Human impacts alter driver-response relationships in lakes of southwest China

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Abstract:	Biodiversity and ecological stability are closely linked, and over recent timescales, anthropogenic impacts have accelerated losses in both from local to global scales. We attempt to show the combined response of diversity and stability of an aquatic community to changes in human activity as a driver. To address this, we measured the diversity and variability of chironomids, and their drivers and nature of response to external conditions over the last century, based on four lake sediment sequences from southwest China, one of world's 36 biodiversity hotspots. Our results showed the driver-response relationship was linear in a lake without direct human impacts but nonlinear in human directly impacted lakes. Recent decreases in alpha diversity and increases in beta diversity were commonly recorded in all four lakes, suggesting that both species loss and a faster replacement of chironomid taxa is a regional phenomenon. However, in the same context of human-induced global warming, increased variability and regime shifts only occurred in lowland lakes, directly disturbed by humans, highlighting that direct human impacts have overcome natural forcing as the determinant driver shaping the chironomid composition in these sites. Additionally, we found that increases in beta diversity occurred prior to a regime shift and its character depends on how the community responds to the key external pressure. Our findings reveal that direct human disturbances have largely reshaped the chironomid composition and induced an earlier regime shift at the cost of species loss, resilience loss and a change in driver-response type.

Scientific Significance Statement Topic

For the first time, we focused on the spatiotemporal changes in chironomid diversity and regime shifts in lakes characterized by different ways of responding to external changes. We found that human impacts changed the pressure- response type of community. Recent decreases in alpha diversity and increases in beta diversity are commonly recorded in all lakes, but increased variability and regime shifts only occurred in human directly impacted lakes, highlighting that direct human impacts have overcome natural forcing as the determinant driver shaping the chironomid composition in these sites. We propose that beta diversity could be applied to evaluate the changes in communities in response to global changes as it can detect the more subtle changes in communities. Additionally, we found that the distance between tipping point and the point at which beta diversity starts to increase is highly related to the way communities respond to external forces.

Scientific Significance Statement Outlet

Biodiversity and stability are critical for maintaining ecosystem functioning, and the connection between them is typically concerned issues for ecologists. We found that the growing beta diversity prior to a regime shift is critical for lake management as the early increase in beta diversity could provide sufficient time to take actions. Another meaningful finding is that the point at which beta diversity starts to increase is highly related to the way communities respond to external forces.

Table 1 Physical and chemical characteristics of the studied lakes

Lake	Lake area (km^2)	Atitude (m a.s.l)	Maximum depth (m)	Total phosphorus (μg/L)	Land cover	Population density (individuals/km^2)
Chenghai	77	1503	35	46	Forest, agriculture, urban	187
Yangzong	31	1770	30	21	Agriculture, urban, forest	473
Lugu	48	2691	94	12	Forest, urban	65
Tiancai	0.021	3898	6.8	14	Forest	0

TITLE PAGE

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ABSTRACT: Biodiversity and ecological stability are closely linked, and over recent timescales, anthropogenic impacts have accelerated losses in both from local to global scales. We attempt to show the combined response of diversity and stability of an aquatic community to changes in human activity as a driver. To address this, we measured the diversity and variability of chironomids, and their drivers and nature of response to external conditions over the last century, based on four lake sediment sequences from southwest China, one of world's 36 biodiversity hotspots. Our results showed the driver-response relationship was linear in a lake without direct human impacts but nonlinear in human directly impacted lakes. Recent decreases in alpha diversity and increases in beta diversity were commonly recorded in all four lakes, suggesting that both species loss and a faster replacement of chironomid taxa is a regional phenomenon. However, in the same context of human-induced global warming, increased variability and regime shifts only occurred in lowland lakes, directly disturbed by humans, highlighting that direct human impacts have overcome natural forcing as the determinant driver shaping the chironomid composition in these sites. Additionally, we found that increases in beta diversity occurred prior to a regime shift and its character depends on how the community responds to the key external pressure. Our findings reveal that direct human disturbances have largely reshaped the chironomid composition and induced an earlier regime shift at the cost of species loss, resilience loss and a change in driver-response type.

KEYWORDS: Diversity, regime shift, driver-response relationship, lake ecosystem, chironomid, southwest China

INTRODUCTION

Lakes constitute important habitats and food resources for humans and other organisms, but under the pressures of accelerated climate change and increasing human impacts, they are fragile ecosystems (Strayer and Dudgeon 2010). The most commonly cited risks are an accelerated loss in biodiversity and ecological collapse (Strayer and Dudgeon 2010; Kardol et al. 2018). Biodiversity is the basis for life-sustaining, ecological processes such as nutrient cycling, photosynthesis, decomposition, climate regulation and removal of pollutants. Ecosystem stability relates to their ability to maintain a natural balance or return to equilibrium quickly after a particular disturbance. Both of these characters are significant aspects for ecosystem services (McCann 2000; Ives and Carpenter 2007; Falkenmark et al. 2019), and it is thus essential to consider both when studying the ecological effects of environmental changes.

A loss or reduction in stability can result in a regime shift, through which the ecological state (hereafter referred to as community state) shifts abruptly into an alternative state due to large external forcing or loss of resilience (Scheffer et al. 2001). Theoretically, communities in different lake ecosystems may respond either smoothly, abruptly, or discontinuously to external forces (Fig. 1). A ‘smooth’ response is indicated by a linear relationship between ecological state and external conditions (Fig. 1a), a regime shift in such a response type can be triggered by high-impact variables (Collie et al. 2004), such as a flood, damming, and overfishing. By contrast, 'abrupt' and 'discontinuous' responses exhibit a nonlinear relationship between ecological state and external conditions (Fig. 1b, 1c), reflecting that the ecosystem is rather insensitive over certain ranges of the external conditions, while responding strongly around a threshold condition, and as such is hard to predict. Regime shifts of these two types are closely related to the loss of resilience, mostly defined as the speed by which the system recovers upon disturbance. Ecosystems with low resilience are relatively easier shift into alternative states even if the perturbation is relatively small. What distinguishes the 'abrupt' (Fig. 1b) and 'discontinuous' type (Fig. 1c) is when the forcing variable decreases, the response variable will follow a different trajectory to the previous equilibrium in a discontinuous regime shift, thus needing a greater effort to reverse the altered state (Barnosky et al. 2012). These three types of regime shift have been observed in contemporary lake ecosystems, mainly focusing on diatom (Xu et al. 2019), macrophyte (Zhang et al. 2018) and *Cladocera* communities (Su et al. 2020).

A number of mechanisms have been proposed to explain the loss of ecological stability (Barnosky et al. 2012), and biodiversity is arguably the most studied (McCann 2000; Ives and Carpenter 2007; Pennekamp et al. 2018). The conventional view is that high biodiversity is often considered to help maintain high stability (McCann 2000), whereas it has been more recently argued that species loss does not always mean a decline in stability, and the biodiversity-stability relationship may be ambiguous (McCann 2000; Ives and Carpenter 2007). Experiments indicate that only the loss or removal of a few species can cause a statistically discernible mean change in the abundance of other species in some communities, whereas most will have weak effects owing to low abundance (Berlow 1999). For example, species extinction only related to ‘weak-interactions’ often happens gradually and locally (Barnosky et al. 2011), whereas the loss of species related to ‘strong interactions’, often playing an important role in supporting the whole community, will result in further extinctions and can lead to abrupt regime shifts via trophic cascades (McCann 2000; Ives and Carpenter 2007).

It has recently been suggested that current extinction rates are higher than would be expected from the fossil record and that the sixth mass extinction may be under way due to anthropogenic pressures (Barnosky et al. 2011). If true, such a sharp decline of biodiversity would likely be accompanied by extensive regime shifts within the biosphere (Barnosky et al. 2012), furtherly leading to damaged ecosystems that are difficult to reverse. For future prediction and lake management, it’s essential to reveal how climate changes and anthropogenic activities affect biodiversity, stability and the driver-response relationships within ecosystem communities. Identifying state shifts in any lake ecosystem demands a temporal context that includes at least a few centuries to encompass the range of ecological variation that would be considered the normal state (Barnosky et al. 2012). Long-term, high resolution ecological and environmental data, are particularly valuable to understand how communities respond to external perturbations. Paleolimnology affords an alternative means of reconstructing temporal trends in biodiversity and provides high resolution (often annual to multi-decadal) time-series, which typically extend far beyond available historical biotic records (Sayer et al. 2010).

