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Critical Transitions in Lake Ecosystem State May Be Driven by Coupled Feedback Mechanisms: A Case Study from Lake Erhai, China

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Abstract: Critical transitions between ecosystem states can be triggered by relatively small external forces or internal perturbations and may show time-lagged or hysteretic recovery. Understanding the precise mechanisms of a transition is important for ecosystem management, but it is hampered by a lack of information about the preceding interactions and associated feedback between different components in an ecosystem. This paper employs a range of data, including paleolimnological, environmental monitoring and documentary sources from lake Erhai and its catchment, to investigate the ecosystem structure and dynamics across multiple trophic levels through the process of eutrophication. A long-term perspective shows the growth and decline of two distinct, but coupled, positive feedback loops: a macrophyte-loop and a phosphorus-recycling-loop. The macrophyte-loop became weaker, and the phosphorus-recycling-loop became stronger during the process of lake eutrophication, indicating that the critical transition was propelled by the interaction of two positive feedback loops with different strengths. For lake restoration, future weakening of the phosphorus-recycling loop or a reduction in external pressures is expected to trigger macrophyte growth and eventually produce clear water conditions, but the speed of recovery will probably depend on the rates of feedback loops and the strength of their coupling.

Keywords: critical transition; positive feedback; regime shift; paleolimnology; eutrophication



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1. Introduction

With growing concerns about widespread ecological instability [1], global ecosystems are now more at risk to rapid change from human-induced critical transitions than at any time in history [2]. The risk comes from a loss of ecological resilience such that a small force or perturbation can shift the system to a contrasting state. The presence of hysteresis means that some shifts in ecosystems may be effectively irreversible, requiring disproportionately large reversals of the key drivers that led to the transition [3]. Therefore, understanding and using the antecedent conditions to critical transitions as possible early warning signals is a major research priority [4–6].

Theories of critical transitions and their early warning signals in ecosystems are largely based on mathematical models [3,5,7], with empirical validation provided by studies of environmental time-series [8,9], manipulated ecosystems [10] and laboratory microcosm experiments [11,12]. Establishing the existence of early warning signals in real-world systems [13] has conventionally used frequency analysis of time-series to identify the increased sensitivity of a system to perturbations implied by a loss of resilience to stress. Fewer studies have sought to understand critical transitions through analyses of a system's structural changes as the system responds or adapts to the stress [9] or through evolutionary simulation models [14]. Knowing how interactions between internal system components,

for example, energy flow and species turnover, change as external forces exert a stress may be key to understanding critical transitions. Interactions between system components determine the nature and strength of self-organizing or positive feedback loops, and these internal mechanisms can drive systems across thresholds and cause critical transitions. However, learning from retrospective analyses of the nature and strength of feedback loops prior to, during, and following a known critical transition is hampered by a lack of case studies.

Lake ecosystems offer an excellent platform for studying critical transitions because numerous observations show shifts between clean and turbid water regimes during eutrophication [4], often associated with an increasing frequency of algal blooms. Here, we develop and apply a methodology to reconstruct the nature and strength of positive feedback loops in Erhai, Yunnan Province, China (Figure 1) before, during, and after an observed critical transition from clear to turbid conditions in 2001 [9], and explore how these loops are affected by external drivers acting alone or in combination. We combine environmental records from instrumental surveys with longer paleolimnological analyses of lake sediments to reconstruct the main elements of the lake-catchment ecosystem, including the dominant positive feedback loops, over several decades. A few previous studies have also used paleolimnological records to help gain insight into structural changes in the biological network of interactions through statistical analyses of nodal connectivity [15,16] and changes in the compositional order of biota through nestedness approaches [17]. However, these studies have focused on only one component of the biological assemblage and have not explicitly identified the feedback dynamics. We expect that feedback dynamics will be characterized by both self-regulating and self-organizing feedback loops, although here our interest is in understanding the functioning of the positive feedback loops that drive abrupt changes in the whole lake ecosystem [18].

