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Cover letter

Dear editor,

With this letter we are submitting the manuscript "*Regime shifts in shallow lake ecosystems along an urban-rural gradient in central China*". This manuscript has 7848 words, 8 figures and 2 tables.

With the process of urbanization, many rural lakes are gradually embedded in cities and turn to suburban or urban lakes. Aquatic ecosystems in different positions along the urban-rural gradient are more likely to experience different developmental trajectories and have diverse ecological status currently. The understanding around how these lakes respond to such stressors is currently not well known but urgently required to ensure the effectiveness of management strategies on different types of lake ecosystems.

This study reconstructed the developmental history of three lakes along the urban-rural gradient a metropolitan area (Wuhan City) in central China using sedimentary chironomid records. Our results revealed that these lakes had undergone regime shifts in the sequence of their distance from city centre, but their responses to external stressors were spatially and temporally different. Urban and suburban lakes have become eutrophic due to anthropogenic pollutants input and climate warming. Hydrological regulation of the connection between river and lake reduced water-level amplitude in the rural lake, and hence stimulated the development of aquatic vegetation that promoted the resilience of the rural lake temporarily. Given rapid urbanization all over the world, more and more lakes will be embedded in the urban landscape, and hence will face the risk of environmental degradation due to increasing external stressors, especially in rapidly developing regions. Different trajectories and driving forces of environmental changes in lakes along the urban-rural gradient highlight active and targeted strategies for different types of lakes, in order to avoid detrimental regime shifts and sustain a desired state.

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Authors

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1. Introduction

Accelerated urbanization is one of the most dramatic changes in post-1950s (Steffen et al., 2015), as the global urban population exceeded the rural population in 2008 for the first time in history (Seto et al., 2010). Rapid urbanization has led to serious environmental and ecological problems, both in urban and surrounding areas, including air, water and soil pollution, land-cover changes, and alteration of ecosystem structure and function (McDonnell et al., 1997; Grimm et al., 2008; Seto et al., 2012). Over the last two decades, research focused on ecological repercussions of rapid urbanization has increased significantly (Teurlincx et al., 2019). Most studies have focused on the responses of terrestrial biota and habitats to urbanization, and relatively less attention has been focused on freshwater habitats, especially lakes (Hill et al., 2017; Liang et al., 2020).

In an urban landscape, lakes are a sink for a wide range of contaminants (e.g. nutrients, trace elements, microplastics, antibiotics) that are released through air, water and detritus (Schueler and Simpson, 2001; Naselli-Flores, 2008). Urban watersheds generally produce higher pollutant loads per unit area from storm water runoff, in comparison with rural watersheds (Schueler and Simpson, 2001). In addition, urban watersheds produce a higher loading of pollutants from municipal wastewater discharges, especially in developing regions with insufficient water infrastructure (Walsh et al., 2005; Lee et al., 2019). Pollutant accumulation should favor disproportionate development of pollution-tolerant species (e.g. harmful cyanobacteria) in urban lakes, subsequently imposing detrimental effects on human health and ecosystem function (Taranu et al., 2015). Importantly, the relative location and morphometry of lakes on the urban-rural gradient will be reshaped with the outward expansion of cities, likely resulting in altered ecosystem functioning across this gradient. Many initial rural lakes gradually became suburban or urban lakes over time adjacent to the newly founded urban centres (Moore et al., 2003). Concomitantly, the bloom of pollution-tolerant species can be expected in lakes around urban regions with rapid urbanization.

Despite recent water quality monitoring schemes in urban regions, available data are spatially and temporally limited. Fortunately, sediment records from multiple lakes can improve our knowledge of long-term aquatic environmental change at a regional scale (Thapalia et al., 2015). Sedimentary records reveal that most urban lakes generally have experienced ecological shifts from a macrophyte-dominated, clear water state to an algal-dominated, turbid water state (Nyenje et al., 2010). Suburban lakes located in the ecotone between urban and rural areas play an important role in regional sustainable development, yet their response to multiple stressors is typically unknown (Zeng et al., 2018; Zhang et al., 2019). It is crucial to reveal the mechanisms behind spatial-temporal evolution of urban lakes in order to avert further environmental degradation and identify effective protection strategies in different lakes along the urban-rural gradient (Hall et al., 1999; Teurlincx et al., 2019).

In the Yangtze floodplain, there are hundreds of shallow freshwater lakes, which provide important ecosystem services such as wildlife habitats, freshwater and food supply, and water regulation (Dearing et al., 2012). Since the early 1980s, Chinese urbanization is unprecedented in scale, with an expansion of urban population from 0.17 billion in 1978 to 0.71 billion in 2013 (Song and Zhang, 2002). As more and more lakes are embedded in the urban landscape, the influxes of anthropogenic pollutants increased markedly (Xu et al., 2010). As a consequence, most lakes in this region have experienced a major alteration from a relatively good water quality to eutrophication during the 1980s (Le et al., 2010) and over 85% of lakes now are eutrophic or hypertrophic (Yang et al., 2010). However, while the status of these systems is known, less is known about the transition processes, and ecosystem trajectories in response to the multiple stressors along the urban-rural gradient, which are important to understand to enable appropriate remediation techniques to be employed.

This study analyzed ecological trajectories of three lakes based on subfossil chironomids (Insecta, Diptera) in sediment cores collected from urban, suburban and rural areas in Wuhan City (central China). We hypothesize that lake responses to multiple stressors would be temporally and spatially different. This study aims to 1) reconstruct ecological trajectories of lakes along the urban-rural gradient with the expansion of urban areas and 2) examine lake responses to past changes in external drivers along the urban to rural gradient.

2. Material and Methods

2.1. Study area

Wuhan is the capital of Hubei Province, located in central China and the middle reach of the Yangtze River (Fig. 1). The region belongs to the subtropical monsoonal climatic zone with a mean annual temperature of 17.4 °C and a mean annual precipitation of 1400 mm. The city is a famous megalopolis having a population of more than 10 million. High population pressure has stimulated city expansion in recent years with the expansion of built-up district area from 30 km^2 in 1950 (3 million people) to 220 km^2 in 2005 (8 million people) and sharply to 550 km^2 in 2014 (10 million people) (Bureau of Statistics of Hubei Province, 2009, 2014; Fig. 2a). The city embraces 166 lakes with surface area of over 0.05 km^2. All of them are shallow lakes with water depth less than 5 m and most are fluvial lakes linked to the evolution of the Yangtze River. Their total area is approximately 867 km^2, occupying 10.2% of the total land area of the city (8,494 km^2). However, 158 out of 166 lakes within the city were eutrophic and 11 were hypertrophic according to the survey in 2017 (Wuhan Environmental Protection

Bureau, 2017). Algal blooms occur frequently, especially in summer in several lakes (e.g. Donghu Lake and Nanhu Lake) near the city centre. The degradation of lake ecosystems in Wuhan has aroused widespread public concern.

Shahu Lake (central location 30°34′7″N, 114°19′40″E; mean water depth of 2.5 m) is the only lake exceeding 3 km^2 in surface area within the inner ring line of Wuhan. Lake surface area was about 6.7 km^2 before the 1910s, with free hydrological connection with the Yangtze River and Donghu Lake. However, its hydrological connection with the Yangtze River was regulated by several local dams after the 1910s. Due to land reclamation with rapid urbanization, the lake became hydrologically closed after the 1990s (Zhang, 2009). Moreover, the lake was divided into two small lakes (named Inner and Outer Shahu Lake) by the construction of Yue-Han Railway in the early 20th century. The water surface area correspondingly reduced to 3.5 km^2 in the late 1980s, and then sharply to current 3.1 km^2 (Compilation Committee of Lakes in Hubei Province, 2014; Fig. 2c, Fig. A.1). About 71% of the lost water surface was converted into built-up areas (Xie et al., 2017). Marginal plants are patched along lakeshore and mainly dominated by *Nelumbo nucifera* and *Alternanthera* with the disappearance of submerged plants (Song, 2008). A survey conducted in August 2016 showed that concentrations of total phosphor~~o~~us (TP), total nitrogen (TN) and chlorophyll *a* (Chl-*a*) were 588, 4300 and 179 μg L^{-1}, respectively (Liang et al., 2020). But in July 2019, the observed TP was 292 μg L^{-1} (Table 1).

Yanxi Lake (30°32′~30°37′N, 114°27′~114°31′E; mean water depth of 1.9 m) is an agriculturally important area and fishery production base, as well as drinking water source for villagers living around the lake. With the expansion of urban area, Yanxi Lake has been transformed from a rural lake to a suburban lake. Many crop lands in its basin have been converted into built-up purpose (Fig. A.1). The lake was freely connected with the Yangtze River before the construction of local Wuhui Dam in 1955 and Beihu Dam in 1965. Lake surface area reduced from 12.7 km^2 in 1936 to 12.6 km^2 in 1982 (Zhang, 2009), and further to current 11.8 km^2 (Fig. 2c). There were more than 20 industrial factories surrounding the lake until the mid-1990s. A large influx of untreated industrial and domestic sewage into the lake has caused the deterioration of water quality (Wu, 1992). After 2000, most of these factories were generally closed and a variety of sewage treatment measures were implemented. Since 2003, the lake has been built into a holiday resort functions as leisure, agriculture tourism and popular science tourism. In August 2016, concentrations of TP and Chl-*a* were 42 and 70 μg L^{-1}, but increased to 160 and 111 μg L^{-1} respectively in July 2019.

Futou Lake is a relatively rural lake (29°57′~30°07′N, 114°09′~114°20′E; mean water depth of 1.65 m), around 57 km away from the city centre. Hydrological connectivity between the lake and the Yangtze River was regulated by the implements of local Jinshui Dam in 1935 and Xinhe Dam in 1973. Presently, this lake is in a macrophyte-dominated state, with high abundances of *Pistia stratiotes*, *Vallisneria natans*, *Potamogeten crispus* and *Ceratophyllum demersum*. Concentration of TP was 43 μg L^{-1} in August 2016 and 70 μg L^{-1} in July 2019. The development trajectory of this lake has been detailed by Zeng et al. (2018), and summary plots of Futou Lake are used to compare with the other two lakes investigated here.

