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Total nitrogen and community turnover determine phosphorus use efficiency of phytoplankton along nutrient gradients in plateau lakes

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ABSTRACT

Numerous studies support that biodiversity predict most to ecosystem functioning, but whether other factors display a more significant direct impact on ecosystem functioning than biodiversity remains to be studied. We investigated 398 samples of the phytoplankton phosphorus resource use efficiency ($RUE_p = \text{chlorophyll-a concentration/dissolved phosphate}$) across two seasons in nine plateau lakes in Yunnan Province, China. We identified the main contributors to phytoplankton RUE_p and analyzed their potential influences on RUE_p at different lake trophic states. The results showed that total nitrogen (TN) contributed the most to RUE_p among the nine lakes, whereas community turnover (measured as community dissimilarity) explained the most to RUE_p variation across the two seasons. Moreover, TN also influenced RUE_p by affecting biodiversity. Species richness (SR), functional attribute diversity (FAD2), and dendrogram-based functional diversity (FDC) were positively correlated with RUE_p in both seasons, while evenness was negatively correlated with RUE_p at the end of the rainy season. We also found that the effects of biodiversity and turnover on RUE_p depended on the lake trophic states. SR and FAD2 were positively correlated with RUE_p in all three trophic states. Evenness showed a negative correlation with RUE_p at the eutrophic and oligotrophic levels, but a positive correlation at the mesotrophic level. Turnover had a negative influence on RUE_p at the eutrophic level, but a positive influence at the mesotrophic and oligotrophic levels. Overall, our results suggested that multiple factors and nutrient states need to be considered when the ecosystem functioning predictors and the biodiversity-ecosystem functioning relationships are investigated.

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Introduction

Ample studies have suggested that biodiversity plays a pivotal role in maintaining the structure and functioning of ecosystems, thus the biodiversity-ecosystem functioning (BEF) re-

lationship has received increasing attention due to concerns on the potential impacts of globally increasing biodiversity loss on ecosystem functioning and stability (Loreau et al., 2001; Balvanera et al., 2006; Allan et al., 2011; Cardinale et al., 2012; Tilman et al., 2014). A high level of biodiversity loss is occurring as a result of multiple environmental stressors

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(Cardinale et al., 2012). Aquatic ecosystems are also suffering from environmental pressures, such as nutrient enrichment, which is considered one of the most important drivers of phytoplankton biodiversity loss (Gudmundsdottir et al., 2013; Przytulska et al., 2017). However, nutrient enrichment has been reported to have multiple effects on phytoplankton diversity. On the one hand, nutrient enrichment may increase phytoplankton diversity by increasing their growth rate and weakening competition intensity between phytoplankton species under low nutrient conditions (Kilham, 2001; Irigoien et al., 2004); on the other hand, nutrient enrichment may reduce the phytoplankton diversity by overproducing one or two algal species under a high trophic state (Taslakian and Hardy, 1976). Given the important impact of nutrients on phytoplankton diversity, we conjecture that nutrients may directly or indirectly affect aquatic ecosystem functioning to some extent. Srivastava and Vellend (2005) have also reported that environmental stressors would influence ecosystem functioning directly or indirectly. The direct effects of environmental stressors on ecosystem functions will reduce the relative importance of biodiversity, while they tend to exert the indirect effects by affecting biodiversity.

In addition to nutrients, community turnover is also an important factor influencing ecosystem functioning and stability (Allan et al., 2011), and it describes the temporal variability of community composition (Tian et al., 2017b). The variation in local environments across different periods will cause species sorting and increase species turnover, therefore, the ecosystem functioning variation across periods might be driven more by species turnover than by species richness variation (Gonzalez et al., 2020). It was found that communities with high species diversity and ecosystems with high functioning rates should also be more stable and display less turnover with time under stable conditions (Ptacnik et al., 2008). However, Zhang et al. (2021a) have revealed that seasonal temperature differences promote spring-summer community turnover, thus improving ecosystem functioning, suggesting that community turnover helps maintain ecosystem functioning through time under fluctuating conditions (Norberg et al., 2001). Although inconsistent relationships between turnover and ecosystem functioning have been observed, it remains to be determined whether turnover plays a predominate role in ecosystem function through time.

Phytoplankton resource use efficiency (RUE) is an ecological concept that reflects the ability of phytoplankton to capture resources, which is an important aspect of ecosystem functioning (Striebel et al., 2009; Tian et al., 2017a). A number of studies defined phytoplankton RUE as the amount of phytoplankton biomass produced per unit of phosphorus (Ptacnik et al., 2008; Filstrup et al., 2014; Tian et al., 2017b; Yang et al., 2022). Phytoplankton RUE has been found to increase with increasing phytoplankton richness in many aquatic systems (Ptacnik et al., 2008; Ye et al., 2019; Yang et al., 2022). However, several subsequent works pointed out that the relationship between species richness and RUE was influenced by nutrient conditions (Filstrup et al., 2014; Gerhard et al., 2021). Tian et al. (2017a) observed that the influence of phytoplankton species richness on RUE changed from positive to negative along the nutrient gradients. Similarly, the relationship between turnover and ecosystem func-

tioning may also be affected by the trophic states of waters. Filstrup et al. (2014) observed a positive relationship between phytoplankton community turnover and RUE, and reported that the relationship between phytoplankton community turnover-ecosystem functioning in low-nutrient aquatic ecosystems might not be applicable to high-nutrient ecosystems. Therefore, the consequences of relationship between phytoplankton diversity, community turnover and RUE is likely to be idiosyncratic, differing quantitatively and qualitatively in different environmental conditions (Cardinale et al., 2006).

The exploration of the BEF relationship will also be hampered by a restricted focus on species richness, since evenness is also an important index in predicting ecosystem functioning (Hodapp et al., 2015; Filstrup et al., 2019). In addition, increasing number of studies have shown that trait-based functional diversity can predict ecosystem functioning better than species diversity (Gagic et al., 2015; Gross et al., 2017; Abonyi et al., 2018; Ye et al., 2019). Functional diversity provides information on species functional traits in communities, and it is directly related to the functioning and maintenance of ecological processes (Goswami et al., 2017). Thus, to improve the predictions and mechanistic understanding of BEF, it has been increasingly accepted that the species functional trait-based diversity should be studied (Cardinale et al., 2012; Gagic et al., 2015).

