

Lake sediment DNA reveals the response of phytoplankton to warming

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ABSTRACT

Phytoplankton can be used as an indicator of aquatic ecological health and to monitor nutrient levels, which are the basis of formulating lake management strategies. However, long-term phytoplankton succession and their response to environmental changes remain poorly understood due to the paucity of ecological monitoring data and the limitation of the traditional paleolimnological indicators used to identify non-fossilized phytoplankton groups (e.g. Cyanobacteria). In this study, we used both paleolimnological and 23S rRNA gene metabarcoding analyses of phytoplankton (eukaryotic algae and cyanobacteria) to probe the impacts of environmental changes on the phytoplankton dynamics over the past millennium in this deep, fault-bounded, eutrophic Lake Chenghai on the Yunnan–Kweichow Plateau, southwest China. The phytoplankton community succession was observed in four periods, including the Medieval Warm Periods (1000s–1400s), the Little Ice Age (1400s–1800s), the early Current Warm Period (1800s–1950s) and the Anthropocene (1950s–present). Specifically, Cyanobacteria dominated during the warm periods, whereas Chlorophyta was abundant during the cold period. Bloom-forming or cyanotoxin-producing taxa (e.g., *Aphanizomenon*) have mainly occurred in recent decades. Co-occurrence network analysis indicated that the community structure became complex and that the diversity has increased markedly during the Anthropocene. Multiple statistical analyses demonstrated that temperature was a key driver controlling phytoplankton succession on the decadal time scales and that anthropogenic warming may have led to an increase in the relative abundance of bloom-forming cyanobacterial taxa in recent decades. These findings further suggest that any efforts to reduce nutrients—and the effects of these efforts—will be offset, and that cyanobacterial blooms may continue to increase in Lake Chenghai if anthropogenic warming conditions continue.

1. Introduction

Not only does phytoplankton affect the abundance, diversity, and functions of a lake ecosystem, it also regulates the ecosystem's response to climate change by mediating the biogeochemical processes the lake (Boyce et al., 2010; Buitenhuis et al., 2013; Spaak et al., 2017). Global lake ecosystems are experiencing continuous degradation in the Great Acceleration period (also called the “Anthropocene”; Huang et al., 2022; Waters et al., 2016), with a worldwide expansion of algal blooms and an apparent loss of aquatic biodiversity (Ho et al., 2019; Qin et al., 2022).

Under the scenario of continuing global warming, outbreaks of algal blooms could be more frequent, and their control will become more difficult because warming could reduce the vertical mixing in lakes, affect the patterns of precipitation, and lengthen the optimal growth periods of some taxa (Huisman, 2018; Qin et al., 2022). The occurrence of algal blooms results from the long-term stress imposed by multiple environmental factors, including temperature, nutrients, solar radiation, and hydrology (Naylor et al., 2021). Therefore, we must comprehensively analyze phytoplanktonic succession processes and their driving mechanisms from a historical perspective in order to assess the future

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responses of lake phytoplankton to climate change.

Previous studies have investigated phytoplankton community structures and their driving mechanisms on short time scales via the analysis of monitoring data (Schindler et al., 2008), controlled experiments (Chapra et al., 2017), ecological model predictions (Gland et al., 2021) and remote sensing (Ho et al., 2019). Remote sensing analyses results have shown that global warming is contributing to a worldwide spread of phytoplankton blooms and promoting the dominance of cyanobacteria in phytoplankton community (Ho et al., 2019; Monchamp et al., 2018). In contrast, many studies have highlighted the temporal changes occurring in the compositions and biomass of phytoplankton communities in response to changes in nutrient composition (Schindler et al., 2008; Salmaso, 2010; H.X. Zhang et al., 2021). For instance, an analysis of phytoplankton data covering 37 years from a small lake (Lake 227, mean depth 4.4 m and maximum depth 10.0 m) in northwestern Ontario, Canada, indicated that the phytoplankton community structure underwent successional progression of Cynobacteria→diatoms→Chlorophyta as the nitrogen (N)/phosphorus (P) ratio increased (Schindler et al., 2008). Based on a global analysis of 573 lakes, Qin et al. (2020) demonstrated briefly that the concentrations of N and P affect the phytoplankton assemblages in a way that is closely related to lake morphology, including water depth. For example, changes in nutrient concentrations have the greatest effect on phytoplankton communities in some deep lakes at the southern end of the Central Alps (Salmaso, 2010). These studies suggested that the human-induced changes in the nutrients (N and P) input to lakes and climate change are the main factors driving changes in phytoplankton community structures, although the relative importance of environmental factors, such as nutrients and temperature, might be site-specific and may depend on the spatial and temporal resolution of the analysis.

The Yunnan-Kweichow Plateau, situated on the southeastern corner of the Qinghai-Tibet Plateau in southwestern China, contains abundant freshwater resources and abundant biodiversity. Most of the lakes in this region are very deep and steep, with little outflow (Hillman et al., 2016). Lake Chenghai, a typical deep, fault-bounded lake in this region, is currently suffering from eutrophication and frequent algal blooms (Dong et al., 2012). Lake Chenghai is also one of the three lakes in the world that naturally produce *Spirulina*, thus raising the populations of Yongsheng county in Yunnan province. Several studies have investigated the temporal-spatial distribution of the phytoplankton diversity and community structure in Lake Chenghai (Cao et al., 2020; Dong et al., 2012; Yan et al., 2019), but these studies have mainly addressed the seasonal and annual dynamics of the cyanobacterial community over the past few decades. Therefore, it remains unclear how the dynamics of the phytoplankton community have changed over the past millennium, which includes the Medieval Warm Period (MWP, 930–1400s), Little Ice Age (LIA, 1400s–1800s), and Current Warm Period (CWP, 1800s–2000s) (Mann and Jones, 2003), and the newly proposed “Anthropocene” (1950s–present; Voosen, 2022). This omission limits our understanding of the characteristics and driving factors of phytoplankton community under both climate and human activity pressures, especially before and after the Great Acceleration.

Lake sediments provide insights into environmental changes and associated variations in the composition of biological communities over time via analyses of physical and chemical indicators, fossils, and biomolecules (Fordham et al., 2020; Wang et al., 2012). Next-generation DNA sequencing technology has recently facilitated the DNA-based analysis of ancient ecology, thus providing long-term information on the diversity and compositions of different species (Bálint et al., 2018; Capo et al., 2021). Sediment DNA analyses also provide an opportunity to investigate bio-invasions (Ficetola et al., 2018), the interactions between taxa at different trophic levels (Ibrahim et al., 2020), and ecosystem restorations (Capo et al., 2021). Furthermore, DNA analyses do not require fossil remains in the sediment; therefore, they allow important components of phytoplankton (like cyanobacteria) to be identified with relatively high taxonomic resolution, which cannot be

provided by using traditional biological indicators. For instance, an analysis of ancient sedimentary DNA showed that the diversity of cyanobacteria in European lakes over the past ~100 years was affected by nutrients cycling and warming (Monchamp et al., 2018). Therefore, a next-generation sequencing analysis of sediment DNA could effectively reconstruct an entire phytoplankton community over longer (decadal-centennial scale) time scales and probe the long-term evolutionary mechanisms underlying the ecological and environmental changes in lakes.

In this study, an integrative analysis of ancient sediment DNA and paleolimnology was used to probe the environmental dynamics of the phytoplankton community in a deep lake over the past millennium. The primary goals of this study were (1) to reconstruct the phytoplankton community succession over the past millennium; (2) to investigate shifts in the co-occurrence network pattern of the phytoplankton community over the past millennium; and (3) to identify the key environmental factors governing phytoplankton community dynamics in a deep and eutrophic lake in the subtropical region at the decadal-centennial scale.

2. Materials and methods

2.1. Study background and sediment cores sampling

Lake Chenghai lies in the subtropical region, and has a surface area of 78.8 km², a catchment area of 318 km², and an average water depth of 20 m (Fig. 1). The lake basin is steeply sloping, and water depth varies by up to 20 m within <0.5 km (Hillman et al., 2016). Consequently, a slight change in the total water volume could lead to a considerable variation in the lake level (Yan et al., 2020). During the period 1960–1990 CE, a large number of pumping stations were gradually established around Lake Chenghai. These stations draw large amounts of water from Chenghai each year and are partly responsible for the rapid decline in the lake level of 0.2 m/year.

The watershed of Lake Chenghai is one of the areas with the most serious soil erosion in Yunnan Province (Zhang et al., 2018). Shrubland, forest land, grassland, dryland, paddy field, rural residential land, and urban land are the predominant land types in the catchment (Fig. 1). In 1942 CE, a large number of people migrated to the Lake Chenghai basin and continue to live there, and the lake has become eutrophic with the increase in agricultural fertilization (Yan et al., 2019).

There are no outflow rivers around the lake, so it is supplied primarily by runoff from the catchment area (~318 km²) and by underground water (Cao et al., 2020). According to the data from Lijiang Meteorological station (in 1954–2020 CE), the annual temperature varies between 6 °C and 21 °C, and the total annual precipitation around the catchment is about 955 mm, with over 80% of precipitation falling in summer.

Several parallel sediment cores were collected from the center of Lake Chenghai using a UWITEC gravity sampler (Fig. 1). The cores were immediately placed in a mobile refrigerator (−20 °C) and shipped back to the laboratory. Upon arriving at the lab, the cores were kept at −86 °C until further analysis. One sediment core was sub-sampled every 1 cm using a core cutter, and the subsamples were used for geochemical/geophysical, and chronological analyses. The other core was also separated into 1 cm sections, and only the heart portion of each subsample was used for the analysis of ancient sedimentary DNA.