2.2. Core collection

Sediment cores were collected using a modified Kajak gravity corer at the approximately centre of Futou Lake (30°03′16.96″N, 114°12′24.67″E; with length of ~65 cm) in April 2014, and Shahu Lake (30°34′12.18″N, 114°20′11.30″E; ~61 cm) and Yanxi Lake (30°34′18.08″N, 114°28′42.49″E; ~61 cm) in October 2011. The cores were sliced at intervals of 1 cm in field. Subsamples were stored in plastic bags and kept in the refrigerator at 4°C before analysis.

2.3. Laboratory analyses

2.3.1. Chronology

Sediment cores were dated mainly by ^{210}Pb, and corrected by the chronomarker of spheroidal carbonaceous particles (SCP). Radioactive isotopes ^{210}Pb, ^{226}Ra and ^{137}Cs were counted at 2-cm intervals on a gamma spectrometer (Ortec HPGe GWL). Chen et al. (2019) displayed the detailed measurements and chronological stratigraphy for each lake.

2.3.2. Particle size

Particle size spectra of samples were measured at 1-cm intervals using a Malvern automated laser optical particle-sizer analyser (Mastersizer-2000) after the removal of carbonate by 10% HCl and organic matter by 30% H_2O_2.

2.3.3. Elements analyses

Element contents (including Cu, Zn and TP) in sediments at 2 cm intervals were determined by the Inductively Coupled Plasma-Atomic Emission Spectrometry (ICP-AES) after digestion with HF-HCl-HNO_3-$HClO_4$.

2.3.4. Chironomid analysis

Sediment samples for chironomid analysis were conducted according to standard techniques proposed by Brooks et al. (2007) at 2 cm intervals. Wet sediment samples were deflocculated in 10% KOH in a water bath at 75 °C for 15 min, and then sieved through 212 and 90 μm meshes. The residue was transferred to a grooved perpex sorting tray and examined manually under a stereo-zoom microscope at x25 magnification with fine forceps. Head capsules were permanently mounted on slides using

Hydromatrix®, ventral side uppermost, and subsequently identified at x100-400 magnification using the taxonomy of Brooks et al. (2007), with reference to Rieradevall & Brooks (2001). A minimum of 50 identifiable whole head capsules from each sample is expected to be representative of the extant fauna (Quinlan and Smol, 2001).

2.4. Climatic data collection

Annual temperature and precipitation data were collected in order to reveal the effects of climate change on lake development. Annual temperature data since 1905 were obtained from Hankou Meteorological Station. Monitored precipitation data were discontinuous as rainfall data from 1944 to 1950 was not measured. Simulated rainfall data of the studied region (29.5-30.5°N,113.5-115.5°E) were then obtained from Koninklijk Nederlands Meteorologisch Instituut (KNMI) (website: http://climexp.knmi.nl/selectfield_obs.cgi). Significant positive correlation exists between rainfall data from Hankou Meteorological Station and KNMI ($r = 0.69$, $p < 0.05$). Annual rainfall data from KNMI, combined with temperature data were then used in subsequent ordination analysis (Fig. 2d).

2.5. Numerical analyses

The enrichment of Cu, Zn and TP can indicate increasing anthropogenic disturbances (Boyle et al., 1999). In order to evaluate the accumulation of elements along time, geoaccumulation index (I_{geo}) for Cu, Zn and TP was calculated as follows:

$$I_{geo} = \log_2(C_n/(1.5*B_n))$$

where, C_n is the measured concentration of element n in sediment; 1.5 is the background matrix correction factor due to lithogenic effects; B_n is the geochemical background value of element n

(Gonzáles-Macías et al., 2006; Ghrefat and Yusuf, 2006; Kim et al., 2018). Considering the different benchmark of elements in different lakes, here we calculated B_n as average concentration before 1900 of element n.

Variance partitioning analysis (VPA) was conducted to distinguish the effects of diverse stressors on fossil chironomid communities. Three explanatory categories were identified as climate, hydrological condition and anthropogenic pollution. The climate-group includes two variables of annual temperature and rainfall. The establishment of local dams was considered as a 1/0 dummy variable for indicating hydrological regulation. Particle size spectra in sediments are closely linked to hydrological dynamics (Zeng et al., 2018). Damming event and particle fractions together were used to reflect hydrological changes in three lakes. The geoaccumulation index of Cu, Zn and TP composed the group of anthropogenic pollution. All explanatory variables were standardized with $\log_{10}(x+1)$-transformation to eliminate the effects of different units among them. Rare chironomid taxa occurred in only one sample or with abundance less than 2% were deleted and would not participate in ordination analyses. Detrended correspondence analysis (DCA) was conducted to extract major changes in chironomid communities of three lakes. It also showed that the gradient length for Shahu, Yanxi and Futou Lake was 2.6, 2.0 and 1.8 standard deviation, respectively, suggesting the linear method was suitable for the subsequent ordination analyses. Redundancy analysis (RDA) was also employed to identify significant explanatory variables and to estimate the fraction of faunal variance explained by three categories in variance partitioning. Monte Carlo permutation tests (499 unrestricted permutations) were conducted to test the significance of variables, and forward selection was used to determine the minimum subset of significant variables. VPA was carried out to evaluate the relative importance of each explanatory group and their explanatory power in each lake. Because of limitation of climate data, the time window analyzed in VPA was 1907-2011 AD for Shahu Lake, 1904-2011 AD for Yanxi Lake and 1914-2014 AD for Futou Lake. All above ordination analyses were based on taxon percentages with square-root transformation, and conducted in CANOCO version 5.0 (Šmilauer and Lepš, 2014).

The possible abrupt shifts in ecosystem structure and function for three lakes were also detected using the Sequential *t*-test Analysis of Regime-shifts algorithm (STARS) proposed by Rodionov (2004). The module shift detection software version 3.2 was initially added in Excel 2010. In parameter setting, significance level was 0.05 and cut-off length was 5. Regime shift index (RSI) was calculated and employed to identify the most potential tipping point. Scores of DCA first axis on chironomid data, which stands for the most important information from chironomids, were involved in the detection. Gaussian kernel density estimation and autoregressive integrated moving average (ARIMA) model were also conducted to verify whether two different regimes existed before and after the tipping point. The former was performed with the R statistical software (R Core Team, 2018) using the 'sm' package (Bowman and Azzalini, 2018), and the latter was conducted using Minitab 17.

3. Results

3.1. Chronology

$^{210}Pb_{ex}$ activities generally declined exponentially with mass depth (Chen et al., 2019). The chronologies of the three sediment cores were calculated based on the constant rate of supply model (Appleby and Oldfield, 1978). The start of the rapid increase in SCP concentrations corresponds to the major expansion in coal consumption from 1970. The final chronologies of sediment cores were established based on the SCP chronomarker-validated ^{210}Pb chronologies (Fig. 3). Generally, sedimentation rates were less than 0.2 g cm^{-2} yr^{-1} before the 1930s, and then increased to a peak. Thereafter sedimentation rates decreased and remained low after the 1980s. Detailed results are presented in Chen et al. (2019).

3.2. Chironomid stratigraphy

More than 40 different species morphotypes of chironomids were identified in three cores (Fig. A.2). Cluster analysis identified significant changes in chironomid composition occurred around 1963, 1975 and 1980 AD for Shahu, Yanxi and Futou Lake, respectively (Fig. 4).

In Shahu Lake, there was a major compositional shift from plant-dwelling taxa to nutrient-tolerant taxa during the past 160 years (Fig. 4a). Before 1963 AD, chironomid assemblages within the lake were dominated by *C. sylvestris*-type (average ca. 18.1%), *D. nervosus*-type (mean of 13.6%) and *Paratanytarsus* (mean of 12.3%). Subsequently, major taxa were replaced by *Tanypus* (average ca. 60.6%), *Propsilocerus akamusi*-type (about 7.9%) and *Procladius* (about 13.3%). The prominence of *Tanypus* after 1990 AD (16 cm-depth), was substantial as the percentage reached up to 90%.

Several different taxa co-existed before 1975 AD in Yanxi Lake (Fig. 4b). Major taxa included *Paratanytarsus* (average percentage of 12.4%), *Microchironomus tener*-type (11.5%), *C. sylvestris*-type (7.5%), *Stempellinella-Zavrelia* (6.6%), *Polypedilum nubifer*-type (4.9%) and *D. nervosus*-type (4.7%). Total abundance of macrophyte-related taxa (*Ablabesmyia*, *Corynonueura edwardsi*-type, *C. sylvestris*-type, *D. nervosus*-type, *Glyptotendipes severini*-type, *Parachironomus vasus*-type, *Paratanytarsus*, *Polypedilum nubeculosum*-type and *P. sordens*-type) in this period was nearly 35.0% in average. Whereafter, chironomid assemblages were dominated by *Tanypus* (ca. 29.9%) and *P. akamusi*-type (10.4%). Concurrently, some other nutrient-tolerant species such as *Chironomus* *plumosus*-type (mean of 3.7%) and *Microchironomus tabarui*-type (4.6%) also increased. After 1999 AD, the abundance of *Tanypus* increased to the maximum (59.7%) at surface samples.

In Futou Lake, chironomid assemblages were dominated by *M. tener*-type before 1980 AD, and then were macrophyte-related *Paratanytarsus* and *C. sylvestris*-type after its damming. Meanwhile, nutrient-tolerant *P. akamusi*-type increased after 1994 AD (Fig. 4c).

3.3. Particle size and elemental concentration

Sediments in three lakes were mainly composed of clay and silt (Fig. 5). Generally, clay decreased in the upper strata of three sediment cores, in contrast to increasing proportions of sand. In spite of low proportions, there were several peaks of sand in three sediment cores.

