophyta, and other phytoplankton groups (Fig. 6). Only Cyanobacteria did not show significant relationship between phytoplankton RUE and disturbance frequency.



**Fig. 4 – Changes in (A) phytoplankton evenness and (B) phytoplankton community turnover in relation to the frequency of disturbances in the four reservoirs. Pearson correlation coefficients ( $r$ ) are provided for regressions of all phytoplankton groups turnover by seasons. All, all phytoplankton groups; Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Other, other phytoplankton groups. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .**



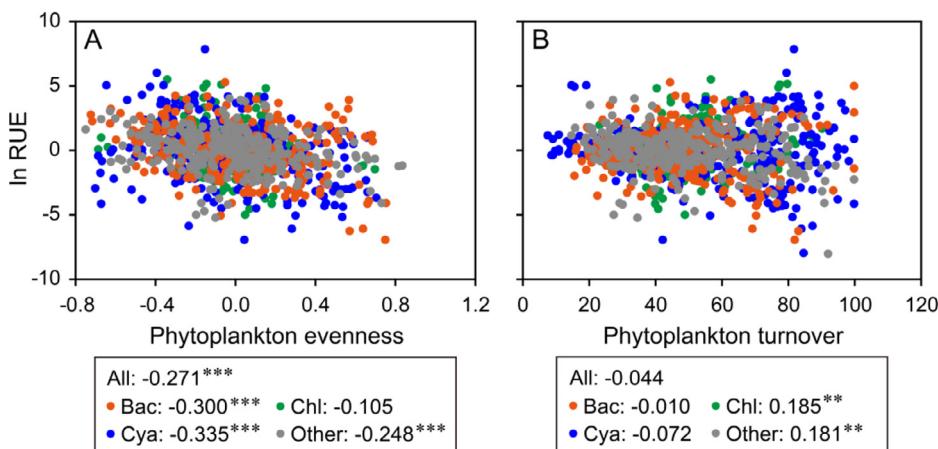
**Fig. 5 – Occurrence frequency as a function of the overall abundance of species among the phytoplankton metacommunity in the four subtropical reservoirs. The solid line represents the predicted occurrence frequency of the neutral model community of Sloan et al. (2006). Species above the model occur more frequently than predicted, and those below occur less frequently than predicted. Each species is colored by its phytoplankton phylum. Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Other, other phytoplankton groups.**

### 2.3. Relationships between phytoplankton community structure and RUE

The change in phytoplankton RUE was significantly associated with phytoplankton evenness across all phytoplank-

**Fig. 6 – Relationships between seasonal change in phytoplankton resource use efficiency (RUE) and disturbance frequency in the four reservoirs. Pearson correlation coefficients ( $r$ ) are provided for regressions of all phytoplankton groups turnover by seasons. All, all phytoplankton groups; Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Other, other phytoplankton groups. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .**

ton groups, but not for phytoplankton turnover (Fig. 7). Decreases in phytoplankton RUE was resulted from an increase in phytoplankton evenness across all phytoplankton groups ( $r = -0.271$ ,  $P < 0.001$ ) and for each phytoplankton group except for Chlorophyta (Fig. 7A). Phytoplankton RUE exhibited a significant and positive relationship with phytoplankton turnover for Chlorophyta and other phytoplankton groups, respectively (Fig. 7B).



**Fig. 7 – Seasonal change in phytoplankton resource use efficiency (RUE) correlated with (A) seasonal change in phytoplankton evenness and (B) interseasonal phytoplankton community turnover. Pearson correlation coefficients ( $r$ ) are provided for regressions of each phytoplankton group. All, all phytoplankton groups; Bac, Bacillariophyta; Chl, Chlorophyta; Cya, Cyanobacteria; Other, other phytoplankton groups. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .**

### 3. Discussion

Our results revealed a substantial variation in environmental variables, phytoplankton community composition, biomass, biodiversity, and functioning in four reservoirs over 7 years. Phytoplankton biomass showed a positive correlation with total phosphorus, which has been well established in limnological literatures (Schindler, 1977; Zhu et al., 2010; De Senerpont Domis et al., 2014; O'Donnell et al., 2017). Following classical ecological theory (the intermediate disturbance hypothesis, IDH), the diversity of communities can be strongly affected by the frequency of disturbance (Connell, 1978). The correlations between disturbances and biodiversity strongly depend on the productivity and the resource supply rate (Huston, 1994). When nutrient supply is insufficient in the environments, the same disturbance may oppositely affect phytoplankton communities as compared to environments with adequate nutrient supply. More eutrophic reservoirs usually harbored less diverse phytoplankton assemblages (Naselli-Flores and Barone, 1994). Thus, the consistency of these results across sampling sites allows us to determine the relationship between the frequency of disturbance and the change in phytoplankton community structure (e.g. evenness and community turnover) and function (e.g. biomass production and nutrient limitation) in these subtropical reservoir ecosystems over seven years.

