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The Relationship Between Phytoplankton Diversity and Ecosystem Functioning Changes with Disturbance Regimes in Tropical Reservoirs

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ABSTRACT

The relationship between species diversity and ecosystem functioning is one of central topics in modern ecology, but variable and controversial patterns have been found depending on ecosystem type, organism type and scale. Such patterns call for mechanistic exploration within an integrative modelling framework. Lakes, especially reservoirs, are highly disturbed ecosystems, and the relationships between species diversity and ecosystem functioning likely differ from those of terrestrial ecosystems. Disturbance can have a great impact on local diversity and resource use efficiency (RUE) of phytoplankton assemblages and thereby influence these relationships. To elucidate how disturbance influences the diversity of phytoplankton and its relationship with ecosystem functioning, we analysed datasets from two groups of waterbodies (large-sized reservoirs and small-sized reservoirs) subjected to different disturbance regimes. We also investigated the mechanisms potentially underlying the relationships using structural equation modelling. A unimodal relationship between species richness and productivity was found in large-sized reservoirs and in small-sized reservoirs in dry seasons, while a positive linear relationship was detected in small-sized reservoirs in wet seasons. Cyanobacteria dominance increased the RUE of phytoplankton and decreased its evenness more significantly in large-sized reservoirs than in small reservoirs. The effects of water temperature and resources availability (TP) on species richness also changed with disturbance regimes. Disturbance is an important factor modifying the responses of phytoplankton communities to environmental gradients, and disturbance regimes at regional scale can largely shape the relationship between phytoplankton diversity and ecosystem functioning.

HIGHLIGHTS

- Relationship between richness and phytoplankton productivity of (sub-)tropical reservoirs varies with disturbance regimes.
- Unimodal and positive relationships between richness and phytoplankton productivity were common for large and small reservoirs, respectively.
- Non-equilibrium under disturbance allows reservoirs to host more species.
- Cyanobacteria decreased evenness but increased resource utilization efficiency of phytoplankton.

INTRODUCTION

Species diversity and ecosystem productivity are essential for the ability of natural systems to provide goods and service (Naeem and others 2009). The relationship between species richness and productivity is of strong interest for ecologists, and much effort has been used to unravel the nature of this relationship (Mittelbach and others 2001; Grace and others 2016). The bivariate relationship between species diversity and productivity in ecosystems has been subject to different interpretations. Community ecologists consider spatial or geographical (latitudinal and altitudinal) variation in species diversity to depend on primary production (energy hypothesis) and on the availability of resources (resource ratio hypothesis). In contrast, ecosystem ecologists are most supportive of the dual relationship linking biodiversity and ecosystem functioning and consider species diversity as a propeller for ecosystem functioning.

A unimodal pattern linking species richness and productivity was first suggested for herbaceous plants (Grime 1973a, 1973b, 2001), with species richness peaking at intermediate levels of net primary productivity. This pattern was later suggested to be ubiquitous and commonly occurring in natural communities (Rosenzweig and Abramsky 1993; Huston and DeAngelis 1994), although also positive relationships were observed (Mittelbach and others 2001). Fraser and others (2014, 2015) highlighted that species richness is limited at low productivity by the minimal/low availability of re-

sources and mainly consists of slow-growing species. In contrast, at high productivity, species richness is limited by interspecific competition since a few fast-growing species monopolise the resources. At intermediate productivity, the diversity peak is derived from/depends on two opposing processes that allow more species to co-occur or coexist. By carrying out a standardised sampling campaign of herbaceous plant communities across the world, Adler and others (2011), by contrast, found that productivity is a poor predictor of plant species richness. Laanisto and Hutchings (2015) found that site selection strongly influenced the relationship between species richness and productivity and that the unimodal pattern disappeared when the site selection was randomly performed.

Long discussions have led to the opinion that the relationship between species richness and productivity is variable and scale dependent and that any dominant pattern at a given scale remains controversial (Whittaker and Heegaard 2003; Gillman and Wright 2006; Whittaker 2010). According to modern community ecology, local species diversity can be regulated or determined not only by local but also by regional processes (Ricklefs 1987; Hubbell 2001; Mittelbach 2012). For example, Fei and others (2018) investigated over 115,000 contiguous forest plots across the USA and found that the relationship was positive in dry climates and unimodal in mesic climates. Graham and Duda (2011) showed that the unimodal patterns are associated with many different processes such as disturbance, herbivory and environmental gradients, and contingent on organisms and environments. The unimodal pattern is thus not ubiquitous as believed before, and it is a contingent rule generated by the interactions between several complex factors. In general, when analysing the local diversity of plants in grassland and of phytoplankton in pelagic waters, the unimodal pattern is more commonly found at moderate levels of productivity. In these habitats, herbaceous plants and phytoplankton are usually limited by a few factors and compete strongly for resources when attaining high biomass (productivity) values (Al-Mufti and others 1977; Zhang and others 2011; Skácelová and Lepš 2014; Török and others 2016; Zhang and others 2018). When shifting to regional scale, the patterns of species diversity are more complex since regional processes such as spatial heterogeneity, dispersal limitation and even species pools may influence the local diversity.

Compared to terrestrial plants, plankton has been less studied despite the pioneering works on species coexistence conducted by Hutchinson (1961). Re-

cently, Vallina and others (2014) found a robust unimodal pattern where the positive slope of the curve was regulated by grazing control, whereas the negative slope was driven by competitive exclusion. According to the competitive exclusion principle, species competing for the same resource cannot coexist at stable environmental conditions (Hardin 1960; Naselli-Flores and others 2003). However, competitive exclusion seldom occurs among phytoplankton species because of the high frequency of environmental changes, preventing the establishment of a competitive equilibrium (Hutchinson 1961). Hutchinson's non-equilibrium hypothesis contributed to clarify the effects of the frequency of environmental variability on species diversity and inspired Connell (1978) to develop the Intermediate Disturbance Hypothesis (IDH). As shown by Reynolds and others (1993), disturbance can play a critical role in determining the relationship between phytoplankton species diversity and productivity. According to Huston (2014), much of the criticism of the IDH can be attributed to the failure in recognising the link between the unimodal pattern and IDH. At low disturbance, more competitive organisms will exclude subordinate species, whereas at high disturbance species growth is inhibited; furthermore, considering the differences in the disturbance history can also help to correctly interpret the relationship between species diversity and productivity.