Distinctive changes in sedimentary Cu, Zn and P were observed in Shahu Lake core. Cu, Zn and P were relatively stable with no notable changes before 1963 AD (Fig. 5a). Cu and Zn sharply increased from 1963 AD to the late 1990s, followed by slight decreases. Sedimentary P continued to increase and trebled between 1963 and 2011 AD.

Variations of Cu, Zn and P in Yanxi Lake were more complex than in Shahu Lake (Fig. 5b). Concentrations of Cu and Zn increased markedly after the 1920s, followed by relatively minor variation after the 1940s. After the 1980s, Cu gradually decreased, while Zn showed an inverse tendency. Sedimentary P remained low values before the1960s, and thereafter continued to rise till the uppermost.

Trends of Cu, Zn and P in Futou Lake were similar as they rose before 1900s and then declined until 1980 (Fig. 5c). Zn and P enriched sharply after 1980 AD, with their concentrations increased by more than 20%. Concurrently, Cu increased slightly from 41 to ~45 mg/kg.

3.4. Variation partitioning analysis

RDA and VPA revealed that chironomid communities in three lakes were significantly influenced by different historical changes in climate, hydrological conditions or anthropogenic pollutants since the early 20th century (Table 2).

In Shahu Lake, three variables (annual temperature, median grain size and I_{geo} (P)) assigned to three explanatory categories comprised the minimum subset of significant variables capturing 60.6% of the total variance in chironomid assemblages. Anthropogenic pollution independently explained 34.7% of total variance, and its combined effect with hydrological conditions captured 22.4% of total variance further (Fig. 6). Climate change was a significant variable but its sole effect was minor. Its interaction with anthropogenic pollution and hydrological conditions explained 6.5% and 2.5% of total variance, respectively. Combined effects of three significant variables were negative and explained -9.6% of species variances.

In Yanxi Lake, climate and hydrological variables failed to explain a significant part of total variance in chironomid communities. The unique effect of anthropogenic pollution captured 44.3% of total variance.

In Futou Lake, the sole effect of hydrological alterations (i.e. damming event and silt fraction) explained more variance (33.7%) in chironomid assemblages than that (13.3%) of anthropogenic pollution. Their interactive effect on chironomids was negative with the value of -10.8%. The sole effect of climate change was not significant.

3.5. Developmental trajectories and regime shifts

The biplot of DCA1 against DCA2 revealed the developmental trajectories and response trends of three lakes to multiple stressors (i.e. different human disturbances) (Fig. 7). Shahu and Yanxi Lake shifted from different ecological status towards an identical homogenized eutrophic state. Futou Lake, however, developed mainly along DCA2 (representing hydrological conditions) and is still in a relatively desired state with established macrophyte communities. Its development took a different trajectory compared with urban Shahu Lake and suburban Yanxi Lake due to the different multi-dimensional stressors impacting it.

STARS captured the possible tipping point in each lake: 1963 AD for Shahu Lake, 1975 AD for Yanxi Lake and 1980 AD for Futou Lake (Table A.1). Gaussian kernel density estimation showed a bimodal distribution, with two divergent peaks for each lake before and after the detected critical point (Fig. 8a). ARIMA displayed obvious divergence between the predicted and observed (sedimentary) biological changes, suggestive of two alternative ecological states for each lake (Fig. 8b). Considering the replacement of dominated taxa in chironomid assemblages, ARIMA confirmed that both Shahu and Yanxi Lake had turned into a completely different and worse ecological state after the regime shift than before. Although experienced regime shift, observed DCA1 scores after 1980 AD in Futou Lake was more stable than the predicted values. In any case, both of these sets of analyses provide evidence of bistability before and after the observed tipping points.

4. Discussion

4.1. History of water quality change

Significant changes in water quality were reflected by sedimentary proxies including geochemical and biotic indicators in three lakes during the past century. Generally, the dominance of macrophyte-related chironomids was replaced by eutrophic species in urban and suburban lakes, suggesting their trajectories toward eutrophication.

Before the 1960s in Shahu Lake, chironomid communities mainly consisted of taxa preferring shallow water with a relatively high density of macrophytes, such as *C. sylvestris*-type, *D. nervosus*-type and *Paratanytarsus* (Brodersen et al., 2001; Davidson et al., 2010). Most of these taxa are often found in productive and mesotrophic to eutrophic waters. They are frequently common in shallow lakes in the Yangtze floodplain, and considered to be indicators of flourishing macrophytes (Langdon et al., 2010; Zhang et al., 2012). Their coexistence and predominance suggested a stable and good ecological state of Shahu Lake during this period. The lake regime collapsed within just a few years (20-30 years) and switched to an alternative state after 1963 AD, since the dominance of clear-water/ plant-preferring taxa (e.g. *Paratanytarsus* genus) were replaced by the rising abundances of pollution- and/or nutrient-tolerant taxa such as *P. akamusi*-type and *Tanypus*. *P. akamusi*-type was firstly described by Sasa (1978) and is often encountered in eutrophic to hypertrophic lakes in China and Japan, with a TP optimum of 118 μg/L in the Yangtze floodplain lakes (Zhang et al., 2012). *Tanypus* can also be found in mesotrophic and hypereutrophic lakes, has a TP optimum of 169 μg/L in the study region (Zhang et al., 2012).

Yanxi Lake was in a relatively desired state before the 1970s, suggested by the dominance of mesotrophic *M. tener*-type (Brooks et al., 2007) and clear-water taxa *Paratanytarsus* (Langdon et al., 2010) and some other plant-inhabiting taxa. After the 1970s, the enrichment of Zn and sedimentary P indicated an increasing influx of external pollutants into Yanxi Lake. The replacement of phytophilous chironomid taxa by eutrophic species indicated that the lake was switching from a mesotrophic state into a eutrophic lake, although the trajectory of change was slower than in Shahu Lake. Until 2010s, Yanxi Lake was still in the process of eutrophication and water deterioration continued as indicated by our results as well as available monitoring data (Wuhan Environmental Protection Bureau, 2012-2017). It might suggest that more effective strategies could be made for suburban lakes, or else the resilience and functional services of these lakes will be lost.

Futou Lake is currently one of the few lakes with flourishing aquatic vegetation in the Yangtze floodplain. This lake has maintained relatively good water quality since the mid-19th century indicated by high abundance of plant-associated chironomids (e.g. *C. sylvestris*-type and *Paratanytarsus*) throughout the sediment core, especially since the 1980s. Vegetation can sequester nutrients in water and plays a critical role in the maintenance of aquatic ecosystem stability (Zhang et al., 2016). However, the enrichment of sedimentary P and heavy metals since the 1980s was suggestive of enhanced human activities in the catchment. As a consequence, *P. akamusi*-type, a eutrophic indicator, started to increase after the mid-1990s, albeit at relatively low abundance. Given the trajectories of the other lakes that contain *P. akamusi*-type, this may be an early warning indicator that the lake may be losing resilience ahead of a switch to an alternative state.

4.2. Anthropogenic pollution

Variance partitioning revealed that anthropogenic pollution was the major driver for changes in chironomid communities in both Shahu and Yanxi Lake. Regional palaeoecology studies confirmed the importance of anthropogenic pollution in regulating water quality in the Yangtze floodplain (Chen et al., 2016; Zhang et al., 2019). Sedimentary phosphor~~o~~us was a significant explanatory variable for Shahu and Yanxi Lake. The enrichment of sedimentary P has accelerated in the urban and suburban lakes since the 1960s, probably linked to recent demographic and economic increases in Wuhan City (Fig. 2).

The dominance of eutrophic species and high sedimentary P content in Shahu Lake indicated that the urban lake suffered from serious eutrophication, because nutrient inputs from sewage discharge were greatest in city centre. The magnitude of increases in sedimentary P and eutrophic taxa was relatively lower in suburban (Yanxi Lake) and rural (Futou Lake) lakes at the same point in time.

In suburban and rural lakes, heavy metal enrichment (i.e. Cu and Zn) explained a significant part of variance in the species data. The enrichment of Cu and Zn is mainly derived from industrial sources (Boyle et al., 1999; Liu et al., 2012). Anthropogenic pollution generally experienced three distinct stages in the study area, i.e. an increase in the early 1900s, a sequent recession and then a rapid rebound after the 1950s. The three stages broadly corresponded to the establishment of modern industry in the early 1900s, Sino-Japanese and Chinese civil wars from the 1930s to 1940s, and the boosting of heavy industry after the 1950s in Wuhan. Heavy metal enrichment would typically reduce chironomid diversity, and promote the proliferation of pollution-tolerant species (Cao et al. 2016). Taken together, variance in chironomid communities explained by anthropogenic pollution decreased along the urban-to-rural gradient, indicating that increased pollutant inputs imposed overwhelming effects on urban and suburban lakes, but relatively minor effects upon the rural lake.

4.3. Hydrological and climate change

Besides anthropogenic pollution, hydrological indicators (i.e. damming and sedimentary particle size) accounted for a significant part of variance in the species data, especially in the rural lake (Futou Lake). In a hydrologically-open lake, sedimentary particle size can be a proxy for hydrodynamic intensity, and an increase in sand percentage may indicate strong inflows that are able to transport coarse particles into the lake (Chen et al. 2011). However, prolonged water retention time after dam construction would promote the deposition of fine particles, resulting in a relative increase in clay (Zeng et al., 2018). In Shahu and Futou Lakes, it is unexpected that the percentage of sand displayed an increasing trend after the 1960s, when both of lakes had suffered from hydrological regulation due to dam construction. This phenomenon is probably linked to a sharp shrinkage of lake area due to land reclamation after the 1950s (Xie et al., 2017). Both Shahu and Futou Lakes have lost more than 25% of surface area during the last century (Zhang et al. 2009; Xie et al., 2017). As a consequence, coarse particles would be readily transported to the lake centre. In the urban lake (Shahu Lake), prolonged hydraulic residence time and lake shrinkage would promote the enrichment of pollutants. Therefore, the combined effect of hydrological alteration and anthropogenic pollution captured a high proportion of total variance in chironomid communities in this lake. In contrast, the combined effect of hydrology and anthropogenic pollution was negative for the rural Futou Lake, as a reduction in water level amplitude after hydrological regulation promoted the development of macrophytes and associated chironomid taxa (Zeng et al., 2018; Zhang et al., 2019), which can have a stabilizing effect on lake ecosystems (Jeppesen et al., 1998).

