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Highlights

- Temporal dynamic network and its structure of phytoplankton were quantified.
- The phytoplankton network architecture was highly dynamic.
- Weak seasonality of phytoplankton network metrics in Taihu Lake, a subtropical lake.
- Eutrophication, warming and decreasing wind speed stabilized phytoplankton networks.
- Human interventions/restoration efforts simplified the phytoplankton networks.
Temporal shifts in the phytoplankton network in a large eutrophic shallow freshwater lake subjected to major environmental changes due to human interventions

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Abstract: Phytoplankton communities are crucial components of aquatic ecosystems, and since they are highly interactive, they always form complex networks. Yet, our understanding of how interactive phytoplankton networks vary through time under changing environmental conditions is limited. Using a 29-year (339 months) long-term dataset on Lake Taihu, China, we constructed a temporal network comprising monthly sub-networks using “extended Local Similarity Analysis” and assessed how eutrophication, climate change, and restoration efforts influenced the temporal dynamics of network complexity and stability. The network architecture of phytoplankton showed strong dynamic changes with varying environments. Our results revealed cascading effects of eutrophication and climate change on phytoplankton network stability via changes in network complexity. The network stability of phytoplankton increased with average degree, modularity, and nestedness and decreased with connectance. Eutrophication (increasing nitrogen) stabilized the phytoplankton network, mainly by increasing its average degree, while climate change, i.e., warming and decreasing wind speed enhanced its stability by increasing the cohesion of phytoplankton communities directly and by decreasing the connectance of network indirectly. A remarkable shift and a major decrease in the temporal dynamics of phytoplankton network complexity (average degree, nestedness) and stability (robustness, persistence) were detected after 2007 when numerous eutrophication mitigation efforts (not all successful) were implemented, leading to simplified phytoplankton networks and reduced stability. Our findings provide new insights into the organization of phytoplankton networks under eutrophication (or re-oligotrophication) and climate change in subtropical shallow lakes.

Keywords: Temporal network, Eutrophication, Complex systems, Climate change, Ecosystem dynamics, Species interactions, Ecosystem stability

1. Introduction

Complex interactions among species, such as competition or symbiosis, play a crucial role in the maintenance of ecosystem structure and functions (Bjorbækmo et al., 2020; Yan et al., 2020; Allen et al., 2022). Previous studies have demonstrated that the more complex interactions among species are, the more stable and multifunctional is the ecosystem (Mougi and Kondoh, 2012; Forster et al., 2021; Yuan et al., 2021; Polazzo et al., 2023). The phytoplankton community plays a vital role in freshwater ecosystems by constituting the base of the pelagic food webs, and its composition and succession affect aquatic biogeochemistry cycles and ecosystem dynamics (Fu et al., 2020; Behrenfeld et al., 2021; Zhang et al., 2021; Douglas et al., 2023). Meanwhile, both eutrophication (or re-oligotrophication) and climate change can have profound impacts on phytoplankton
communities (Deng et al., 2020; Wu et al., 2023) and their interspecific interactions (Frossard et al., 2018; Escalas et al., 2019). As the intensification of eutrophication coupled with the ongoing climate change exacerbate shifts of freshwater ecosystems (Ho et al., 2019; Woolway et al., 2020; Zhou et al., 2022), a holistic understanding of the ecological role of phytoplankton in a changing environment and of the dual effects of eutrophication and climate changes is needed.

The interactions between species can be distilled into a complex network with species as nodes and their relationships as edges, where diverse interactions connect species in a complex network (Delmas et al., 2018; Yeakel et al., 2020). The network theory provides a holistic insight into complex systems (e.g., internet (Barabási and Albert, 1999), brains (Menardi et al., 2022), and societies (Bodin et al., 2019; Wu et al., 2022)) and has been widely used in studies of complex interactions of microorganisms (Barberan et al., 2012; Wang et al., 2023) and molecules (Deng et al., 2012; Meyer et al., 2020) in the last decade. Network parameters can be used to explore the characteristics of species interactions and reveal how these complex interactions change with environmental variations (Escalas et al., 2019; Wang et al., 2019; Felipe-Lucia et al., 2020; Merz et al., 2023). While previous studies on interaction networks are largely based on the assumption that interactions are fixed and constant over time (Blonder et al., 2012; Escalas et al., 2019; Merz et al., 2023), it is unclear how temporally highly dynamic ecosystem components, such as phytoplankton, respond.

