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Abrupt Ecological Shift and Recovery Trajectory of a Peri-Urban Lake in the Anthropocene: Insights From Paleoecology and Modeling Projection

Shixin Huang[1,2,3], Qi Lin[2], Ke Zhang[2], Yaoyao Han[2,3], Chenliang Du[1], and Ji Shen[1]

[1]School of Geography and Ocean Science, Nanjing University, Nanjing, China, [2]State Key Laboratory of Lake and Watershed Science for Water Security, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, China, [3]University of Chinese Academy of Sciences, Beijing, China

Shixin Huang and Qi Lin contributed equally to this paper.

Key Points:

- The peri-urban lake has experienced an abrupt shift and a cross-over reversal under human impacts
- Total algal biomass is projected to further increase despite management efforts
- Climate warming is weakening the efforts of nutrient reductions and enhancing the hysteresis of recovery

Supporting Information:

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

Correspondence to:

K. Zhang and J. Shen,
kzhang@niglas.ac.cn;
jishen@nju.edu.cn

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Author Contributions:

Conceptualization: Shixin Huang, Qi Lin, Ke Zhang
Data curation: Shixin Huang, Ke Zhang
Formal analysis: Shixin Huang
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Investigation: Qi Lin, Ke Zhang
Methodology: Shixin Huang, Yaoyao Han, Chenliang Du
Project administration: Ke Zhang, Ji Shen
Supervision: Ke Zhang, Ji Shen
Visualization: Shixin Huang
Writing – original draft: Shixin Huang

Abstract Urban and peri-urban lakes are undergoing significant ecological deterioration in the fast-changing Anthropocene, leading to toxic algal proliferation jeopardizing ecosystem services and public health. Nevertheless, the ecological response of these lakes to anthropogenic disturbances, management interventions, and climate change remains inadequately understood. This study examined the dynamic trajectory of the algal community from Luoma Lake, a representative peri-urban lake in eastern China, from the 1900s to 2050, based on comprehensive paleoecological investigations and model projections. Phototrophic pigment analysis indicated an exponential increase in algal abundances since the early 2000s, coupled with an abrupt community shift toward eutrophic taxa driven by rapid urbanization, agricultural and fishery practices. Recent rate-based observations suggested a reversal in algal production and cyanobacterial proliferation due to management efforts, signaling an early ecological recovery. However, model projections under two representative climate scenarios (SSP1-2.6 and SSP5-8.5) suggested continued algal abundance growth and accelerated ecological response rates until 2050. This highlighted that the anticipated benefits of nutrient reductions may be diluted by climate warming, posing a significant challenge for future urban lake management. This study underscores the necessity of incorporating climate adaptation into rate-focused management strategies to mitigate adverse ecological impacts. Our findings provide valuable insights for policymakers and contribute to the broader understanding of urban lake ecosystem responses to combined anthropogenic and climatic stressors, offering new perspectives for effective lake restoration in the context of global climate change.

Plain Language Summary Urban and peri-urban lakes worldwide not only face growing threats from multiple human disturbances and climatic forcings, but also encounter challenges from accompanying protection strategies. However, how these lakes responded to human disturbances, management efforts, and climate warming at multi-decadal scales is largely unknown. In this study, we investigated a peri-urban lake (Luoma Lake) in eastern China using lake sediment archives and projection models. Our results showed that the lake trophic level and algal community shifted to eutrophic status since the early 2000s. Human-induced nutrient loads and climate warming were the main determinants. Recently, algal abundances have decreased under effective policy-driven management, suggesting that the dynamic trajectory of the peri-urban lake does not follow the traditional, persistent degradation pathway, but in a fast reversal way. However, models predicted that future climate warming will restrain the recovery of freshwater lakes. Consequently, policymakers should take measures to mitigate global warming to prevent the exacerbation of harmful phytoplankton blooms and manage degraded lakes at a safe operating rate of ecological response.

1. Introduction

Urban/peri-urban lakes in human-dominated landscapes, being among the most vulnerable freshwater ecosystems worldwide, have been undergoing severe deterioration within the fast-changing Anthropocene. Peri-urban lakes refer to water bodies that are situated in the transition zone between urban and rural areas, often at the outskirts or fringes of expanding cities or towns (Swann et al., 2019), providing significant ecological services and economic values, such as flood control, regulating local climate, providing habitats for diverse species, recreational and esthetic value. The ecological dynamics of these lakes are shaped by the interactions between the natural environment and the effects of nearby urbanization. Currently, 55% of the global population resides in urban areas and

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Shixin Huang, Qi Lin, Ke Zhang, Yaoyao Han, Chenliang Du, Ji Shen

accompanying urban expansion results in over 80% of natural habitat degradation and significant wetlands loss (Ke et al., 2018).

Multiple anthropogenic disturbances have been posing substantial threats to urban freshwater security (Gauthier et al., 2021). Numerous studies have suggested that residential development and wastewater discharge associated with anthropogenic contamination have caused extensive lake eutrophication with the overenrichment of nutrients, harmful algal blooms, and intensified lacustrine hypoxia, leading to the significant loss of ecosystem services, and even catastrophic socio-ecological transformations (Carpenter, 2005; Janssen et al., 2021; Jenny et al., 2016; Lin et al., 2023; Scheffer et al., 2001). Future continuous urban expansion and climate change could further exacerbate lake algal proliferation and more nuisance cyanobacterial blooms (Kakouei et al., 2021; Radosavljevic et al., 2022). However, few studies provide a continuous spectrum of lake ecosystem response to environmental disturbances from the past to the future.