In the urban Shahu Lake, changes in chironomid communities were significantly correlated with increasing temperature. It is noteworthy that the combined effect of temperature and sedimentary phosphorus explained a higher proportion of variance than the sole effect of temperature (Fig. 7). The results indicated that rising temperature could indirectly promote the development of nutrient-tolerant species (Chen et al. 2013). In shallow lakes, climate warming usually accelerates nutrient release from sediments and renew nutrient supplies into the water column (Jensen and Andersen 1992). However, in the suburban (Yanxi) and rural (Futou) lakes, the effects of climate variables failed to be significant, neither their sole effects nor combined effects with other drivers. The effect of climate warming on chironomids would thus likely be amplified in the eutrophic lake (Shahu Lake) with high nutrient loading.

4.4. Regime shifts in lakes along an urbanization gradient

Regime shifts are increasingly happening in terrestrial and aquatic environments in the context of continuous human influences (Folke, 2004; Reid et al., 2016). In most cases, ecosystems' regime tends to shift from a desired state with high resilience to an undesired state with low ability of self-organization and feedback (Wang et al., 2012, 2019; Zhang et al., 2018), and this appears to have occurred rapidly in Shahu Lake. Hydrologic regulation can also induce critical transition through altering vegetation coverage in lake ecosystems (Schooler et al., 2011; Bertani et al., 2016). For example, water level alteration stemming from dam establishment caused the disappearance of submerge vegetation (the first regime shift) and then the increase of nutrients triggered the second state alteration (algal blooms thereafter) in Chaohu Lake, which is located in the same region with our study (Kong et al., 2017). However, rural Futou Lake in our study seems to respond markedly different from urban Shahu Lake and Chaohu Lake. Massive macrophytes beds developed as a result of stabilized hydrological conditions after the detected tipping point in Futou Lake around 1980. The hydrological change and stabilizing effect of macrophytes promoted ecological resilience in Futou Lake. The ARIMA results (Fig. 8b) showed that the lake trajectory, based on the previous ecosystem data, was to further change and decline towards an alternative (eutrophic) state, similar to the Shahu and Yanxi lakes. But this never happened, due to the altered hydrology and macrophyte growth across the lake. Nevertheless, the increasing abundance of pollution-tolerant taxa (*P. akamusi*-type) indicated the continued enrichment of pollutants and nutrients in Futou Lake, and based on the trajectories of the other lakes in this study, would suggest that despite hydrological and macrophyte stability, nutrients are still increasing and the lake may yet be losing resilience ahead of a transition to an alternative state. As such, the chironomid data may provide an early warning to this, and other rural lakes, on the edge of city expansion and subject to enhanced nutrient pollution. While Shahu lake has transited to an alternative state, and Futou lake currently appears to have partially stabilized (for now at least), Yanxi lake may still be mid-transition regarding its ecological state. Given the location of the transition region, Yanxi Lake was suffering from multiple stressors with varying types and magnitude resulting from the expansion of Wuhan city and increasingly altered land-use patterns and population. The lake is still in a self-adjustment process to the new regime system as DCA1 scores of Yanxi Lake are still declining, which may indicate the altering biological compositions as ARIMA analyses also predicted.

4.5. Implication for sustainable management

Palaeoecological records provide useful implications for sustainable management of urban freshwater ecosystems. Regional comparison demonstrated that anthropogenic impacts were overwhelming in urban and suburban lakes, but relatively weak in the rural lake. Variance partitioning suggested that the precise management strategy should vary with lake position along the urban-to-rural gradient. The urban lake has experienced transitions from a phase of exponential pollution to a relatively stable polluted state. In contrast, the suburban lake is suffering from exponential pollution, and hence it is urgent to implement effective control measurements (e.g. installation of new sewage treatment plants) in the rapidly urbanized area. For the rural lake, both moderate hydrological regulation (e.g. water level stabilization) and reduction of external pollutant input are important for the development of macrophytes, which can increase resilience of lake ecosystems buffering against external disturbances (e.g. anthropogenic nutrient input) (cf. Scheffer et al. 2003). Additionally, although climate warming was also important, it cannot be regulated. Under a scenario of increasing temperature in future, nutrient release from lake sediments would increase the risk of environment deterioration in urban lakes.

5. Conclusions

Chironomid stratigraphies, combined with geochemical records and climatic data, demonstrated that the response of shallow lakes to external stressors was temporally and spatially different along the urban-rural gradient in a metropolitan area (central China) during the past century. All three lakes had experienced critical transitions which occurred in the sequence of their distance from city centre. Anthropogenic disturbance triggered regime shifts within lakes and drove them toward different states. Given the input of massive pollutants, urban Shahu Lake and suburban Yanxi Lake shifted from clear water to turbid state in 1963 and 1975, respectively. Climate warming acted as an amplifier of ecological change in urban lake with high pollution pressures. The dam impoundment in Futou Lake stabilized hydrological conditions, which facilitated the development of macrophytes after 1980. However, due to prolonged hydraulic retention time, nutrient enrichment in Futou Lake might be accelerated. Contrary to the new stable state in Shahu and Futou Lake, suburban Yanxi Lake, located in the transition region along the rural-urban gradient, now is still in self-adjustment resulting from the varying stressors in types and magnitude. With the city expansion, lakes along the urban-rural gradient exist in different ecological states due to the impact of varying drivers. This study also implies that active and targeted strategies on not only urban lakes but also suburban-rural lakes will be strongly required to avoid detrimental shifts and sustain a desired state in aquatic ecosystems.

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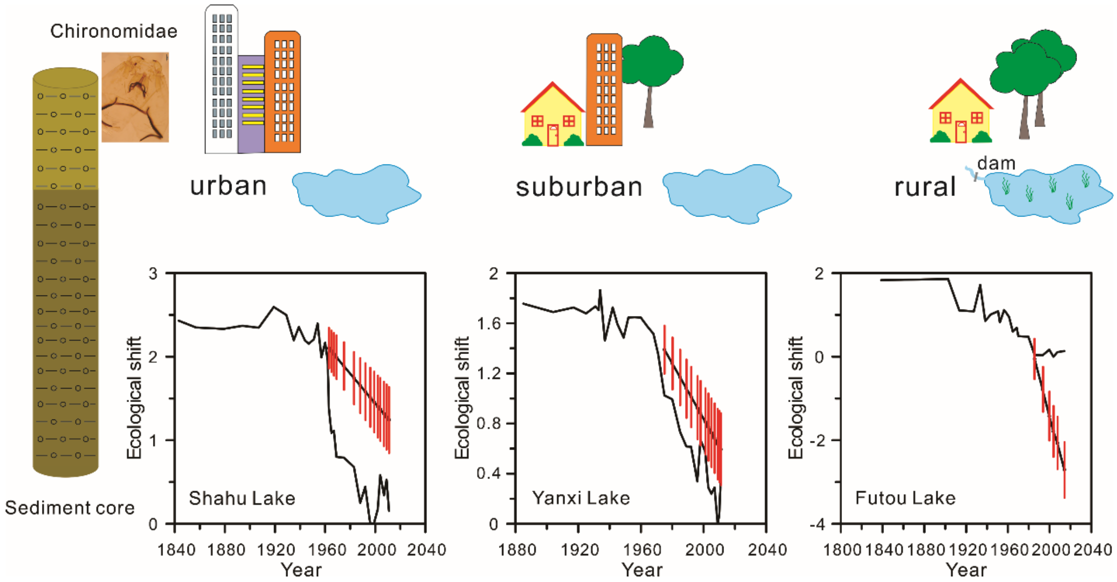
***Graphical Abstract**



***Highlights (for review : 3 to 5 bullet points (maximum 85 characters including spaces per bullet point)**

Highlights

- Past environmental changes in lakes along the urban-rural gradient were assessed.
- Urban, suburban and rural lakes experienced critical transitions at different times.
- Urban-rural lakes are currently in different ecological states.
- The external driving forces varied among different types of lakes.
- Warming acts as an amplifier of ecological change when pollution pressures are high.

Regime shifts in shallow lake ecosystems along an urban-rural gradient in central China

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Abstract: Due to differential exploitation pressure, ecosystems along the urban to rural gradients often exhibit different status in ecological structure and function. This can be challenging for lake restoration, given the relative strengths, magnitudes and speed of the exploitation. In this paper, we reconstructed the ecological changes over the past century and identified the regime shifts based on subfossil aquatic biota (chironomid records) in three shallow lakes (Shahu, Yanxi and Futou Lake) along an urban-rural gradient in the Yangtze floodplain, China. Our results illustrated the differences among lakes in trajectories, timing of critical transition and current ecological status. Eutrophic chironomid taxa increased markedly and replaced macrophyte-related taxa in urban Shahu Lake and suburban Yanxi Lake, indicated by the shift from a stable, vegetation-dominated state to an alternative, algal-dominated state in 1963 AD and 1975 AD respectively. The ecological regime in rural Futou Lake transited around 1980 AD but it is still in a relatively clear water state with abundant macrophytes due to anthropogenic hydrological controls. The greatest variance of chironomid compositional changes in both Shahu and Yanxi Lake was captured by anthropogenic pollutants, and analyses show that when these pressures are high they may be further amplified by climate warming. Responses along the urban-rural gradient are exemplified by urban Shahu Lake having shifted to a fragile regime with weak resistance and resilience, while rural Futou Lake has stabilized in a new regime with improved ecological resilience. Suburban Yanxi Lake is still moving toward a new state, and as such is unstable, because the types and magnitudes of external stressors are changing with urbanization in the city. It is suggested that active and precise management strategies for lakes should be established along the urban-rural gradient given their distinct development trajectories, drivers and current status.