In this study, we identified the independent contributions of environmental variables, phytoplankton community turnover, taxonomic diversity (species richness and evenness), and functional diversity (dendrogram-based functional diversity, FDC; functional attribute diversity, FAD2) on phytoplankton RUE_P in the nine plateau lakes across two seasons (the end of the dry and rainy seasons). Additionally, the relationships among biodiversity, community turnover, and phytoplankton RUE_P were also examined under different nutrient levels. We hypothesize that 1) nutrients can affect RUE_P by affecting biodiversity, and it also has a direct impact on RUE_P; 2) community turnover contributes the most to the seasonal difference in RUE_P; 3) the effects of phytoplankton diversity and community turnover on RUE_P are restricted by the nutrient state in lakes.

1. Materials and methods

1.1. Study area

The Yunnan Plateau, located in the southeastern Tibetan Plateau, is one of the areas rich in natural plateau lakes (Ma et al., 2011). There are nine major lakes in Yunnan Plateau with the area of each lake above 30 km², including Lake Dianchi (LDC), Lake Yangzong (LYZ), Lake Fuxian (LFX), Lake Xingyun (LXY), Lake Qilu (LQL), Lake Erhai (LEH), Lake Lugu (LLG), Lake Chenghai (LCH), and Lake Yilong (LYL). The morphological parameters of these nine plateau lakes are shown in Appendix A Table S1. The area covered by the nine plateau lakes is characterized by a semihumid monsoon climate with obviously distinctive dry and rainy seasons. The population living in the nine plateau lake basins accounts for approx-

imately 11% of the province's total population, but it is the most densely populated area with the strongest human activities and the most developed economy in the province. The nine plateau lakes play a vital role in water resource regulation, flood control and drainage, agricultural irrigation, lake and land ecosystem circulation regulation, and they provide habitats for aquatic animals and plants. Therefore, they are important for the regional economic development and ecological environments. Fast economic development in the nine plateau lake area results in the deterioration of the water quality, posing a great threat to ecological environment. At present, LDC and LXY are absolutely dominated by *Microcystis* genera with frequent cyanobacterial blooms. LQL and LYL are seriously polluted by nutrients with low water transparency (Yu et al., 2021). The nutrient concentrations in LEH, LCH and LYZ reach the mesotrophic level, of which LYZ is seriously polluted with arsenic (Zhang et al., 2020). Although LFX and LLG are in an oligotrophic state, these two lakes have presented a trend of nutrient concentration increase in recent years (Zhou et al., 2018; Lin et al., 2021).

1.2. Phytoplankton and environmental sample collection and treatment

Samples were collected from April to May (the end of the dry season, e-dry season) and from October to November (the end of the rainy season, e-rainy season) in 2020. A total of 398 samples (194 from the e-dry season and 204 from the e-rainy season) were collected from the nine plateau lakes in Yunnan Province (Fig. 1). Water samples were collected at 0.5 m below the lake surface, and stratified sampling was carried out at three sampling sites for each lake (Fig. 1). The stratified lake water was sampled from the lakes with a water depth of less than 10 m at vertical intervals of 1–2 m and from the lakes with a water depth greater than 10 m at intervals of 5 m (Appendix A Table S2).

Water temperature (WT), pH, and dissolved oxygen (DO) were measured *in situ* using a multiparameter probe (EXO, Yellow Springs Instruments, USA). Transparency was measured using a Secchi disk (SD). The concentrations of total nitrogen (TN), total phosphorus (TP), dissolved phosphate ($\text{PO}_4^{3-}\text{-P}$), and permanganate index (COD_{Mn}) in lake water were determined following standard methods (State Environmental Protection Administration of China, 2002). The samples were filtered with a Whatman GF/F filter (biomass intercepted by 0.7 μm pore size) for chlorophyll determination. The filter membranes were immersed in 90% acetone, and the chlorophyll was extracted in the dark at 4°C for 24 hr. The absorbance of the chlorophyll solution was measured using a spectrophotometer (TU-1810, DPC, China), and the concentration of chlorophyll *a* (Chl-*a*) was calculated by the previously reported method (Arar, 1997). The precipitation data were obtained using the R environment, as previously described (Sparks, 2018).

Phytoplankton samples and the environmental samples were collected simultaneously. The water samples were preserved with Lugol's solution for phytoplankton cell counting and species identification. All taxa of phytoplankton were counted with a counting chamber (0.1 mL) under mi-

croscope (Olympus, Japan, 400 \times magnification). More than 500 cells were counted for each sample. The phytoplankton was identified at species level or genus level according to the following literature (Krammer and Lange-Bertalot, 1991; Hu and Wei, 2006; Liu and Hu, 2012; Wei, 2017; Wei, 2018).

1.3. Phosphorus resource use efficiency (RUE_P) of Phytoplankton

Phosphorus is considered the primary limiting nutrient in most freshwater ecosystems (Harke et al., 2012). Generally, the N/P molar ratio above the Redfield ratio (16:1) indicates P-limitation. In this study, 94% of the sampling sites in this study had N/P molar ratios greater than 16 (Appendix A Fig. S1). Therefore, phosphorus was used as a proxy to evaluate the phosphorus use efficiency of phytoplankton in this study. The phytoplankton RUE_P of dissolved phosphate was calculated according to the following equation:

$$\text{RUE}_\text{P} = \text{Chl-}a : \text{PO}_4^{3-}\text{-P}$$

1.4. Biodiversity indices

Species richness referred to the number of algal taxa of each sampling site, and phytoplankton evenness was calculated as Pielou's evenness based on the abundance of each algal taxon of each sampling site (species abundance-site matrix). These two indices were calculated by the "diversity" function in the R package *vegan* (Hill, 1973).

Three functional traits of the phytoplankton distributed in 18 categories were included in this analysis: morphological traits (size class, life forms), physiological traits (nitrogen fixation, silicon requirements, mixotrophy, chl-*b*, chl-*c*, phycobiliproteins, toxin production), and behavioral traits (motility). The size class was subdivided into small (<100 μm^3), medium (100–1000 μm^3), large (1000–10000 μm^3), and extra-large (>10000 μm^3). Life forms were subdivided into single-celled, filamentous, chain-like, stellate, and colonial. Motility was further divided into vacuolated and flagellar. The categorization of functional traits referred to several literature (Weithoff, 2003; Litchman and Klausmeier, 2008; Abonyi et al., 2018). The functional trait categories of each taxon were specified based on presence-absence data (functional traits-species matrix, Appendix 1) (Abonyi et al., 2018).

The species abundance-sites matrix and functional trait-species matrix were used to calculate the second generation functional attribute diversity (FAD2) and the dendrogram-based functional diversity (FDc) (Petchev and Gaston, 2006). FAD2 and FDc were calculated using *FDiversity* software (Casanoves et al., 2011).

