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# Global and Planetary Change

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#### Research article

# Ecological shift and resilience in China's lake systems during the last two centuries



Ke Zhang<sup>a,\*</sup>, Xuhui Dong<sup>a</sup>, Xiangdong Yang<sup>a</sup>, Giri Kattel<sup>a,b,c</sup>, Yanjie Zhao<sup>a</sup>, Rong Wang<sup>a</sup>

- a State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China
- b Environmental Hydrology and Water Resources Group, Department of Infrastructure Engineering, The University of Melbourne, Parkville, Victoria 3010, Australia
- <sup>c</sup> Faculty of Science and Technology, Federation University Australia, Mt. Helen, Victoria 3353, Australia

#### ARTICLE INFO

Keywords: Resilience Regime shift Social-ecological systems Paleoenvironment

#### ABSTRACT

The worldwide decline of wetland ecosystems calls for an urgent reassessment of their current status from a resilience perspective. Understanding the trajectories of changes that have produced the current situation is fundamental for assessing system resilience.

Here, we examine long-term dynamics of wetland ecosystem change by reviewing paleoecological records from 11 representative lakes in China. We identify unprecedented change in alga communities in the context of last two centuries. Striking ecological shifts have occurred in all lakes, yet with spatial and temporal differences. The long-term trajectories of change in diatom species composition and structure indicate gradually eroded system resilience. These ecological shifts were shaped by socio-economic activities as China transformed from a rural agricultural to an industrialized society within the last several decades, during which multiple drivers have accumulated and acted synergistically. The balance between ecosystem and society, which appeared to exist for thousands of years, was broken by increasing population, new technology, and urbanization since the 1980s. The consequences are the emergence of new positive feedbacks with the potential to drive the coupled systems into undesirable states. By linking long-term social and ecological change at a regional scale, our study provides a novel contribution to the understanding of lake ecosystems resilience in present-day China. We argue that sustaining wetland ecosystems requires integrated approaches that incorporate a deeper understanding of social-ecological dynamics over decadal-centennial timescales to address the complex underlying mechanisms leading to the current degradation.

#### 1. Introduction

Wetlands have been supporting human livelihoods for millennia, yet today most wetland ecosystems are experiencing severe degradation worldwide (Petrescu et al., 2015). Widespread decline in ecological condition, loss of biodiversity and dramatic shifts in ecosystem composition and function have been reported across the world (Davidson, 2014; Kirwan and Megonigal, 2013). However, the extent to which these changes are irreversible, and how much of it reflects the inherent variability of these systems, is poorly known. Understanding whether or not species, ecological communities or ecosystems have reached a tipping point, beyond which changes are irrevocable and restoration unfeasible, has significant implications for future sustainable management (Scheffer et al., 2012). Major shifts in the state of wetland ecosystems may have predated the onset of monitoring programs by many decades (Ramstack Hobbs et al., 2016), thereby misrepresenting the extent of changes in response to anthropogenic pressures, as well as the baselines

targeted by managerial actions (Zedler and Kercher, 2005). Moreover, how social system changes (such as demographic change, opening market, and technological innovation) have shaped the lake ecosystem in the past cannot be well assessed without the long-term environmental data (Dakos et al., 2012a). Therefore, there is a great need to expand the temporal scope of our wetland assessment, to better understand the trajectories of dynamic interactions between ecological and social systems (Pearson et al., 2015). Palaeolimnological research provides a valuable means of obtaining a long-term insight into which has been advocated as crucial for the assessment of ecosystem shifts and resilience, which ensures the robustness of the rationale and scientific basis underpinning future managerial actions (Gillson and Marchant, 2014; Kidwell, 2015).

As a harbinger of global environmental change, China has been facing greater challenges to cope with rapid degradation of wetland ecosystems (Murray et al., 2014; Wang et al., 2012b). As a significant part of wetland ecosystems, lakes in China cover an area of 78000 km<sup>2</sup>,

E-mail address: kzhang@niglas.ac.cn (K. Zhang).

<sup>\*</sup> Corresponding author.

and more than 10 million livelihoods depend on lakes (Wang, 2015). The area of eutrophic lakes in China has increased from 135 km<sup>2</sup> to  $8700\,\mathrm{km}^2$  between 1970 and 2010, and more than 1000 lakes (> 1 km<sup>2</sup>) with an area of 13000 km<sup>2</sup> have disappeared in the middle and lower Yangtze River Basin during the last five decades (Wang, 2015). Lake deterioration has led to the loss of biodiversity (Wang et al., 2013), damage to ecological services, as well as increased environmental disasters, such as catastrophic Yangtze floods in 1998 and Taihu water crisis in 2007 (Qu et al., 2014). Given the current predictions of rapid socio-economic development (annual GDP growth rate around 7%) (Li et al., 2017; Peng, 2011), the growing threat of climate change (Deng et al., 2017), and the potential synergy between these threats (Wang, 2015), the situation for China's lake systems is not promising. In many cases, local strategies aimed at protecting and restoring lake ecosystems have failed to stop or reverse the regional-scale decline (Qu et al., 2014). Though considerable progress has been made to better understand and manage lake ecosystems in China, much research focuses on the most recent "symptoms" of the problems rather than their deep historical causes (Zhao et al., 2013). The extent and spatiotemporal variability of lake ecosystem change, in particular, is still poorly known.

