Received: 3 June 2020 | Accepted: 26 October 2020

DOI: 10.1111/1365-2745.13544

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RECONCILING RESILIENCE ACROSS
ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Long-term empirical evidence, early warning signals and multiple drivers of regime shifts in a lake ecosystem

Haojie Su[1,2] | Rong Wang[3] | Yuhao Feng[2] | Yanling Li[4] | Yun Li[1,3] | Jun Chen[1] | Chi Xu[5] | Shaopeng Wang[2] | Jingyun Fang[2] | Ping Xie[1,4]

[1]Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

[2]Department of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing, China

[3]Nanjing Institute of Geography & Limnology, Chinese Academy of Sciences, Nanjing, China

[4]Institute for Ecological Research and Pollution Control of Plateau Lakes, School of Ecology and Environmental Science, Yunnan University, Kunming, China

[5]School of Life Sciences, Nanjing University, Nanjing, China

Correspondence
Ping Xie
Email: xieping@ihb.ac.cn

Funding information
The Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDB31000000; The Major Science and Technology Program for Water Pollution Control and Treatment, Grant/Award Number: 2017ZX07203-004; The National Key Research and Development Program of China, Grant/Award Number: 2017YFA0605201

Handling Editor: Guillaume de Lafontaine

Abstract

1. Catastrophic regime shifts in various ecosystems are increasing with the intensification of anthropogenic pressures. Understanding and predicting critical transitions are thus a key challenge in ecology. Previous studies have mainly focused on single environmental drivers (e.g. eutrophication) and early warning signals (EWSs) prior to population collapse. However, how multiple environmental stressors interact to shape ecological behaviour and whether EWSs were detectable prior to the recovery process in lake ecosystems are largely unknown.
2. We present long-term empirical evidence of the critical transition and hysteresis with the combined pressures of climate warming, eutrophication and trophic cascade effects by fish stocking in a subtropical Chinese lake in the Yangtze floodplain. The catastrophic regime shifts are cross-validated by 64-year multi-trophic level monitoring data and paleo-diatom records.
3. We show that EWSs are detectable in both the collapse and recovery trajectories and that including body size information in composite EWSs requires shorter time-series data and can improve the predictive ability of regime shifts. Although full recovery has not yet been observed, EWSs prior to recovery provide us with the opportunity to take measures for a clear-water regime.
4. Climate warming and top-down cascade effects have a negative influence on water clarity by altering lower trophic level abundance and body size, which, in turn, have a negative effect on macrophyte abundance. Furthermore, we identify a shift in the dominant driving forces from bottom-up to top-down after regime shifts, decoupling the relationships between nutrients and biological components and thus decreasing the efficiency of nutrient reduction.
5. *Synthesis*. This study provides new insights into ecological hysteresis under multiple external stressors and improves our understanding of trait-based early warning signals in both the collapse and recovery processes in natural freshwater ecosystems. For management practice, our work suggests that slowing down climate warming and weakening the fish predation pressure on food webs are necessary to increase the effectiveness of nutrient reduction in the restoration of lakes.

KEYWORDS
body size, catastrophic transitions, climate warming, ecological resilience, eutrophication, hysteresis, paleolimnology, trophic cascade

1 | INTRODUCTION

A burgeoning literature shows that ecosystems (freshwater, marine and terrestrial) respond nonlinearly to environmental drivers, as an abrupt transition occurs when a driver exceeds a threshold (Beisner et al., 2003; Scheffer et al., 2001). Ecosystems often exhibit hysteresis even when external drivers return to previous conditions, leading to not only serious degradation of ecological functions and services but also difficulty in restoration practice (Hilt et al., 2017). Intensive efforts have been made to understand regime shifts using mathematical models (Biggs et al., 2009; Holling, 1973; May, 1977; Scheffer et al., 2009), the reconstruction of paleo-ecological communities (Bruel et al., 2018; Kong et al., 2017; Mcgowan et al., 2005; Wang et al., 2012) and population-level and whole-lake experiments (Carpenter et al., 2011; Faassen et al., 2015). However, there is little direct empirical evidence to confirm system-level nonlinear changes in natural ecosystems (Capon et al., 2015), as monitoring programmes are often limited by short time-series lengths and low sampling resolutions. Although regime shifts can also be tested indirectly using methods of space-for-time substitutions in field observations (Su, Wu, et al., 2019; van Nes & Scheffer, 2005; Ward et al., 2018) or remote sensing archives (Staver et al., 2011; Xu et al., 2016), spatial data often have different temporal contexts and cannot provide site-specific mechanisms of change.

Ecological resilience is the capacity of an ecosystem to maintain its structure, functions and processes in the face of perturbations (Holling, 1973). Theory suggests that early warning signals (EWSs) can be used to monitor subtle changes in the spatial and temporal behaviour of ecological systems as they approach a threshold (Carpenter & Brock, 2006; Clements & Ozgul, 2018; Dakos et al., 2012; Guttal & Jayaprakash, 2008; Kefi et al., 2014; Scheffer et al., 2009). These statistical metrics are based on the phenomenon of critical slowing down (CSD), which is characterized by a reduction in the recovery rate after a small disturbance as an ecosystem approaches a catastrophic transition (Dakos et al., 2008). EWSs indicate a loss of resilience, in the sense that an ecosystem becomes more vulnerable and can more easily tip to an alternative state. Increases in variance and autocorrelation in systems prior to a transition have been shown both theoretically and experimentally (Carpenter & Brock, 2006; Spears et al., 2017), providing an ideal method for depicting the dynamics of resilience. Composite EWSs have also been proposed to increase overall predictive ability by combining multiple indicators (Drake & Griffen, 2010). In addition, including trait information (e.g. body size) in composite EWSs provides more robust predictions than traditional abundance-based time-series indicators alone (Arkilanian et al., 2020; Baruah et al., 2020; Clements et al., 2017; Clements & Ozgul, 2016). However, most studies on ecological resilience and/or EWSs focused on the deterioration of environments, whereas ecological resilience in the recovery process received much less attention (but see Clements et al., 2019).

Climate warming, eutrophication and fish stocking are three major anthropogenic stressors undermining the functioning of aquatic ecosystems (Daskalov et al., 2007; Moss et al., 2003; Smith & Schindler, 2009). For instance, unprecedented rates of climate warming can induce phenological mismatches within food webs (Durant et al., 2007; Schweiger et al., 2008; Winder & Schindler, 2004), alter the forging behaviour of consumers (Woodward et al., 2010) and reduce the body size of aquatic individuals (Forster et al., 2012; Yvon-Durocher et al., 2011), which may alter the feedbacks that maintain a stable regime and the resilience of ecosystems to disturbance (Wernberg et al., 2010). Furthermore, warming and fish stocking may interact in a synergistic way through ecological networks (Christensen et al., 2006; Jackson et al., 2016), which enlarge the strength of top-down cascade effects. Thus, clarifying how multiple stressors interact and shape the structure and functioning of ecosystems is critical for understanding the dynamics of ecological behaviour.

Plankton community abundance and body size are important ecosystem properties and can be used to explore the mechanisms through which water clarity functionally declines. Body size is an important species trait that links the structure and stability of food webs (Brose et al., 2019; Spanbauer et al., 2016). This metric is related to energy requirements, gape size and life history, and it plays a vital role in determining the strength of trophic cascades (Delong et al., 2015). A previous study showed that bottom-up effects from nutrients primarily structure plankton abundance, whereas community composition and body size distributions are mainly determined by top-down cascade effects from fish (Lemmens et al., 2018). Water clarity is functionally correlated with not only phytoplankton abundance but also body size. Under the same biomass conditions, it is generally accepted that systems with smaller body sizes of suspended particles have lower water clarity (Bhargava & Mariam, 1991). As ecosystems in nature are often affected by multiple stressors simultaneously (Crain et al., 2010), changes in the relative importance of bottom-up and top-down effects may decouple the relationships between nutrients and biological processes, which cause the hysteretic response of an ecosystem to nutrient reduction in the backward recovery trajectory.

In the present work, using monitoring data spanning 64 years (1956–2019) and microfossil records reconstructed from dated sediment cores in the subtropical shallow Lake Donghu (Figure S1), we provide empirical quantitative evidence of abrupt shifts and hysteresis at the ecosystem level. We then assess whether trait-based composite EWSs were reliably detectable in advance of both the collapse and recovery processes and evaluate how short the time-series data are required to be before a collapse/recovery is present in composite EWSs. Finally, we unravel the underlying mechanisms of how climate warming, fish stocking and eutrophication interact in driving nonlinear regime shifts. We highlight that the transition of the dominant driving forces from bottom-up to top-down caused hysteresis that prevented the recovery efforts of nutrient reduction.