Here we present subfossil chironomid records from four lakes in the southwest China. As a biodiversity hotspot (Myers et al. 2000), southwest China possesses many lakes with different backgrounds of natural properties and human impacts and some of them are faced with risks of continuous loss in biodiversity (Lu et al. 2020). Previous studies related to diversity or regime shifts in this region were mainly focused on bacteria, phytoplankton and plants (Wang et al. 2016; Wang et al. 2020; Song et al. 2019). In this study, we focus on chironomids - one of the most abundant and diverse benthic macroinvertebrate groups in aquatic ecosystems worldwide (Giller and Malmqvist 1998). Chironomids play a supporting role in lake food webs (an important link between basal food resources and predators) and are well preserved in lake sediments (Serra et al. 2017). Our aim is to test how driver-response relationships vary across a gradient of human impacted lakes, and what further diversity-stability relationships exist with different diversity metrics prior to and post regime shifts.

MATERIALS AND METHODS

Study region

Yunnan province is situated in southwest China, between 21°N and 29°N of latitude and 97°E and 106°E of longitude, with an altitude gradient of ~6663 m. Due to the 'synergistic effect' of changes in latitude and altitude, the province, spanning only 8° in latitude, holds all climate zones and the highest biodiversity in China (Yang et al. 2004). Under the pressures of global changes, Yunnan is also the most threatened province in terms of biodiversity loss (Yang et al. 2004; Qian et al., 2020; Wang et al. 2020). Disturbances from agriculture, chemical fertilizer consumption, overfishing, coal consumption and tourism are mainly distributed and increased in the lowland areas (Fig. S1), leading to the degradation of many ecosystems. Other highland ecosystems away from direct human perturbation have also suffered from the impacts of recent climate warming (Fig. S2, Wang et al. 2020) and indirect human impacts such as nitrogen deposition (Hu et al. 2014).

In this study, four lakes (Fig. 2) in Yunnan were selected to investigate the stability, driver-response type and diversity of chironomid communities across a human impact gradient using a paleolimnological approach. Tiancai Lake (26°38'N, 99°43'E; 3898 m a.s.l.) is a freshwater lake away from direct human impacts (Chen et al. 2018), as there is no land used for agriculture or buildings around its catchment. Hence we regard Tiancai as a lake not directly affected by human activities and our control site. Conversely, the other three lakes selected for study have suffered from a range of direct human impacts. Lugu Lake (27°41'-27°45'N, 100°45'-100°50'E; 2691 m a.s.l.) is a remote, oligotrophic freshwater lake, but is facing multiple pressures due to increased tourism and mechanized agriculture in recent years (Zhang et al. 2013);

Lake Chenghai (26°27’-26°38’N, 100°38’-100°41’E; 1500 m a.s.l.) and Yangzong (24°51’-24°58’N, 102°58’-103°01’E; 1771 m a.s.l.) are situated in catchments with strong human impacts (Zhang et al. 2012), and have been suffering from eutrophication since the 1990s. Table 1 is a summary of the key physical and chemical characteristics of these four lakes. According to previous studies (Zheng et al. 2019; Zhang et al., 2012), different types of activity, such as non-point source nutrient inputs and cultivation of *Spirulina* in Chenghai, fish cultivation and mining in Yangzong, soil erosion caused by deforestation in Lugu are potentially the main drivers for shifts in ecological compositions (Zhang et al. 2013). Additional details about each lake can be found in the supplementary information.

Sample processing

Sediment cores were collected from the four lakes using a Kajak gravity corer in 2007 and 2008 (Renberg 1991). These cores were sliced in the field at 0.5 cm or 1 cm intervals and stored at < 4 °C prior to analysis. The ages of these samples ranging from ~1900 to ~2007CE were determined from the activity of ^{210}Pb, ^{226}Ra and ^{137}Cs radioisotopes. The cores’ chronologies and environmental data including TOC (total organic carbon), TN (total nitrogen), grain size, elemental geochemistry and mean annual average temperature (MAAT) inferred from measurements from branched archea bacteria (brGDGT) used in this study have been reported in (i) Zheng et al. (2019) for Chenghai Lake, (ii) Zhang et al. (2012) for Yangzong Lake, (iii) Zhang et al. (2013) for Lugu Lake; (iv) Zhang et al. (2017), Xiao et al. (2014), Chen et al. (2018) and Feng et al (2019) for Tiancai Lake.

Sediment samples for chironomid analysis were processed using standard techniques (Brooks et al. 2007). The sediments were firstly deflocculated with 10% KOH at 75°C for 15 min in a water bath, and then rinsed through 212 and 90-µm sieves. The residue from the 90-µm sieve was then transferred to a grooved Perspex sorting tray from which chironomid head capsules were picked using a stereo-zoom microscope at ×25 magnification. Head capsules were then sealed on glass slides with Hydromatrix®. A minimum of 50 identifiable whole head capsules were counted for each sample (Quinlan et al. 2001). The head capsules were identified mainly at a ×100 to ×400 magnification, using the reference literatures (Brooks et al. 2007; Rieradevall et al., 2001).

Statistical methods

The constrained incremental sum of squares (CONISS) analysis was used to identify the chironomid zones in the sediment core, which were based on the square-root transformed species data (Grimm 1991). Principal components analysis (PCA) was conducted to extract the major components of the chironomid assemblages in each lake because the length of the first axis of detrended correspondence analysis (DCA1) was < 2 in three of the four lakes (1.17 for Tiancai, 1.73 for Lugu, 0.88 for Chenghai and 3.1 for Yangzong) (ter Braak and Smilauer 2012). Statistically significant shifts in the dominant modes of variability, which are characterized by the scores on the first axis of PCA (PCA1), were identified using sequential T-test analysis performed in the Regime-Shifts algorithm (STARS) with a cut-off length of 10 (p<0.01) (Rodionov 2006). We also ran the cumulative sum of difference (CUSUM) of PCA1 for evidence of sharp changes in slope, which has been proposed as an integral part of trend detection in long-term environmental data (Nicholls 2001). For the sake of ensuring the accuracy of shift-detection, the existence of regime shift is jointly determined by CONISS, STARS and CUSUM. In order to reflect the periodic changes of chironomid communities, all relative abundance data of chironomids were divided into three periods according to the symbolic events marking changes in the intensity of human activities (e.g., 1950-the founding of New China and the time of regime shift or 1980-the reform and opening). Relative abundance of chironomids in each period was then averaged to obtain the compositional dynamics of the four biostratigraphic profiles using DCA (ter Braak and Smilauer 2012). Redundancy analysis (RDA) was performed on the four lakes to investigate the forcing variables that led to the change in chironomids. The residuals of PCA1 after detrended by Gaussian kernel smoothing method were employed to represent variabilities of chironomids. CONISS was performed using Tilia (Grimm 1991). PCA and DCA were performed with the 'vegan' package in R version 3.32 (Dixon 2003) and chironomid variabilities were performed with the 'earlywarnings' packages in R (version 3.32; http://www.r-project.org/). RDA were performed using CANOCO version 5 program package (ter Braak and Smilauer 2012).

Both alpha and beta diversity in time series were calculated. Alpha diversity, referred to as point diversity, is the species richness that occurs within a given area. Beta diversity is the rate of change in species composition including species richness and abundance that occurs in spatial or temporal scale. Based on the relative abundance of chironomids, alpha diversities were calculated employing species richness and beta diversities were calculated between adjacent communities by Jaccard index using the 'vegan' package in R version 3.32 (Oksanen et al. 2018).

RESULTS

The spatiotemporal dynamics of subfossil chironomids

Clear changes in the replacement of the dominant chironomid taxa were identified by CONISS in the lakes directly impacted by human activities (Fig. 3). *Procladius* is the dominant taxon (average abundance of ~60%, the following abundance are mean value) in Chenghai Lake before ~1998 CE, Yangzong Lake (~82%) before ~1988 CE and Lugu Lake (~54%) before ~1970 CE. Afterwards, *Procladius* has been gradually replaced by *Chironomus plumosus*-type and *Microchironomus* in Chenghai and Yangzong lakes (Fig. 3a and 2b), and by *Tanytarsus mendax*-type and *Polypedelum nubeculosum*-type in Lugu Lake. However, no substantial changes are observed in Tiancai Lake (only indirectly impacted by humans) except for the loss of some rare taxa such as *Eukiefferiella gracei*-type (~0.6%), *Micropsectra* type A (~0.6%) and

Micropsectra type B (~0.9%) after the 1990s. *Heterotrissocladius marcidus-type* (~20%), *Micropsectra insignilobus*-type (~10%) and *Tvetenia tamafalva*-type (~8%) dominate the assemblages throughout the Tiancai record.

DCA was used to assess the dissimilarity of the sites species composition as measured by their turnover distance in standard deviation (SD) units (ter Braak and Smilauer 2012) (Fig. 4). Tiancai Lake (green symbols) is distant from the other three lakes and almost unchanged over the past century, as the three green symbols are almost overlapping. For the other three lakes, their communities are characterized by greater deviation, which is most significant in Yangzong Lake, followed by Chenghai and Lugu lakes.