2.2. Sediment core chronology and geochemical-geophysical measurements

The sediment core's age distribution was determined using ¹³⁷Cs–²¹⁰Pb and accelerator mass spectrometry (AMS) ¹⁴C analyses (Yan et al., 2020). Geochemical and geophysical parameters were used to reconstruct the past environmental changes. The total organic carbon (TOC), δ¹³C_{org}, total nitrogen (TN), and C/N ratio of the sediments were determined as described by Yan et al. (2020). The total phosphorus (TP)

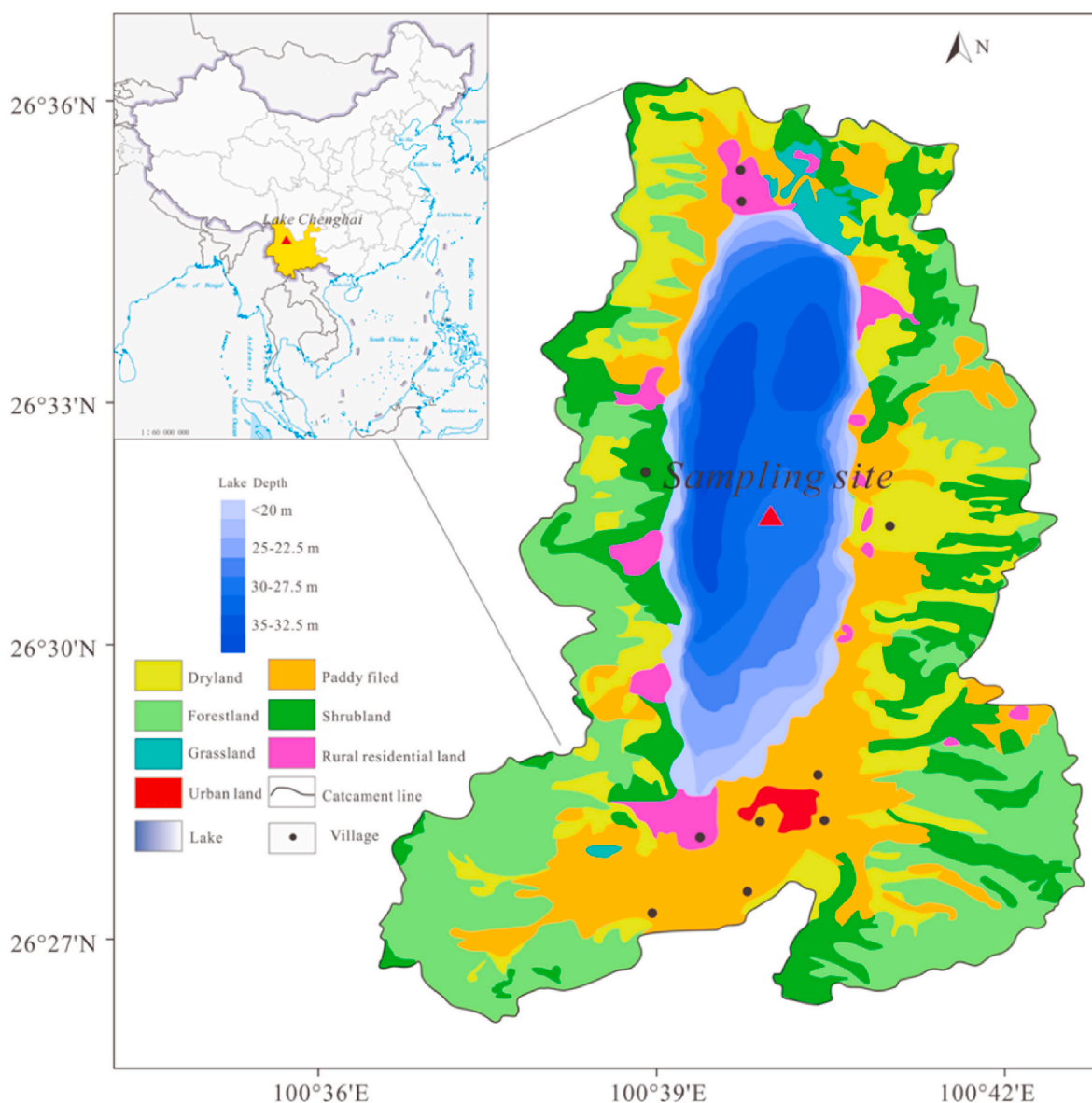


Fig. 1. Geographical location of Lake Chenghai in Yunnan Province, Southwestern China. The bathymetry of the lake and the coring location.

concentrations in the sediments were measured using a spectrophotometer with an experimental error of <0.5%. Grain size was measured using a Malvern Mastersizer 2000 laser grain-size analyzer, in the range of 0.02–2000 μm .

2.3. DNA extraction, Illumina MiSeq sequencing, bioinformatic analysis

The sediment DNA was extracted as described by Yan et al. (2019). In brief, the FastDNA™ SPIN Kit for Soil DNA Extraction (MP Biomedical, USA) was used to extract the DNA, and the extracted DNA solutions were stored at -86°C . Phytoplankton-specific primers p23SrV_f1 (5'-GGACAGAAAGACCCTATGAA-3') and p23SrV_r1 (5'-TCAGCCTGTTATCCCTAGAG-3') were designed to amplify a 410-bp fragment of the 23S rDNA (Sherwood and Presting, 2007; Yan et al., 2019). Sample-specific 7-bp barcodes were incorporated into the primers for multiplex sequencing. Each PCR amplification, including the negative control, was performed in a 25 μL reaction containing 5 μL of 5 $\times$ reaction buffer, 5 μL of 5 $\times$ GC buffer, 2 μL of dNTP (2.5 mM), 1 μL of forward primer (10 μM), 1 μL reverse primer (10 μM), 2 μL of DNA template, 0.25 μL of Q5®DNA Polymerase, and 8.75 μL of ddH₂O. The thermal cycling parameters for PCR amplification were: initial

denaturation at 98°C for 2 min; 25 cycles of denaturation at 98°C for 15 s, annealing at 55°C for 30 s and extension at 72°C for 30 s, and a final extension at 72°C for 5 min. All PCRs were performed in triplicate, and the products from each of the three samples were mixed. Sterile disposable materials, including gloves and experimental masks, and sterilized laboratory equipment were used throughout the experiments (sediment subsampling, DNA extraction, and PCR amplification), and the different procedures were performed in different rooms to avoid contamination. Negative controls were included for DNA extractions and PCR, and all the control products were negative for the 23S rRNA gene amplifications. The control products were not included in the sequencing library.

The PCR products were visualized on 2% agarose gels and then purified using the MiniBEST Agarose Gel DNA Extraction Kit (TaKaRa, Japan). The purified products were quantified using the Quant-iT™ PicoGreen™ dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). After the individual quantification step, the amplicons were pooled in equal amounts, and pair-end 2 $\times$ 250-bp sequencing was performed using the Illumina MiSeq platform with MiSeq Reagent Kit v3 at Shanghai Personal Biotechnology Co., Ltd. (Shanghai, China).

Quantitative Insights into Microbiology Ecology (QIIME 2; Bolyen

et al., 2019) was used to assemble the raw reads and filter the sequences according to the official tutorials (<https://docs.qiime2.org/2019.4/tutorials/>). In brief, the raw sequence data were demultiplexed using the demux plugin, followed by primers cutting using the cutadapt plugin. The sequences were then merged, quality filtered, and dereplicated using functions of fastq_mergepairs, fastq_filter, and derep_fulllength, respectively, in the Vsearch plugin. All the unique sequences were then clustered at 98% (via cluster_size), followed by the removal of chimera (via uchime_denovo). Finally, the nonchimeric sequences were reclustered at a 97% similarity to generate operational taxonomic units (OTUs). Representative sequences were selected and an OTU table was constructed. The representative sequences selected from each OTU were annotated with taxonomic information by comparison with the National Center for Biotechnology Information (NCBI) database. Non-algal OTUs were removed and were not considered in any further analyses.

2.4. Statistical analysis

To investigate the historical temporal trends in phytoplankton diversity, the α -diversity indices (including richness, Chao1, Pielou's evenness, abundance-based coverage estimator [ACE], Shannon's index, and Simpson's index) were calculated using the *alpha_diversity.py* (Caporaso et al., 2010). To measure the homogenization of the phytoplankton composition, Nonmetric Multidimensional scaling (NMDS) was performed using the Bray–Curtis dissimilarity calculated from the OTU abundance data (Anderson et al., 2006). Then, four groups were defined: the Medieval Warm Period (MWP, 1000s–1400s), the Little Ice Age (LIA, 1400s–1800s), the Early Current Warm Period (Early CWP, 1800s–1950s), and the Anthropocene (1950s–present). Analysis of similarities (ANOSIM) was used to assess the significance of the differences in data between groups. Further, STAMP analysis (Parks et al., 2014) was used to examine the statistical significance of differences among the different groups, and Welch's *t*-test with a false discovery rate (FDR) correction was used to identify the taxa with significantly different abundances.

Co-occurrence networks were constructed to describe and compare the interactions among communities during the four periods, based on Spearman's correlation with a correlation coefficient of $r > |0.6|$ and statistically significance of $p < 0.05$ (Bastian et al., 2009). The co-occurrence network patterns were visualized using the Gephi software (Bastian et al., 2009) with the Fruchterman-Reingold algorithm. To characterize the topologies of the networks, the numbers of edges and nodes, the proportions of negative and positive links, the average degrees, and average path lengths were calculated.

To identify the environmental factors driving the phytoplankton community structure over the past millennium, a variation inflation factor (VIF) analysis was used to detect the multicollinearity of the environmental variables. Variables that correlated strongly with each other were excluded, and the remaining variables were used for a redundancy analysis (RDA). Three kinds of key environmental factors were defined: climate change (temperature, precipitation and total solar irradiance [TSI]), human activities (reflected by sedimentary $\delta^{13}\text{C}_{\text{org}}$), and nutrients (TN, TP). To clarify the contributions of the key environmental factors to the diversity and community structures of the phytoplankton, a variation partitioning analysis (VPA) analysis was performed (Peres-Neto et al., 2006) using the *vegan* package in R.

Partial least squares path modelling (PLS-PM) was used to probe the direct and indirect relationships between community structure, diversity, and environmental variables. Six latent variables were defined and used to construct the models: climate changes (temperature, precipitation, TSI), human activities (represented by sedimentary $\delta^{13}\text{C}_{\text{org}}$), nutrients (TOC, TN, TP, N/P, C/N), lake level (represented by sedimentary grain size), α -diversity (Shannon diversity index, richness), and the community structure of the phytoplankton (indicated by NMDS1 and NMDS2, extracted from NMDS). The direction and intensity of the associations between the latent variables were illustrated by the path

coefficients, and the reliability of the constructed model was evaluated using goodness-of-fit (GOF) statistics (Tian et al., 2019). Correlations between the selected environmental parameters and NMDS1 were calculated using a linear regression analysis. Pearson's correlations between the taxa and environment variables were calculated using the *vegan* package.