Human activities have increased the productivity of aquatic ecosystems since the industrial revolution, promoting eutrophication processes and a decrease in species diversity (for example, Ansari and others 2011). As a consequence of eutrophication, high cyanobacterial biomass, often composed of a single species, is limitedly transferred to higher trophic levels, thus greatly modifying ecosystem functions. Species losses and a decrease in species evenness result in reduced resource use efficiency and ultimately lower ecosystem functioning (Filstrup and others 2014, 2019).

In addition to local, within-lake factors, regional, among-lakes factors also need to be considered in the attempt to assess phytoplankton diversity. Phytoplankton assemblages across a regional productivity gradient share a common pool of species, and the diversity of local phytoplankton assemblages can be quickly shaped by the regional species pool that is airborne dispersed and even by the water flow among waterbodies during flooding periods (Naselli-Flores and Padisak 2016; Hu and others 2017).

Reservoirs are man-made waterbodies with both lakes and rivers characteristics (Thornton and others 1990). As part of river systems, the reservoirs have a variable water flow (amount and direction) and other hydrological properties that affect the structure of phytoplankton assemblages (Straškraba and others 1993; Han and others 2003). Compared to natural lakes and due to their operational regimes, reservoirs are more hydrodynamic systems. In monsoonal regions like southern China, 75% of the total precipitation occurs in summer and results in a strong disturbance of the phytoplankton communities in late dry season and early wet season, when large reservoirs are managed for irrigation and flooding control. Due to their small catchments, small reservoirs are less managed, exhibit stronger hydrological dynamics than large reservoirs, and become dry earlier. Shifts in the regime of disturbance may have a great impact on local diversity and on phytoplankton resource use efficiency.

In the present study, 107 (sub)tropical reservoirs located in southern China were studied to test the following hypotheses: (1) the relationships between species diversity and productivity are unimodal for phytoplankton at regional scales where a common species pool exists; (2) the unimodal pattern can be largely influenced by disturbance but to a different extent in small- and large-sized reservoirs; (3) cyanobacterial dominance significantly influences resource use efficiency, but this influence also varies with disturbance; (4) similar to the finding in natural lakes, resource use efficiency (RUE) is negatively associated with the species evenness of phytoplankton in reservoirs.

MATERIALS AND METHODS

Sampling Design and Data Collection

We assumed that disturbance regimes differ between large-sized and small-sized reservoirs. Due to longer water residence time (RT), large-sized reservoirs are more hydrodynamically stable than small-sized reservoirs, especially in the wet or flooding seasons. We studied 107 reservoirs (Figure 1) divided into two groups: 34 large-sized reservoirs (storage capacity $\geq 10^8$ m^3, RT ≥ 360 days) and 73 small-sized reservoirs (storage capacity $< 10^8$ m^3, RT ≈ 100 days). Here, RT is theoretical residence time and equal to water volume at normal water level divided by total inflow (Straškraba and others 1993). For our small reservoirs, water was pumped directly for navigation from September to November, that is, their actual RT is much shorter than 100 days. All the reservoirs were sampled in both dry (from November to
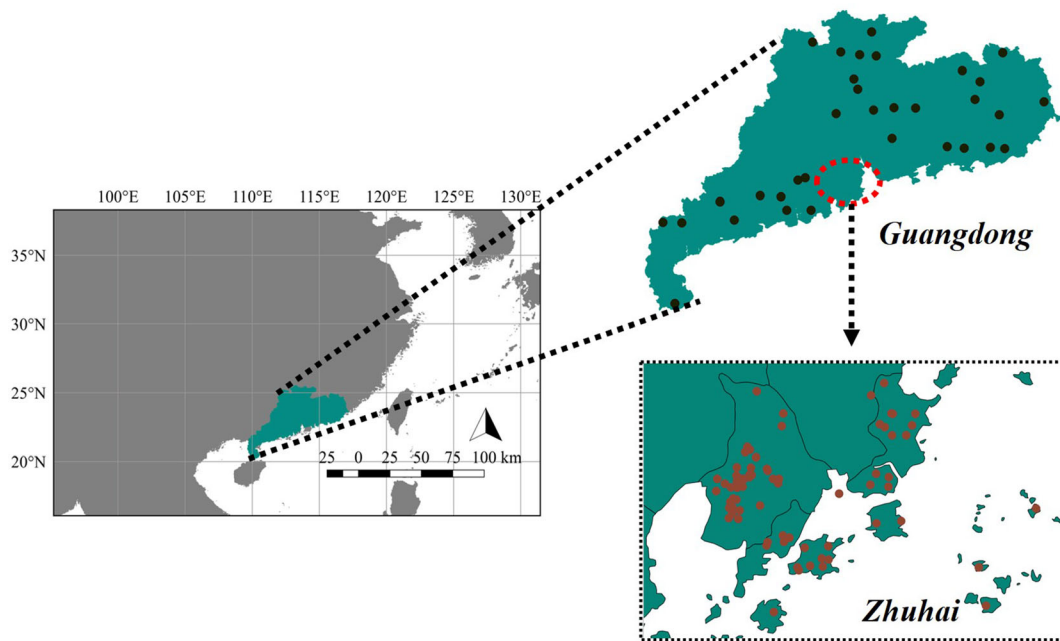
Figure 1. The locations of the reservoirs investigated in the present study in Guangdong Province, southern China. Black circles represent large-sized reservoirs and red circles represent small-sized reservoirs. Right, top: location of the large-sized reservoirs; right, bottom: location of the small-sized reservoirs.

March) and wet (from June to September) seasons, when they were at high water level. The large-sized reservoirs were sampled from 2014 to 2015, in the dry season (from October to January) and in the wet season (from June to September) and the small-sized reservoirs from 2017 to 2018 in the dry season (October) and in the wet season (August). Reservoir morphological variables (that is, volume and watershed characteristics) and sampling sites at each reservoir are shown in Table A1. For the small-sized reservoirs, one sampling site was located near the dam and another away from the dam so that that the two sites had rather dissimilar phytoplankton assemblages. For the large-sized reservoirs, several sites were sampled along the environmental gradient from the riverine zone to the lacustrine zone. Data on the surface area and the catchment area of each reservoir were provided by the local department of water resource management and checked using Google Earth.

Water samples for phytoplankton and chemical measurements were collected from the epilimnion with a hard plastic tube sampler (length: 6 m, diameter: 0.02 m). Water temperature (T, °C) was measured with a YSI85 (yellow spring) probe. TP and TN were measured following standard method (APHA 2012) (Figure A1).