In this paper, we review and synthesize long-term paleolimnological-records of diatom communities from 11 different lakes from various part of China to illustrate how lake ecosystems have evolved during the past 150 years. We focus on three key questions: (i) Are there comparable trends of lake ecosystem change in China during the last two centuries across geographic regions, ecosystem types or species? (ii) Do these changes represent major shifts in ecological characters? (iii) How did socio-economic developments shape the lake ecosystem? Finally, we provide recommendations for incorporating a resilience approaches to China's wetland ecosystem research and management.

#### 2. Methods

#### 2.1. Data collection

We examine and synthesize diatom assemblage records retrieved from the sediment cores of 11 representative lakes from different parts of China (Fig. 1). Eleven lakes range from the shallow open lakes on the Yangtze flood plain with elevation less than 10 m a.s.l to the thermally stratified deep mountain lakes in the west Yunnan Plateau with

elevation up to 1900 m a.s.l (Table 1). The social and economic development level around these lakes also shows clear gradients, covering from the most developed region in the east to the most under developed region in the west. Most of these paleo-records have been published and interpreted in details (Chen et al., 2014; Chen et al., 2015; Dong et al., 2016; Liu et al., 2012; Liu et al., 2017; Wang et al., 2012a; Zhang et al., 2016; Zhao et al., 2016). Diatom species are closely related to environmental parameters (such as increasing temperature or nutrient) and respond quickly to ecological perturbations (Ruehland et al., 2015), and thus serve as primary indicators of change providing reliable information of lake ecosystem change. Field and laboratory methods used in each of these studies are detailed in the literature cited above. In broad terms, sediment records at each site are derived from sediment cores taken from the deepest sections of each lake, and cores were subsampled at a resolution of 0.5-1.0 cm, freeze-dried, and prepared for diatom analysis. All sediment core samples were dated using  $^{210}\mathrm{Pb}$  and <sup>137</sup>Cs by non-destructive gamma spectrometry.

# 2.2. Statistical approaches

Multiple statistical approaches were employed to detect significant ecological shifts in the diatom communities. First, a standardized principal component analysis (PCA) was applied to extract major components of diatom assemblages in each lake. Second, we identified potential abrupt changes in the dominant modes of variability, characterized by the first principal component (PCA1) of diatom assemblages, using the sequential T-test Analysis of Regime-Shifts algorithm (STARS) designed to detect statistically significant shifts in the mean level and the magnitude of fluctuations (Rodionov, 2006), using a cutoff length of 20 years (p < 0.05). We also run the cumulative sum of difference (CUSUM) of PCA1 for evidence of sharp changes in slope, which has been proposed as an integral part of trend detection in longterm environmental data (Nicholls, 2001). As a further regime shift detection technique, a stratigraphically constrained cluster analysis, with a Bray-Curtis similarity index, was performed to determine the most significant shifts in the diatom communities over the past 150 years. Following these regime shift detection techniques, it was possible to identify significant ecological shifts in the diatom communities. Furthermore, the time series of PCA1 prior to the significant shift in each lake were detrended with a single exponential smoothing method to remove any long-term trends. Then we calculated the lag-1

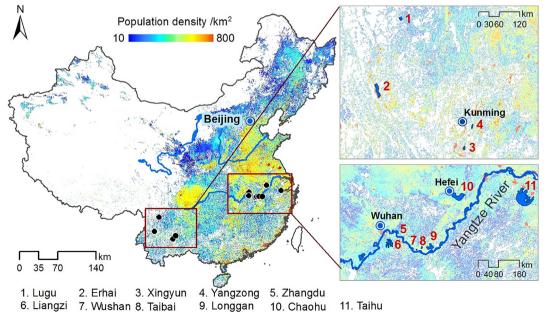


Fig. 1. Maps showing the geographical distribution of the 11 studied lakes in China.

Table 1
Physical, chemical, biological and socioeconomic description of the 11 studied lakes. TP, total phosphorus; TN, total nitrogen; DO, dissolved oxygen; COD, Chemical Oxygen Demand; Lake supply coefficient is the ratio of lake surface area to lake catchment area.

Lake	Latitude (N)	Longitude (E)	Elevation (m)	Lake area (km²)	Catchment areas (km²)	Lake supply coefficient	Mean depth (m)	Secchi depth (m
Lugu	27.70	100.78	2690.00	48.45	171.40	3.54	40.00	11.00
Erhai	25.78	100.21	1793.00	249.00	2785.00	11.18	10.70	2-6.5
Xingyun	24.90	102.99	1722.00	34.70	378.00	10.89	5.30	1.20
Yangzong	24.85	102.98	1770.00	31.68	192.00	6.06	19.50	4.50
Zhangdu	30.66	113.38	20.00	35.00	514.00	14.69	1.20	0.55
Liangzi	30.22	114.61	20.00	304.00	3265.00	10.74	4.16	1.19-2.4
Wushan	29.91	115.60	18.20	16.10	469.00	29.13	3.10	
Taibai	29.97	115.82	16.00	25.10	960.00	38.25	3.20	0.3-0.6
Longgan	29.96	116.2	15.00	316.00	5511.00	17.44	3.80	2-2.3
Chaohu	31.30	117.58	8.37	769.55	9258.00	12.03	2.70	0.15-0.25
Taihu	30.36	119.73	3.14	2425.00	36500.00	15.05	2.10	0.35-0.5
Lake	TP (ml/L)	TN (ml/L)	DO (ml/L)	COD (ml/L)	Mean temperature(°C)	Mean precipitation	Population density (P/	GDP/capita
						(mm)	km2)	(Yuan)
Lugu	0.03	0.23	7.88	1.69	12.70	920.00	43.20	21084.00
Erhai	0.05	0.59	8.20	2.72	15.00	1056.00	118.00	19282.00
Xingyun	0.0.263	1.21	7.20	3.98	15.00	947.00	221.00	25463.00
Yangzong	0.01	0.49	5.60	3.01	14.50	963.00	309.00	15305.00
Zhangdu	0.05	1.03	7.60	4.10	16.30	1461.00	967.80	89000.00
Liangzi	0.02	1.06	8.90	2.89	16.90	1263.00	660.00	57358.00
Wushan	0.19	2.39	8.46	6.05	16.80	1330.00	621.00	39783.00
Taibai	0.02	0.47	7.70	3.80	16.70	1272.00	739.00	21657.00
Longgan	0.09	1.83	7.57	5.25	16.60	1291.00	334.00	25432.00
Chaohu	0.03	1.56	9.47	3.48	16.10	995.00	456.00	34007.00
Taihu	0.03	1.32	11.50	3.24	16.00	1084.00	1405.00	141453.00