1.5. Classification of lake trophic state

In order to classify the nine lakes into different nutrient level groups, a hierarchical clustering analysis was performed on all the samples of the nine lakes based on TN, TP, and Chl-*a* concentrations (Appendix A Table S3). The samples from the nine lakes were divided into three groups (Appendix A Fig. S2). The first group contained all the samples from LFX and LLG,

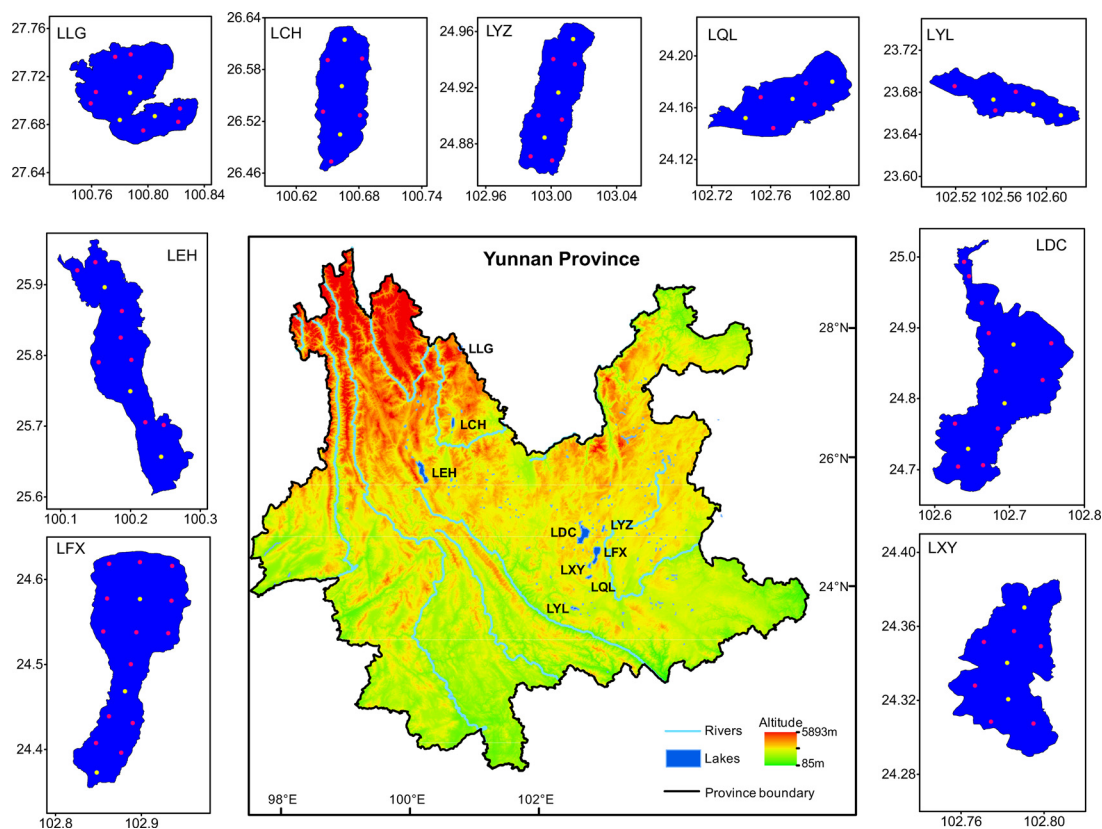


Fig. 1 – Location of the nine plateau lakes and distribution of the sampling sites (Lake Qilu, LQL; Lake Yilong, LYL; Lake Xingyun, LXY; Lake Dianchi, LDC; Lake Chenghai, LCH; Lake Erhai, LEH; Lake Yangzong, LYZ; Lake Fuxian, LFX; Lake Lugu, LLG). The red points in the lake indicate the sampling sites where water samples were collected at 0.5 m below the water surface, and the yellow points denote the stratified sampling sites.

characterized by low concentrations of TN, TP, and Chl-*a*; the second group contained all the samples from LCH, LEH and LYZ, characterized by intermediate concentrations of TN, TP, and Chl-*a*; and the third group contained all the samples of LQL, LYL, LXY and LDC, characterized by high concentrations of TN, TP, and Chl-*a*. Such grouping results are in line with most studies that LFX and LLG are oligotrophic lakes, LCH, LEH and LYZ are mesotrophic lakes, and LQL, LYL, LXY and LDC are eutrophic lakes (Bao and Cui, 2012; Dong, 2014).

1.6. Statistical methods

Canonical analysis of principal coordinates (CAP, Anderson and Willis, 2003) was performed to examine the differences in phytoplankton community structure across the different lakes and different seasons. CAP displayed a cloud of multivariate points to determine the axis that best discriminates a priori defined groups. It allowed the performance of a constrained ordination on the basis of any distance or dissimilarity measure. The first axis score of CAP (CAP1) was extracted as one of the explanatory variables for RUE_P in the subsequent analysis. The analysis of similarity (ANOSIM) was conducted to determine the significant dissimilarities in phytoplankton communities across the different lakes and seasons, based on 999 permutations (Clarke, 1993).

CAP, ANOSIM, and clustering analysis were performed using PRIMER 6.0.

Correlation analysis was conducted to detect the relationships between the environmental variables, biodiversity indices, community turnover and RUE_P, as well as the relationships between the seasonal differences in all the variables. The hierarchical partitioning method was employed to determine the contribution of environmental variables, biodiversity indices, and community turnover to RUE_P via the *rdacca.hp* package in R (Lai et al., 2022). Permutation tests for linear regression was conducted to compute a linear regression between the explanatory variables (environmental variables, biodiversity indices, and community turnover) and response variables (RUE_P). The significance of the equation parameters (R^2 and regression coefficients) was performed using the function *lmorigin* in R (Anderson and Legendre, 1999; Legendre and Desdevises, 2009). Partial least squares path modeling (PLSPM) was performed to show the linkage among the environmental variables, phytoplankton community structure (CAP1, diversity), community turnover, and phytoplankton RUE_P. The partial correlation coefficients and goodness-of-fits (GoF) was computed using the "plspm" package in the R. Intra-annual phytoplankton community turnover between the two sampling events was calculated according to the Bray–Curtis dissimilarity matrix (Pacnik et al., 2008) using the "vegan" package in the R.