Recent studies have suggested that the changes of abiotic environments not only affect the structure of species communities (e.g., species composition) but also their complexity (e.g., number of edges, connectance) of their interaction networks (Escalas et al., 2019; Yuan et al., 2021; Zhang et al., 2022; Li et al., 2023a; Fu et al., 2024a). For instance, climate warming may enhance the complexity and stability of microbial networks (Yuan et al., 2021; Fu et al., 2024a) and reduce the connectance of the plankton network in lakes (Forster et al., 2021; Merz et al., 2023). Adverse environments, such as pollutants, might reduce the network stability by reducing the modularity (Hernandez et al., 2021; Li et al., 2023a), and nutrient increases in lakes have been shown to reduce the connectance of plankton networks (Merz et al., 2023). Therefore, examining the temporally dynamic aspects of ecological networks may provide fresh perspectives on how abiotic environments shape variations in species interactions being affected by ongoing climate changes and human activities (Blonder et al., 2012; Tylianakis and Morris, 2017; Wang et al., 2019; Deutschmann et al., 2023; Fu et al., 2024a).

Lake Taihu, a large, shallow, and eutrophic lake, has been extensively studied since the well-known drinking water crisis occurred in May 2007 (Guo, 2007; Qin et al., 2019). Due to its unique geographical location (see Method section) and continuous long-term monthly monitoring (since 1991), it is one of the most limnologically studied lakes in China (Deng et al., 2019; Zhang et al., 2020). Thus, numerous studies have examined the effects of eutrophication and climate change on
the phytoplankton community composition in the lake over the past decade (Xu et al., 2010; Xu et al., 2017; Zhang et al., 2018; Deng et al., 2020). However, so far research has not been conducted into the network structure of phytoplankton communities and its temporal dynamics. Here, we assembled a long-term (1991-2019) monitoring dataset from eight sites in Lake Taihu to investigate the effects of climate change, eutrophication, and restoration efforts on the temporal dynamics of phytoplankton network complexity and stability. We constructed a temporal network of phytoplankton communities for each site based on “extended Local Similarity Analysis” (eLSA) and sub-networks for each sampling month, and then we measured the indices of network complexity and stability for each sub-network. We tested the long-term variation of network complexity and stability and the relative importance of global, regional and local environments in determining this in three time periods: before (Pre-IRE:1991-2007) and after (Post-IRE:2008-2019) the implementation of intensive restoration efforts (IRE) which has been indicated as a major determinant for the remarkable changes in phytoplankton community composition as well as their feedbacks with external drivers (Qin et al., 2019; Liu et al., 2023; and Fu et al., 2024b), as well as the entire study period (1991-2019). We addressed the following questions: 1) How will the complexity and stability of phytoplankton network in a shallow, eutrophic lake change over time? 2) How will phytoplankton network complexity affect network stability in the context of climate change, eutrophication, and restoration? 3) How do global, regional and local environments affect phytoplankton network properties?

2. Methods

2.1 Study area description

Lake Taihu, the third largest freshwater lake in China, is located in a large, heavily urbanized (>40 million inhabitants), and agricultural catchment (36,500 km²) in the Changjiang (Yangtze) River Delta region (Fig. S1)(Qin et al., 2019). The lake has a surface area of 2,338 km² and a mean depth of 1.9 m. Since the 1990s, the lake has experienced accelerated eutrophication accompanied by algal blooms due to increases in anthropogenic nutrient (e.g., nitrogen and phosphorus) loads (Xu et al., 2017; Qin et al., 2019). In May 2007, a massive bloom overwhelmed the lake's drinking water plants, leaving millions of residents of Wuxi City without potable water for nearly a week, which became a highly publicized drinking water crisis (Guo, 2007). Since this crisis, a series of intensive restoration efforts (IRE), including effluent diversion, stocking of filter-feeding fish, flushing, and dredging, have been implemented. However, these efforts have not achieved the desired outcome (Qin et al., 2019).