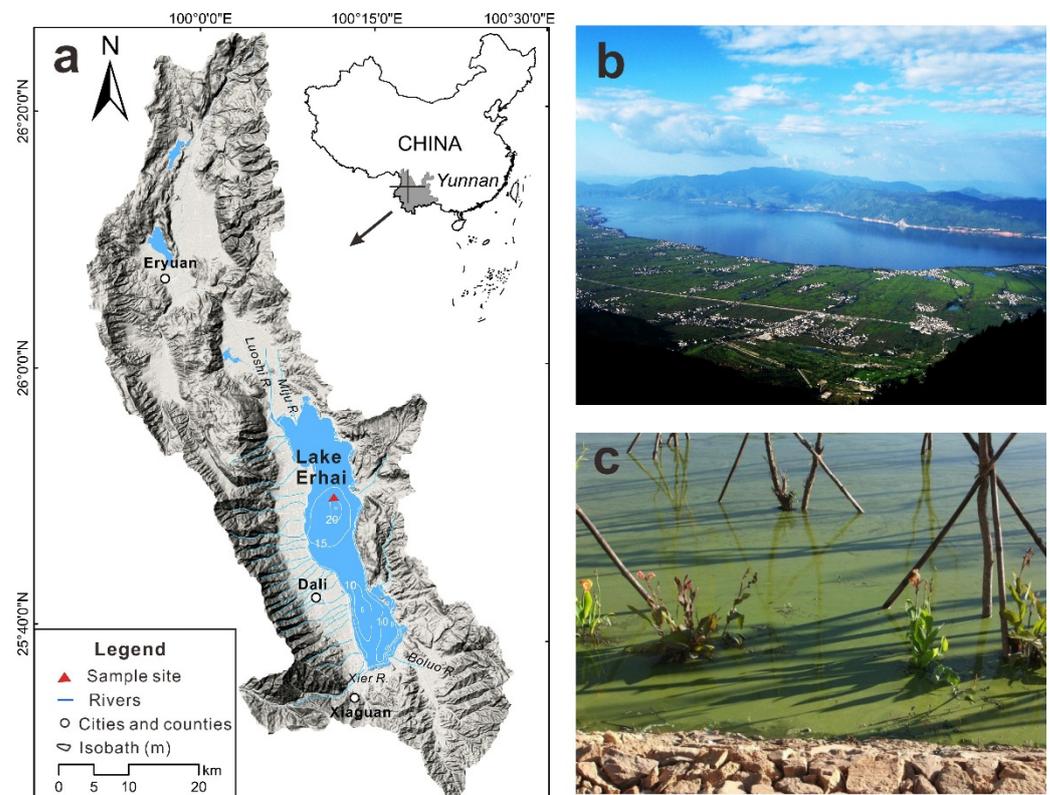


Figure 1. Erhai, Yunnan Province, China. (a) Lake location and its catchment showing lake outflow, water depths (5 m intervals) and the main core location (red dot), that provided the paleolimnological data [9]. (b) Photograph from western mountains looking across the deepest and widest part of the lake (taken in 2010). (c) Photograph from western mountains looking across the deepest and widest part of the lake (taken in 2010) showing algal blooms.

by the author). (c) Photograph of algae bloom in 2010 on the NE shoreside (http://blog.sina.com.cn/s/blog_4c4985580100mmm0.html with permission, accessed on 31 December 2021).

2. Materials and Methods

2.1. Study Site

Erhai is one of the largest tectonic lakes in Yunnan Province (25°36′–25°58′ N, 100°05′–100°18′ E). Lying at an altitude of 1974 m, it is approximately 40 km long and 7–8 km wide, with a surface area ~256 km² and catchment area ~2250 km² (Figure 1). The mean depth of Erhai is ~10 m and the maximum depth is ~21 m. The catchment comprises two administrative regions, the City of Dali (Xiaguan) and Eryuan County (Figure 1). Dali includes all areas directly bordering the lake, and Eryuan County mainly includes the northern catchment drained by the largest inflowing river, the Miju. Erhai drains out through the West Erhe River to the south (Figure 1a). There are 4 large towns and 52 villages in the catchment, with a total population presently exceeding 800,000: a doubling since 1985.

Land cover in the mountainous parts of the catchment is classified as forest (53% area), but most of the natural Cangshan Fir (*Abies*) was cut during the Great Leap Forward (1958–1961) and Cultural Revolution (1966–1976), and now only exists above 3300 m. Crop land is the second largest land cover in the catchment (19% area), existing mainly in the northern Miju catchment and the western alluvial plain, where there is typically a double-cropping system of rice, wheat, legumes, and tobacco. The forest cover declined from 62% in 1990 to 53% in 2006 but, in most areas, the deforested land was used for infrastructural development rather than croplands.

The lake can be divided into a northern deeper basin (maximum depth ~20 m) characterized by monomictic summer stratification [19] and a shallower mixed southern basin (maximum depth ~10 m) (Figure 1a). The lake was defined as mesotrophic in the early 1990s [20] but became steadily more eutrophic as a result of non-point pollution, mainly from agricultural runoff [21]. In 1992, the mean concentration of total phosphorus (TP) in lake water was around 0.015 mg/L, rising to over 0.035 mg/L in 2003 [20]. The first records of algal blooming date to 1996, and blooms have been recorded subsequently in each year since 2003 (Figure 1c). Before 2001, the water clarity remained high at more than 3 m Secchi Disc (SD) depth, but within two years declined to ~1.5 m, indicating that the lake had shifted from a clear to a turbid state. Since 2001–2003, the lake quality has been classified as Class III–IV ‘eutrophic’ [22]. The main nutrient sources (~75–90% TP) are non-point rural and agricultural: livestock breeding, village wastewater and agricultural runoff [21,22]. Drawing on water monitoring data from 1997 to 2003, [9] argued that the rapid change between 1992 and 2009 could be defined as a critical transition, closely tracking a theoretical fold bifurcation where three system states exist but only two are stable.

2.2. Causal Loop and Hypotheses

We compiled available data (Table 1) and background information to create a narrative of environmental changes since ~1950 and a hypothetical causal loop diagram (Figure 2) to show the potential interactions between the lake components and external drivers. From this, we hypothesized that four possible positive feedback loops [23–25] could play a role in controlling water turbidity:

- Loop I Macrophyte-dissolved nutrient-algae-turbidity-macrophytes;
- Loop II Macrophyte-zooplankton-algae-turbidity-macrophytes;
- Loop III Macrophyte-waves-resuspended sediment-turbidity-macrophytes;
- Loop IV Algae-organic material-bottom water anoxia-nutrient release-algae.

Table 1. Indicator data for different lake system components with time-series date range.