2. Results

2.1. Variation of phytoplankton community structures

A total of 343 phytoplankton taxa were identified in the two seasons, including 267 taxa in the e-dry season and 263 taxa in the e-rainy season (Appendix A Table S4). The mesotrophic lake LEH had the largest number of taxa (164), while the eutrophic lake LXY had the minimum taxa (105) in the overall season (Appendix A Table S4). The four eutrophic lakes LQL, LYL, LXY, and LDC were dominated by cyanobacteria species in both seasons (Appendix A Table S5). LCH was dominated by cyanobacteria and chlorophyte species in the e-dry season, and by cyanobacteria species in the e-rainy season. LEH was absolutely dominated by one cyanobacteria species in the e-dry season, while by cyanobacteria and diatom species in the e-rainy season (Appendix A Table S5). LYZ was dominated by cyanobacteria and diatom species in both seasons. LFX was dominated by chlorophyte, diatom, chrysophyte, and cryptophyte species in the e-dry season, but by cyanobacteria species in the e-rainy season. LLG was the only lake without cyanobacteria among the dominant species, it was dominated by diatoms in the e-dry season, and by diatom and chlorophyte species in the e-rainy season (Appendix A Table S5).

CAP and ANOSIM analyses indicated that phytoplankton community structure differed significantly among the nine lakes in both the e-dry ($R=0.994$, $P<0.001$, Fig. 2a) and e-rainy seasons ($R=0.994$, $P<0.001$, Fig. 2b). Besides, the phytoplankton community structure for each lake was also significantly different between the two seasons (LDC, $R=0.868$, $P=0.001$; LYZ, $R=1$, $P=0.001$; LXY, $R=0.998$, $P=0.001$; LFX, $R=1$, $P=0.001$; LQL, $R=0.999$, $P=0.001$; LYL, $R=0.999$, $P=0.001$; LEH, $R=0.993$, $P=0.001$; LCH, $R=0.996$, $P=0.001$; LLG, $R=0.908$, $P=0.001$; Fig. 2c).

2.2. Contributions of environmental factors, diversity indices, and community turnover to RUE_p

Spearman correlation analysis indicated that RUE_p was significantly positively correlated with TN, TP, SR, and FAD2, and negatively correlated with CAP1 and water depth in the e-dry season, e-rainy season, and the overall season (Fig. 3a, c and e). Precipitation was negatively correlated with RUE_p in the e-dry season and e-rainy season, but had no significant correlation with RUE_p in the overall season (Fig. 3a, c and e). In terms of the seasonal changes (the differences between the two seasons), turnover exhibited the strongest negative correlation with the seasonal difference of RUE_p (Fig. 3g). The seasonal difference of precipitation was negatively correlated with the seasonal difference of RUE_p (Fig. 3g). Hierarchical partitioning analysis showed that TN was the most important factor influencing RUE_p in both seasons and the overall season, followed by TP and CAP1. However, turnover had the most important effect on the seasonal difference of RUE_p (Fig. 3h). Among the four diversity indices, FAD2 made the highest independent contribution to RUE_p in all the seasons, followed by the species richness.

The partial least squares path models indicated that TN influences RUE_p by two pathways in the overall season (Fig. 4a), namely, a direct way, and an indirect way via affecting bio-

diversity (SR, FAD2, and FDC). The permutation tests for linear regression also showed that TN exhibited not only a direct significant positive linear correlation with RUE_p (Appendix A Fig. S4), but also a significant positive linear correlation with diversity indices (SR, FAD2, and FDC) (Appendix A Fig. S5). Accordingly, SR, FAD2, and FDC showed a significant positive correlation with RUE_p in both seasons (Appendix A Fig. S6 a, c, and d). However, evenness displayed a negative correlation with TN and RUE_p in the e-rainy season (Appendix A Fig. S5; Fig. S6), whereas no significant relationship with TN and RUE_p in the e-dry season (Appendix A Fig. S5; Fig. S6) and the overall season (Fig. 4a). Therefore, evenness was not included in the diversity in the PLSPM analysis.

For the seasonal difference, turnover showed the most important direct negative effect on RUE_p (Fig. 4b), and it was positively affected by precipitation-induced changes in evenness and community structure (CAP1), whereas it was less affected by SR, FAD2 and FDC (Fig. 4b).

2.3. Relationships between phytoplankton diversity, community turnover and RUE_p were influenced by the trophic state

The effects of biodiversity and community turnover on RUE_p were influenced by the trophic states in the studied lakes. SR and FAD2 exhibited a significant positive influence on RUE_p at all trophic states, and their positive correlation was enhanced with the increasing trophic state, namely, the estimated slope was highest in the eutrophic group, followed by the mesotrophic and oligotrophic groups (Fig. 5a and c). Evenness showed a negative correlation with RUE_p in the eutrophic and oligotrophic groups, but a positive correlation with RUE_p in the mesotrophic group (Fig. 5b). In contrast to evenness, FDC displayed a significant positive correlation with RUE_p in the eutrophic and oligotrophic groups, but no significant correlation with RUE_p in the mesotrophic group (Fig. 5d). Phytoplankton intra-annual turnover exhibited a significant negative correlation with RUE_p in the eutrophic group, but a positive correlation with RUE_p in the mesotrophic and oligotrophic groups (Fig. 5e).

3. Discussion

3.1. Effects of TN on phytoplankton biodiversity

Our data indicated that TN had distinct effects on different diversity indices. In terms of species richness, the positive relationship between it and TN was attributed to the fact that the two nutrient-rich lakes LQL and LYL had high species richness. These two lakes are different from the general *Microcystis*-dominated eutrophic lakes (such as LDC and LXY) that will inhibit the growth of other algae by forming blooms and thick algal mats (Liu et al., 2021) and producing algal toxins (we detected algal toxin in both LDC and LXY but not in LQL and LYL, the data not shown). LQL and LYL were dominated by several smaller cyanobacteria instead of *Microcystis* with no thick algae mats formed, then there is enough space and less competition to support more species in high nutrient conditions. These results indicated that the biodiversity of eutrophic lakes