A 100 ml subsample of water was fixed immediately with Lugol's solution and stored for phytoplankton enumeration. Phytoplankton species were identified and enumerated using an inverted microscope (Utermöhl 1958). For each species, the biovolume was estimated based on the morphology of cells (Hillebrand and others 1999) and through direct measurements of cell dimensions in at least 25 randomly selected individuals. Colonial species, for example, *Microcystis* spp., were measured and the individuals were counted. When the cell size changed largely within the population of a species at a given sampling site, the population was divided into several classes of cell size to determine the average cell volume. The biomass of each species was calculated as abundance × cell volume by assuming a wet weight density of 1 $g \cdot cm^{-3}$; total phytoplankton biomass was calculated as the sum of the biomass of all the species present. We also measured the Chl*a* concentration as a surrogate for primary (phytoplankton) productivity, which was determined spectrophotometrically after acetone extraction (Pápista and others 2002; Lin and others 2005).

Phytoplankton RUE was calculated as the ratio of Chl*a* to TP (RUE = Chl*a*: TP) (Ptacnik and others 2008). Simpson evenness (E) was calculated as: $E = 1/(S \times \sum p_i^2)$, where p_i is the proportion of

individuals belonging to species i; S is the number of species in the sample (Morris and others 2014). The genus richness value was obtained by counting the number of genera for every sampling site. The dissimilarity between any pair of phytoplankton assemblages was measured as Bray–Curtis dissimilarity. If one pair of phytoplankton assemblages within one single reservoir was rather similar (that is, BC dissimilarity $\leq$ 0.2), only one assemblage in the pair of assemblages was used to reduce pseudo replication in the data analysis. Finally, a total of 381 samples were analysed in our study, and AN-OVA did not show a significant difference in the Bray–Curtis dissimilarities between among-reservoirs and within-reservoirs with occurrence/absence data (Figure A2).

Data Analysis

Regression analysis was performed to determine the relationships between phytoplankton diversity (that is, species richness and evenness) and productivity (that is, Chl$a$ concentrations). Linear and quadratic regressions were performed for each dataset and were considered significant when the coefficients of determination had a p-value < 0.05.

Structural equation modelling (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 hypothesised set of causal pathways (Arhonditsis and others 2006; Grace and others 2010; Shipley 2016). Compared to multiple-regression analysis, SEM considers both direct and indirect effects of potential variables on response variables. The effect of measurement error (both random and systematic) on structural relationships can be taken into account, while multi-regression analysis assumes that measurement occurs without error (Hox and Bechger 2009; Stein and others 2012). In the present study, we aimed to elucidate potential factors or variables influencing directly or indirectly the relationship between diversity (species richness) and ecosystem productivity (Chl$a$). In the SEM, we considered the reservoir morphological variables including catchment area and lake size as well as physical and chemical factors including temperature (T) and TP. The ratio between the surface area of the waterbodies and the catchment area (SA/CA) was calculated to indicate the buffering capacity of waterbodies to external disturbance (Hu and others 2014; Morales-Baquero and others 1999). SEM was run not only for the combined datasets of two seasons, but also the datasets for each season. The Akaike information

criterion (AIC) was used to select the most parsimonious model. Using AIC, the final model was chosen based on the likelihood (AICL) that the model was the best fit to the current data set among the candidate models.

All analyses were undertaken in R (R Core Team 2014), regression analyses were performed with functions from package vegan (Oksanen and others 2018), and SEM was performed with package lavaan (Rosseel 2012).

RESULTS

Species Composition and Richness of Phytoplankton

Cyanobacteria were most frequently dominant in the large-sized reservoirs (Figure 2a and b), with filamentous species like *Raphidiopsis* (*Cylindrospermopsis*) *raciborskii*, *Pseudanabaena* spp. and *Limnothrix* spp. being dominant in the dry season (Figure 2a). In contrast, in the small-sized reservoirs, the most commonly dominant phytoplankton taxa belonged to green algae (Chlorophyta and Charophyta) (Figure 2c and d).

In general, few species dominated in each reservoir, and the difference in phytoplankton species richness between the dry and the wet season was mainly due to variation in rare species (relative biomass $< 1\%$) (Figure 3a and b). In the large-sized reservoirs, the species richness of phytoplankton was lower in the dry season than in the wet season (Figure 3a, $t = -3.39$, $df = 54.82$, $p < 0.05$). By contrast, in the small-sized reservoirs, phytoplankton species richness was higher in the dry season (Figure 3b, $t = 10.30$, $df = 138.54$, $p < 0.05$).

Relationship Between Species Richness and Productivity

The relationships between species richness and productivity (Chl$a$) showed a unimodal pattern for the large-sized reservoirs in both the dry and the wet season (Figure 4c and e) when the samples collected in two seasons were integrated (Figure 4a), whereas the relationships for the small-sized reservoirs had a more linear pattern (Figure 4b, d and f).

Relationship Between Resource Use Efficiency and Evenness

Resource use efficiency (RUE) for both the large-sized and the small-sized reservoirs significantly decreased with phytoplankton evenness when
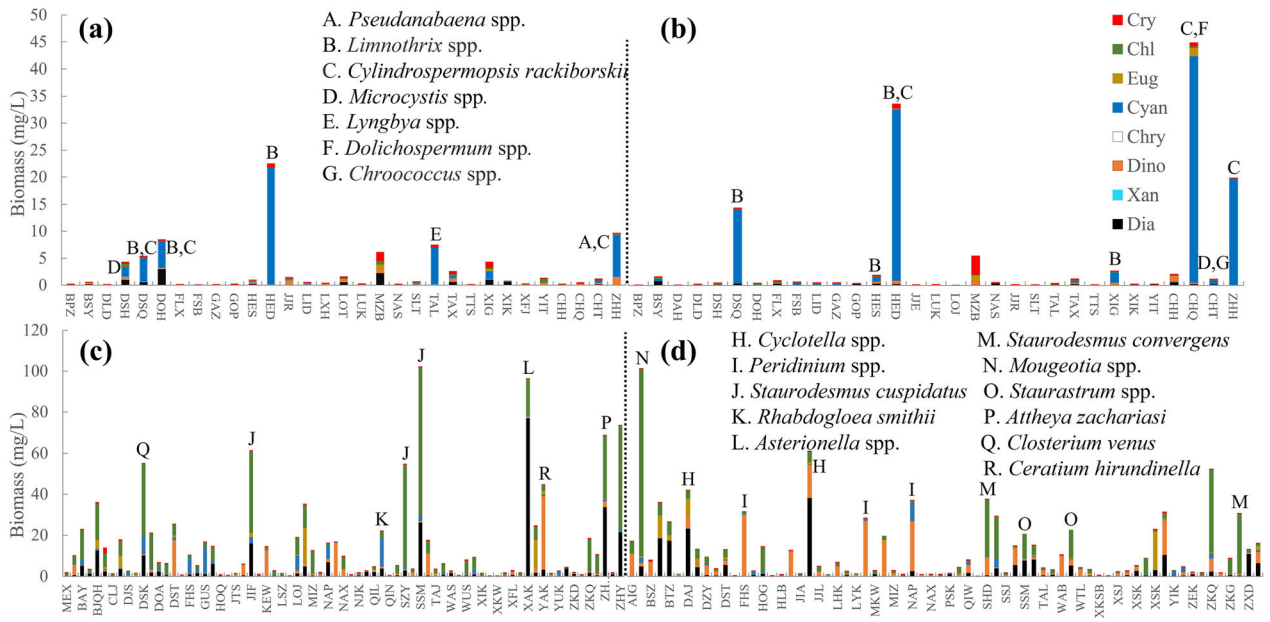
Figure 2. Phytoplankton biomass grouped in eight classes in the dry (**a** and **c**) and the wet (**b** and **d**) season in 34 large-sized (**a** and **b**) and 73 small-sized (**c** and **d**) reservoirs, and the dominant phytoplankton species (see information of reservoirs in Table A1). Notes: Cry—Cryptophyta, Chl—Chlorophyta, Eug—Euglenophyta, Cyan—Cyanobacteria, Chry—Chrysophyta, Dino—Dinophyta, Xan—Xanthophyta, Dia—Bacillariophyta). Capital letters indicate the dominant species.