2 | MATERIALS AND METHODS

2.1 | Study site

Lake Donghu (30°33′02″N, 114°21′40″E), a subtropical shallow lake in the middle and lower Yangtze Plain, is a city-central lake located in Wuhan, Hubei Province (Figure S1). The mean depth of Lake Donghu is 2.21 m, and the lake surface area is 32 km^2. The ever-growing human population and rapid development of industry, agriculture and animal husbandry in the drainage basin have led to severe eutrophication since the 1970s. The total nitrogen (TN) concentration increased from 0.76 mg/L in the 1950s to 2.35 mg/L in the 1990s and decreased to 1.31 mg/L in the 2010s; the total phosphorus (TP) concentration increased from 0.068 mg/L in the 1950s to 0.176 mg/L in the 1990s and decreased to 0.107 mg/L in the 2010s. From 2002, municipal engineering was carried out to separate rain and sewage water around the lake. Consequently, the water nutrient concentration has shown a decreasing trend in recent years (Figure S2a,b).

Beginning in 1972, fish stocking activities were implemented to increase the fish yield of the lake (Figure S2c), including increasing the stocking densities of bighead carp and silver carp, improving the proportion of large fingerlings, reconstructing fish screens and controlling predatory fish. These juvenile fishes subsist on natural food resources in the water column without artificial feeding. The fish yield increased from 98.25 kg/ha before the 1970s to 1,194.23 kg/ha in 2003 and then decreased to 757.6 kg/ha after the 2010s. The mean proportion of planktivorous fish (i.e. silver carp and bighead carp) was 84.71% from 1973 to 1978 and increased to 98% after the 1990s. The fish yield of grass carp *Ctenopharyngodon idellus* was 8.9% from 1973 to 1976 and decreased to less than 1% after that time. Before the 1970s, submerged macrophyte vegetation was abundant in the lake. An investigation in 1962–1963 showed that the vegetation coverage was 83%, with a mean biomass of 1,614 g/m^2. Submerged macrophyte vegetation decreased to 5.8 g/m^2 in 1975, and the once dominant species, *Potamogeton maackianus*, disappeared in that year and since then has never recovered (Liu, 1991).

2.2 | Long-term field observations

Long-term monitoring data (1956–2019) were obtained from the Donghu Experimental Station, which is under the framework of the Chinese Ecosystem Research Network (CERN). The monitoring programme collects ecosystem-level abiotic (e.g. TP, TN, water clarity and temperature) and biotic variables (e.g. phytoplankton, zooplankton and fish). Surveys were conducted monthly at two sampling stations in the Guozheng Lake area representing coastal (Station I) and pelagic zones (Station II; Figure S1). As water temperature is highly correlated with air temperature (Figure S3), the monthly mean air temperature was used as a substitute for the water temperature in further analyses. Water samples from each site were collected 0.5 m below the water surface and 0.5 m above the lake bottom using a 5 L Schindler sampler and then mixed together for subsequent analyses. The water clarity was characterized as the Secchi depth, which was measured with a Secchi disk. The water samples were taken to the laboratory to analyse gross primary productivity, TN and TP concentrations in accordance with standard methods (Huang et al., 1999). Fish yield data were obtained annually from the Fishery Management Committee of Lake Donghu.

Mixed water samples (1 L) were preserved with 4% formaldehyde and 1% Lugol's solution and concentrated to 50 ml after sedimentation for at least 48 hr. Phytoplankton and rotifers were counted in the concentrated samples under 400× magnification. The biomass of each taxon was calculated using the approximating geometric forms. Mixed water samples (10 L) were sieved through 64-μm plankton nets and preserved with 5% formalin for further analysis of crustacean zooplankton. To maintain the consistency of the data, phytoplankton and zooplankton were sampled and identified with the same method in recent decades to reduce observation bias. We considered functional groups (e.g. cladocerans, copepods and rotifers for zooplankton) in our analysis, which is rarely influenced by species identification. The phytoplankton were categorized into six major groups with distinct sizes and functions, including Cyanophyta, Chlorophyta, Bacillariophyta, Pyrrophyta, Euglenophyta and Chrysophyta. Furthermore, to ensure the accuracy of the data, we resampled, reanalysed or recounted the samples if abnormal values were found. The body sizes of the cladocerans and phytoplankton were calculated as the biomass divided by the density, with mg per individual (mg/ind.) as the unit.

2.3 | Paleo-limnological records

On 8 July 2010, a 50-cm sediment core was collected in Lake Donghu (30°33′02″N, 114°21′40″E) at a water depth of 2 m using a Kajak gravity corer with a 58 mm diameter. The sediment core was sliced at 0.5 cm intervals for dating and diatom analyses. The chronologies of the core were obtained by measuring ^{210}Pb and ^{137}Cs radionuclide activities in contiguous samples at the State Key Laboratory of Lake Science and Environment of the Chinese Academy of Sciences (CAS), Nanjing, China. A total of 98 sediment samples were prepared for diatom analysis using the standard method (Battarbee et al., 2001). Diatom species were identified using oil immersion at 1,000 magnification under an Olympus microscope (BX51). Diatom concentrations were estimated using DVB microspheres, which are expressed as relative percent abundances.

2.4 | Statistical analyses

Change-point analysis was used to test the changes in the mean value of water clarity. The sequential *F*-statistic of water clarity was calculated at a confidence level of $p < 0.01$ with a moving window of 5% of the time series using the STRUCCHANGE package in R 4.0.0 (Zeileis et al., 2001). The change point occurred at the maximum of the *F*-statistic, which was determined by the 'breakpoints' function. The same method was also applied to nine other state variables to test the reliability of the estimated breakpoint date, that is, the abundance of cladocerans, copepods, rotifers, Cyanophyta and total phytoplankton, the PC1 of phytoplankton community composition, the proportion of Cyanophyta to total phytoplankton abundance, and the body size of cladocerans and phytoplankton. Furthermore, diatom assemblage records over time retrieved from the sediment core were analysed using principal component analysis (PCA) and chronological clustering to confirm the identification of breakpoints. Changes in the mean principal component (PC) of diatoms were also assessed by change-point analysis. Chronological clustering was performed using the 'coniss' method on a bray distance matrix using the RIOJA package in R (Juggins, 2015). The output of the dendrogram indicated the main temporary regimes.

To demonstrate hysteresis in the ecosystems, we plotted the response state variables (i.e. water clarity, total phytoplankton abundance, cladoceran abundance, the body size of phytoplankton and the body size of cladocerans) against the main environmental stress over time. PCA was used to extract the main time trends from the multiple environmental stresses. The first PC axis scores are theoretical variables that contain the most information regarding the original total variance (Jolliffe, 2002). Here, the main environmental stress was calculated as the first PC of TN, TP, temperature and fish (which explained 53.5% of the total variance).

Composite EWSs were first proposed by Drake and Griffen (2010) and have since been commonly used (Arkilanian et al., 2020; Clements et al., 2017, 2019; Clements & Ozgul, 2016). Following Clements and Ozgul (2016), we also consider body size decline prior to a population approaching a collapse as an EWS. In doing so, the normalized value of body size was multiplied by −1 so that it can be included in the composite EWS (i.e. increasing when approaching a tipping point). To derive the composite EWS, we first normalized each leading indicator (AR1, CV and body size) by subtracting the long-run average of the respective indicator and dividing by the long-run standard deviation (Drake & Griffen, 2010). Thus, each statistic at time *t* ($\widehat{w}_t$) was calculated as follows:

$$\widehat{w}_t = \frac{w_t - \overline{w}_{1:t}}{SD\left(w_{1:t}\right)},$$

where $\overline{w}_{1:t}$ is the mean of a statistic from times 1 to *t* and $SD\left(w_{1:t}\right)$ is the standard deviation over the same period. The composite EWS was then calculated by summing the values for the leading indicators to be included at each time point (e.g. Figure S4 for AR1 + CV + Size.phytoplankton). An EWS was considered to be present if the composite metric at any time exceeds its running mean value by more than 2σ (more than 2 when the composite metric was normalized).

We present the composite EWS in two different ways. The first is an analysis using the entire time series. This method exhibits the detailed dynamics of the composite EWS and provides general information on how predictable the tipping point was. Second, we also calculated the minimum length of required time-series data to generate an EWS, as the length of data used in the analysis may affect the predictive ability. We did so by analysing the whole time series prior to the tipping point and then iteratively −1 year to the analysis until all composite EWSs vanished. This approach provides information on whether our results are sensitive to the window size and whether including trait-based EWSs are more predictive than traditional leading indicators. In this study, we analysed the EWSs prior to the collapse and recovery independently to avoid the effects of state shift itself on the resilience indicators. The diatom data used in the collapse path are the sum abundance of macrophyte-attached species (i.e. *Eunotia* sp., *Epithemia sorex* and *Gyrosigma accuminatum*), which are the dominant species in a clear-water regime. The diatom data used in the recovery path are the sum abundance of pelagic species. In addition, we used the traditional single early warning indicator '*SD*' to test whether flickering was observed before a bifurcation (Figure S5). Water clarity and the PC1 of phytoplankton community composition were used as state variables. Significance was determined by comparing the original nonparametric Kendall tau correlation coefficient to the trends obtained from the surrogate data (Dakos et al., 2012). The 'surrogates_ews' function in the early warnings package was used to perform this analysis, and the default setting was used. That is, the size of the rolling window was 50%, and the Gaussian detrending method was used (bandwidth was 10%) prior to analysis.

