

Seasonality of water temperature and conductivity regulates phytoplankton richness dynamics by changing turnovers rates in a freshwater shallow lake

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Abstract

Phytoplankton are crucial components of aquatic ecosystems, with their richness dynamics playing an important role in regulating ecological functions. However, seasonal variations of phytoplankton turnover associated with water properties remain unclear. Based on a two-year survey in a freshwater lake, we showed that phytoplankton richness was primarily affected by water temperature (WT) and conductivity (EC). WT seasonality exerted opposite contributions to phytoplankton gain and loss rates, leading to complex temporal changes in turnover and subsequent richness dynamics. In addition, Cyanophyta and Chlorophyta richness dominated the seasonal variations of phytoplankton richness, and their turnover rates were mainly influenced by WT and EC. The gain and loss rates of non-dominant phyla (Chrysophyta, Cryptophyta and Pyrrophyta) were closely related to water N:P ratios and WT. These discrepancies suggest the differential competitive strategies of dominant and non-dominant phyla under environmental fluctuations. Our findings highlight that phytoplankton turnover, especially the gain process, drives the richness dynamics of community and plays crucial roles in maintaining water carbon storage, and provide basis and proposals for the management and conservation of aquatic ecosystems.

Introduction

Phytoplankton play fundamental roles as primary producers in aquatic ecosystems (Field et al. 1998; Schaum et al. 2017), converting carbon dioxide into organic matter through photosynthesis and providing essential energy for food webs. Phytoplankton biomass are highly sensitive to climate change and water eutrophication (Henson et al. 2021). The optimal growth conditions for different phytoplankton species vary substantially due to interspecific variations and environmental adaptability (Sandgren et al. 1992; Bao et al. 2022). Phytoplankton communities undergo rapid succession under environment change (Mock et al. 2017; Krasovec et al. 2019). Their succession can affect water carbon cycling by altering community function (Allan et al. 2011).

Phytoplankton richness serves as a crucial indicator for the shifts of community composition and function in aquatic ecosystems (Allan et al. 2011). Studies on variations in phytoplankton richness and elucidating their underlying maintenance mechanisms, succession dynamics, and ecological consequences not only advances the theoretical understanding of aquatic ecosystem functioning but also provides a scientific basis for lake management policies formulation and ecological restoration practices (Rosińska et al. 2017; Ye et al. 2024). Most studies focus only on changes in richness (Armengol et al. 2019; Bestion et al. 2020; Dittrich et al. 2023). However, changes of phytoplankton richness do not necessarily represent community composition variation, because both species gain and loss processes are important components of community succession (Fox et al. 2012; Staude et al. 2023). The effects of phytoplankton gains and losses on community characteristics vary with different taxa. Non-random gains of dominant phytoplankton may suppress persisting taxa biomass (Fox et al. 2012), whereas loss processes directly contribute to the declined of community diversity and functions (Jochum et al. 2020).

Turnover rate, defined as mean of gain and loss rates, provides a more detailed account of richness shifts (Anderson 2007) and is widely used in the study of terrestrial ecosystems. For example, nitrogen addition reduces plant community turnovers by simultaneously suppressing species gain and loss rates in a typical grassland (Zhao et al. 2022), but increases those in an old field primarily through elevating species loss rate only (Xu et al. 2012). Phytoplankton turnovers could also be greatly affected by the seasonal variations of temperature, nutrients, and other physiochemical properties by changing either gain or loss processes over time (Zhang et al. 2016; Zhang et al. 2021). Growing evidence indicates a progressive increase in phytoplankton turnover rates by the end of this century under a changing climate in the oceans, with an elevated occurrence of ephemeral taxa and more extinctions of persistent taxa (Henson et al. 2021). However, the relative contributions of abiotic variables to phytoplankton and specific taxa turnover in freshwater ecosystems are still unclear.

Differing from deep lakes with higher environmental capacity and lower exogenous nutrient load, shallow lakes are more sensitive to the changes of climate and aquatic environment, which may induce faster turnover and differential responses of phytoplankton phyla. Based on a two-year survey in Baiyangdian Lake (BYDL), the largest freshwater shallow lake in North China Plain, this study aims to examine the temporal changes of phytoplankton richness and their responses to aquatic environments variations. The specific objectives were to address: (1) how does phytoplankton richness change with season? (2) how do water physicochemical properties affect seasonal phytoplankton turnover?

Materials and Methods

Study site and sampling sites

The sampling sites are located within open water area of BYDL (115°45'–116°07' E, 38°43'–39°02' N), the largest lake in North China Plain. The region has a typical temperate monsoon climate, with annual mean air temperature of 12.9°C, and annual precipitation of 525 mm (1955 – 2019). 70 – 80% precipitation is concentrated in June-August (Zeng et al. 2021). The lake is consistent with 3700 ditches and 143 ponds, and its average depth is 1.8 meters. The main vegetation account for 49.8% of the area of is *Phragmites australis*. Eight rivers and one canal were in the basin. Zhaowangxin river in the east of lake is the downstream river only. The Yellow River, the middle pathway of the South-to-North Water Diversion Project, and upstream reservoirs supplied most of the water to BYDL during different seasons of the year.

Samples collection

In 2022–2023, we collected water and phytoplankton samples at 10 sites three times per year (April, August and October represent spring, summer and autumn, respectively), with three replicates for each site (Fig. 1). Latitude and longitude information of all the sampling sites are represented in Table S1. Two-year sampling using consistent sampling standard were used to eliminate interference from

interannual random fluctuations. 200 mL water samples and 1 L phytoplankton samples were collected 0.5 m below the water surface from 9 a.m. to 3 p.m. and stored in ice bags. Phytoplankton samples were added with Lugol's iodine solution (final concentration 2%) before transported to laboratory for subsequent analysis.

Water properties analyses

All water samples were pathed through 0.45 µm filter. Water total nitrogen (TN) contents were measured by TOC analyzer, and water total phosphorus (TP) contents were measured by auto analyzer (smartchem 450, AMS Alliance, Rome, Italy). Water temperature (WT), turbidity, conductivity (EC), and pH were measured *in situ* at each sampling site using portable water quality monitors (EXO2, YSI, United States).

Phytoplankton detection and turnover rate calculation

Phytoplankton samples were stored for 48h by settlement flasks, and the settled phytoplankton approximately 25 mL were transferred to smaller bottles. Phytoplankton taxa were identified and quantified with an optical microscope (E100, Nikon, Tokyo, Japan). Each sample was analyzed in a 0.1 mL counting chamber at a magnification of 400x using 100 randomly selected fields. The taxonomic identification of phytoplankton was performed according to “Freshwater algae in China: System, Classification and Ecology” (Hu et al. 2006).

The gain (G_p), loss (L_p) and turnover rates (T_p) for adjacent seasons were calculated using the equations proposed by Anderson (2007):

$$G_p = S_{\text{gain}} / [(1/2) (S_1 + S_2)]$$

$$L_p = S_{\text{loss}} / [(1/2) (S_1 + S_2)]$$

$$T_p = (S_{\text{gain}} + S_{\text{loss}}) / (S_1 + S_2)$$

where S_{gain} and S_{loss} represent gain and loss rate, respectively, between any two adjacent sampling intervals. S_1 and S_2 were phytoplankton richness at two adjacent sampling dates. This formula is mainly used to quantify and examine the temporal patterns of species gain, loss, and turnover rates during succession, as well as to reconstruct the true dynamics of succession.