3. Results

3.1. Temporal trends in geochemical and geophysical characteristics

The TOC in the sediment was 0.6%–6% (mean, 1.1%), and the content of TN was 0.6%–0.1% (mean of 0.144%) (Fig. 2). Both TOC and TN were relatively high during the 1000s–1350s; stabilized at relatively low levels during 1350–1900s; and increased rapidly thereafter. The concentrations of TP ranged from 1.2 mg/g to 0.4 mg/g, with an average of 0.75 mg/g; the trend in TP was roughly similar to those in TOC and TN (Fig. 2). The C/N ratio ranged from 6 to 11 (mean, 8). C/N stabilized at relatively low values before the 1980s and gradually increased thereafter (Fig. 2). N/P showed a pattern of change similar to that of TOC. As shown in Fig. 2, $\delta^{13}\text{C}_{\text{org}}$ ranged from -27.5‰ to -24.5‰ , and a significant reduction in $\delta^{13}\text{C}_{\text{org}}$ was observed over the past millennium was observed. The medium of particle size was relatively larger in the 1000s–1350s than in the 1350s–present time interval (Fig. 2).

The temperature data were taken from Feng et al. (2019), and higher temperatures were noted during the 1000s–1350s than during the 1350s–1900s, with the highest values being recorded during the 1950s–present. TSI showed a similar pattern of change to temperature (Fig. 2), decreasing during the 1000s–1900s and increasing during 1900s–present (Coddington et al., 2016). The precipitation index (Tian et al., 2019) showed an opposite trend to temperature and TSI, increasing during the 1000s–1900s and then decreasing from the 1900s (Fig. 2).

3.2. Changes in the phytoplankton diversity and community structure

In total, 93 sediment samples were subjected to amplicon sequencing, generating 9,300,000 raw sequences (mean, 100,000 sequences per sample). In total, 5518 OTUs were annotated with barcodes in the 23S rDNA region. OTUs assigned to non-algae were removed, and only phytoplankton groups, which included 2897 OTUs, were included in the analysis. These OTUs were classified into 11 algal groups, and the detailed taxonomic information is summarized in Table 1. The relative abundance of Cyanobacteria, Chlorophyta, Rhodophyta, Dinohyta, Cryptophyta, Bacillariophyta, Phaeophyta, Euglenida, Haptophyta, Streptophyta accounted for 70.85%, 13.00%, 5.70%, 1.73%, 1.40%, 0.35%, 0.14%, 0.35%, 0.14%, 0.02%, 0.01%, 0.01%, and 0.01%, in the total phytoplankton sequences of the total samples, respectively (Table 1). As shown in Fig. 3, among these groups, Cyanobacteria, Chlorophyta, Rhodophyta, and Dinohyta were the dominant groups over the past millennium, accounting for 35%–95%, 50%–1%, 44%–1%, and 40%–1%, in the per sample, respectively.

To evaluate the changes in the α -diversity of the phytoplankton over the past millennium, the α -diversity indices, including richness, Chao1, ACE, Shannon's index, Pielou's evenness, and Simpson's index, were calculated. As shown in Fig. 4, richness, Chao1, and ACE showed similar changes, with significant increases since the 1950s. The patterns of change in Shannon's index, Simpson's index, and Pielou's evenness were similar, with a fluctuating increasing trend over the past millennium (Fig. 4).

To analyze the variance in the phytoplankton structure over time, NMDS was performed at the OTU level. The low stress value indicated that NMDS1 could significantly explained the temporal changes in the community structure (Fig. 5), so NMDS1 was used to evaluate the changes in the phytoplankton community structure over the past millennium in order to identify the change points in the community

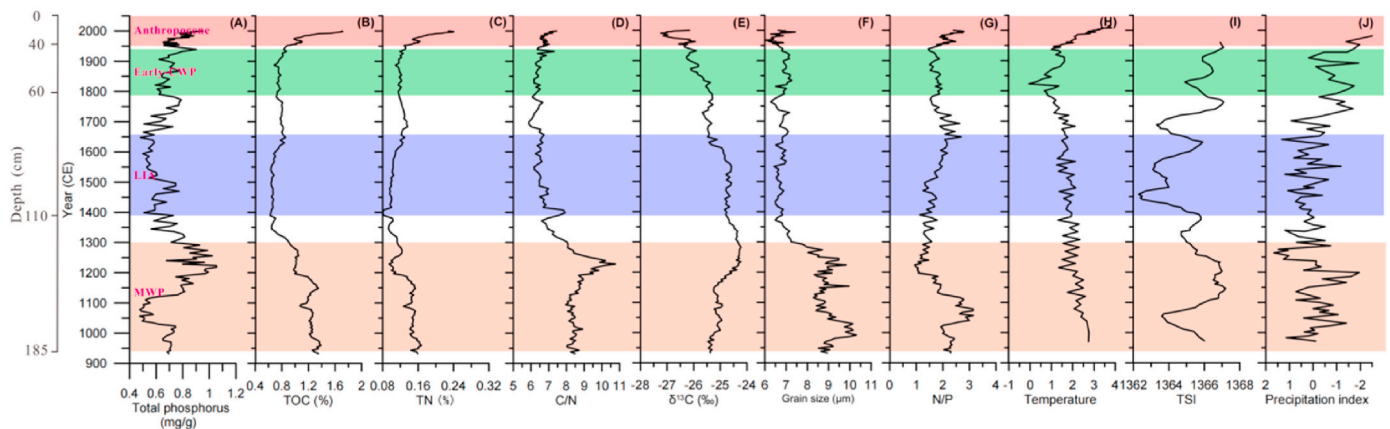


Fig. 2. Patterns of temporal change patterns in multiple environmental variables over the past millennium. (A) Total phosphorus (TP); (B) total organic carbon (TOC); (C) total nitrogen (TN); (D) C/N ratio; (E) $\delta^{13}\text{C}_{\text{org}}$; (F) grain size; (G) N/P ratio; (H) reconstructed temperature anomaly based on the brGDGTs in Tiancai Lake, southwestern China (Feng et al., 2019); (I) reconstructed total solar irradiance (TSI; Coddington et al., 2016); (J) reconstructed precipitation index in southwestern China (Tan et al., 2018). Note: The four historical periods are also shown in the figure: MWP (Medieval Warm Period, 1000s–1400s), LIA (Little Ice Age, 1400s–1800s), Early CWP (Early Current Warm Period, 1800s–1950s), and the Anthropocene (1950s–present).

structure. Three significant change points were detected in the 1400s, 1800s, and 1950s, defining four time-intervals: MWP (1000s–1400s), LIA (1400s–1800s), Early CWP (1800s–1950s), and the Anthropocene (1950s–present). The ANOSIM test results suggested that the composition of phytoplankton differed significantly between the four intervals ($R = 0.589$, $p = 0.001$).

MWP was dominated by *Synechococcaceae* (80%–95%, mean 88%), followed by *Trebouxiphyceae* (1%–10%, mean 3%), *Chroococcaceae* (0.1%–4%, mean 1.5%), *Rhodochaetaceae* (1%–6%, mean 1.4%) (Figs. 3 and 5). LIA was a cold period, in which the relative abundance of *Synechococcaceae* decreased significantly (3%–40%, mean 36%), with a concurrent increase in *Trebouxiphyceae* (3%–70%, mean 23%), *Rivulariaceae* (1%–20%, mean 4%), and *Monodopsidaceae* (0.1%–15%, mean 3%). The phytoplankton community during Early CWP was mainly composed of *Synechococcaceae* (20%–40%, mean 44%), *Rhodochaetaceae* (1%–35%, mean 12%), *Rivulariaceae* (0.1%–20%, mean 6%), *Prochlorotrichaceae* (1%–5%, mean 5%), *Chroococcaceae* (2%–14%, mean 6%), *Dinophysiaceae* (1%–12%, mean 3%). The Anthropocene was marked by sharp increases in *Aphanizomenonaceae* (2%–70%, mean 18%), *Prochlorotrichaceae* (1%–40%, mean 11%), *Nostocaceae* (1%–40%, mean 11%).

Co-occurrence network analyses further demonstrated the differences between the four stages (Fig. 6). The keystone taxa differed among the four time-intervals, suggesting marked changes in the phytoplankton community structure. The complexity of the network and the number of nodes were greatest during the Anthropocene, which was consistent with the higher phytoplankton diversity during the Anthropocene than the other periods over the past millennium (Fig. 6). Moreover, the number of edges, the average path length, and the average node degree during the Anthropocene were also much greater than during the other three time intervals, suggesting that more interactions between species occurred during this time interval. The keystone taxa also differed across the four time-intervals (Fig. 6), implying significant changes in the phytoplankton assemblages and interactions. The proportion of negative links during the Anthropocene was much higher than during the other time intervals (Fig. 6).

3.3. Environmental drivers of the phytoplankton community dynamics

A VIF analysis showed that the environmental variables TOC, N/P, and C/N shared the multicollinearity problems with other environmental variables. Therefore, only the variables TN, TP, $\delta^{13}\text{C}_{\text{org}}$, grain size, temperature, precipitation, and TSI were used for the further RDA and VPA analyses. The RDA results showed that seven environmental

variables accounted for 35.6% of the total variance in the phytoplankton community structure throughout the whole time-interval (Fig. 7A). Temperature and $\delta^{13}\text{C}_{\text{org}}$ were the most statistically significant variables, explaining more variation in the phytoplankton than the other environmental variables. This was also supported by the results of a linear correlation analysis (Supplementary Fig. 1).

The abovementioned environmental variables could be categorized into three kinds of environmental factors according to the environmental significance of the variable: climate change, human activities, and nutrients (for details, see the Discussion). The contributions of environmental factors during the MWP–LIA–Early CWP period (1000s–1950s), the Anthropocene (1950s–present), and the whole period were calculated using a VPA analysis (Fig. 7B). As shown in Fig. 7B, the environmental factors that provided the maximum explanatory power accounted for 35.03%, 57.39%, and 30.26% of the variation in the phytoplankton community during the whole period, the Anthropocene, and the MWP–LIA–Early CWP interval, respectively. Specifically, during the MWP–LIA–Early CWP interval, human activities explained 13.12% of the variance in the phytoplankton community; climate change explained 19.44% of the community change; and nutrients accounted for the largest amount of variance, 24.45% (Fig. 7B). During the Anthropocene, human activities, climate change, and nutrients explained 35.18%, 37.94%, and 35.89% of the variance in phytoplankton diversity and composition, respectively (Fig. 7B). Human activities and climate variables also separately explained 1.03% and 3.82% of the community changes, respectively, during the MWP–LIA–Early CWP interval, whereas during the Anthropocene, human activities and climate change independently explained 15.16% and 8.54% of the changes, respectively.