Theil–Sen regression was used to robustly explore the effects of fish stocking and temperature on water clarity, plankton abundance and body size. Theil–Sen estimation is a robust method that determines the slope of the regression line via the median of the slopes. The MBLM package in R was used to perform this analysis. Bottom-up and top-down control are known to be critical determinants of ecosystem structure and functions in aquatic habitats. The correlation coefficient between the time series of nutrients (or fish) and population abundance has probably been commonly used to assess the type and strength of trophic control within ecosystems (Boyce et al., 2015; Carpenter & Kitchell, 1996; Frank et al., 2005; Ripple et al., 2016). Strong positive correlations indicate bottom-up control, and strong negative correlations between adjacent trophic levels indicate top-down control, as predators suppress the abundance of their prey. We tested whether the dominant forces changed before and after regime shifts using the Pearson correlation coefficient.

Structural equation modelling (SEM) was used to explore the pathways by which fish stocking, temperature and nutrients affected water clarity through the food web and to test a positive feedback between water clarity and macrophyte abundance (represented by the macrophyte-attached diatom abundance). We first constructed a full model that included all possible pathways; then, nonsignificant pathways were eliminated to optimize the model. SEM, which involved sets of multiple regression analyses, allowed a rigorous estimation of the causal relationship network (Grace, 2006). The standardized path coefficients between two variables represented the relative strength of a relationship. For the category of nutrients that encompassed more than one parameter (i.e. TN and TP), the first PC (PC1), which explained 78.1% of the total variance, was introduced as a new variable into the SEM. We used a χ^2 test and p values to evaluate the fit of the models (e.g. models were considered to have a good fit when the p values ranged from 0.1 to 1). As missing values are not allowed for many analyses (e.g. composite EWS analysis and SEM), we used the linear interpolation method in the analysis. We conducted the SEM analyses using AMOS 21.0 (Amos Development Corporation).

3 | RESULTS

3.1 | Abrupt transition of multiple state variables

The lake experienced a regime shift in the mid-1980s from a clear-water state to a phytoplankton-dominated turbid state. The ecosystem exhibited hysteresis, as the values of environmental drivers dropped below the values at which bi-stability was observed in the forward collapse. We provide direct evidence of regime shifts for multiple 'state variables' in the mid-1980s in Lake Donghu. Specifically, we selected 10 state variables that comprehensively represented the biotic and abiotic conditions of the ecosystem to robustly assess the existence of regime shifts (Table 1; Figure 1). The species composition of phytoplankton has shown profound changes in recent decades (Figure S6). Water clarity, as well as the parameters of the abundance, species composition and body size of phytoplankton and zooplankton, all generally showed abrupt changes in the middle of the 1980s (Table 1; Figure 1), except for rotifer (1982) and copepod abundances (1996). All state variables presented in Table 1 showed significant differences ($p < 0.001$) in their mean values before and after regime shifts, for example, water clarity showed an abrupt change in 1985, with the mean water clarity decreasing from 1.77 to 0.86 m after the shift (Table 1). In addition, Lake Donghu has experienced increasing environmental stresses in recent decades. The annual mean air temperature increased significantly ($R^2 = 0.31$, $p < 0.001$; Figure S2; Table 1), with the mean temperature increasing from 16.70 ± 0.41 ℃ to 17.30 ± 0.49 ℃ after the regime shift. The fish stocking density also showed a significant increase ($R^2 = 0.69$, $p < 0.001$; Figure S2), with the mean fish yield increasing from 263.09 ± 210.10 to 903.67 ± 180.49 kg/ha after the regime shift. The TN in the water column also increased significantly ($p = 0.015$) after the regime shift, but for TP, the change was not statistically significant.

3.2 | Hysteresis in the recovery path

By plotting these same state variables—namely, water clarity, log10 total phytoplankton density, cladoceran density, the body size of phytoplankton and body size of cladocerans—as a function of environmental stress, we reveal a folded bifurcation, which indicates a

TABLE 1 Overview of the 10 state variables and four stressors. The breakpoint and mean value (mean ± *SD*) of the clear-water regime and turbid-water regime, the direction of the shift and the significance of the difference after regime shifts are listed. Here, the breakpoint is the last year of the clear-water regime, and 1985 was used as the breakpoint to compare the mean values of the stressors before and after the critical transition

	Parameter	Breakpoint	Clear-water regime	Turbid-water regime	Direction of shift	*p*
State variables	Water clarity, m	1985	1.77 ± 0.32	0.86 ± 0.13	Decrease	<0.001
	Cladoceran, ind./L	1986	29.46 ± 12.03	6.07 ± 4.88	Decrease	<0.001
	Copepods, ind./L	1996	61.24 ± 35.52	14.60 ± 14.83	Decrease	<0.001
	Rotifer, ind./L	1982	842.17 ± 7,499.13	2,406.23 ± 945.06	Increase	<0.001
	Log10 total phytoplankton, ind./L	1986	5.88 ± 0.40	7.74 ± 0.34	Increase	<0.001
	Log10 Cyanophyta, ind./L	1986	5.32 ± 0.56	7.52 ± 0.30	Increase	<0.001
	PC1 of the phytoplankton assemblages	1985	−0.51 ± 0.33	0.34 ± 0.19	Increase	<0.001
	Cyanophyta, %	1985	30.13 ± 17.95	72.24 ± 14.10	Increase	<0.001
	Body size of cladoceran, mg/ind.	1986	0.06 ± 0.02	0.02 ± 0.01	Decrease	<0.001
	Log10 body size of phytoplankton, mg/ind.	1986	−4.60 ± 0.28	−7.08 ± 0.37	Decrease	<0.001
Stressors	Total nitrogen, mg/L	—	1.32 ± 0.53	1.90 ± 0.91	Increase	0.015
	Total phosphorus, mg/L	—	0.12 ± 0.08	0.15 ± 0.07	Increase	0.245
	Temperature, ℃	—	16.70 ± 0.41	17.30 ± 0.49	Increase	<0.001
	Fish, kg/ha	—	263.09 ± 210.10	917.54 ± 185.82	Increase	<0.001

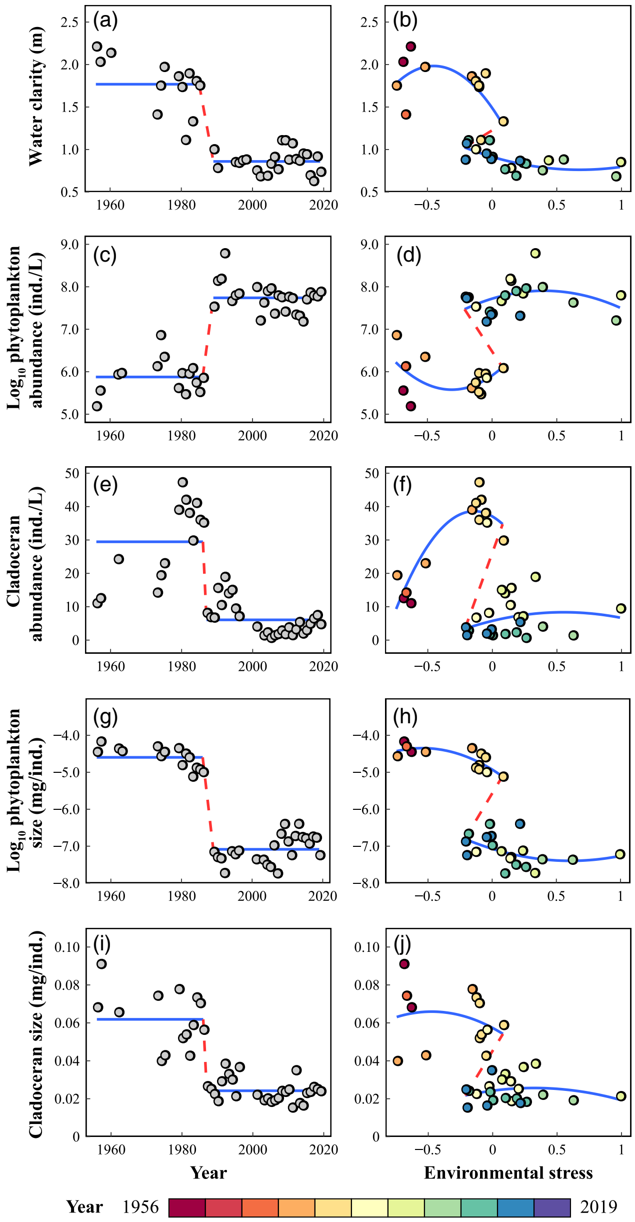


FIGURE 1 Abrupt shifts and hysteresis, respectively, in Lake Donghu in state variables (a, b) water clarity, (c, d) log10 phytoplankton abundance, (e, f) cladoceran abundance, (g, h) log10 phytoplankton body size and (i, j) cladoceran body size. A sequential *F*-statistic with a 5% sliding window was used to detect regime shifts for the entire period. The blue horizontal lines in the left column represent the mean value before and after regime shifts. The blue curves in the right column were fitted using the quadratic parabola equation. The red dashed lines indicate the border of the two alternative stable states. Data points are coloured by year and clearly show the hysteretic trajectory along environmental stress. Here, environmental stress was calculated as the first principal component of temperature, water total nitrogen, total phosphorus and the fish yield

symptom of hysteresis (Figure 1, right column). The ecosystem was alternatively in either a clear or a turbid state when the stress was in the range of values between −0.21 and 0.08. The temporal trajectory followed by the ecosystem state suggests a different forward and backward path characterizing hysteresis in the lake's recovery (Figure 1, right column).

