LIMNOLOGY and OCEANOGRAPHY

ASLO

Limnol. Oceanogr. 9999, 2021, 1–16

doi: 10.1002/lno.11878

Synergistic impacts of nutrient enrichment and climate change on long-term water quality and ecological dynamics in contrasting shallow-lake zones

Qi Lin,[1] **Ke Zhang**,[1*] **Suzanne McGowan**,[2] **Eric Capo**,[3] **Ji Shen**[4]

[1]State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China
[2]School of Geography, University of Nottingham, Nottingham, UK
[3]Department of Chemistry, Umeå University, Umeå, Sweden
[4]School of Geographic and Oceanographic Sciences, Nanjing University, Nanjing, China

Abstract

Anthropogenic and climatic stressors on freshwater ecosystems are of global concern. However, the interactions and effects of multiple stressors (e.g., nutrient enrichment, climate warming, altered wind and precipitation) acting over different spatial and temporal scales are often complex and remain controversial. Here, we reconstructed one-century dynamics of eutrophication and primary producer communities in algal-dominated and macrophyte-dominated zones of a large shallow lake (Taihu, China), by integrating sedimentary photosynthetic pigments and geochemical records with water monitoring and historical archives. We aimed to explore the long-term underlying mechanisms of the responses of water quality and lake biota to multiple environmental perturbations. We found that water quality degradation and algal community modification showed similar trends but distinct timings and trajectories in contrasting ecological zones. Onset and intensity of eutrophication in north Meiliang Bay (since the 1950s) exceeded far beyond that of macrophyte-dominated Eastern Taihu (~1990s). Anthropogenic nutrients overtook past climatic control on production and composition of phototrophic assemblages. More importantly, lake phytoplankton responded markedly to climate warming, decreasing wind speed, and extreme weathers after cultural eutrophication. Synergistic interactions of nutrients and climate on lake ecosystems became increasingly significant in promoting harmful algal blooms (HABs) dominated by *Microcystis*, close to the hyper-eutrophic north lake zones. The asynchronous limnological and ecological responses also indicated the modulating roles of lake ecological regime and catchment hydrogeomorphic characteristic. Collectively, our findings suggest that mitigation of eutrophication and HABs calls for a triple management strategy integrating anthropogenic nutrients, climate change, and lake-catchment setting.

Over the past century, global freshwater ecosystems have been widely affected by increased climate change, pollution, and hydrological manipulation (Birk et al. 2020; Jenny et al. 2020; Jeppesen et al. 2020). Consequently, there has been a widespread increase in intense phytoplankton blooms, particularly harmful algal blooms (HABs) (Taranu et al. 2015), resulting in a considerable decline in water quality, which is threatening the world's water resources used for drinking, fisheries, and recreational purposes (Ho et al. 2019). Such disturbances are likely to occur more frequently under predicted future conditions of anthropogenic and climatic variability (Carey et al. 2012; O'Neil et al. 2012). Understanding how multiple stressors have influenced aquatic ecosystems over long time scales in the past is crucial for the prediction of future responses, and to facilitate ecological restoration and watershed management (Bennion and Battarbee 2007).

In particular, shallow water and short water residence times make shallow lakes more vulnerable to the combined effects of anthropogenic activity and climate change (Scheffer and Jeppesen 2007; Janssen et al. 2014). Nutrient enrichment and disturbances of shallow lakes has been increasing significantly in densely populated regions due to diffuse and point inputs of sewage, agriculture, and aquaculture wastes

*Correspondence: kzhang@niglas.ac.cn

Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: Q.L. and K.Z. conceived the study; K.Z., J.S., and Q.L. acquired the funding and administered the project; Q.L., S.M., and E.C. led the experimental investigations and formal analysis; Q.L., S.M., and K.Z. wrote the manuscript, and all authors contributed to discussion of analyses, interpretation, and editing the paper.

(McGowan et al. 2012; Kusmer et al. 2018), as well as hydrological regulation (Chen et al. 2016; Kong et al. 2017), leading to elevated primary production, changes in benthic habitats and algal communities, and the dominance of nuisance cyanobacteria in lake ecosystems (Maheux et al. 2016; Yang et al. 2017). Regionally and globally, climate change has been altering weather patterns, via increasing temperature and extreme weather events as well as changes in wind and rainfall, all of which can translate into different levels of influence/impairment of water quality (O'Neil et al. 2012; Yang et al. 2016). For instance, global warming and declining wind speed due to atmospheric stilling (Wu et al. 2018) could affect phytoplankton productivity and communities by enhancing the stability and stratification of the water column (Janatian et al. 2019), to favor the occurrence of HABs especially in eutrophic shallow lakes (Paerl and Huisman 2008; Posch et al. 2012; Deng et al. 2018). A meta-analysis based on modern surveys from > 1000 U.S. lakes suggests that the interaction of temperature and nutrients is not synergistic in determining phytoplankton and cyanobacterial biovolume in most cases, whereas eutrophic and hyper-eutrophic lakes usually exhibit a significant interaction between nutrients and temperature (Rigosi et al. 2014). A more recent study from 33 freshwater mesocosm experiments also drew similar conclusions about interactions of multiple stressors on freshwater biota (Birk et al. 2020). However, interactive mechanisms of anthropogenic activity and climate change on lake ecosystem modifications are rarely investigated at multidecadal scales (with some exceptions such as McGowan et al. 2012; Capo et al. 2017, Monchamp et al. 2018), especially in ecologically fragile and strongly human-impacted regions. Such studies could shed light on the relative importance of different disturbances as well as the additive and/or synergistic effects on the water quality and biological structure over long-time scales.

Considering lake-catchment characteristics and ecological regimes as "filters" of multiple stressors can further improve our understanding of catchment-scale development and context-dependent ecological responses (Leavitt et al. 2009; Maheux et al. 2016; Chen et al. 2021). Taihu Lake, the third-largest freshwater and shallow lake in the most densely populated region of eastern China, provides an ideal model system to study how the interaction of anthropogenic activity and climate change over a variety of spatial scales affects lake water quality and ecosystem functioning. First, the lake basin has experienced dramatic social and economic transitions since the 1980s, with remarkable economic growth (annual rate of 15.7%), population expansion (annual rate of 3.0%), intensive agricultural development, industrialization, and urbanization (Qin 2008; Xu et al. 2017). Coupled with considerable eutrophication and climate warming, annual cyanobacterial blooms started in the northern bays from the 1980s, with *Microcystis* spp. dominating, then the bloom coverage expanded into the open lake areas since the early 1990s (Duan et al. 2009), threatening the water security of millions of people inhabiting the basin (Qin et al. 2019). Second, Taihu Lake is characterized by two distinct ecological regimes: the algae-dominated zones in the north and west, and the macrophyte-dominated zones in the east (Zhao et al. 2013; Janssen et al. 2014), which offer a chance for direct comparisons between sub-basins with different ecological regimes, drainage networks, and anthropogenic pressures.

Autotrophic communities are key components in determining ecosystem state, and they are strong indicators of water quality degradation in lakes (Maheux et al. 2016; Yang et al. 2016; Moorhouse et al. 2018). Paleolimnological analysis of fossil photosynthetic pigments is an effective method to determine past ecological responses from nutrient enrichment, acidification, and climate change, with different algal groups responding to different environmental drivers (McGowan 2013; Chen et al. 2016). In this study, by integrating sedimentary photosynthetic pigments and geochemical records with water monitoring and historical archives, we examined one-century of algal community dynamics and ecological state changes in algae- and macrophyte-dominated zones of Taihu Lake to determine the underlying mechanisms of the responses of lake biota to multiple environmental perturbations. Our first goal was to quantify past changes in primary production, algal abundance, and community composition in two contrasting lake zones (Meiliang Bay in the north and Eastern Taihu) by measuring the concentrations of chlorophylls, carotenoid pigments, and nutrients in dated sediments spanning the last 100 yr. Second, we sought to quantitatively compare anthropogenic, climate, and catchment changes with limnological variability, using multivariate analysis and generalized additive models (GAMs), to elucidate the importance of interactive effects in structuring long-term phototrophic assemblages. We hypothesized that: (1) the contrasting lake ecological zones would show distinctive timings and intensity of eutrophication and algal community modification due to their basin-specific responses to anthropogenic pressure, climate change, and drainage effect; (2) anthropogenic nutrient loading exerts a stronger control than climate on algal communities; (3) synergistic effects of multiple stressors would play an increasingly important role in regulating photoautotrophs with increasing eutrophication. Ultimately, this study seeks to generate new knowledge to aid integrated strategies and prioritization of watershed management.

Materials and methods

Study area and sampling

Taihu Lake (30°55′40″N–31°32′58″N, 119°52′32″E–120°36′10″E) is a large, shallow, and eutrophic lake situated in the Yangtze River Delta, which is one of the most rapidly developing and densely populated regions in China (Fig. 1). It has a surface area of ~2338 km^2 and an average water depth of 1.9 m. The watershed area is ~36,500 km^2, with an average