The distance of a lake from surrounding urban areas has been considered as a predominant factor influencing lake ecosystem health (Han et al., 2023). Given the significant socio-ecological value of urban/peri-urban lakes, massive restoration efforts have been implemented globally to alleviate eutrophication symptoms and improve ecological quality (Qin et al., 2023; Sarvilinna et al., 2018). Successes in lake restoration have been documented in Europe and other developed, densely populated regions, where improved water quality with reduced nutrient levels and phytoplankton biomass have been achieved under the great and costly treatment (Ibrahim et al., 2021; Jeppesen et al., 2005). For instance, the ecological status of Lake Jyvasjarvi, an urban lake in Central Finland, has shown marked improvement following a gradual recovery over 20 years since the 1990s (Meriläinen et al., 2003). In contrast, many urban/peri-urban lakes in China, such as Lake Taihu, Chaohu, and Dianchi experienced abrupt ecological shifts around the 1980s and thereafter continued to be plagued with cyanobacterial blooms despite extensive restoration efforts spanning several decades (Lin et al., 2023; Qin et al., 2019). Internal nutrient loadings, such as phosphorus, resulting from wind action and salinization associated with the expansion of urban stormwater management systems and impervious land cover, and extreme climate are impeding these lake restorations even though the substantial abatement of the external nutrient loadings (Lin et al., 2021; Qin et al., 2021; Radosavljevic et al., 2022; Slowinski et al., 2023; Yin et al., 2022). This restoration dilemma is rooted in the conflict between economic growth and pollution management in many developing areas globally (Qin et al., 2022). Therefore, given their profound ecological significance and economic value, effectively managing and restoring these highly human-impacted, degraded lakes remains a challenging and contentious issue, raising the critical question of how peri-urban lake ecosystems in developing regions respond to multiple anthropogenic disturbances and nutrient reductions in a warming world.

Aquatic algae communities act as natural "gauges" to measure the linear/non-linear responses of ecosystems to external disturbances (Scheffer et al., 2001). Understanding the long-term dynamics of the algal community is a priority for the sustainable management of human-impacted lakes. In this study, we investigated Luoma Lake, a typical peri-urban lake in the Huai River Basin of eastern China, utilizing multi-proxy paleolimnological records (photosynthetic pigments, nutrient indicators, and their isotopes) and model projections to explore the historical trajectory and future trend of the ecosystem state. Specifically, we aimed to address two key questions: (i) what are the dynamic trajectories of trophic status and phytoplankton community in Luoma Lake over the past century? (ii) How do the lake's primary productivity and ecosystem dynamics respond to multiple local to regional environmental forcings in the past and coming decades? This study further explored the rates of ecological change responding to human activities and climate forcings, and predicted their trends under future warming by 2050.

2. Materials and Methods

2.1. Study Area

The Huai River Basin (HRB), one of the most densely populated regions, is located in eastern China (Figure 1a), whose population density (611 persons/km^2) was more than four times as much as the average population density of China. Luoma Lake (34.0°–34.2°N, 118.0°–118.3°E) is situated in the middle-lower reach of the HRB (Figure 1a), which is a shallow lake with a mean depth of 3.3 m (maximum depth of 5.5 m), an area of 290 km^2, and a water volume of 9.18×10^8 m^3. The annual volume of inflows and outflows (2009–2020 CE) were 30.0×10^8 and 24.7×10^8 m^3, respectively. The water of Luoma Lake is exchanged 10 times a year. The concentrations of TN, TP, and Chl-a in Luoma Lake were 2.32, 0.05, and 18.84 μg L^{-1} in 2018, respectively, which was considered as lightly eutrophic based on comprehensive trophic level index (TLI > 50) (Hu et al., 2022). The

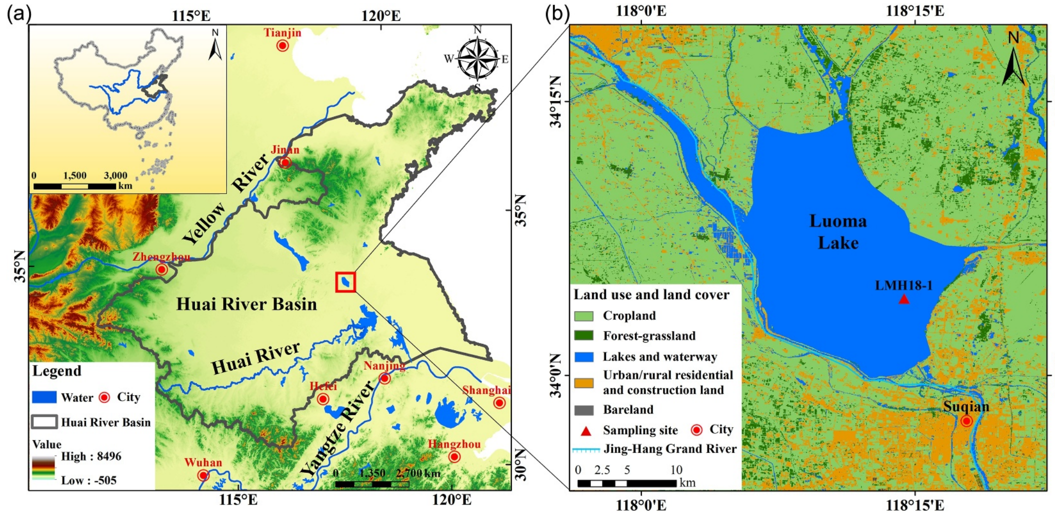

Figure 1. Geographical maps of (a) the Huai River Basin and (b) Luoma Lake, depicting the land-use and land-cover changes and the sampling site of the LMH18-1 sediment core.

lake basin is mainly dominated by the warm temperate semi-humid monsoon climate. The annual average temperature and total precipitation (1960–2018 CE) were approximately 14.9°C and 831.5 mm, respectively.