Statistics analysis

Statistical significance of the differences in water nutrients, physicochemical properties, and diversity indexes between seasons and years were tested by Duncan's Multiple Range Test and Wilcoxon test, respectively, in SAS 8.01 (SAS Institute, Cary, North Carolina, USA). Linear regression analyses were conducted in GraphPad Prism 9.3.1 (GraphPad Software, LLC, San Diego, Carolina, USA). The scatters

referred to the Y-axis mirror, and the slope difference of two regression lines were compared by GraphPad Prism. Random forest analyses were implemented in R version 4.3.3 (R Core Team, 2024) using the *randomForest* package.

Results

Temporal dynamics of water properties

Water nutrients in BYDL exhibited significantly interannual changes between 2022 and 2023. Annual mean water total nitrogen (TN) dropped from 1.62 mg L⁻¹ in 2022 to 0.96 mg L⁻¹ in 2023 (Wilcoxon test, $P < 0.001$; Fig. 2a). The highest concentration of TN occurred in spring 2022 (2.18 mg L⁻¹). However, annual mean water total phosphorus (TP) increased from 0.09 mg L⁻¹ in 2022 to 0.41 mg L⁻¹ in 2023 (Wilcoxon test, $P = 0.012$). TP reached its peak at 0.90 mg L⁻¹ in summer 2023 (Fig. 2b). Annual mean water N:P ratios decreased from 446 in 2022 to 18.7 in 2023 (Wilcoxon test, $P < 0.001$). The seasonal mean N:P ratios showed a strong seasonal fluctuation with peaks occurring in summer and autumn 2022 (730 and 570, respectively; Fig. 2c).

Annual mean water conductivity (EC) was 784 $\mu\text{S cm}^{-1}$ and 790 $\mu\text{S cm}^{-1}$ in 2022 and 2023, respectively. EC remained relatively stable and peaked at 1148 $\mu\text{S cm}^{-1}$ in spring 2023 (Fig. 2d). Annual mean water turbidity was 2.98 FNU in 2022 and slightly decreased to 2.73 FNU in 2023, with the lowest value of 1.37 FNU in summer 2023 (Fig. 2e). Annual mean water temperature (WT) was 23.1°C and 22.0°C in 2022 and 2023, respectively. Seasonal mean WT varied from 15.9°C to 32.6°C and peaked in summer of the two years (Fig. 2f). No clear spatial patterns of environmental factors across sampling sites were observed (Fig. S1).

Changes in phytoplankton richness and taxa turnover rate

Phytoplankton richness was relatively stable over the two years, with an annual mean of 20.8 in 2022 and 22.4 in 2023, respectively. Phytoplankton richness was higher in summer (23.4 in 2022 and 27.6 in 2023) than spring (18.6 in 2022 and 17.2 in 2023) and autumn (20.5 in 2022 and 22.4 in 2023; Fig. 3a). Cyanophyta, Bacillariophyta, and Chlorophyta were the dominant phyla, accounting for 82.4% of phytoplankton richness, and two years mean of Chrysophyta, Cryptophyta, and Pyrrophyta were all less than 1 (Fig. S2). Principal Component Analysis (PCA) conducted at the phylum level revealed that two axes explained 84.3% and 10.2% of the total variability (Fig. 3b). The first axis (PC1) was primarily influenced by Chlorophyta (-0.79) and Cyanophyta richness (-0.59), whereas the second axis (PC2) was attributed by Cyanophyta (0.75), Chlorophyta (-0.55), Cryptophyta (-0.22), and Euglenophyta richness (-0.20).

Mean gain rate of phytoplankton at genus level was 0.41 (Fig. 4) and decreased dramatically from spring-summer (0.50 in 2022, 0.69 in 2023) to summer-autumn (0.26 in 2022, 0.21 in 2023) both in 2022 and 2023. Loss rate remained relatively stable, with a mean value of 0.35 and the lowest loss rate (0.21)

in spring-summer 2023. Consequently, turnover rate had the highest value of 0.45 in spring-summer 2023, and the lowest values in summer-autumn 2022 and 2023 (both 0.34).

Dependences of phytoplankton richness and turnover rates on water properties

Phytoplankton richness was positively correlated with TP (Fig. S3b; $R^2 = 0.13$, $P = 0.004$) and WT (Fig. S3f; $R^2 = 0.19$, $P < 0.001$), but was negatively related to EC (Fig. S3d; EC: $R^2 = 0.08$, $P = 0.027$) across all the sampling dates in 2022 and 2023.

Gain rate at the community level showed positive dependences on the changes in TP (Fig. 5b; $R^2 = 0.10$, $P = 0.027$) and WT (Fig. 5f; $R^2 = 0.45$, $P < 0.001$), but a negative relationships with those in EC (Fig. 5d; $R^2 = 0.22$, $P < 0.001$). Loss rate increased with increasing EC (Fig. 5j; $R^2 = 0.13$, $P = 0.011$) and declining WT (Fig. 5l; $R^2 = 0.20$, $P = 0.001$). The regression slope of gain rate on the changes in WT was higher than that of the mirrored loss rate in the Y axis (Fig. S4; $P = 0.077$). Turnover rate was negatively correlated with the changes in turbidity (Fig. 5q; $R^2 = 0.12$, $P = 0.013$) but positively with those of WT (Fig. 5r; $R^2 = 0.13$, $P = 0.009$), respectively. In addition, the Jaccard dissimilarity of phytoplankton community showed negative and positive dependences on the changes in turbidity (Fig. S5; $R^2 = 0.16$, $P = 0.004$) and WT ($R^2 = 0.19$, $P = 0.002$), respectively. The replacement was the major component of Jaccard dissimilarity (Fig. S6), but was not regulated by environment factors (Fig. S7), whereas the nestedness component was positively correlated with the changes in TN (Fig. S7g; $R^2 = 0.11$, $P = 0.017$) and TP (Fig. S7h; $R^2 = 0.08$, $P = 0.041$).

The gain rates of both Cyanophyta and Chlorophyta were related negatively with the changes in EC (Cyanophyta: $R^2 = 0.31$, $P < 0.001$; Chlorophyta: $R^2 = 0.29$, $P < 0.001$) but positively with those in WT (Fig. S8d, f; Cyanophyta: $R^2 = 0.62$, $P < 0.001$; Fig. S9d, f; Chlorophyta: $R^2 = 0.41$, $P < 0.001$). The gain rates of Chlorophyta increased with the changes in TP (Fig. S9b; $R^2 = 0.13$, $P = 0.010$) and that of Euglenophyta increased with the changes WT only (Fig. S10f; $R^2 = 0.18$, $P = 0.003$). The gain rate of other phyla, including Chrysophyta, Cryptophyta, and Pyrrophyta, negatively correlated with the changes in N:P ratios ($R^2 = 0.39$, $P < 0.001$) and WT ($R^2 = 0.25$, $P < 0.001$), but positively with those in EC (Figs. S11c, d, f; $R^2 = 0.15$, $P = 0.006$). The loss rates of both Cyanophyta and Chlorophyta positively depended upon the changes in EC (Cyanophyta: $R^2 = 0.28$, $P < 0.001$; Chlorophyta: $R^2 = 0.22$, $P < 0.001$), but negatively upon those in WT (Figs. S8j, l, S9j, l; Cyanophyta: $R^2 = 0.27$, $P < 0.001$; Chlorophyta: $R^2 = 0.37$, $P < 0.001$). The loss rate of Chlorophyta, Bacillariophyta, and other phyla demonstrated negative relationships with the changes in TP (Fig. S9h; $R^2 = 0.12$, $P = 0.012$), turbidity (Fig. S12k; $R^2 = 0.21$, $P < 0.001$), and N:P ratios (Fig. S11i; $R^2 = 0.14$, $P = 0.007$), respectively. The turnover rates of Cyanophyta and Bacillariophyta positively depended upon the changes in WT (Cyanophyta: $R^2 = 0.26$, $P < 0.001$; Bacillariophyta: $R^2 = 0.13$, $P = 0.010$), whereas those of Cyanophyta and Bacillariophyta were also negatively correlated with the changes in turbidity (Figs. S8q, r; $R^2 = 0.09$, $P = 0.035$) and EC (Figs. S12p, r; $R^2 = 0.13$, $P = 0.010$), respectively. The turnover rate of Euglenophyta and other phyla showed negative correlations with the changes in turbidity (Fig. S10q; $R^2 = 0.12$, $P = 0.015$) and WT (Fig. S11r; $R^2 = 0.13$, $P = 0.009$), respectively.