autocorrelation based on the residuals between interpolated data and fitted data under half-time series moving window size, in order to assess the change of lake ecosystem resilience (Dakos et al., 2008).

#### 3. Results and discussion

# 3.1. Ecological shifts in diatom communities

Our results show that most lake ecosystems examined have experienced dramatic ecological change within the last 150 years (Fig. 2). The general patterns of PCA1 from 11 lakes show the long-term trajectories and variability of diatom assemblage change. The phase-space plot of the first two principal components (PC1 and PC2) indicates abrupt changes in the reduced data set (Fig. A.1). Both the STARS and CUSUM analyses identified significant shifts among the 11 lakes (Fig. 2). Results from the constrained cluster analysis complemented the STARS and CUSUM, and also show distinct changes in diatom assemblages (Fig. 2 and Fig.A.2). Multiple lines of evidence suggest that striking community shifts have occurred during the last 150 years, yet with considerable spatial and temporal differences (Table A.1). In Middle and East China, especially around the lower Yangtze River Basin, most diatom communities underwent an abrupt shift between the 1950s and 1980s. For instance, in Taibai, Wushan, and Zhangdu lake, clear shifts happened around the 1950s, when the diatom communities showed a substantial decrease in the relative abundance of epiphytic species and increase in the planktonic species (Zhao et al., 2016). In Chaohu and Taihu lake, the shift occurred around the 1970s with pronounced increase in eutrophic planktonic diatoms (Chen et al., 2011; Dong et al., 2008). For lakes from the western part of China, shifted diatom community structure shifts occurred relatively later compared to that of east China. In Lugu and Xingyun Lake, the diatom assemblage composition shift occurred in the 1990s from assemblages dominated by larger planktonic diatoms and a variety of benthic diatoms, to an assemblage dominated by small-moderate and fast-growing planktonic diatom (Chen et al., 2014; Liu et al., 2017). In Erhai and Yangzong Lake, profound transitions were also noticed in the algal community in the early 2000s (Chen et al., 2015; Wang et al., 2012a).

Our long-term results suggest the abrupt changes in species

composition are unprecedented in the context of the last two centuries. The general patterns of ecological shifts revealed by diatom communities in our study are also supported by zooplankton community change in other studies (Cao et al., 2014; Kattel et al., 2016). Zoological remains provide strong support that limnological response to stressors have been transmitted to higher trophic levels (Smol et al., 2005). Chironomid and cladoceran microfossils in many lakes also show significant change in both concentration and assemblage diversity. For example, the abundance of littoral cladoceran species increased significantly to become dominant from the late 1960s at Zhangdu and Liangzi Lake (Kattel et al., 2016). In Taibai Lake, a rapid decline of macrophyte-dwelling chironomid taxa during the 1950-1970s was observed with increasing eutrophic/anoxic taxon Chironomus plumosus (Cao et al., 2014). Such a decline in plant-attached species if often interpreted as a direct response to the collapse of the submerged macrophyte community (Sayer et al., 2010). Collectively, these evidence suggest that large-scale ecological shifts and rapid reorganizations may have occurred in many lakes ecosystem across China, indicating an increasingly deteriorated conditions in the lake ecosystem.

#### 3.2. Trajectories of lake degradation from resilience perspective

Assessing ecosystem degradation from a resilience perspective is increasingly viewed as crucial for management and restoration (Müller et al., 2016; Sasaki et al., 2015). Resilience is the inherent ability of a system to absorb various disturbances and reorganize while undergoing state changes to maintain critical functions (Holling, 1973). Directly measuring and quantifying system resilience has been difficult, especially in the real world ecosystems (Standish et al., 2014). Mathematical modeling has revealed some generic indicators (such as rising variance, lag-1 autocorrelation) which could be used to indirectly represent reduced resilience (Scheffer et al., 2015). For instance, when a degraded system with declining resilience approaches the tipping point, the system recovers more and more slowly from a small perturbation, so that the system tends to become more similar to its own past, resulting in an increase in autocorrelation at lag-1 (Dakos et al., 2012b; Wang et al., 2012a). In most of examples of abrupt diatom community change we analyzed, autocorrelation showed an increasing trend in the period