combining the data from the dry and the wet seasons (Figure 5a and b). When the relationship was investigated separately, RUE decreased significantly with evenness in both seasons (Figure 5c and f), though only slightly in the small-sized reservoirs in the dry season (Figure 5d). The RUE relationship for small-sized reservoirs in the dry season was strongly influenced by the point at the far right in Figure 5d; otherwise, the slopes would be more negative than that in the wet season.

In the large-sized reservoirs, phytoplankton assemblages were dominated by only a few genera (that is, low evenness) and had the highest proportions of cyanobacteria. The phytoplankton communities without clearly dominant species had lower proportions of cyanobacteria (Figure 6). The relative abundance of cyanobacteria was significantly and negatively related to phytoplankton evenness, indicating that phytoplankton assemblages dominated by cyanobacteria had a relatively high RUE. The trends were similar for the dry and the wet season. However, the relative abundance of cyanobacteria and phytoplankton evenness showed no significant relationship in the small-sized reservoirs, and phytoplankton RUE did not show a clear pattern in relation to the relative abundance of cyanobacteria in the two seasons (Figure 6).

Important Factors Influencing Species Richness and Productivity

The datasets from the two seasons were combined to build two SEMs, one for large-sized reservoirs and the other for small-sized reservoirs. In SEM, the relationship between species richness and productivity was assumed to change with resource availability (TP), buffering capacity to external disturbance (SA/CA), water temperature (T) and resource use efficiency (RUE), and with the relative abundance of cyanobacteria (Figure 7). For the large-sized reservoirs, the model revealed significant effects of three variables (T, Cyano and TP) on primary productivity (Figure 7a). Species richness correlated positively with productivity (0.362), and T (0.239). Both TP (0.645) and Cyano (0.305) correlated positively with productivity. For the small-sized reservoirs, species richness was positively and slightly affected by RUE (Figure 7b). T had a negative effect on species richness (−0.303). SA/CA was negatively related to TP (−0.215). Species richness correlated positively with productivity (0.294) (Figure 7b). SEM for the datasets of single seasons overall supported the above results, but showed seasonal difference between large-sized reservoirs and small-sized reservoirs (Figure A3).
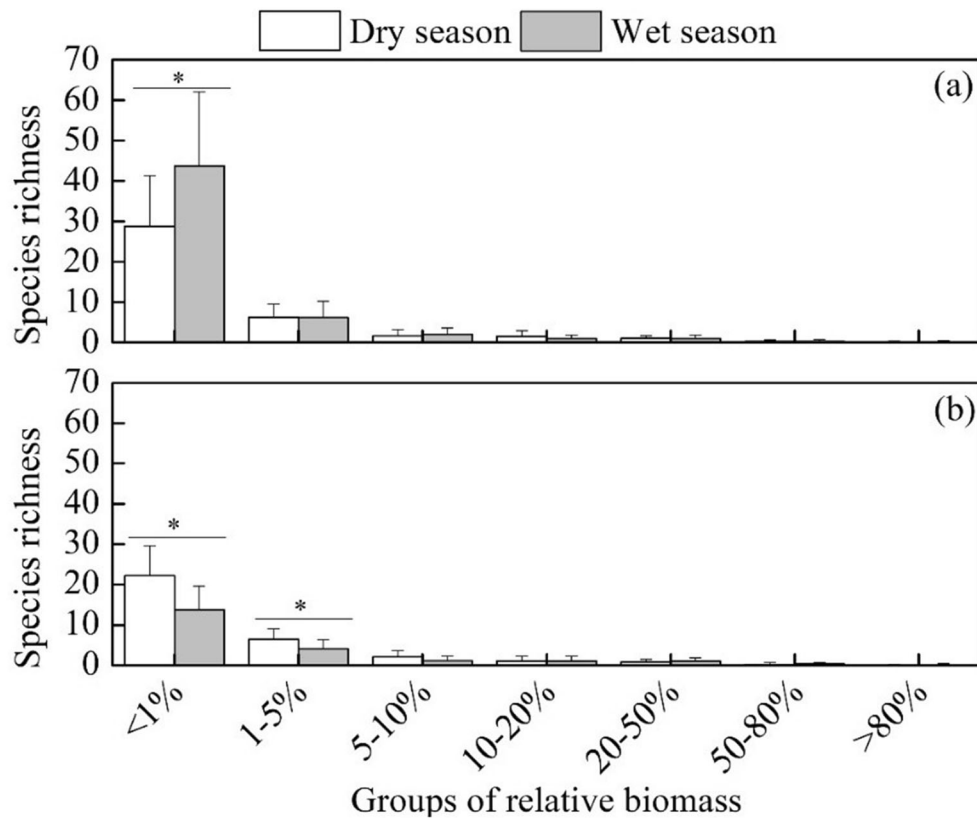
Figure 3. Comparison of phytoplankton species richness based on relative biomass between the dry and wet season in the large- and small-sized reservoirs. The species were grouped into seven relative biomass groups in the dry and wet season: **a** phytoplankton species richness in large-sized reservoirs; **b** phytoplankton species richness in small-sized reservoirs. * above the bar indicates statistically significant differences in species richness between the dry and wet seasons ($p < 0.05$).