3.3 | Evidence of regime shifts from paleo-diatom records

Our paleo-diatom records retrieved from sediment cores also detected the presence of a regime shift (Figure 2), in agreement with the patterns found in the long-term ecological monitoring data. The chronological clustering of diatom assemblages identified two temporal groups, with a division in 1984. These findings were consistent with a visual inspection of the PC1 (accounting for 83.5% of the total variance) of the sediment core. Specifically, the diatom community was dominated by planktonic *Aulacoseira granulata* before 1984 (49–16 cm), which had a mean abundance of 60.6%. After 1984 (16–0 cm), *A. granulata* declined rapidly, and *Stephanodicus minutulus* became the dominant species. The periphytic taxa, such as *Eunotia* sp., *Epithemia sorex* and *Gyrosigma accuminatum*, which are often attached to submerged macrophytes, showed a decreasing trend after the mid-1980s.

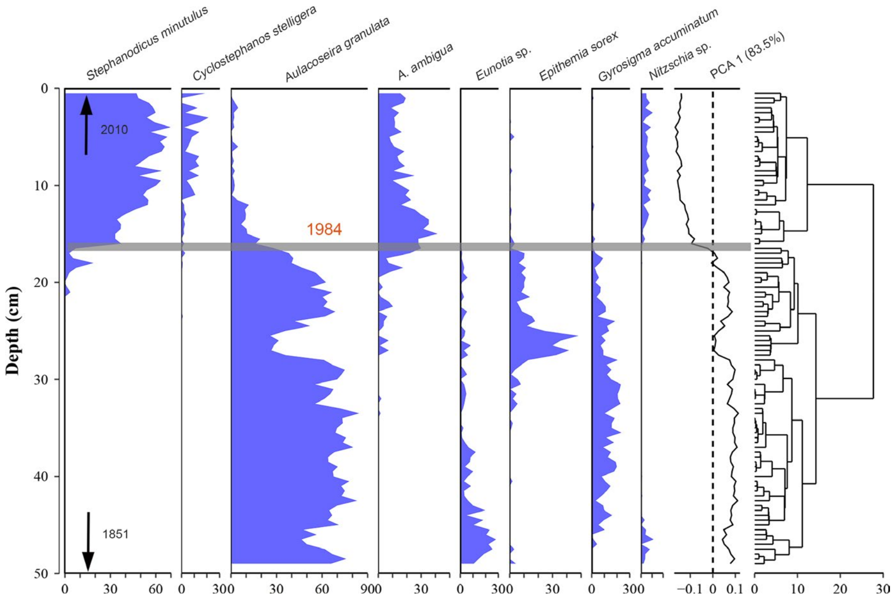
3.4 | EWS analysis

The maximum values of normalized composite EWSs were greater than the 2σ threshold, indicating that EWSs were present for different organisms (phytoplankton, cladocerans and paleo-diatom) in both the collapse and recovery trajectories (Figure 3a,c). In addition, composite metrics that include body size information generally have smaller value of minimum length of required data and higher proportion of years with detectable EWS (Table S1). That is, including trait-based EWSs have stronger predictive ability than abundance-based metrics alone in both the collapse and recovery trajectories (Figure 3b,d). EWSs were detectable up to 10 years before a collapse when macrophyte-attached diatom abundance data were used (AR1 + CV), whereas detectable EWSs prior to recovery would take at least 13 years when trait-based cladoceran data were used (AR1 + CV + Size). The normalized *SD* score increased in both the collapse ($p = 0.015$ and 0.095 for water clarity and phytoplankton PC1, respectively) and recovery ($p = 0.025$ and 0.005 for water clarity and phytoplankton PC1, respectively), which showed an increasing variation approaching the tipping point (Figure S5).

3.5 | Multiple factors in driving the ecosystem to a turbid state

Theil–Sen regressions showed that both the fish yield and temperature had negative relationships with water clarity (both $p < 0.001$; Figure 4a,b) and cladoceran abundance (both $p < 0.001$; Figure 4e,f) and positive relationships with the abundance of total phytoplankton (both $p < 0.001$; Figure 4c,d). Furthermore, the fish yield and temperature exhibited negative relationships with phytoplankton

FIGURE 2 Evidence for regime shifts in Lake Donghu from paleolimnological diatom records. Only taxa with a mean abundance above 2% are shown. The first principal components of diatom community assemblages account for 83.5% of the total variance. The grey horizontal line represents the critical transition year, that is, 1984. Chronological clustering analysis with the Bray–Curtis distance was used



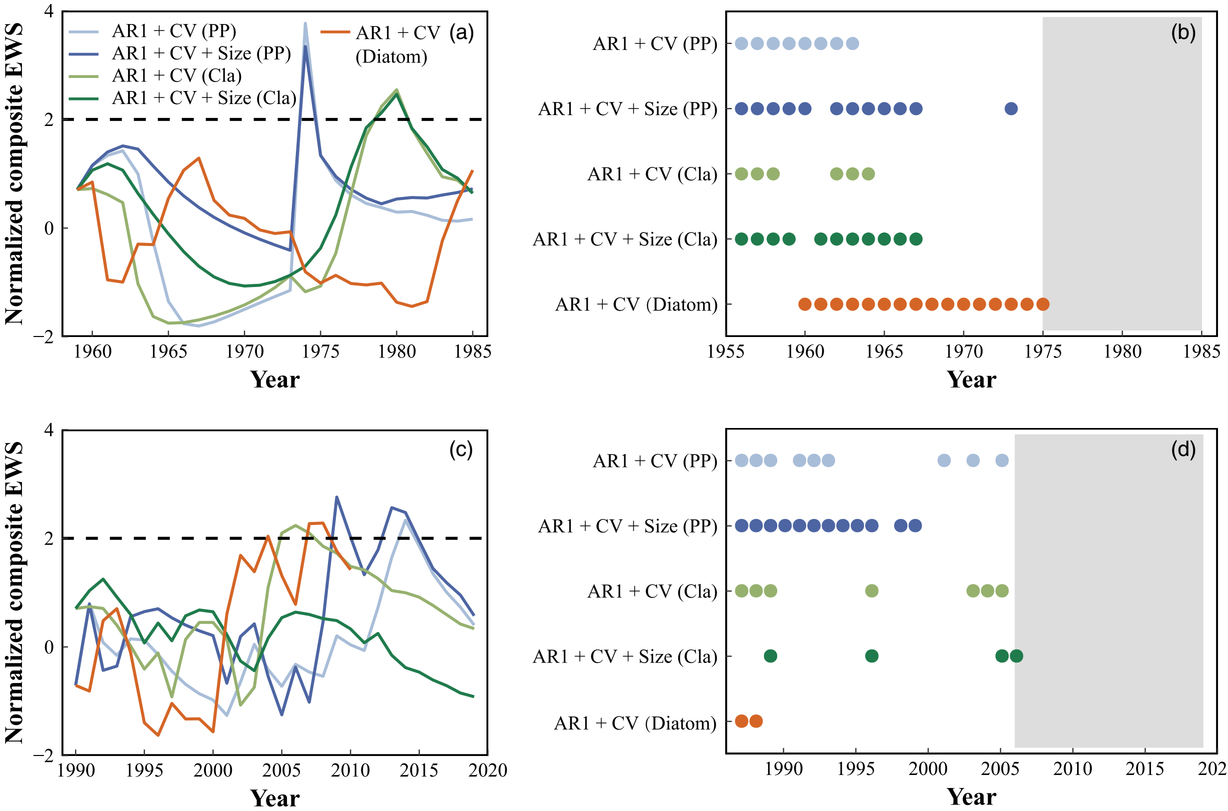


FIGURE 3 Performance of the composite early warning signal (EWS) prior to the (a, b) collapse and (c, d) recovery processes. (a, c) show the mean trends of the normalized composite EWS using whole time-series data and (b, d) show how short the EWS is present prior to the tipping point. The horizontal black dashed line indicates a 2σ threshold where an EWS was considered to be present. The solid dots in (b, d) indicate that EWSs are present in that year and the colours represent the different composite EWSs (see legends in the top left of Figure 3a). Grey shaded areas indicate the shortest length of required time-series data for the appearance of the EWSs. EWSs were detectable with as little as 10 years (collapse) and 13 years (recovery). PP, phytoplankton; Cla, cladoceran

body size (both $p < 0.001$; Figure 4g,h) and cladoceran body size (both $p < 0.001$; Figure 4i,j).