2.2 Data collection

A long-term (1991-2019) monthly monitoring dataset on water quality variables and
phytoplankton was compiled by the Taihu Laboratory for Lake Ecosystem Research, Chinese Ecosystem Research Network (TLLER, http://thl.cern.ac.cn/), and relevant data were obtained from the National Ecosystem Science Data Center (http://www.nesdc.org.cn/). The data were collected at eight sites (No. THL00, THL01, and THL03~THL08) covering a range from Meiliang Bay to the center of the lake (Fig. S1). The water quality variables include total nitrogen (TN), total phosphorus (TP), orthophosphate (PO$_4$), nitrate (NO$_3$), ammonium (NH$_4$), dissolved oxygen (DO), Secchi depth (SD), pH, and chlorophyll-$a$ (Chla), while the phytoplankton samples include the biomasses of the species. Descriptions of the survey and measurement methods for all parameters can be found in Deng et al. (2019) and Guo et al. (2019). Monthly data on meteorological variables (1991-2019) came from the Dongshan Meteorological Station, located on Dongshan Island in Lake Taihu, including air temperature (AirTemp), precipitation (Precip), and wind speed (WindSpeed), and were accessed from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/). The monthly anomalies (1991-2019) of El Niño and Southern Oscillation (ENSO) were considered as a proxy of the global climatic oscillation and were obtained from the website of NOAA Physical Sciences Laboratory (https://psl.noaa.gov/data/climateindices/list/).

2.3 Data cleaning

Before analysis, all tested variables were converted into monthly average values, and a total of 29 years and 339 months of data were generated, yielding a total of 2775 data records for local environmental variables across the eight sampling sites and 339 data records on the variables of the meteorological and global climatic oscillation (1991.10~2019.12, one data record for each month). Limited missing values (<5%) were interpolated using the na_seadec function from the imputeTS (Moritz and Bartz-Beielstein, 2017) R-package, which is particularly well-suited to interpolate missing value in time series data. All phytoplankton taxa were aggregated to genus level.

2.4 Temporal network construction

Rare phytoplankton genera were excluded from the analysis, retaining only those with an occurrence frequency >5% (i.e., at least 17 months) of the samples (n = 339). The counts of genera presented in the occurrence tables varied from 29 (site THL08) to 40 (site THL00). Temporal networks for the phytoplankton community were constructed for each site following three steps. First, we combined the phytoplankton biomass data with the tested abiotic water quality data for each site and month to construct a comprehensive association network for all sample months by extended Local Similarity Analysis (eLSA) as reported by Xia et al. (2011). By capturing additional time-dependent
associations, including both local and time-lagged associations, eLSA sheds light on the natural dynamics of biological systems. We performed eLSA on the biomass data with subsampled reads including z-score transformation by using the median and median absolute deviation. $p$-values were estimated by performing a random permutation test (iterations = 2000) for co-occurrences where the comparison's theoretical $p$-values were below 0.05. Bonferroni false discovery rates ($q$-values) for all potential edges (associations) were estimated based on the $p$-values using the `p.adjust` function from the *stats* R-package. Significance thresholds of 0.001 for the $p$ and $q$ values were adopted, as suggested by Weiss et al. (2016) and Krabberod et al. (2022). Second, the EnDED (environmentally driven edge detection) (Deutschmann et al., 2021) program, which combines the method interaction information (with a 0.05 significance threshold and 10000 iterations) and data processing inequality, was applied to detect and remove environmentally driven edges. The links between two genera related to the same environmental driver were removed from the integrative association network, so we ended up with a single static network for each site. Third, following the methodology outlined by Deutschmann et al. (2023), we established the temporal network consisting of 339 monthly sub-networks for each site from October 1991 to December 2019.

2.5 Temporal network properties

As network properties reflect both the complexity and stability of the networks (Newman et al., 2006), we calculated two groups of variables, including seven global network metrics, to characterize the complexity and stability for each monthly sub-network using the `igraph` R package. As complexity is typically associated with the taxonomic diversity, connectivity, and interactions within a community (May, 1972; Deng et al., 2012), we evaluated four network metrics: average degree (A.degree), connectance, modularity, and nestedness as proxies of network complexity (detailed information present in Table S1). For these four metrics, average degree characterizes the average links for each phytoplankton genus, exhibiting a notable positive correlation with both the quantity of nodes (i.e., diversity) and edges (i.e., interactions) (Jamakovic and Uhlig, 2008). Connectance represents the density and proportion of actual edges from all potential links in the network (Wasserman and Faust, 1994). Higher average degree and connectance indicate more nodes and edges. Ecological network complexity can also be expressed by network topological characteristics: modularity and nestedness (Bascompte, 2010; Li et al., 2022). Modularity delineates the degree to which a network is partitioned into distinct modules, wherein species exhibit strong interactions, primarily within their own module and less so with species from other modules (Newman, 2006).
Nestedness is quantified using the NODF metric (nestedness overlap and decreasing fills), representing a pattern of interactions where specialists interact with only a subset of the species that generalists interact with (Almeida-Neto et al., 2008; Mariani et al., 2019).