Keywords: Critical transition; Urban-rural lakes; Urbanization; Subfossil chironomids; Palaeolimnology

1. Introduction

Accelerated urbanization is one of the most dramatic changes in post-1950s (Steffen et al., 2015), as the global urban population exceeded the rural population in 2008 for the first time in history (Seto et al., 2010). Rapid urbanization has led to serious environmental and ecological problems, both in urban and surrounding areas, including air, water and soil pollution, land-cover changes, and alteration of ecosystem structure and function (McDonnell et al., 1997; Grimm et al., 2008; Seto et al., 2012). Over the last two decades, research focused on ecological repercussions of rapid urbanization has increased significantly (Teurlincx et al., 2019). Most studies have focused on the responses of terrestrial biota and habitats to urbanization, and relatively less attention has been focused on freshwater habitats, especially lakes (Hill et al., 2017; Liang et al., 2020).

In an urban landscape, lakes are a sink for a wide range of contaminants (e.g. nutrients, trace elements, microplastics, antibiotics) that are released through air, water and detritus (Schueler and Simpson, 2001; Naselli-Flores, 2008). Urban watersheds generally produce higher pollutant loads per unit area from storm water runoff, in comparison with rural watersheds (Schueler and Simpson, 2001). In addition, urban watersheds produce a higher loading of pollutants from municipal wastewater discharges, especially in developing regions with insufficient water infrastructure (Walsh et al., 2005; Lee et al., 2019). Pollutant accumulation should favor disproportionate development of pollution-tolerant species (e.g. harmful cyanobacteria) in urban lakes, subsequently imposing detrimental effects on human health and ecosystem function (Taranu et al., 2015). Importantly, the relative location and morphometry of lakes on the urban-rural gradient will be reshaped with the outward expansion of cities, likely resulting in altered ecosystem functioning across this gradient. Many initial rural lakes gradually became suburban or urban lakes over time adjacent to the newly founded urban centres (Moore et al., 2003). Concomitantly, the bloom of pollution-tolerant species can be expected in lakes around urban regions with rapid urbanization.

Despite recent water quality monitoring schemes in urban regions, available data are spatially and temporally limited. Fortunately, sediment records from multiple lakes can improve our knowledge of long-term aquatic environmental change at a regional scale (Thapalia et al., 2015). Sedimentary records reveal that most urban lakes generally have experienced ecological shifts from a macrophyte-dominated, clear water state to an algal-dominated, turbid water state (Nyenje et al., 2010). Suburban lakes located in the ecotone between urban and rural areas play an important role in regional sustainable development, yet their response to multiple stressors is typically unknown (Zeng et al., 2018; Zhang et al., 2019). It is crucial to reveal the mechanisms behind spatial-temporal evolution of urban lakes in order to avert further environmental degradation and identify effective protection strategies in different lakes along the urban-rural gradient (Hall et al., 1999; Teurlincx et al., 2019).

In the Yangtze floodplain, there are hundreds of shallow freshwater lakes, which provide important ecosystem services such as wildlife habitats, freshwater and food supply, and water regulation (Dearing et al., 2012). Since the early 1980s, Chinese urbanization is unprecedented in scale, with an expansion of urban population from 0.17 billion in 1978 to 0.71 billion in 2013 (Song and Zhang, 2002). As more and more lakes are embedded in the urban landscape, the influxes of anthropogenic pollutants increased markedly (Xu et al., 2010). As a consequence, most lakes in this region have experienced a major alteration from a relatively good water quality to eutrophication during the 1980s (Le et al., 2010) and over 85% of lakes now are eutrophic or hypertrophic (Yang et al., 2010). However, while the status of these systems is known, less is known about the transition processes, and ecosystem trajectories in response to the multiple stressors along the urban-rural gradient, which are important to understand to enable appropriate remediation techniques to be employed.

This study analyzed ecological trajectories of three lakes based on subfossil chironomids (Insecta, Diptera) in sediment cores collected from urban, suburban and rural areas in Wuhan City (central China). We hypothesize that lake responses to multiple stressors would be temporally and spatially different. This study aims to 1) reconstruct ecological trajectories of lakes along the urban-rural gradient with the expansion of urban areas and 2) examine lake responses to past changes in external drivers along the urban to rural gradient.

2. Material and Methods

2.1. Study area

Wuhan is the capital of Hubei Province, located in central China and the middle reach of the Yangtze River (Fig. 1). The region belongs to the subtropical monsoonal climatic zone with a mean annual temperature of 17.4 °C and a mean annual precipitation of 1400 mm. The city is a famous megalopolis having a population of more than 10 million. High population pressure has stimulated city expansion in recent years with the expansion of built-up district area from 30 km^2 in 1950 (3 million people) to 220 km^2 in 2005 (8 million people) and sharply to 550 km^2 in 2014 (10 million people) (Bureau of Statistics of Hubei Province, 2009, 2014; Fig. 2a). The city embraces 166 lakes with surface area of over 0.05 km^2. All of them are shallow lakes with water depth less than 5 m and most are fluvial lakes linked to the evolution of the Yangtze River. Their total area is approximately 867 km^2, occupying 10.2% of the total land area of the city (8,494 km^2). However, 158 out of 166 lakes within the city were eutrophic and 11 were hypertrophic according to the survey in 2017 (Wuhan Environmental Protection

Bureau, 2017). Algal blooms occur frequently, especially in summer in several lakes (e.g. Donghu Lake and Nanhu Lake) near the city centre. The degradation of lake ecosystems in Wuhan has aroused widespread public concern.

Shahu Lake (central location 30°34′7″N, 114°19′40″E; mean water depth of 2.5 m) is the only lake exceeding 3 km^2 in surface area within the inner ring line of Wuhan. Lake surface area was about 6.7 km^2 before the 1910s, with free hydrological connection with the Yangtze River and Donghu Lake. However, its hydrological connection with the Yangtze River was regulated by several local dams after the 1910s. Due to land reclamation with rapid urbanization, the lake became hydrologically closed after the 1990s (Zhang, 2009). Moreover, the lake was divided into two small lakes (named Inner and Outer Shahu Lake) by the construction of Yue-Han Railway in the early 20th century. The water surface area correspondingly reduced to 3.5 km^2 in the late 1980s, and then sharply to current 3.1 km^2 (Compilation Committee of Lakes in Hubei Province, 2014; Fig. 2c, Fig. A.1). About 71% of the lost water surface was converted into built-up areas (Xie et al., 2017). Marginal plants are patched along lakeshore and mainly dominated by *Nelumbo nucifera* and *Alternanthera* with the disappearance of submerged plants (Song, 2008). A survey conducted in August 2016 showed that concentrations of total phosphorus (TP), total nitrogen (TN) and chlorophyll *a* (Chl-*a*) were 588, 4300 and 179 μg L^{-1}, respectively (Liang et al., 2020). But in July 2019, the observed TP was 292 μg L^{-1} (Table 1).

Yanxi Lake (30°32′~30°37′N, 114°27′~114°31′E; mean water depth of 1.9 m) is an agriculturally important area and fishery production base, as well as drinking water source for villagers living around the lake. With the expansion of urban area, Yanxi Lake has been transformed from a rural lake to a suburban lake. Many crop lands in its basin have been converted into built-up purpose (Fig. A.1). The lake was freely connected with the Yangtze River before the construction of local Wuhui Dam in 1955 and Beihu Dam in 1965. Lake surface area reduced from 12.7 km^2 in 1936 to 12.6 km^2 in 1982 (Zhang, 2009), and further to current 11.8 km^2 (Fig. 2c). There were more than 20 industrial factories surrounding the lake until the mid-1990s. A large influx of untreated industrial and domestic sewage into the lake has caused the deterioration of water quality (Wu, 1992). After 2000, most of these factories were generally closed and a variety of sewage treatment measures were implemented. Since 2003, the lake has been built into a holiday resort functions as leisure, agriculture tourism and popular science tourism. In August 2016, concentrations of TP and Chl-*a* were 42 and 70 μg L^{-1}, but increased to 160 and 111 μg L^{-1} respectively in July 2019.

Futou Lake is a relatively rural lake (29°57′~30°07′N, 114°09′~114°20′E; mean water depth of 1.65 m), around 57 km away from the city centre. Hydrological connectivity between the lake and the Yangtze River was regulated by the implements of local Jinshui Dam in 1935 and Xinhe Dam in 1973. Presently, this lake is in a macrophyte-dominated state, with high abundances of *Pistia stratiotes*, *Vallisneria natans*, *Potamogeten crispus* and *Ceratophyllum demersum*. Concentration of TP was 43 μg L^{-1} in August 2016 and 70 μg L^{-1} in July 2019. The development trajectory of this lake has been detailed by Zeng et al. (2018), and summary plots of Futou Lake are used to compare with the other two lakes investigated here.

2.2. Core collection

Sediment cores were collected using a modified Kajak gravity corer at the approximately centre of Futou Lake (30°03′16.96″N, 114°12′24.67″E; with length of ~65 cm) in April 2014, and Shahu Lake (30°34′12.18″N, 114°20′11.30″E; ~61 cm) and Yanxi Lake (30°34′18.08″N, 114°28′42.49″E; ~61 cm) in October 2011. The cores were sliced at intervals of 1 cm in field. Subsamples were stored in plastic bags and kept in the refrigerator at 4°C before analysis.

2.3. Laboratory analyses

2.3.1. Chronology

Sediment cores were dated mainly by ^{210}Pb, and corrected by the chronomarker of spheroidal carbonaceous particles (SCP). Radioactive isotopes ^{210}Pb, ^{226}Ra and ^{137}Cs were counted at 2-cm intervals on a gamma spectrometer (Ortec HPGe GWL). Chen et al. (2019) displayed the detailed measurements and chronological stratigraphy for each lake.