DISCUSSION

Species diversity—ecosystem productivity relationships have received much attention by ecologists, but have yielded extremely variable results, as they are affected by many factors, including scale, disturbance, ecosystem type, species pool and the methods used for estimating productivity and diversity (Miller and others 2011; Daam and others 2019; Cardinale and others 2009a, 2009b; Ptacnik and others 2010; Lisner and others 2021). We found a unimodal relationship in the large-sized reservoirs where competition can be strong at high productivity thanks to a longer residence time (Figure 4a). In contrast, a positive and more linear pattern was found for the small-sized reservoirs (Figure 4b), especially in the wet season, indicating complementary effects among species. Disturbance does not allow competitive exclusion to play out, thereby lessening competition intensity (Hutchinson 1961; Naselli-Flores and others 2003). Since the studied reservoirs were productive, cyanobacteria dominance was common and had a negative effect on phytoplankton evenness and a positive

effect on RUE, especially in the large reservoirs (Figure 6).

Unimodal and Positive Linear Relationship Between Species Richness and Productivity

As predicted by the dynamic equilibrium model (Huston 1997, 2014), we detected a unimodal and a linear relationship between phytoplankton species richness and productivity (Chl*a*) in the large- and small-sized reservoirs, respectively. In tropical China, the total yearly average precipitation is about 1800 mm, and it is mainly occurring in summer (that is, flooding season, 1000 mm from June to August) and late autumn (300 mm in November). The average theoretical water residence time was about 100 days for small-sized reservoirs and at least 360 days for large-sized reservoirs (Han and others 2003). Small-sized reservoirs have a low buffering capacity against external disturbance such as high precipitation in wet season in the tropics. They are subjected to
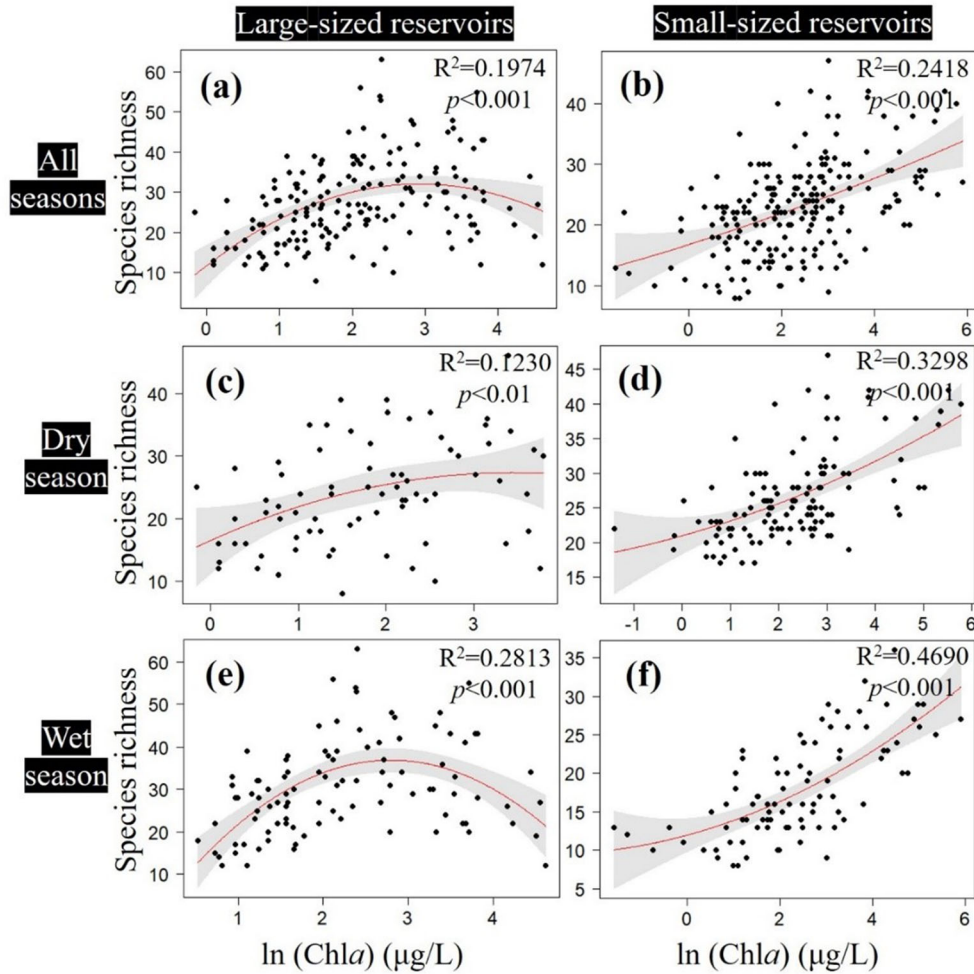
Figure 4. Regression models of species richness of phytoplankton against productivity (indicated by Chl*a* concentration) for the two groups of reservoirs in the two seasons. **a** and **b** are the regressions between species richness and productivity for the integrated dataset of the two seasons; **c** and **d** are the regressions between species richness and productivity in the dry season for the large-sized **(c)** and small-sized reservoirs **(d)**; **e** and **f** are the regressions between species richness and productivity in the wet season for the large-sized **(e)** and small-sized reservoirs **(f)**.

much more frequent and intense flushing (that is, disturbance) compared to large-sized reservoirs, and the frequency of flushing is likely closer to the phytoplankton generation time in small-sized than in large-sized reservoirs, promoting a shift in the seasonal succession of species that hampers the probability of reaching ecological equilibrium (Reynolds and others 1993; Reynolds 1994). These disturbance events allow coexistence of both ''fitting'' and ''less fitting'' species, resulting in apparent violation of the principle of competitive exclusion (Hutchinson 1961; Naselli-Flores and others 2003). Flushing dilutes existing populations and simultaneously favours dispersal in connected waterbodies (Hu and others 2017), brings new nutrients and eventually modifies the underwater light climate by increasing the turbidity. All these