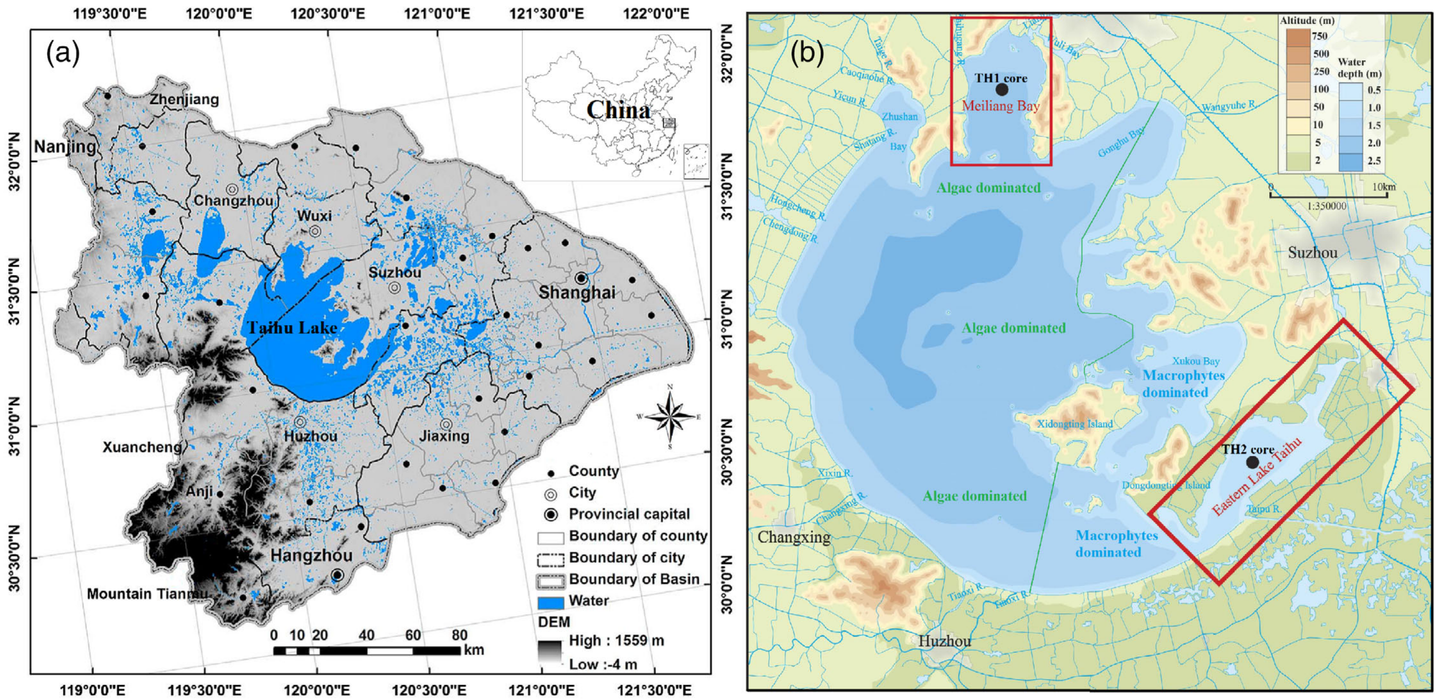

Fig. 1. Sketch map of the Taihu Lake Basin (**a**) and sampling sites of the sediment cores (**b**). The green line (**b**) generally divides Taihu Lake into two typical ecological zones: algae-dominated zones in the north and west, and macrophyte-dominated zones in the east.

elevation of 34.4 m, varying between −4 and 1559 m. The mountainous lands are in the southwest of the basin, whereas other areas are dominated by plains, accounting for approximately 80% of the basin area. The dominant soil types are yellow-brown soil, red soil, and paddy soil (agricultural land). Currently, agricultural land, urban and building land, and waterbodies account for 47.9%, 24.3%, and 13.6% of the total area of the basin, respectively (Supporting Information Fig. S1; Xu et al. 2017). There are approximately 219 rivers, with inflows going to the northern and western sides of the lake, and outflows occurring on the eastern sides (Supporting Information Fig. S2, Table S1). The lake area has a subtropical monsoon climate, with an annual average temperature of 15–17°C, annual precipitation of 1010–1400 mm, and annual evaporation of ~1001 mm.

There are seven large cities surrounding Taihu Lake (Fig. 1a) with approximately 35 million people using it as a drinking water source (Qin et al. 2008). However, water pollution (especially eutrophication) is increasing and water quality is deteriorating rapidly in the lake due to a variety of anthropogenic interventions, including forest clearance, land reclamation, agricultural fertilizer use, discharge of industrial wastewater and raw sewage, aquaculture, and intensive use of water resources (Qin et al. 2008). In May 2007, a heavy cyanobacterial bloom overwhelmed the waterworks that supplies Wuxi city on Taihu's northern shore (Fig. 1a), depriving more than 2 million people of drinking water for nearly a week, which has posed great threats to regional sustainable development and has caused significant public concern worldwide (Guo 2007). A series of countermeasures costing ~100 billion RMB (US$14 billion) addressing effluent diversion and water quality improvement were implemented after the "water crisis" (Qin et al. 2019). However, the severity of blooms in Taihu Lake has not lessened, and annual cyanobacterial blooms persist in northern and northwestern lake zones (Yang et al. 2016; Guo et al. 2019). Concurrently, the macrophyte-dominated zones and the marshy areas along the eastern shoreline are suffering from nutrient enrichment attributed to enhanced agriculture and aquaculture activities (Fig. 1b) (Zhao et al. 2013; Janssen et al. 2014).

To reconstruct primary producer community dynamics in contrasting zones of Taihu Lake, two sediment cores (~40 cm) with an intact sediment-water interface were retrieved from the center of typical ecological zones of the lake in March 2017 using a Kajak sampler (Fig. 1b). The TH1 core was obtained from Meiliang Bay, a hyper-eutrophic and algal-dominated area close to Wuxi in the north, and TH2 core was collected from Eastern Taihu Lake, a meso-eutrophic and macrophyte-rich zone (Table 1). The cores were sectioned into 0.5-cm contiguous intervals in the field, and the samples were stored frozen at −4°C. All subsamples were freeze-dried (48 h, 0.1 Pa), weighed before and after drying to calculate the water content, and then processed for dating and subsequent analyses.

Table 1. Summary of key physical and limnological characteristics of Taihu Lake.

Parameter	Meiliang Bay	Eastern Taihu
Mean depth (m)	2.7	1.2
Water area (km^2)	140	131
Macrophyte coverage (%)	<0.5	67–95
pH (mean ± 1SD)	8.6 ± 0.6	8.3 ± 0.1
TP (mean ± 1SD, $\mu g\ L^{-1}$)	128 ± 79	49 ± 10
TN (mean ± 1SD, $mg\ L^{-1}$)	2.26 ± 0.78	1.11 ± 0.38
Chl *a* (mean ± 1SD, $\mu g\ L^{-1}$)	46.34 ± 42.30	6.52 ± 3.54
SDD (mean ± 1SD, m)	0.48 ± 0.26	0.68 ± 0.24

Water quality parameter: SDD, secchi disk depth; TN, total nitrogen; TP, total phosphorus. Data collated from Taihu Laboratory for Lake Ecosystem Research and Zhang et al. (2016).

Lithology and geochemical analysis

The core sediments are composed of > 90% silt (4–63 μm) and clay (< 4 μm), and colored gray to brown/dark-brown from the bottom to the top of the cores (Lin et al. 2020). To measure total organic carbon (TOC) and total nitrogen content, samples were ground and pretreated with 1 mol L^{-1} HCl to remove carbonate, and measured using a Euro 3000 elemental analyzer. Results are expressed as percent of dry weight sediment. Standard reference materials GSS-9, GSS-13, and GSS-16 (lacustrine sediment and soil from National Institute of Metrology of China) were used as quality control, and the measured values were all within the ranges of certified values. The concentrations of sediment total phosphorus (TP) were determined by inductively coupled plasma-atomic emission spectrometry (Leeman Labs, Profile DV) after sequential digestion as described by Liu et al. (2013). The phosphorus enrichment factor, an indicator of sediment nutrient level and changes in anthropogenic nutrient loading, was calculated based on the sedimentary phosphorus concentration profiles following the method as described in Supporting Information. The ^{210}Pb age model of both sediment cores were computed with *serac* R package (Bruel and Sabatier 2020), and the chronological results have been reported in detail in our previous study (Lin et al. 2020), which suggested mean sedimentation rates of 0.39 and 0.42 cm yr^{-1} for Meiliang Bay core and Eastern Taihu Lake core, respectively, over the past ~100 yr (Supporting Information Fig. S3).

Pigment analysis

Sedimentary chlorophyll and carotenoid pigments were analyzed using an Agilent 1200 series high performance liquid chromatography (Agilent Technologies, Mississauga, Ontario, Canada) with quaternary pump, autosampler, ODS Hypersil column (250 × 4.6 mm; 5 μm particle size), and photo-diode array detector as described in McGowan (2013) with the extraction and separation conditions modified from Chen et al. (2001). Pigments were calibrated using authentic standards (DHI, Denmark) and are expressed in nmol pigment g^{-1} TOC. The ultraviolet radiation (UVR)-absorbing pigment (scytonemin derivative) identified in Leavitt et al. (1997) was divided by the sum of key carotenoids (diatoxanthin, lutein-zeaxanthin, and alloxanthin) and multiplied by 100 to derive a UVR index. Calibration in whole-lake experiments revealed that this index increases as a linear function of the depth of UVR penetration, such that higher index values indicate greater exposure to potentially damaging UVR (Leavitt et al. 1997), namely better light conditions and indicate higher water clarity.

Numerical analysis

The timings of sedimentary pigment changes were determined by a stratigraphically constrained incremental sum of squares (CONISS) cluster analysis and was performed on the standardized data in the Tilia program. For all subsequent numerical analyses, pigment abundances were $\log(x + 1)$ transformed to normalize the data and labile pigments (such as fucoxanthin) were excluded to minimize the influence of pigment degradation. Nonmetric multidimensional scaling (NMDS) analysis based on Bray-Curtis distances was performed to analyze the variations in the pigment assemblage (algal community) composition over the last ~100 yr. Three-dimensional solutions were produced to meet the criterion of a final stress < 0.2, and the algal communities were categorized into discrete groups according to the average scores (Clarke 1993).

Redundancy analysis (RDA) was conducted to explore potential relationships between fossil pigments and environmental drivers over the past several decades, when significant changes in pigment assemblages occurred and document archives were available (ter Braak and Šmilauer 2012). Up to 20 environmental variables from climate (annual mean temperature, wind speed, and total precipitation), agricultural (gross output value of agriculture, fertilizer and pesticide consumption, grain production, and cultivated land area), aquaculture (pen-fishing area), and sewage (population numbers and gross domestic product indicators) categories (Supporting Information Fig. S4) were included in the initial analysis. Archival data sets have an annual resolution to cover the fossil pigment data sets (2.5-yr resolution) for explanation. Thus, environmental data sets were adjusted to include data specific to the sub-basins of Meiliang Bay since 1960 and Eastern Taihu Lake since 1950. Data sets were checked for normal distributions and transformed as appropriate. A series of partial-RDAs were performed to evaluate to what extent the forward-selected environmental variables independently explained the variation in the fossil pigment assemblages. Redundant environmental variables with a variance inflation factor > 20 were removed before the analysis. The variance explained in all cases is that after the removal of the effect of other variables, and the significance was determined using restricted Monte Carlo permutation tests (n = 999). The gradient length of < 1 total standard deviations unit suggested that a linear model was suitable for unconstrained (NMDS) and constrained (RDA) ordinations of pigments using the program Canoco 5 (ter Braak and Šmilauer 2012).