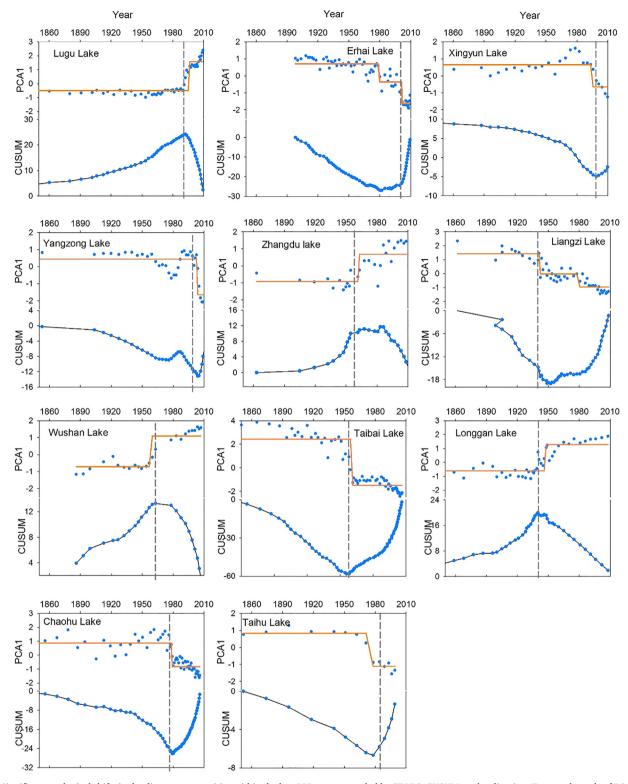


Fig. 2. Significant ecological shifts in the diatom communities within the last 150 years, revealed by STARS, CUSUM, and ordination. Temporal trends of PCA 1 score are used as holistic indicators of ecological states. The thick brown line depicts the changes in mean identified by the STARS algorithm. The dark gray dash line indicates the major transition identified by the constrained cluster analysis (for detailed cluster analysis, see Fig. A.2).

before the shift, except for Zhangdu Lake showing decline trend (Fig. 3). The broad pattern of increasing autocorrelation in the diatom community indicates the decline of the ecological resilience prior to the detected shift. However, we caution that the resilience concept outlined here does not just focus on short-term recovery to a single, static equilibrium (Holling, 1973; Scheffer et al., 2001).

Lake ecosystems are composited of multiple communities with complex biotic interactions, and show strong temporal asynchrony between different groups when facing disturbance (O'Gorman and Emmerson, 2009; Rooney et al., 2006). As pressure increases, certain communities (i.e. diatoms) respond quickly and show small-scale shifts in composition and structure. However, at the whole ecosystem level,

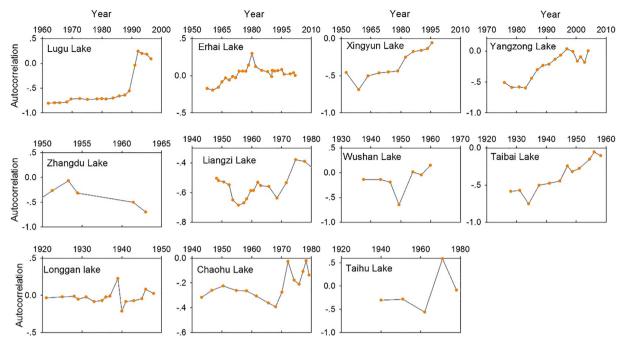


Fig. 3. Increasing trends in autocorrelation indicate declined diatom community resilience before the shift. The lag-1 autocorrelation is calculated based on the residuals of PCA1 under half-time series moving window size.

the ecosystem may have degraded into another temporally stable but non-equilibrium state, whilst still sitting in the realm of wider basin of attraction (Fig. A.3, S3a, and S3b) (Ghazoul et al., 2015). For instance, a clear shift in diatom community occurred around 1956 in Taibai Lake (Fig. 2), while chironomid communities did not show big change until the early 1990s (Cao et al., 2014). These evidence suggest that substantial changes of ecosystem function due to the alternation of both phytoplankton and zooplankton communities, though at ecosystem level the lake still retained its clear and relatively stable state, with macrophyte coverage greater than 20% in the 1960s (Zhao et al., 2016). However, continued loss of functionally-important species can increase the vulnerability to any future disturbances, and cause dramatic changes in the structure and diversity of other communities(O'Gorman and Emmerson, 2009). Furthermore, such changes can cause complex biotic interactions at multiple trophic levels (Sayer et al., 2010). The 2013 field survey showed a complete disappearance of the submerged macrophyte communities from the Taibai Lake (Zhao et al., 2016). As this degradation trajectory goes through, thresholds may be surpassed in response to either external drivers or internal reorganization, resulting in the collapse of the whole ecosystem (Scheffer et al., 2015).

This transient behavior is often ignored because of the common expectation that regime shifts are necessarily sudden (Villa Martín et al., 2015). However, their existence indicates that regime shift is close and not yet irreversible, and thus recognition provides new and important information for lake management. Furthermore, it is being increasingly realized that ecosystem-level shifts from one equilibrium to another might be gradual or even more protracted (Hughes et al., 2013; Sayer et al., 2010). Our paleoecological records have revealed pronounced multi-decadal ecological variability and transient dynamics during the last 150 years. A lack of awareness of this long history of change has led some researchers focusing on recent events or current conditions as the sole or major causes of the lake ecosystem shift (Le et al., 2010). A more appropriate interpretation is that we are now witnessing the tail-end of a much longer transition caused by long-term accumulating slow and fast drivers.