We calculated three indices: robustness, vulnerability, and persistence, to estimate the stability (detailed information present in Table S1) of each monthly sub-network. The robustness of a network is determined as the proportion of the remaining nodes (genera in this study) in a network after random node removal (Pocock et al., 2012). We calculated the robustness as the proportion of remaining nodes when 50% of the random nodes were removed. Vulnerability measures the effect of a node on system performance if it and all its associated links are removed, which quantifies the relative contribution of the node to the global network efficiency (Deng et al., 2012; Yuan et al., 2021). Persistence is defined as the proportion of coexisting species (of the total number of species) in an ecological regime (Jason et al., 2010; Landi et al., 2018). We thus calculated the persistence of a monthly sub-network as the percentage of nodes (genera) present in the sub-network in total number of species (genera) in the month.

2.6 Statistical analysis

To conduct our analysis, we used two types of datasets as local, regional and global environmental drivers for phytoplankton network complexity and stability. TN, TP, DO, and SD represent local key environmental variables related to phytoplankton growth in lakes (Deng et al., 2016; Zou et al., 2020). Regional meteorological variables included AirTemp, Precip, and WindSpeed, while ENSO was used to represent global climate oscillation. As the implementation of a series of intensive restoration efforts since 2007 (Qin et al., 2019), a sudden shift in phytoplankton biomass and composition (Guo et al., 2019; Liu et al., 2023) and a significantly loosening in the ecosystem causal feedback networks (Fu et al., 2024b) were observed. We thus divided our dataset into three time series: Pre-IRE (1991~2007), Post-IRE (2008~2019), and the entire research period (1991~2019) to compare the changes of phytoplankton network properties before and after the implementation of intensive restoration efforts (IRE) were initiated.

We tested the long-term trends of all variables from each time series using the non-parametric Mann-Kendall trend test (*mk.test* from the *trend* R package. In addition, we separated the variance of all tested variables (environmental drivers and network properties) from each time series into seasonal trends, long-term trends, and residuals using generalized additive models (GAM) by the *gam* function in the *mgcv* R package. In each GAM model, a Gaussian normal distribution was specified
as family for the predictors. The relative contribution and significance of each component to the total variance of the time series were also calculated using the GAM models.

We tested the differences in all variables between Pre-IRE (1991~2007) and Post-IRE (2008~2019) using Wilcoxon test with post-hoc comparisons by the wilcox.test function from the stats R package.

Furthermore, to avoid long-term and seasonal trend effects, in some of the analyses we detrended the data to remove long-term and seasonal trends and standardized the data to enhance comparability among variables (hereafter called detrended data), which improved the stationarity and reduced the autocorrelation of the time series. Here we followed the methods provided by Chang et al.(2020). We used random forests regression (RF) on detrended data of each time series to assess the relative importance of the tested drivers in determining network complexity and stability. For network complexity, we constructed RF complexity models using the local, regional and global environmental drivers as predictors, and for network stability we applied the environmental drivers plus the network complexity parameters as predictors. The potential predictors were randomly resampled to generate 500 un-pruned decision trees. The relative importance of each explanatory variable was evaluated according to the increments in mean standard error (%Inc MSE) for the RF model predictions. Random Forests regression was performed in the randomForest R package.