Luoma Lake is a peri-urban lake close to Suqian City and Xuzhou City in Jiangsu province, which is passed through by the Beijing-Hangzhou Grand Canal, the longest artificial river worldwide. Luoma Lake provides significant ecosystem services, including drinking water, tourism, aquaculture, flood control, navigation, and agricultural irrigation. Moreover, Luoma Lake serves as a vital regulating reservoir for China's South-to-North Water Diversion Project, Eastern Route, whose water quality greatly affects the drinking water safety of northern China.

2.2. Sampling and Laboratory Analyses

2.2.1. Sediment Coring and Chronology

A 54-cm long sediment core (LMH18-1) with an intact water-sediment interface was collected from the eastern section of Luoma Lake (Figure 1b) in July 2018 using a Kajak sampler. The sampling site is close to Suqian City with minimal disturbance of sediments, providing a good case to explore the ecological effect of urbanization. The sediment core was subsampled at 0.5-cm intervals. Subsamples for pigment analysis were freeze-dried in darkness and stored in the freezer before analysis. The other freeze-dried samples were prepared for subsequent analyses of radioactive isotope dating, and physicochemistry proxies.

The sediment core chronology was determined by radioactive isotope ^{210}Pb, ^{226}Ra, and ^{137}Cs activities of sediments at 1.5-cm intervals on a gamma spectrometry (Appleby, 2002). The concentration of excess ^{210}Pb ($^{210}\text{Pb}_{\text{ex}}$) was calculated by subtracting the specific activity of ^{226}Ra-supported ^{210}Pb ($^{210}\text{Pb}_{\text{sup}}$) from the total ^{210}Pb activities ($^{210}\text{Pb}_{\text{total}}$). The analytic methods of sediment grain size, total phosphorus (TP), total organic carbon (TOC), total nitrogen (TN), stable isotopes of organic carbon (δ^{13}C) and nitrogen (δ^{15}N) are detailed in Text S1 in Supporting Information S1.

2.2.2. Sedimentary Pigment Analysis

Pigment analysis was conducted at 1-cm intervals at the Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences. Sedimentary chlorophyll and carotenoid pigments were extracted and purified following the standard procedures (Leavitt & Hodgson, 2001; McGowan, 2013), to reflect changes in the abundance and composition of the algae community (see, Text S2 in Supporting Information S1). Individual compounds were separated and quantified using an Agilent High-Performance Liquid Chromatography (HPLC) 1260 series with a quaternary pump, auto-sampler, Poroshell 120 EC-C18 column (150 × 3.0 mm, 2.7 μm particle size). The concentrations of pigments are expressed as nmole pigment g^{-1} TOC.

Altogether 12 pigment biomarkers were separated and identified from the LMH18-1 sediment core. Chlorophyll-a (Chl-a), its general derivative pheophytin-a (Pheo-a), and β-carotene (β-car) were used as indicators of the total algae (Leavitt & Hodgson, 2001). Diatoxanthin (Diato) was applied to estimate siliceous algae (diatoms and chrysophytes), and alloxanthin (Allox) for cryptophytes. Lutein, chlorophyll-b (Chl-b), pheophytin-b (Pheo-b), and its deviation pheophytin-b' (Pheo-b') were selected to indicate the chlorophytes, and canthaxanthin (Canth), echinenone (Ech) and zeaxanthin (Zea) for cyanobacteria. Here, the sum of concentrations of Chl-a and Pheo-a (expressed as Chl-a + Pheo-a) was used to indicate the total algal productivity, and the sum of canthaxanthin, echinenone, and zeaxanthin concentrations was calculated to represent total cyanobacterial abundances.

2.3. Historical Climate Records and Future Scenarios

Annual air temperature and annual precipitation data spanning 1901−2018 CE were obtained from the Climatic Research Unit database (CRU; http://www.cru.uea.ac.uk/) of the University of East Anglia with a 0.5° × 0.5° resolution (CRU TS v4.0) (Harris et al., 2020).

Projected annual near-surface air temperature time series spanning 2019−2050 CE under two scenarios of combinations of the Shared Socioeconomic Pathway (SSP) and Representative Concentration Pathway (RCP) (i.e., SSP1-2.6, SSP5-8.5) were extracted from the ensemble of 27 global climate projection models in Coupled Model Inter-comparison Project Phase 6 (CMIP6) experiment (https://esgf-node.llnl.gov/search/cmip6/). These two scenarios provide a comprehensive framework by considering the potential pathways and uncertainties of future socio-economic factors and span a broad range of potential future anthropogenic forces and risks (see details in Text S3 in Supporting Information S1).

2.4. Numerical Analyses

Non-metric multidimensional scaling (NMDS) was performed on pigment assemblages to reflect the algae community structure using Bray-Curtis distance in the *R* package *vegan* (Oksanen et al., 2018). Temporal trends in pigment assemblages were estimated using generalized additive models (GAMs) in the *mgcv* package (Wood, 2018). Additionally, the Rates of Change (RoC) analysis was conducted using the *mgcv* and *gratia* packages (Simpson, 2018, 2019) to estimate rates of ecological response and environmental forcing change per unit of time following the detailed method in the reference (Huang et al., 2022) (Texts S4.1 and S4.4 in Supporting Information S1).

Random forest analysis was used to estimate the relative significance of predictor variables to the phytoplankton community (Breiman, 2001) using the *R* packages *randomForest* (https://cran.r-project.org/web/packages/randomForest) and *rfPermute* (Archer, 2020) (Text S4.2 in Supporting Information S1). The significant environmental stressors were selected as predictor variables (Figure S1 and Text S3 in Supporting Information S1), including the Gross Domestic Product (GDP), fishery outputs (Fishery), agriculture outputs (Agri), annual average temperature (Tem), and annual precipitation (Pre), to examine the possible effect of urbanization, agriculture and aquaculture activities, and climate forcings on lake algal community.