The links between phytoplankton diversity, community structure, and the selected environmental parameters in the four time intervals and the entire period were also synthetically illustrated using PLS-PM models. As shown in Fig. 8, during both the MWP and Early CWP time intervals, the climate factors showed positive impacts on the community structure, with path coefficients of 0.677 and 0.953, respectively. During the LIA interval, the effects of each path on the phytoplankton diversity and the community structure were weak, with absolute path coefficients of 0.104 and 0.456. During the Anthropocene, human activities seem to significantly influence the diversity and community structure of the phytoplankton by affecting the supply of nutrients to the lake (Fig. 8). Furthermore, the PLS-PM models during the Anthropocene and pre-Anthropocene (including the MWP, LIA, and the Early CWP) differed significantly, with human activities also playing a significant role in driving community structure and diversity during the

Table 1
Detailed description of the taxa measured in Lake Chenghai.

Phylum	Class	Family	Relative abundance (%)
Cyanobacteria	<i>Chroococcales</i>	<i>Aphanothecaceae</i> ; <i>Chroococcaceae</i> ; <i>Cyanobacteriaceae</i> ; <i>Microcystaceae</i>	70.85%
	<i>Chroococcidiopsidales</i>	<i>Chroococcidiopsidaceae</i>	
	<i>Nostocales</i>	<i>Aphanizomenonaceae</i> ; <i>Chlorogloeopsidaceae</i> ; <i>Hapalosiphonaceae</i> ; <i>Nostocaceae</i> ; <i>Rivulariaceae</i> ; <i>Tolypothrichaceae</i>	
	<i>Oscillatoriales</i>	<i>Coleofasciculaceae</i> ; <i>Cyanothecaceae</i> ; <i>Microcoleaceae</i> ; <i>Oscillatoriaceae</i>	
	<i>Pleurocapsales</i>	<i>Dermocarpellaceae</i> ; <i>Hyellaceae</i>	
	<i>Spirulinales</i>	<i>Spirulinaceae</i>	
	<i>Synechococcales</i>	<i>Chamaesiphonaceae</i> ; <i>Leptolyngbyaceae</i> ; <i>Merismopediaceae</i> ; <i>Prochloraceae</i> ; <i>Prochlorotrichaceae</i> ; <i>Pseudanabaena</i> ;	
Chlorophyta	<i>Chlorophyceae</i>	<i>Synechococcaceae</i>	13.00%
		<i>Carteria</i> ; <i>Asteromonadaceae</i> ; <i>Haematococcaceae</i> ; <i>Chromochloris</i> ; <i>Hydrodictyceae</i> ; <i>Neochloridaceae</i> ;	
		<i>Scenedesmaceae</i> ; <i>Selenastraceae</i> ; <i>Treubariaceae</i>	
	<i>Chloropiciphyceae</i>	<i>Chloropicaceae</i>	
	<i>Pedinophyceae</i>	<i>Resultomonadaceae</i> ; <i>Pedinomonadaceae</i>	
	<i>Pyramimonadales</i>	<i>Pyramimonadales</i>	
	<i>Trebouxiophyceae</i>	<i>Botryococcus</i> ; <i>Chlorellaceae</i> ; <i>Chlorellales</i> ; <i>Oocystaceae</i> ; <i>Choricystis</i> ; <i>Prasiolaceae</i>	
Rhodophyta	<i>Ulvophyceae</i>	<i>Ulvaceae</i>	5.70%
	<i>Bangiophyceae</i>	<i>Bangiaceae</i> ; <i>Pyropia</i> ; <i>Porphyririaceae</i>	
	<i>Compsopegonophyceae</i>	<i>Erythrotrichiaceae</i> ; <i>Erythrotrichiaceae</i> ; <i>Rhodochaetaceae</i>	
	<i>Florideophyceae</i>	<i>Ahnfeltiaceae</i> ; <i>Rhodomelaceae</i> ; <i>Corallinaceae</i> ; <i>Gracilariaceae</i> ; <i>Halymeniaceae</i> ; <i>Liagoraceae</i> ; <i>Rhodogorgonaceae</i> ;	
		<i>Sebdeniaceae</i>	
Dinophyta	<i>Stylonematophyceae</i>	<i>Stylonemataceae</i>	1.73%
	<i>Eustigmataphyceae</i>	<i>Eustigmataceae</i> ; <i>Monodopsidaceae</i> ; <i>Trachydiscus</i>	
	<i>Dinophyceae</i>	<i>Dinophysaceae</i>	
Cryptophyta	<i>Cryptomonadales</i>	<i>Cryptomonadaceae</i>	0.35%
	<i>Pyrenomonadales</i>	<i>Chroomonadaceae</i> ; <i>Geminigeraceae</i> ; <i>Pyrenomonadaceae</i>	
Bacillariophyta	<i>Bacillariophyceae</i>	<i>Gomphonemataceae</i>	0.14%
	<i>Coscinodiscophyceae</i>	<i>Stephanodiscaceae</i>	
	<i>Mediophyceae</i>	<i>Plagiogrammaeae</i>	
Phaeophyta	<i>Phaeotophyceae</i>	<i>Dictyotaceae</i> ; <i>Dictyotaceae</i> ; <i>Sargassaceae</i>	0.02%
Euglenida	<i>Euglenales</i>	<i>Euglenaceae</i> ; <i>Phacaceae</i>	0.01%
Haptophyta	<i>Haptophyceae</i>	<i>Pavlovaceae</i> ; <i>Phaeocystaceae</i> ; <i>Chrysochromulinaceae</i>	0.01%
Streptophyta	<i>Charophyceae</i>	<i>Characeae</i>	0.01%

Anthropocene (Fig. 8). Across the whole interval, climate change was the key factor controlling phytoplankton diversity and community structure.

The linkages between specific phytoplankton taxa and environmental variables were determined using two correlation analyses. As shown in Fig. 9, cyanobacterial taxa, such as *Aphanizomenonaceae*, were more sensitive to temperature than they were to other factors (Supplementary Fig. 2), while *Synechococcus* was more sensitive to nutrients than to other factors. Most Chlorophyta taxa, including *Chromochloridaceae*, *Hydrodictyceae*, *Neochloridaceae*, *Selenastraceae*, *Sphaeropleales*, *Treubariaceae*, *Chloropicaceae*, *Chlorellaceae*, and *Oocystaceae*, correlated negatively with precipitation and temperature, but positively correlated with TN, N/P, and C/N. The Rhodophyta taxa, such as *Rhodochaetaceae*, correlated negatively with $\delta^{13}\text{C}$ and precipitation and positively with TSI. The Dinophyta taxa, such as *Trachydiscus*, correlated positively with TN, N/P, and C/N and negatively with precipitation (Fig. 9).

4. Discussion

4.1. Temporal changes in climate, human activity intensity, lake levels, and trophic status

The reconstructed temperature changes over the past millennium in southwestern China based on sedimentary branched glycerol dialkyl glycerol tetraethers (brGDGTs) in Tiancai Lake track the global paleotemperature records (Feng et al., 2019), and show that the climate over the past millennium could be divided into several distinct intervals: the MWP (930–1400s), LIA (1400–1800s), and CWP (1800s–present) (Mann and Jones, 2003). It is noteworthy that the temperature and the intensity of human activities have been greater since the 1950s than in any preceding interval of human history, and this period is called the “Anthropocene” (Crutzen, 2002; Voosen, 2022). Therefore, in our analysis of Lake Chenghai, we chose to identify discrete intervals of time

within the CWP as 1800–1950 ‘Early Current Warm eriod’ (Early-CWP), and 1950s to present as Anthropocene. Precipitation in Lake Chenghai over the past millennium was reconstructed from speleothem oxygen isotope records (Tan et al., 2018), and the reconstructed was consistent with the changing pattern of precipitation in southwestern China (Hillman et al., 2016; Tan et al., 2018; Xu et al., 2019). Overall, the climate in Lake Chenghai has shown warm–dry and cold–wet condition over the past millennium (Yan et al., 2020).

Changes in lake levels offer a sensitive index of changes in the hydrological equilibrium that are attribute to variations in temperature and rainfall (Williamson et al., 2009; Xu et al., 2019). The medium grain size could reflect fluctuations in the levels of some lakes well (Chen et al., 2000; Hillman et al., 2016). An apparent inverse correlation between grain size and water depth was found in Lake Chenghai; i.e., a coarser grain size corresponded to a shallower water depth and vice versa (Ye et al., 2018). Moreover, the changes in sedimentary grain size were similar to those in the reconstructions of the lake level in Lake Chenghai based on physical beach evidence (Xu et al., 2019; Ye et al., 2018), supporting the notion that the high values of median grain size during the MWP period and small size during the LIA represent the relatively lower and higher lake levels, respectively (Ye et al., 2018). Therefore, changes in the lake level could be the main control factor regulating the changes in grain size, especially before the 1800s.