GAMs are nonparametric data-driven regression models (Hastie and Tibshirani 1986), which are effective in assessing nonlinear relationships between response and predictor variables without any restrictive assumptions. They can improve predictive results over long-time series (Simpson and Anderson 2009; Capo et al. 2017). In the present study, GAM analysis was performed to investigate the relationships between algal community dynamics and two main forcing factors. The enrichment factors of phosphorus (anthropogenic nutrients) and the ratios of annual average air temperature to wind speed (climate) were selected as representative predictor variables as discussed below, while the response variables were sedimentary pigment concentrations of the total (ubiquitous) algal community and specific taxonomic groups (cyanobacteria, chlorophytes, chrysophytes, siliceous algae). Response variables that did not follow a Gaussian distribution were log-transformed prior to modeling. The functions *gam* and *predict.gam* from the "mgcv" package in R software were used and GAM parameterization was performed following technical recommendations from Simpson and Anderson (2009). Based on *F* tests, correlations with a significance level of $p \leq 0.05$ were considered significant for all GAM analyses. Diagnostic plots (i.e., residuals vs. fitted values plots and residuals vs. time plots) were visualized to check the robustness of performed GAMs.

Results

Lake eutrophication process

The long-term perspective beyond modern monitoring provided by the paleolimnological records of chlorophyll *a* (Chl *a*) and nutrient proxies, such as TOC, carbon to nitrogen ratio, TP, and its enrichment factors (Fig. 2), shows that both lake zones have been subjected to substantial cultural eutrophication that started asynchronously and reached different magnitudes. In Meiliang Bay where nutrient loading and lake production were higher, there is evidence of eutrophication starting ~1950 and intensifying ~ 1980. Sediment TP and Chl *a* concentrations have risen nearly 1.5-fold and 21-fold over the past six decades, respectively, with annual average of recent water TP and Chl *a* concentrations reaching nearly 126 $\mu g\ L^{-1}$ and 42 $\mu g\ L^{-1}$, respectively (Fig. 2). Our sedimentary records agree with many previous eutrophication reconstructions from this lake area, for example, sediment phosphorus chemical fractions (Liu et al. 2013), organic stable isotopes ($\delta^{13}C$, $\delta^{15}N$) (Wu et al. 2007), diatoms (Dong et al. 2008), and cladocera (Cheng et al. 2020). Diatom-inferred epilimnetic TP and sediment TP records can reasonably be used to reconstruct past lake water phosphorus concentration (Moyle and Boyle 2021), despite potential limitations necessitating caution in the application of these techniques (Juggins 2013). Our sediment phosphorus content and enrichment factor profiles in Meiliang Bay core show similar historical changes with that of previous diatom reconstruction ($r^2 = 0.85$, $p < 0.01$) (Fig. 2; Dong et al. 2008) and sediment bioavailable phosphorus (Liu et al. 2013), all of which characterize long-term increases in the lake trophic level. Moreover, recently exacerbated eutrophication is supported by modern water quality monitoring (Fig. 2), despite some peaks that cannot be captured by the sediment records due to potential sedimentation mix and limited resolution. The timings of Meiliang Bay trophic status change generally coincide with regional socioeconomic transitions in rapidly developing north Taihu Lake Basin due to the birth of the People's Republic of China in 1949 and the economic reform and open up since 1978 (Lin et al. 2019). In Eastern Taihu Lake, in agreement with increasing TP and Chl *a* from water quality monitoring, the sedimentary records indicate dramatic nutrient enrichment starting from the mid-1990s. The sediment TP and Chl *a* concentrations have risen nearly twofold and 10-fold over the past two decades, with annual average of recent water TP and Chl *a* concentrations reaching almost 48 $\mu g\ L^{-1}$ and 10 $\mu g\ L^{-1}$, respectively (Fig. 2).Therefore, multiple paleolimnological records and monitoring data collectively suggest that Meiliang Bay has longer history of eutrophication (~70 yr) and a higher trophic level than Eastern Taihu Lake (~30 yr) (Fig. 2; Table 1).

Variations in algal abundance and community structure

Similar to other shallow lakes with rapid sedimentation and burial rates (Zastepa et al. 2017; Zhang et al. 2019), our fossil pigment records in Taihu Lake suggest limited degradation issues (Supporting Information Fig. S5) (Cuddington and Leavitt 1999), and can be used to accurately track past primary productivity and algal succession. Cluster analysis of pigment assemblages in the Meiliang Bay core suggested that the algal community changed most markedly in ~1950 and ~2002 (Fig. 3a), and that pigment abundance started significantly increasing after ~1980. Notably, Chl *a* and echinenone (from cyanobacteria) in this lake area were inseparable on the liquid chromatography, so we simply merged them into one record—Chl *a* + Ech. Before 1950, the concentrations of pigments from all algae (Chl *a* and β-carotene), siliceous algae (diatoxanthin), cryptophytes (alloxanthin), colonial cyanobacteria (canthaxanthin), chlorophytes (pheophytin *b* and *b′* which are degradation products of chlorophyll *b*), and coeluted pigments from chlorophytes and cyanobacteria (lutein-zeaxanthin) were stable and relatively low, consistent with the high UVR index indicating high water clarity. After 1950, water clarity declined, and concentrations of all pigments substantially increased, indicating increasing autotrophic productivity in Meiliang Bay. Concentrations of most pigments reached a maximum in 2002 (4- to 20-fold of the 1950s levels), and then declined to intermediate levels around 2010.

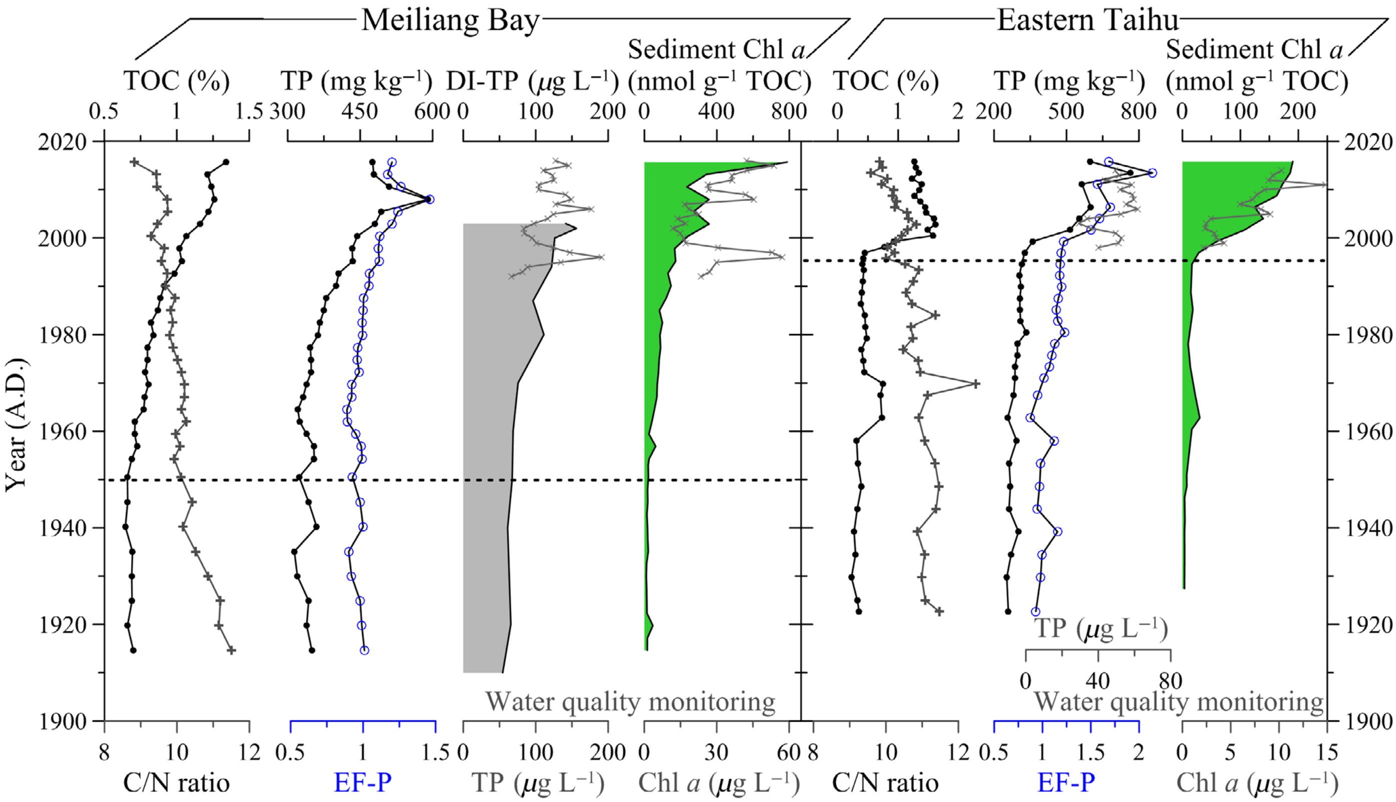

Fig. 2. Comparison of temporal changes in sedimentary nutrient proxies, Chl *a*, and modern water quality monitoring records (gray curves and text) in Meiliang Bay and Eastern Taihu Lake. Horizontal dashed lines indicate the beginnings of lake nutrient enrichment. Abbreviations of the proxies: C/N ratio, ratio of total organic carbon to total nitrogen in sediments; DI-TP, diatom-inferred epilimnetic total phosphorus from Dong et al. (2008); EF-P, enrichment factor of sediment total phosphorus.

All pigment concentrations in the top sediments were relatively high except that of canthaxanthin.

In the Eastern Taihu Lake core, cluster analysis of pigment assemblages identified periods of rapid changes centered around 1960 and 1995 (Fig. 3b). Before 1960, concentrations of β-carotene, siliceous algae, and cryptophyte pigments were too low to be detected, whereas there was low abundance of total autotrophic assemblages, colonial cyanobacteria, and chlorophytes. Between 1960 and 1995, elevated UVR index values indicated high water clarity while pigment concentrations were intermediate, except for the pigments from siliceous algae which first appeared in the sediments around 1980. After 1995, water clarity declined sharply, and there was an abrupt and substantial increase in total autotrophic assemblages (Chl *a*) and in pigments from all algal groups, which were maintained at a relatively high level after the mid-2000s (3- to 10-fold of the pre-1995 levels), indicating dramatically increased phytoplankton biomass in Eastern Taihu Lake. In contrast, the significantly lower β-carotene after 2000 may be related to the decline in macrophytes and benthic algae in this lake area, which was confirmed by remote sensing observations (Zhao et al. 2013; Zhang et al. 2016).