2.3.2. Particle size

Particle size spectra of samples were measured at 1-cm intervals using a Malvern automated laser optical particle-sizer analyser (Mastersizer-2000) after the removal of carbonate by 10% HCl and organic matter by 30% H_2O_2.

2.3.3. Elements analyses

Element contents (including Cu, Zn and TP) in sediments at 2 cm intervals were determined by the Inductively Coupled Plasma-Atomic Emission Spectrometry (ICP-AES) after digestion with $HF\text{-}HCl\text{-}HNO_3\text{-}HClO_4$.

2.3.4. Chironomid analysis

Sediment samples for chironomid analysis were conducted according to standard techniques proposed by Brooks et al. (2007) at 2 cm intervals. Wet sediment samples were deflocculated in 10% KOH in a water bath at 75 °C for 15 min, and then sieved through 212 and 90 μm meshes. The residue was transferred to a grooved perpex sorting tray and examined manually under a stereo-zoom microscope at x25 magnification with fine forceps. Head capsules were permanently mounted on slides using

Hydromatrix®, ventral side uppermost, and subsequently identified at x100-400 magnification using the taxonomy of Brooks et al. (2007), with reference to Rieradevall & Brooks (2001). A minimum of 50 identifiable whole head capsules from each sample is expected to be representative of the extant fauna (Quinlan and Smol, 2001).

2.4. Climatic data collection

Annual temperature and precipitation data were collected in order to reveal the effects of climate change on lake development. Annual temperature data since 1905 were obtained from Hankou Meteorological Station. Monitored precipitation data were discontinuous as rainfall data from 1944 to 1950 was not measured. Simulated rainfall data of the studied region (29.5-30.5°N,113.5-115.5°E) were then obtained from Koninklijk Nederlands Meteorologisch Instituut (KNMI) (website: http://climexp.knmi.nl/selectfield_obs.cgi). Significant positive correlation exists between rainfall data from Hankou Meteorological Station and KNMI ($r = 0.69$, $p < 0.05$). Annual rainfall data from KNMI, combined with temperature data were then used in subsequent ordination analysis (Fig. 2d).

2.5. Numerical analyses

The enrichment of Cu, Zn and TP can indicate increasing anthropogenic disturbances (Boyle et al., 1999). In order to evaluate the accumulation of elements along time, geoaccumulation index (I_{geo}) for Cu, Zn and TP was calculated as follows:

$$I_{\mathrm{geo}} = \log_2(C_n/(1.5*B_n))$$

where, C_n is the measured concentration of element n in sediment; 1.5 is the background matrix correction factor due to lithogenic effects; B_n is the geochemical background value of element n

(Gonzáles-Macías et al., 2006; Ghrefat and Yusuf, 2006; Kim et al., 2018). Considering the different benchmark of elements in different lakes, here we calculated B_n as average concentration before 1900 of element n.

Variance partitioning analysis (VPA) was conducted to distinguish the effects of diverse stressors on fossil chironomid communities. Three explanatory categories were identified as climate, hydrological condition and anthropogenic pollution. The climate-group includes two variables of annual temperature and rainfall. The establishment of local dams was considered as a 1/0 dummy variable for indicating hydrological regulation. Particle size spectra in sediments are closely linked to hydrological dynamics (Zeng et al., 2018). Damming event and particle fractions together were used to reflect hydrological changes in three lakes. The geoaccumulation index of Cu, Zn and TP composed the group of anthropogenic pollution. All explanatory variables were standardized with $\log_{10}(x+1)$-transformation to eliminate the effects of different units among them. Rare chironomid taxa occurred in only one sample or with abundance less than 2% were deleted and would not participate in ordination analyses. Detrended correspondence analysis (DCA) was conducted to extract major changes in chironomid communities of three lakes. It also showed that the gradient length for Shahu, Yanxi and Futou Lake was 2.6, 2.0 and 1.8 standard deviation, respectively, suggesting the linear method was suitable for the subsequent ordination analyses. Redundancy analysis (RDA) was also employed to identify significant explanatory variables and to estimate the fraction of faunal variance explained by three categories in variance partitioning. Monte Carlo permutation tests (499 unrestricted permutations) were conducted to test the significance of variables, and forward selection was used to determine the minimum subset of significant variables. VPA was carried out to evaluate the relative importance of each explanatory group and their explanatory power in each lake. Because of limitation of climate data, the time window analyzed in VPA was 1907-2011 AD for Shahu Lake, 1904-2011 AD for Yanxi Lake and 1914-2014 AD for Futou Lake. All above ordination analyses were based on taxon percentages with square-root transformation, and conducted in CANOCO version 5.0 (Šmilauer and Lepš, 2014).

The possible abrupt shifts in ecosystem structure and function for three lakes were also detected using the Sequential *t*-test Analysis of Regime-shifts algorithm (STARS) proposed by Rodionov (2004). The module shift detection software version 3.2 was initially added in Excel 2010. In parameter setting, significance level was 0.05 and cut-off length was 5. Regime shift index (RSI) was calculated and employed to identify the most potential tipping point. Scores of DCA first axis on chironomid data, which stands for the most important information from chironomids, were involved in the detection. Gaussian kernel density estimation and autoregressive integrated moving average (ARIMA) model were also conducted to verify whether two different regimes existed before and after the tipping point. The former was performed with the R statistical software (R Core Team, 2018) using the ‘sm’ package (Bowman and Azzalini, 2018), and the latter was conducted using Minitab 17.

3. Results

3.1. Chronology

$^{210}Pb_{ex}$ activities generally declined exponentially with mass depth (Chen et al., 2019). The chronologies of the three sediment cores were calculated based on the constant rate of supply model (Appleby and Oldfield, 1978). The start of the rapid increase in SCP concentrations corresponds to the major expansion in coal consumption from 1970. The final chronologies of sediment cores were established based on the SCP chronomarker-validated ^{210}Pb chronologies (Fig. 3). Generally, sedimentation rates were less than 0.2 g cm^{-2} yr^{-1} before the 1930s, and then increased to a peak. Thereafter sedimentation rates decreased and remained low after the 1980s. Detailed results are presented in Chen et al. (2019).

3.2. Chironomid stratigraphy

More than 40 different species morphotypes of chironomids were identified in three cores (Fig. A.2). Cluster analysis identified significant changes in chironomid composition occurred around 1963, 1975 and 1980 AD for Shahu, Yanxi and Futou Lake, respectively (Fig. 4).

In Shahu Lake, there was a major compositional shift from plant-dwelling taxa to nutrient-tolerant taxa during the past 160 years (Fig. 4a). Before 1963 AD, chironomid assemblages within the lake were dominated by *C. sylvestris*-type (average ca. 18.1%), *D. nervosus*-type (mean of 13.6%) and *Paratanytarsus* (mean of 12.3%). Subsequently, major taxa were replaced by *Tanypus* (average ca. 60.6%), *Propsilocerus akamusi*-type (about 7.9%) and *Procladius* (about 13.3%). The prominence of *Tanypus* after 1990 AD (16 cm-depth), was substantial as the percentage reached up to 90%.

Several different taxa co-existed before 1975 AD in Yanxi Lake (Fig. 4b). Major taxa included *Paratanytarsus* (average percentage of 12.4%), *Microchironomus tener*-type (11.5%), *C. sylvestris*-type (7.5%), *Stempellinella-Zavrelia* (6.6%), *Polypedilum nubifer*-type (4.9%) and *D. nervosus*-type (4.7%). Total abundance of macrophyte-related taxa (*Ablabesmyia*, *Corynonueura edwardsi*-type, *C. sylvestris*-type, *D. nervosus*-type, *Glyptotendipes severini*-type, *Parachironomus vasus*-type, *Paratanytarsus*, *Polypedilum nubeculosum*-type and *P. sordens*-type) in this period was nearly 35.0% in average. Whereafter, chironomid assemblages were dominated by *Tanypus* (ca. 29.9%) and *P. akamusi*-type (10.4%). Concurrently, some other nutrient-tolerant species such as *Chironomus* *plumosus*-type (mean of 3.7%) and *Microchironomus tabarui*-type (4.6%) also increased. After 1999 AD, the abundance of *Tanypus* increased to the maximum (59.7%) at surface samples.

In Futou Lake, chironomid assemblages were dominated by *M. tener*-type before 1980 AD, and then were macrophyte-related *Paratanytarsus* and *C. sylvestris*-type after its damming. Meanwhile, nutrient-tolerant *P. akamusi*-type increased after 1994 AD (Fig. 4c).

3.3. Particle size and elemental concentration

Sediments in three lakes were mainly composed of clay and silt (Fig. 5). Generally, clay decreased in the upper strata of three sediment cores, in contrast to increasing proportions of sand. In spite of low proportions, there were several peaks of sand in three sediment cores.

Distinctive changes in sedimentary Cu, Zn and P were observed in Shahu Lake core. Cu, Zn and P were relatively stable with no notable changes before 1963 AD (Fig. 5a). Cu and Zn sharply increased from 1963 AD to the late 1990s, followed by slight decreases. Sedimentary P continued to increase and trebled between 1963 and 2011 AD.

Variations of Cu, Zn and P in Yanxi Lake were more complex than in Shahu Lake (Fig. 5b). Concentrations of Cu and Zn increased markedly after the 1920s, followed by relatively minor variation after the 1940s. After the 1980s, Cu gradually decreased, while Zn showed an inverse tendency. Sedimentary P remained low values before the1960s, and thereafter continued to rise till the uppermost.

Trends of Cu, Zn and P in Futou Lake were similar as they rose before 1900s and then declined until 1980 (Fig. 5c). Zn and P enriched sharply after 1980 AD, with their concentrations increased by more than 20%. Concurrently, Cu increased slightly from 41 to ~45 mg/kg.

3.4. Variation partitioning analysis

RDA and VPA revealed that chironomid communities in three lakes were significantly influenced by different historical changes in climate, hydrological conditions or anthropogenic pollutants since the early 20th century (Table 2).