System Component	Indicator	Date Range	Resolution of Sampling	Data Source
turbidity	Secchi disk depth	1989–2013	monthly	Chen, 2015 [26]
dissolved nutrient	total P in water column	1992–2014	monthly	Wang, 2016 [27]

Table 1. Cont.

System Component	Indicator	Date Range	Resolution of Sampling	Data Source
bottom oxygen	fossil chironomid head capsules	1822–2007	sedimentation rate dependent	Wang et al., 2012 [9]
P from catchment	P fertilizer use	1990–2012	annual	Chen, 2015 [26]
sediment organic	total organic carbon in sediment	1900–2010	sedimentation rate dependent	Wang et al., 2012 [9]
sediment P	P in sediment	1900–2010	sedimentation rate dependent	Wang et al., 2012 [9]
sediment P release	the ratio of sediment P and Fe	1900–2010	sedimentation rate dependent	Wang et al., 2012 [9]
macrophytes	maximum macrophyte depth	1957–2009	single survey	Wu et al., 2013 [28]
algae	chlorophyll-a concentration	1988–2013	monthly	Chen, 2015 [26]
zooplankton	fossil Cladocera	1956–2012	sedimentation rate dependent	Liu et al., 2014 [29]
fish	fish yield	1990–2012	annual	Chen, 2015 [26]
water level	monitoring lowest water level	1952–2011	annual	Wang et al., 2012 [9]
temperature	monitoring temperature in Dali station	1951–2010	daily	National Meteorological Information Center (http://data.cma.cn , accessed on 31 December 2021)
rainfall	monitoring rainfall in Dali station	1951–2009	daily	National Meteorological Information Center (http://data.cma.cn , accessed on 31 December 2021)
wind	monitoring wind in Dali station	1951–2010	daily	National Meteorological Information Center (http://data.cma.cn , accessed on 31 December 2021)