#### 3.1. Increased frequency of disturbance lead to no significant changes in biodiversity

In our study of the four subtropical reservoirs, phytoplankton evenness, one important aspect of biodiversity, had no significant relationship with frequent environmental disturbances, thereby refuting the hypothesis 1a. Variations in phytoplankton communities were not detected in the diversity metric. Disturbances have a profound impact on biodiversity (e.g. Connell, 1978; Huston, 1994; Verbeek et al., 2018), and that

the relationship between biodiversity and disturbance often shows a peak at intermediate levels of disturbance. However, based on a large number of published studies, Mackey and Currie (2001) reported that disturbance did not affect the diversity, richness, and evenness in 28%, 35%, and 50% of studies, respectively. In our study, the frequency of disturbances did not impact diversity.

This lack of a significant relationship between biodiversity and disturbance might be due to two possible reasons. First, many populations can be easily affected under frequent disturbances leading to further reduce species diversity (Connell, 1978). Species that declined in abundance can be replaced by newly immigrated or evolved species in such a way that the existing niches were fully occupied and, thus, the diversity stayed almost the same (taxonomic turnover). Our study also showed that the evenness index declined and maintained at a low level in response to frequent disturbances. Second, species replacement may mask the variations in the diversity metric (Pannard et al., 2008). The neutral model predicted that neutral processes of ecological drift and dispersal were powerful enough on their own to generate a large amount of composition variation both within and among phytoplankton communities, and these neutral or stochastic processes can explain a significant portion of the community assembly (Fig. 5).

#### 3.2. Increased frequency of disturbance lead to high phytoplankton community turnover

Our results indicated that a high frequency of disturbance appears to be associated with a high phytoplankton community turnover across the reservoirs, thereby supporting the hypothesis 1b. By resampling of 38 ponds in Belgium after 10 years, Verbeek et al. (2018) demonstrated that differentiation in biotic composition may occur at a faster rate under harsh environmental conditions. At a broad-scale from 131 Midwestern United States lakes, Filstrup et al. (2014) also found that high phytoplankton species turnover associated with low even-

ness, once the lakes dominated by few cyanobacterial genera (e.g. *Microcystis*). The change in phytoplankton compositional turnover is the sum of the differentiations between each species within two sampling dates, so that a modification in the density of a dominant species, such as cyanobacteria, can strongly affect the dynamics of the other species (Yang et al., 2017). Therefore, the high phytoplankton community turnover rate recorded here was likely a good indicator of the high sensitivity of plankton in the subtropical reservoirs.

Previous studies clearly support an opposite diversity-stability relationship in phytoplankton. Phytoplankton community would display a lower compositional turnover rate due to the larger number of species involved (Ptacnik et al., 2008). Tian et al. (2017) discovered that phytoplankton community turnover significantly decreased with increasing phytoplankton evenness. However, Filstrup et al. (2014) found that in nutrient-enriched lakes, phytoplankton communities dominated by a few species would show a slower community turnover rate than more even communities. In this study, we also found that phytoplankton evenness was positively correlated with community turnover rate (Appendix A Fig. S3), indicating different diversity-stability relationships occurred in aquatic and terrestrial ecosystems (Tilman and Downing, 1994).

Global aquatic communities may become more vulnerable under the combined effects of multiple environmental disturbances, such as human activity and climate change (Michalak et al., 2013; Yang et al., 2017). The stability of phytoplankton communities could be potentially altered by climate change and anthropogenic disturbances through modifying air temperature (Jöhnk et al., 2008), precipitation patterns (Reichwaldt and Ghadouani, 2012; Michalak et al., 2013), water level fluctuations (Zohary and Ostrovsky, 2011; Yang et al., 2016), and watershed characteristics including land use and runoff (Hayes et al., 2015). Community turnover can be used to describe the ability of species composition to adapt to fluctuating environments, as well as the stability of ecosystems (Verbeek et al., 2018).