In general, $\delta^{13}\text{C}$ is a valuable tool for detecting anthropogenic contamination processes, and tracing the assimilation of nutrients and organic matter sources (Vilhena et al., 2021; Wolfe et al., 2013). $\delta^{13}\text{C}_{\text{org}}$ values range from -25.55‰ to -27.25‰ and show overall depletion trends (Dean et al., 2014; Han et al., 2022). This result is in good agreement with the previous reports of changes in global atmospheric $\delta^{13}\text{C}$ preserved in sediments, tree rings, and ice cores (Rubino et al., 2013; Han et al., 2022). The consensus view of this proxy is that it is related to the anthropogenic inputs of radiocarbon-dead and ^{13}C -depleted CO_2 from the combustion of fossil fuels (Francey et al., 1999; Han et al., 2022; Wolfe et al., 2013). Therefore, $\delta^{13}\text{C}_{\text{org}}$ can be

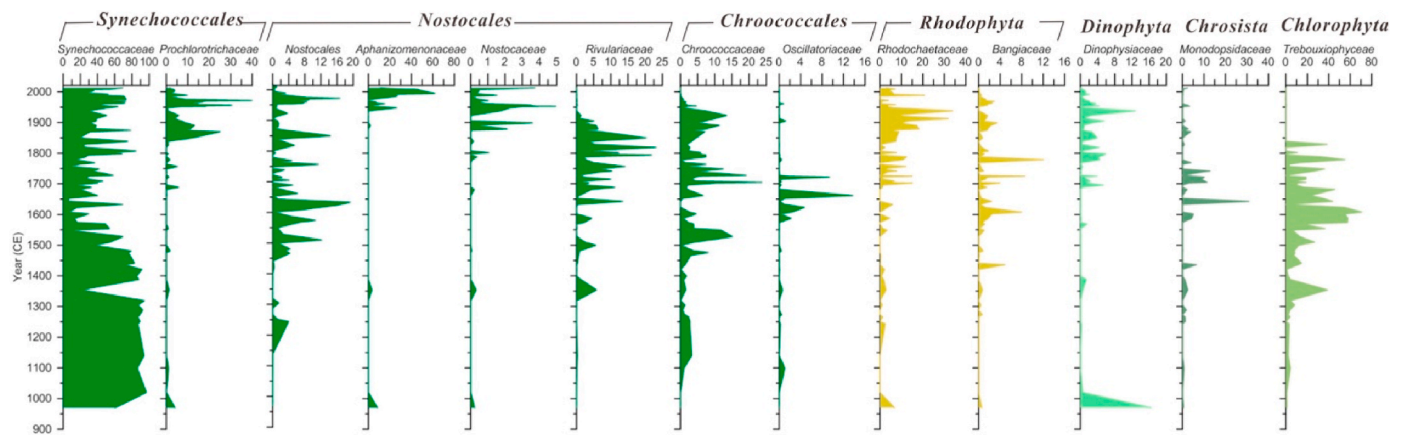


Fig. 3. Relative abundances of main phytoplanktonic taxonomic groups (at the family level) in Lake Chenghai throughout the past millennium.

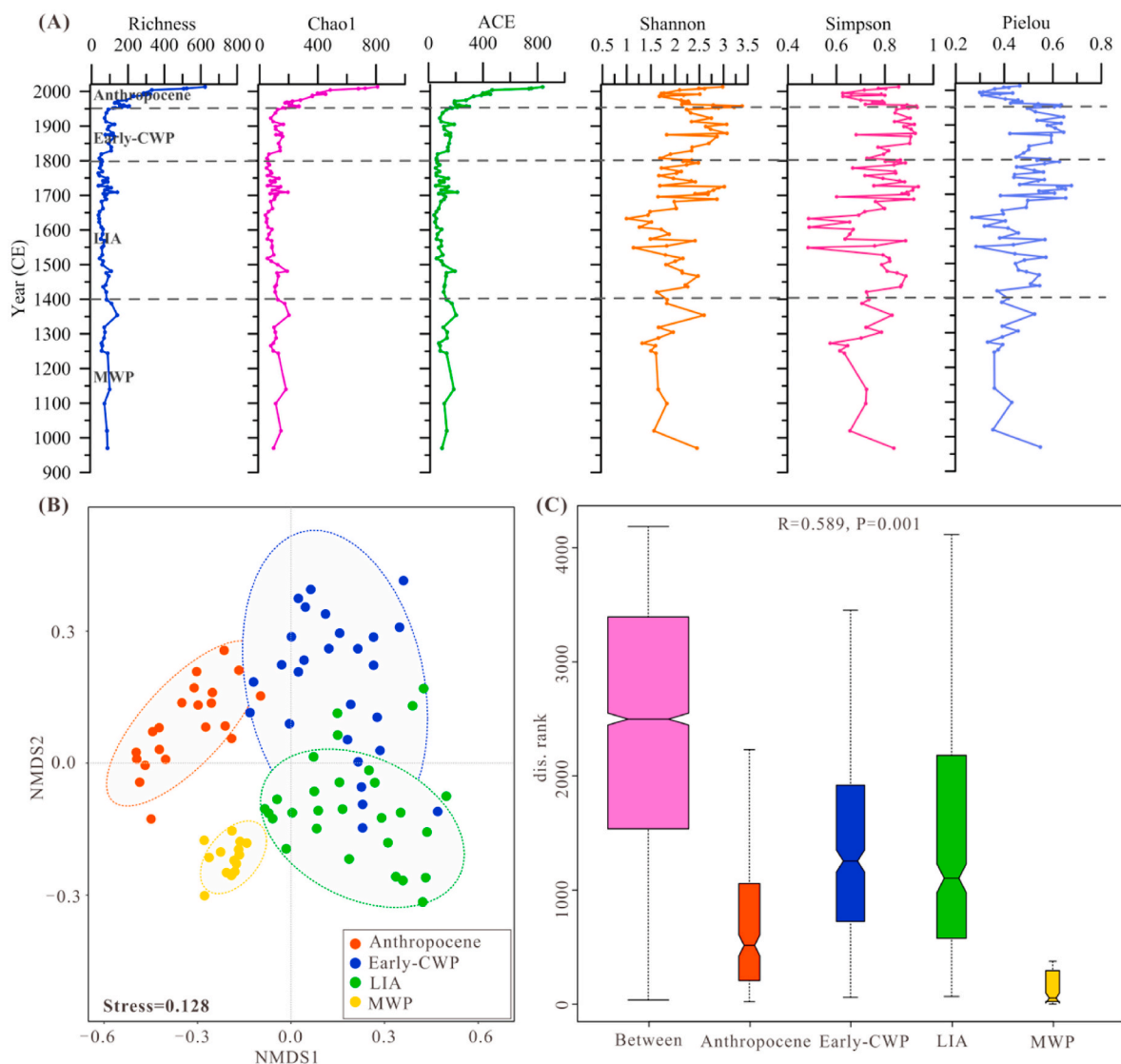


Fig. 4. Temporal variations in α -diversity indices and β -diversity comparisons of phytoplankton communities in Lake Chenghai in the four intervals: Medieval Warm Period (MWP, 1000s–1400s), Little Ice Age (LIA, 1400s–1800s), Early Current Warm Period (Early CWP, 1800s–1950s), and Anthropocene (1950s–present). (A) Changes in α -diversity indices including richness, Chao1, ACE, Shannon's index, Simpson's index, and Pielou's evenness over the past millennium; (B) nonmetric multidimensional scaling (NMDS) analysis based on operational taxonomic units (OTUs); (C) violin plots displaying the dissimilarity of phytoplankton communities in the four historical periods, estimated using analysis of similarities (ANOSIM). Between represents the different between compositions of the four periods samples.

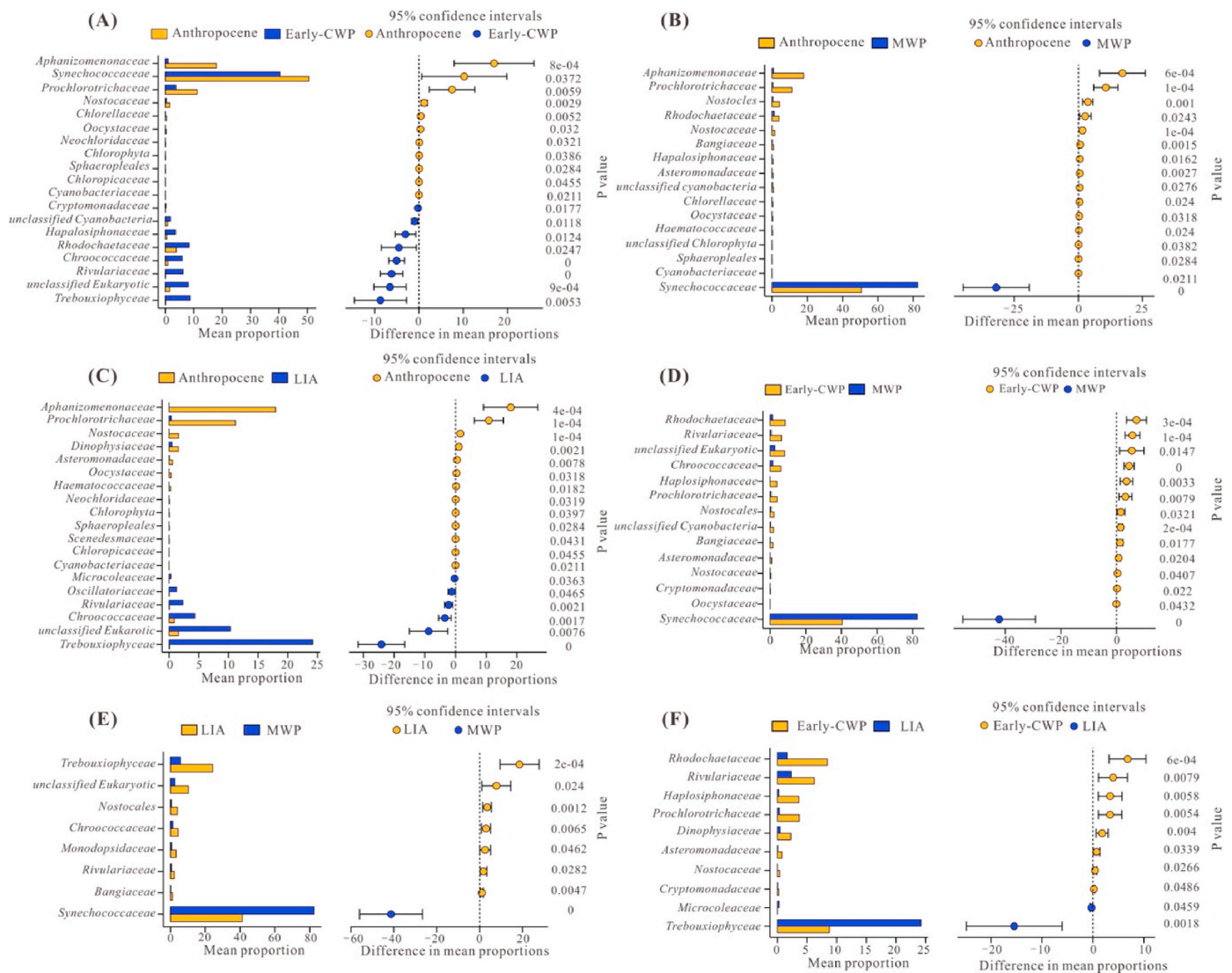


Fig. 5. Comparisons of phytoplankton taxa in the four historical periods. The Mann-Whitney U test was used to examine the significant differences between the periods compared in each sub-figure (A–F). (A) Anthropocene and Early-CWP; (B) Anthropocene and MWP; (C) Anthropocene and LIA; (D) Early-CWP and MWP; (E) LIA and MWP; (F) Early-CWP and LIA. Note: Medieval Warm Period (MWP, 1000s–1400s), Little Ice Age (LIA, 1400s–1800s), Early Current Warm Period (Early-CWP, 1800s–1950s), Anthropocene (1950s–present).

taken as a second anthropogenic marker (Han et al., 2022; Waters and Turner, 2022), and we regarded its changes in $\delta^{13}\text{C}_{\text{org}}$ as indicating the intensity of human activity in this study.