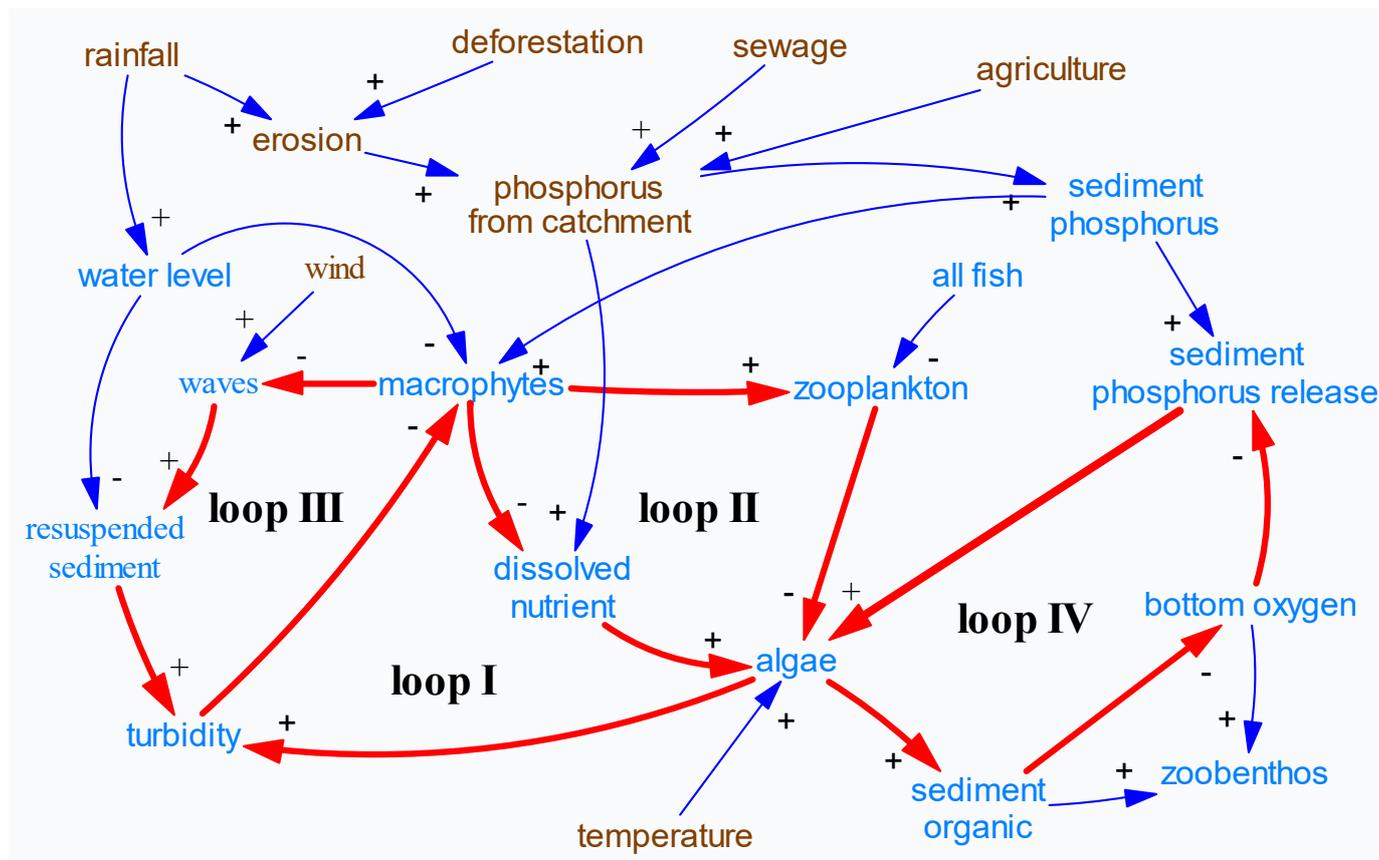


Figure 2. A causal loop diagram for the Erhai catchment system based on the literature and the key components within the lake (blue labels) and its catchment (brown labels). The arrows show the direction of the effects of one component on another, where the ‘+’ and ‘-’ signs denote positive and inverse relationships, as envisaged in bivariate scatter plots with positive and negative correlation coefficients, respectively. Specific interactions that define loops I–IV are shown in red.

Loops I–III involve interactions between macrophytes growing in relatively shallow water and turbidity, mediated through nutrients, zooplankton populations and suspended sediment. Macrophytes can help maintain low levels of turbidity by absorbing dissolved nutrients that promote phytoplankton productivity (loop I), by providing cover for zooplankton from fish predation which feed on phytoplankton (loop II), or by reducing the exposure of the lake bed to wind stress and the re-suspension of sediments (loop III). In each case, a greater biomass, distribution or density of macrophytes improves the lake conditions that allow macrophytes to flourish further. Conversely, losses of macrophytes or increases in turbidity driven by external drivers cause the loops to reverse. These interactions are most likely to play out in shallow lakes where the potential photic zone is large relative to the size of the lake and where wind-generated currents reach the lake bed. With a potential fetch over much of Erhai's surface measured in kilometers, wind stress at the lake bed through exceedance of critical orbital velocities for fine sediment could extend to water depths of 5–10 m [30]. Water depths in the shallower edges of the northern basin and most of the southern basin are mostly 10 m. Therefore, the potential role of macrophytes in affecting water quality through different mechanisms means that none of the loops I–III may be excluded a priori.

Despite arguments that redox-mediated phosphorus-release (loop IV) is a simplification of complex processes [31], it remains widely accepted that sediment organic matter and hypolimnetic dissolved oxygen determine the magnitude of the nutrient release and potential recycling from lake sediments. In loop IV, increasing phytoplankton productivity results in more sedimented organic matter, greater oxygen depletion of bottom waters through decomposition, the generation of anoxia in the hypolimnion and upper sediments, and the release of previously fixed nutrients, such as phosphorus, capable of boosting phytoplankton growth (Figure 2). The presence of stratification where a stable hypolimnion is protected from mixing with the oxygenated epilimnion makes loop IV a candidate in relatively deep lakes. In Erhai, the deeper northern basin is known to stratify, indicating the potential for loop IV. Indeed, Wang et al. [9] used the lack of chironomid head capsules in the recent sediments as evidence for the presence of anoxia and P-release prior to the critical transition, but no other loops were tested.

2.3. Analyses

We tested the validity of the plausible positive feedback loops using a large database of monitored and paleolimnological time-series [9]. This was a qualitative analysis in combination with linear correlation between variables to evaluate the hypothesized loops. We assumed that a strong positive feedback loop will show significant correlations between different variables within the loop over time. Statistical analysis of the time-series data used a common time range of data, even though the time ranges varied between datasets. Dated paleolimnological records were transformed to annual time-series by linear interpolation. We analyzed Pearson correlations between different variables to describe the linear relationship and used p -values to evaluate the significance, and we set $p > 0.01$ as non-significant. The statistical analysis was performed in Minitab® 16 Statistical Software.

3. Results

3.1. Long-Term Change (1950s–2010s)

Information about potential external drivers was drawn from a variety of time-series (Table 1 and Figure 3). Potential drivers of the lake ecosystem for which time-series are available included climate, lake water level, external nutrients, and the introduction of exotic fish. The mean annual temperature has been rising since the 1990s with recent high temperatures equaling historical values found in the 1950s (Figure 3a, Mann–Kendall trend test: $z = 2.50$, $n = 20$, p -value = 0.01) and rainfall data show that droughts occurred in 1960, 1978, 1988 and 2006 (Figure 3b). Before 1975, the lake water level was stable at around 1973–1974 m above sea level with a maximum depth of ~21 m (Figure 3c). In the period 1978–1982, lake levels were controlled by both precipitation and outflow

management, linked to the construction and operation of the hydropower station in the West Erhe River, with a maximum 25.6% loss of volume in 1982 compared to pre-1978 volumes [20]. Figure 3d shows the phosphorus-fertilizer (P-fertilizer) consumption in the catchment rising from 400×10^4 t in 1990 to 1600×10^4 t in 2012. The lake water TP was around 0.014 mg/L in 1992 and increased to around 0.034 mg/L in 2003, although declined to around 0.020 mg/L in 2014 (Figure 3e). Macrophytes covered the lake to a depth of 3 m before the 1950s, but that they rapidly expanded to cover the whole southern shallower basin by the end of the 1970s (Figure 3g).