The NMDS analysis tracked four and three clustering groups for the fossil pigment assemblage compositions in Meiliang Bay and Eastern Taihu Lake, respectively (Fig. 3c, d), referring to the stratigraphic zones identified in the temporal cluster analysis. The main gradient of phototrophic assemblage change in both lake areas was associated with increased levels of pigments from the total algae and major taxonomic groups, all of which were highly correlated with NMDS axis 1 (95% and 73%, respectively; Fig. 3c,d). Overall, the modification in the composition of the algal community, inferred from pigment concentrations, was similar in both lake areas, indicating increased abundance in cyanobacteria, cryptophytes, chlorophytes, and siliceous algae during the transition from clear-water to turbid-water systems since ~1950 in Meiliang Bay (Fig. 3a) and ~1995 in Eastern Taihu Lake (Fig. 3b). The dominant algal community composition inferred from fossil pigments is consistent with existing algal monitoring in north Taihu Lake during 1992–2017, which suggested that cyanobacterial biomass accounted for more than half of the total phytoplankton biomass recently (Zhang et al. 2018*a*; Guo et al. 2019).

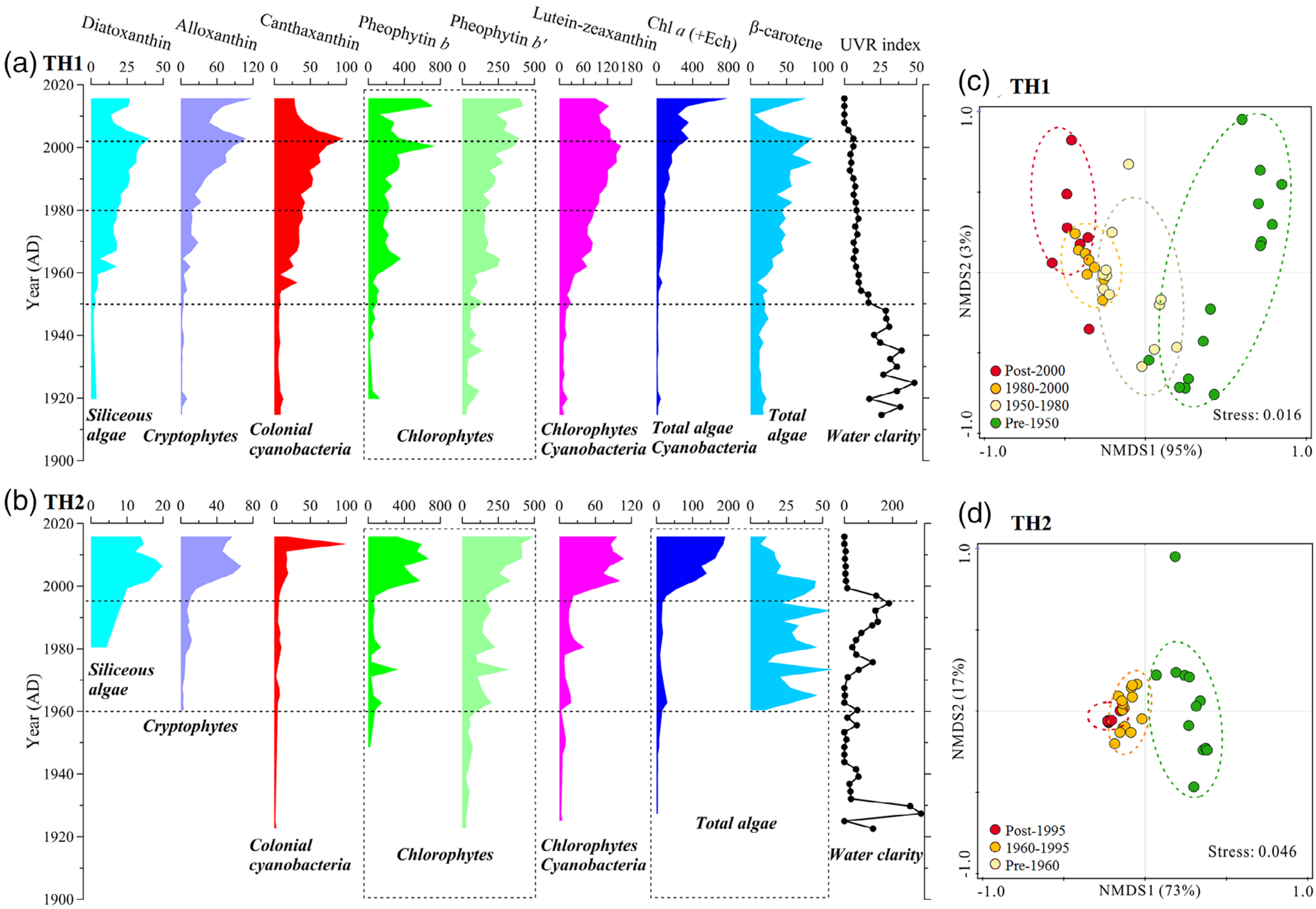

Fig. 3. Historical changes in sedimentary chlorophyll and carotenoid pigments (nmol g^{-1} TOC) and UVR index for TH1 core from Meiliang Bay (**a**) and TH2 core from Eastern Taihu Lake (**b**), and NMDS analysis of the pigment assemblage compositions (**c**, **d**). Horizontal dotted lines (**a**, **b**) indicate periods of change as determined by the CONISS cluster analysis, and dotted circles (**c**, **d**) indicate the corresponding clustering groups.

The observed covariations among fossil pigments (Fig. 3) are driven by shifts in both phototrophic communities and degradation intensity (which affects all pigments) through time. Alternatively, considering the relatively steady preservation conditions, our fossil pigment records indicated that the disturbance-induced variations in environmental factors in this large shallow lake was the dominant driver of algal biomass as synchronous algal abundance dynamics prevailed over the past century. Moreover, competitive interactions among algal communities are potential factors in modulating their composition and structure (Houlahan et al. 2007; Ewing et al. 2020). The different rates and magnitudes of changes in pigment concentrations (Fig. 3a,b) indicate variations in algal community structure. Percentage shifts in the dominant pigment types (Supporting Information Fig. S6) suggest that the community structure has been altered continuously in both lake areas during different eutrophic phases, with preferential growth of mixotrophic and eutrophic taxa, such as cryptophytes, some siliceous algae, and cyanobacteria (in Meiliang Bay only), similar to eutrophication succession sequences in many previous investigations (Sparber et al. 2015; Hu et al. 2019; Ewing et al. 2020). This pattern is also consistent with previous sedimentary diatom records in north Taihu Lake, which suggested that diatom communities changed from *Aulacoseira*-dominated to other eutrophic planktonic species (*Stephanodiscus minutulus*, *Cyclostephanos tholiformis*, and *Cyclotella meneghiniana*) as lake trophic status improved (Dong et al. 2008).

As a consequence of severe eutrophication in Meiliang Bay, however, the sedimentary pigments particularly canthaxanthin and β-carotene declined after the 2000s (Fig. 3a). This is likely to be linked to (1) self-shading and restricting light penetration of the water column caused by overall increases in phytoplankton (Zhang et al. 2018*a*), which would result in an overall decline in primary production (Bergström and Karlsson 2019); (2) production of surface cyanobacterial (*Microcystis*) blooms (Guo et al. 2019), which would be susceptible to senescence and degradation through photo-oxidation of HAB pigments, reducing their incorporation into sediments; (3) anthropogenic salvage of cyanobacterial blooms for lake management, for instance, over 10 million tons of wet algae has been harvested since 2007 (Qin et al. 2019).

Multiple anthropogenic and climatic drivers

Human activities and climate change are considered to be major drivers of freshwater ecosystem dynamics including algae succession (McGowan et al. 2012; Yang et al. 2017). Our RDA ordination included long-term environmental variables from agriculture (gross output value of agriculture), aquaculture (pen-fishing area, Eastern Taihu Lake only), sewage (population numbers), and climate (annual mean temperature and wind speed) categories. The results suggest that both anthropogenic (sewage, aquaculture, agriculture) and climate variables were strongly correlated with variations in pigment abundance and composition of both lake areas (Fig. 4).

In Meiliang Bay, axis 1 of the RDA explained 61.5% of variance and was correlated negatively with most algal pigments, and especially associated with increased population, agricultural output value, and air temperature (Fig. 4a). Wind speed was negatively related to major algal changes. Axis 2 explained 12.4% of the pigment variance and was correlated negatively with β-carotene and wind speed. According to the forward selection results of environmental variables, population, temperature, wind speed, and agriculture significantly explained 27.9%, 24.4%, 15.6%, and 6.8% of the variability in algal community, respectively (Fig. 4c). In Eastern Taihu Lake, RDA axis 1 explained 63.8% of the variance in the data sets and was correlated positively and strongly with all algal pigments except for β-carotene. The first gradient of the analysis represented all anthropogenic factors with increased aquaculture, population, and elevated air temperature (Fig. 4b). Axis 2 only explained 5.5% of the pigment variance and showed week correlation with β-carotene. The forward selection results suggested that aquaculture, temperature, and population independently explained 55.6%, 11.2%, and 4.0% of the variability in algal community, respectively (Fig. 4d). Taken together, high fossil pigment abundance was associated strongly with increased anthropogenic impacts (sewage, agriculture, and aquaculture) and elevated air temperature with distinct contributions in different lake areas. However, wind speed, which declined through time in the region (Supporting Information Fig. S4) probably associating with changes in atmospheric circulation patterns and aerosol emissions (Wu et al. 2018), only contributed to changes in the pigment assemblages in Meiliang Bay.

To further explore the impacts of anthropogenic activity and climate change on long-term algal dynamics in the contrasting lake zones, GAM analysis was performed following Capo et al. (2017) to estimate when and to what extent anthropogenic nutrient and climate variables contributed to the variations in total and taxonomic algal biomass (Fig. 5 and Supporting Information Fig. S7). Phosphorus enrichment factor and the ratios of annual average air temperature to wind speed were thus selected as representative predictor variables. In Meiliang Bay, nutrient and climate variables explained together 75.6%, 60.4%, 70.9%, 70.7%, and 69.9% of the variance in total algae and cyanobacteria (Chl a + echinenone), siliceous algae (diatoxanthin), cryptophytes (alloxanthin), cyanobacteria (canthaxanthin), and chlorophytes (pheophytin b and b'), respectively (Supporting Information Table S2). The smooth functions illustrated a linear response of total algal pigment concentration to nutrients and a significantly strong response to climate ($p < 0.001$). Siliceous algae and cryptophytes appeared to respond similarly to both predictors with nonlinear relationships because of their similar temporal changes in abundance. Cyanobacteria responded significantly to nutrients ($p = 0.015$) and climate ($p < 0.001$) while chlorophytes were only driven by nutrients ($p = 0.002$). In contrast, the GAM analysis from records of Eastern Taihu Lake showed that nutrients and climate explained 93.6%, 98.4%, 97.3%, 87.3%, and 72.6% of the variance in total algae, siliceous algae, cryptophytes, cyanobacteria, and chlorophytes, respectively, and suggested nutrient enrichment was the predominant factor influencing all algal abundance ($p < 0.001$) (Supporting Information Table S2, Fig. S7). The fitted relationships between total algae, siliceous algae, and climate were nonlinear for Eastern Taihu Lake ($p < 0.05$), indicating a certain degree of climate impacts.