Driving forces for taxa gain, loss and turnover rate

Across the two-year period, random forest analyses demonstrated that changes in WT (IncMSE = 22.2, $P < 0.010$) contributed 43.8% (full model $P < 0.001$) of the variations in gain rate at the community level (Fig. 6a). Changes in WT (IncMSE = 14.9, $P = 0.049$) and EC (IncMSE = 10.1, $P = 0.089$) together accounted for 26.6% (full model $P = 0.002$) of the variations in loss rate (Fig. 6a).

Changes in WT (IncMSE = 29.6, $P < 0.010$) and EC (IncMSE = 12.8, $P < 0.010$) jointly explained 60.7% (full model $P < 0.001$) of the variations in Cyanophyta gain rate (Fig. 6b). Changes in WT (IncMSE = 20.9, $P < 0.010$) were responsible for 49.4% (full model $P < 0.001$) of the variations in Chlorophyta gain rate (Fig. 6c). Changes in N:P ratios (IncMSE = 16.1, $P < 0.010$) and WT (IncMSE = 12.5, $P < 0.010$) together accounted for 45.1% (full model $P < 0.001$) of the variations in other phyla gain rate (Fig. 6d).

Changes in WT and EC jointly contributed 55.8% (full model $P < 0.001$) and 37.7% (full model $P < 0.001$) to the variations in the loss rates of Cyanophyta (WT: IncMSE = 22.3, $P < 0.010$; EC: IncMSE = 15.0, $P < 0.010$) and Chlorophyta (WT: IncMSE = 16.8, $P < 0.010$; EC: IncMSE = 7.8, $P = 0.020$), respectively (Figs. 6b, c). Changes in N:P ratios (IncMSE = 12.7, $P = 0.020$) explained 12.5% (full model $P = 0.023$) of the variations in other phyla loss rate (Fig. 6d).

Changes in WT (IncMSE = 13.8, $P < 0.010$) were responsible for 7.6% (full model $P = 0.066$) of the variations in Cyanophyta turnover rate (Fig. 6b). Changes in WT (IncMSE = 9.8, $P < 0.010$) and N:P ratios (IncMSE = 9.6, $P = 0.020$) together accounted for 13.6% (full model $P = 0.015$) of the variations in the other phyla turnover rate (Fig. 6d).

In addition, there were positive dependences of fluorescent dissolved organic matter (fDOM) on gain (Fig. 7a; $R^2 = 0.13$, $P = 0.009$) and turnover rates (Fig. 7c; $R^2 = 0.07$, $P = 0.067$) over the two-year period.

Discussion

Water properties influence phytoplankton richness dynamics

Temporal succession of phytoplankton community, characterized by the adherence to ecological niches and adaptation to environmental change (Vallina et al. 2023), is a crucial mechanism influencing biodiversity and ecosystem functions (Abonyi et al. 2018). Phytoplankton richness is regulated by local environmental filters (Catherine et al. 2016; Da Silva et al. 2024) and exhibits significant temporal-variability. Our results suggest a temperature-dependent change in phytoplankton richness at the community level across different seasons (Fig. 3) and the predominance of water temperature in affecting phytoplankton richness dynamics (Fig. S3), which is consistent with the results reported in 71 lakes of Yangtze River basin (Zhang et al. 2018) and 20 lakes of English Lake District (Maberly et al. 2022). Similarly, the diversity indices, richness and evenness, recorded in summer are higher than those

in winter at El-Temsah Lake (Essa et al. 2024), demonstrating the response patterns of phytoplankton diversity to temperature changes. Increased richness under rising temperature is likely attributable to the promoted water column stratification, which provides more ecological niches for phytoplankton survival (Allen et al. 2002; Allen and Gillooly 2006; Wang et al. 2024). In addition, the correlation between richness and water temperature has also been attributed to the temporal dynamics of phytoplankton niche assembly. Warming enhances phytoplankton growth and metabolisms, leading to accelerated phytoplankton gains and losses process (Elahi et al. 2015; Tonkin et al. 2017; Anderson and Ryneerson 2020).

Large-scale ecological management has been carried out with the establishment of Xiong'an New Area in BYDL. The annual mean TN was significantly decreased (Fig. 2a), but TP exhibits significant spatial-temporal variation in summer due to blooms of aquatic macrophyte species in spring and summer (Figs. 2b, S1b; Yang et al. 2020). These phenomena led to significant interannual difference in N:P ratios. It has been demonstrated that both TN and TP have a positive effect on phytoplankton richness across spatiotemporal scales (Lehtinen et al. 2017), suggesting that nutrient limitation decreases phytoplankton richness (Hou et al. 2024). The relationships of phytoplankton with TN and TP are shown to closely associated with N:P ratios. When N:P ratios exceed 17, phytoplankton growth and community composition change from N-dependent to P-dependent (Sakamoto 1966; Dodds et al. 2002; Lv et al. 2011). Our findings of the stimulated phytoplankton richness under TP enrichment demonstrate that P limitation is the dominant state in BYDL (Figs. 2c, S3). On the one hand, this indicates the higher demand of phytoplankton for available P to maintain active metabolisms. On the other hand, the N-fixing capacity of Cyanobacteria might induce the diminished requirement of phytoplankton for TN relative to TP (Chen et al. 2022a).

EC conducts the ion concentration and dissolved solids contents in water, including sodium, potassium, chloride, carbonate, sulfate, calcium, and magnesium, and exerts a predominant influence on the chemical composition and physical characteristics of water, and is associated with nutritional status (Pal et al. 2015). The influence of EC on phytoplankton richness has been widely observed in marine, lagoons, and inland freshwater (Olli et al. 2019; Saifullah et al. 2019; Stefanidou et al. 2020; Reid et al. 2021; Bharathi et al. 2022; Melles et al. 2023; Stanković et al. 2023). The negative correlations of phytoplankton richness with water EC agree with some previous studies that rapidly increased EC may affect the osmotic equilibrium and nutrients absorption capability of microorganisms (Kinsman-Costello et al. 2023), furthermore reducing the phytoplankton richness and biomass (Moffett et al. 2023). As a crucial environmental filter of phytoplankton community in spring and autumn in BYDL, higher EC exerts greater negative influences on Cyanobacteria and Chlorophyta, which account for over 80% of phytoplankton abundance, but positive effects on Chrysophyta, Cryptophyta, and Pyrrophyta, all these observations may be attributed to the differing adaptability of these taxa to environmental stresses (Yang et al. 2024).