In Shahu Lake, three variables (annual temperature, median grain size and I_{geo} (P)) assigned to three explanatory categories comprised the minimum subset of significant variables capturing 60.6% of the total variance in chironomid assemblages. Anthropogenic pollution independently explained 34.7% of total variance, and its combined effect with hydrological conditions captured 22.4% of total variance further (Fig. 6). Climate change was a significant variable but its sole effect was minor. Its interaction with anthropogenic pollution and hydrological conditions explained 6.5% and 2.5% of total variance, respectively. Combined effects of three significant variables were negative and explained -9.6% of species variances.

In Yanxi Lake, climate and hydrological variables failed to explain a significant part of total variance in chironomid communities. The unique effect of anthropogenic pollution captured 44.3% of total variance.

In Futou Lake, the sole effect of hydrological alterations (i.e. damming event and silt fraction) explained more variance (33.7%) in chironomid assemblages than that (13.3%) of anthropogenic pollution. Their interactive effect on chironomids was negative with the value of -10.8%. The sole effect of climate change was not significant.

3.5. Developmental trajectories and regime shifts

The biplot of DCA1 against DCA2 revealed the developmental trajectories and response trends of three lakes to multiple stressors (i.e. different human disturbances) (Fig. 7). Shahu and Yanxi Lake shifted from different ecological status towards an identical homogenized eutrophic state. Futou Lake, however, developed mainly along DCA2 (representing hydrological conditions) and is still in a relatively desired state with established macrophyte communities. Its development took a different trajectory compared with urban Shahu Lake and suburban Yanxi Lake due to the different multi-dimensional stressors impacting it.

STARS captured the possible tipping point in each lake: 1963 AD for Shahu Lake, 1975 AD for Yanxi Lake and 1980 AD for Futou Lake (Table A.1). Gaussian kernel density estimation showed a bimodal distribution, with two divergent peaks for each lake before and after the detected critical point (Fig. 8a). ARIMA displayed obvious divergence between the predicted and observed (sedimentary) biological changes, suggestive of two alternative ecological states for each lake (Fig. 8b). Considering the replacement of dominated taxa in chironomid assemblages, ARIMA confirmed that both Shahu and Yanxi Lake had turned into a completely different and worse ecological state after the regime shift than before. Although experienced regime shift, observed DCA1 scores after 1980 AD in Futou Lake was more stable than the predicted values. In any case, both of these sets of analyses provide evidence of bistability before and after the observed tipping points.

4. Discussion

4.1. History of water quality change

Significant changes in water quality were reflected by sedimentary proxies including geochemical and biotic indicators in three lakes during the past century. Generally, the dominance of macrophyte-related chironomids was replaced by eutrophic species in urban and suburban lakes, suggesting their trajectories toward eutrophication.

Before the 1960s in Shahu Lake, chironomid communities mainly consisted of taxa preferring shallow water with a relatively high density of macrophytes, such as *C. sylvestris*-type, *D. nervosus*-type and *Paratanytarsus* (Brodersen et al., 2001; Davidson et al., 2010). Most of these taxa are often found in productive and mesotrophic to eutrophic waters. They are frequently common in shallow lakes in the Yangtze floodplain, and considered to be indicators of flourishing macrophytes (Langdon et al., 2010; Zhang et al., 2012). Their coexistence and predominance suggested a stable and good ecological state of Shahu Lake during this period. The lake regime collapsed within just a few years (20-30 years) and switched to an alternative state after 1963 AD, since the dominance of clear-water/ plant-preferring taxa (e.g. *Paratanytarsus* genus) were replaced by the rising abundances of pollution- and/or nutrient-tolerant taxa such as *P. akamusi*-type and *Tanypus*. *P. akamusi*-type was firstly described by Sasa (1978) and is often encountered in eutrophic to hypertrophic lakes in China and Japan, with a TP optimum of 118 μg/L in the Yangtze floodplain lakes (Zhang et al., 2012). *Tanypus* can also be found in mesotrophic and hypereutrophic lakes, has a TP optimum of 169 μg/L in the study region (Zhang et al., 2012).

Yanxi Lake was in a relatively desired state before the 1970s, suggested by the dominance of mesotrophic *M. tener*-type (Brooks et al., 2007) and clear-water taxa *Paratanytarsus* (Langdon et al., 2010) and some other plant-inhabiting taxa. After the 1970s, the enrichment of Zn and sedimentary P indicated an increasing influx of external pollutants into Yanxi Lake. The replacement of phytophilous chironomid taxa by eutrophic species indicated that the lake was switching from a mesotrophic state into a eutrophic lake, although the trajectory of change was slower than in Shahu Lake. Until 2010s, Yanxi Lake was still in the process of eutrophication and water deterioration continued as indicated by our results as well as available monitoring data (Wuhan Environmental Protection Bureau, 2012-2017). It might suggest that more effective strategies could be made for suburban lakes, or else the resilience and functional services of these lakes will be lost.

Futou Lake is currently one of the few lakes with flourishing aquatic vegetation in the Yangtze floodplain. This lake has maintained relatively good water quality since the mid-19th century indicated by high abundance of plant-associated chironomids (e.g. *C. sylvestris*-type and *Paratanytarsus*) throughout the sediment core, especially since the 1980s. Vegetation can sequester nutrients in water and plays a critical role in the maintenance of aquatic ecosystem stability (Zhang et al., 2016). However, the enrichment of sedimentary P and heavy metals since the 1980s was suggestive of enhanced human activities in the catchment. As a consequence, *P. akamusi*-type, a eutrophic indicator, started to increase after the mid-1990s, albeit at relatively low abundance. Given the trajectories of the other lakes that contain *P. akamusi*-type, this may be an early warning indicator that the lake may be losing resilience ahead of a switch to an alternative state.

4.2. Anthropogenic pollution

Variance partitioning revealed that anthropogenic pollution was the major driver for changes in chironomid communities in both Shahu and Yanxi Lake. Regional palaeoecology studies confirmed the importance of anthropogenic pollution in regulating water quality in the Yangtze floodplain (Chen et al., 2016; Zhang et al., 2019). Sedimentary phosphorus was a significant explanatory variable for Shahu and Yanxi Lake. The enrichment of sedimentary P has accelerated in the urban and suburban lakes since the 1960s, probably linked to recent demographic and economic increases in Wuhan City (Fig. 2).

The dominance of eutrophic species and high sedimentary P content in Shahu Lake indicated that the urban lake suffered from serious eutrophication, because nutrient inputs from sewage discharge were greatest in city centre. The magnitude of increases in sedimentary P and eutrophic taxa was relatively lower in suburban (Yanxi Lake) and rural (Futou Lake) lakes at the same point in time.

In suburban and rural lakes, heavy metal enrichment (i.e. Cu and Zn) explained a significant part of variance in the species data. The enrichment of Cu and Zn is mainly derived from industrial sources (Boyle et al., 1999; Liu et al., 2012). Anthropogenic pollution generally experienced three distinct stages in the study area, i.e. an increase in the early 1900s, a sequent recession and then a rapid rebound after the 1950s. The three stages broadly corresponded to the establishment of modern industry in the early 1900s, Sino-Japanese and Chinese civil wars from the 1930s to 1940s, and the boosting of heavy industry after the 1950s in Wuhan. Heavy metal enrichment would typically reduce chironomid diversity, and promote the proliferation of pollution-tolerant species (Cao et al. 2016). Taken together, variance in chironomid communities explained by anthropogenic pollution decreased along the urban-to-rural gradient, indicating that increased pollutant inputs imposed overwhelming effects on urban and suburban lakes, but relatively minor effects upon the rural lake.

4.3. Hydrological and climate change

Besides anthropogenic pollution, hydrological indicators (i.e. damming and sedimentary particle size) accounted for a significant part of variance in the species data, especially in the rural lake (Futou Lake). In a hydrologically-open lake, sedimentary particle size can be a proxy for hydrodynamic intensity, and an increase in sand percentage may indicate strong inflows that are able to transport coarse particles into the lake (Chen et al. 2011). However, prolonged water retention time after dam construction would promote the deposition of fine particles, resulting in a relative increase in clay (Zeng et al., 2018). In Shahu and Futou Lakes, it is unexpected that the percentage of sand displayed an increasing trend after the 1960s, when both of lakes had suffered from hydrological regulation due to dam construction. This phenomenon is probably linked to a sharp shrinkage of lake area due to land reclamation after the 1950s (Xie et al., 2017). Both Shahu and Futou Lakes have lost more than 25% of surface area during the last century (Zhang et al. 2009; Xie et al., 2017). As a consequence, coarse particles would be readily transported to the lake centre. In the urban lake (Shahu Lake), prolonged hydraulic residence time and lake shrinkage would promote the enrichment of pollutants. Therefore, the combined effect of hydrological alteration and anthropogenic pollution captured a high proportion of total variance in chironomid communities in this lake. In contrast, the combined effect of hydrology and anthropogenic pollution was negative for the rural Futou Lake, as a reduction in water level amplitude after hydrological regulation promoted the development of macrophytes and associated chironomid taxa (Zeng et al., 2018; Zhang et al., 2019), which can have a stabilizing effect on lake ecosystems (Jeppesen et al., 1998).

In the urban Shahu Lake, changes in chironomid communities were significantly correlated with increasing temperature. It is noteworthy that the combined effect of temperature and sedimentary phosphorus explained a higher proportion of variance than the sole effect of temperature (Fig. 7). The results indicated that rising temperature could indirectly promote the development of nutrient-tolerant species (Chen et al. 2013). In shallow lakes, climate warming usually accelerates nutrient release from sediments and renew nutrient supplies into the water column (Jensen and Andersen 1992). However, in the suburban (Yanxi) and rural (Futou) lakes, the effects of climate variables failed to be significant, neither their sole effects nor combined effects with other drivers. The effect of climate warming on chironomids would thus likely be amplified in the eutrophic lake (Shahu Lake) with high nutrient loading.