#### 3.3. Dynamics of linked social-ecological lake systems

The broad patterns of lake ecological degradation and shifts are caused by increasing anthropogenic stressors during the last century, including population expansion, over exploitation, agriculture intensification and climate change (Wang, 1998). The spatially different temporal trends of socio-economic developments coupled with sitespecific bio-geophysical characteristics of each lake (Table 1) all contribute to the variations in the timing of the ecological shifts in different lakes. Furthermore, long-term complex interactions between multiple drivers and lake ecosystems can result in different press-response relationships. Ecosystem shift can be triggered either by abrupt environment drivers (extrinsic regime shift) or by gradually changing environment drivers with internal reorganizations and feedbacks (intrinsic regime shift) (Magnuson, 2007; Seddon et al., 2014; Williams et al., 2011). For example, in Erhai Lake, the environmental conditions remained relatively stable with no substantial change around 2001 when a profound transition in the diatom community occurred (Fig. A.4) (Wang et al., 2012a). In this case, the shift appears to be a nonlinear discontinuous response to environmental drivers. In contrast, upstream dam construction in Taibai Lake during the late 1950s, which significantly altered hydrological conditions, played a key role in triggering the diatom community shift around 1956 (Zhao et al., 2016), while other environmental drivers did not show significant change at that time (Fig. A.4). However, not all ecosystem shifts behavior fall neatly into the two types of shift, as ecosystems are complex and are usually governed by a mixture of external drivers, positive and negative feedback loops, and fast and slow processes (Hughes et al., 2010). The results from the general additive model also suggest that the diatom community in the two lakes responded to different drivers both at a liner and nonlinear way (Fig. 4). It is more possible that these ecological shifts resulted from long-term complex interactions of multiple drivers, some of which gradually undermine ecosystem resilience (e.g., climate change, overfishing), while the others (e.g., dam construction) give the final impulse for abrupt change (Anthony et al., 2015).

In general, the lake degradation in China has gone through several distinct stages corresponding to different socio-economic regimes within the last two centuries (Fig. 5). Before the 1950s, most lake

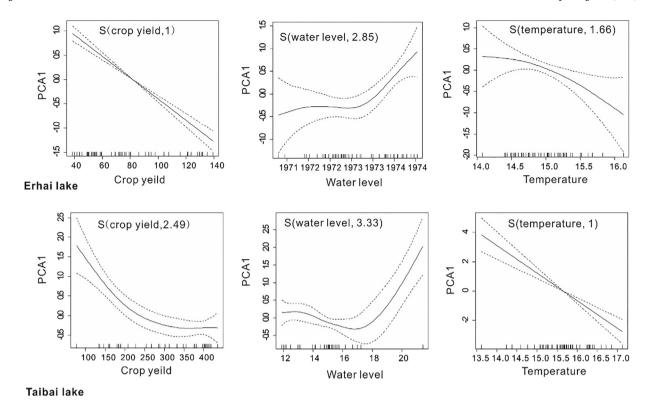


Fig. 4. Examples of pressure-response relationship of lake ecosystem, exemplified in Erhai lake (a) and Taibai Lake (b). The figure shows fitted smooth function between diatom assemblages (PCA1 scores) and different drivers from a general additive model (GAM). Two dotted lines mark the 95% uncertainty interval of the fitted function. On the x-axis, ticks show the distribution of observed values for the two variables. The number in parenthesis within each figure is the effective degrees of freedom (edf) of the smooth function. For the original plot of each drivers, please refer to SI (Fig. A.4).

ecosystems appear to be relatively stable, as seen by the relative stability of natural variability in the assemblage PC1 trends (Fig. 2). Although some lakes had been surrounded and exploited by people for a long period (e.g. Taihu lake basin for thousands of years), the impact was relatively small and was restricted to a local scale (Wang, 1998). For instance, communities have been in existence around Taihu lake basin for thousands of years, but the impacts on the lake ecosystem appeared to have been relatively limited compared with the present.

This may be due to technological limitation and/or low population density, where traditional agriculture techniques have not been changed around the Taihu lake region for at least 500 years before the new China (Ellis and Wang, 1997). We argue that many lake ecosystems maintained its capacity to recovery after disturbance during these periods, and the local equilibrium between the lake ecosystem and anthropogenic disturbance was also maintained.

However, after the 1950s, the fine balance between the ecological

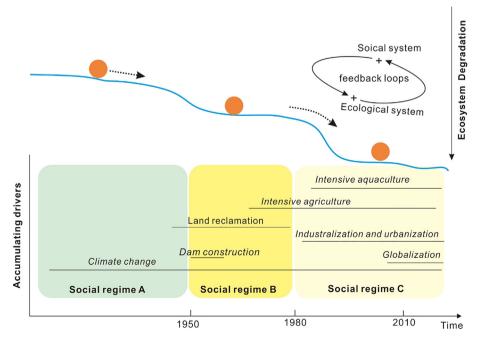


Fig. 5. The conceptual figure shows temporal cooccurrence of multiple accumulating drivers in China through the last 150 years (lower panel), which caused ecosystem degradation and reduced system resilience (upper panel). The colored boxes represent three distinctive social regimes: Social Regime A (before the 1950s), Social Regime B (between the 1950s and 1980s), and Social Regime C (from the 1980s to present). The dark lines in each colored boxes represent the starting point and duration of the drivers that affect the lake ecosystem. For detailed temporal trend of these drivers, please see Fig. A.5 in the Appendix A. The positive feedback loop formed and enhanced since the 1980s (upper panel), which indicates the potential force to cause further collapse of the lake ecosystem.