Based on the pattern of driver-response described in Supporting Information Fig. S7, the GAM analysis revealed the contributions of anthropogenic nutrient and climate variables to the long-term changes in algal abundance (Fig. 5). In Meiliang Bay, the simultaneous effects of changing nutrients and climate were detected for most algae (except chlorophytes) since the 1950s, followed by significant effects detected mainly since the 1980s when lake eutrophication intensified. For total algae and cyanobacteria, the contribution of climate increased and sometimes even surpassed that of nutrients. In contrast, nutrients were the leading factor determining long-term dynamics in phototrophic assemblages in Eastern Taihu Lake; the simultaneous effects of climate were only detected for total algae and siliceous algae, which were particularly prevalent since the late-1990s.

Discussion

Synergy of anthropogenic and climatic effects

Increasing anthropogenic nutrient loading has been documented as having the most pronounced effects on primary producer communities, such as increasing algal abundance and changing community structure (Moorhouse et al. 2018; Zhang et al. 2018*a*). The north Taihu Lake Basin has

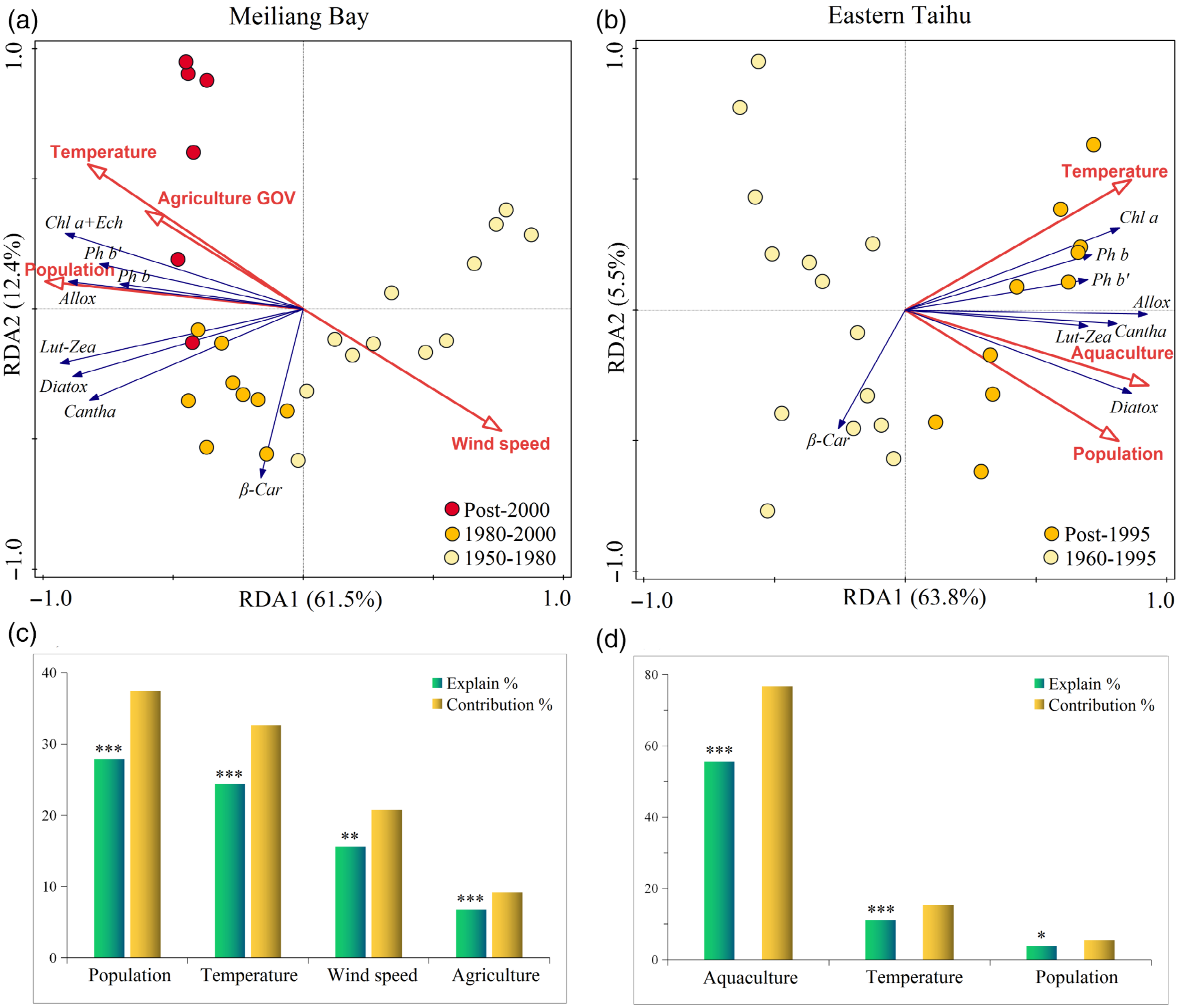

Fig. 4. Redundancy analysis illustrating the relationships between sedimentary pigments and significant ($p < 0.05$) environmental variables in core samples (filled circles) from Meiliang Bay (**a**, **c**) and Eastern Taihu Lake (**b**, **d**). Chl *a*, diatoxanthin (diatox), alloxanthin (allox), canthaxanthin (cantha), echinenone (ech), pheophytin *b* (ph *b*), pheophytin *b*′ (ph *b*′), lutein-zeaxanthin (lut-zea), and β-carotene (β-car) were included in the analysis (blue arrows, italics). Environmental variables include agriculture (gross output value [GOV] of agriculture), aquaculture (pen-fishing area, Eastern Taihu Lake only), sewage (population), and climate (annual mean temperature and wind speed) categories (red arrows, bold text). For both lake areas, independent variance explained and contribution of environmental variables with corresponding significance levels (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$) are shown.

experienced agricultural development since the 1950s, and agricultural intensification and urbanization since the 1970s–1980s (Supporting Information Figs. S1, S4) (Xu et al. 2017; Lin et al. 2019). Human disturbances on Eastern Taihu Lake are dominated by aquaculture (pen-fishing) and agriculture which has intensified since the 1990s with less urbanization (Supporting Information Fig. S4) (Zhao et al. 2013; Lin et al. 2020). Concomitantly, increasing influx of bioavailable nitrogen and phosphorus from agricultural effluent, domestic sewage and aquaculture fertilizer sources to the lake (Supporting Information Table S1, Fig. S2) increased water nutrient concentrations and accelerated algae production since ~1950 in Meiliang Bay and since the mid-1990s in Eastern Taihu Lake (Fig. 2). The most pronounced changes in phototrophic

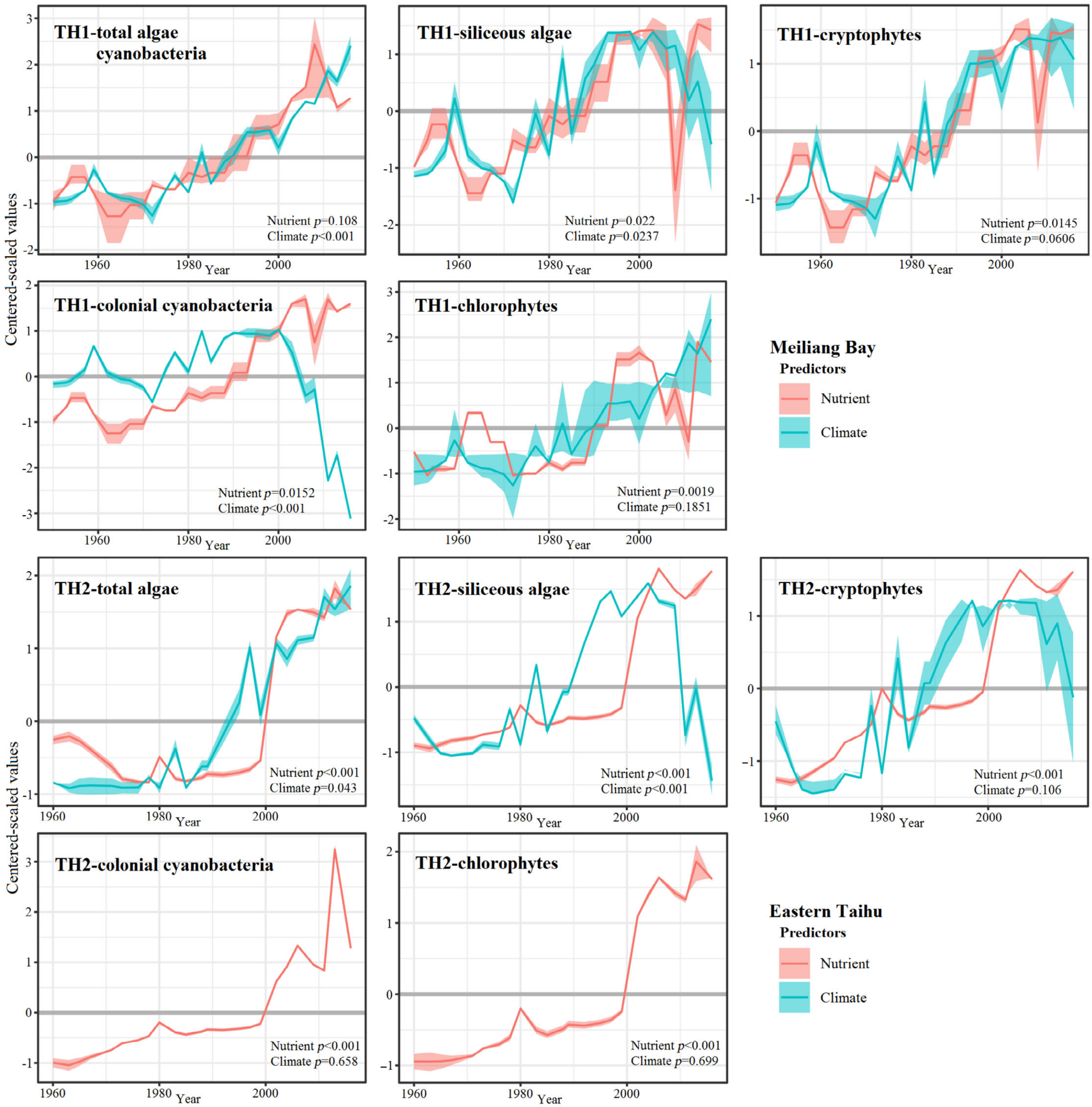

Fig. 5. Generalized additive model analysis results for total (ubiquitous) and taxonomic algal biomass. This figure presents the contribution (curves) of nutrient and climate variables (i.e., predictors) to the pigment temporal changes (i.e., response variables) from total algae and cyanobacteria (Chl *a* + echinenone), siliceous algae (diatoxanthin), cryptophytes (alloxanthin), colonial cyanobacteria (canthaxanthin), and chlorophytes (pheophytin *b* and *b*′) in Taihu Lake cores. The considered predictor variables are phosphorus enrichment factor and the ratios of annual average air temperature to wind speed. The graphs show (1) when each predictor contributes significantly (positively or negatively) and (2) how much each predictor contributes (relative importance of each predictor is deduced from the centered-scaled values on y-axis scale) to the temporal changes (increase/decrease) in a response variable (Simpson and Anderson 2009). The shaded bands are 95% confidence intervals on the estimated effect. Where the shaded bands include the zero lines, the contribution of the covariate is not statistically significantly different from the intercept. Significant correlations with predictors are shown for each response variable referring to Supporting Information Table S2.

assemblages of both lake zones occurred along with the changes in lacustrine trophic status, confirming that anthropogenic nutrient supply is the main driver of algal dynamics and HABs in most freshwater lakes (Ho et al. 2019; Birk et al. 2020).