Finally, we utilized generalized multilevel path models (GMPMs) fitted with detrended data with multiple component models to test multivariate relationships among environmental drivers, network complexity, and stability. Compared to the standard structure equation models, GMPMs can deal with non-normal data and temporal and spatial dependence error structures that occur widely in ecological datasets (Shipley, 2009). Our GMPMs included several hypothesized paths: 1) ENSO affects regional climate variables; 2) regional meteorological drivers affect water quality and phytoplankton networks architecture and stability; 3) local environments (water quality) affect networks architecture and stability; 4) phytoplankton network complexity affects network stability and mediate the effects of environmental on network stability. In each component model within the GMPMs, linear mixed effects models (LMEs) were used to fit the predictors with sites as random variable. We computed $\chi^2$ and Fisher’s C statistics to estimate goodness of model fit and significance. We used the coefficient of determination ($R^2$) for each predictor to assess each component model in the GMPMs. We present the final model with only significant paths, showing standardized path coefficients.

All statistical analyses were performed using R version 4.2.3 (R Core Team, 2023), LMEs were
performed in the *nlme* package, GMPMs were conducted in the *piecewiseSEM* (Lefcheck, 2016) package, and plots were drawn by the *ggplot2* and *ggpubr* packages.

### 3. Results

#### 3.1 Long-term and seasonal trends

TN and TP increased, and SD decreased significantly during the Pre-IRE period (1991-2007), while TN decreased significantly during the Post-IRE (2008~2019) period (Table 1, Fig. S2). For the network metrics, modularity increased and NODF decreased significantly from 1991 to 2019. Furthermore, the network properties showed distinct trends both in the Pre-IRE and Post-IRE periods. Except for connectance (non-significant) and vulnerability (decreased significantly), all network metrics increased significantly during the Pre-IRE period (Table 1, Fig. 1), while connectance decreased significantly and modularity, robustness, and persistence increased during the Post-IRE period (Table 1, Fig. 1).

We found that all the test environmental variables exhibited significant long-term trends; thus, long-term variation explained between 0.6% (SD) and 39.9% (persistence) of the variability in the data (Table 2). By contrast, all the network parameters showed significant and weak seasonal trends, and seasonality only explained 0.5% (vulnerability) to 1.8% (persistence) of the variability (Table 2, Fig. S3).

#### 3.2 Temporal changes in network properties

The network properties exhibited significant differences between the two periods (Wilcoxon test, \( P < 0.05 \)) (refer to Fig. 2, Table S2). For instance, A.degree, modularity, NODF, robustness, and persistence showed higher values and lower vulnerability during the Pre-IRE period than during the Post-IRE period (1991-2007).

We also found that the number of edges (species interactions) frequently varied (lost, gained, and preserved compared to the previous month) between two consecutive monthly sub-networks (Fig. 3A, Fig. S4). In addition, specific edges and nodes experienced significant shifts in number or degree between Pre-IRE and Post-IRE. Specifically, some dominant edges (e.g., *Aulacoseira* vs. *Microcystis*) during Pre-IRE were lost during Post-IRE (Fig. 3B, Fig. 4, Fig. S5), and some hub-nodes (e.g., SP18: *Closteriopsis*) occurred in the Pre-IRE period but disappeared during Post-IRE, while new hub-nodes (e.g., SP4: *Ankistrodesmus*) appeared subtly. The degree of nodes generally decreased (Fig. 3C, Fig. 4, Fig. S6).

#### 3.3 Contribution of environmental drivers to network property variability
During the Pre-IRE period (1991-2007), the RF models contributed 16% to 51% of the total variance of network complexity and 64% to 96% of network stability (Fig. 5A, Fig. 6A). TN was the most important predictor of network complexity, and A.degree was most important for network stability. During the Post-IRE period (2008-2019), the RF models contributed 12% to 28% of the total variance of network complexity and 72% to 93% of network stability (Fig. 5B, Fig. 6B). ENSO was the most important predictor of A.degree, followed by precipitation and wind speed. Wind speed was the most important predictor for connectance and modularity. ENSO was the most important driver of NODF, followed by wind speed and air temperature. A.degree remained the most important predictor of network stability during the Post-IRE period.

During the entire period (1991-2019), RF models contributed 22% to 48% of the total variance of network complexity and 72% to 96% of network stability (Fig. 5C, Fig. 6C). Total nitrogen (TN) was the most important driver of network complexity, with an Inc MSE value of >50% (Fig. 5C), and A.degree was the most important predictor of network stability with all Inc MSE values >70% (Fig. 6C). Additionally, ENSO was the secondary most important driver of network complexity.