events, depending on the intensity and frequency of disturbance, can contribute to an increased species richness (Naselli-Flores 2000). Conversely, in large and deep reservoirs, especially when they are stratified, even a major meteorological event may not disturb the phytoplankton assembly and its succession (Sommer and others 1993). The ecological effects of a disturbance can be quantitatively interpreted from changes in the mortality and birth rate of species and in the carrying capacity of the ecosystems (Sousa 1984; Dornelas 2010). At a regional scale, large reservoirs differ from small ones mainly in the intensity of disturbance and degree of stratification. Large and deep (stratified) reservoirs have higher nutrient retention in the sediments and can buffer disturbance by minimizing the intensity of disturbance effects
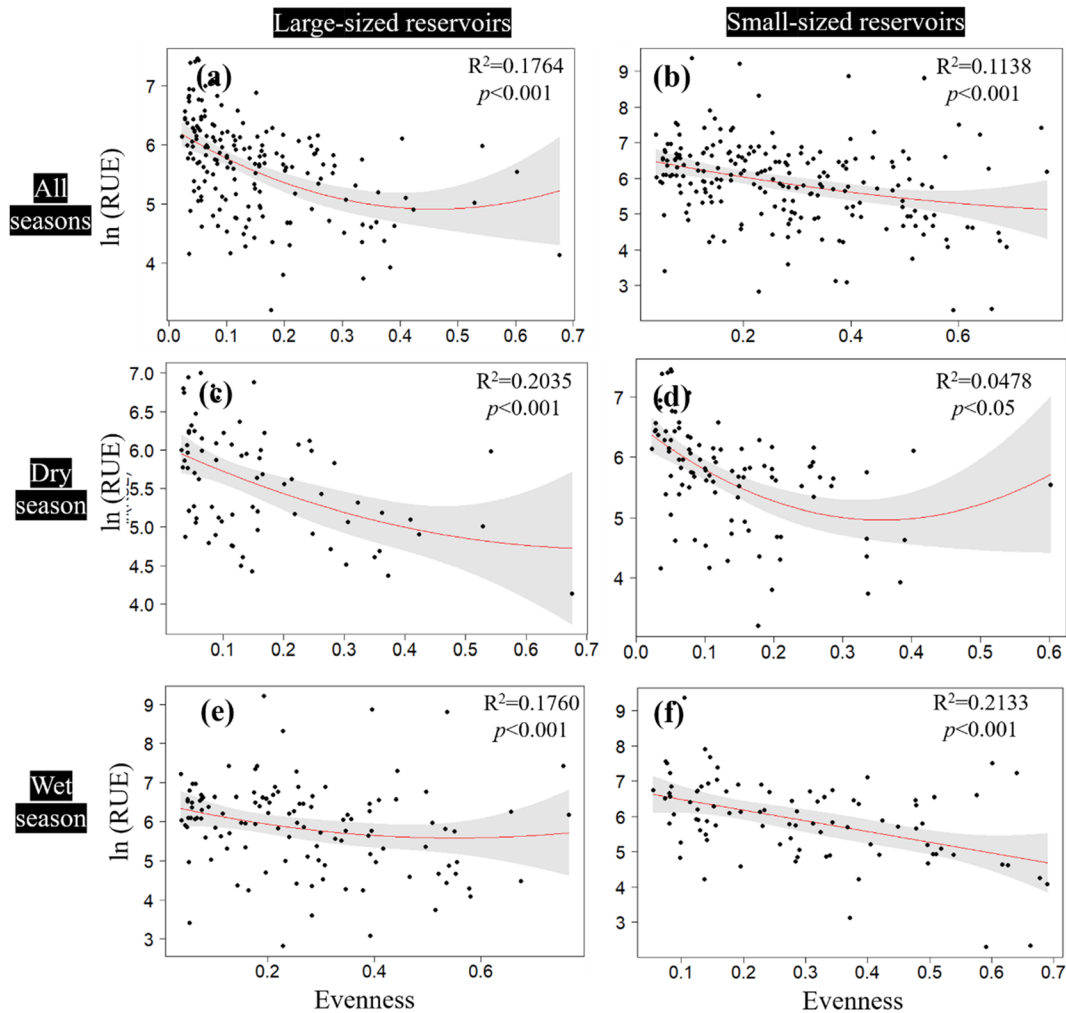
Figure 5. Regression models showing resource use efficiency (RUE) against evenness of phytoplankton in the study reservoirs in the wet and dry seasons. **a** RUE-evenness regression with the integrated data on large-sized reservoirs, **b** with the integrated data on small-sized reservoirs; **c** RUE-evenness regression with the data on the large-sized reservoirs in the dry season, and **e** in the wet season; **d** RUE-evenness regression with the data on small-sized reservoirs in the dry season and **f** in the wet season.

(Friedl and Wüest 2002). As a consequence, stable water columns and low carrying capacity in the epilimnion promote competition among phytoplankton species, and dominance of a few species, especially cyanobacteria, reduces phytoplankton diversity in eutrophic lakes (Jeppesen and others 2000; Downing and others 2001; Hautier and others 2009; Watson and others 1997; Filstrup and others 2014). High hydraulic disturbance, especially in shallow waterbodies, reduces the growth rates of many phytoplankton species through dilution but may increase the carrying capacity of the ecosystem by increasing both endogenous (from the littoral and the bottom zones through mixing) and exogenous (from their catchment or from connected waterbodies) nutri-

ents. The small-sized reservoirs in our study were much shallower than the large ones, both in the dry and wet seasons, and they were thus more prone to be affected by disturbance. Moreover, all the reservoirs became shallow in the dry season and were exposed to higher levels of hydrodynamic disturbance due to increased vertical mixing. This increased disturbance in the large reservoirs may explain their approximately linear relationship in the dry season (Figure 4c).