and social systems became disturbed in response to extensive modifications. The pressure of an increasing population and growing food demand resulted in a rapid expansion of agriculture, and the post 1950s period witnessed a number of policies and institutional change in order to maximize ecosystem goods and services (Wang, 1998), such as the Great-Leap Forward (1958-1961) and the People's Commune (1958-1982). This was enabled by widespread wetland reclamation, intensive river regulation and flow abstraction under the planned economy, which caused serious ecosystem degradation across China's lakes (Wang et al., 2012b). For instance, land reclamation caused a reduction in lake areas from 28859 km<sup>2</sup> to 7600 km<sup>2</sup> in the Middle and Lower Yangtze River Basin during the two decades alone since the foundation of new China (Wang, 2015). More than 50000 dams and sluices were built since 1950 along the Yangtze River in order to minimize flooding, facilitate irrigation, furnish hydroelectric power and store water (Yang et al., 2011). During this phase, fluctuations in the main biophysical processes led to significant change in species composition and altered food webs structure of lake ecosystems (Kattel et al., 2016).

The situation accelerated after the 1980s, especially since the opening-up market reforms. With rapid industrialization and unprecedented urbanization, the scale of human impacts on lakes has grown exponentially. China's urbanization increased from 19.4% to 52.6% between 1980 and 2012 (Yang, 2013). Social and economic activities under intensification and extensification strategies were coincident with large-scale degradation of lake ecosystems. As societies become more affluent, they are able to extract resources from further extent and contribute increasingly to larger-scale and more complex problems confronting lakes, such as lake modification (e.g., dredging), land-based pollution (e.g., incorporating pesticides and fertilizers in agriculture, sewage), and industrialized aquaculture (Wang, 2015). For instance, China has become the largest producer and consumer of N fertilizer, accounting for one-third of world fertilizer production in 2010 alone (Li et al., 2013). The freshwater aquaculture yield increased more than 25 fold during the last 30 years. More importantly, the chronic impacts of pollution and overfishing are increasingly compounded by the more recent, superimposed impacts of global warming and globalization of market (Liu and Diamond, 2005). The effects are synergistic so that the whole response is much greater than the sum of individual disturbances. As a result, multiple drivers accumulate and act synergistically in reducing ecosystem resilience to change (Fig. A.4 and Fig. A.5). We would argue that many lake ecosystems may have exceeded their regenerative capacity during this period, causing dramatic shifts in ecological species composition, structure, and function.

The transitions of lake social-ecological system occur through feedbacks between technological advancement, population growth, and ecosystem change. The interacting and mutually reinforcing processes contribute to the rapid decline of ecosystems resilience through these complex feedbacks (Liu et al., 2015). For instance, fishers often respond by increasing fishing efforts as catch rates decline, and if declines are prolonged, demand and value increase, which increases the incentive to more intensive fishing activities (Jia et al., 2013). Previous research shows that positive feedback loops between social process and ecological dynamics have already emerged in some lake systems in China (Liu et al., 2015; Zhang et al., 2015), which potentially lead the coupled social-ecological system toward an undesirable state that may be difficult or impossible to reverse. Moreover, degradation of lake ecosystem had far-reaching consequences for the social systems. For instance, prior to the 1980s, water quality in many lakes in China was negatively affected by the anthropogenic pressures, now water quality has adverse effect on human wellbeing. The Taihu mega-blooms in 2007 caused the loss of millions of dollars and generated a set of cascading negative impacts (Qu et al., 2014). Indeed it is being increasingly realized that these kinds of social-ecological feedbacks have the potential to drive the society into poverty traps (Kittinger et al., 2013). Ignoring these critical social-ecological linkages can result in unintended consequences that are too significant to ignore (Folke et al., 2016).

## 4. Research and management implications

Into the future, lakes in China and elsewhere will face multiple accelerating stressors from global climate change to local stressors as a whole. Our evidence indicates that the likelihood of non-linear shifts in lake ecosystems may increase as the pressures continue to accumulate, with potentially large social-economic impacts. Solving these pressing challenges requires new perspectives and a suite of more vigorous, innovative and adaptive management strategies that emphasize enhancing lake ecosystem resilience. Here we propose three major recommendations.

First, better integration of paleoecological perspectives into restoration and adaptive ecosystem management are needed. Paleo-records provide invaluable information for understanding the natural range of system variability, the resilience of social-ecological system to past changes, and can also inform the Anthropocene reference condition and restoration target (Kidwell, 2015; Kopf et al., 2015). However, the application of long-term data from paleoecology is often hindered as the management and policy implications are not made explicit, and data sets are often not accessible or amenable to stakeholders (Gillson and Marchant, 2014). There needs to be an enhanced collaboration between paleoecological communities and different potential user groups, and translate these data into forms that are accessible and useful to environmental managers and decision makers.