Interestingly, despite the negative effects of fish and warming on crustacean zooplankton, cladocerans showed an increasing trend before regime shifts (Figure 1e). Furthermore, we found that TN and TP had positive relationships with gross primary productivity ($r = 0.727$ and 0.676, $p < 0.001$ and $p = 0.001$), rotifer abundance ($r = 0.653$ and 0.562, $p < 0.001$ and $p = 0.005$),

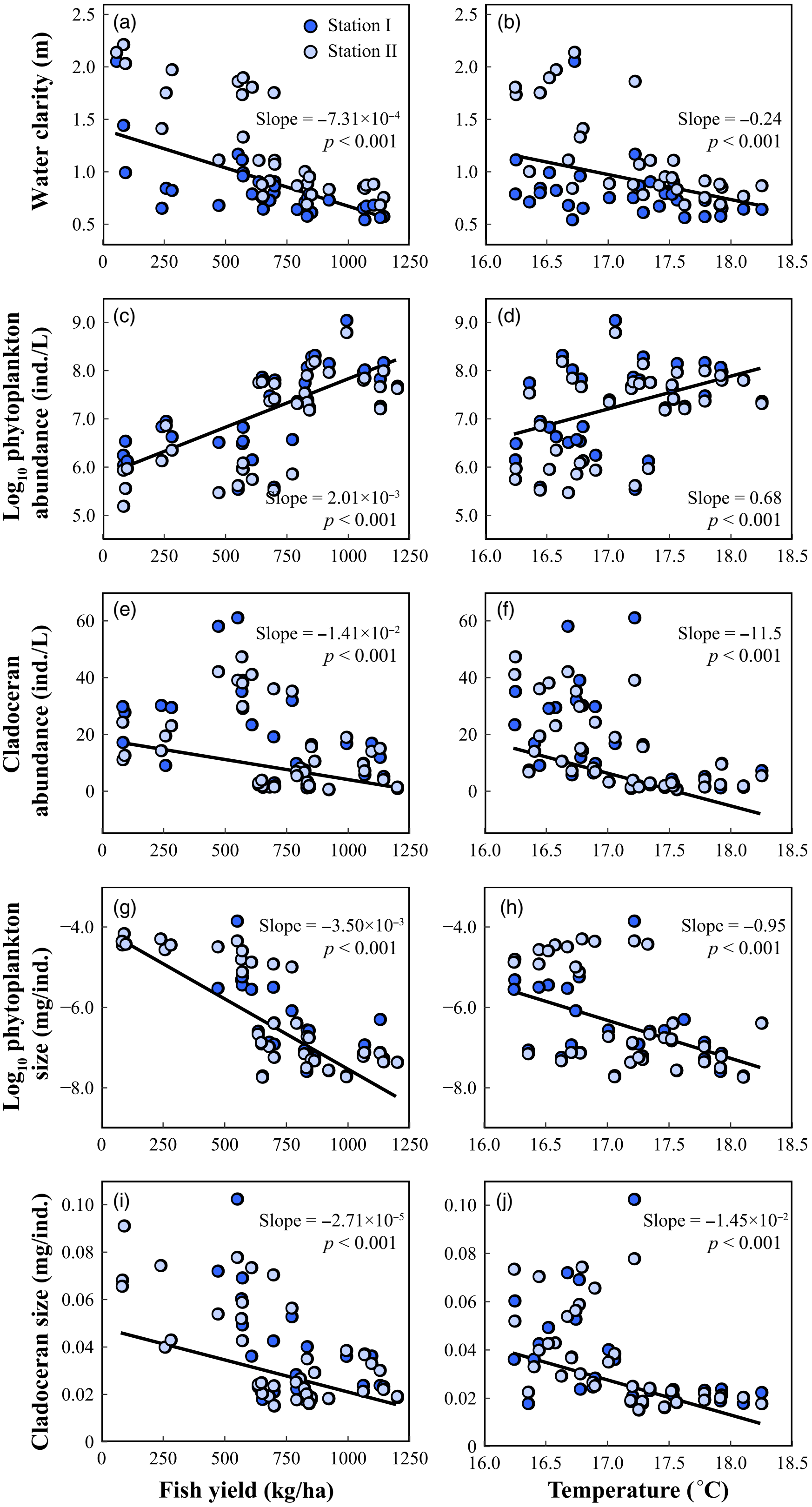


FIGURE 4 Effects of the fish yield and temperature, respectively, on (a, b) water clarity, (c, d) log10 phytoplankton abundance, (e, f) cladoceran abundance, (g, h) log10 phytoplankton size and (i, j) cladoceran size. Slopes of the regression line were determined by the Theil–Sen slope estimator. Body size was calculated as the ratio of biomass to abundance, with mg per individual as the unit

copepod abundance (r = 0.675 and 0.638, both $p < 0.001$) and cladoceran abundance (r = 0.567 and 0.373, p = 0.005 and p = 0.079) in the clear-water state while these relationships weakened or disappeared after regime shifts (Table 2). These results suggest that the bottom-up effect was dominant in the clear-water stage, whereas top-down forces were dominant in the turbid-water stage. Changes in the relative importance of environmental drivers may influence ecosystem responses and

TABLE 2 Pearson correlations between lake water nutrients (TN and TP) and primary production and zooplankton abundance (rotifer, copepods and cladoceran) in the clear-water regime and turbid-water regime. The number of observation years (*n*), correlation coefficients (*r*) and significance values (*p*) are indicated

	Clear-water regime			Turbid-water regime		
Correlated variables	*n*	*r*	*p*	*n*	*r*	*p*
TN-gross primary production	20	0.727	<0.001	35	0.61	<0.001
TN-rotifer	23	0.653	<0.001	49	0.157	0.281
TN-copepods	23	0.675	<0.001	47	0.292	0.046
TN-cladoceran	23	0.567	0.005	49	0.123	0.401
TP-gross primary production	20	0.676	0.001	35	0.414	0.013
TP-rotifer	23	0.562	0.005	49	0.164	0.260
TP-copepods	23	0.638	<0.001	47	0.223	0.132
TP-cladoceran	23	0.373	0.079	49	0.067	0.649

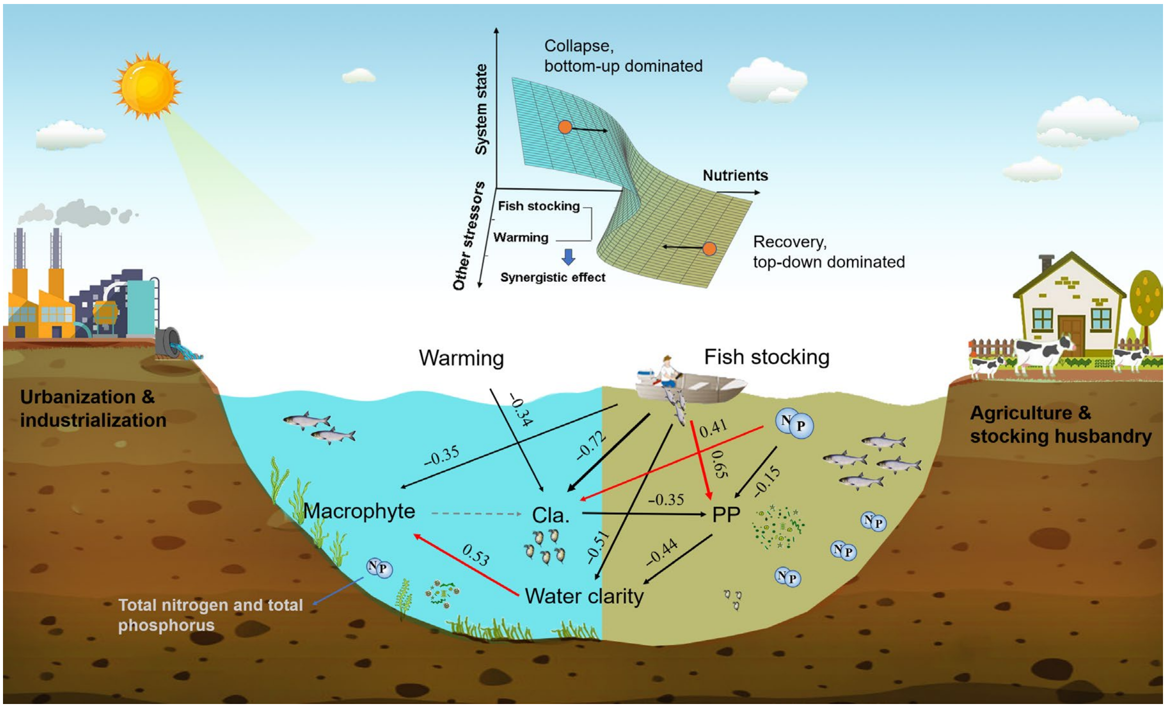


FIGURE 5 Infographic representing the characteristics of the clear-water state (left, before the mid-1980s) and the turbid-water state (right, after the mid-1980s) in the Donghu Lake ecosystem. Compared with the vegetated clear-water state, the turbid state is characterized by a loss of submerged macrophytes, a high water nutrient concentration, a high fish stocking density, a low abundance of crustaceans, a high density of phytoplankton and a smaller body size of zooplankton and phytoplankton. A schematic diagram summarizes how fish stocking, climate warming and eutrophication influence the feedbacks between water clarity and submerged macrophytes. Red arrows represent positive effects, black arrows represent negative effects and the grey dashed arrow represents a nonsignificant path. The arrow width is proportional to the strength of the relationship. The numbers above the arrows indicate the path coefficients. Model fit summary: $\chi^2 = 10.83$, $df = 7$, $p = 0.146$. A three-dimensional conceptual model in the upper graph shows ecosystem behaviour under different pressure scenarios of eutrophication, fish stocking and climate warming. The nutrient-limited bottom-up effect was predominant in the forward clear-water regime, whereas the top-down cascade effect was predominant in the backward turbid-water regime. With the increase in the fish stocking density and temperature, the hysteresis of the pressure response increased (indicated by the lower recovery threshold). In addition, the possible synergic effects of fish stocking and warming will further strengthen hysteresis, and lake recovery efforts (e.g. nutrient reduction) will be less effective as a result

behaviours, consequently leading to hysteretic recovery in response to nutrient reduction.