### 3.3. Phytoplankton community functional change increases with increasing disturbance frequency

Variation in phytoplankton RUE was positively related to the disturbance frequency for all phytoplankton with an exception of Cyanobacteria (Fig. 6), thereby partially supporting the hypothesis 2. With higher nutrient loadings in an aquatic ecosystem, a large increase in productivity of phytoplankton or cyanobacteria-dominated state can occur (Reynolds, 2006). Cyanobacterial species (i.e. *Cylindrospermopsis raciborskii* in Shidou and Bantou reservoirs in this study) tend to have a higher efficiency of resource use (e.g. light, CO<sub>2</sub>, and nutrients) than non-cyanobacteria species, which may eventually cause some non-cyanobacteria sensitive species disappeared under cyanobacteria-dominant conditions (Burford et al., 2016; Yang et al., 2017). More importantly, the bloom-forming Cyanobacteria (e.g. *Microcystis* sp. and diazotrophic cyanobacteria) could produce the highest RUE under certain conditions (Filstrup et al., 2014; Olli et al., 2015).

In highly productive reservoirs of this study, phytoplankton RUE was negatively correlated with phytoplankton even-

ness (Fig. 7). The relationship between phytoplankton RUE and diversity was counter to expectations from most of the empirical studies (Ptacnik et al., 2008; Striebel et al., 2009; Tian et al., 2017), but was consistent with the finding of Filstrup et al. (2014). The opposing phytoplankton evenness-RUE relationships in these subtropical reservoirs likely result from the high frequency of environmental disturbances. Climate change and human activities may alter weather patterns and intensity of anthropogenic disturbances, via increased temperature, heavy precipitation events, agricultural and urban nutrient surpluses, and decline in water level, which all can result in the dominance of Cyanobacteria in reservoir ecosystems (Reichwaldt and Ghadouani, 2012; Yang et al., 2016, 2017). As bloom-forming cyanobacteria have a higher efficiency of resource use and competition advantage than other phytoplankton species (Burford et al., 2016; Yang et al., 2017), this can lead to a noticeable degradation in water quality and aquatic ecosystems.

Phytoplankton functioning is usually related to community turnover. Under a theoretical framework, Norberg et al. (2001) demonstrated that community turnover can variously affect ecosystem functioning depended on the disturbance regime. Phytoplankton RUE only displayed a significant relationship with the change in Chlorophyta and other phytoplankton groups (Fig. 7B), but it exhibited a positive correlation with the disturbance frequency for Bacillariophyta, Chlorophyta, and other phytoplankton groups (Fig. 6), indicating strong environmental effects on phytoplankton communities depending on the phytoplankton taxonomic group. A high disturbance frequency can lead to higher community turnover rate (Fig. 4B), which perhaps resulted in greater biodiversity and phytoplankton RUE in our reservoir ecosystems. This finding is consistent with one answer to the Paradox of Plankton (Hutchinson, 1961), namely that constantly changing environmental conditions could promote phytoplankton biodiversity. In general, fluctuating environments allow a greater number of species coexistence, even in a limited-resource environment (Hutchinson, 1961; Kenitz et al., 2013).

Our results were based on a broader seasonal sampling of four subtropical reservoirs. There are, however, some limitations in the current study. One of them is that we only focused on observational research rather than a controlled experiment, the other is high-frequency sampling is required to obtain the detail impacts of multiple disturbances at short-term period. The occurrence of disturbances is likely to be of more frequent under future climate change and human activity (i.e. urbanization), a key priority for the current scientific research should focus on a higher frequency of data collection and additional field manipulative experiments.

## 4. Conclusions

Our work highlights the influence of multiple disturbances on phytoplankton community structure and function in four subtropical reservoirs over seven years. The results demonstrated that frequent disturbances would translate into changes in phytoplankton communities. Phytoplankton biomass and evenness were significantly related to total phosphorus con-

centration across all phytoplankton groups. A high frequency of environmental disturbance was not significantly related to phytoplankton evenness, but it was associated with a high phytoplankton community turnover. The relationship between phytoplankton evenness and community turnover was significant across the four reservoirs. Further, we found strong positive effects of the disturbance frequency on phytoplankton RUE, and phytoplankton community structure and function had contrasting relationships, indicating significant and complex environmental effects on phytoplankton communities. As BEF relationships remains unclear in most ecosystems, our study provides insights into understanding the role of environmental disturbances in shaping the structure and function of phytoplankton communities in changing aquatic ecosystems.