TOC, TN, and TP and their ratios are all essential for phytoplankton growth; therefore, their contents or concentrations can be used to reconstruct the trophic status and paleo-productivity in Lake Chenghai (Li et al., 2019; Zan et al., 2012). The relatively high values for sedimentary TOC and TN during the MWP and the Anthropocene demonstrate the eutrophic status of the lake, whereas the low values during the LIA indicate oligotrophic conditions in the lake.

4.2. Shifts in the phytoplankton community on decadal-centennial scales

Ancient sediment DNA provides a taxonomically sensitive method for reconstructing the long-term changes in phytoplankton communities in lakes (Keck et al., 2020). Several studies have shown that the degradation of sediment DNA over time and the presence of active microbes in the archive sediments should be considered in any analysis of ancient sedimentary DNA (Capo et al., 2021). Therefore, explaining why the DNA in the sediment is not completely degraded is critical when

evaluating the reconstructed results of ancient DNA analyses. The anoxic depositional environments in Lake Chenghai may contribute to the preservation of sediment DNA (Parducci et al., 2017). Moreover, the reconstructed phytoplankton compositions identified here are consistent with the phytoplankton composition recorded from water samples and historical monitoring (Dong et al., 2012; Yan et al., 2019), providing further evidence that the degradation of DNA and differences in the state of preservation across layers are not evident at this scale.

Diversity is one of the most commonly used quantitative descriptors of communities when assessing the characteristics of a system, such as its complexity, stability, or function (Borics et al., 2014; Carvalho et al., 2013). However, changes in phytoplankton diversity in deep lakes over the past millennium have not been fully investigated. The findings of the present study suggest that phytoplankton diversity was higher during the historical warm periods (e.g. the MWP) than during the cold period (e.g., LIA) (Fig. 4A), as indicated by the richness and Pielou indices. More importantly, phytoplanktonic diversity was significantly higher during the Anthropocene than during any other time intervals. This is similar to the results of recent studies that have reported a significant increase in phytoplankton diversity over recent decades (Li et al., 2019;

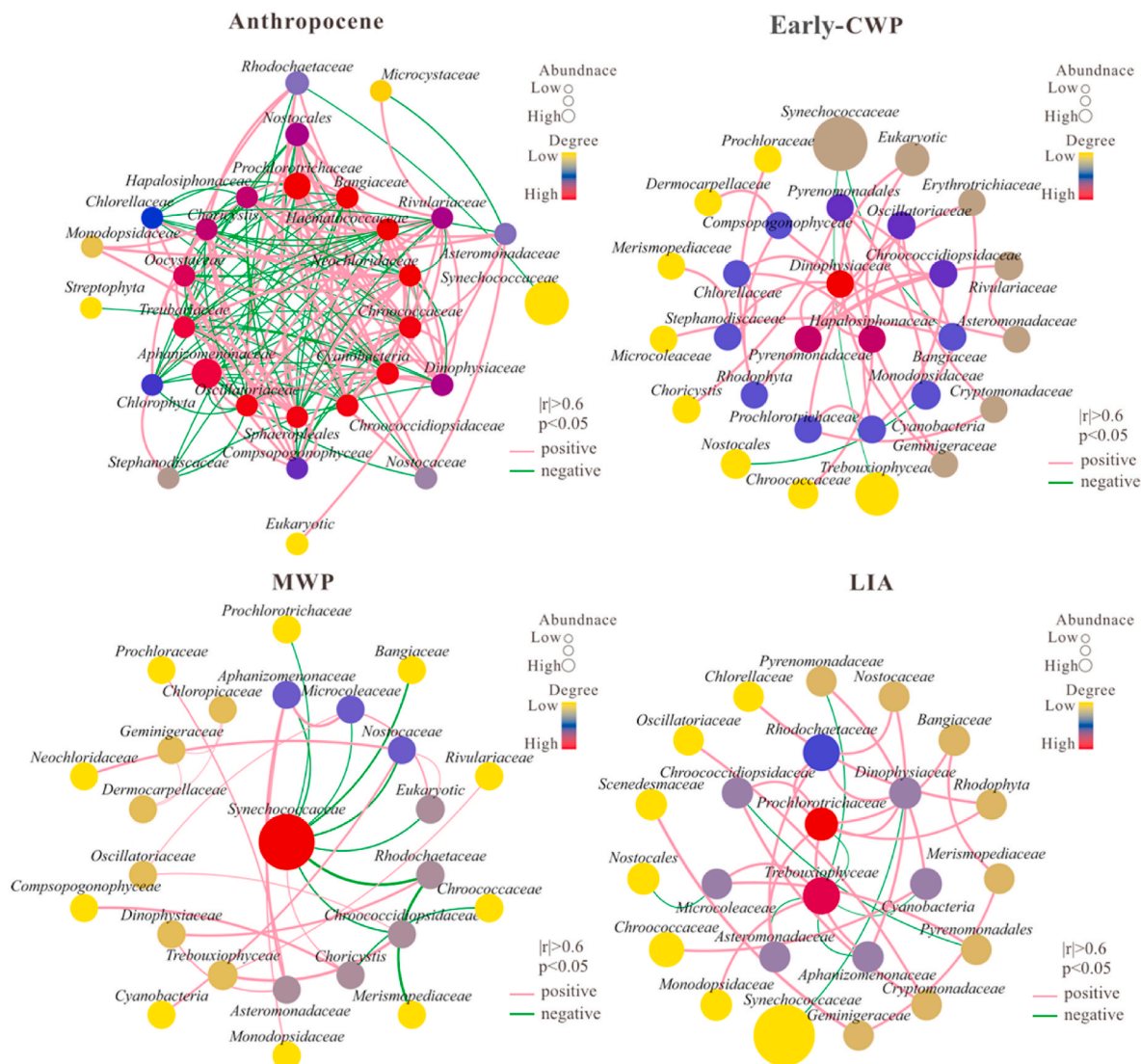


Fig. 6. Comparisons of the co-occurrence network patterns of phytoplankton taxa (at the family level) in the four intervals: the Medieval Warm Period (MWP, 1000s–1400s), Little Ice Age (LIA, 1400s–1800s), Early Current Warm Period (Early-CWP, 1800s–1950s), and Anthropocene (1950s–present). Note: The size of a circle represents the relative abundance of the taxon, and the color represents the important degree of the taxon; the thickness of each connecting line represents the important degree of the significant Spearman's correlations ($|r| > 0.6$, $p < 0.05$) between the nodes; green edges indicate the negative correlations, and pink edges indicate the positive correlations.

Zhang et al., 2022). Based on an analysis of ancient sediment DNA from 10 lakes in the European peri-alpine region, Monchamp et al. (2018) also observed a significant increase in photosynthetic taxa at the regional scale over the past 100 years. Together, these findings suggest that the increase in phytoplankton diversity in recent decades is a global phenomenon, but further detailed surveys of different types of lakes are required to confirm this inference.

Three significant change-points in the community structure occurred during the 1400s, 1800s, and 1950s. After these points, the phytoplankton communities gradually became more complex. As shown in Fig. 6, the degree of ecological network complexity and the key taxa present during the Anthropocene differ from those in earlier historical periods, suggesting the occurrence of a large-scale biological reorganization during the Anthropocene (Cael et al., 2021; Henson et al., 2021; Keck et al., 2020). The complexity and proportion of negative links are much greater during the Anthropocene than during the other intervals (Fig. 6), which is consistent with the results for other lakes (e.g., Lake Taihu, Zhang et al., 2022; Lake Chaohu, Li et al., 2019). It is noteworthy that the keystone taxa during Anthropocene were mainly

Aphanizomenon, *Microcystis*, *Nostocaceae*, and *Prochlorococcus*, which have increased progressively since the 1950s, whereas there is a corresponding reduction in the previously dominant taxon *Synechococcales* (Figs. 5 and 6). The former taxa have been reported to produce a variety of cyanotoxins and can form cyanobacterial blooms (Cao et al., 2020; Kosten et al., 2012; Monchamp et al., 2018). Moreover, these taxa were mainly detected during the Anthropocene (Figs. 3 and 5), suggesting that cyanobacterial blooms have only occurred in this lake in recent decades. This may be related to the fact that changes during the Anthropocene differ from those in past major warming periods and include greenhouse gases emissions, aerosol emissions, and land-use changes (Liu et al., 2017; Zhang et al., 2022).