The SEM results suggest that fish stocking, warming and eutrophication had cascade effects on the food webs in various ways. Our model fit the data well ($\chi^2 = 10.83$, $df = 7$, $p = 0.146$) and explained 49%, 79%, 72% and 81% of the variation in cladoceran abundance, phytoplankton abundance, macrophyte abundance and water clarity, respectively (Figure 5). Fish had a direct negative influence on macrophyte abundance (−0.35). In addition, fish and temperature directly and indirectly had negative effects on water clarity, which, in turn, exerted a negative feedback effect on macrophyte abundance.

4 | DISCUSSION

In recent decades, the concepts of regime shift and alternative stable states in multiple ecosystem types, such as lakes, oceans, coral reefs and arid lands (Scheffer et al., 2001), have gained much attention. However, a previous study reviewed 135 papers on freshwater ecosystems and showed that there is little empirical evidence in natural ecosystems to confirm pressure-induced nonlinear changes (Capon et al., 2015). It is generally accepted that regime shifts should occur at the system-wide level, with changes being detectable across multiple physical and biological components, including reconstructed palaeontological communities (Dong et al., 2020; Kong et al., 2017; Zhang et al., 2018). Although the methods for reconstructing microfossil records are restricted by low resolution and the few taxa, paleo-limnological proxies can provide long-term reference data to track ecosystem dynamics. In the present study, we provided cross-validated multidisciplinary evidence to verify critical transitions in multiple trophic levels and water environments and the existence of alternative stable states within a range of environmental conditions.

4.1 | EWS detection prior to the collapse and recovery processes

Ecosystems worldwide are facing biodiversity loss and ecosystem function degradation under multiple anthropogenic pressures. Thus, predicting ecosystem collapse (forward shift) and recovery (backward shift) is a critical challenge because it is related to management costs and conservation efficiency. Many efforts have been made to predict a regime shift; however, whether EWSs can be detectable in a real-world recovery process is largely overlooked. Although Clements et al. (2019) observed EWSs of recovery with marine fish catch data, tests in natural freshwater ecosystems have not yet been conducted. In this study, a composite EWS is detectable prior to regime shifts in both the collapse and recovery processes. Although the full recovery (shift back to a clear state) has not yet been observed, EWSs indicate a loss of resilience of the turbid state, which points to the system being on a recovery trajectory. We also found that including body size information in composite EWSs can be more robust for signalling abrupt changes in ecosystem structure and functions (Clements et al., 2017; Clements & Ozgul, 2016). As the upper bound of the diatom series data is 2010, the composite EWS of diatoms (AR1 + CV) has a lower predictive ability of recovery than that of phytoplankton and cladocerans (Figure 3d), indicating that an EWS metric closer to the tipping point has higher predictive ability. Our results suggested that EWSs can be detectable even when full recovery was not observed, which provides us with the opportunity to take measures to restore a clear-water ecosystem. In management practice, in addition to nutrient reduction, more positive measures are needed (e.g. a reduction in the fish stocking density and the planting of submerged macrophytes) to promote the recovery transition to a macrophyte-dominated clear-water state.

4.2 | Mechanisms underlying the critical transition and hysteresis

This study included data on multiple stressors and trophic levels, which allowed us to explore internal trophic interactions and reveal the mechanisms underlying critical transitions in the whole ecosystem. Multiple anthropogenic stressors potentially exert positive feedbacks that provoke an unpredictable 'ecological surprise' in lake ecosystems (Birk et al., 2020; Davis et al., 2010; Jackson et al., 2016). For instance, the synergistic effects of herbivory and periphyton shading trigger macrophyte loss and regime shifts (Hidding et al., 2016). Our results showed that climate warming and the trophic cascade by fish stocking had direct and indirect negative influences on water clarity (Figure 5), jointly driving the ecosystem to a turbid state and decoupling the relationships between nutrients and biological components. Body size miniaturization of plankton and the flourishing of phytoplankton abundance are probably key to understanding the decline in water clarity, as small organisms floating in the water column have a high specific surface area and can more efficiently scatter and reflect light. In turn, the decline in water clarity has a negative effect on macrophyte abundance, forming a positive feedback loop in which 'the more turbid the water, the fewer macrophytes there are' (Su, Chen, et al., 2019; van der Heide et al., 2011; this study, Figure 5).

Understanding the mechanisms of hysteresis is critical for management practices. It has been assumed that the recovery to a macrophyte-dominated ecosystem can be hampered by low water clarity, grazing by fish or birds, water-level fluctuations and a lack of propagules or seeds in the sediment (Hilt et al., 2006). In the present study, we propose a three-dimensional conceptual model to iconically depict the mechanisms of critical transition and hysteresis (Figure 5). In the forward bottom-up controlled system, according to the theory of alternative lake equilibria, eutrophication facilitates primary producers and thereby reduces water clarity. In the backward trajectory, fish-driven top-down forces control ecosystem behaviour, forming an ecological hysteresis of recovery even when the nutrient levels drop below the values at which the ecosystem collapses. As respiration is more sensitive to warming than photosynthesis (Allen et al., 2005; Yvon-Durocher et al., 2010), warmer temperatures will strengthen the top-down forces due to the increased metabolic rate and resource demand (Kratina et al., 2012). Furthermore, it is suggested that both fish stocking and warming will increase water nutrient availability, for example, by direct excretion of fish, elevated nutrient release from sediment, enhanced mineralization rates and increased evaporation (Domis et al., 2013; Gudasz et al., 2010), further weakening the efforts of nutrient reduction and enhancing hysteresis. Moreover, food webs may show evolutionary responses to top-down effects (e.g. altering genotype frequencies in the cladoceran population), making the recovery process slow or even impossible (Kuparinen & Merilä, 2007; Stokes & Law, 2000).

5 | CONCLUSIONS

We provide convincing empirical evidence for pressure-induced nonlinear ecological changes in a subtropical shallow lake, cross-validated by long-term monitoring and paleo-diatom data. The Donghu Lake ecosystem shifts from a macrophyte-dominated clear-water state to a phytoplankton-dominated turbid-water state under the combined pressures of climate warming, eutrophication and trophic cascade by fish stocking. We found that EWSs were detectable in both the forward collapse and backward recovery trajectories and that including body size information in composite EWSs was more robust for assessing ecological resilience approaching a transition. In a multi-driver-controlled ecosystem, dominant drivers changing from bottom-up to top-down forces after the critical transition lowered the effectiveness of nutrient reduction in the turbid regime. Therefore, in practice, in addition to nutrient reduction, more positive management measures, such as reducing the fish stocking density, slowing climate warming and carrying out macrophyte planting, are important and necessary for the anticipatory recovery to a clear-water state.

ACKNOWLEDGEMENTS

We would like to thank all members who have ever participated in the monitoring programme of the Donghu Lake ecosystem. This work was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000), the National Key Research and Development Program of China (2017YFA0605201) and the Major Science and Technology Program for Water Pollution Control and Treatment (2017ZX07203-004). We would like to thank Sonia Kefi for providing useful feedback on earlier versions of the manuscript. The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

P.X. and H.S. designed the research; H.S., Y.L., Ya.L. and J.C. contributed to the sampling and data collection; H.S. and Y.F. devised the figure structure and performed the data analyses; H.S. wrote the manuscript and P.X., R.W., C.X., S.W. and J.F. substantially contributed to revisions.

DATA AVAILABILITY STATEMENT

Long-term monitoring data can be obtained from Donghu Experimental Station of Lake Ecosystems (http://dhl.cern.ac.cn/meta/metaData). Data were also available from the Dryad Digital Repository https://doi.org/10.5061/dryad.7m0cfxpsf (Su et al., 2020).