Regime shift, variability and response type of chironomids

Results of regime shift detection are presented in the left panel of Fig. 5. Significant shifts detected by STARS and CUSUM are found in Chenghai (Fig. 5a), Yangzong (Fig. 5c) and Lugu (Fig. 5e) lakes, and their date of regime shift is consistent with the results of CONISS. The earliest change point was identified in Lugu lake around 1970 CE, followed by Yangzong Lake in 1988 CE and Chenghai Lake in the late 1998 CE. No regime shift was detected in Tiancai either by CONISS, STARS or CUSUM.

Variability of chironomids are listed in the right panel of Fig. 5. It is clear that the community variability increased prior to the regime shift in lakes Chenghai (Fig. 5b), Yangzong (Fig. 5d) and Lugu (Fig. 5f). The difference among them is that variability of Chenghai and Lugu increase gradually when the regime shift was still far away (2-3 decades), while Yangzong only increase rapidly when it is was close to the regime shift (2-3 years).

The results of the RDA are shown in Fig. 6 and show that TOC is the main driver in Chenghai (Fig. 6a). In Yangzong lake, the concentration of the elements, TOC as well as grain size compositions are the drivers for chironomid changes. Here, TOC in Tiancai Lake have not yet passed a regime shift. Sedimentary TOC and brGDGTs-inferred MAAT were respectively regarded as the primary drivers for Chenghai and Tiancai lakes. TOC instead of grain size is used as an external driver for chironomid assemblage changes in Yangzong and Lugu lakes. This is because, due to soil erosion, changes in TOC, sediment elemental chemistry and grain size are synchronous and highly correlated in these lakes. Furthermore, TOC is closely related to the food supply, habitats, and oxygen concentrations for the survival of chironomids (Brodersen and Quinlan 2006; Frossard et al. 2013), and as such considered to be a local driver of chironomid assemblages (Zheng et al. 2019; Zhang et al. 2013). However, in Tiancai (Fig. 6d), the recent increase in temperature is the clear main driver for the continuous loss of chironomids.

We compare the response type of chironomid communities to changing external drivers in phase plots at each site (Fig. 7). Correlation coefficients between external forcing and community state are not significant in most phases and the responses of community in each lake vary, and can be mainly classified into three different types. The first type corresponds to a smooth type, represented by Tiancai Lake (Fig. 7d), where chironomids gradually changed with the increasing MAAT. The second type, i.e., the abrupt type, correspond to Chenghai (Fig. 7a) and Lugu (Fig. 7c) lakes, where the TOC content of Chenghai (Lugu) Lake increases from 12.7 to 13.8 g/kg (from 61.6 to 59.3 g/kg), and PCA1 values jumped from 0.6 to 2.3 (from -0.1 to -2.5), reflecting a large shift in chironomid communities. The third type, i.e., discontinuous type, describing Yangzong (Fig. 7b), displays two linear clusters of points, 1898–1988 CE (upper line) and 1988–2007 CE (lower line), suggesting two alternative chironomid states for all TOC values in the range 7.1-16.7 g/kg, which is equivalent to ~14% of the whole TOC scale.

Diversity dynamics of subfossil chironomids

As shown in Fig. 8, the range of alpha diversity (richness) in Tiancai Lake (12-26) is higher than that of Lugu (3-12), Yangzong (3-12) and Chenghai (2-7) lakes (Fig. 8a-8j). In detail, alpha diversity displays a decreasing trend in Chenghai Lake (Fig. 8f) (from 6 to 2), while Yangzong (from 4 to 9) and Lugu (from 6 to 10) lakes show an increasing trend prior to their regime shift. Tiancai lake's alpha diversity is stable before 1990s and is followed by a continuous decline afterwards (from 22 to 15). Beta diversity (dissimilarity, measured as Jaccard in Fig. 8) is generally higher in Tiancai Lake (~0.4) than in other lakes (~0.1-0.2), However, an abrupt increase in beta diversity occurs in Yangzong and Lugu lakes after their respective regime shifts, especially in Yangzong Lake. Contrary to changes in alpha diversity, beta diversity in the four lakes share an increasing trend in the recent decades. More specifically, beta diversity slowly increases in Chenghai Lake from an ‘initial’ medium value of 0.15 to the current 0.23 (Fig. 8e); Yangzong Lake’s beta diversity increases abruptly after 1980s (from 0.10 to 0.65) (Fig. 8f); Lugu lake’s beta diversity increases step by step since the 1940s (from 0.21 to 0.49) (Fig. 8g), while beta diversity in Tiancai Lake shows a minor increase after 1990s (from 0.45 to 0.48) (Fig. 8h).

DISCUSSION

As shown in Fig. 3, the species composition of Tiancai Lake is different from the other three lakes. Tiancai Lake is mainly composed of cold and oligotrophic tolerant taxa, e.g., *Heterotrissocladius marcidus*-type, *Micropsetra insignilobus*-type and *Tvetenia tamafalva*-type, and species loss in this lake barely occurs apart for some cold-stenotrophic taxa with low abundance including *Eukiefferiella gracei*-type, *Micropsetra* type A, *Micropsetra* type B and *Macropelopia* taxa (Fig. 3e) as the climate warms. By contrast, the other three lakes have recently been dominated by *Chironomus*, which can tolerate anoxic conditions associated with lake eutrophication, and often increases quickly after abrupt environmental changes, and

Tanytarsus, often related to warm and eutrophic conditions (Brodersen et al., 2004; Thorp and Covich, 2001). Based on the ecological attributes of chironomids in these lakes, such discrepancy in species composition between Tiancai and the other lakes is likely based on lake temperature as Tiancai is situated at a higher altitude. The relatively stable community composition of Tiancai is likely the result of its location, i.e., a highland area that has not been disturbed by direct human activities. Community changes in this kind of lake are generally caused by climate change or indirect human impacts such as nitrogen deposition (Hu et al. 2014), given the relative remoteness of the site. Comparatively, dominant taxa in the other three lakes have recently shifted from predator, e.g., *Procladius*, or genera associated with fine sediments in the profundal zone such as *Microchironomus* to eutrophic and anaerobic tolerant taxa, belonging mainly to the genera *Chironomus* and *Tanytarsus* (Thorp and Covich, 2001). Located in the lowland areas, the significant changes in species composition of these three lakes are likely related to the intensified human activities in catchment, including the expansion of agriculture, aquaculture, deforestation and mining (Zhang et al. 2012; Zhang et al. 2013).

In this study, regime shifts have only been detected in lakes directly influenced by human impacts. The growing variability before a regime shift and the abrupt (Chenghai and Lugu) or discontinuous (Yangzong) driver-response curves jointly indicate that abrupt changes in these lakes were not caused by the sudden intensification of external stressors but resilience loss (Scheffer et al. 2001). The decreasing time resolution with depth implies that samples represent approximately 1 year in the upper part and approximately 4-8 years in the deeper part of the sediment profile. Greater temporal aggregation in the deeper profile is likely to reduce the temporal variation in chironomid composition, giving a reduced variability for the oldest data (Wang et al. 2013). We therefore suggest that these may be an artefact of the numerical methods used and the inherent problems in time-series analysis of samples with uneven temporal spacing from sediment cores. Results of this study (Fig. 5) show that the increased variability does exist in lakes Chenghai, Yangzong and Lugu, but only occurs before the regime shift. It doesn't increase in Tiancai and even conversely decreases after the regime shift in the other three lakes, showing that reconstructing the loss of resilience in directly human impacted lakes is possible in uneven temporally spaced cores. Human induced loss in aquatic ecosystem resilience was also previously identified using diatom assemblages (Wang et al. 2012; Wang et al. 2019), and manifested as shifts in species composition, from specialists in west China lakes with a history of low human impacts, to predominantly generalists in highly disturbed lakes of east China. A possible explanation for such a loss in resilience is the emergence of positive feedbacks produced by synergies among habitat fragmentation, pollution, overfishing, invasive species and soil erosion negatively affecting the ecological structure of previous desired regimes (Barnosky et al. 2011). As secondary consumers, chironomids are sensitive to changes in temperature (Brooks and Birks 2001), which has been increasing recently in Tiancai (Feng et al. 2019). Combining the results of the RDA (Fig. 6d) and the ecology of taxa lost in Tiancai Lake, we consider that climate warming could explain the species loss there. Furthermore, ecological changes in Tiancai Lake are typically driver-mediated and still possesses relative high resilience at the present (Fig. 5h). Sasaki and Lauenroth (2011) show that the a stable regime of aquatic communities is typically regulated by dominant species rather than rare ones as dominant species are the most abundant ones and may play major roles in controlling the rates and directions of many community and ecosystem processes. Indeed, in the three lowland lakes, where regime shifts are detected, their dominant taxa are commonly replaced, leading to a less stable community (McCann 2000; Mayfield et al. 2020). Conversely, in Tiancai Lake, changes in species composition are limited to rare taxa only, and as such a critical point has not been reached yet and the community remains in the same (current) regime with little structural change (McCann 2000; Mayfield et al. 2020). Actually, the current climate change is occurring at an unprecedented rate that will continue over the coming decades (Smith et al. 2015; Mayfield et al. 2021). Limited by their low abundance, rare species will be firstly eliminated from such continuous climate change, leading to a loss of weak structural interactions within the communities (Burlakova et al. 2007; Wang et al. 2019; Mayfield et al. 2021). As rare species are a critical component in defining the uniqueness of unionid communities, their continuous loss may eventually affect the capacity of communities to absorb climate impacts (Berlow 1999; Grimm et al. 2013; Mayfield et al. 2021).