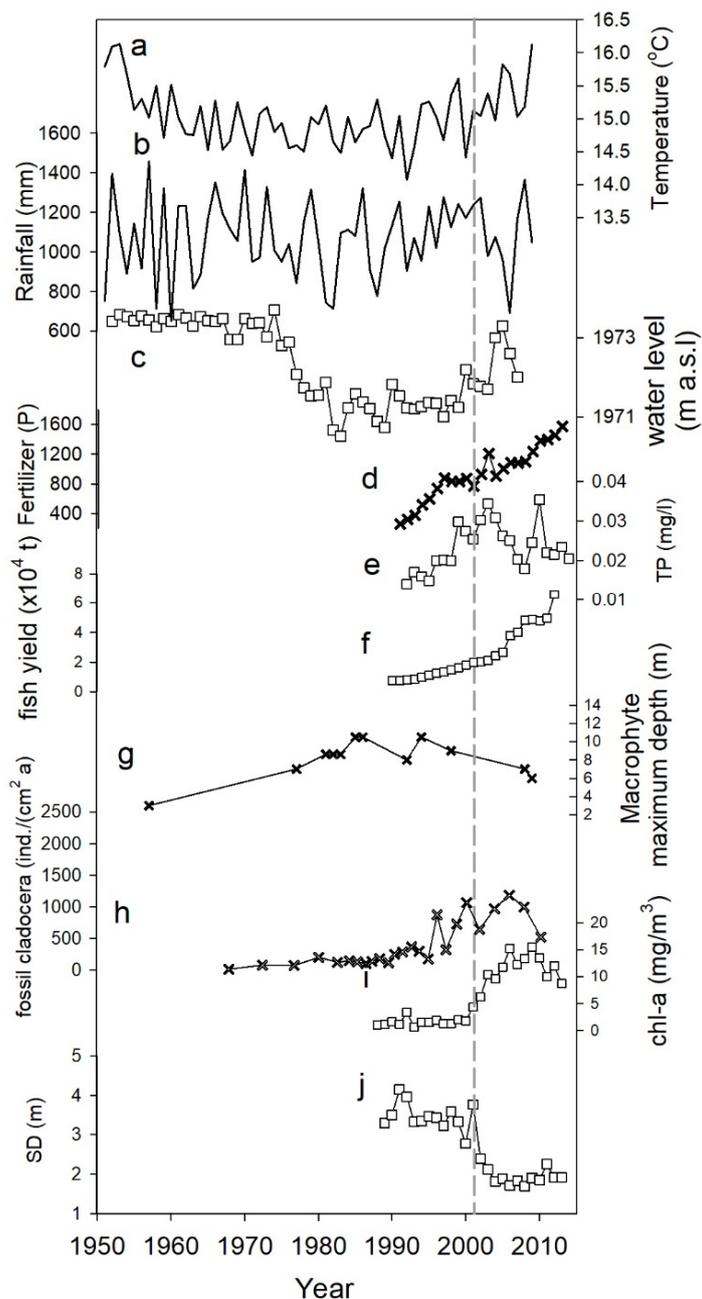


Figure 3. Monitoring data in Erhai. (a) Temperature variability between 1950 and 2010; (b) rainfall variability between 1950 and 2010; (c) water level between 1950 and 2010 (meters above sea level); (d) consumed phosphorus fertilizer ($\times 10^4$ t) in Dali city administration area; (e) total phosphorus (TP) in water; (f) fish yield from the lake; (g) maximum depth covered by macrophytes; (h) fossil Cladocera from the lake sediments; (i) concentration of chlorophyll-a (chl-a) in the water; (j) water clarity (SD).

Fish may play an important role in lake ecosystem feedback loops. In the early 1950s, there were 17 fish species, with no exotic fish recorded [32]. However, in 1961, Grass Carp (*Ctenopharyngodon idellus*) feeding on macrophytes, Silver Carp (*Hypophthalmichthys molitrix*) feeding on phytoplankton, and Bighead Carp (*Aristichthys nobilis*) feeding on zooplankton were introduced to increase fishery production. Silver Fish (*Neosalanx taihuensis*), feeding only on zooplankton, were introduced from Taihu lake in eastern China during the 1990s [32]. Several other species, including gobies (e.g., *Ctenogobius cliffordpopei* and *C. giurinus*), were also accidentally introduced into the lake [32]. The fish yield rose significantly, from 0.8×10^4 t in 1990 to around 6.6×10^4 t in 2012 (Figure 3f, Mann–Kendall trend test: $z = 6.55$, $n = 23$, p -value < 0.0001). Zooplankton, represented by fossil cladocera [29], increased from 1950s, but showed no clear trend after the 1980s (Figure 3h). The phytoplankton concentration, measured as chlorophyll-a (chl-a), increased from around 2 mg/m^3 in the late 1980s, peaking at 12 mg/m^3 in the mid-2000s (Figure 3i), a long-term trend which mirrors the decline in SD from around 3.5 m before 2001 to around 1.7 m in the mid-2000s (Figure 3j).