ORCID

Haojie Su https://orcid.org/0000-0003-4780-1094
Chi Xu https://orcid.org/0000-0002-1841-9032
Shaopeng Wang https://orcid.org/0000-0002-9430-8879

REFERENCES

Allen, A., Gillooly, J., & Brown, J. (2005). Linking the global carbon cycle to individual metabolism. *Functional Ecology*, *19*(2), 202–213. https://doi.org/10.1111/j.1365-2435.2005.00952.x

Arkilanian, A. A., Clements, C. F., Ozgul, A., & Baruah, G. (2020). Effect of time series length and resolution on abundance- and trait-based early warning signals of population declines. *Ecology*, *101*(7), e03040. https://doi.org/10.1002/ecy.3040

Baruah, G., Clements, C. F., & Ozgul, A. (2020). Eco-evolutionary processes underlying early warning signals of population declines. *Journal of Animal Ecology*, *89*(2), 436–448. https://doi.org/10.1111/1365-2656.13097

Battarbee, R., Jones, V., & Flower, R. (2001). *Tracking environmental change using lake sediments: Volume 3: Terrestrial, algal, and siliceous indicators* (Vol. 3): Springer.

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. *Frontiers in Ecology and the Environment*, *1*(7), 376–382. https://doi.org/10.2307/3868190

Bhargava, D., & Mariam, D. W. (1991). Effects of suspended particle size and concentration on reflectance measurements. *Photogrammetric Engineering and Remote Sensing*, *57*(5), 519–529.

Biggs, R., Carpenter, S. R., & Brock, W. A. (2009). Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(3), 826–831. https://doi.org/10.1073/pnas.0811729106

Birk, S., Chapman, D., Carvalho, L., Spears, B. M., Andersen, H. E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A. D., Cardoso, A. C., Couture, R.-M., Cremona, F., de Zwart, D., … Hering, D. (2020). Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nature Ecology & Evolution*, *4*(8), 1060–1068. https://doi.org/10.1038/s41559-020-1216-4

Boyce, D. G., Frank, K. T., Worm, B., & Leggett, W. C. (2015). Spatial patterns and predictors of trophic control in marine ecosystems. *Ecology Letters*, *18*(10), 1001–1011. https://doi.org/10.1111/ele.12481

Brose, U., Archambault, P., Barnes, A. D., Bersier, L.-F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., … Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, *3*(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x

Bruel, R., Marchetto, A., Bernard, A., Lami, A., Sabatier, P., Frossard, V., & Perga, M. E. (2018). Seeking alternative stable states in a deep lake. *Freshwater Biology*, *63*(6), 553–568. https://doi.org/10.1111/fwb.13093

Capon, S. J., Lynch, A. J. J., Bond, N., Chessman, B. C., Davis, J., Davidson, N., Finlayson, M., Gell, P. A., Hohnberg, D., Humphrey, C., Kingsford, R. T., Nielsen, D., Thomson, J. R., Ward, K., & Nally, R. M. (2015). Regime shifts, thresholds and multiple stable states in freshwater ecosystems; a critical appraisal of the evidence. *Science of the Total Environment*, *534*, 122–130. https://doi.org/10.1016/j.scitotenv.2015.02.045

Carpenter, S. R., & Brock, W. A. (2006). Rising variance: A leading indicator of ecological transition. *Ecology Letters*, *9*(3), 311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x

Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W. A., Cline, T., Coloso, J., Hodgson, J. R., Kitchell, J. F., Seekell, D. A., Smith, L., & Weidel, B. (2011). Early warnings of regime shifts: A whole-ecosystem experiment. *Science*, *332*(6033), 1079–1082. https://doi.org/10.1126/science.1203672

Carpenter, S. R., & Kitchell, J. F. (1996). *The trophic cascade in lakes*. Cambridge University Press.

Christensen, M. R., Graham, M. D., Vinebrooke, R. D., Findlay, D. L., Paterson, M. J., & Turner, M. A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, *12*(12), 2316–2322. https://doi.org/10.1111/j.1365-2486.2006.01257.x

Clements, C. F., Blanchard, J. L., Nash, K. L., Hindell, M. A., & Ozgul, A. (2017). Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nature Ecology & Evolution*, *1*(7), 188. https://doi.org/10.1038/s41559-017-0188

Clements, C. F., McCarthy, M. A., & Blanchard, J. L. (2019). Early warning signals of recovery in complex systems. *Nature Communications*, *10*. https://doi.org/10.1038/s41467-019-09684-y

Clements, C. F., & Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. *Nature Communications*, *7*. https://doi.org/10.1038/ncomms10984

Clements, C. F., & Ozgul, A. (2018). Indicators of transitions in biological systems. *Ecology Letters*, *21*(6), 905–919. https://doi.org/10.1111/ele.12948

Crain, C. M., Kroeker, K., & Halpern, B. S. (2010). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Dakos, V., Carpenter, S. R., Brock, W. A., Ellison, A. M., Guttal, V., Ives, A. R., Kéfi, S., Livina, V., Seekell, D. A., van Nes, E. H., & Scheffer, M. (2012). Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS ONE*, *7*(7). https://doi.org/10.1371/journal.pone.0041010

Dakos, V., Scheffer, M., van Nes, E. H., Brovkin, V., Petoukhov, V., & Held, H. (2008). Slowing down as an early warning signal for abrupt climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(38), 14308–14312. https://doi.org/10.1073/pnas.0802430105

Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(25), 10518–10523. https://doi.org/10.1073/pnas.0701100104

Davis, J., Sim, L., & Chambers, J. (2010). Multiple stressors and regime shifts in shallow aquatic ecosystems in antipodean landscapes. *Freshwater Biology*, *55*, 5–18. https://doi.org/10.1111/j.1365-2427.2009.02376.x

De senerpont domis, L. N., Elser, J. J., Gsell, A. S., Huszar, V. L. M., Ibelings, B. W., Jeppesen, E., Kosten, S., Mooij, W. M., Roland, F., Sommer, U., Van donk, E., Winder, M., & Lürling, M. (2013). Plankton dynamics under different climatic conditions in space and time. *Freshwater Biology*, *58*(3), 463–482. https://doi.org/10.1111/fwb.12053

DeLong, J. P., Gilbert, B., Shurin, J. B., Savage, V. M., Barton, B. T., Clements, C. F., Dell, A. I., Greig, H. S., Harley, C. D. G., Kratina, P., McCann, K. S., Tunney, T. D., Vasseur, D. A., & O'Connor, M. I. (2015). The body size dependence of trophic cascades. *The American Naturalist*, *185*(3), 354–366. https://doi.org/10.1086/679735

Dong, X., Kattel, G., & Jeppesen, E. (2020). Subfossil cladocerans as quantitative indicators of past ecological conditions in Yangtze River Basin lakes, China. *The Science of the Total Environment*, *728*, 138794. https://doi.org/10.1016/j.scitotenv.2020.138794

Drake, J. M., & Griffen, B. D. (2010). Early warning signals of extinction in deteriorating environments. *Nature*, *467*(7314), 456–459. https://doi.org/10.1038/nature09389

Durant, J. M., Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, *33*(3), 271–283. https://doi.org/10.3354/cr033271

Faassen, E. J., Veraart, A. J., Van Nes, E. H., Dakos, V., Lürling, M., & Scheffer, M. (2015). Hysteresis in an experimental phytoplankton population. *Oikos*, *124*(12), 1617–1623. https://doi.org/10.1111/oik.02006

Forster, J., Hirst, A. G., & Atkinson, D. (2012). Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(47), 19310–19314. https://doi.org/10.1073/pnas.1210460109

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, *308*(5728), 1621–1623. https://doi.org/10.1126/science.1113075

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge University Press.

Gudasz, C., Bastviken, D., Steger, K., Premke, K., Sobek, S., & Tranvik, L. J. (2010). Temperature-controlled organic carbon mineralization in lake sediments. *Nature*, *466*(7305), 478–481. https://doi.org/10.1038/nature09186

Guttal, V., & Jayaprakash, C. (2008). Changing skewness: An early warning signal of regime shifts in ecosystems. *Ecology Letters*, *11*(5), 450–460. https://doi.org/10.1111/j.1461-0248.2008.01160.x

Hidding, B., Bakker, E. S., Hootsmans, M. J., & Hilt, S. (2016). Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. *Oikos*, *125*(10), 1489–1495. https://doi.org/10.1111/oik.03104

Hilt, S., Brothers, S., Jeppesen, E., Veraart, A. J., & Kosten, S. (2017). Translating regime shifts in shallow lakes into changes in ecosystem functions and services. *BioScience*, *67*, 928–936. https://doi.org/10.1093/biosci/bix106

Hilt, S., Gross, E. M., Hupfer, M., Morscheid, H., Mählmann, J., Melzer, A., Poltz, J., Sandrock, S., Scharf, E.-M., Schneider, S., & van de Weyer, K. (2006). Restoration of submerged vegetation in shallow eutrophic lakes – A guideline and state of the art in Germany. *Limnologica*, *36*(3), 155–171. https://doi.org/10.1016/j.limno.2006.06.001

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology Evolution and Systematics*, *4*(4), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Huang, X., Chen, W., & Cai, Q. (1999). *Survey, observation and analysis of lake ecology. Standard methods for observation and analysis in Chinese Ecosystem Research Network, Series V*. Standards Press of China.