3.4 Multivariate relationships among environmental drivers, network complexity, and stability

The stepwise model selection process linking phytoplankton community network stability to two groups of environmental variables (climate and water quality) and network complexity variables led to a final path model that was well supported by the detrended data (Fig. 7, $\chi^2 = 33.81$, $d.f = 48$, $P = 0.94$). The model explained 61% of the variation of robustness (Fig. 7), 46% of vulnerability (Fig. S7A), and 92% of persistence (Fig. S7B). Except for the weak direct impact of wind speed and air temperature on network stability, all environmental drivers affected the network stability indirectly through network complexity. Specifically, TP and TN changed NODF and modularity. The climate drivers affected network stability indirectly, mainly by water nutrients (TN, TP). Additionally, TN had a positive effect on network complexity.

4. Discussion

The dynamic changes in the architecture of species interaction (e.g. competition, mutualism, co-occurrence) networks are crucial for determining the complexity and stability of communities (Mougi and Kondoh, 2012; Yuan et al., 2021). By using a long-term dataset covering 29 years on Lake Taihu, we constructed a temporal network comprising 339 monthly sub-networks based on extended Local Similarity Analysis (eLSA) and quantified the extent to which the phytoplankton community network changed over time. The network parameters of phytoplankton showed significant long-term trends,
with marked shifts in network architecture and complexity among consecutive time periods (at least monthly). The result indicated that the phytoplankton networks in the lake varied in terms of gain and loss of genera, as well as their interactions, and our observed reorganization of phytoplankton networks is consistent with previous findings of strong dynamic changes of biotic networks with environmental changes (Thompson and Gonzalez, 2017; Deutschmann et al., 2023).

We found significant but weak seasonality in the metrics for the phytoplankton network compared with observations from north temperate freshwater lakes (Fu et al., 2020; Forster et al., 2021; Deutschmann et al., 2023; Fu et al., 2024a), likely reflecting effects of higher temperatures in winter (Khaliq et al., 2024). In north temperate lakes, a seasonal behavior with yearly periodicity of species interaction networks has been shown to be tightly associated with the seasonal succession of species driven by the seasonal variation of temperature (Giner et al., 2019; Fu et al., 2020; Forster et al., 2021; Deutschmann et al., 2023). Supporting our findings, recent studies on the long-term succession of phytoplankton communities in Lake Taihu showed weak seasonality trends (Zhang et al., 2018; Liu et al., 2023), and they suggested that wind speed was a major driver of temporal succession and that other potential drivers (e.g., light availability) could also be important in determining the seasonal dynamics of the phytoplankton community, especially after 2007 (Zhang et al., 2018; Deng et al., 2020). This concurs with the observed dominant role of wind speed in determining phytoplankton biomass (Fu et al., 2024b) as well as network complexity (especially after 2007) and stability in our study. Furthermore, the zooplankton grazing pressure, identified as a major biotic force in stabilizing the seasonal succession of phytoplankton communities in north temperate lakes (Fu et al., 2021), is typically substantially lower in subtropical than in temperate lakes due to higher fish predation (Jeppesen et al., 2020; Rao et al., 2023), and this likely contributes further to the weak seasonality in Lake Taihu.