## Acknowledgements

This work was supported by the National Natural Science Foundation of China (Nos. 91851104, 41703074 and 41901135), the National Key Research and Development Program of China (No. 2017YFA0605203), and the Natural Science Foundation of Fujian Province of China (No. 2019J02016).

## Appendix A Supplementary data

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.jes.2020.07.026](https://doi.org/10.1016/j.jes.2020.07.026).

## REFERENCES

- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D., et al., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Burford, M.A., Beardall, J., Willis, A., Orr, P.T., Magalhaes, V.F., Rangel, L.M., et al., 2016. Understanding the winning strategies used by the bloom-forming cyanobacterium *Cylindrospermopsis raciborskii*. *Harmful Algae* 54, 44–53.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., et al., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Chai, Z.Y., Wang, H., Deng, Y., Hu, Z., Tang, Y.Z., 2020. Harmful algal blooms significantly reduce the resource use efficiency in a coastal plankton community. *Sci. Total Environ.* 704, 135381.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- De Senerpont Domis, L.N., Van De Waal, D.B., Helmsing, N.R., Van Donk, E., Mooij, W.M., 2014. Community stoichiometry in a changing world: combined effects of warming and eutrophication on phytoplankton dynamics. *Ecology* 95, 1485–1495.
- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébaud, E., Loreau, M., 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecol. Lett.* 10, 522–538.
- Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folmar, A., Huberty, A., et al., 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408, 578–580.
- Evtimova, V.V., Donohue, I., 2014. Quantifying ecological responses to amplified water level fluctuations in standing waters: an experimental approach. *J. Appl. Ecol.* 51, 1282–1291.
- Filstrup, C.T., Hillebrand, H., Heathcote, A.J., Harpole, W.S., Downing, J.A., 2014. Cyanobacteria dominance influences resource use efficiency and community turnover in phytoplankton and zooplankton communities. *Ecol. Lett.* 17, 464–474.
- Fisher, J.L., Peterson, W.T., Rykaczewski, R.R., 2015. The impact of El Niño events on the pelagic food chain in the northern California Current. *Glob. Change Biol.* 21, 4401–4414.
- Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44, 864–877.
- Greenberg, A.E., Clesceri, L.S., Eaton, A.D. (Eds.), 1992. Standard Methods for the Examination of Water and Wastewater. American Public Health Association, Washington (DC), USA.
- Hayes, N.M., Vanni, M.J., Horgan, M.J., Renwick, W.H., 2015. Climate and land use interactively affect lake phytoplankton nutrient limitation status. *Ecology* 96, 392–402.
- Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., et al., 2017. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *J. Appl. Ecol.* 55, 169–184.
- Hillebrand, H., Dürselen, C.D., Kirschtel, D., Pollingher, U., Zohary, T., 1999. Biovolume calculation for pelagic and benthic microalgae. *J. Phycol.* 35, 403–424.
- Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., et al., 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proc. Natl. Acad. Sci. U. S. A.* 104, 10904–10909.
- Hillebrand, H., Matthiessen, B., 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecol. Lett.* 12, 1405–1419.
- Hodapp, D., Hillebrand, H., Blasius, B., Ryabov, A.B., 2016. Environmental and trait variability constrain community structure and the biodiversity-productivity relationship. *Ecology* 97, 1463–1474.
- Hodapp, D., Hillebrand, H., Striebel, M., 2019. Unifying the concept of resource use efficiency in ecology. *Front. Ecol. Evol.* 6, 233.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., et al., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.
- Hu, H., Wei, Y. (Eds.), 2006. The Freshwater Algae of China: Systematics, Taxonomy and Ecology. Science Press, Beijing, China (in Chinese).
- Huston, M.A. (Ed.), 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.
- Hutchinson, G.E., 1961. The Paradox of the Plankton. *Am. Nat.* 95, 137–145.
- Isabwe, A., Yang, J.R., Wang, Y.M., Liu, L.M., Chen, H.H., Yang, J., 2018. Community assembly processes underlying phytoplankton and bacterioplankton across a hydrologic change in a human-impacted river. *Sci. Total Environ.* 630, 658–667.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, T.C., et al., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577.
- Jeppesen, E., Brucet, S., Naselli-Flores, L., Papastergiadou, E., Stefanidis, K., Noges, T., et al., 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. *Hydrobiologia* 750, 201–227.
- John, D.M., Whitton, B.A., Brook, A.J. (Eds.), 2002. The Freshwater