Jackson, M. C., Loewen, C. J., Vinebrooke, R. D., & Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, *22*(1), 180–189. https://doi.org/10.1111/gcb.13028

Jolliffe, I. (2002). *Principal component analysis*. Springer.

Juggins, S. (2015). *rioja: Analysis of Quaternary science data*. R package version (0.9-5). The Comprehensive R Archive Network.

Kéfi, S., Guttal, V., Brock, W. A., Carpenter, S. R., Ellison, A. M., Livina, V. N., Seekell, D. A., Scheffer, M., van Nes, E. H., & Dakos, V. (2014). Early warning signals of ecological transitions: Methods for spatial patterns. *PLoS ONE*, *9*(3), e92097. https://doi.org/10.1371/journal.pone.0092097

Kong, X., He, Q., Yang, B., He, W., Xu, F., Janssen, A. B. G., Kuiper, J. J., van Gerven, L. P. A., Qin, N., Jiang, Y., Liu, W., Yang, C., Bai, Z., Zhang, M., Kong, F., Janse, J. H., & Mooij, W. M. (2017). Hydrological regulation drives regime shifts: Evidence from paleolimnology and ecosystem modeling of a large shallow Chinese lake. *Global Change Biology*, *23*(2), 737–754. https://doi.org/10.1111/gcb.13416

Kratina, P., Greig, H. S., Thompson, P. L., Carvalho-Pereira, T. S. A., & Shurin, J. B. (2012). Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, *93*(6), 1421–1430. https://doi.org/10.1890/11-1595.1

Kuparinen, A., & Merilä, J. (2007). Detecting and managing fisheries-induced evolution. *Trends in Ecology & Evolution*, *22*(12), 652–659. https://doi.org/10.1016/j.tree.2007.08.011

Lemmens, P., Declerck, S. A., Tuytens, K., Vanderstukken, M., & De Meester, L. (2018). Bottom-up effects on biomass versus top-down effects on identity: A multiple-lake fish community manipulation experiment. *Ecosystems*, *21*(1), 166–177. https://doi.org/10.1007/s10021-017-0144-x

Liu, J. K. (1991). *Ecological studies of Lake Donghu*. Science Press.

May, R. M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, *269*(5628), 471–477. https://doi.org/10.1038/269471a0

McGowan, S., Leavitt, P. R., Hall, R. I., Anderson, N. J., Jeppesen, E., & Odgaard, B. V. (2005). Controls of algal abundance and community composition during ecosystem state change. *Ecology*, *86*(8), 2200–2211. https://doi.org/10.1890/04-1029

Moss, B., Mckee, D., Atkinson, D., Collings, S. E., Eaton, J. W., Gill, A. B., Harvey, I., Hatton, K., Heyes, T., & Wilson, D. (2003). How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms. *Journal of Applied Ecology*, *40*(5), 782–792. https://doi.org/10.1046/j.1365-2664.2003.00839.x

Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., Motley, J. L., Self, K. E., Taylor, D. S., & Wolf, C. (2016). What is a trophic cascade? *Trends in Ecology & Evolution*, *31*(11), 842–849. https://doi.org/10.1016/j.tree.2016.08.010

Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., van Nes, E. H., Rietkerk, M., & Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature*, *461*(7260), 53–59. https://doi.org/10.1038/nature08227

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*, 591–596. https://doi.org/10.1038/35098000

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, *89*(12), 3472–3479. https://doi.org/10.1890/07-1748.1

Smith, V. H., & Schindler, D. W. (2009). Eutrophication science: Where do we go from here? *Trends in Ecology & Evolution*, *24*(4), 201–207. https://doi.org/10.1016/j.tree.2008.11.009

Spanbauer, T. L., Allen, C. R., Angeler, D. G., Eason, T., Fritz, S. C., Garmestani, A. S., Nash, K. L., Stone, J. R., Stow, C. A., & Sundstrom, S. M. (2016). Body size distributions signal a regime shift in a lake ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1833). https://doi.org/10.1098/rspb.2016.0249

Spears, B. M., Futter, M. N., Jeppesen, E., Huser, B. J., Ives, S., Davidson, T. A., Adrian, R., Angeler, D. G., Burthe, S. J., Carvalho, L., Daunt, F., Gsell, A. S., Hessen, D. O., Janssen, A. B. G., Mackay, E. B., May, L., Moorhouse, H., Olsen, S., Søndergaard, M., … Thackeray, S. J. (2017). Ecological resilience in lakes and the conjunction fallacy. *Nature Ecology & Evolution*, *1*(11), 1616–1624. https://doi.org/10.1038/s41559-017-0333-1

Staver, A. C., Archibald, S., & Levin, S. A. (2011). The global extent and determinants of savanna and forest as alternative biome states. *Science*, *334*(6053), 230–232. https://doi.org/10.1126/science.1210465

Stokes, K., & Law, R. (2000). Fishing as an evolutionary force. *Marine Ecology Progress*, *208*, 307–309. Retrieved from https://www.jstor.org/stable/24863829

Su, H., Chen, J., Wu, Y., Chen, J., Guo, X., Yan, Z., Tian, D. I., Fang, J., & Xie, P. (2019). Morphological traits of submerged macrophytes reveal specific positive feedbacks to water clarity in freshwater ecosystems. *Science of the Total Environment*, *684*, 578–586. https://doi.org/10.1016/j.scitotenv.2019.05.267

Su, H., Wang, R., Feng, Y., Li, Y., Li, Y., Chen, J., Xu, C., Wang, S., Fang, J., & Xie, P. (2020). Data from: Long-term empirical evidence, early warning signals and multiple drivers of regime shifts in a lake ecosystem. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.7m0cfxpsf

Su, H., Wu, Y., Xia, W., Yang, L., Chen, J., Han, W., Fang, J., & Xie, P. (2019). Stoichiometric mechanisms of regime shifts in freshwater ecosystem. *Water Research*, *149*, 302–310. https://doi.org/10.1016/j.watres.2018.11.024

van der Heide, T., van Nes, E. H., van Katwijk, M. M., Olff, H., & Smolders, A. J. (2011). Positive feedbacks in seagrass ecosystems–evidence from large-scale empirical data. *PLoS ONE*, *6*(1), e16504. https://doi.org/10.1371/journal.pone.0016504

van Nes, E. H., & Scheffer, M. (2005). Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology*, *86*(7), 1797–1807. https://doi.org/10.1890/04-0550

Wang, R., Dearing, J. A., Langdon, P. G., Zhang, E., Yang, X., Dakos, V., & Scheffer, M. (2012). Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature*, *492*(7429), 419–422. https://doi.org/10.1038/nature11655

Ward, D. F., Wotherspoon, S., Melbourne-Thomas, J., Haapkylä, J., & Johnson, C. R. (2018). Detecting ecological regime shifts from transect data. *Ecological Monographs*, *88*(4), 694–715. https://doi.org/10.1002/ecm.1312

Wernberg, T., Thomsen, M. S., Tuya, F., Kendrick, G. A., Staehr, P. A., & Toohey, B. D. (2010). Decreasing resilience of kelp beds along a latitudinal temperature gradient: Potential implications for a warmer future. *Ecology Letters*, *13*(6), 685–694. https://doi.org/10.1111/j.1461-0248.2010.01466.x

Winder, M., & Schindler, D. E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, *85*(8), 2100–2106. https://doi.org/10.1890/04-0151

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Xu, C., Hantson, S., Holmgren, M., Nes, E. H., Staal, A., & Scheffer, M. (2016). Remotely sensed canopy height reveals three pantropical ecosystem states. *Ecology*, *97*(9), 2518–2521. https://doi.org/10.1002/ecy.1470

Yvon-Durocher, G., Jones, J. I., Trimmer, M., Woodward, G., & Montoya, J. M. (2010). Warming alters the metabolic balance of ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2117–2126. https://doi.org/10.1098/rstb.2010.0038

Yvon-Durocher, G., Montoya, J. M., Trimmer, M., & Woodward, G. (2011). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology*, *17*(4), 1681–1694. https://doi.org/10.1111/j.1365-2486.2010.02321.x

Zeileis, A., Leisch, F., Hornik, K., & Kleiber, C. (2001). strucchange: An R package for testing for structural change in linear regression models. *Journal of Statistical Software*, *7*(2), 1–38. https://doi.org/10.18637/jss.v007.i02

Zhang, K., Dong, X., Yang, X., Kattel, G., Zhao, Y., & Wang, R. (2018). Ecological shift and resilience in China's lake systems during the last two centuries. *Global and Planetary Change*, *165*, 147–159. https://doi.org/10.1016/j.gloplacha.2018.03.013

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Su H, Wang R, Feng Y, et al. Long-term empirical evidence, early warning signals and multiple drivers of regime shifts in a lake ecosystem. *J Ecol*. 2020;00:1–13. https://doi.org/10.1111/1365-2745.13544