Changes in biodiversity before the regime shifts are complex. Resilience loss occurs in Yangzong, Chenghai and Lugu lakes, but their patterns of alpha diversity are varied, confirming that higher species richness does not always equate to a more stable community (McCann 2000; Ives and Carpenter 2007). Beta diversity increased prior to the regime shift, but the distance between the tipping point and the point of initial increases in beta diversity varies greatly among the three lakes. In lakes marked by abrupt responses, beta diversity shows a much earlier (decadal) but gradually increasing trend before their shifts. Whereas in the lake displaying a discontinuous response to forcing, it only shows an abrupt increasing trend a few years (2-3 years) prior to the tipping point. Regime shifts in this kind of lake, where hysteresis occurs, is hence difficult to predict in advance. As such, the diversity dynamics is likely highly dependent on the response type of communities. Over the recent decades, a declining alpha diversity (species richness) and increasing beta diversity (Jaccard dissimilarity) is observed in all four lakes. In southwest China, such reshaped patterns of lake biodiversity, either caused by anthropogenic activities (Wang et al. 2016) or climate warming (Wang et al. 2020) have already been found in bacteria and diatom communities. It not only suggests that regime shifts will likely result in species loss and greater variability, but also reveals that both species loss and a faster replacement of chironomid taxa could be a regional phenomenon. It is important here to consider why an increases in beta diversity is detected in all four lakes while only three of them show a regime shift. In general, only large changes in dominant species tend to induce regime shifts, but increased beta diversity can reflect changes in dominant or rare species, producing a faster replacement of communities and a much more unstable community (Mayfield et al. 2021). As such, a dataset that shows increased beta diversity over recent years/decades may be a critical tool for lake management as the early increase in beta diversity could provide sufficient time to take appropriate actions ahead of an oncoming regime shift.

CONCLUSIONS

For the first time, we focused on the spatiotemporal changes in chironomid diversity and regime shifts in lakes characterized by different response patterns to external changes. We found that human impacts changed the linear (smooth) response of communities into a nonlinear response (either abrupt or discontinuous), along with the great changes in the dominant taxa. In the same context of human-induced global warming, a recent decrease in alpha diversity and increase in beta diversity are commonly recorded in the four lakes. However, increased variability and regime shifts only occurred in lowland lakes, directly disturbed by humans, highlighting that direct human impacts have overcome natural forcing as the determinant driver shaping the chironomid composition in these sites. Therefore, chironomid communities in lowland, human impacted lakes lost their resilience and shifted earlier than those in highland, relatively unimpacted lakes. We propose that beta diversity could be applied to evaluate the changes in communities in response to global changes as it can detect the more subtle, but important, changes in communities, such as the loss of rare species, which is difficult to capture by traditional ordination (e.g., PCA). Additionally, the growing beta diversity prior to a regime shift is critical for lake management as its early increase could provide sufficient time to take appropriate actions in advance. Through this study, we find that the distance between the tipping point and the point at which beta diversity starts to increase is highly related to the way communities respond to external forces. It is notable that in the lakes we studied, such distance is much longer in lakes characterized by smooth and abrupt responses than that by discontinuous response to those forces.

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Conflict of Interests: None

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Table

Table 1 Physical and chemical characteristics of the studied lakes

Lake	Lake area (km^2)	Altitude (m a.s.l.)	Maximum depth (m)	Total phosphorus (µg/L)	Land cover	Population density (individuals/km^2)
Chenghai	77	1503	35	46	Forest, agriculture, urban	187
Yangzong	31	1770	30	21	Agriculture, urban, forest	473
Lugu	48	2691	94	12	Forest, urban	65
Tiancai	0.021	3898	6.8	14	Forest	0

Figure legends

Fig. 1 Different types of community state respond to external driver (Scheffer et al. 2001), including (a) smooth type, without tipping point (b) abrupt-continuous type, only a tipping point (F_1) and (c) nonlinear-discontinuous type, having two tipping points (F_2 and F_1). The lines indicate the equilibrium points between the ecosystem states and the environmental conditions. A solid line means a stable equilibrium and a dotted line means an unstable equilibrium.

Fig. 2 Maps showing the location of (a) sampling sites and the outline of Lake (b) Chenghai, (c) Yangzong, (d) Lugu and (e) Tiancai. More details can be found in Table 1.

Fig. 3 The main chironomid taxa (relative abundance >20%) and taxa mentioned in the text. Yangzong and Chenghai are modified from Zheng et al. (2019); Lugu from Zhang et al. (2013); Tiancai from Zhang et al. (2017). Note that the black dashed line represents shifts in the chironomid composition according to CONISS.

Fig. 4 DCA ordinations of paleo-samples in the four lakes. The arrows represent the trajectory of the temporal changes in community in each lake. Percentage on the axis of DCA is the variance in communities that can be explained by the axis.

Fig. 5 Regime shifts (left panel) and variability (right panel) of chironomids in Lake (a) (b) Chenghai, (c) (d) Yangzong, (e) (f) Lugu, (g) (h) Tiancai. In the left panel, results of T-test and CUSUM are shown in red line and black line, respectively. In the right panel, purple lines are variability of four lakes, measured using residuals of PCA1, and the red solid circles are the dates of regime shift.

Fig. 6 Sample-environmental variable plot of RDA between fossil chironomids and sedimentary proxies in (a) Chenghai, (b) Yangzong, (c) Lugu and (d) Tiancai lake cores. Xlf: magnetic susceptibility of low frequency; <4 μm: the percentage of grain size smaller than 4 μm; 4-16 μm: the percentage of grain size between 4 and 16 μm; 32-64 μm: the percentage of grain size between 32 and 64 μm; >64 μm: the percentage of grain size larger than 4 μm; TOC: total organic carbon; TP: total phosphorus; Al, Fe, Ti, Ca, Mn, P: Elemental concentrations; BrGDGT-inferred MAAT: BrGDGT-inferred mean annual air temperature.

Fig. 7 Phase-space plots of the driving variables (TOC or temperature) versus the chironomid state response variable (PCA1) over the last century. Plot (a) Chenghai (b) Yangzong and (c) Lugu describe two linear clusters of points before (orange line) and after (blue line) their respective date of regime shifts, while (d) Tiancai Lake does not display any regime shift.

Fig. 8 Alpha (richness index) and beta diversity (Jaccard index) in time series and boxplot for (a) (e) (i) (m) Chenghai, (b) (f) (j) (n) Yangzong, (c) (g) (k) (o) Lugu and (d) (h) (l) (p) Tiancai. Note that the gray dashed line indicates the point of regime shift.

Supplementary Information for:

Human impacts alter driver-response relationships in lakes of southwest China

1. Supplementary figures

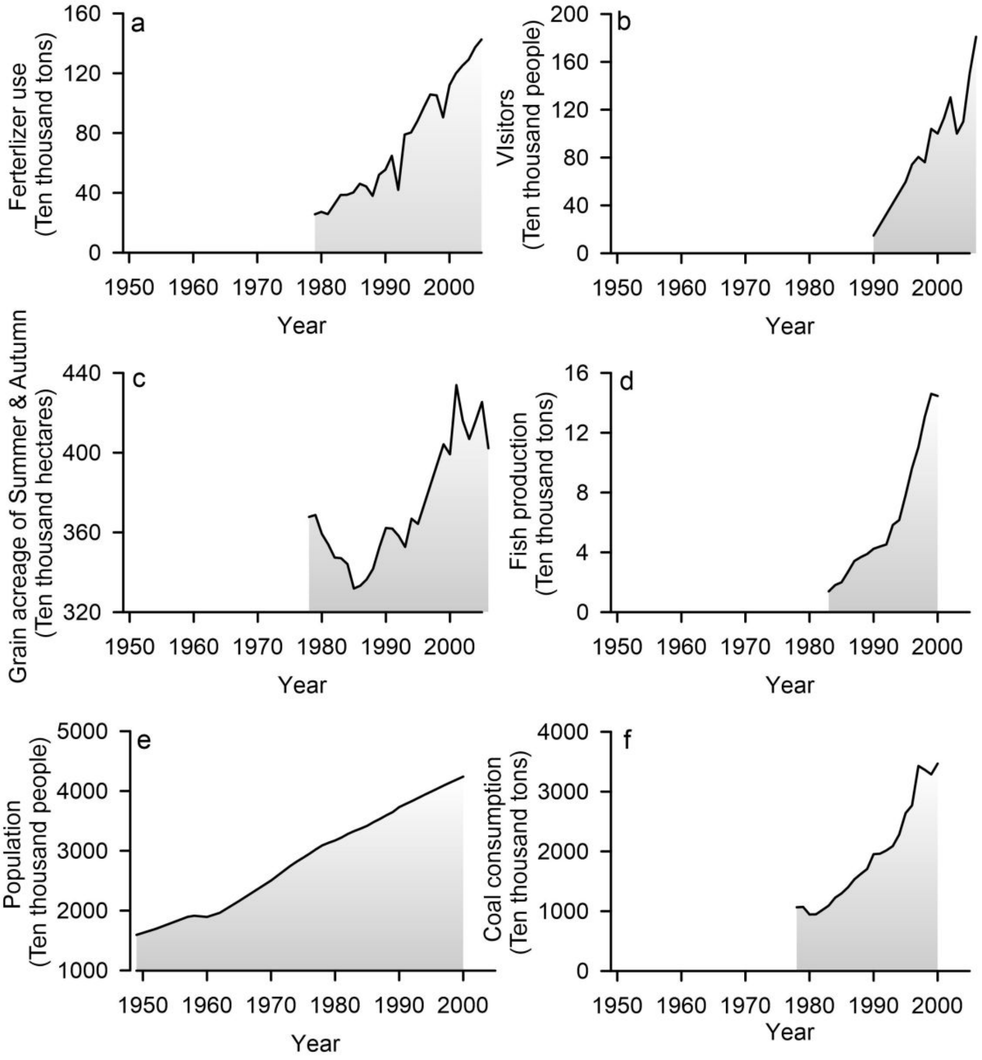

Fig. S1 Proxies related to human activities in Yunnan Province. The general increased (a) fertilizer use between 1979 and 2005 CE, (b) visitors between 1990 and 2006CE, (c) grain acreage of Summer and Autumn between 1978 and 2006 CE, (d) fish production between mid-1980s and 2000, (e) human population between 1950 and 2000, and (f) coal consumption between 1978 and 2000 CE. All data were derived from the *Yunnan Statistical Yearbook* (1950-2000 CE).

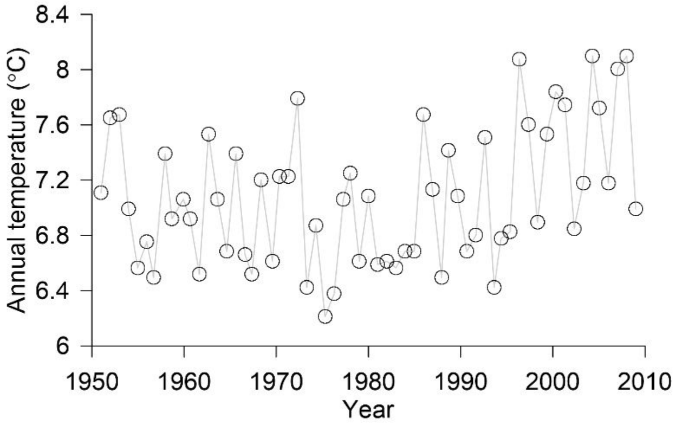

Fig. S2 The temperature changes from 1952 to 2010 as recorded at Kangding Weather Station (revised from Wang et al. 2020).

The details of study sites

Chenghai Lake (26°27′-26°38′N, 100°38′-100°41′E) (Fig. 1) covers a surface area about 77 km^2 and catchment area about 318 km^2 (Wu et al., 2004). The maximum depth is 35 m and the SD is 2.6 m. The lake is mainly fed by precipitation and groundwater, and there are no perennial inlet and outlet rivers in the catchment. The water level decreased obviously in recent decades due to human withdrawal (Sun et al. 2017). After 1940s, a large population immigrated and settled in the basin, since then, vegetation in the lower valley has been seriously disturbed by human (Zhou et al. 1999; Sun et al. 2017). After 1989 CE, Spirulina farming has been the dominant industry in Chenghai Lake, and the amount of wastewater, which is rich in high COD (chemical oxygen demand), TP (total phosphorus), TN (total nitrogen) and pH, discharged into the lake increased from 1.23 million tons in 1993CE to 3.08 million tons in 2000CE (Zhou et al. 1997). Due to cage culture and alien fish introduction (such as Neosalanx taihuensis Chen, Abbottina rivularis, Pseudorasbora parva) after 1980s, more than 50% native fish species died out when compared to historical records (Yuan 2010). The biodiversity loss and breaking out of blue green algae occurred in 1990s (Liu et al. 2015).

Yangzong Lake (24°51′-24°58′N, 102°58′-103°01′E) covers an area of 31 km^2, and its catchment area is 192 km^2. The maximum depth is 30 m and the SD is 4.3 m. The lake is mainly fed by precipitation and inflow rivers of Qixing River and Yangzong River in the southwest as well as some temporal streams. The main pollution source of Yangzong Lake is domestic sewage and agricultural non-point source pollution (Wang 2003; Zhang 2017). It mainly accepts domestic sewage from nearby villages and towns, and cooling circulating water from Yangzonghai power station, which fundamentally increased water temperature of some areas of the lake (Zheng et al. 2019). In 2004, around 65% of the catchment area of Yangzong Lake was suffering from the influence of soil erosion (Zhu 2008).

Lugu Lake (27°41'–27°45'N, 100°45'–100°50'E) covers a surface area of 48.45 km^2, and a drainage area of 171.4 km^2 and still in a oligotrophic state. The maximum depth is 94 m, and it shows thermal stratification in summer. Forestland is the dominant land-use type (~85.95%), followed by agricultural land (~8.44%), and grass/pasture land (~5.47%) (Bai et al. 2008). It has been suffered from human impacts in last decades, mainly due to deforestation and the development of tourism and agriculture. Data based on lake sediment and instrumental monitoring showed that soil erosion, global warming and sewage input were the main drivers for ecosystem change in Lugu Lake (Guo et al. 2013; Lin et al. 2017). Soil erosion in the catchment increased markedly from 1950 onwards, particularly after 1970 (Zhang et al. 2013).

Tiancai Lake (26°38'N, 99°43'E) has a surface area of ~0.02 km^2 and a drainage area of ~3 km^2. It's a sub-alpine lake located on Laojun Mountains near the timberline

(4000 m a.s.l.) - sensitive to the global warming and is hydrologically open with the inflow from the south and an outflow to the north and lake water is supplied by precipitation and surface runoff from the catchment. The annual mean temperature and precipitation is 2.5°C and 910 mm (Xiao et al. 2011). The primary forest around the lake is well preserved and consists mainly of conifer forest comprising *Abies* sp. and *Picea* sp. There are about 200 m^2 of Rhododenfron bushes in the west of lake, and the top of mountain (4200 m a.s.l.) consists of alpine meadow and rocky beach desert. As reported, dissolved organic matter of this lake is dominated by terrestrially-derived source (Du et al. 2016).

The dynamics of main environmental variables

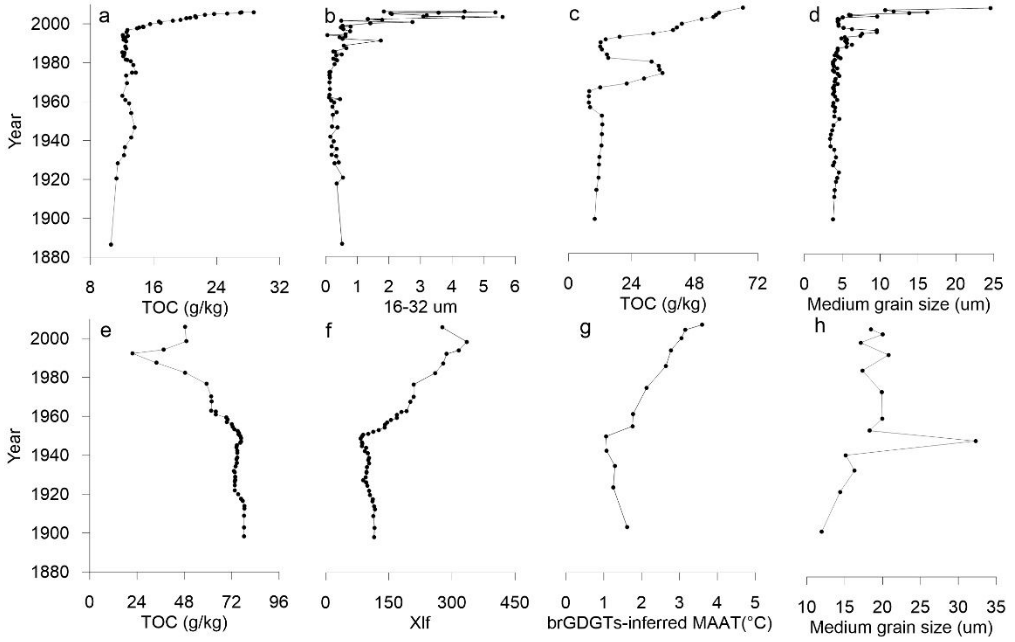

Fig. S3 The long term changes of main drivers for chironomid communities in Lake (a) and (b) Chenghai (Zheng et al. 2019); (c) and (d) Yangzong (Zhang et al. 2012); (e) and (f) Lugu (Zhang et al. 2013); (g) and (h) Tiancai (Chen et al. 2018; Feng et al. 2019). TOC: total organic carbon; Xlf: magnetic susceptibility; 4-16 µm: the percentage of grain size between 4 and 16 µm; BrGDGT-inferred MAAT: BrGDGT-inferred mean annual air temperature.