Climate change has been widely acknowledged as a primary factor affecting eutrophication and algal communities. Temperature and light are crucial factors affecting photosynthesis and growth of photoautotrophs (Paerl and Huisman 2008; Bergström and Karlsson 2019). Warming can enhance algae growth rates and extend the growing season. Wind is also a key climatic factor affecting the function of aquatic ecosystems (Janatian et al. 2019). Wind speed plays vital roles in water stability which affects the vertical stratification, sediment resuspension, nutrient cycling, and persistence of cells in the euphotic layer of lakes (Paerl et al. 2006; Zhang et al. 2018*a*). A recent study based on ~22 yr monitoring and microcosm experiments suggested that decreasing wind speeds may strongly affect eutrophication in shallow lakes by enhancing vertical stratification, increasing bottom hypoxia, and subsequently promoting the release of nutrients from the sediments (Deng et al. 2018). Meteorological conditions within the Taihu Lake Basin changed measurably during the period of 1950–2016, including an increase in the annual average air temperature of 1.39°C, and a decline in the annual average wind speed of 1.42 m s^{-1} (Supporting Information Fig. S4). Therefore, our RDA analysis probably suggested that increasing water temperatures and decreasing wind speeds synergistically contributed to water column stability, nutrient cycling, and bioavailability as well as long-term algal growth and community dynamics in eutrophic to hyper-eutrophic north Taihu zones (Fig. 4), which is consistent with observations from the modern monitoring program (Zhang et al. 2018*b*). The significantly increased ratios of temperature to wind speed further enhanced light limitation, favoring the phytoplankton succession toward buoyant cyanobacteria—the prevalent species in nutrient-rich lakes (Carey et al. 2012; Posch et al. 2012), such as *Microcystis* in Meiliang Bay (Guo et al. 2019). In contrast, the primary producer communities in Eastern Taihu Lake mostly consist of macrophytes, benthic algae, and phytoplankton under mesotrophic conditions, which are also affected by global warming effects but at less extent (Ho et al. 2019).

Similar to previous studies (Jeppesen et al. 2005; Dong et al. 2012), partial correlations of pigment assemblages with the independent environmental variables (Fig. 4c,d) demonstrate that anthropogenic nutrients overwhelm climatic control on long-term algal community dynamics in Taihu Lake. However, in contrast with Eastern Taihu Lake where nutrient supply contributed most (82.2%) of explained variance in phototrophic assemblages, climatic effects (contribution of 53.4%) were greater in Meiliang Bay, where increasing water temperatures and decreasing wind speeds could also promote nutrient recycling via algal uptake and degradation, and sediment release processes (Fig. 6). This points to the likelihood that interactive effects of nutrients and climate can enhance eutrophication and HABs under eutrophic to hyper-eutrophic conditions, consistent with the observations by Rigosi et al. (2014) and Richardson et al. (2019).

The analyses have captured the most important drivers of lake ecosystem state changes, whereas the remaining unexplained variances (25.3% and 29.2%) seem likely to be related to hydrological fluctuations and extreme weathers (Wei et al. 2020). The annual mean water level in Taihu Lake increased by 0.38 m (~20% of lake mean water depth) from 1992 to 2016 due to climate and human disturbances (Zhang et al. 2018*b*). This hydrological fluctuation might have ecological impacts on the lake, such as decreasing underwater light availability (Zeng et al. 2018; Janatian et al. 2019), increasing phytoplankton biomass, and changing community composition (Chen et al. 2016; Yang et al. 2017), even leading to ecological shifts (Scheffer and Jeppesen 2007). Although the rising lake level would increase the risk of pigment exposure to degradation processes during sinking (Cuddington and Leavitt 1999), our fossil pigment records of Chl *a* showed generally upward trends (Fig. 3), which reinforced the interpretation of elevated primary production in Taihu Lake. Additionally, increased heavy rainfall might have accelerated lake nutrient loading through wet deposition and runoff within the cultivated catchment (Kusmer et al. 2018), and stronger winds might have promoted internal nutrient release and recycling from polluted sediments in eutrophic lakes like Taihu (Yang et al. 2016), all of which stimulate algal growth and subsequent HABs formation (Fig. 6). Overall, our results provide empirical support for the stronger responses of long-term algal abundance and community composition to synergistic effects of anthropogenic forcing and climate change than single disturbances (Yang et al. 2017; Ho et al. 2019).

Contrasting lake ecological responses

Sedimentary pigments show that there has been an overall increase in algal production over the past ~100 yr, but distinct timings and processes of community dynamics in contrasting Taihu Lake zones. In Meiliang Bay, algal production started to increase ~1950 and accelerated after 1980, with particularly substantial increases in cyanobacteria and cryptophytes, as observed in other studies of long-term lake eutrophication (McGowan et al. 2012; Zhang et al. 2019). In contrast, primary production showed abrupt increases between 1995 and 2005 in Eastern Taihu Lake, and alternating phototrophic assemblages where macrophytes, chlorophytes, and cyanobacteria (during 1960–1990) or cryptophytes and siliceous algae (after 1990) assumed greater importance. The differences in phototrophic responses, first, should be attributed to the longer and stronger anthropogenic pressures in northern parts of Taihu Lake (Qin et al. 2008; Lin et al. 2020), with more nutrient loading and accumulation, and higher trophic level. Eastern Taihu Lake is located downstream and is relatively isolated because of the poor internal connectivity that limits nutrient

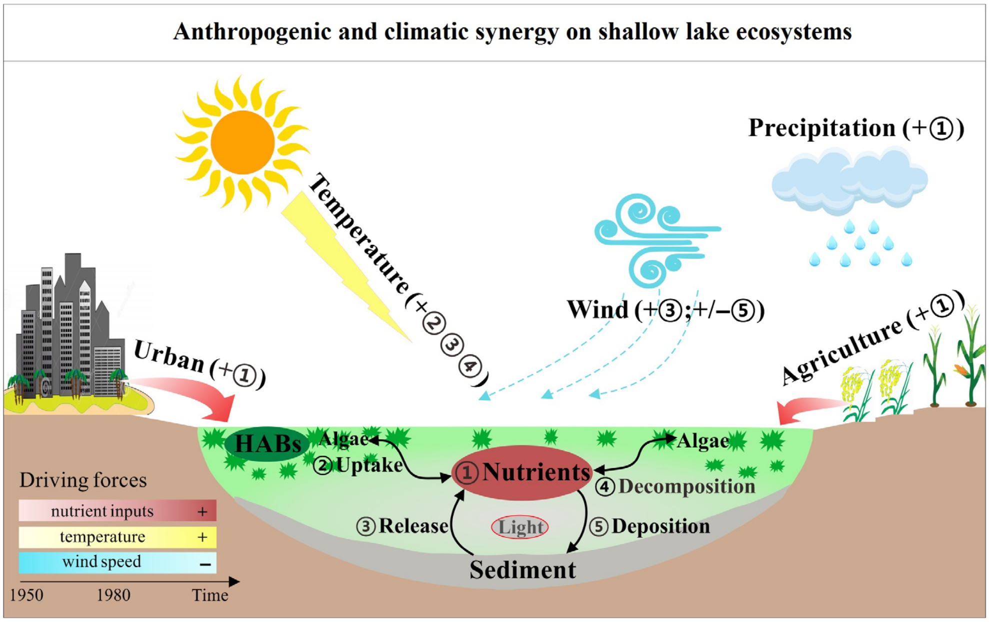

Fig. 6. Conceptual model showing the mechanisms responsible for the synergistic effects of anthropogenic nutrients and climate change on shallow lake ecosystems from a long-term perspective. The scenario of algal-dominated zone (Meiliang Bay) with HABs is depicted. ①, ②, ③, ④, and ⑤ are five main processes of nutrient cycling in the lake, namely occurrence in water, uptake by phototrophic assemblages, release from sediments, decomposition from phototrophic assemblages, and deposition into sediments. Symbols "+" and "−" denote the increasing and decreasing effects, respectively. Long-term driving forces, including anthropogenic nutrient inputs from urban and agriculture, increasing temperature, changing patterns of wind (decreasing speeds, windstorm, and constant directions to HABs), and precipitation (heavy rainfall), have intensified lake nutrient cycling and dynamics in phototrophic assemblages. Algal self-shading and underwater light attenuation are underlying factors affecting algal growth and community succession.

transport (Supporting Information Fig. S2) (Janssen et al. 2014). Second, Eastern Taihu Lake has been a macrophyte-rich area for the past century (Zhao et al. 2013) (Fig. 1b), which could absorb nutrients and buffer against the lake shift toward an algae-dominated state (Scheffer and Jeppesen 2007; Zeng et al. 2018). Even so, this lake zone has probably undergone a transition from a macrophyte-dominated to algae-dominated state, with the loss of macrophytes and increase in phytoplankton production driven by cultural eutrophication, elevated lake level, and light limitation (Zhang et al. 2016). Third, two lake zones might have responded differently to climate-related variables (e.g., warming, wind, and extreme weathers) due to their differences in drainage characteristics and ecological regime, as observed in other lake catchments (Maheux et al. 2016; Moorhouse et al. 2018; Chen et al. 2021).