Reservoirs are river–lake hybrids, and their physical, chemical and biological features are extremely sensitive to hydrological forces (Thornton and others 1990). The more the reservoir dimension decreases, the more it will act as a river. Linear and positive relationships between species richness
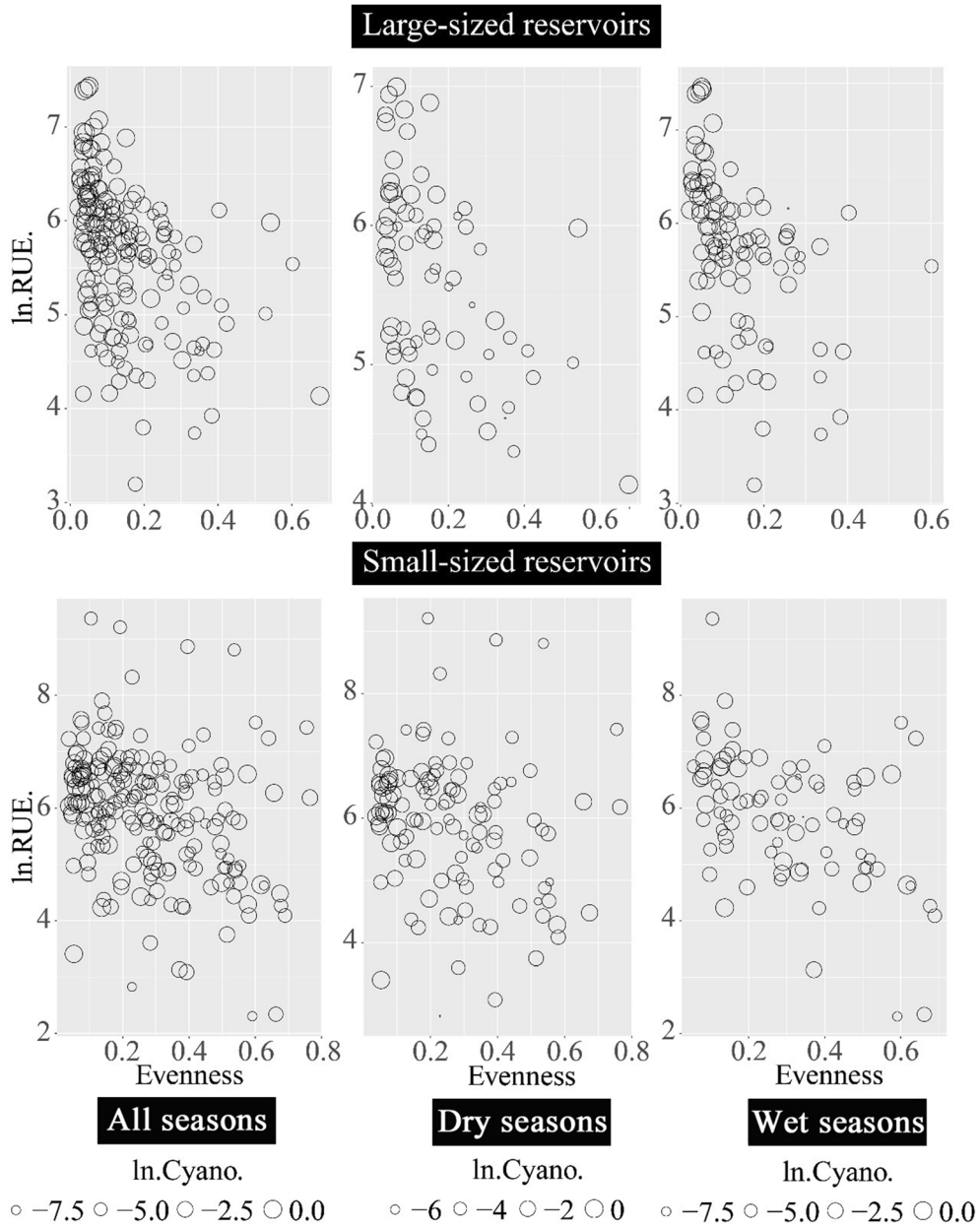
Figure 6. Cyanobacterial dominance (percentage of cyanobacteria) in the relationship between RUE and phytoplankton evenness for large-sized and small-sized reservoirs in the dry and wet seasons.

and productivity are common in streams where low competition and high complementary effects among coexisting species occur (Cardinale and others 2005; 2009a, 2009b). Small productive reservoirs, thanks to reduced competition and increased carrying capacity, are able to support more rare species than large reservoirs (Naselli-Flores and Barone and 1994; Abrams 1995; Connell and Orias 1964; Rosenzweig and Abramsky 1993). Moreover, according to Gross and Cardinale (2007), at intermediate degrees of nutrient avail-

ability species coexistence can be enhanced by niche partitioning.

In summary, our results show that unimodal relationships between species richness and productivity are often detectable in phytoplankton, and they support the hypothesis that the degree of disturbance influences the relationship between species richness and productivity; periodic disturbance can increase phytoplankton biodiversity by reducing the effects of interspecific competition and promotes the coexistence of species adapted to different environmental conditions and resource
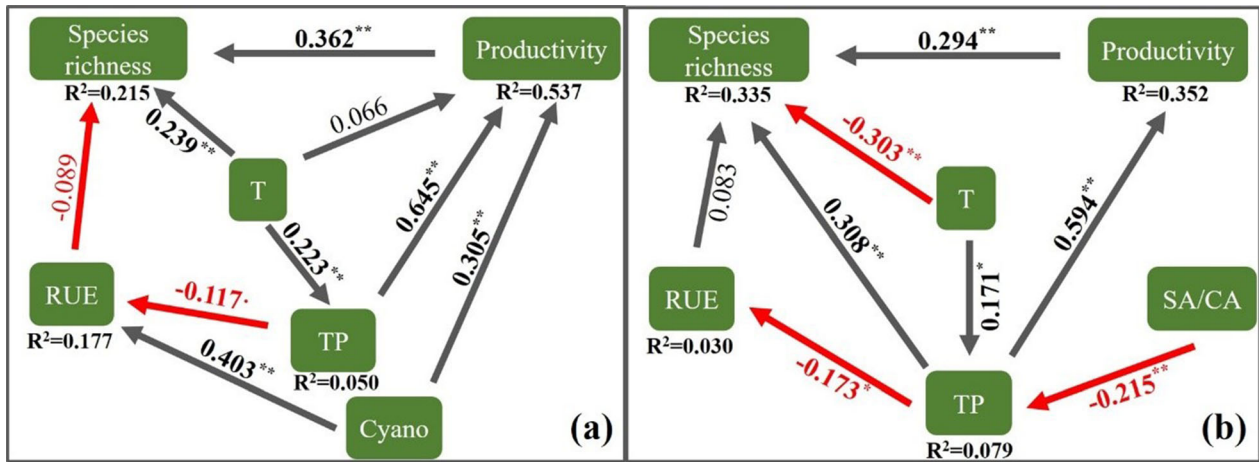
Figure 7. Structural equation modelling of phytoplankton diversity explained by productivity and exogenous variables using data from large- **(a)** and small-sized reservoirs **(b)**. SA/CA is the ratio of surface area (SA) to catchment area (CA). T is water temperature, RUE = Resource use efficiency, Cyano = the relative abundance of Cyanobacteria. Numbers adjacent to arrows and arrows indicate the relationship's effect size and the associated bootstrap P value. $\bullet = p < 0.1$; $* = p < 0.05$; $** = p < 0.001$. Black and red lines indicate positive and negative relationships, respectively.

levels (Sommer and others 1993; Connell 1978; Janousek and Dreitz 2020; Petraitis and others 1989).