Two distinct phytoplankton assemblages in Lake Chenghai appeared alternately before the 1950s and varied with environmental factors, especially temperature. Comparisons of the community compositions during the MWP, LIA, and Early CWP period revealed that the abundance of cyanobacteria was significantly higher during the warm periods than during the cold period, whereas the cold periods were mainly dominated by Chlorophyta (Figs. 3 and 5). Specifically, two major

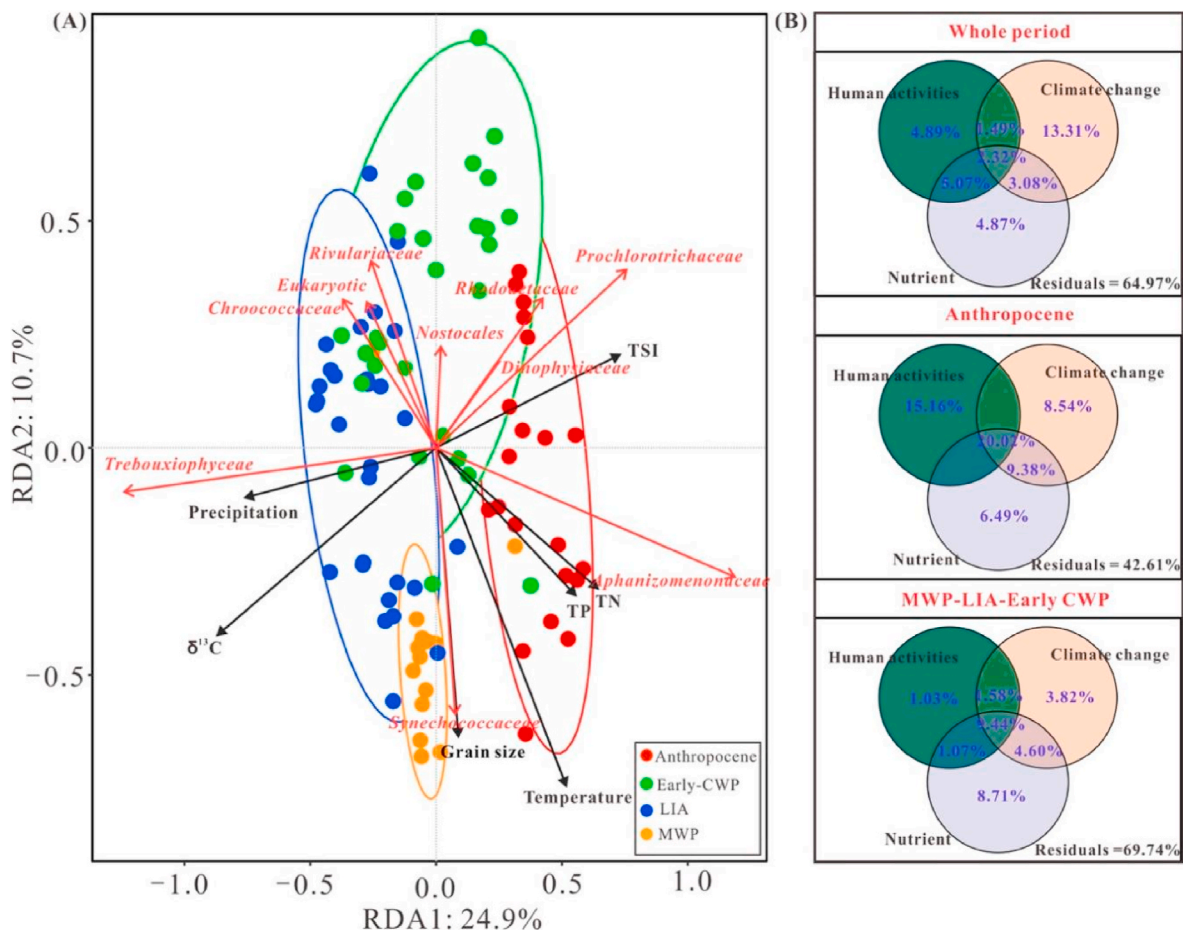


Fig. 7. Redundancy analysis (RDA) and variance partitioning analysis (VPA) illustrating the relationships between the phytoplankton community at the operational taxonomic units (OTU) level and environmental variables. (A) RDA of the whole-period samples. The legend shows the four periods: Medieval Warm Period (MWP, 1000s–1400s), Little Ice Age (LIA, 1400s–1800s), Early Current Warm Period (Early CWP, 1800s–1950s), and Anthropocene (1950s–present). Significant taxonomic drivers of variation are shown by red arrows, and significant environmental variables are shown by black arrows. (B) VPA of the whole-period samples, the Anthropocene (1950s–present) samples, and the MWP–LIA–Early CWP (1000s–1950s) samples. Note: Environmental variables $\delta^{13}\text{C}$, total phosphorus (TP), total nitrogen (TN), and grain size are from the present study; temperature data are from Feng et al. (2019); precipitation data are from Tan et al. (2018); total solar irradiance (TSI) data are from Coddington et al. (2016). Climate change is represented by temperature, precipitation, and TSI; human activities are represented by sedimentary $\delta^{13}\text{C}_{\text{org}}$; nutrients are represented by TN and TP.

phytoplankton assemblages, *Synechococcales-Dinophyceae* and *Synechococcales-Monodopsidaceae-Trebouxiophyceae*, appear alternately, with the former occurring mainly during warm periods and the latter during the cold period (Figs. 3 and 5). This is consistent with the seasonal dynamics of phytoplankton traits, with Chlorophyta dominating in spring but being rapidly replaced by Cyanobacteria in summer (Gilbert, 2013). Taken together, these results provide further evidence that (a) abrupt ecological changes and cyanobacterial blooms occurred in the lakes during the Anthropocene; and (b) Cyanobacteria are dominant in the phytoplankton of the medium-deep and shallow lakes during the warm periods.

4.3. Mechanisms controlling the phytoplankton community dynamic

Our analysis of ancient sediment DNA showed that the phytoplankton community succession was almost synchronous with changes in climate and human activities across the past millennium, with four successive intervals corresponding to the MWP, LIA, Early CWP, and the Anthropocene. Previous studies have investigated the impacts of climate variables (e.g., temperature, precipitation, TSI) and nutrients (e.g., P, N) on phytoplankton dynamics in freshwater lakes worldwide (e.g., Gland et al., 2021; Paerl and Paul, 2012; Qin et al., 2020), but the viewpoints on the relative importance of those parameters driving phytoplankton

community successions have been quite variable. Several studies based on monitoring and paleolimnology data have demonstrated that nutrient enrichment is the most important factor driving phytoplankton succession and even algal blooms (Elliott, 2021; Schindler et al., 2008; Sinha et al., 2017; Nwosu et al., 2023), whereas some studies suggested that climate warming dominates the phytoplankton successions, because the frequency of algal blooms has not declined in the recent decades despite a reduction in the nutrients inputs into lakes (e.g., Ho et al., 2019; Zhang et al., 2022). In the present study, the onset of the Anthropocene coincided with a marked shift in the composition of the phytoplankton community, which began to occur with the dominance of the eutrophication-associated and potentially toxic *Aphanizomenon*. At the same time, the contributions of environmental factors controlling the phytoplankton community during the Anthropocene differed from those in the MWP–LIA–Early CWP, indicating that the changes observed in the phytoplankton community in the 1950s could be attributable to the anthropogenic warming and eutrophication that have occurred with the development of agriculture and factories in the catchment and the attendant nutrient loading over the recent decades (Figs. 7 and 8). Other environmental variables, such as precipitation and lake levels, mainly affected phytoplankton taxonomy via mixing and changes in nutrient concentrations. For example, declines in the lake level and precipitation could have increased the concentrations of nutrients and the turbidity of

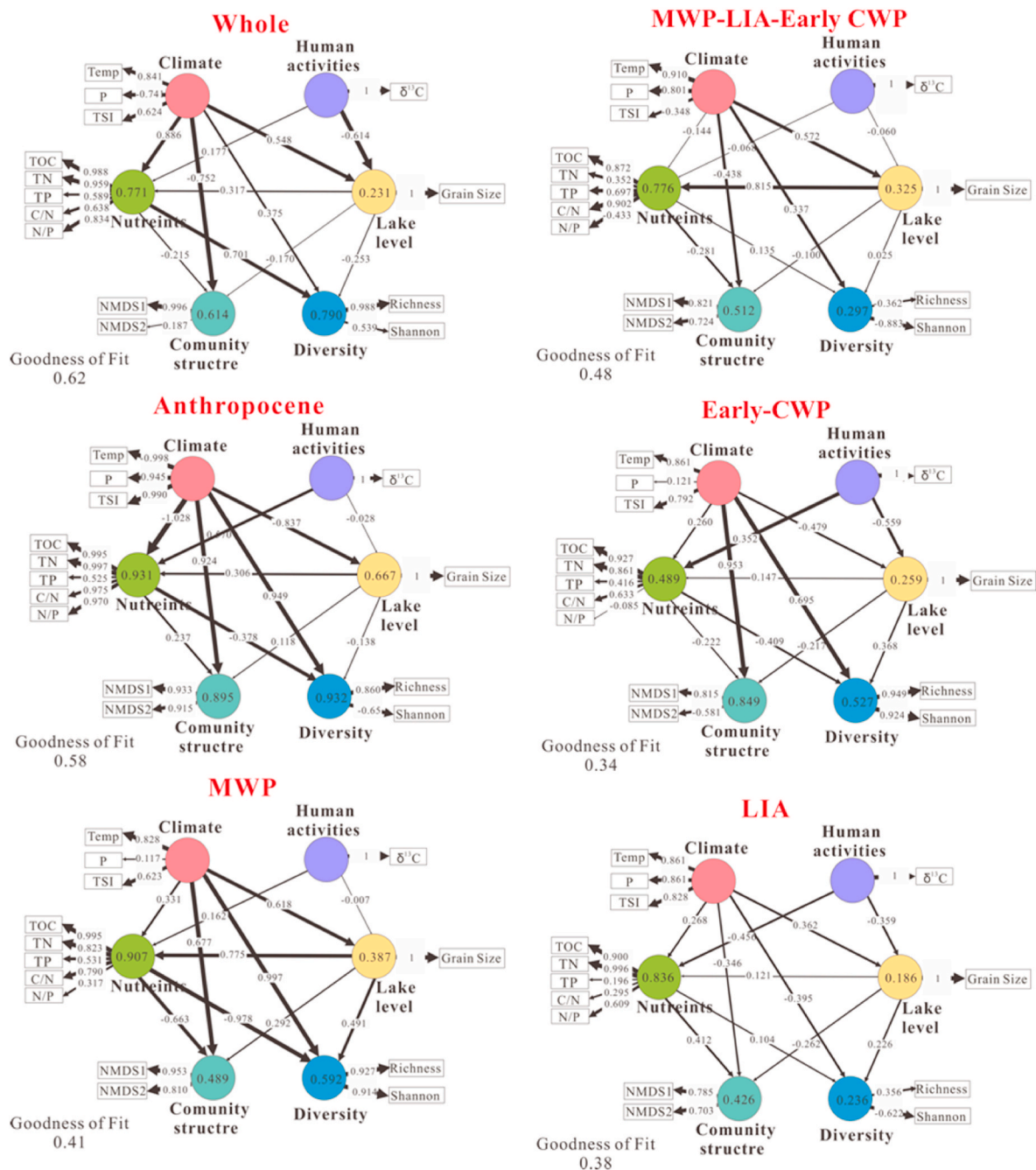


Fig. 8. Direct effects and indirect effects of environmental variables on the phytoplankton diversity and community structure determined with the partial least squares path modeling (PLS-PM) for the whole period, MWP-LIA-Early CWP (1000s–1950s), Anthropocene (1950s–present), Early Current Warm Period (Early-CWP, 1800s–1950s), Little Ice Age (LIA, 1400s–1800s), and Medieval Warm Period (MWP, 1000s–1400s) in this study. Note: Arrow thickness represents the absolute path coefficient value, with higher absolute values representing stronger correlations. Environmental variables, including $\delta^{13}\text{C}$, total phosphorus (TP), total nitrogen (TN), total organic carbon (TOC), C/N, N/P, and grain size, are from the present study; temperature (Temp) data are from [Feng et al. \(2019\)](#); precipitation (P) data are from [Tan et al. \(2018\)](#); total solar irradiance (TSI) data are from [Coddington et al. \(2016\)](#). NMDS1 and NMDS2 were extracted from a nonmetric multidimensional scaling (NMDS) analysis.

the lake (Fig. 8), and further altering the phytoplankton community structure.