Given the potential effect of different warming scenarios on lake primary productivity and cyanobacteria, GAMs here were performed to project total algal and cyanobacterial abundances during 2019–2050 CE using the *mgcv* package based on empirical relationships between historical algal abundances and environmental data. More details are presented in Text S4.3 in Supporting Information S1.

3. Results

3.1. Sediment Lithology and Chronology

LMH18-1 sediment core was mainly composed of clay (<4 μm) and fine silt (4–16 μm), and the median grain size (Md) ranged from 2.7 to 7.9 μm (Figure S2 in Supporting Information S1). The $^{210}Pb_{ex}$ activities generally declined exponentially with depth ($R^2 = 0.81$). The Constant Rate of Supply (CRS) model could provide a good age model for LMH18-1, allowing changes in initial concentrations and sedimentation rates over time (Appleby & Oldfield, 1978). The ^{137}Cs activity profile showed one well-defined ^{137}Cs peak at 39 cm, corresponding to the fallout peak of ^{137}Cs from nuclear weapons testing in 1963 CE (Ritchie & McHenry, 1990), which was consistent with many lakes in China (Lan et al., 2020). The well-defined 1963-^{137}Cs fallout peak could be used as an independent time marker to constrain the chronology. Thus, the ^{137}Cs-corrected CRS model was established for

LMH18-1 using the *R* package *serac* (Bruel & Sabatier, 2020), covering the past ∼120 years (Figure S2 in Supporting Information S1).

3.2. Sedimentary Geochemistry and Lake Trophic Status

Sedimentary geochemical records of TOC and TN exhibited an obvious increase during the 1990–2000s, followed by a stable phase and slightly declined contents in the recent decade (Figure S3a and Text S5 in Supporting Information S1). TOC contents varied between 0.43% and 1.89% and TN contents ranged from 0.09% to 0.30%. Sedimentary burial rates of TOC and TN showed a similar changing trend to their contents, presenting a steady trend before the 2000s with an average burial rate of 17.62 and 2.97 g m^{-2} yr^{-1}, respectively, a significantly elevated phase during the 2000–2010s with a maximum burial rate of 101.69 and 15.96 g m^{-2} yr^{-1}, respectively, particularly as well as a declining trend in the recent decade (Figure S3b in Supporting Information S1). The molar ratio of TOC to TN (C/N) was lower than 10 (ranging from 4.67 to 9.27) and relatively stable throughout the sediment core. Corrected sediment δ^{13}C values (−22.81‰ to −19.93‰) declined steadily from the 1950s, while δ^{15}N values (5.54–8.65‰) increased markedly after the 2000s and stabilized. The concentration of TP, ranging from 588.16 to 681.51 mg kg^{-1}, depicted a gradually declined trend, followed by an abrupt increase and then decrease in the recent decade. However, the TP burial rates, ranging from 0.23 to 3.60 g m^{-2} yr^{-1}, presented the opposite temporal trend before the 2000s and thereafter showed a similar abrupt shift. The enrichment factor of phosphorus (EF-P) showed a similar increasing trend to that of TP burial rates, followed by a downward trend in recent years. The molar ratio of TOC to TP, ranging from 17.16 to 77.23, has increased since the 1990s and stabilized at a high level until the 2000s with an average of 72.03, resembling the general trend of TOC. The constrained incremental sum of squares (CONISS) analysis of TN, TOC, C/N, EF-P, and δ^{15}N in Tilia 2.6.1 (Grimm, 2011), indicated a shift in lake trophic status in the 2000s (Figure S3 in Supporting Information S1).

3.3. Historical Changes in Algal Productivity and Community

Analyses of sedimentary pigments, including major carotenoid and chlorophyll pigments, revealed good preservation conditions and significant changes in the abundance and composition of phytoplankton community over the past century (Figure 2a, Figure S4 in Supporting Information S1). The ratio of chlorophyll-a to pheophytin-a (Chl-a/Pheo-a) was used to follow the preservation conditions of sedimentary pigments in this study (Leavitt & Hodgson, 2001). The temporal trend of Chl-a/Pheo-a showed a little variation before the 2000s, and thereafter increased significantly, coeval with increases in TOC contents and TOC/TP (Figure S3 and S4 in Supporting Information S1), suggesting the enhanced preservation of pigments in an anoxic environment as the improved lake primary productivity (McGowan et al., 2012; Slowinski et al., 2023). Additionally, whether labile pigments with oxygen- or N-rich functional assemblages (e.g., Chl-a) or less labile and chemically reliable pigments (e.g., Pheo-a, Allox) exhibited a similar historical trend indicated the limited variations in post-depositional pigment degradations of LMH18-1 sediments (Figure S4 in Supporting Information S1; more details in Text S6 in Supporting Information S1) (Leavitt & Hodgson, 2001; McGowan et al., 2012; Reuss et al., 2005). Pigment concentrations of total algae (Chl-a, Pheo-a, β-car), siliceous algae (Diato), cryptophytes (Allox), chlorophytes (Lutein, Chl-b, Pheo-b, Pheo-b'), and cyanobacteria (Canth, Ech, Zea) were generally low and stable across the 20th century. Subsequently, all pigment abundances increased exponentially after the early 2000s (Figure 2a). Particularly, total algal abundances (Chl-a + Pheo-a) increased 10-fold, and some bloom-forming algal pigment abundances increased 20-fold (e.g., Zea and Lutein). However, many pigment abundances have begun to decline recently, especially total cyanobacteria (Canth + Ech + Zea) (Figures 2 and 3). Temporal dynamics in the algal community structure measured as changes in NMDS1 scores of pigment assemblages showed a substantial turnover during the 2000s (Figure 2d and Figure S5 in Supporting Information S1).