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COMMENTS TO THE AUTHORS

Editor-in-Chief:

In addition to addressing all reviewer and editor comments in your revision, **please also make sure that your revised manuscript conforms to the style and formatting requirements for** *Limnology and Oceanography*, as specified in the online instructions for authors (https://aslopubs.onlinelibrary.wiley.com/hub/journal/19395590/about/author-guidelines#9). Please pay particular attention to journal policy regarding citations (≤3 in support of any given statement).

Associate Editor:

Associate Editor

Comments to the Author:

Thank your for submission and your careful attention to the Reviewer comments. We have decided to accept your manuscript for publication in the Special Issue on nonlinear dynamics and regime shifts in aquatic ecosystems. Reviewer 2 has suggested several additional changes to improve clarity. These changes are very minor and should be made prior to uploading your final document.

Reviewer(s):

Reviewer: 1

Comments to the Author

The authors made a good-faith effort to address every comment. Although it is still not entirely clear to me that chironomids changed due to loss of resiliency rather external stressors (Reviewer 2 had similar doubts), the authors now provide justification for their argument. This manuscript adds to the growing body of work on ecological resilience/stability theory and will contribute new data to the debate on this topic.

Reviewer: 2

Comments to the Author

I reviewed the response to reviewers and the revised manuscript, and the authors did a great job responding to the reviewers concerns. I only had a few small suggestions – mostly copy-editing type comments.

Minor comments

Scientific statement – Consider changing “Besides, we find that the distance between tipping point and the point at which beta diversity…” to “Additionally, we found that the distance between tipping point and the point at which beta…”

Scientific statement – Consider revising for clarity. “Spatiotemporal changes of biodiversity and stability are topics most concerned by ecologists.”

Re: We try to clarify this sentence as follows. “Biodiversity and stability are two critical aspects for maintaining ecosystem functioning, and the connection between them is one of the most concerning issues for ecologists and managements. We found that the growing beta diversity prior to a regime shift is critical for lake management as the early increase in beta diversity could provide sufficient time to take appropriate actions in advance. Another meaningful finding is that the point at which beta diversity starts to increase is highly related to the way communities respond to external forces.”

Scientific statement – Insert ‘to’ between ‘sufficient time’ and ‘take appropriate’

Re: Changed.

Scientific statement – Consider changing “Another founding that the point at which beta diversity starts to increase is highly related to the way communities respond to external forces is also meaningful, related to the way communities respond to external forces.” to “Another meaningful finding is that the point at which beta diversity starts to increase is highly related to the way communities respond to external forces.”

Re: Changed.

Line 33 – humans are contributing to climate change, so this passage could use clarification between anthropogenic and non-anthropogenic change and the conclusion.

Re: Agreed, we couldn’t completely distinguish the respective contribution of anthropogenic and non-anthropogenic changes to chironomid communities. However, it is clear that both lowland and highland lakes have been affected by climate change, and only lakes with direct human impacts are more unstable. Hence, the sentence was changed to “However, in the same context of human-induced global warming, increased variability and regime shifts only occurred in lowland lakes, directly disturbed by humans, highlighting that direct human impacts have overcome natural forcing as the determinant driver shaping the chironomid composition in these sites ”

Line 34 – insert chironomid before community (since the whole lake community was not the focus)

Re: Changed.

Line 90 – most instead of mostly

Re: Changed.

Line 164 – add an ‘its’ before catchment

Re: Changed.

Line 166 – perhaps ‘Conversely’ instead of “On the contrary”

Re: Changed.

Supp Line 2-3 – This appears to be the older title

Re: We have changed the older title to the new one.

Supp Figure 1 – Are there references for these data? Consider including them in the figure caption

Re: Thanks, the data of Fig. S1 were derived from the *Yunnan Statistical Yearbook* (1950-2000 CE). We have added this information in the figure caption.

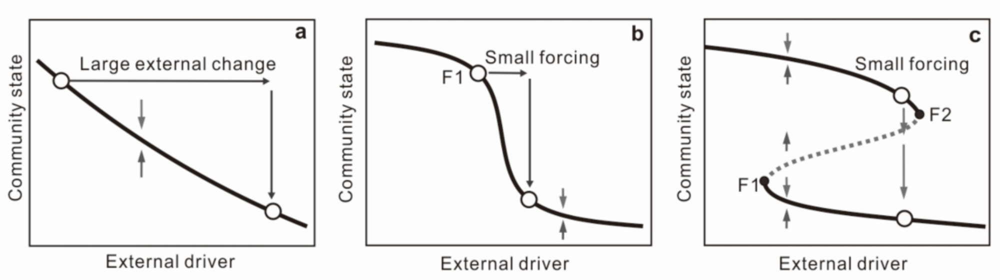

Fig. 1 Different types of community state respond to external driver (Scheffer et al. 2001), including (a) smooth type, without tipping point (b) abrupt-continuous type, only a tipping point (F1) and (c) nonlinear-discontinuous type, having two tipping points (F2 and F1). The lines indicate the equilibrium points between the ecosystem states and the environmental conditions. A solid line means a stable equilibrium and a dotted line means an unstable equilibrium.

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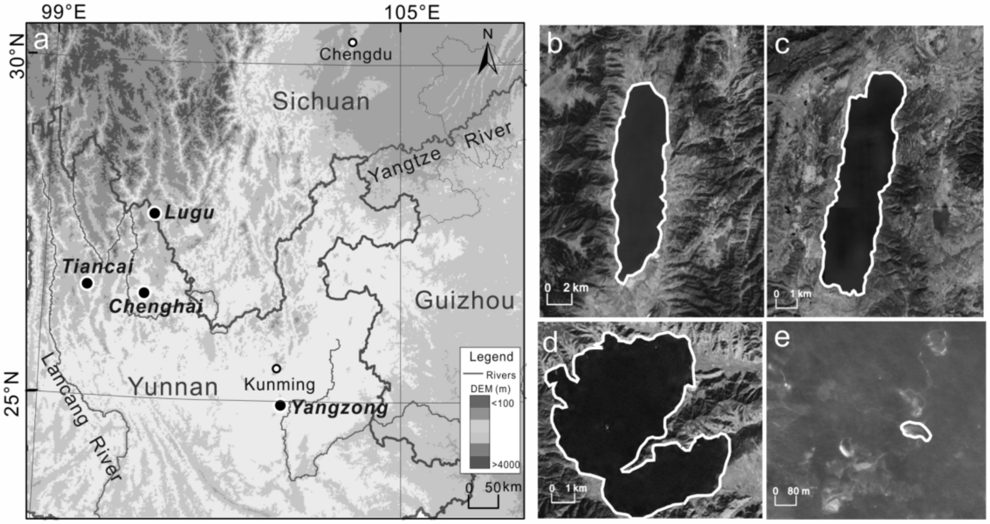

Fig. 2 Maps showing the location of (a) sampling sites and the outline of Lake (b) Chenghai, (c) Yangzong, (d) Lugu and (e) Tiancai. More details can be found in Table 1.