Phytoplankton turnover under changing environments

Gain and loss significantly influence phytoplankton richness dynamics. Under varying environmental conditions, gain and loss rates can exhibit two types of relationships. First, gain and loss rates altogether increase or decrease with environmental factors increase. For instance, high turnover rate may arise from the joint increases of gain and loss in fertile habitats following external disturbances (Kaarlejärvi et al. 2021). Second, gain and loss rates change in opposite directions in response to environment fluctuations, and the asymmetrical responses of gain and loss rates to environmental variabilities could result in the biased changes of turnover rates.

Warming has been documented to accelerate turnovers of plants and soil microorganisms in terrestrial ecosystems (Tonkin et al. 2017; Xiao et al. 2023; Xu et al. 2023). Moreover, global change can increase phytoplankton turnover in most marine regions (Henson et al. 2021). Our observations of WT affecting phytoplankton turnover through the asymmetrical responses of their gains and losses to WT (Figs. 5f, i) indicate that the process of loss is longer than that of gain in this temperate freshwater lake (Fig. S4). This phenomenon might be attributed to phytoplankton's tolerance to low temperature or the resistance conferred by higher community diversity during cooling (Ptacnik et al. 2008; Chen 2022b; Fernández-González et al. 2022). Such mechanisms may help to explain the reduced turnover rate during summer-autumn (Fig. 4). In addition, our observations that increased EC symmetrically suppresses gain but enhances loss (Figs. 5d, j) are in accordance with the results of previous studies (Berger et al. 2019; Greco et al. 2023; Kaushal et al. 2023). The inhibition of some phytoplankton nutrient absorption under increased EC leads to the rapid loss of ecological niches and richness under interspecific competition (Kinsman-Costello et al. 2023). Furthermore, the differential impacts of TP on gain and loss rates in our study indicate that decreasing TP does not necessarily result in species losses due to the tolerance of phytoplankton to TP lack in P limitation water column (Lin et al. 2016).

Moreover, turnover rate is modified from the Jaccard dissimilarity index which reflects the sum of taxa replacement and nestedness. Replacement consists of gain and loss, whereas nestedness represents loss process only (Baselga et al. 2010). Both turnover rate and Jaccard dissimilarity index are influenced by turbidity and WT (Figs. 5q, r, S5), which may be due to that light is more limited than nutrients in eutrophication lakes (Yang et al. 2023). Specific to different components, the major replacement component is unaffected by environmental factors (Figs. S6, S7), likely attributing to that the gain and loss of replacement differentially response to same factors. The negative influences of TN and TP on the nestedness component in our study indicate that water eutrophication leads to some taxa loss in water body (Lanza et al. 2024).

Specific responses of phytoplankton taxa to environmental changes

Richness changes of dominant phyla can substantially affect phytoplankton diversity and community composition (Zhao et al. 2022) and exhibit similar trends during environment change. However, these phyla can also show phylum-specific responses to environmental change. For instance, Cyanophyta and Chlorophyta richness could be greatly regulated by water temperature, with Chlorophyta richness

exhibiting the highest value at 20°C, but Cyanophyta richness peaking at 23°C (Moresco et al. 2024). In addition, Cyanophyta gain rate changes faster than loss rate under changing WT in our study (Figs. S8f, I), whereas Chlorophyta gain rate does not, indicating that Cyanophyta community changes more aggressively relative to Chlorophyta when WT rise. Bacillariophyta have a "mix-and-match genome" (Armbrust 2009), which endows them with a variety of advantageous traits, such as tough silicified cell walls, vacuoles for storing nutrients, rapid responses to light changes, and the formation of a resting stage (Bowler et al. 2010). These attributes enhance the tolerance of Bacillariophyta to environmental fluctuations compared to other phyla (Bowler et al. 2010; Figs. 5, 6).

In contrast to the dominant phyla, the non-dominant phyla (Euglenophyta, Chrysophyta, Cryptophyta, and Pyrrophyta) exhibit lower richness levels, and the responses of these phyla to environmental change significantly differ from those of dominant phyla (Cyanophyta, Bacillariophyta, and Chlorophyta). Limited nutrients have been proved to show greater influences on non-dominant phyla than dominant phyla (Carroll et al. 2023), supported by our results that the gain rates of Chrysophyta, Cryptophyta, and Pyrrophyta are primarily affected by N:P ratios and WT (Fig. 6d). Decrease in N:P ratios could produce more niches in P-limited water that can be occupied by non-dominant phyla in the aquatic environment (Lehtinen et al. 2017). For instance, a survey in New York Bay suggests that nitrate N reduction leads to the decreased Bacillariophyta biomass, but increased Cryptophyta and Euglenophyta biomass (Brown et al. 2024). Our study site is a P-limited freshwater lake, and slight changes in water nutrients, especially P contents, could result in substantial variability of N:P ratios, thus impacting turnover processes of the nutrient-sensitive non-dominant phyla. Non-dominant phyla are more adaptable than dominant phyla to low temperature environments. For instance, Cryptophyta are found to dominate in spring (Wang et al. 2024), with *Cryptomonas sp.* and *Peridinium sp.* exhibiting obviously higher biomass at lower temperatures (Weisse et al. 2016). This adaptation to low WT may represent a strategic response of non-dominant phyla to competitive pressures, replacing some dominant phyla to colonize new niches when environment changes, which is important for maintaining ecosystem function.

Implications for water carbon storage and management of aquatic ecosystems

Dissolved organic matter (DOM) constitutes one of the largest carbon pools in aquatic environments (Bianchi, 2011). Faster turnover can drive more diverse functions of phytoplankton community to maintain higher productivity and stability of aquatic ecosystems (Allan et al. 2011; Gonzalez et al. 2020), thus releasing more DOM into the water column. Our findings demonstrate that water fDOM might be significantly regulated by higher phytoplankton turnover through increasing phytoplankton gain, but not loss process. This is likely due to that the reduced productivity resulting from phytoplankton loss could be compensated by the elevated water DOM originated from massive apoptosis (Hooper et al. 2012; Bestion et al. 2020). Nevertheless, further research is required to clarify the ecological mechanisms by long-term monitoring.

Our study also reveals the impact of freshwater EC on phytoplankton diversity. In the context of global freshwater salinization (Bolotin et al. 2020), decreased water EC does not affect carbon uptake in the water column, but reduces phytoplankton richness loss. Lake management strategies was generally focused on controlling water N and P contents, we call for measures to reduce the use of de-icing road salts, groundwater for agricultural irrigation, and the weathering of soils and infrastructure around lakes, especially those similar to Baiyangdian Lake (Kaushal et al. 2023; Moffett et al. 2023), where the replacement of components is the main driver of β -diversity.

Conclusions

Through a two-year sampling survey in a freshwater lake, we observed that WT and EC predominantly regulated phytoplankton richness dynamics. In specific, phytoplankton gain increased with rising WT, whereas phytoplankton loss decreased with increasing WT and EC. The influences of WT on phytoplankton gain and loss were asymmetric, contributing to a complex temporal change in turnover rates. In addition, Cyanophyta and Chlorophyta dominated the seasonal variation of phytoplankton richness in BYDL, whose gain and loss rates were primarily affected by WT and EC. By contrast, the gain and loss rates of non-dominant phyla, Chrysophyta, Cryptophyta and Pyrrophyta, exhibited strong dependences on water N:P ratios. Our findings suggest the different adaptation strategies of dominant and non-dominant phyla turnovers to environmental change, highlight that phytoplankton turnover, especially the gain process, drives the richness dynamics of phytoplankton community and plays crucial roles in maintaining water carbon storage, and establish recommendations for the governance and preservation of aquatic ecosystems.