Additionally, random forest analysis revealed that GDP, agriculture outputs, aquaculture outputs, temperature, and precipitation were strongly correlated with historical variations in lake primary production, total cyanobacteria, and phytoplankton community (NMDS1), which together captured 77%, 92%, and 86% of explained variation, respectively (Figures 2e–2g). The GDP, agriculture and aquaculture activities are equally the most significant, indicating the effect of substantial nutrient influxes on lake algal community dynamics, especially cyanobacterial proliferation (Figure 2). Importantly, both the total algae and cyanobacteria community exhibited non-linear responses to environmental forcings (Figure S6 in Supporting Information S1).

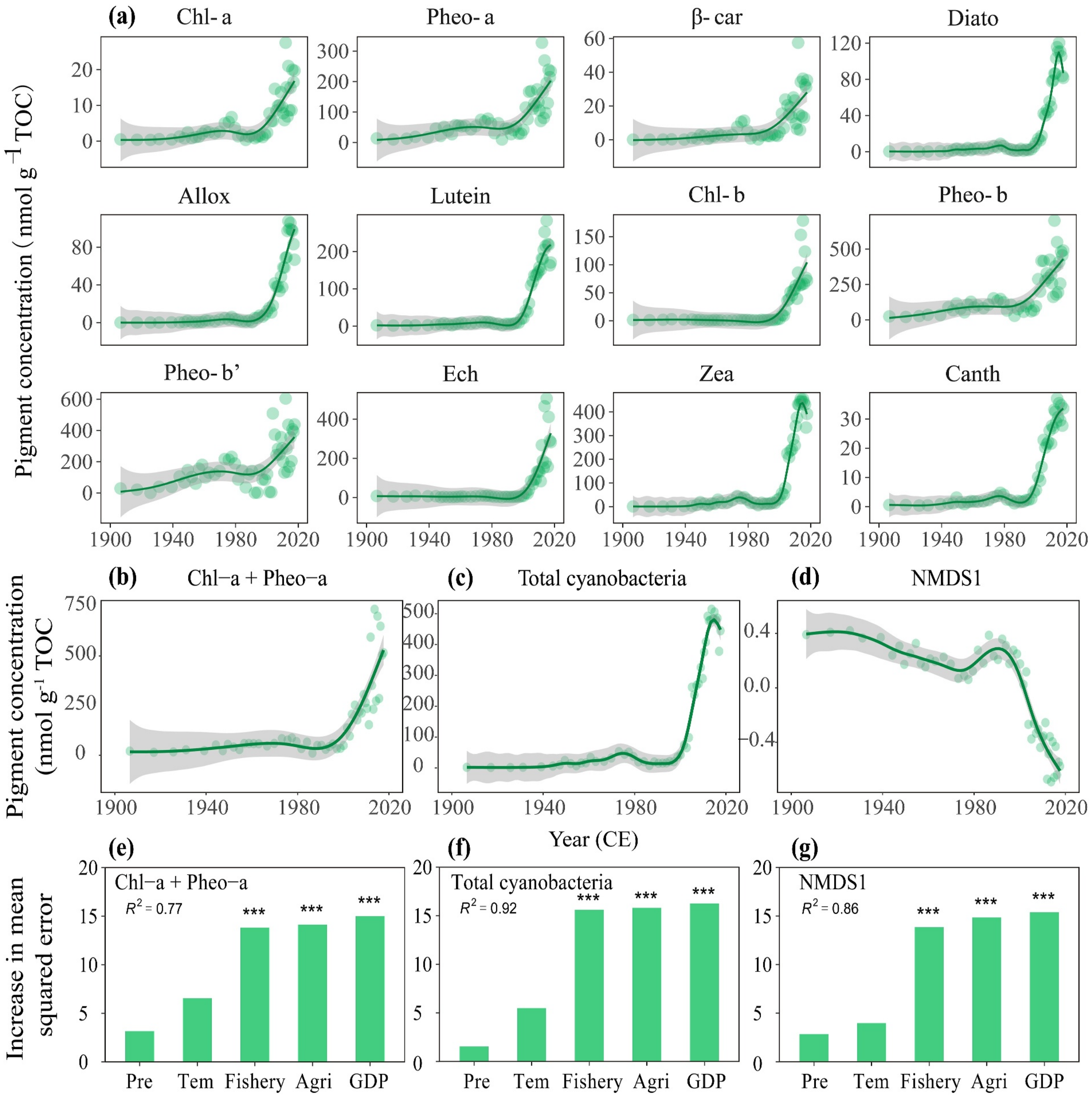

Figure 2. Sedimentary pigment records and environmental driver analyses. Algal abundances are fitted using GAMs (solid lines) with 95% confidence intervals shown as shadow areas (a–d). The ranking of significant drivers of phytoplankton changes was conducted using random forest (e–g; ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Detailed model summaries of GAMs for pigment assemblages are listed in Table S1 in Supporting Information S1. Full names of abbreviations in (a–b) are chlorophyll-a (Chl-a), pheophytin-a (Pheo-a), β-carotene (β-car), diatoxanthin (Diato), alloxanthin (Allox), lutein (Lutein), chlorophyll-b (Chl-b), pheophytin-b (Pheo-b), pheophytin-b' (Pheo-b'), echinenone (Ech) and zeaxanthin (Zea), canthaxanthin (Canth), and the sum of concentrations of Chl-a and Pheo-a (expressed as Chl-a + Pheo-a).

3.4. Projected Trends of Temperature, Total Algal and Cyanobacterial Abundances

Climate warming played a significant role in affecting phytoplankton variations (Figure 2). To estimate the effect of future climate change on algal abundances and explore the potential range of ecological responses, this study defined two 20-year periods, one as a historical baseline condition (1980–2000 CE) and one as a future projection period (2030–2050 CE). The historical period was set to account for the pre-period of the algal community shift during the 2000s. Projection models in CMIP6 illustrated that temperature was projected to increase by 11.5% (1.70°C) and 13.5% (1.98°C) in the future horizon under the SSP1-2.6 and SSP5-8.5 scenarios, respectively, as compared to the historical condition.