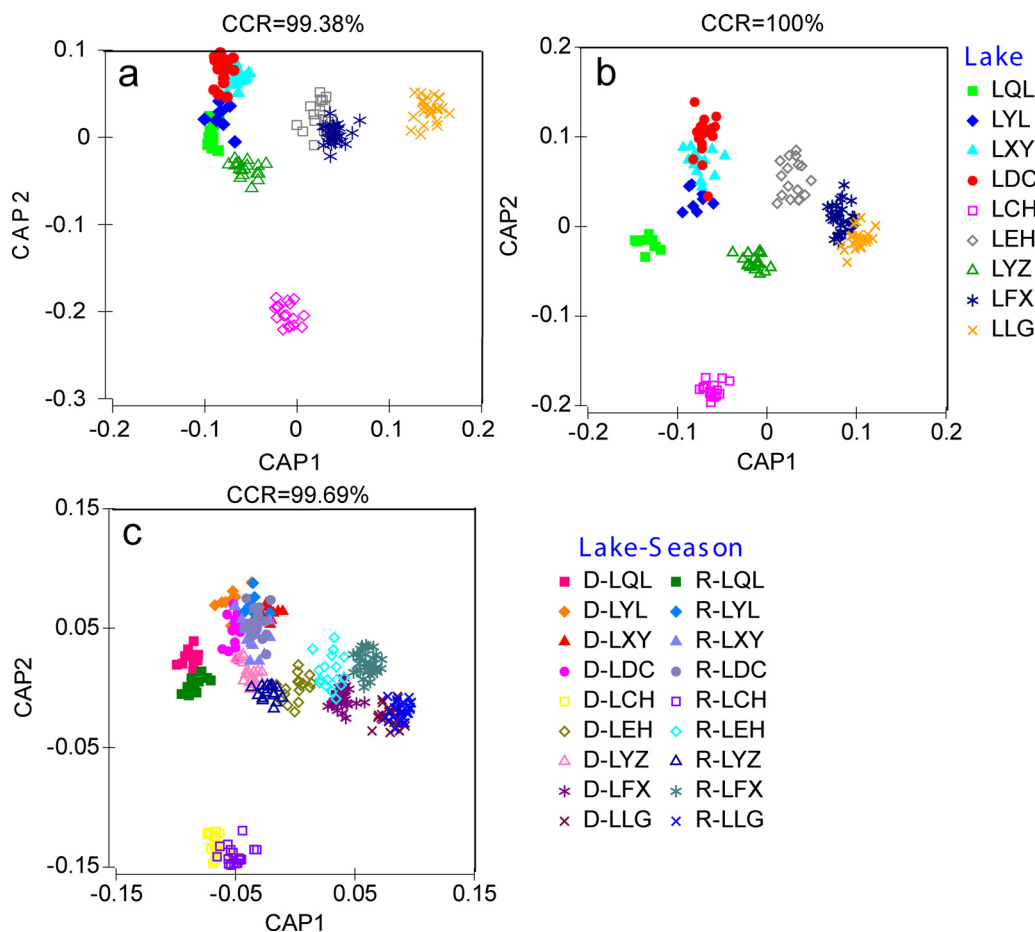


Fig. 2 – Ordination plot of canonical analysis of the principal coordinates (CAP) for phytoplankton abundance in the e-dry season (a), the e-rainy season (b), and the overall season (c) based on Bray–Curtis coefficient. CCR, the correct classification rate; D, the end of the dry season; R, the end of the rainy season.

was not necessarily very low, which might be related to certain properties in lakes.

Consistent with species richness, FAD2 also showed significant positive correlations with TN in both seasons. The high TN supporting high functional diversities may be due to the fact that under the sufficient resource conditions, the niche differentiation among coexisting species promotes the differences in phytoplankton functional traits, and thereby increases the functional diversity. In addition, FAD2 is estimated by the sum of the distances between species in traits space (Walker et al., 1999), thus it is related to both species traits and species richness. Therefore, the newly added species caused by the increase of TN may have different functional traits from existing species, and thus the functional diversity increases. Our data showed that both SR and functional diversities were low in oligotrophic lakes and *Microcystis*-dominated eutrophic lakes, which might be due to the possibility that the smaller the species number is, the less traits the species is likely to contain. However, FDC showed no significant correlation with TN in the e-dry season. FDC is calculated by the total branch length of the dendrogram based on the functional traits (Petchey and Gaston, 2002). Mathematically, FDC is depend largely on the

trait differences among species rather than species richness, thus adding a non-unique species (the traits is identical to one already existed) will leave FDC unchanged (Ye et al., 2019).

However, compared with species richness, evenness showed a strong negative correlation with TN in the e-rainy season, which was in line with the common tendency that the evenness of freshwater species was decreased with increasing nutrient concentrations in the lakes worldwide (Liess et al., 2009; Lehtinen et al., 2017; Wang et al., 2017). The decreased evenness with increasing nutrient concentrations indicates that few species are favored by nutrient enrichment (Larson and Belovsky, 2013). Consistently, in the present study, LDC and LXI were overwhelmingly dominated by *Microcystis* with both low species richness and low evenness. Although LQL and LYL had high species richness, several cyanobacteria species (such as *Cylindrospermopsis* sp., *Raphidiopsis curvata*, and *Pseudanabaena* sp.) still had high dominance, resulting in low evenness. However, in the e-dry season and the overall season, TN showed no significant effect on evenness (Appendix A Fig. S5; Fig. 4), which was attributed to the fact that LEH and LYZ with mesotrophic nitrogen level had the lowest evenness during the dry season. The low evenness in LEH was