Declarations

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contribution

Z. J., F. J., and W. S. contributed to conceptualization. F. J., and W. S. contributed to funding acquisition. W. S. contributed to validation. F. J. contributed to methodology. Z. J., W. Y., Z. L., Z. L., C. S., and Q. X. contributed to investigation. Z. J. contributed to data curation, original draft and manuscript writing, visualization, software. Q. X. contributed to resources. R. J., F. J., and W. S. contributed to review and edit manuscript. L. Y., F. J., and W. S. supervised the study.

Data availability statement

The data and code associated with this study are available on Figshare and can be accessed via the following DOI: [10.6084/m9.figshare.30901532](https://doi.org/10.6084/m9.figshare.30901532)

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Figures

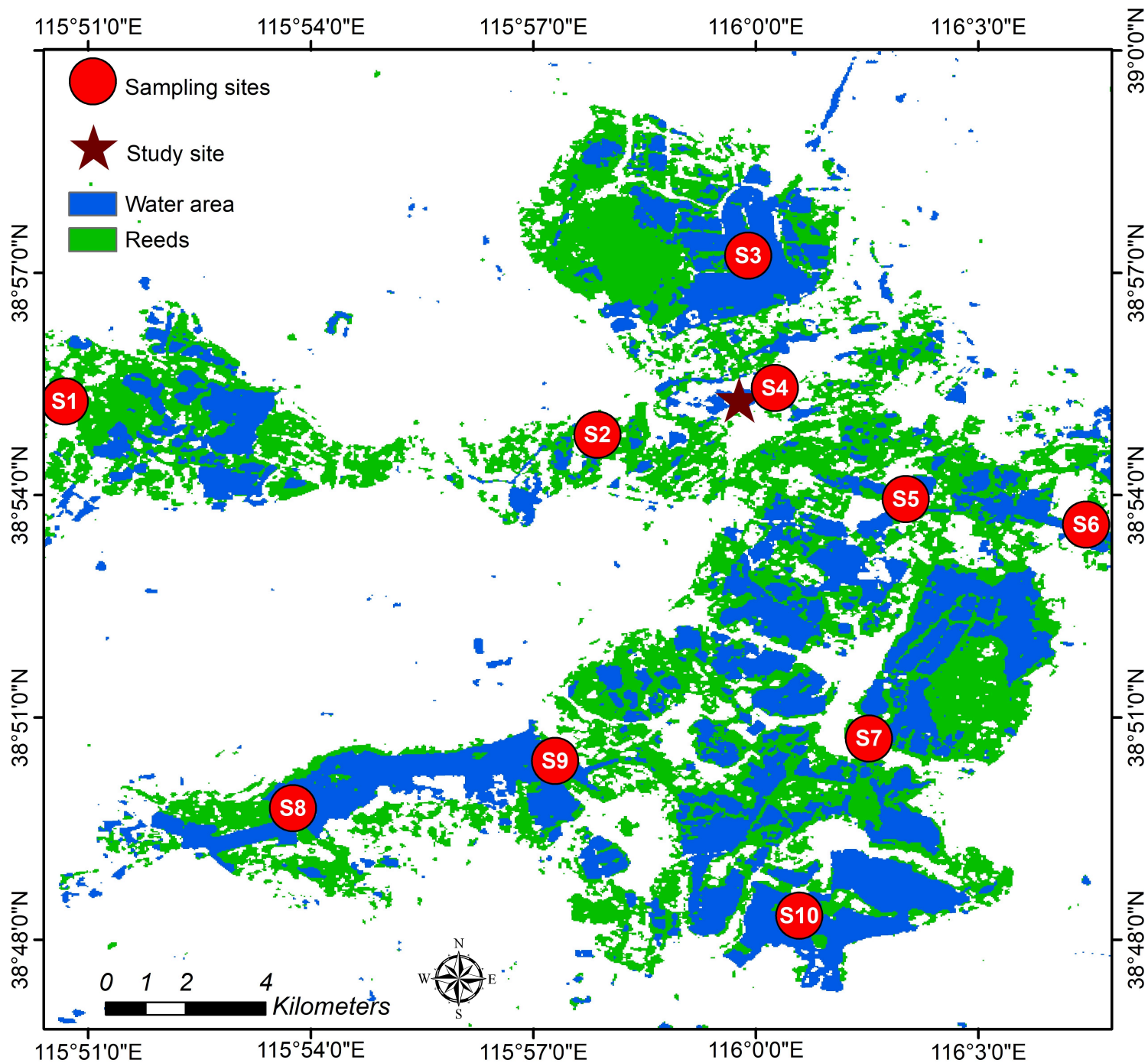


Figure 1

Spatial distribution of the sampling sites in Baiyangdian lake

Note: S1: Zaozhadian, S2: Baodaoleyuan, S3: Shaochedian, S4: Daguanyuan, S5: Guangdian, S6: Zaolinzhuang, S7: Hupidian, S8: Guancheng, S9: Duancun, S10: Caiputai