The path model revealed that long-term eutrophication stabilized the phytoplankton network mainly by enhancing the average degree. This suggests that greater diversity (A.degree, i.e., number of phytoplankton genera) would largely strengthen the resistance of the network to environmental fluctuations, which is consistent with the results of Thébault and Fontaine (2010), who demonstrated that increased diversity promotes mutualistic network resilience. Previous studies on microbial networks showed that environmental stress reduced network stability by decreasing species diversity (Hernandez et al., 2021; Li et al., 2023a). We found that eutrophication fostered a conducive environment for phytoplankton, leading to increased phytoplankton diversity (i.e., number of nodes
and average degree), which stabilized the phytoplankton networks. Notably, our analysis revealed a significant decrease in phytoplankton network complexity (average degree, nestedness) and stability (robustness, persistence), as well as antagonistic interactions (negative links, Fig. 1, Fig. 3, Fig. S5) after 2007 when a series of intensive restoration efforts (IRE) were implemented (Guo et al., 2019; Deng et al., 2023; Fu et al., 2024b). Our results suggested that the major shifts in TN exerted dominant controls on phytoplankton network complexity and thus stability across the studied periods. This is supported by recent findings from the lake that a sudden shift in phytoplankton biomass and composition (a sudden shift from green algae and flagellate co-dominance to dominance of diatoms) was strongly coupled with a sudden decrease in N (ammonium) concentrations around 2007 (Liu et al., 2024 Figure 1&2). Importantly, we found that the average degree and abundance of core genera (with high ranks of degree in the network) as well as the link edges also showed abrupt shifts in 2007 (Fig. 3, Fig. 4, Fig. S8), providing a mechanistic explanation for the temporal shifts in the phytoplankton network. The major changes in the phytoplankton network around 2007 occurred in association with major human interventions, including an increase in the water level due to the operation of the Water Diversion from Yangtze River to Lake Taihu project (Dai et al., 2020) (Fig. S9), a reduction in the discharge of industrial waste water and fertilizers application from the lake catchment (leading especially to a lower N concentration in the lake), and a reduction in conductivity (Qin et al., 2021). Moreover, massive repeated stocking of Bighead Carp (Hypophthalmichthys nobilis) and Silver Carp (Hypophthalmichthys molitrix), which failed to mitigate algae expansion as aimed for, led to less zooplankton grazing on phytoplankton (Mao et al., 2020) and thus enhanced the biomass and density of phytoplankton (Mao et al., 2020; Liu et al., 2023). This weakened top-down control on algae by zooplankton may contribute to stabilizing the phytoplankton network by indirectly increasing phytoplankton diversity. In addition, a recent study on 20 Danish lakes showed that the phytoplankton network tends to be more stable during algae blooms (Fu et al., 2024a) and that released top-down control on zooplankton by fish (i.e., intensify the top-down control of zooplankton on phytoplankton) after nutrient loading reduction caused significant shifts in zooplankton communities, potentially also leading to higher phytoplankton richness and higher network stability (Jeppesen et al., 2005; Fu et al., 2024a). The restoration attempts, including effluent diversion, flushing, and fish stocking in Lake Taihu (Qin et al., 2021) might have simplified the phytoplankton networks and reduced their stability through both a trophic cascade (released grazing control of zooplankton on phytoplankton due to fish stockings) and bottom-up (N reduction) forces. While the
top-down effects on phytoplankton biomass and diversity have received much attention, their controls on phytoplankton networks warrant further research.

Our findings indicate that both global and regional climate variables significantly affect network stability of phytoplankton, mainly through direct or indirect paths. Global climate change (e.g., ENSO) appears to stabilize the phytoplankton network indirectly through its influence on regional meteorological variables like rainfall and wind speed. In Lake Taihu, Qin et al. (2021) indicated that ENSO increased the extreme climate events (regional climate anomalies) and exacerbated eutrophication and aggravated algae blooms, which could stabilize the phytoplankton network according to our previous study (Fu et al., 2024a) and this research. Our path model also showed that increasing in global climatic oscillation led to decreased wind speed, which could greatly intensify internal nutrient cycling and thus interactions between phytoplankton and nutrients in Taihu Lake (Deng et al., 2018). This might cause great complementary nutrients usage as well as niche differentiation (modularity in a network), and thus enhance community diversity (A-degree in a network), increasing network stability of phytoplankton. However, the long-term change of regional meteorological variables (warming and decreasing wind speed) directly enhanced the phytoplankton network stability to a certain extent. Warming and decreasing wind speed stabilize the water column and thereby provide a favorable environment for phytoplankton growth (Deng et al., 2018; Li et al., 2023b) which likely then stabilized the phytoplankton communities and their associated networks. In addition, stronger bottom-up control in warmer lakes could further enhance the stability of plankton networks (Merz et al., 2023). A decrease in wind speed may not only affect the cohesion of phytoplankton communities (less wind drift, Deng et al., 2020), but also release its controls on the causal linkages between phytoplankton and environmental drivers (Fu et al., 2024b), both of which would influence the temporal dynamics of phytoplankton network.