3.2. Critical Transition (2000–2004)

The new monitored data presented for the period 2010–2013 reaffirm the earlier observations [26] of a critical transition in lake turbidity (Figure 4). A comparison between the turbidity state measured by a Secchi disk (SD) and the main TP driver showed two alternate states: a clear state with the SD at around 3.5 m; and a turbid state with the SD at around 1.7 m (Figure 4a). The clear state existed when $\text{TP} < \sim 0.030 \text{ mg/L}$ (before 2001), but turbidity rapidly declined within 3 years (2001–2003) as TP approached 0.035 mg/L . Between 2005 and 2008, TP levels declined to as low as 0.018 mg/L , but with no improvement in turbidity. Since 2009, TP levels have fluctuated within the range 0.021 – 0.035 mg/L , but with no significant improvement or deterioration in turbidity. The lowest TP value of 0.018 mg/L reached in 2008 is equivalent to levels in the early 1990s but has the lowest water clarity (c. 1.7 m). Since 2004, turbidity has been insensitive to TP concentrations, suggesting a hysteretic phenomenon associated with a fold bifurcation. The comparison of TP with chl-a also showed alternative low and high algal states over the TP range ~ 0.018 – 0.035 mg/L (Figure 4b) [26].

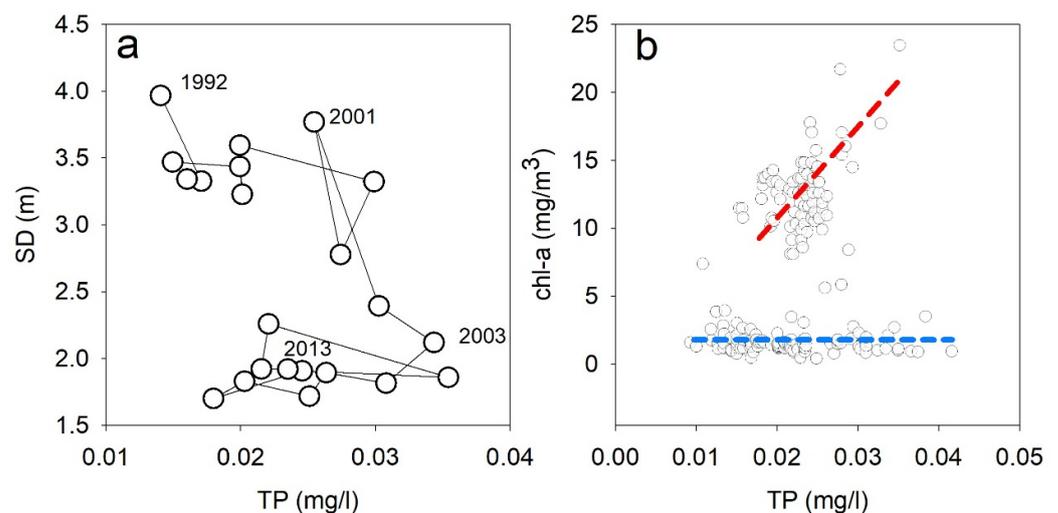


Figure 4. Phase plots of total phosphorus (TP) against water clarity (SD) and chlorophyll-a (chl-a) as a proxy for phytoplankton concentrations during the period 1992 to 2013. (a) The TP vs. SD plot of mean annual data from one sampling site tracks a fold bifurcation between the lake’s main driver (TP) and lake’s state (SD), with a transition between two stable states during the period 2001–2003. For TP values 0.018 – 0.040 mg/L , the lake can exist in either clear or turbid alternate states. (b) The TP vs. chl-a plot of mean annual data from 12 regular monitoring sites [26] shows a linear, positive relationship for a high algal state (red dashed line) and no relationship for a low algal state (blue dashed line).

3.3. Testing the Hypothesized Loops—Long-Term Analysis (1950s–2010s)

We first tested for the presence or absence of positive feedback loops through visual description, aided by simple statistical correlations between interacting elements. Over the period 1992–2013, there was a strong inverse correlation between SD and chl-a ($r = -0.90$, $p < 0.0001$) and a strong positive correlation between SD and macrophyte coverage ($r = 0.69$, $p < 0.0001$), indicating that clear water states are generally associated with low phytoplankton production and high macrophyte coverage, findings that support the presence of loops I and II. Loop III is mediated through sediment re-suspension. Although data for wave and suspended sediment are lacking, we found only a weak positive correlation between wind and SD ($r = 0.19$, $p = 0.367$), which suggests that loop III was likely ineffective during this period. Although a comparison of zooplankton and macrophyte data revealed the highest abundance of Cladocera at the end of the 1970s, when the macrophytes reached the highest coverage, there was also a significant positive correlation ($r = 0.70$, $p < 0.01$) between chl-a, and zooplankton over the period 1988–2012, indicating that loop II did not dominate over the long term.

The evidence for loop IV over the longer timescale is ambivalent. Chl-a was significantly correlated with the accumulation of organic sediment (TOC) ($r = 0.98$, $p < 0.001$) over the period 1988–2009, indicating that aquatic productivity drives the accumulation of organic sediment. Over the same period, chironomid head capsule abundance was strongly negatively correlated with the sediment P:Fe ratio (P-release) ($r = -0.87$, $p < 0.001$), supporting the link between organic sediment, increasing anoxia and P-release from the sediments to the hypolimnion. Moreover, the statistical correlation between chl-a and TP ($r = 0.39$, $p = 0.077$) in the period 1992–2013 is also non-significant, suggesting that TP has, at best, a weak direct control on aquatic productivity. Although conditions for P-release caused by anoxia in the deep-water zone of the core location are certain, the effects on lake-wide productivity are unclear.