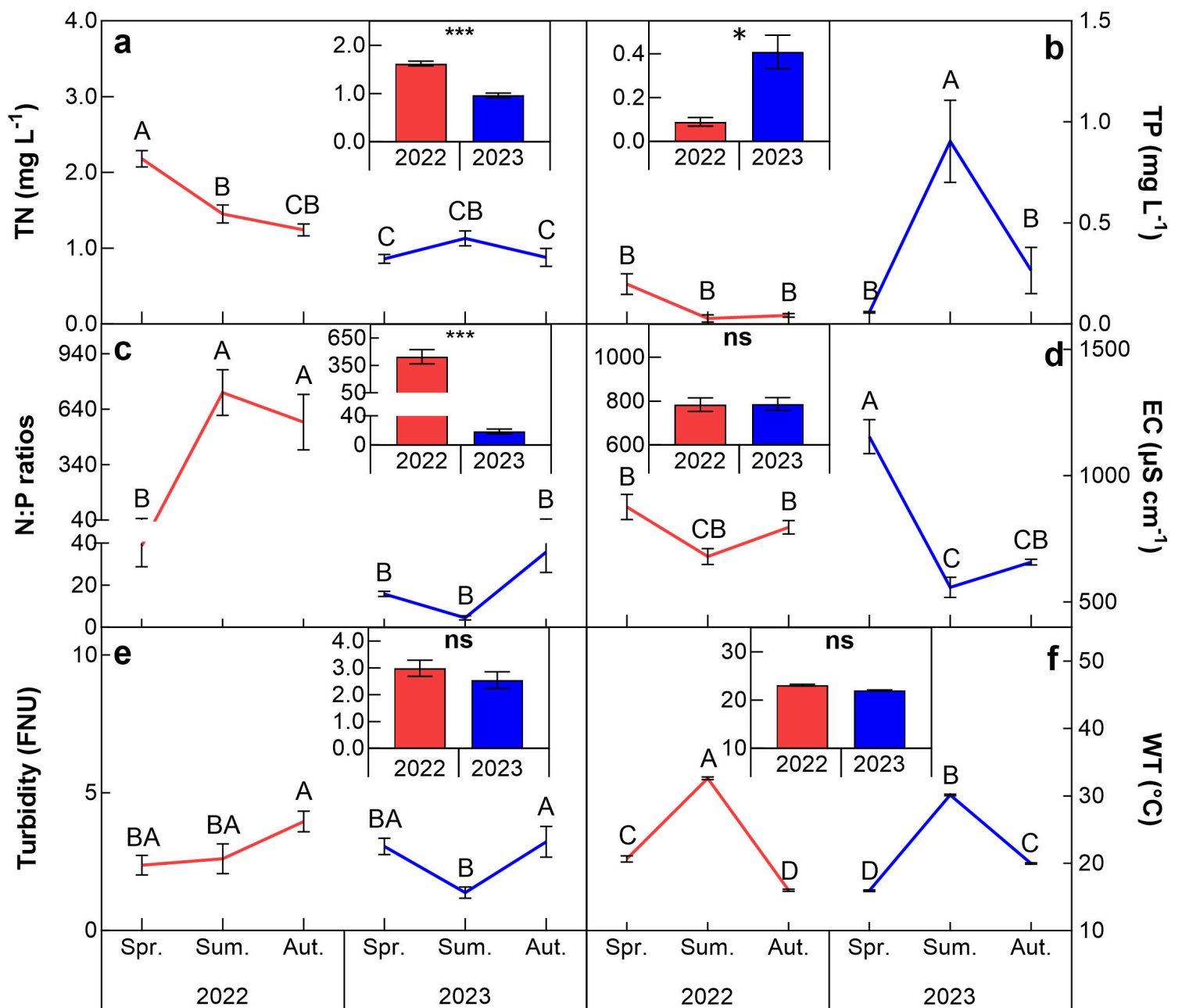


Figure 2

Seasonal and annual (*insets*) mean total nitrogen (TN; **a**), total phosphorus (TP; **b**), N:P ratios (**c**), conductivity (EC; **d**), turbidity (**e**), and water temperature (WT; **f**) across all the sampling sites in Baiyangdian Lake in 2022 and 2023. Different upper-case letters above the error bars indicate statistical significances at $P < 0.05$ (Duncan test) among the three seasons. ns, *, and ***: $P > 0.10$, < 0.05 , and < 0.001 , respectively

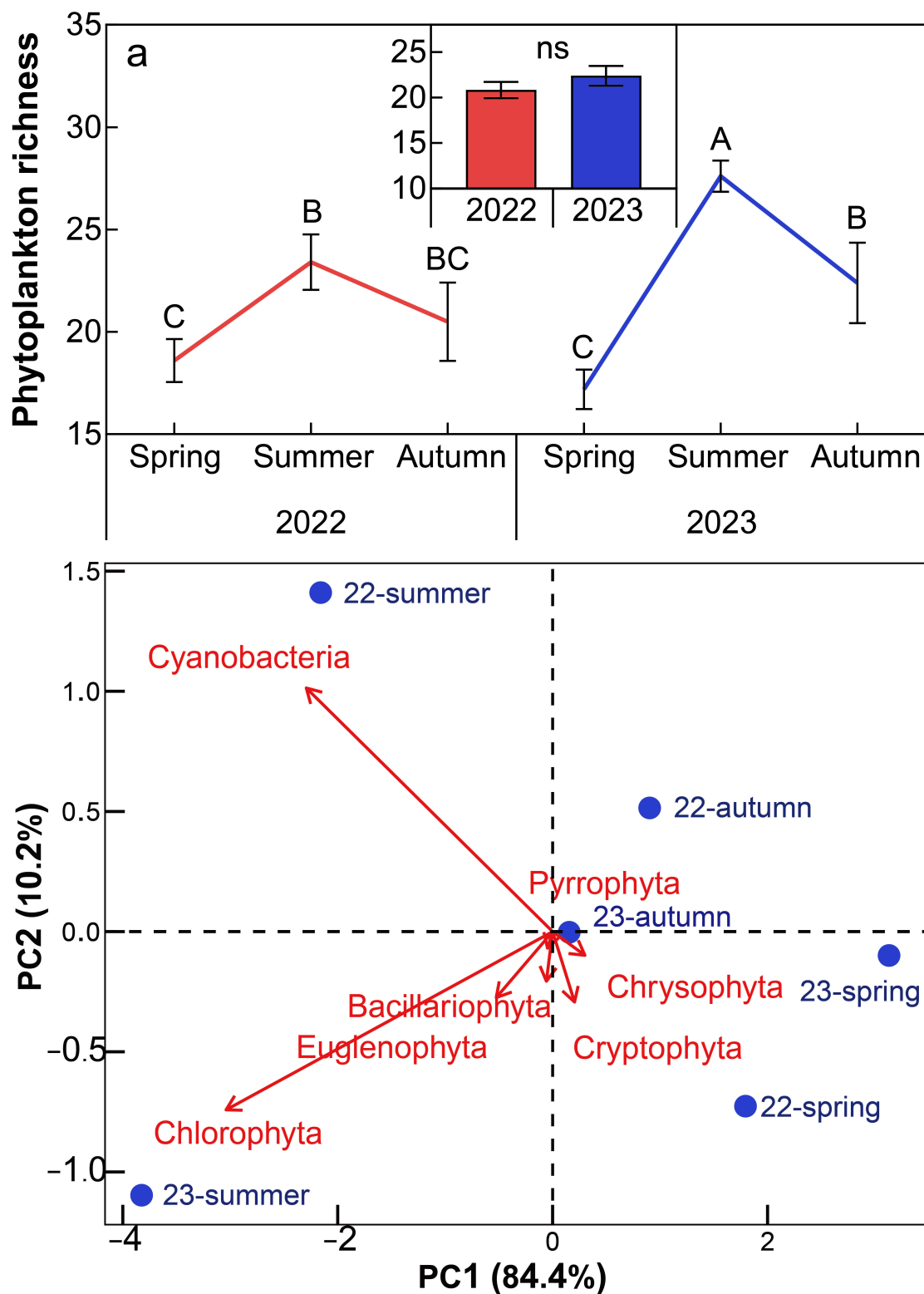


Figure 3

Seasonal and annual (*insets*) mean phytoplankton richness across all the sampling sites in Baiyangdian Lake in 2022 and 2023 (**a**). Different uppercase letters above the error bars indicate statistical significances at $P < 0.05$ among the three seasons. ns: $P > 0.10$. Principal component analysis (PCA) of seasonal variations in phytoplankton richness over the two years (**b**). Each data point indicates seasonal mean value