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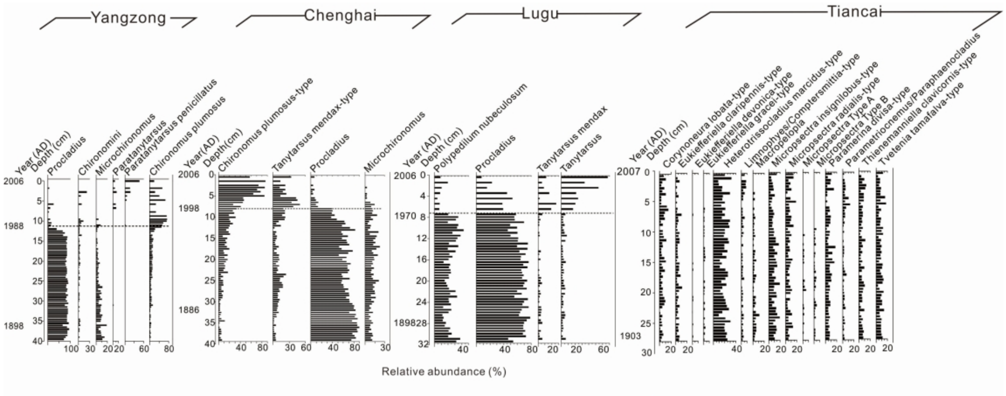

Fig. 3 The main chironomid taxa (relative abundance >20%) and taxa mentioned in the text. Yangzong and Chenghai are modified from Zheng et al. (2019); Lugu from Zhang et al. (2013); Tiancai from Zhang et al. (2017). Note that the black dashed line represents shifts in the chironomid composition according to CONISS.

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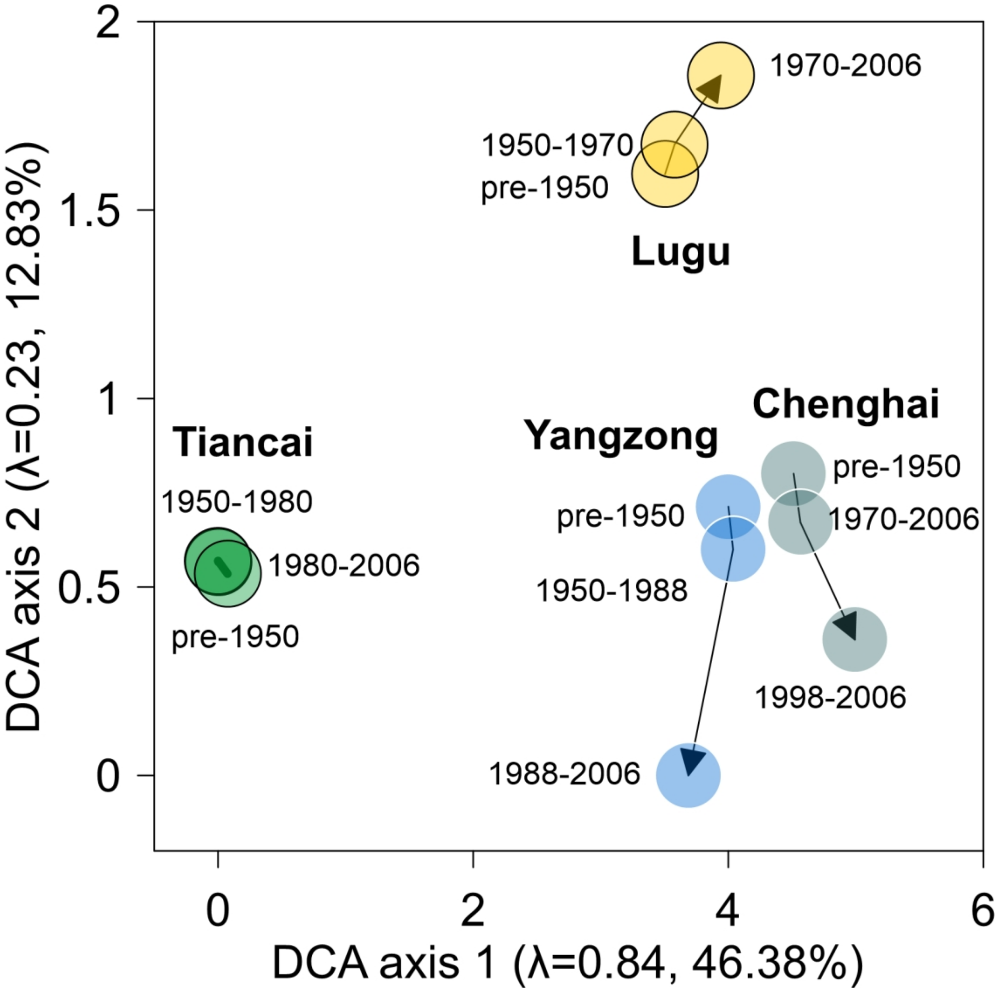

Fig. 4 DCA ordinations of paleo-samples in the four lakes. The arrows represent the trajectory of the temporal changes in community in each lake. Percentage on the axis of DCA is the variance in communities that can be explained by the axis.

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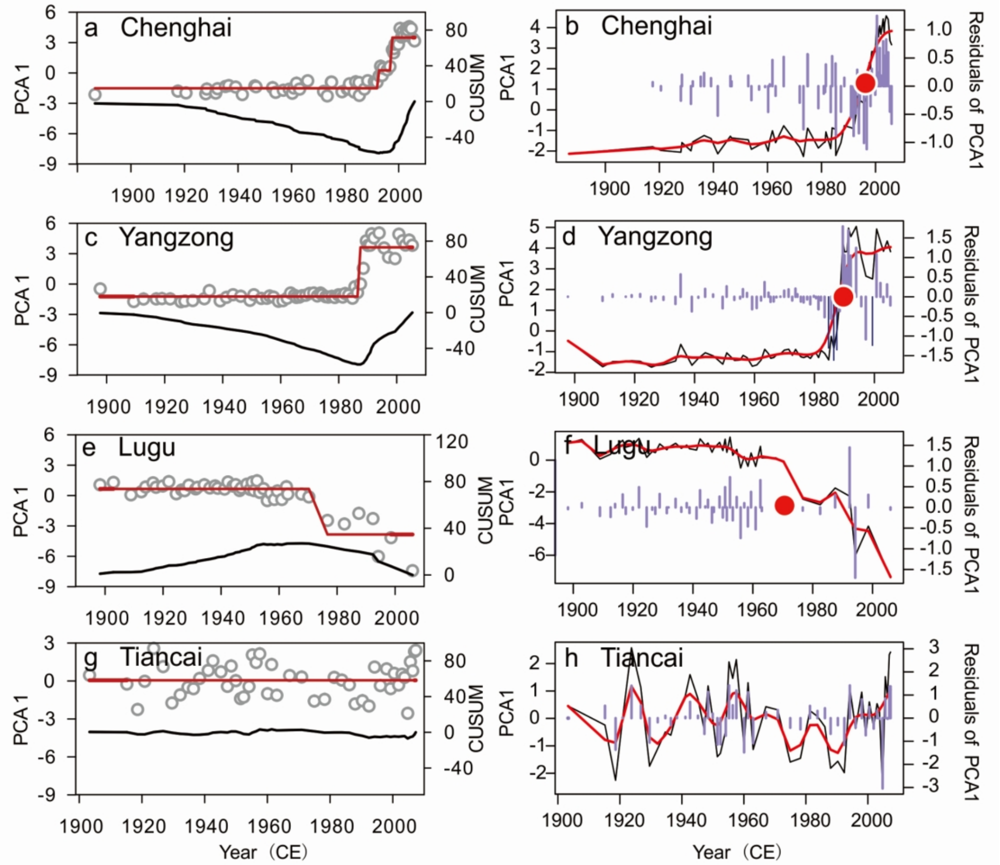

Fig. 5 Regime shifts (left panel) and variability (right panel) of chironomids in Lake (a) (b) Chenghai, (c) (d) Yangzong, (e) (f) Lugu, (g) (h) Tiancai. In the left panel, results of T-test and CUSUM are shown in red line and black line, respectively. In the right panel, purple lines are variability of four lakes, measured using residuals of PCA1, and the red solid circles are the dates of regime shift.