In terms of external drivers, runoff of catchment P (as indicated by P fertilizer consumption, Figure 3d) was significantly positively correlated with SD ($r = 0.80$, $p < 0.0001$) and chl-a ($r = 0.78$, $p < 0.0001$). In addition, catchment P was also significantly negatively correlated ($r = -0.82$, $p < 0.0001$) with chironomid head capsules, indicating it to be a potentially important driver of phytoplankton concentrations and the development of anoxic conditions. Lake water levels were significantly positively correlated ($r = 0.76$, $p < 0.0001$) with chl-a over the period 1988–2007, and negatively ($r = -0.72$, $p < 0.0001$) with SD, supporting a view that the water level is a significant indirect driver of both phytoplankton production and turbidity, mediated through its effect on macrophytes. A visual comparison shows that the highest macrophyte coverage between 1975 and 2000 coincided with the lowest water levels (Figure 3c,g), and a statistical correlation between macrophytes and water level also showed a significant inverse correlation ($r = -0.82$, $p < 0.001$). For the other potential external drivers, there was a significant and positive correlation between fish yield and zooplankton ($r = 0.64$, $p = 0.002$). However, correlations with fish yield data alone are insufficient to make strong inferences because the changing proportions of herbivorous, planktivorous and piscivorous species are unknown. There was a positive correlation ($r = 0.56$, $p = 0.007$) between temperature and chl-a over the period 1988–2007, indicating that phytoplankton production might also be affected by temperature.

3.4. Testing the Hypothesized Loops—Short Term Analysis (2000–2004)

The findings for the short-term analyses over the transition period (2000–2004) indicated that macrophytes are negatively correlated with TP and turbidity, whereas turbidity is positively correlated with chl-a. Additionally, zooplankton are negatively correlated with chl-a and positively correlated with macrophytes. These interactions are predicted for functioning loop I (Figure 4). Small correlation coefficients for macrophytes vs. zooplankton ($r = 0.16$, $p = 0.801$), and zooplankton vs. chl-a ($r = -0.25$, $p = 0.681$) suggest that loop II was weak over the same period.

Lake water level and temperature, as potential external drivers, showed far less impact over the transition period than in the long term (linear correlations $p > 0.10$). Exotic fish yield showed a significant, negative correlation with macrophytes ($r = -0.96$, $p = 0.01$), suggesting that there may be a positive feedback loop that links together phytoplankton, planktivorous fish, macrophytes and phytoplankton, through which the increasing planktivorous fish effect significant change in the abundance of macrophytes and phytoplankton. However, the proportions of herbivorous, planktivorous and piscivorous species were unknown, so this potential loop cannot be confirmed. Stress from various external drivers, rather than from one dominant driver, seems to have gradually reduced ecosystem resilience and caused the transition, thus excluding a driver-mediated regime shift.

The functioning of loop IV is supported by positive and negative correlations between the potential for sediment P-release (P:Fe ratio) and TP and hypolimnion oxygen levels, respectively. Additionally, chl-a was positively correlated with TP and sediment organic matter, and sediment organic matter was negatively correlated with hypolimnion oxygen. Despite the lack of statistical significance, all these associations are predicted by the causal loop diagram (Figure 2) and support a qualitative transition in the aquatic ecosystem driven by a short-term functioning loop IV. Prior to the transition, there is a sequence of changes in other variables (Figure 3) that are consistent with a strengthening loop IV: (i) chironomid head capsule concentrations declining from at least 1996 indicate declining oxygen levels in the hypolimnion [9]; (ii) chemical oxygen demand ($\text{COD}_{\text{Mn}} < 2 \text{ mg/L}$ before 1998 but increasing to $\sim 4 \text{ mg/L}$ in 2003 indicating the rapid increase in oxidizable organic material in the water with the potential to reduce dissolved oxygen [26]; (iii) an interannual jump in TP by 50% in 1998–1999; (iv) the start of the major rise in diatom eutrophic species *Fragilaria crotonensis* in 1999 [9]; and (v) the rise in sediment carbon from 2001 [9]. The whole period in which loop IV operated was therefore about 5 years (1998–2003), with an unusually high influx of TP from the catchment in 1998–1999 possibly acting as a trigger for the process.

4. Discussion

Drawing on water monitoring data collected in 1992–2009 and lake sediment reconstructions between 1883 and 2010, Wang et al. [9] argued for a critical transition between two alternative states occurring around 2001. The implications were: (i) the lake can exist with alternative states over a TP range 0.018–0.030 mg/L; (ii) there was a strengthening positive feedback loop prior to 2001 that could transgress the nutrient threshold [18]; and (iii) a restoration of lake turbidity would likely involve the strengthening of another feedback loop that can shift the current state to its original form, or a similar state. The same study also reasoned that the strong positive feedback loop in the period leading up to the critical transition in 2001 involved high levels of nutrient-driven planktonic productivity, oxygen depletion and anoxia in the hypolimnion, resulting in a secondary fertilization effect, whereby P is recycled from the lake sediments to the water column [9]. These findings are supported in the present study from both qualitative and quantitative analyses that indicate that different positive feedback loops showed varied levels of stability during the eutrophication process before and after the transition.