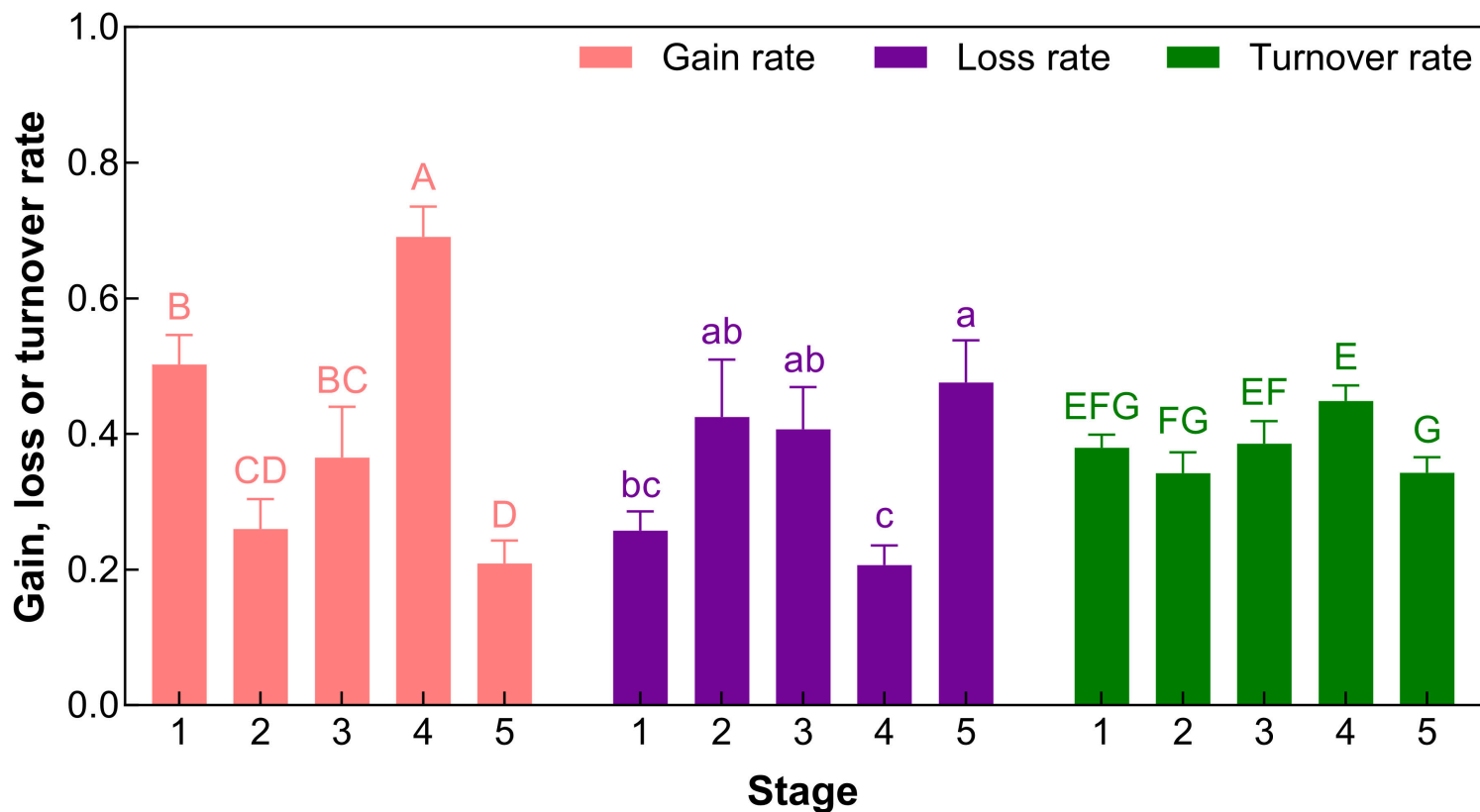


Figure 4

Phytoplankton gain (pink), loss (purple), and turnover (green) rates between two adjacent seasons in 2022 and 2023. Different upper and lowercase letters with the same color above the error bars indicate statistical significances at $P < 0.05$ (Duncan test) among different stages

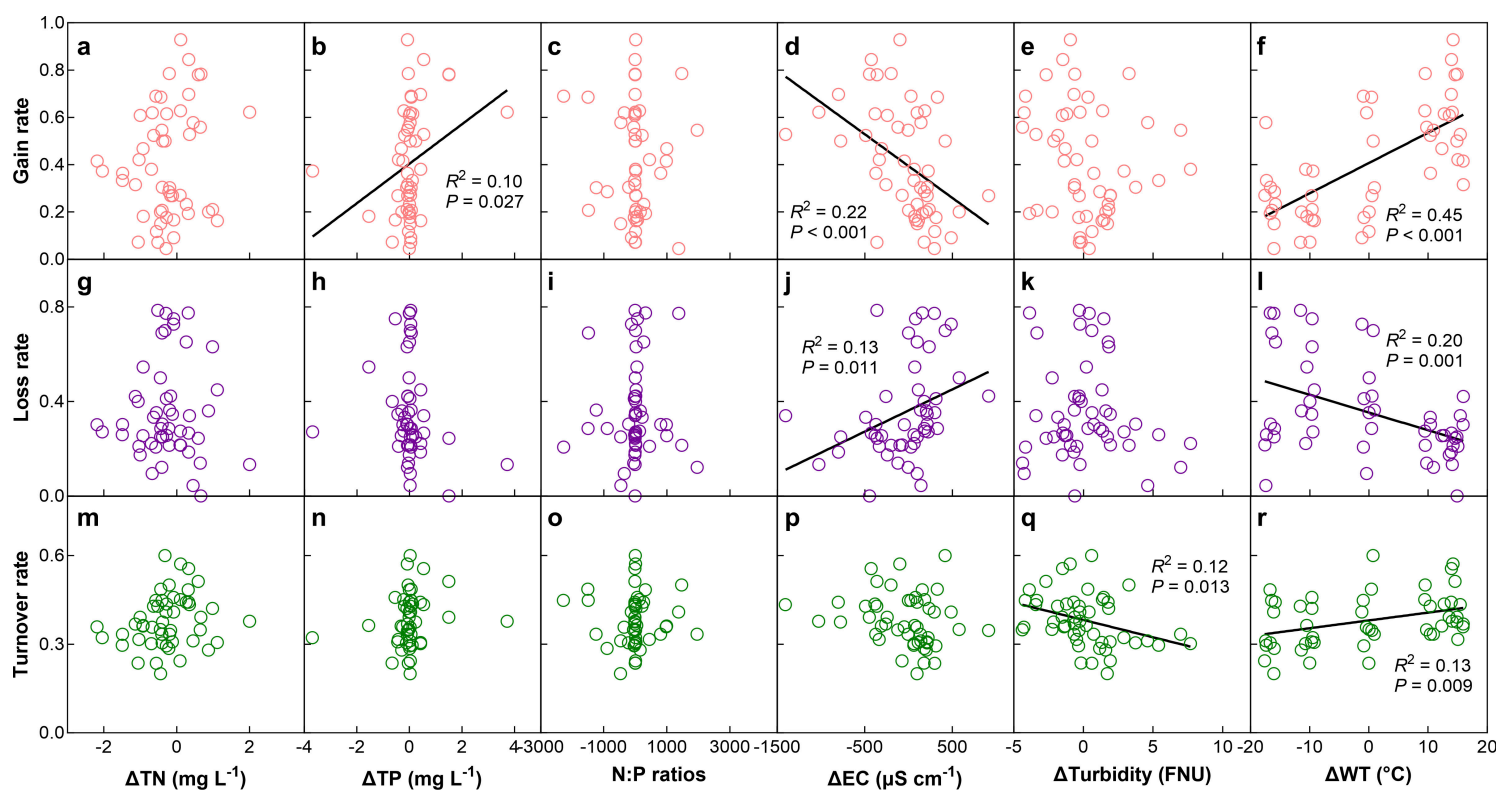


Figure 5

Relationships of phytoplankton gain, loss, and turnover rates with the changes in total nitrogen (Δ TN; **a, g, m**), total phosphorus (Δ TP; **b, h, n**), N:P ratios (Δ N:P ratios; **c, i, o**), conductivity (Δ EC; **d, j, p**), turbidity (Δ Turbidity; **e, k, q**), and water temperature (Δ WT; **f, l, r**) over the two years. Each date point represents the value between two adjacent seasons at each sampling site