As discussed previously, human activities have been a widespread force in shaping the structure and function of Earth's environment ([Waters et al., 2016](#)), causing significant global warming, an increase of nutrient loading, and other changes to water ([Huang et al., 2022](#)). For example, anthropogenic warming profoundly affects phytoplankton communities either directly through higher temperature or indirectly through changes in nutrients ([Huo et al., 2022](#); [Kosten et al., 2012](#)).

Temperature plays a crucial role in controlling metabolic rates and thus increases species richness during warm periods ([Allen et al., 2002](#); [Brown et al., 2004](#)). Moreover, warming could potentially promote the dominance of cyanobacterial in the phytoplankton communities of eutrophic lakes because cyanobacteria are better adapted to higher temperatures than are other taxa ([Gilbert, 2013](#); [Ho et al., 2019](#); [J.F. Zhang et al., 2021](#)), which is supported by the findings of the present study. It has also been argued that the land-use types in the Lake Chenghai catchment, especially agriculture land (which is the main

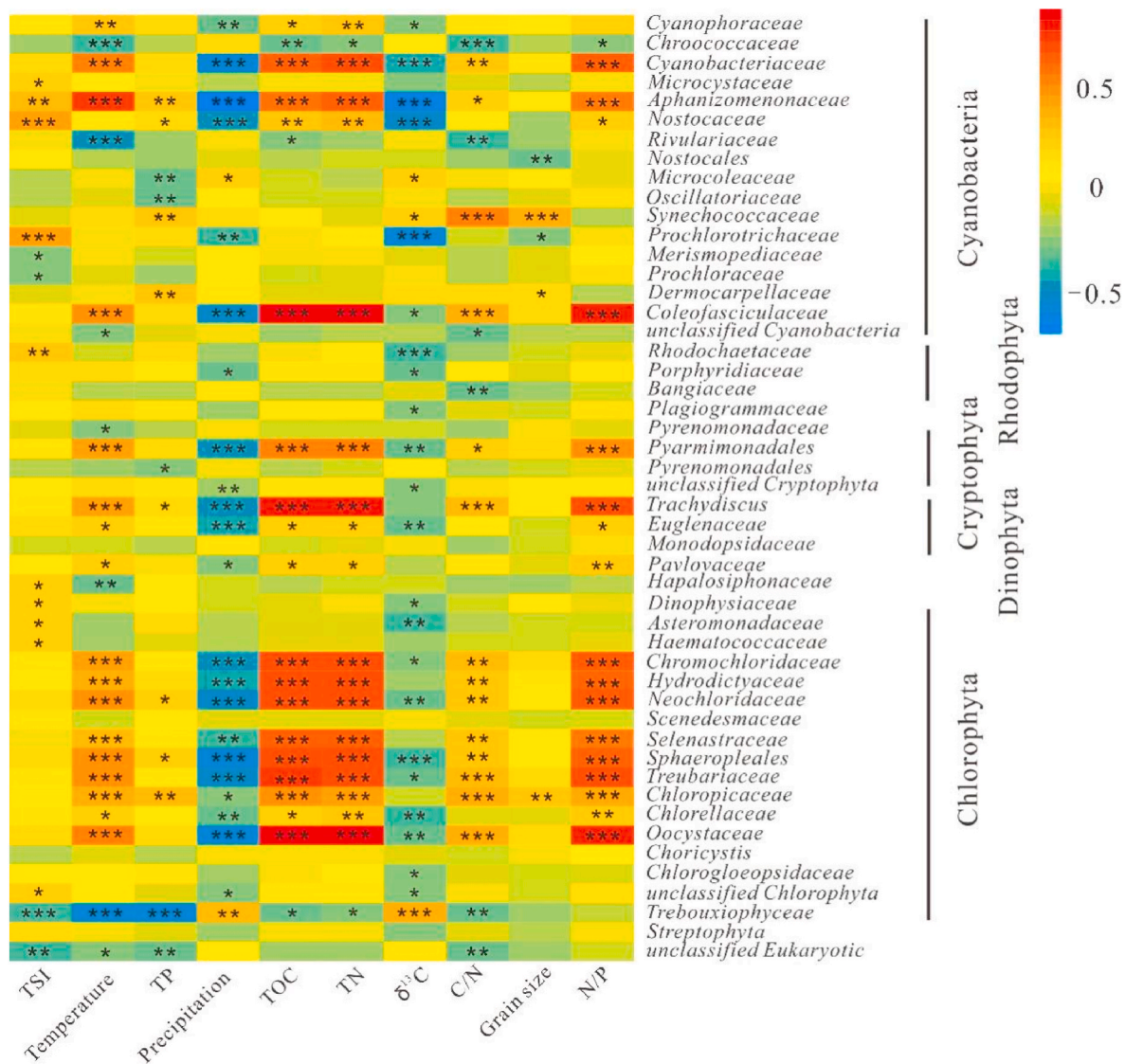


Fig. 9. Spearman's correlations between taxa abundance and environmental variables. Note: Environmental variables, including $\delta^{13}\text{C}$, total phosphorus (TP), total nitrogen (TN), total organic carbon (TOC), C/N, N/P, and grain size are from the present study; temperature data are from Feng et al. (2019); precipitation data are from Tan et al. (2018); total solar irradiance (TSI) data are from Coddington et al. (2016).

sources of nutrient inputs into the lake; Chen et al., 2018), play an important role in shaping the composition and distribution of the cyanobacterial (Liao et al., 2016). Based on the present study, changes in P concentration during the Anthropocene are similar to those in the MWP (Fig. 2), whereas the changes in the phytoplankton community composition are unprecedented in the Anthropocene (Fig. 3), suggesting that other key factors control the composition of phytoplankton community, and especially the occurrence of bloom-forming taxa. Nitrogen levels and temperature have been significantly higher in the recent decades than in other historical periods (Fig. 2), which could partly explain the significant increase in *Aphanizomenon* abundance (Fig. 3 & Supplementary Fig. 2), because *Aphanizomenon* blooms have been reported in 102 German lakes displaying N enrichment (Dolman et al., 2012).

It is noteworthy that TP strongly affected the abundance of the dominant taxon *Synechococcus* in Lake Chenghai (Fig. 9), although it has not been previously reported as a toxic-producing cyanobacterium. To the best of our knowledge, *Synechococcus*, fast-growing 'r-strategy' picocyanobacteria, is more sensitive to nutrients than to temperature, and is more abundant in nutrient-rich conditions than in nutrient-poor conditions (Behrenfeld et al., 2021; Henson et al., 2021; Zhang et al.,

2022). Chlorophyta taxa, such as *Selenastraceae*, *Sphaeropleales*, *Treubariaceae*, *Chloropicaceae*, *Chlorellaceae*, *Oocystaceae*, and *Choricystis*, are sensitive to most environmental parameters, especially the nutrients (Fig. 9). This suggests that some Chlorophyta taxa that cannot be identified by morphologically may be the potential indicators of changes in the nutrient status and temperature conditions of lakes (Capo et al., 2017). Our results also show that different microbial groups have unique responses to environmental variables, and that the DNA preserved in the sediments can provide valuable information about past changes in the biodiversity and community structure in the lakes.

5. Conclusions

Using traditional paleoclimatological and ancient sedimentary DNA analyses, we have reconstructed the temporal changes in the phytoplankton community (cyanobacterial and eukaryotic algae) and environmental conditions of Lake Chenghai, a deep lake in the subtropical area, over the past millennium. The succession of phytoplankton communities resolved into four discrete intervals: the Medieval Warm Period (MWP, 1000s–1400s), the Little Ice Age (LIA, 1400s–1800s), the Early Current Warm Period (here defined as the 1800s–1950s) and the

Anthropocene (1950s–present; which is the latter part of the Current Warm Period). Cyanobacteria dominated during the warm intervals, whereas Chlorophyta became abundant during the cold intervals. Significantly, bloom-forming taxa (e.g., *Aphanizomenon*) have only occurred in recent decades, and the phytoplankton diversity in this eutrophic lake has increased significantly during the Anthropocene. Multiple statistical analyses suggested that temperature is the main driver of change in the phytoplankton assemblage, and that anthropogenic warming in recent decades may promote bloom-forming cyanobacterial growth. We conclude that cyanobacterial blooms may become a more serious problem in the subtropical regions under continuing anthropogenic warming conditions.

Credit authors statement

Dongna Yan: conceptualization, visualization, methodology, data curation, formal analysis, writing—original draft, funding acquisition. **Bashir Bolaji Tihamiyu:** conceptualization, writing—review & editing. **Jiaozhao Liu:** writing – review & edit. **Jianghu Lan:** sampling, methodology. **Hai Xu:** validation, writing—review & editing. **Weiguo Hou:** writing—review & editing, formal analysis. **Hanfeng Wen:** sampling, formal analysis. **Maolin Gu:** sampling, formal analysis. **Hong Yan:** validation, writing—review & editing. **Zhihai Tan:** validation, writing—review & editing. **Zhisheng An:** validation, Writing—review & editing, funding acquisition. **Yongming Han:** validation, writing—review & editing, funding acquisition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2023.108293>.

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