Cyanobacteria Dominance and RUE of Phytoplankton Assemblages

The role of species diversity in ecosystems is remarkable and dual. It can be considered both as a cause and consequence of primary production (Gross and Cardinale 2007; Korhonen and others 2011). The positive relationship between species diversity and productivity in the biodiversity-ecosystem functioning framework implies that coexisting species enhance ecosystem functioning. Resource use efficiency (RUE) is another important measure of ecosystem functioning. In freshwater ecosystems, where phosphorus is often the limiting factor for growth, RUE can be defined as the ratio between phytoplankton biomass and total phosphorus, the latter indicating the potential productivity of the ecosystem. Ptacnik and others (2008) integrated a large dataset on Fennoscandia lakes and the Baltic Sea and found a positive relationship between RUE and the richness of phytoplankton genera. Filstrup and others (2019) also detected a positive relationship using a lake dataset from continental USA. These authors also suggested that a negative relationship between RUE and evenness is more common than a positive one and that this kind of relationship do not differ significantly among regions. Moreover, several authors have highlighted that evenness has stronger effects on ecosystem functioning than richness (for example,

Wilsey and Potvin 2000; Hodapp and others 2015). As hypothesised, we found that phytoplankton RUE decreased significantly with evenness in the large-sized reservoirs where cyanobacterial dominance causes a decrease in both species richness and evenness (Figure 5b). As the relative abundance of cyanobacteria increased, phytoplankton evenness declined, and its RUE increased (Figure 6b). Cyanobacterial species, like *Microcystis* spp. and *Raphidiopsis* (*Cylindrospermopsis*) *raciborskii*, commonly dominate in southern China reservoirs, which often show quite low phosphate concentrations. Cyanobacterial growth can be favoured under phosphorus-limiting conditions (Isvánovics and others 2000; Reynolds 2006; Ferber and others 2004 Shen and Song 2007), and these organisms can also, to some extent, resist zooplankton grazing (McCauley and Briand, 1979). In tropical freshwater ecosystems where there is a high fish predation (Han and others 2003; Jeppesen and others 2010), small grazers (for example, small cladocerans and rotifers) dominate and exert a lower control on phytoplankton biomass (Aka and others 2000). Moreover, the grazing pressure can be further reduced because of the increased occurrence of toxic cyanobacterial species (Kâ and others 2012). Light availability can be another limiting factor for eukaryotic phytoplankton growth in reservoirs with high cyanobacterial biomass (Stauffer 1991; Tessier and Woodruff 2002; Caputo and others 2008). Hence, a negative relationship between phytoplankton RUE and evenness is likely more common in eutrophic reservoirs in the tropics.

We checked evenness and richness for large and small reservoirs (Figure A6), and our analysis supported that evenness was strongly and negatively related with RUE indicating dominance increases RUE. Richness was weakly and positively related with RUE. Our results show evenness effect is stronger than richness effect on RUE, which is consistent with earlier studies (Wilsey and Potvin 2000; Hodapp and others 2015).

Potential Factors Influencing Species Diversity Productivity Patterns

The dynamic equilibrium model proposed disturbance as just one among several potential factors, which influence the relationship between richness and productivity (Huston 1979, 1994, 2014). Admittedly, the relationship needs to be investigated in a multivariate framework of hypotheses to reveal its variability among ecosystem types, organism types and scales. In fact, as shown by Padisák and others (2010), although ecological processes such as competition, predation, parasitism and all the activities aimed at the flow of matter and energy are ubiquitous in all ecosystems, these are interpreted differently for organisms under different physical, chemical and biological constraints and disturbances. With the structural equation modelling (SEM) approach, an integrative model can be established that has a substantially higher explanation power that the traditional model for the bivariate relationship (Grace and others 2014, 2016). In both large- and small-sized reservoirs, species richness significantly increased with productivity, and total phosphorus increased productivity but decreased RUE. In the large reservoirs, cyanobacterial dominance increased the productivity and RUE of phytoplankton, but decreased species richness. We used SA/CA to indicate the buffering ability of a reservoir to disturbance and found that it was negatively related to total phosphorus and species richness in the small-sized reservoirs. This implies that external disturbance increased total phosphorus and favoured the occurrence of coexisting species. We found an opposite influence of water temperature (T) on species richness in large- and small-sized reservoirs. Increasing temperature promoted phytoplankton growth in the large reservoirs but seemed to have an inhibitory effect on growth in the small-sized reservoirs during summer. Given their low average water depth, shallow water columns can be more easily subjected to a faster and higher warming compared to deep water columns (that is, the large-sized reservoirs in this study)

(Toffolon and others 2014; Woolway and others 2016). The relatively high temperature in (sub)tropical lakes, especially in the wet season (including summer), probably slowed down population growth of most phytoplankton species but cyanobacteria and some species of green algae due to their higher temperature optima and tolerances (Butterwick and others 2005; Lüring and others 2013; Huisman and others 2018). SEM for large-sized reservoirs showed a different relationship between species richness and productivity in the dry and wet seasons (Figure A3). Negative relationship may result from heavy cyanobacterial blooms usually occurring in dry seasons. In contrast, cyanobacteria of small-sized reservoirs usually bloom in wet seasons. Although they only slightly increased primary productivity, it significantly correlated with species richness.

CONCLUSION

The role of species diversity in ecosystems is remarkable, and the relationship between species diversity and productivity can greatly change among ecosystem types, organismal types, and scales. The relationship is mediated by many factors in natural systems. The Intermediate Disturbance Hypothesis (Connell 1978) highlights the important role of disturbance on diversity, more or less implicitly assuming a potential link between disturbance and productivity. Later, the dynamic equilibrium model (DEM) proposed a broad interaction disturbance and productivity that influences species diversity (Huston 1979, 1994, 2014). We explored the relationship between species richness and productivity of phytoplankton assemblages in two groups of reservoirs with contrasting regimes of disturbance and found that the relationship between species diversity and productivity, and even its underlying processes, is different among ecosystem types characterized by different disturbance regimes. Unimodal pattern was common in large and deep reservoirs, whereas a positive and linear pattern was common for small and shallow reservoirs, especially in wet seasons. Cyanobacterial dominance significantly decreased phytoplankton evenness but increased RUE of phytoplankton under low disturbance, that is, depending on the morphology and size of the waterbody. Structural equation modelling revealed that other environment chemical and physical variables, as nutrient availability and water temperature, can indirectly contribute to species richness. Our study emphasizes the role of disturbance in shaping the relationship between species diver-

sity and productivity for freshwater ecosystems and shows that the relationship largely depends on both the local characteristics of waterbodies and those of the regional network where single waterbodies are embedded.

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DATA AVAILABILITY

Data for reservoir and water quality data are available in the supplementary materials, and the other metadata are deposited as Dryad Dataset, https://doi.org/10.5061/dryad.rbnzs7hf3.

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