Second, developing new metrics for stewardship of lake ecosystem resilience is vital for coping with uncertainty and surprise. Ecosystem metrics for monitoring the status of lake ecosystems needs to move beyond macrophyte cover and counts of targeted species, to include multiple resilience measurements approaches across organism groups and focus on ecosystem structure and function (e.g. connectivity, diversity etc) that underpin ecosystem resilience. Lake degradation should be classified based on the declining level of resilience, and also recognize that individual lakes have unique social-economic background and history that has shaped the lake system (e.g. historical contingency). This will help take appropriate actions in maintenance of resilience.

Third, the lake management programs should incorporate tipping point and threshold in their management strategies, and fully consider the potential collapse of the lake ecosystems. Identifying lake ecosystems that have not yet tipped and prioritize the design and implementation of new management practices that could stabilize the system at an appropriate level. Meanwhile, management should focus on enhancing system resilience to cope with future uncertainties. For lake ecosystems that have already crossed the threshold, reduce drivers solely is not enough to reverse the shift, practical ways to break the detrimental feedbacks that locked the new system is also needed. Furthermore, to sustain lake ecosystems, we must move toward an integrated social-ecological systems approach that better understands and incorporates the socio-economic factors that shape the ways that societies interact with lakes.

#### 5. Conclusion

Taken together, our study shows that all lake ecosystems examined have experienced dramatic and unidirectional shifts well before the contemporary monitoring programs commenced. For those sites where longer paleoecological records are available, recent change in species composition and structure appear unparalleled within at least the last several centuries. The similar patterns of ecological shifts in diatom communities are driven by complex interactions among biophysical, ecological and socioeconomic mechanisms through time. Given the increasing pressures in the foreseeable future, the ability of the deteriorated lake ecosystem in China to cope with local and global change may be irretrievably compromised. Restoration and management

strategies that aim to increase system resilience and avoiding detrimental shifts will require deeper understanding of the dynamics of the coupled social-ecological system over the long-term perspective, such as decadal to centennial scales.

## Acknowledgements

This work was supported by National Key Research and

Development Program of China NBRPC (#2017YFA0605200), Science Fund for Creative Research Groups of the National Natural Science Foundation of China (#41621002), the National Natural Science Foundation of China (NSFC) (#41530753, #41472314, #41772378), and One Hundred Talent Program of the Chinese Academy of Sciences (#Y6SL011001 to Zhang Ke). We would like to thanks John Dearing and two anonymous reviewers for constructive comments and suggestions on an early draft of the paper.

# Appendix A. Appendix

Table A.1 Statistically significant (p < 0.01) breakpoints for PCA1 of diatom assemblages aggregated by site using sequential Student's *t*-test with different cut-off lengths (l = 20). Only RSI value bigger than 1 are presented. Selected breakpoint dates in the paper were shown in bold.

Lake	Year	Breakpoint value (RSI index)
Lugu	1995	4.453268169
Erhai	1998	1.33888478
	1980	1.321355098
Xingyun	1996	2.215724995
Yangzong	2000	1.718578215
Zhangdu	1991	1.009950221
	1975	1.595791761
	1961	2.844742692
	1909	1.313104966
Liangzi	1996	1.205886564
· ·	1948	2.464789185
	1933	1.324864182
Wushan	1991	1.14483813
	1975	1.601484764
	1961	2.856681603
	1909	1.318529808
Taibai	1957	3.708771611
Longgan	1957	1.629442019
	1945	1.842693962
	1877	1.314226059
Chaohu	1989	1.553871795
	1978	1.98410759
Taihu	30.36	119.73
	1985	1.811346645
	1974	3.492337119

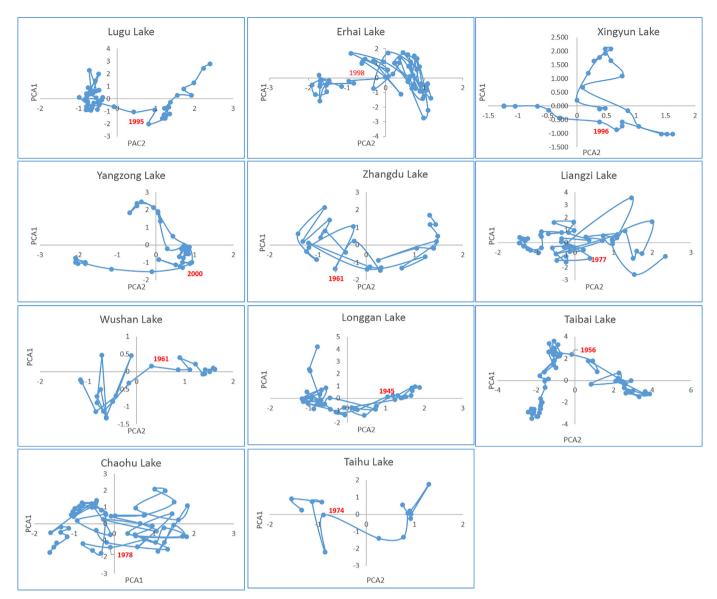


Fig. A.1. Phase plot of PCA 1 again PCA2 in each lakes. Temporal trends of principal components (PC1 and PC2) are used as holistic indicators of ecosystem states, and phase-space plots of two principal components are used to graphically illustrate abrupt changes in the reduced data set (Weijerman et al., 2005). The PCA results of Yangzong and Xingyun Lake are from Cheng and Liu (Chen et al., 2015; Liu et al., 2017). Blue lines connect stratigraphically contiguous assemblages. The number in red color are the time of significant break point detect by STARS.