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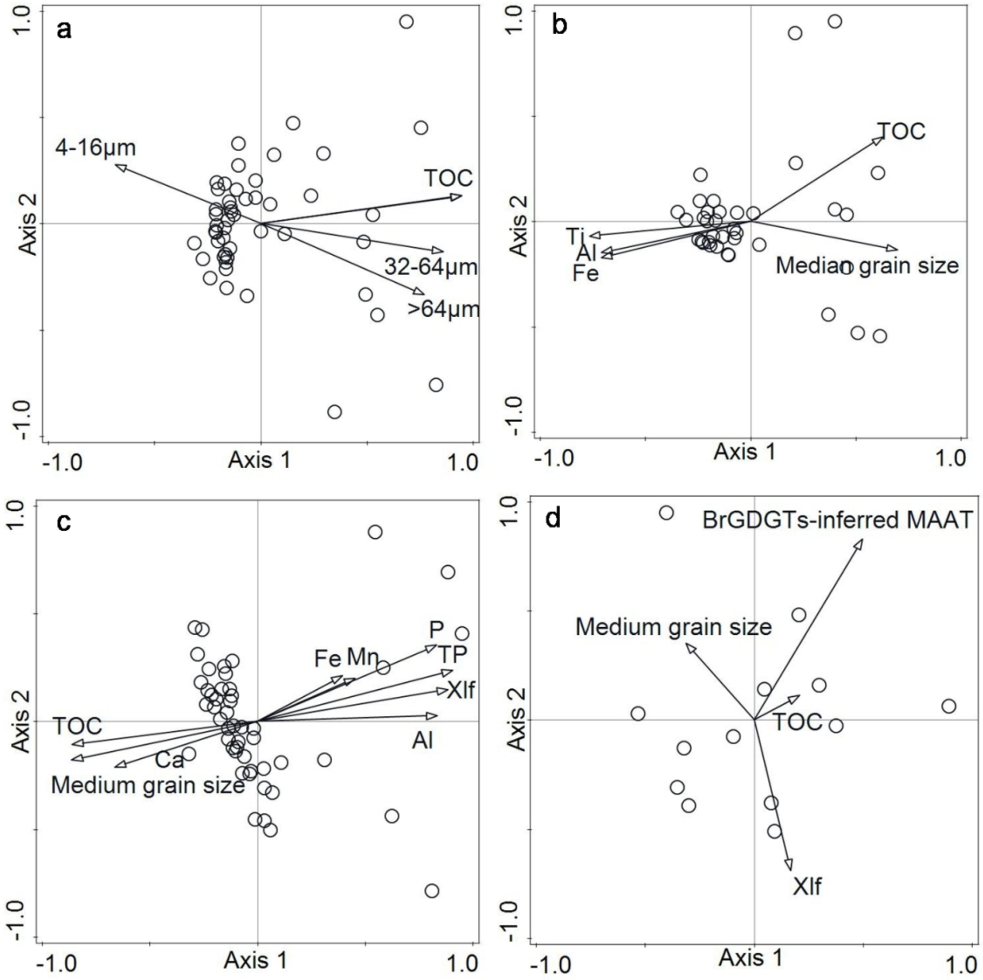

Fig. 6 Sample-environmental variable plot of RDA between fossil chironomids and sedimentary proxies in (a) Chenghai, (b) Yangzong, (c) Lugu and (d) Tiancai lake cores. Xlf: magnetic susceptibility of low frequency; <4 μm: the percentage of grain size smaller than 4 μm; 4-16 μm: the percentage of grain size between 4 and 16 μm; 32-64 μm: the percentage of grain size between 32 and 64 μm; >64 μm: the percentage of grain size larger than 4 μm; TOC: total organic carbon; TP: total phosphorus; Al, Fe, Ti, Ca, Mn, P: Elemental concentrations; BrGDGT-inferred MAAT: BrGDGT-inferred mean annual air temperature.

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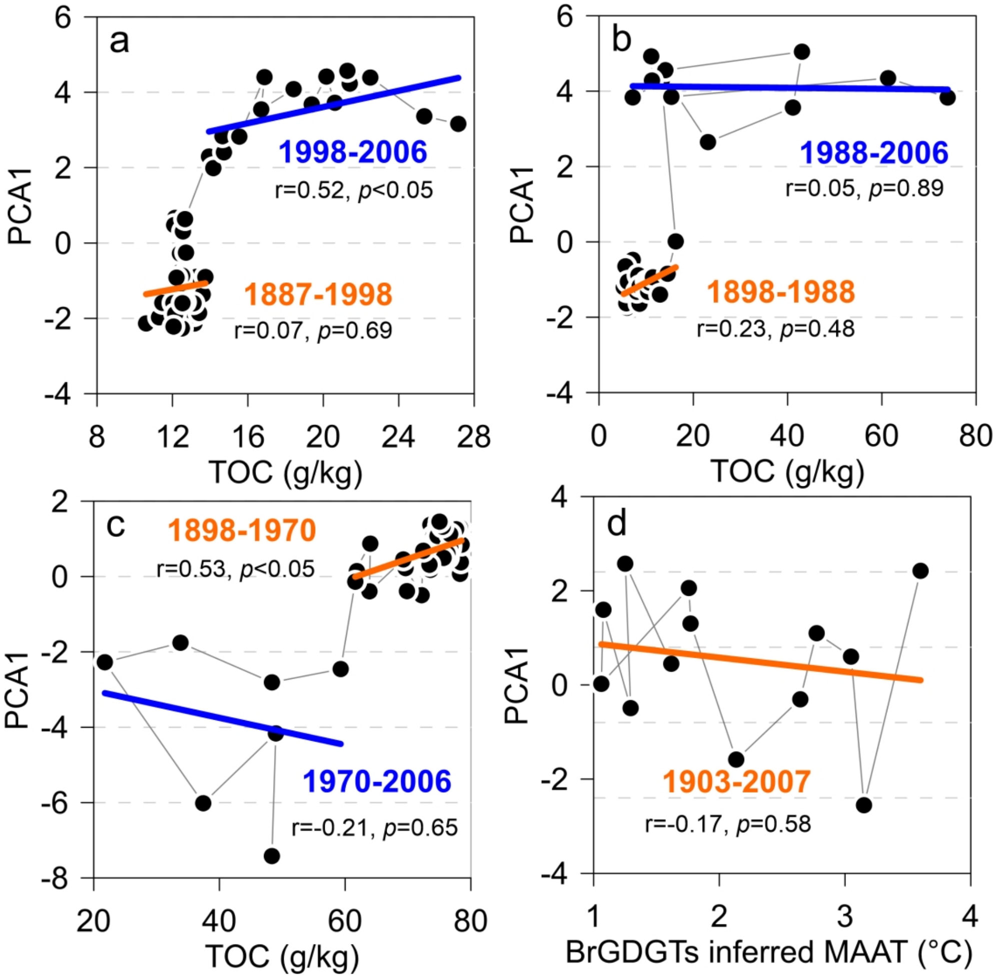

Fig. 7 Phase-space plots of the driving variables (TOC or temperature) versus the chironomid state response variable (PCA1) over the last century. Plot (a) Chenghai (b) Yangzong and (c) Lugu describe two linear clusters of points before (orange line) and after (blue line) their respective date of regime shifts, while (d) Tiancai Lake does not display any regime shift.

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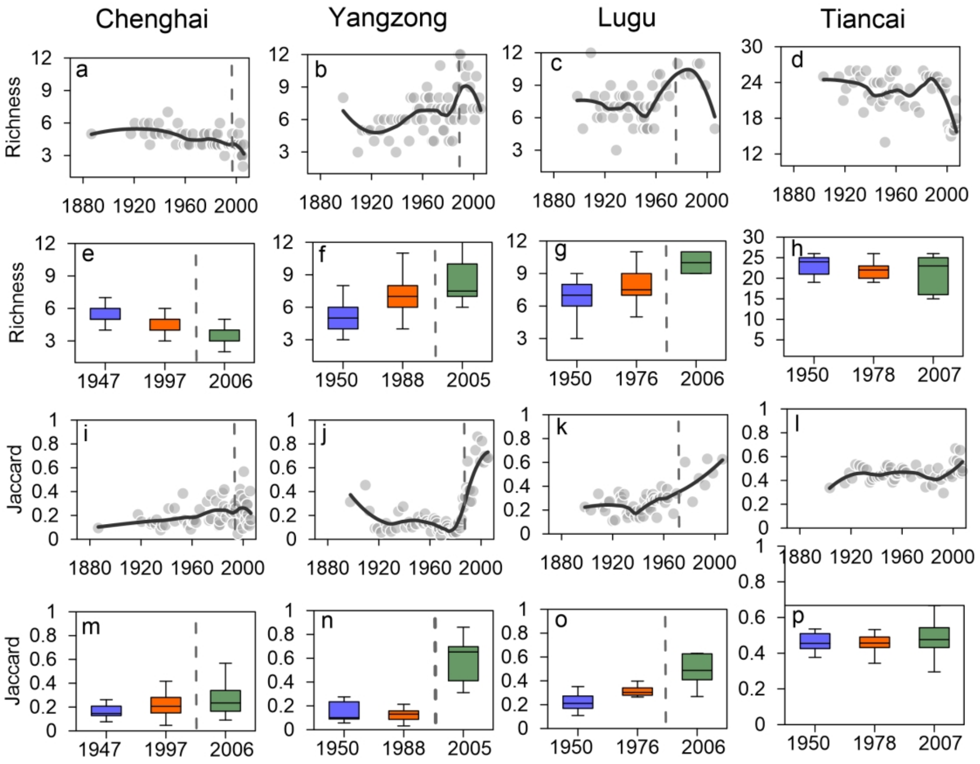

Fig. 8 Alpha (richness index) and beta diversity (Jaccard index) in time series and boxplot for (a) (e) (i) (m) Chenghai, (b) (f) (j) (n) Yangzong, (c) (g) (k) (o) Lugu and (d) (h) (l) (p) Tiancai. Note that the gray dashed line indicates the point of regime shift.

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