According to the GAM analysis results (Fig. 5), the contribution of nutrients to long-term changes in algal biomass mostly exceeds that of climate in both lake zones, but the majority of the coupled effects of two predictors were cumulative with simultaneous positive effects from the intensification of eutrophication. For instance, after nutrient enrichment from the 1950s in Meiliang Bay, major phytoplankton responded markedly to fluctuations in climate, such as enhanced warming, lower wind speed, and extreme weathers (Yang et al. 2016). This is probably because the dominant cyanobacteria (*Microcystis*) in hyper-eutrophic Meiliang Bay could take advantage of warming both directly, from increased growth rates, and indirectly, from enhanced stability of the water column suited to its ability for buoyancy regulation (Carey et al. 2012). The resulting bloom outbreaks in the northern bays also benefited from southerly or southeasterly winds for cyanobacteria aggregation (Zhang et al. 2018*b*). Furthermore, high trophic levels, rising water levels, and climate-induced water stability can, in combination, accentuate algal self-shading and underwater light attenuation as underlying factors affecting photoautotroph growth and succession (Bergström and Karlsson 2019; Janatian et al. 2019). Taken together, the synergistic interactions of nutrients and climate acting on eutrophied shallow lake ecosystems can become more significant (Fig. 6) according to: (1) the direct effects of elevated algal growth rates and successions as well as enhanced nutrient bioavailability and cycling, and (2) the indirect effects of enhanced underwater light limitation, all which are recognized factors in promoting HABs.

Additionally, the relative importance of anthropogenic nutrients and climate change on the long-term algal dynamics was also dependent on intrinsic lake status. In lake zone with oligo-mesotrophic to eutrophic state, nutrient loading was strongly linked to primary producer biomass such as algae and macrophytes in Eastern Taihu Lake, whereas climate change only affected total and siliceous algae to some extent after the beginning of enrichment. With the development of lake eutrophication (from eutrophic to hyper-eutrophic Meiliang Bay), synergistic effects of nutrients and climate appeared to occur and became increasingly important, which also differed between algal taxa (Fig. 5 and Supporting Information Fig. S7) according to their different ecophysiological adaptations (Carey et al. 2012). For example, most chlorophytes were more sensitive to nutrients, whereas major bloom-forming cyanobacteria were more sensitive to temperature, particularly in a nutrient-sufficient environment (Jensen et al. 1994). The long-term pattern of algal response in Taihu Lake can be supported by some previous findings from in situ observations, experiments, and modeling analyses (Rigosi et al. 2014; Richardson et al. 2019; Birk et al. 2020). Therefore, the past status and development of lake ecosystems can affect the nature and magnitude of the responses to future anthropogenic and climatic stressors.

References

Bennion, H., and R. W. Battarbee. 2007. The European Union Water Framework Directive: Opportunities for palaeolimnology. J. Paleolimnol. **38**: 285–295. doi:10.1007/s10933-007-9108-z

Bergström, A. K., and J. Karlsson. 2019. Light and nutrient control phytoplankton biomass responses to global change in northern lakes. Glob. Chang. Biol. **25**: 2021–2029. doi:10.1111/gcb.14623

Birk, S., and others. 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nat. Ecol. Evol. **4**: 1060–1068. doi:10.1038/s41559-0201216-4

Bruel, R., and P. Sabatier. 2020. *serac*: A R package for ShortlivEd RAdionuclide chronology of recent sediment cores. J. Environ. Radioact. **225**: 106449. doi:10.1016/j.jenvrad.2020.106449

Capo, E., D. Debroas, F. Arnaud, M. E. Perga, C. Chardon, and I. Domaizon. 2017. Tracking a century of changes in microbial eukaryotic diversity in lakes driven by nutrient enrichment and climate warming. Environ. Microbiol. **168**: 335–351. doi:10.1111/1462-2920.13815

Carey, C. C., B. W. Ibelings, E. P. Hoffmann, D. P. Hamilton, and J. D. Brookes. 2012. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. Water Res. **46**: 1394–1407. doi:10.1016/j.watres.2011.12.016

Chen, N., T. S. Bianchi, B. A. McKee, and J. M. Bland. 2001. Historical trends of hypoxia on the Louisiana shelf: Application of pigments as biomarkers. Org. Geochem. **32**: 543–561. doi:10.1016/S0146-6380(00)00194-7

Chen, X., S. McGowan, L. Xu, L. Zeng, and X. Yang. 2016. Effects of hydrological regulation and anthropogenic pollutants on Dongting Lake in the Yangtze floodplain. Ecohydrology **9**: 315–325. doi:10.1002/eco.1637

Chen, X., S. McGowan, J. Peng, T. Zheng, X. Bai, and L. Zeng. 2021. Local and regional drivers of environmental changes in two subtropical montane ponds (central China) over the last two centuries. Ecosystems **24**: 565–582. doi:10.1007/s10021-020-00535-2

Cheng, L., G. Kattel, B. Xue, S. Yao, L. Li, and J. Liu. 2020. Application of subfossil *Bosmina* and its $\delta^{13}C$ values in tracing the long-term food web dynamics of shallow eutrophic lakes: A case in Taihu Lake, southeast China. Sci. Total Environ. **730**: 138909. doi:10.1016/j.scitotenv.2020.138909

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. **18**: 117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Cuddington, K., and P. R. Leavitt. 1999. An individual-based model of pigment flux in lakes: Implications for organic biogeochemistry and paleoecology. Can. J. Fish. Aquat. Sci. **56**: 1964–1977. doi:10.1139/f99-108

Deng, J., H. W. Paerl, B. Qin, Y. Zhang, G. Zhu, E. Jeppesen, Y. Cai, and H. Xu. 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. Sci. Total Environ. **645**: 1361–1370. doi:10.1016/j.scitotenv.2018.07.208

Dong, X., H. Bennion, R. Battarbee, X. Yang, H. Yang, and E. Liu. 2008. Tracking eutrophication in Taihu Lake using the diatom record: Potential and problems. J. Paleolimnol. **40**: 413–429. doi:10.1007/s10933-007-9170-6

Dong, X., H. Bennion, S. C. Maberly, C. D. Sayer, G. L. Simpson, and R. W. Battarbee. 2012. Nutrients exert a stronger control than climate on recent diatom communities in Esthwaite Water: Evidence from monitoring and palaeolimnological records. Freshw. Biol. **57**: 2044–2056. doi:10.1111/j.1365-2427.2011.02670.x

Duan, H., R. Ma, X. Xu, F. Kong, S. Zhang, W. Kong, J. Hao, and L. Shang. 2009. Two-decade reconstruction of algal blooms in China's Lake Taihu. Environ. Sci. Technol. **43**: 3522–3528. doi:10.1021/es8031852

Ewing, H. A., and others. 2020. "New" cyanobacterial blooms are not new: Two centuries of lake production are related to ice cover and land use. Ecosphere **11**: e03170. doi:10.1002/ecs2.3170

Guo, C., G. Zhu, B. Qin, Y. Zhang, M. Zhu, H. Xu, Y. Chen, and H. W. Paerl. 2019. Climate exerts a greater modulating effect on the phytoplankton community after 2007 in eutrophic Lake Taihu, China: Evidence from 25 years of recordings. Ecol. Indic. **105**: 82–91. doi:10.1016/j.ecolind.2019.05.034

Guo, L. 2007. Ecology—doing battle with the green monster of Taihu Lake. Science **317**: 1166. doi:10.1126/science.317.5842.1166

Hastie, T., and R. Tibshirani. 1986. Generalized additive models. Stat. Sci. **1**: 297–310. doi:10.1214/ss/1177013604

Ho, J. C., A. M. Michalak, and N. Pahlevan. 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. Nature **574**: 667–670. doi:10.1038/s41586-019-1648-7

Houlahan, J. E., and others. 2007. Compensatory dynamics are rare in natural ecological communities. Proc. Natl. Acad. Sci. USA **104**: 3273–3277. doi:10.1073/pnas.0603798104

Hu, K., G. Chen, I. Gregory-Eaves, L. Huang, X. Chen, Y. Liu, and P. R. Leavitt. 2019. Hydrological fluctuations modulate phototrophic responses to nutrient fertilization in a large and shallow lake of Southwest China. Aquat. Sci. **81**: 37. doi:10.1007/s00027-019-0633-4

Janatian, N., K. Olli, F. Cremona, A. Laas, and P. Nõges. 2019. Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. Limnol. Oceanogr. **65**: 717–731. doi:10.1002/lno.11342

Janssen, A. B. G., S. Teurlincx, S. An, J. H. Janse, H. W. Paerl, and W. M. Mooij. 2014. Alternative stable states in large shallow lakes? J. Great Lakes Res. **40**: 813–826. doi:10.1016/j.jglr.2014.09.019

Jenny, J. P., and others. 2020. Scientists' warning to humanity: Rapid degradation of the world's large lakes. J. Great Lakes Res. **46**: 686–702. doi:10.1016/j.jglr.2020.05.006

Jensen, J. P., E. Jeppesen, K. Olrik, and P. Kristensen. 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. Can. J. Fish. Aquat. Sci. **51**: 1692–1699. doi:10.1139/f94-170

Jeppesen, E., and others. 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshw. Biol. **50**: 1747–1771. doi:10.1111/j.1365-2427.2005.01415.x

Jeppesen, E., M. Beklioğlu, K. Özkan, and Z. Akyürek. 2020. Salinization increase due to climate change will have substantial negative effects on inland waters: A call for multifaceted research at the local and global scale. Innovation **1**: 100030. doi:10.1016/j.xinn.2020.100030

Juggins, S. 2013. Quantitative reconstructions in palaeolimnology: New paradigm or sick science? Quat. Sci. Rev. **64**: 20–32. doi:10.1016/j.quascirev.2012.12.014

Kong, X., and others. 2017. Hydrological regulation drives regime shifts: Evidence from paleolimnology and ecosystem modeling of a large shallow Chinese lake. Glob. Chang. Biol. **23**: 737–754. doi:10.1111/gcb.13416

Kusmer, A. S., J. O. Goyette, G. K. Macdonald, E. M. Bennett, R. Maranger, and P. J. A. Withers. 2018. Watershed buffering of legacy phosphorus pressure at a regional scale: A comparison across apace and time. Ecosystems **22**: 91–109. doi:10.1007/s10021-018-0255-z

Leavitt, P. R., R. D. Vinebrooke, D. B. Donald, J. P. Smol, and D. W. Schindler. 1997. Past ultraviolet radiation environments in lakes derived from fossil pigments. Nature **388**: 457–459. doi:10.1038/41296

Leavitt, P. R., and others. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnol. Oceanogr. **54**: 2330–2348. doi:10.4319/lo.2009.54.6_part_2.2330

Lin, Q., K. Zhang, J. Shen, and E. Liu. 2019. Integrating long-term dynamics of ecosystem services into restoration and management of large shallow lakes. Sci. Total Environ. **617**: 66–75. doi:10.1016/j.scitotenv.2019.03.307

Lin, Q., K. Zhang, E. Liu, P. Sabatier, F. Arnaud, and J. Shen. 2020. Deciphering centurial anthropogenic pollution processes in large lakes dominated by socio-economic impacts. Anthropocene **32**: 100269. doi:10.1016/j.ancene.2020.100269

Liu, E., J. Shen, H. Yuan, E. Zhang, and C. Du. 2013. The spatio-temporal variations of sedimentary phosphorus in Taihu Lake and the implications for internal loading change and recent eutrophication. Hydrobiologia **711**: 87–98. doi:10.1007/s10750-013-1465-1

Maheux, H., P. R. Leavitt, and L. J. Jackson. 2016. Asynchronous onset of eutrophication among shallow prairie lakes of the Northern Great Plains, Alberta, Canada. Glob. Chang. Biol. **22**: 271–283. doi:10.1111/gcb.13076

McGowan, S. 2013. Pigments studies, p. 326–338. *In* S. Elias [ed.], The encyclopedia of quaternary science, v. **3**, 2nd ed. Elsevier.