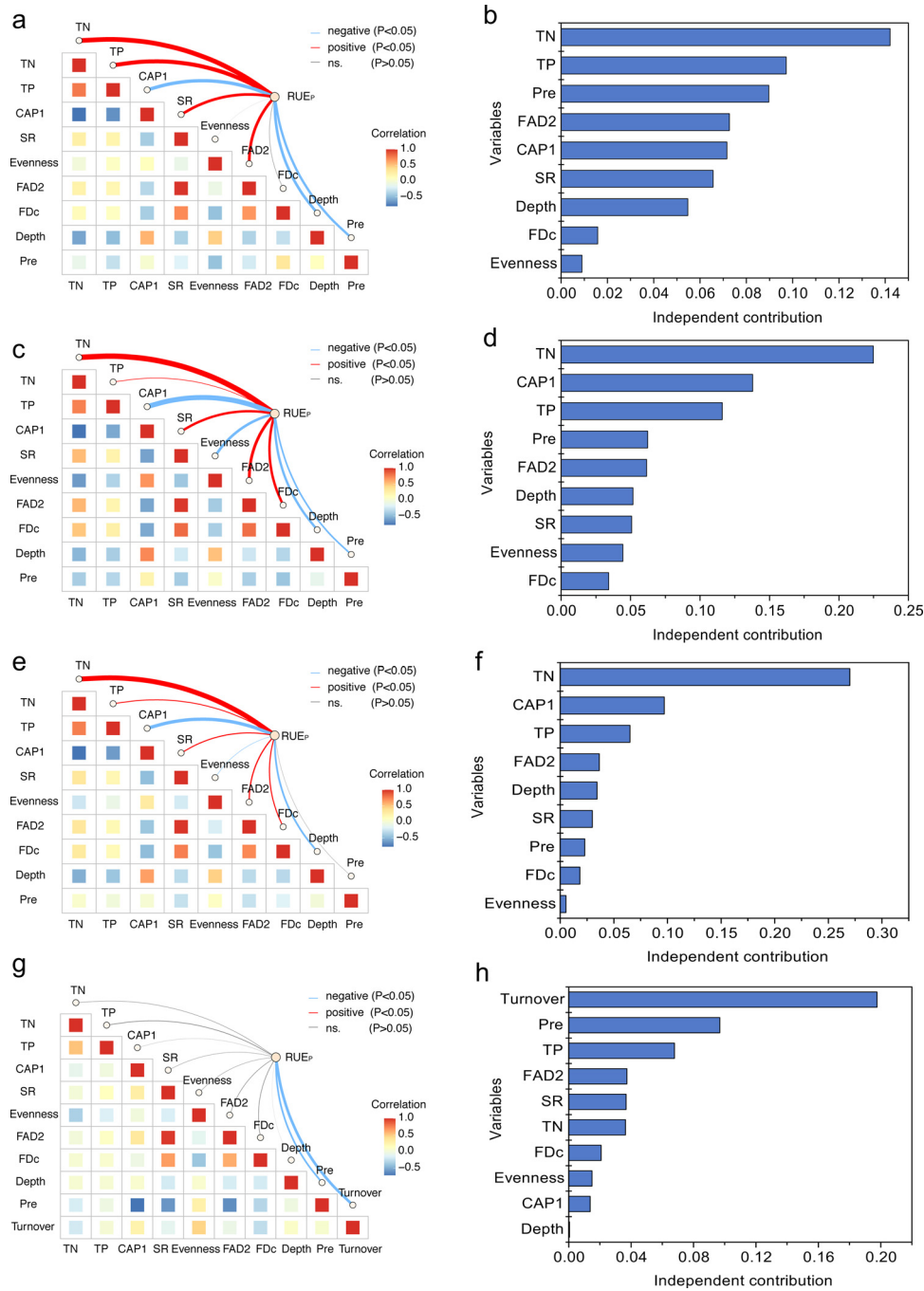


Fig. 3 – Correlation analysis and hierarchical partitioning analysis between explanatory variables and RUE_p . (a) Correlation analysis in the e-dry season. (b) Hierarchical partitioning analysis in the e-dry season. (c) Correlation analysis in the e-rainy season. (d) Hierarchical partitioning analysis in the e-rainy season. (e) Correlation analysis in the overall season. (f) Hierarchical partitioning analysis in the overall season. (g) Correlation analysis between the seasonal differences in explanatory variables and RUE_p . (h) Hierarchical partitioning analysis of the seasonal difference in explanatory variables to RUE_p . The thickness of the line indicates the strength of the correlation. The thicker the line, the stronger the correlation. The red line represents positive correlation, whereas the blue line represents negative correlation. TN, total nitrogen; TP, total phosphorus; CAP1, the first axis score for the canonical analysis of principal coordinates (Fig. 2); SR, species richness; FAD2, functional attribute diversity; FDc, dendrogram-based functional diversity; Pre, precipitation.

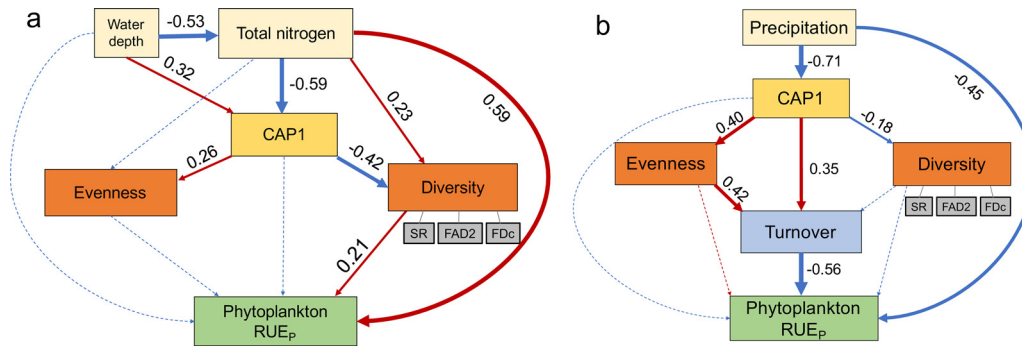


Fig. 4 – Partial least squares path models showing the relationships among the environmental variables, phytoplankton community structure (CAP1, diversity), and phytoplankton phosphorus use efficiency in the overall season (a), and the relationships among the turnover, the seasonal differences in precipitation, phytoplankton community structure (CAP1, diversity), and phytoplankton phosphorus use efficiency across the two seasons (b). The goodness of fit indices (GoF) for a and b were 0.62 and 0.59 respectively. The red line represents a significant positive relationship ($P < 0.05$), whereas the blue line represents a significant negative relationship ($P < 0.05$). The dashed line represents a non-significant relationship ($P > 0.05$). CAP1 was the first axis score of the canonical analysis of principal coordinates (Fig. 2). The numbers indicate partial correlation coefficients associated with each causal relationship. Other variables such as TP, precipitation (a) or water depth (b) were not included in the model as they would reduce the goodness-of-fits of the model. Diversity included species richness (SR), functional attribute diversity (FAD2), and dendrogram-based functional diversity (FDc), but did not include evenness because its relationship with total nitrogen (TN), turnover and RUE_p was different from that of SR, FAD2, and FDc.

caused by a high dominance of *Aphanocapsa elachista* (0.91), which has been reported to be a frequently dominant species in moderate trophic shallow lakes (Becker et al., 2010). Similarly, the low evenness in LYZ was caused by the high dominance of *Pseudanabaena* sp. (0.87). The predominance of these two species during the dry season of mesotrophic lakes may be due to the possibility that mesotrophic nitrogen levels are sufficient for them to thrive, and the environmental conditions such as temperature and light in the dry season are suitable for their growth.

3.2. TN promotes the phosphorus use efficiency of phytoplankton by impacting diversity

Besides the direct pathway to RUE_p, TN also had a path that affected RUE_p through altering biodiversity (Fig. 4). Consistent with the relationship between TN and RUE_p, SR, FAD2, FDc were significantly positively correlated with RUE_p. However, evenness was significantly negatively correlated with RUE_p in the e-rainy season, and weakly correlated with RUE_p in the e-dry season and the overall season. For species richness, the positive correlation between phytoplankton RUE and SR is widely acknowledged. For instance, Ptacnik et al. (2008) have discovered that phytoplankton RUE is significantly positively correlated with phytoplankton genus richness. Striebel et al. (2009) have also reported a positive correlation between species richness and RUE by natural phytoplankton communities. Consistently, our data also showed that SR was significantly positively correlated with RUE at all three trophic states. Previous study has demonstrated that increased lake resource is transferred to autotrophic organism with the increasing number of coexisting species (Ptacnik et al., 2008), suggesting that species richness may have consistent directional relationships (albeit of differing strengths) on resource use efficiency across nutri-

ent ranges. In this study, the positive correlation between SR and RUE_p was enhanced with the increasing trophic states. Phytoplankton communities in highly eutrophic lakes including LQL and LYL are generally dominated by Cyanophyta species. It is reported that Cyanophyta species is more efficient in phosphorus use than other phytoplankton species (Filstrup et al., 2014), which might explain why the four eutrophic lakes had relatively higher RUE_p than other lakes. In the case of the dominance by Cyanophyta species, the more phytoplankton species, the higher the efficiency of resources capture (Tian et al., 2017a), thus LQL and LYL had higher RUE_p than LDC and LXY since the former (LQL and LYL) had more phytoplankton species. In effect, the three mesotrophic lakes were also dominated by Cyanophyta species, which might be the reason why they had higher RUE_p than oligotrophic lakes.