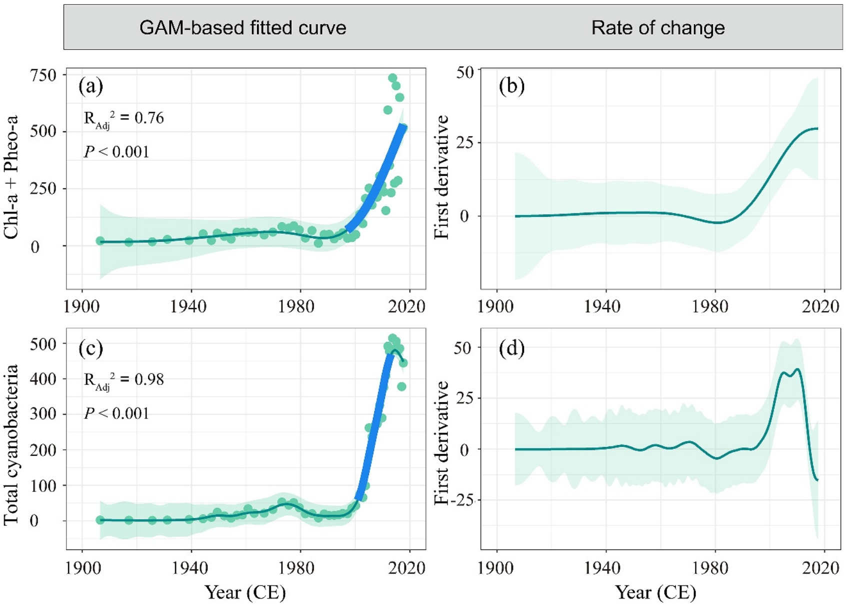

Figure 3. Rates of change analyses of historical sedimentary pigment concentrations of total algae and total cyanobacteria. The bolded sections (blue lines) in the first column demonstrate significant increases in algal abundances, which were identified from the periods of their first derivatives and 95% simultaneous confidence intervals of GAM-fitted trends deviating from zero.

In GAMs, the fitting model of the training data set revealed the significant relationships between the historical abundances of the total algae ($R^2 = 0.83$, $p < 0.001$) and total cyanobacteria ($R^2 = 0.98$, $p < 0.001$) with predictor variables, providing the well empirical model for predicting the algal response. Under two warming scenarios with current environmental policy, projected total algal and cyanobacterial abundances also indicated highly fitting relationships with their historical variations and were expected to increase continuously (Figure S7 in Supporting Information S1). Total algal and cyanobacterial abundances under the sustainable scenario (SSP1-2.6) were projected to increase 12-fold and 18-fold, respectively, compared with average abundances during the historical period (1980–2000 CE). Changes in total algal abundances under the aggressive scenario (SSP5-8.5) were greater than those under the sustainable scenario, while cyanobacterial abundances were slightly different under these two scenarios.

3.5. Rates of Changes in Ecological Response

The temporal trends of algal pigment abundances provided a significant record, allowing the estimation of historical changes in lake primary production and cyanobacterial biomass, and the rate of ecological response over the past ~120 years (Figure 3). We observed that, unlike the ever-increasing trend of total algal abundances since the late 1990s, the RoC of total algae exhibited a rapid increase and reached a peak during the early 2010s (Figure 3b). The RoC of cyanobacterial abundances showed a steady trend before the late 1990s, and thereafter increased significantly to the obvious plateau during the 2000s, followed by a downward trend (Figure 3d).

The projected temperature under SSP1-2.6 exhibited a slight increase by 2050 CE, while the SSP5-8.5 scenario revealed a most severe warming trend (Figure 4a). Under these two scenarios, we explored the whole range of possible variability in algal abundances responding to future warming. By the mid-21st century, changes in rates of algal responses to the magnitude of warming under SSP5-8.5 would be significantly greater than those under SSP1-2.6. Although a rather low RoC was projected for cyanobacteria, total algal abundances would continue to increase at a uniformly steady rate under the sustainable scenario, while accelerating under the aggressive scenario (Figure 4, Figure S7 in Supporting Information S1). However, the RoC of phytoplankton abundances in future scenarios was significantly lower than that during the historical accelerated period (the 2000s–2018).