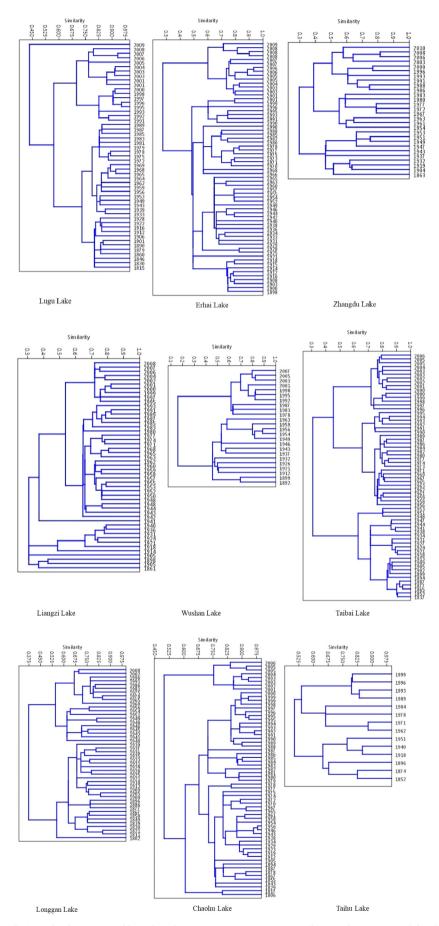


Fig. A.2. Constrained cluster analysis on the diatom assemblages based on Bray-Curtis community similarity index. We carried the cluster analysis on 9 lakes, while the cluster results of Yanzong and Xingyun lakes are from Chen and Liu (Chen et al., 2015; Liu et al., 2017).

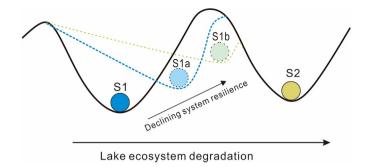


Fig. A.3. The conceptual model shows the trajectory of reduced ecosystem resilience and shift. The depth of the basin indicates the resilience of a particular ecosystem state. The ball in the basin represents the state of the ecosystem. Disturbance may be cumulative, and slowly eroding ecosystem resilience, which can push the system to transient to several intermediate stable but non-equilibrium states (i.e. from S1 to S1a to S1b) before collapsed to other stable state S2, modified from (Ghazoul et al., 2015).

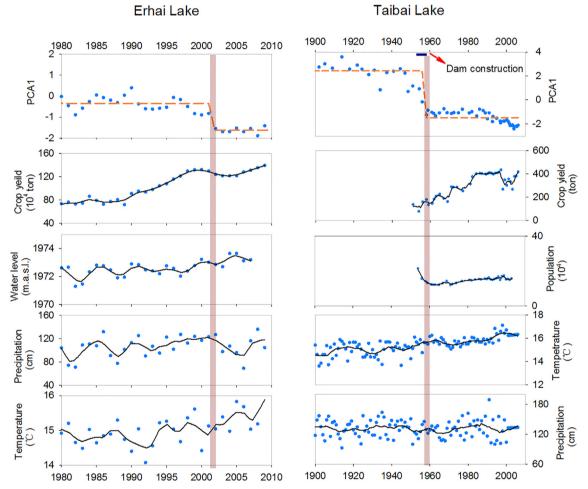


Fig. A.4. Examples of press-response type of lake ecosystem, exemplified in Erhai lake (a) and Taibai Lake (b). The vertical band shows the timing of the ecological shift identified. In Erhai Lake, clear shift of diatom community happened around 2001, while climate change, water level and agriculture activities did not show significant change. In Taibai lake, Dam construction between in the last 1950s act as a key trigger that caused diatom community shift (Liu et al., 2012).

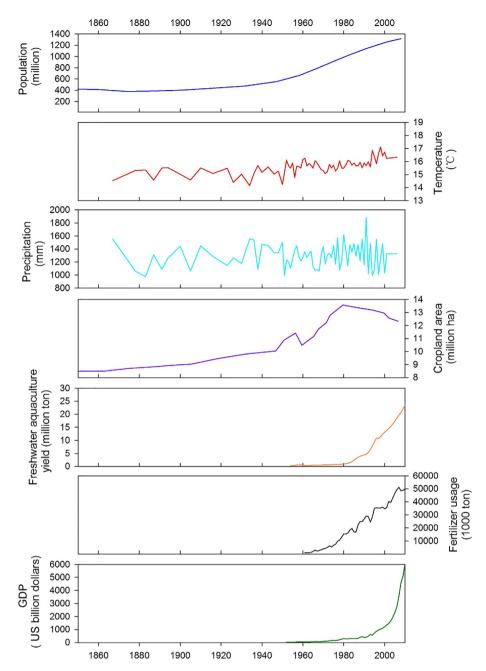


Fig. A.5. Multiple drivers of ecosystem change in China since the 1850s. The magnitude of drivers increased significantly over time, especially during the last 30 years. Note that the Annual temperature and precipitation is for east China only. GDP data are collected form the China Statistical Yearbook and the China Compendium of Statistics (1949–2008) published by the national Bureau of Statistics of China (http://www.stats.gov.cn/). The fresh aquaculture yield are collected from China Fishery Statistical Yearbook. The fertilizer usages of whole China are downloaded from Earth Policy Institute data center (http://www.earthpolicy.org/data\_center/). Annual temperature and precipitation in east China are from regional climate model output (Liu et al., 2005). The cropland area and population data are from (Miao et al., 2016).

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