McGowan, S., P. Barker, E. Y. Haworth, P. R. Leavitt, S. C. Maberly, and J. Pates. 2012. Humans and climate as drivers of algal community change in Windermere since 1850. Freshw. Biol. **57**: 260–277. doi:10.1111/j.1365-2427.2011.02689.x

Monchamp, M. E., P. Spaak, I. Domaizon, N. Dubois, D. Bouffard, and F. Pomati. 2018. Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. Nat. Ecol. Evol. **2**: 317–324. doi:10.1038/s41559-017-0407-0

Moorhouse, H. L., S. McGowan, Z. E. Taranu, I. Gregory-Eaves, P. R. Leavitt, M. D. Jones, P. Barker, and S. A. Brayshaw. 2018. Regional versus local drivers of water quality in the Windermere catchment, Lake District, United Kingdom: The dominant influence of wastewater pollution over the past 200 years. Glob. Chang. Biol. **24**: 4009–4022. doi:10.1111/gcb.14299

Moyle, M., and J. Boyle. 2021. A method for reconstructing past lake water phosphorus concentrations using sediment geochemical records. J. Paleolimnol. **65**: 461–478. doi:10.1007/s10933-021-00174-0

O'Neil, J. M., T. W. Davis, M. A. Burford, and C. J. Gobler. 2012. The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. Harmful Algae **14**: 313–334. doi:10.1016/j.hal.2011.10.027

Paerl, H. W., L. M. Valdes, B. L. Peierls, J. E. Adolf, and L. J. W. Harding. 2006. Anthropogenic and climatic influences on the eutrophication of large estuarine ecosystems. Limnol. Oceanogr. **51**: 448–462. doi:10.4319/lo.2006.51.1_part_2.0448

Paerl, H. W., and J. Huisman. 2008. Climate: Blooms like it hot. Science **320**: 57–58. doi:10.1126/science.1155398

Posch, T., O. Köster, M. M. Salcher, and J. Pernthaler. 2012. Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. Nat. Clim. Change **2**: 809–813. doi:10.1038/nclimate1581

Qin, B. 2008. Lake Taihu, China: Dynamics and environmental change. Springer.

Qin, B., and others. 2019. Why Lake Taihu continues to be plagued with cyanobacterial blooms through 10 years (2007-2017) efforts. Sci. Bull. **64**: 354–356. doi:10.1016/j.scib.2019.02.008

Richardson, J., L. Feuchtmayr, C. Miller, P. D. Hunter, S. C. Maberly, and L. Carvalho. 2019. Response of cyanobacteria and phytoplankton abundance to warming, extreme rainfall events and nutrient enrichment. Glob. Chang. Biol. **25**: 3365–3380. doi:10.1111/gcb.14701

Rigosi, A., C. C. Carey, B. W. Ibelings, and J. D. Brookes. 2014. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. Limnol. Oceanogr. **59**: 99–114. doi:10.4319/lo.2014.59.1.0099

Scheffer, M., and E. Jeppesen. 2007. Regime shifts in shallow lakes. Ecosystems **10**: 1–3. doi:10.1007/s10021-006-9002-y

Simpson, G. L., and N. J. Anderson. 2009. Deciphering the effect of climate change and separating the influence of confounding factors in sediment core records using additive models. Limnol. Oceanogr. **54**: 2529–2541. doi:10.4319/lo.2009.54.6_part_2.2529

Sparber, K., C. Dalton, E. de Eyto, E. Jennings, D. Lenihan, and F. Cassina. 2015. Contrasting pelagic plankton in temperate Irish lakes: The relative contribution of heterotrophic, mixotrophic, and autotrophic components, and the effects of extreme rainfall events. Inland Waters **5**: 295–310. doi:10.5268/IW-5.3.828

Taranu, Z. E., and others. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. Ecol. Lett. **18**: 375–384. doi:10.1111/ele.12420

ter Braak, C. J. F., and P. Šmilauer. 2012. CANOCO reference manual and user's guide: Software for ordination (version 5.0). Microcomputer Power.

Wei, K., C. Ouyang, H. Duan, Y. Li, M. Chen, J. Ma, H. An, and S. Zhou. 2020. Reflections on the catastrophic 2020 Yangtze River Basin flooding in southern China. Innovation **1**: 100038. doi:10.1016/j.xinn.2020.100038

Wu, J., C. Huang, H. Zeng, G. H. Schleser, and R. Battarbee. 2007. Sedimentary evidence for recent eutrophication in the northern basin of Lake Taihu, China: Human impacts on a large shallow lake. J. Paleolimnol. **38**: 13–23. doi:10.1007/s10933-006-9058-x

Wu, J., J. Zha, D. Zhao, and Q. Yang. 2018. Changes in terrestrial near-surface wind speed and their possible causes: An overview. Clim. Dyn. **51**: 2039–2078. doi:10.1007/s00382-017-3997-y

Xu, X., G. Yang, Y. Tan, X. Tang, H. Jiang, X. Sun, Q. Zhuang, and H. Li. 2017. Impacts of land use changes on net ecosystem production in the Taihu Lake Basin of China from 1985 to 2010. J. Geophys. Res. Biogeosci. **122**: 690–707. doi:10.1002/2016JG003444

Yang, J., H. Lv, A. Isabwe, L. Liu, X. Yu, H. Chen, and J. Yang. 2017. Disturbance-induced phytoplankton regime shifts and recovery of cyanobacteria dominance in two subtropical reservoirs. Water Res. **120**: 52–63. doi:10.1016/j.watres.2017.04.062

Yang, Z., M. Zhang, X. Shi, F. Kong, R. Ma, and Y. Yu. 2016. Nutrient reduction magnifies the impact of extreme weather on cyanobacterial bloom formation in large shallow Lake Taihu (China). Water Res. **103**: 302–310. doi:10.1016/j.watres.2016.07.047

Zastepa, A., Z. E. Taranu, L. E. Kimpe, J. M. Blais, I. Gregory-Eaves, R. W. Zurawell, and F. R. Pick. 2017. Reconstructing a long-term record of microcystins from the analysis of lake sediments. Sci. Total Environ. **579**: 893–901. doi:10.1016/j.scitotenv.2016.10.211

Zeng, L., S. McGowan, Y. Cao, and X. Chen. 2018. Effects of dam construction and increasing pollutants on the ecohydrological evolution of a shallow freshwater lake in the Yangtze floodplain. Sci. Total Environ. **621**: 219–227. doi:10.1016/j.scitotenv.2017.11.181

Zhang, H., S. Huo, K. M. Yeager, Z. He, B. Xi, X. Li, C. Ma, and F. Wu. 2019. Phytoplankton response to climate changes and anthropogenic activities recorded by sedimentary pigments in a shallow eutrophied lake. Sci. Total Environ. **647**: 1398–1409. doi:10.1016/j.scitotenv.2018.08.081

Zhang, M., X. Shi, Z. Yang, Y. Yu, L. Shi, and B. Qin. 2018*a*. Long-term dynamics and drivers of phytoplankton biomass in eutrophic Lake Taihu. Sci. Total Environ. **645**: 876–886. doi:10.1016/j.scitotenv.2018.07.220

Zhang, Y., X. Liu, B. Qin, K. Shi, J. Deng, and Y. Zhou. 2016. Aquatic vegetation in response to increased eutrophication and degraded light climate in Eastern Lake Taihu: Implications for lake ecological restoration. Sci. Rep. **6**: 23867. doi:10.1038/srep23867

Zhang, Y., B. Qin, G. Zhu, K. Shi, and Y. Zhou. 2018*b*. Profound changes in the physical environment of Lake Taihu from 25 years of long-term observations: Implications for algal bloom outbreaks and aquatic macrophyte loss. Water Resour. Res. **54**: 4319–4331. doi:10.1029/2017WR022401

Zhao, D., M. Lv, H. Jiang, Y. Cai, D. Xu, and S. An. 2013. Spatio-temporal variability of aquatic vegetation in Taihu Lake over the past 30 years. PLoS One **8**: e66365. doi:10.1371/journal.pone.0066365

Acknowledgments

We are grateful to Linghan Zeng, Teresa Needham, Yuxin Zhu, Weilan Xia, Yilan Liu, Yanjie Cai, and Xi Yang for their assistance during the laboratory analyses, and Drs. Pierre Sabatier and Min Xu for the help in chronology construction. We thank the Taihu Laboratory for Lake Ecosystem Research (TLLER) for providing the water monitoring data. We would also like to thank the editors and two anonymous reviewers for constructive comments that improved the paper. This work was financially supported by the National Key Research and Development Program of China (2017YFA0605200), Science Fund for Creative Research Groups of the National Natural Science Foundation of China (41621002), the National Natural Science Foundation of China (42007284, 41772378, 41530753), the Natural Science Foundation of Jiangsu Province of China (BK20201099), and "One Hundred Talent Program" of the Chinese Academy of Sciences (Y6SL011001 to Ke Zhang).

Conflict of Interest

None declared.

Submitted 23 September 2020
Revised 02 June 2021
Accepted 05 June 2021

Associate editor: Grace Wilkinson