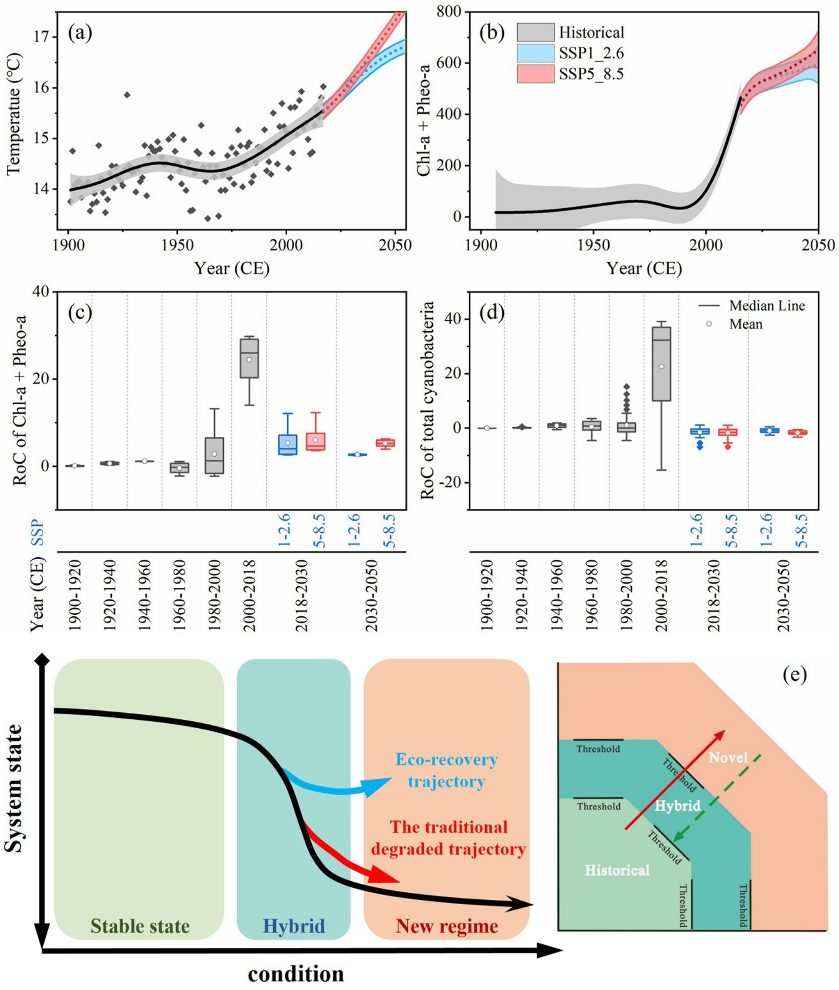

Figure 4. Simulation and projection of long-term lake ecological responses. Variations in GAM-fitted historical annual temperature and total algal abundances, as well as their projections under the SSP1-2.6 and SSP5-8.5 scenarios, are presented (a–b). Box plots display the RoC of the historical and projected total algal and cyanobacterial abundances every 20 years (c–d). The conceptual framework of the long-term lake ecological trajectories and potential regime shifts of degraded lakes is depicted in (e) referring to Hobbs et al. (2009).

4. Discussion

4.1. The Mechanism Underlying Peri-Urban Lake Ecosystem Dynamics

High-resolution paleolimnological analyses of sediment geochemistry and fossil pigments revealed an abrupt ecological shift in pei-urban Luoma Lake during the 2000s, characterized by fast elevated lake trophic level and primary productivity, as well as the abnormal proliferation of eutrophic algal taxa and nauseous cyanobacteria. Random forest and GAMs analyses suggested that these shifts in the lake phytoplankton community were primarily attributed to long-term nutrient enrichments from urbanization, aquaculture, and agricultural practices, in conjunction with rising temperature (Figure 2 and Figure S3 in Supporting Information S1). Moreover, the phytoplankton community exhibited a non-linear response to anthropogenic disturbances (Figure S6 in Supporting Information S1), indicating that the lake ecosystem has deviated from its equilibrium states under external perturbations (Scheffer et al., 2001). Nutrient enrichment and climate warming are the most pervasive and intractable causes driving algal community dynamics in freshwater lakes, pushing lakes into unprecedented ecological states (Lin et al., 2021; Oleksy et al., 2020). In specific, anthropogenic nutrient over-enrichment promoted algal production, particularly the proliferation of bloom-forming cyanobacteria, and smothered aquatic macrophytes, which could thereby suppress important invertebrate and fish habitats. Moreover, this dynamic process may have diminished the stability and resilience of lake ecosystems, resulting from an adverse feedback mechanism (Paerl & Huisman, 2008; Scheffer & Jeppesen, 2007; Scheffer et al., 2012).

The rapid expansion of enclosure aquaculture in Luoma Lake, increasing from approximately 20 km^2 in 1994 to 88 km^2 in 2015, has placed significant pressure on lake water quality due to non-point source pollution and in-lake nutrient enrichments (Figure S1 in Supporting Information S1). Additionally, agriculture outputs have nearly tripled over the past three decades, and the urbanization rate of Suqian City escalated from 24% in 2000 to 60% by 2018, leading to substantial nutrient influxes and serious water environmental problems. Nevertheless, in pursuit of regional sustainable development, various lake-watershed management efforts have been implemented, such as the “Fishing Ban” policy, “No sand mining”, “Returning farmland to the lake”, lake rehabilitation through dredging, and upgrading of sewage treatment plants. In recent years, fertilizer usage and enclosure aquaculture areas have dropped significantly (Figure S1 in Supporting Information S1). Particularly, the enclosure aquaculture areas have declined to 74 km^2, and natural lake areas have expanded from 207 km^2 in 2015 to 222 km^2. These proactive management efforts have resulted in recent declining trends of sedimentary nutrients, algal production, and cyanobacterial abundances, as an alternative stable state has not yet been established (Figures 2 and 3). Regulating nutrient loading therefore could be a preferred option for bringing degraded aquatic ecosystems to a desired state before catastrophic transitions, thereby maintaining ecological resilience, especially for those in densely populated developing areas (Scheffer et al., 2001). In contrast, considerable empirical evidence illustrated that the ecological status of highly degraded lakes in developed urban landscapes has been improved by costly restoration efforts but is hard to reverse due to ecological hysteresis with a positive feedback loop associated with an alternative stable state (Ibrahim et al., 2021; Makri et al., 2018; Su et al., 2020).