Although both FAD2 and species richness showed a positive correlation with RUE_p at all three trophic states, FAD2 had higher independent contribution to RUE_p than species richness across the seasons and the nutrient gradients (Fig. 3). It has been well reported that functional diversity performs better in predicting ecosystem functioning than species diversity (Gross et al., 2017; Abonyi et al., 2018; Ye et al., 2019), since adding or losing species with the same functional traits has negligible effect on ecological functions (Carmona et al., 2016). Essentially, the functional diversity of organisms is realized through the utilization of huge heterogeneous resources within an ecosystem, that is, large differences in resource utilization indicate high functional diversity and high ecosystem functioning (Cadotte et al., 2011). Díaz and Cabido (2001) also found a better explanation for the impact of functional diversity on ecosystem functions: the variation of functional eigenvalues increases due to the heterogeneity of habitats, resulting in a high functional diversity and enhanced ecosystem functions.

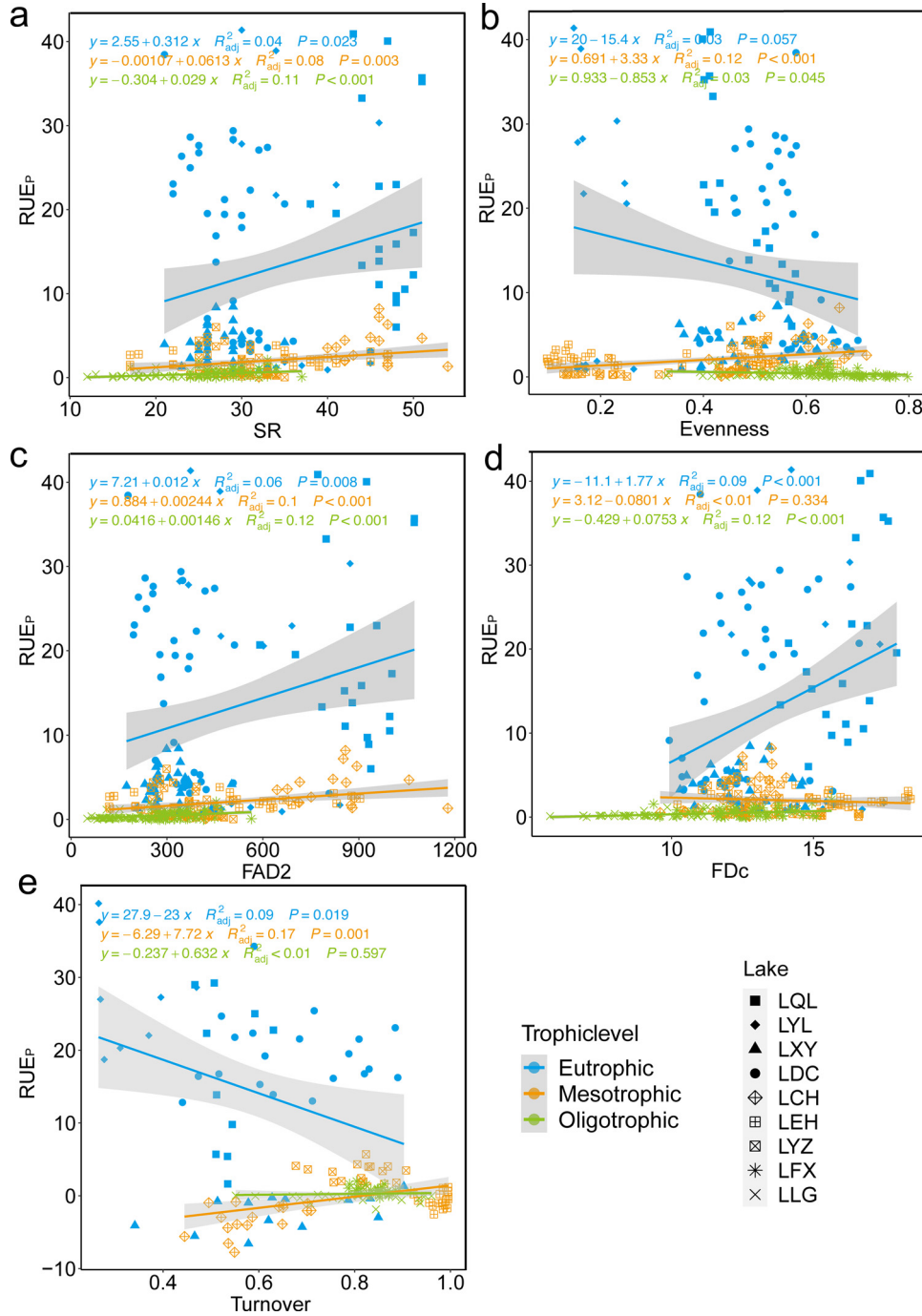


Fig. 5 – Linear regression analysis between diversity indices (a, b, c, d), community turnover (e) and resource use efficiency (RUE_p) at eutrophic, mesotrophic, and oligotrophic states.

Compared to species richness, evenness had more complex relationships with RUE_p. Tian et al. (2017b) have reported that RUE_p is positively correlated with both phytoplankton species richness and evenness, whereas Lehtinen et al. (2017) have observed a negative correlation between RUE_p and both species richness or evenness. Filstrup et al. (2014) have discovered that RUE_p is increased with increasing phytoplankton species richness, but is decreased with increasing evenness. In the present study, phytoplankton evenness was strongly negatively cor-

related with RUE_p in the e-rainy season, and also negatively correlated with RUE_p in the eutrophic and oligotrophic lakes. Our results were consistent with those of Filstrup et al. (2014), who found that the effects of species richness and evenness on RUE_p differed. The opposing phytoplankton evenness-RUE_p relationship in the eutrophic level likely results from the dominance of cyanobacteria since they are able to use phosphorus more efficiently than other phytoplankton taxa (Filstrup et al., 2014). In our study, eutrophic LYL exhibiting the lowest even-

ness but a high RUE_P might be due to the fact that *Cylindrospermopsis raciborskii* (a main dominant species in LYL) has been reported to have strategic flexibility to use environmental phosphorus (Fang et al., 2014). The negative evenness- RUE_P relationship in the oligotrophic level might be attributed to the higher RUE_P and lower evenness in LLG (Fig. 5). The predominant species (*Fragilaria crotonensis*) in LLG reduced the evenness and was also reported to be a good P competitor in the multiple species competition experiments (Interlandi and Kilham, 1999). In the mesotrophic lakes, a positive correlation between evenness and RUE_P was observed, which might be attributed to the fact that mesotrophic condition supported more species, thus presenting more pronounced niche differentiation, eventually resulting in more rational and efficient use of the resources.