- Algal Flora of the British Isles—An Identification Guide to Freshwater and Terrestrial Algae. Cambridge University Press, Cambridge, UK.
- Jöhnk, K.D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P.M., Stroom, J.M., 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Glob. Change Biol.* 14, 495–512.
- Johnson, N., Revenga, C., Echeverria, J., 2001. Managing water for people and nature. *Science* 292, 1071–1072.
- Kelner, M., Migeon, S., Tric, E., Couboulex, F., Dano, A., Lebourg, T., et al., 2014. Recent morphological changes of the nice continental slope. In: Lollino, G., Manconi, A., Locat, J., Huang, Y., Artigas, M.C. (Eds.). In: Engineering Geology for Society and Territory, 4. Springer, Switzerland, pp. 221–225.
- Kenitz, K., Williams, R.G., Sharples, J., Selsil, Ö., Biktashev, V.N., 2013. The paradox of the plankton: species competition and nutrient feedback sustain phytoplankton diversity. *Mar. Ecol. Prog. Ser.* 490, 107–119.
- Lenihan, H.S., Oliver, J.S., 1995. Anthropogenic and natural disturbances to marine benthic communities in Antarctica. *Ecol. Appl.* 5, 311–326.
- Loreau, M., Naeem, S., Inchausti, P. (Eds.), 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, UK.
- Lu, X., Lu, Y., Chen, D., Su, C., Song, S., Wang, T., et al., 2019. Climate change induced eutrophication of cold-water lake in an ecologically fragile nature reserve. *J. Environ. Sci.* 75, 359–369.
- Lv, H., Yang, J., Liu, L.M., Yu, X.Q., Yu, Z., Chiang, P.C., 2014. Temperature and nutrients are significant drivers of seasonal shift in phytoplankton community from a drinking water reservoir, subtropical China. *Environ. Sci. Pollut. Res.* 21, 5917–5928.
- Mackey, R.L., Currie, D.J., 2001. The diversity-disturbance relationship: is it generally strong and peaked? *Ecology* 82, 3479–3492.
- Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., et al., 2013. Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6448–6452.
- Naselli-Flores, L., Barone, R., 1994. Relationship between trophic state and plankton community structure in 21 Sicilian dam reservoirs. *Hydrobiologia* 275/276, 197–205.
- Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casagrandi, R., Levin, S.A., 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proc. Natl. Acad. Sci. U. S. A.* 98, 11376–11381.
- O'Donnell, D.R., Wilburn, P., Silow, E.A., Yampolsky, L.Y., Litchman, E., 2017. Nitrogen and phosphorus colimitation of phytoplankton in Lake Baikal: insights from a spatial survey and nutrient enrichment experiments. *Limnol. Oceanogr.* 62, 1383–1392.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., et al., 2013. vegan: Community Ecology Package. R package version 2, 0–10. <http://CRAN.R-project.org/package=vegan>.
- Olli, K., Klais, R., Tamminen, T., 2015. Rehabilitating the cyanobacteria-niche partitioning, resource use efficiency and phytoplankton community structure during diazotrophic cyanobacterial blooms. *J. Ecol.* 103, 1153–1164.
- Paillisson, J.M., Marion, L., 2011. Water level fluctuations for managing excessive plant biomass in shallow lakes. *Ecol. Eng.* 37, 241–247.
- Pannard, A., Bormans, M., Lagadeuc, Y., 2008. Phytoplankton species turnover controlled by physical forcing at different time scales. *Can. J. Fish. Aquat. Sci.* 65, 47–60.
- Pielou, E.C. (Ed.), 1969. An Introduction to Mathematical Ecology. Wiley, New York, USA.
- Pires, A.P., Srivastava, D.S., Marino, N.A., MacDonald, A.A.M., Figueiredo-Barros, M.P., Farjalla, V.F., 2018. Interactive effects of climate change and biodiversity loss on ecosystem functioning. *Ecology* 99, 1203–1213.
- Ptacnik, R., Solimini, A.G., Andersen, T., Tamminen, T., Brettm, P., Lepistö, L., et al., 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. *Proc. Natl. Acad. Sci. U. S. A.* 105, 5134–5138.