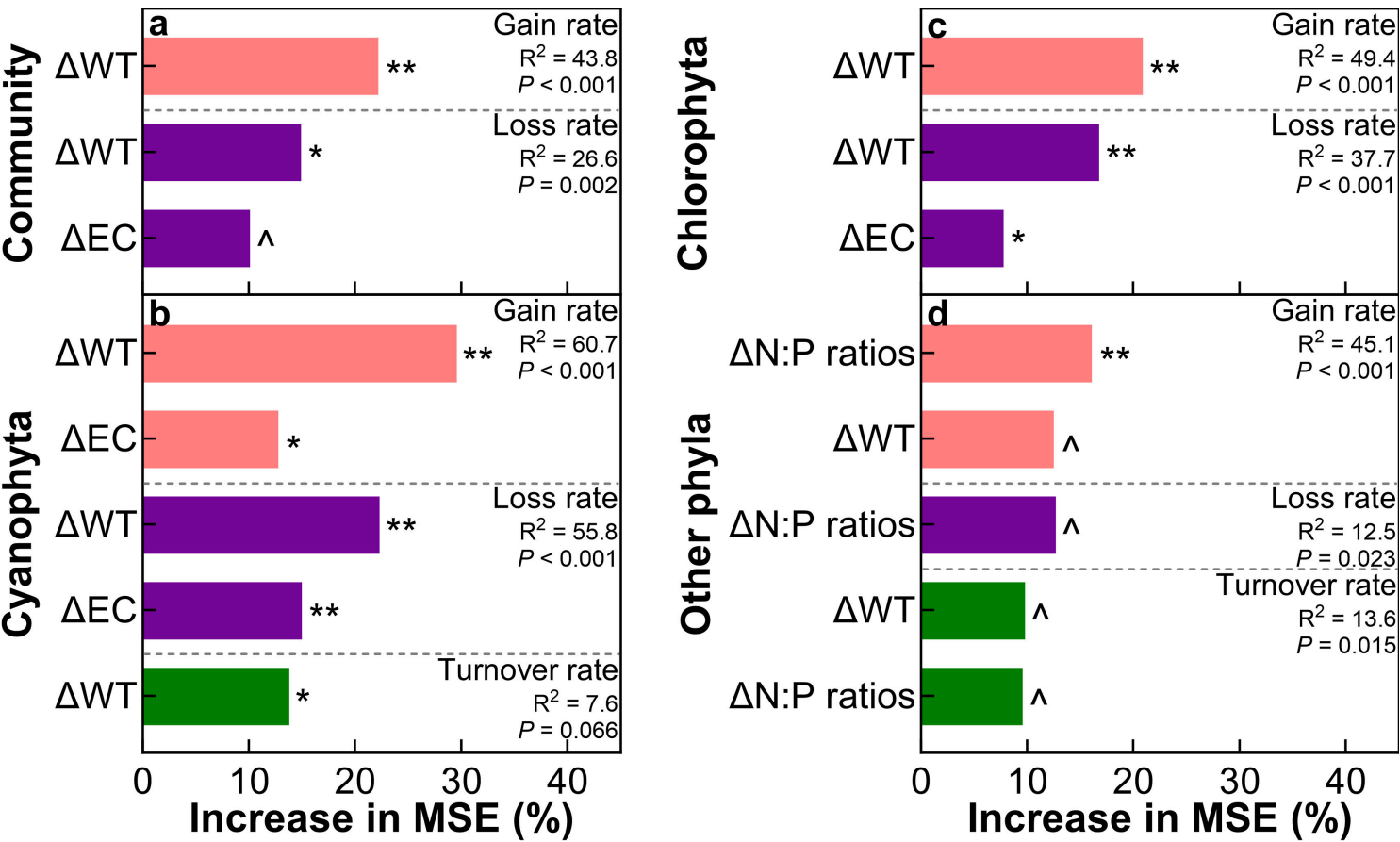


Figure 6

Random forest analyses on the gain, loss, and turnover rates of at community (**a**), Cyanophyta (**b**), Chlorophyta (**c**), and other phyla levels (**d**) on the changes in total nitrogen (Δ TN), total phosphorus (Δ TP), N:P ratios (Δ N:P ratios), conductivity (Δ EC), turbidity (Δ Turbidity), and water temperature (Δ WT) over the two years (Only significant variables were shown). Other phyla include Chrysophyta, Cryptophyta, and Pyrrophyta. Δ value is the differences between two adjacent seasons at each sampling site. ^, *, and **: $P < 0.10$, 0.05 , and 0.01 , respectively

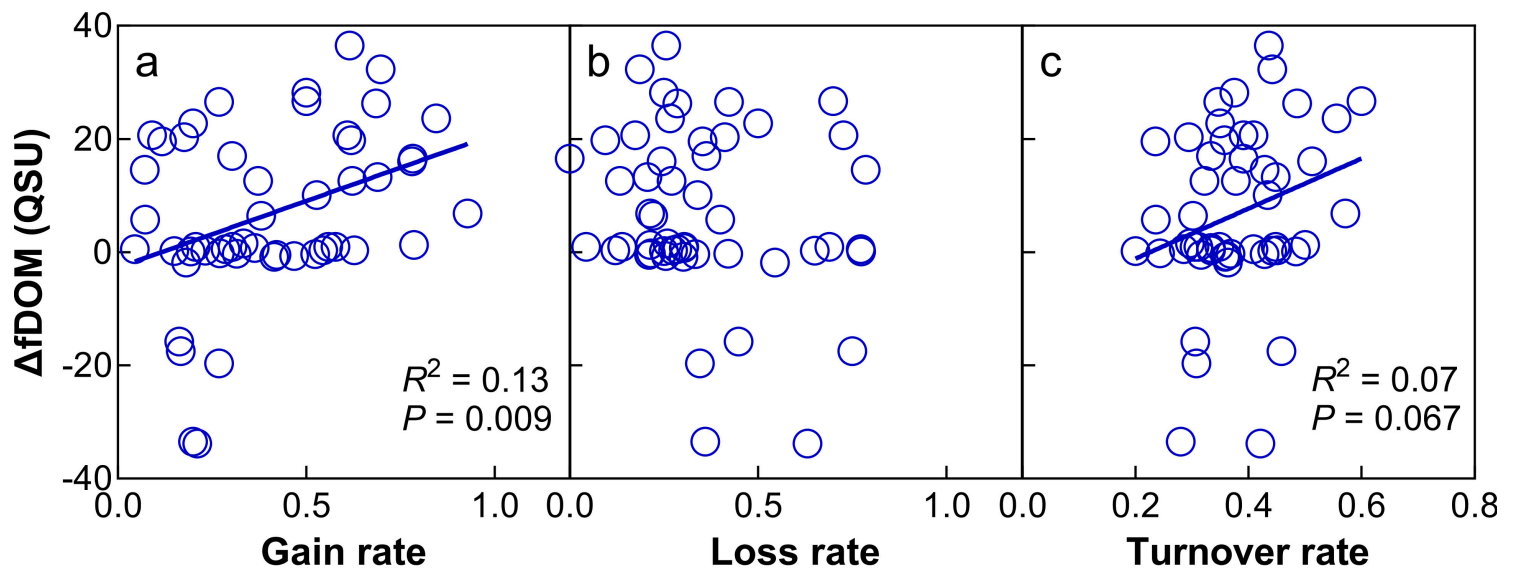


Figure 7

Relationships of the changes in fluorescent dissolved organic matter (fDOM) with phytoplankton gain (a), loss (b), and turnover rates (c) in 2022 and 2023. Each date point represents the value between two adjacent seasons at each sampling site

Supplementary Files

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