It was noticeable that all the biodiversity indices showed stronger relationships with RUE_P in the e-rainy season than in the e-dry season, and evenness even showed no significant correlation with RUE_P in the e-dry season (Fig. 3; Appendix A Fig. S6). Although SR, FAD2, and FDC showed significant correlation with RUE_P in both seasons, higher slopes were observed in the e-rainy season than in the e-dry season (Appendix A Fig. S6). The precipitation during the rainy season has a strong impact on the aquatic ecosystem, and it brings a high nutrient load from runoff into the lakes, resulting in a rapid increase in the concentration of nutrients (Barçante et al., 2020). Consistently, our results revealed that eutrophic lakes had higher nutrient concentrations in the e-rainy season than in the e-dry season (Appendix A Table S3), resulting in higher phytoplankton phosphorus use efficiency in the e-rainy season (Appendix A Fig. S6). In addition, the change in the light intensity can also influence the nutrient uptake by phytoplankton (Meseck et al., 2005). Lean and Pick (1981) have reported that more phosphate is taken up by phytoplankton at a low light intensity ($55 \mu\text{Einst}/\text{m}^2/\text{s}$) than at a high light intensity ($240 \mu\text{Einst}/\text{m}^2/\text{s}$). In our study area, the rainy season has relatively lower solar radiation than the dry season (Zhang et al., 2021b), and the excessively high solar radiation in the dry season even causes photoinhibition of phytoplankton in the lake (Zhou et al., 2015). This might explain why the phytoplankton phosphorus use efficiency in the eutrophic lakes was higher in the e-rainy season than in the e-dry season in the present study. The above findings made the changing trend of RUE_P along the biodiversity gradients more significant in the e-rainy season than in the e-dry season.

3.3. TN promotes the phosphorus use efficiency of phytoplankton directly

When studying the relationships between biodiversity and ecosystem function, we need to focus not only on the factors that affect biodiversity, but also on the direct impact of these factors on ecosystem functioning (Gonzalez and Chanton, 2002; Schmid and Hector, 2004). In this study, the highest independent contribution of TN to RUE_P in the two seasons (Fig. 3) and the strongest significant direct effect of TN on RUE_P in the partial least squares path model (Fig. 4) indicated that TN was the most important environmental driver promoting phytoplankton RUE_P among the nine lakes. The positive correlation between TN and Chl-*a* (Appendix A Fig. S3) in-

dicated that the increasing TN promoted the growth of phytoplankton and increased phytoplankton biomass, thus promoting more inorganic phosphorus uptake by the phytoplankton. This is also proved by the field observation that increased nitrogen levels improve the phosphorus use efficiency by phytoplankton community (Zhang et al., 2021a). Laboratory experiment also discovered that nitrate addition can stimulate phytoplankton growth and increase the phosphorus utilization by phytoplankton, thus promoting phosphorus release from sediments to overlying water (Ma et al., 2021). In addition, the enrichment of nitrogen has been proved to increase the alkaline phosphatase activity (APA), which can further stimulate the uptake and utilization of phosphorus by phytoplankton (Ma et al., 2018).

3.4. Community turnover declines phytoplankton resource use efficiency

Community turnover can affect ecosystem functioning in a disturbance regime-dependent manner (Norberg et al., 2001). It is reported that community turnover reduces phytoplankton RUE in the cyanobacteria-dominated eutrophic lakes (Filstrup et al., 2014), but promotes phytoplankton RUE in drinking water reservoirs (Yang et al., 2021). In our study, we also found various effects of community turnover on RUE_P at different trophic states. The negative correlation between community turnover and RUE_P in the eutrophic lakes (Fig. 5e) suggested that environmental conditions did not fluctuate dramatically in these eutrophic lakes, which allowed the cyanobacteria to maintain their dominant status over time (Norberg et al., 2001; Filstrup et al., 2014), suggesting that environmental conditions in the eutrophic lakes might be relatively stable compared with those in other nutrient-level lakes (Filstrup et al., 2014). Conversely, a positive correlation was observed between RUE_P and turnover in the mesotrophic and oligotrophic lakes, which was owing to the fact that most species were replaced on the intra-annual scale in mesotrophic and oligotrophic lakes, leading to a more complementary niche among the phytoplankton species and a more comprehensive utilization of efficient resources. The positive turnover-ecosystem functioning relationship implies that coexistence between species would be promoted if they had different responses to temporally changing environments in the mesotrophic and oligotrophic levels over time (Allan et al., 2011).

4. Conclusion

Our work investigated the predictors of phytoplankton phosphorus use efficiency (RUE_P) along nutrient gradients in the nine plateau lakes across the two seasons (the end of the dry and rainy seasons). The results demonstrated that TN had the dominant independent contribution and the strongest direct effect to phytoplankton RUE_P among the nine lakes, whereas turnover contributed the most to RUE_P across the two seasons. The largest independent contribution and significant positive effect of TN on RUE_P demonstrated that increased nitrogen levels can directly improve the phytoplankton RUE_P . Moreover, TN influenced RUE_P also by affecting biodiversity. Specif-

ically, species richness, FAD2, and FDC were positively correlated with TN and RUE_P in both seasons, while evenness was negatively correlated with TN and RUE_P at the end of the rainy season. We also found that the effects of phytoplankton diversity and community turnover on RUE_P depended largely on the trophic state of lakes. Species richness and FAD2 were positively correlated with RUE_P in all three trophic states. Evenness showed a negative correlation with RUE_P at the eutrophic and oligotrophic levels, but a positive correlation with RUE_P at the mesotrophic level. Turnover had a negative influence on RUE_P at the eutrophic level, but a positive influence at the mesotrophic and oligotrophic levels. Our results suggested that multiple biodiversity indices and nutrient levels need to be taken into consideration when we determine the ecosystem functioning predictors and examine BEF relationships.

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Appendix A Supplementary data

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jes.2022.02.005.

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