Climate change acts as a potent catalyst for the further expansion of bloom-forming algal taxa despite nutrient reductions (Paerl & Huisman, 2008, 2009). The more pronounced increase in temperature under the SSP5-8.5 scenario lengthens the optimal growth period for algae, resulting in enhanced warming effects and increased algal biomass (Chapra et al., 2017; Kakouei et al., 2021). Furthermore, the potential synergistic effect of anthropogenic nutrients and climate warming from a long-term perspective, could be more prone to stimulate algal growth (Figure S8 in Supporting Information S1), particularly buoyant cyanobacteria, and further result in catastrophic ecological shifts (Gauthier et al., 2021; Lin et al., 2021, 2023; Rigosi et al., 2014; Zhang et al., 2024). However, it should not be neglected that the limited effect of short-term natural disturbances (e.g., cooling, rainfall events) on cyanobacterial blooms (Luo et al., 2022; Yang et al., 2017). Collectively, both historical records and future projections of algal abundances demonstrated that the increasing temperature substantially contributes to changes in lake primary productivity, exacerbating cultural eutrophication. Furthermore, the modern monitoring data of Luoma Lake in 2019 CE (TN: 2.63 $mg\ L^{-1}$, TP: 0.057 $mg\ L^{-1}$, Chl-a: 20.87 $\mu g\ L^{-1}$) indicated the elevated lake primary production in a warming world, validating the substantial influence of climate warming (Hu et al., 2022). Nevertheless, it is worth mentioning that there were still several uncertainties and limitations of the ecological projection model based on GAMs. For instance, GAMs assumed additive effects among predictive variables when capturing nonlinear response relationships, potentially neglecting critical synergistic interactions to ecological dynamics. Furthermore, it is hard to model the complex ecological response using the limited environmental forcings due to the inherent variability of ecosystems. Therefore, GAMs were employed here to preliminarily identify potential stressor-response relationships between algal abundances and significant environmental variables (temperature and anthropogenic nutrient influxes) using a centurial scale sedimentary archive. Based on this empirical relationship, we emphasized the exploration of the great influence of future warming on algal dynamics under two scenarios with distinct warming magnitudes.

4.2. Managing Rates of Lake Ecological Response and Degradation Pathway

Rates of change analyses revealed the unprecedented acceleration in algal productivity and cyanobacterial proliferation in Luoma Lake since the 2000s, making a significant shift over the past century (Figure 3). The recent decline in RoC evidenced that the rapidly elevated cyanobacterial abundance has been depressed by management efforts. However, under different magnitudes and rates of future warming scenarios in CMIP6, the ecological dynamics of lake primary producers and cyanobacteria exhibited distinct responses at varying rates.

Under the sustainable SSP1-2.6 scenario, the slow increase in annual temperature by the mid-21st century contributed to a stable ecological response, supported by proactive and pragmatic government management (Figure S7 in Supporting Information S1). In contrast, a substantial increase in ecological response rates under

SSP5-8.5 proved that higher temperatures would weaken the effects of nutrient reductions by multiple interactive mechanisms (Smol et al., 2005). In addition, climate warming could retard the eco-recovery process. The ecological hysteresis of recovery, seen in urban shallow lakes such as Donghu Lake in eastern China, highlights the diminished effectiveness of nutrient control, even when extensive management measures were employed (Su et al., 2020). Additionally, internal nutrient release and top-down control may also influence recovery in shallow lakes (Bennion et al., 2015). Ecosystem recovery, thereafter, is not merely a straightforward reversal of the degradation pathway, it may require several decades of concerted efforts to achieve a relatively ideal ecological status with a safe operating rate of ecological response.

Despite the pronounced ecological deterioration observed in urban/peri-urban lakes, these ecosystems are also receiving more attention for restoration due to serving significant landscape functions, including substantial environmental investments and high resident participation (Han et al., 2023; Sarvilinna et al., 2018). Our analysis of the dynamic trajectory of the peri-urban Luoma Lake ecosystem has demonstrated an unusual crossover reversal toward the eco-recovery pathway and increased resilience, deviating from the traditional, persistently degraded pathway that typically crosses the critical thresholds and exhibits a regime shift pattern (Figure 4e) (Scheffer et al., 2001). For instance, the variance and RoC of phytoplankton continuously increased after the ecological shift in China's Taihu Lake located in the highly urbanized Yangtze River Delta, suggesting increased ecosystem vulnerability and resilience loss with the potential risk of shifting to a novel normal (Lin et al., 2023).

Taken together, more rate-focused strategies should be integrated into adaptive lake management. Controlling the rate of ecological response within a reasonable range is imperative to prevent catastrophic consequences stemming from undesired ecological changes in the coming decades. In addition, reducing rates of future climate change as indicated in the sustainable scenario should be prioritized universally by multilateral and international efforts. For instance, advocating for policies and agreements aimed at reducing global greenhouse gas emissions and preserving natural ecosystems and biodiversity, as well as investing in scientific research to facilitate the advancement of innovative technologies for climate change mitigation and adaptation provide a significant opportunity to effectively combat climate change on a global scale. Local management strategies for peri-urban/urban lakes should also focus on retaining nutrients within urban landscapes to prevent further non-point source pollution from worsening lake ecosystems (Jeppesen et al., 2005). Decreasing rates will buy much time for aquatic communities to adapt and evolve, thereby minimizing the risks of pushing ecological systems across tipping points and avoiding catastrophic abrupt ecological shifts (Williams et al., 2021).

5. Conclusions

This study highlights a significant surge in phytoplankton abundances and an abrupt community shift in peri-urban Luoma Lake during the early 2000s, which was mainly attributed to substantial nutrient loading from rapid urbanization, aquaculture, and agriculture activities in the watershed, alongside climate warming. In recent years, lake trophic levels and algal abundances particularly cyanobacteria have decreased under various management policies, exhibiting a swift ecological reversal pathway before crossing a catastrophic threshold. Despite these improvements, projected future warming is expected to further stimulate phytoplankton growth, even in the face of anticipated nutrient reductions under two representative climate scenarios (SSP1-2.6 and SSP5-8.5). The projections presented in this study embodied a broad range of possible variability in lake ecological responses to future climate warming, providing policy decision-makers with a comprehensive array of references and plausible choices to guide their decisions. This study offers a novel perspective on the dynamic trajectory of degraded lake ecosystems in developing regions, presenting new challenges and insights for understanding ecological responses of peri-urban lakes to anthropogenic stressors and management efforts, as well as future climate warming. The findings can help develop rates-focused climate adaptation management strategies.

Data Availability Statement

All data are available on the online data repository Figshare https://doi.org/10.6084/m9.figshare.24588102.v2.

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