5. Conclusion

Using a 29-year (339 months) long-term dataset of phytoplankton from a eutrophic shallow lake, we constructed a temporal network comprising 339 monthly sub-networks, which was quantitatively evaluated to the extent where phytoplankton networks change across time. Our study provided a holistic view on how the phytoplankton network responds to environmental fluctuation in terms of temporal dynamic shifts in their topography, complexity, and stability. The results create new insights into the reorganization of phytoplankton networks under re-oligotrophication and climate change in a subtropical lake, and they revealed that the network architecture was highly dynamic, showing
frequent gain and loss of nodes (genera). We found that the stability of phytoplankton networks increased with average degree and nestedness and decreased with connectance and that it was mainly determined by average degree. Our findings highlighted that eutrophication and climate change (warming and decreasing wind speed) stabilized the phytoplankton network in Lake Taihu, especially during bloom periods. Although the major environmental changes caused by human interventions in Lake Taihu simplified the phytoplankton networks, phytoplankton communities have the potential to re-establish the network complexity and stability through increased node degrees, link edges, and modularity (Fig. 1, Fig. S10). Thus, we are confident that the present eutrophication restoration efforts, especially the reduction of nutrient loading, are effective and should be continued. In addition, some alternative measures aiming for targeted removal of core nodes (genera, e.g., *Cryptomonas*) that form algae bloom, to destabilize phytoplankton networks stability would be beneficial.

**Acknowledgements**

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**Competing financial interests**

The authors declare no competing financial interests.

**References**


Behrenfeld, M.J., Boss, E.S. and Halsey, K.H. 2021. Phytoplankton community structuring and succession in a


local similarity analysis (eLSA) of microbial community and other time series data with replicates. BMC Syst. Biol. 5(2). https://doi.org/10.1186/1752-0509-5-S2-S15


Table 1 Mann Kendall trend test results of variables in different periods.

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<td>P</td>
<td>tau</td>
<td>P</td>
<td>tau</td>
<td>P</td>
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<td>0.000</td>
<td>-4.032</td>
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<td>Total phosphorus (TP)</td>
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<td>0.107</td>
<td>0.915</td>
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<td>0.780</td>
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<td>0.842</td>
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<td>0.418</td>
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<td>Connectance</td>
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<tr>
<td>Robustness</td>
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<td>1.263</td>
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<td>-0.523</td>
<td>0.601</td>
<td>-0.677</td>
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Table 2 Explained variance (Var.exp.) and significance (P) of seasonal and annual trends from generalized additive models for each variable.

<table>
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<tr>
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<td>0.008</td>
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<tr>
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<td>0.164</td>
<td>0.000</td>
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<td>Network stability</td>
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<tr>
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<td>0.000</td>
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<td>0.070</td>
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Fig. 1 Long-term trends of network complexity (A) and stability (B) tested by Mann-Kendall $\tau$ test, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, ns: not significant. The vertical dashed line represents the division by December 2007.

Fig. 2 Differences in network complexity (A) and stability (B) between two distinct periods (Pre-IRE: 1991-2007, Post-IRE: 2008-2019) as tested by wilcox.test.
Fig. 3 Dynamics of temporal network results from site THL04. A: Variation in the number of edges compared to the last month (red: lost, black: kept, blue: gained). B: Changes in edges (interactions); each row represents a specific edge, red indicates positive links, blue indicates negative links. C: Changes in node degree; each row represents a specific node (genus). No data on phytoplankton species from January to October in 1991 and 2004.
Fig. 4 Temporal dynamics of the degree of nine core genera (nodes). No data on phytoplankton species from January to October in 1991 and 2004.
Fig. 5 Random Forest analysis showing the mean predictor importance of each environmental driver in determining the network complexity of the phytoplankton community for three times series: A. Pre-IRE(1991-2007), B. Post-IRE(2008-2019), C. the entire research period (1991-2019).
Fig. 6 Random Forest analysis showing the mean predictor importance of each environmental driver in determining the network stability of the phytoplankton community for three times series; A. Pre-IRE: 1991-2007, B. Post-IRE: 2008-2019, C. the entire research period (1991-2019).
Fig. 7 Generalized multilevel path models showing multivariate relationships among environmental drivers (first to third row), network complexity (fourth and fifth row), and network stability (sixth row): robustness. ENSO: El Niño and Southern Oscillation, AirTemp: air temperature, TP: total phosphorus, TN: total nitrogen; A.degree: average degree, NODF: nestedness. Blue arrows represent positive effects and red arrows negative effects. Only significant paths are shown. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$
Graphical abstract

Declaration of interests

☑ 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.