Over the long term, the results point to the importance of a macrophyte-driven loop I or II, with no strong evidence for the sediment-resuspension loop III. If loop II, involving zooplankton, had dominated over loop I, involving nutrients, we would expect the extension of macrophytes to drive an increase in zooplankton with the subsequent predation and reduction in phytoplankton. However, the presence of a weak inverse correlation between macrophytes and dissolved nutrients (Figure 2) increased the likelihood that loop I would dominate over loop II. Prior to the transition, the positive relationship between P-release and TP suggests that the P-recycling loop IV may have existed, although the statistical insignificance ($r = 0.20$, $p = 0.43$) suggests that the amount of released P from sediment was secondary to P from other sources. Indeed, between 1993 and 2003, the P:Fe ratio used to infer P-release increased by 37.5 % but TP increased by $\sim 100\%$. Overall,

the descriptive/statistical analysis favored the presence of the macrophyte-mediated loop I dominating over loop II, where catchment P and lake water level act as primary drivers, and temperature act as possible secondary drivers. The evidence for conditions that allow P-release through loop IV is strong, but quantitatively, the process may be less significant. We can surmise that, in the clear stable state, loop I drove higher levels of macrophyte coverage until under conditions of increased stress, where it reversed and drove the loss of macrophytes. Loop IV may, initially, have been relatively weak, but strengthened in response to high levels of organic matter accumulation and hypolimnetic oxygen depletion in the lake bottom. This accelerated the shift to the alternate stable state across the critical transition to strongly turbid conditions. In the alternate state, loop IV remained stable, whereas loop I became much less stable.

Alternative stable state theory predicts that crossing a tipping point requires the operation of a positive feedback loop [3,10–12,33–35]; however, the existence of positive feedback alone is not a sufficient condition for alternative stable states but is rather the sign and intensity of the net effect of all the interacting positive and negative feedback which matters [35]. This was well-illustrated in a simulation study in coral reefs [36] which showed how weak positive feedbacks can lead to alternate stable states if they act in concert and reinforce each other. At Erhai, the evidence also suggests that the tipping point and transition involved the interaction of two positive feedback loops, I and IV. It seems that the dominance of loop I over the long term would have led to a continued reduction in macrophytes as the lake water became more turbid. However, because both loops shared phytoplankton as a key component, the strengthening of loop IV leading up to 2001 led to a synchronization of loops, which resulted in the dramatic shift from relatively clear to phytoplankton-dominated states during 2001–2003. As such, loop IV advanced the transition and caused the tipping point to arrive earlier than had loop I continued as the sole positive feedback mechanism. The coupled loops were accommodated during 2001–2003 by the changes in boundary conditions of low lake water levels, nutrient loading from the catchment, fishing, and high temperatures. This finding is consistent with other studies in lake ecosystems [37], where two positive feedback loops involving climate warming and nutrient loading determined the lake state.

There are important implications of coupled feedback loops for lake restoration. From a practical standpoint at Erhai, it seems that recovery to the clear stable state needs the re-establishment of a strong loop I so that macrophytes can again maintain clear water, restrict phytoplankton biomass, and provide shelter for zooplankton. A reduction in nutrient loading to the lake would be expected to reverse loop I and allow the recovery of macrophytes. However, based on our findings, the coupling through phytoplankton productivity to loop IV means that P-release from the sediments may maintain the turbid state, leading to the continued shading of benthic macrophytes. The hysteresis observed between TP and turbidity (Figure 4) is essentially the product of P-release in loop IV, even though loop IV was not the sole cause of the transition at that time. The evidence for loop IV functioning as early as 1996 (the first recorded algal bloom) points to long-term fluctuations in the strength of the loop with different sets of triggering conditions. For lake managers at Erhai, the immediate challenge is to reverse as many of the changed boundary conditions that maintain the dominance of loop IV over loop I, especially the exotic fish communities and low lake water levels, as well as the more obvious driver of nutrient loading.

Classic fold bifurcation theory shows a threshold-induced return to the original stable state as the main driver is reduced. Although critical transitions and regime shifts are often described as ‘abrupt changes’, it is unlikely that recovery in the real world will be matched in terms of similar rates of change: the strengthening of feedback mechanisms that drive relatively rapid destructive effects on system complexity is unlikely to be mirrored in the recovery phase. At Erhai, any future weakening of loop IV or reduction in external stress is expected to trigger macrophyte growth and eventually produce clear water conditions as an internal threshold is crossed. However, the system will take far longer under the control of loop I to regain the diversity of niches and species associated with clear water

conditions. We suggest that the speed of threshold-induced transitions in forward and recovery phases can vary greatly, depending on the rates of feedback loops and the strength of their coupling.

5. Conclusions

1. Using a range of paleolimnological, monitored and documentary data sources from Erhai, China, we reconstructed the significant positive feedback loops prior to a state shift from clear to turbid water conditions in 2001 brought about by multiple stresses;
2. We identified the growth and decline of two significant and positive feedback loops coupled through phytoplankton: a macrophyte-loop and a P-recycling loop. As the regulating macrophyte-loop became weaker during the process of lake eutrophication, the re-organizing P-recycling-loop became stronger and was ultimately responsible for transitioning the lake state across a tipping point;
3. This insight suggests that management aimed at restoring the lake to the earlier clear, stable state needs to focus initially on weakening the P-recycling loop through controls on nutrient loading, water levels and fish farming;
4. The presence of a critical transition preceded by changing feedback loops agrees with alternative stable state theory, but we suggest that the lake's hysteretic path will be asymmetrical with an incremental, rather than abrupt, recovery phase.

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