- R Development Core Team, 2018. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria.
- Reichwaldt, E.S., Ghadouani, A., 2012. Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: between simplistic scenarios and complex dynamics. *Water Res* 46, 1372–1393.
- Reynolds, C.S. (Ed.), 2006. The Ecology of Phytoplankton (Ecology, Biodiversity, and Conservation). Cambridge University Press, Cambridge, UK.
- Rigosi, A., Carey, C.C., Ibelings, B.W., Brookes, J.D., 2014. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. *Limnol. Oceanogr.* 59, 99–114.
- Schindler, D.W., 1977. Evolution of phosphorus limitation in lakes. *Science* 195, 260–262.
- Schindler, D.W., 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* 58, 18–29.
- Sloan, W.T., Lunn, M., Woodcock, S., Head, I.M., Nee, S., Curtis, T.P., 2006. Quantifying the roles of immigration and chance in shaping prokaryote community structure. *Environ. Microbiol.* 8, 732–740.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391.
- Steudel, B., Hector, A., Friedl, T., Lofke, C., Lorenz, M., Wesche, M., et al., 2012. Biodiversity effects on ecosystem functioning change along environmental stress gradients. *Ecol. Lett.* 15, 1397–1405.
- Striebel, M., Behl, S., Stibor, H., 2009. The coupling of biodiversity and productivity in phytoplankton communities: consequences for biomass stoichiometry. *Ecology* 90, 2025–2031.
- Supp, S.R., Ernest, S.K., 2014. Species-level and community-level responses to disturbance: a cross-community analysis. *Ecology* 95, 1717–1723.
- Tian, W., Zhang, H., Zhang, J., Zhao, L., Miao, M., Huang, H., 2017. Biodiversity effects on resource use efficiency and community turnover of plankton in Lake Nansihu, China. *Environ. Sci. Pollut. Res.* 24, 11279–11288.
- Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. *Nature* 367, 363–365.
- Verbeek, L., Vanhamel, M., van den Berg, E., Hanashiro, F.T., Gianuca, A.T., Striebel, M., et al., 2018. Compositional and functional consequences of environmental change in Belgian farmland ponds. *Freshwater Biol.* 63, 581–596.
- Vinebrooke, R.D., Schindler, D.W., Findlay, D.L., Turner, M.A., Paterson, M., Mills, K.H., 2003. Trophic dependence of ecosystem resistance and species compensation in experimentally acidified Lake 302S (Canada). *Ecosystems* 6, 101–113.
- Wardle, D.A., Zackrisson, O., 2005. Effects of species and functional group loss on island ecosystem properties. *Nature* 435, 806–810.
- Wetzel, R.G., Likens, G.E. (Eds.), 2000. Limnological Analyses, 3rd ed.. Springer-Verlag New York Inc., New York, USA.
- Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P., Polunin, N.V., 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient. *Glob. Change Biol.* 12, 2220–2234.
- Yang, J., Lv, H., Yang, J., Liu, L.M., Yu, X.Q., Chen, H.H., 2016. Decline

- in water level boosts cyanobacteria dominance in subtropical reservoirs. *Sci. Total Environ.* 557, 445–452.
- Yang, J., Yu, X.Q., Liu, L.M., Zhang, W.J., Guo, P.Y., 2012. Algae community and trophic state of subtropical reservoirs in southeast Fujian, China. *Environ. Sci. Pollut. Res.* 19, 1432–1442.
- Yang, J.R., Lv, H., Isabwe, A., Liu, L.M., Yu, X.Q., Chen, H.H., et al., 2017. Disturbance-induced phytoplankton regime shifts and recovery of cyanobacteria dominance in two subtropical reservoirs. *Water Res.* 120, 52–63.
- Ye, L., Chang, C.W., Matsuzaki, S.I.S., Takamura, N., Widdicombe, C.E., Hsieh, C.H., 2019. Functional diversity promotes phytoplankton resource use efficiency. *J. Ecol.* 107, 2353–2363.
- Zhu, W., Wan, L., Zhao, L., 2010. Effect of nutrient level on phytoplankton community structure in different water bodies. *J. Environ. Sci.* 22, 32–39.
- Zohary, T., Ostrovsky, I., 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland Waters* 1, 47–59.