4.4. Regime shifts in lakes along an urbanization gradient

Regime shifts are increasingly happening in terrestrial and aquatic environments in the context of continuous human influences (Folke, 2004; Reid et al., 2016). In most cases, ecosystems' regime tends to shift from a desired state with high resilience to an undesired state with low ability of self-organization and feedback (Wang et al., 2012, 2019; Zhang et al., 2018), and this appears to have occurred rapidly in Shahu Lake. Hydrologic regulation can also induce critical transition through altering vegetation coverage in lake ecosystems (Schooler et al., 2011; Bertani et al., 2016). For example, water level alteration stemming from dam establishment caused the disappearance of submerge vegetation (the first regime shift) and then the increase of nutrients triggered the second state alteration (algal blooms thereafter) in Chaohu Lake, which is located in the same region with our study (Kong et al., 2017). However, rural Futou Lake in our study seems to respond markedly different from urban Shahu Lake and Chaohu Lake. Massive macrophytes beds developed as a result of stabilized hydrological conditions after the detected tipping point in Futou Lake around 1980. The hydrological change and stabilizing effect of macrophytes promoted ecological resilience in Futou Lake. The ARIMA results (Fig. 8b) showed that the lake trajectory, based on the previous ecosystem data, was to further change and decline towards an alternative (eutrophic) state, similar to the Shahu and Yanxi lakes. But this never happened, due to the altered hydrology and macrophyte growth across the lake. Nevertheless, the increasing abundance of pollution-tolerant taxa (*P. akamusi*-type) indicated the continued enrichment of pollutants and nutrients in Futou Lake, and based on the trajectories of the other lakes in this study, would suggest that despite hydrological and macrophyte stability, nutrients are still increasing and the lake may yet be losing resilience ahead of a transition to an alternative state. As such, the chironomid data may provide an early warning to this, and other rural lakes, on the edge of city expansion and subject to enhanced nutrient pollution. While Shahu lake has transited to an alternative state, and Futou lake currently appears to have partially stabilized (for now at least), Yanxi lake may still be mid-transition regarding its ecological state. Given the location of the transition region, Yanxi Lake was suffering from multiple stressors with varying types and magnitude resulting from the expansion of Wuhan city and increasingly altered land-use patterns and population. The lake is still in a self-adjustment process to the new regime system as DCA1 scores of Yanxi Lake are still declining, which may indicate the altering biological compositions as ARIMA analyses also predicted.

4.5. Implication for sustainable management

Palaeoecological records provide useful implications for sustainable management of urban freshwater ecosystems. Regional comparison demonstrated that anthropogenic impacts were overwhelming in urban and suburban lakes, but relatively weak in the rural lake. Variance partitioning suggested that the precise management strategy should vary with lake position along the urban-to-rural gradient. The urban lake has experienced transitions from a phase of exponential pollution to a relatively stable polluted state. In contrast, the suburban lake is suffering from exponential pollution, and hence it is urgent to implement effective control measurements (e.g. installation of new sewage treatment plants) in the rapidly urbanized area. For the rural lake, both moderate hydrological regulation (e.g. water level stabilization) and reduction of external pollutant input are important for the development of macrophytes, which can increase resilience of lake ecosystems buffering against external disturbances (e.g. anthropogenic nutrient input) (cf. Scheffer et al. 2003). Additionally, although climate warming was also important, it cannot be regulated. Under a scenario of increasing temperature in future, nutrient release from lake sediments would increase the risk of environment deterioration in urban lakes.

5. Conclusions

Chironomid stratigraphies, combined with geochemical records and climatic data, demonstrated that the response of shallow lakes to external stressors was temporally and spatially different along the urban-rural gradient in a metropolitan area (central China) during the past century. All three lakes had experienced critical transitions which occurred in the sequence of their distance from city centre. Anthropogenic disturbance triggered regime shifts within lakes and drove them toward different states. Given the input of massive pollutants, urban Shahu Lake and suburban Yanxi Lake shifted from clear water to turbid state in 1963 and 1975, respectively. Climate warming acted as an amplifier of ecological change in urban lake with high pollution pressures. The dam impoundment in Futou Lake stabilized hydrological conditions, which facilitated the development of macrophytes after 1980. However, due to prolonged hydraulic retention time, nutrient enrichment in Futou Lake might be accelerated. Contrary to the new stable state in Shahu and Futou Lake, suburban Yanxi Lake, located in the transition region along the rural-urban gradient, now is still in self-adjustment resulting from the varying stressors in types and magnitude. With the city expansion, lakes along the urban-rural gradient exist in different ecological states due to the impact of varying drivers. This study also implies that active and targeted strategies on not only urban lakes but also suburban-rural lakes will be strongly required to avoid detrimental shifts and sustain a desired state in aquatic ecosystems.

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Table 1 Summarized characteristics of three lakes.

Lake	Water area (km^2)	Mean depth (m)	Total phosphorous (μg L^{-1})		Land use type	Lake type
			August 2016	July 2019		
Shahu	3.1	2.5	588	292	Urban land	Urban
Yanxi	14.2	1.9	42	160	Cropland, aquaculture, urban land	Suburban
Futou	126	2.9	43	70	Cropland, aquaculture	Rural

Table 2 Significant explanatory variables used in variation partitioning analyses, and their total explained variances of chironomid data for three lakes. Variables are listed according to the variable categories of climate (C), hydrological changes (H) and pollutant input (P). *I*geo is the geoaccumulation index of elements in sediments.

Lake	Time period	Significant variables			
		C	H	P	Total explained (%)
Shahu	1907-2011	Annual Temp.	median grain size	*I*geo(P)	60.6
Yanxi	1904-2011	--	--	*I*geo(P), *I*geo(Zn), Igeo(Cu)	44.3
Futou	1914-2014	--	Dam, silt	*I*geo(Cu)	36.3

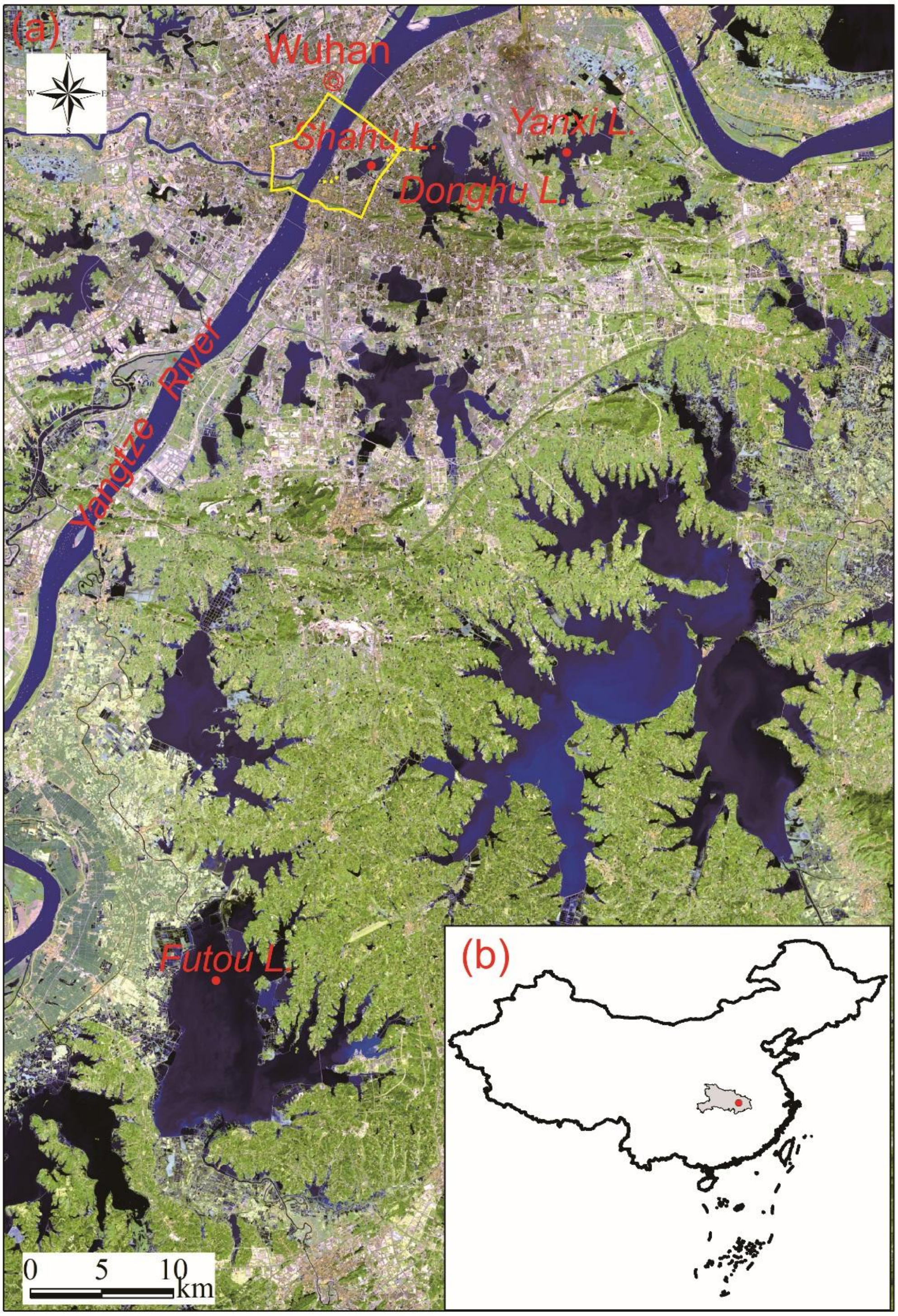


Figure 1 Maps showing the location of lakes in Wuhan (a) and the city in China (b). The *solid yellow* line is the inner ring line of the city, and the *dotted yellow* lines represent the hydrological connections between Shahu Lake and the Yangtze River before 1910s, and between Shahu Lake and Donghu Lake before 1990s.

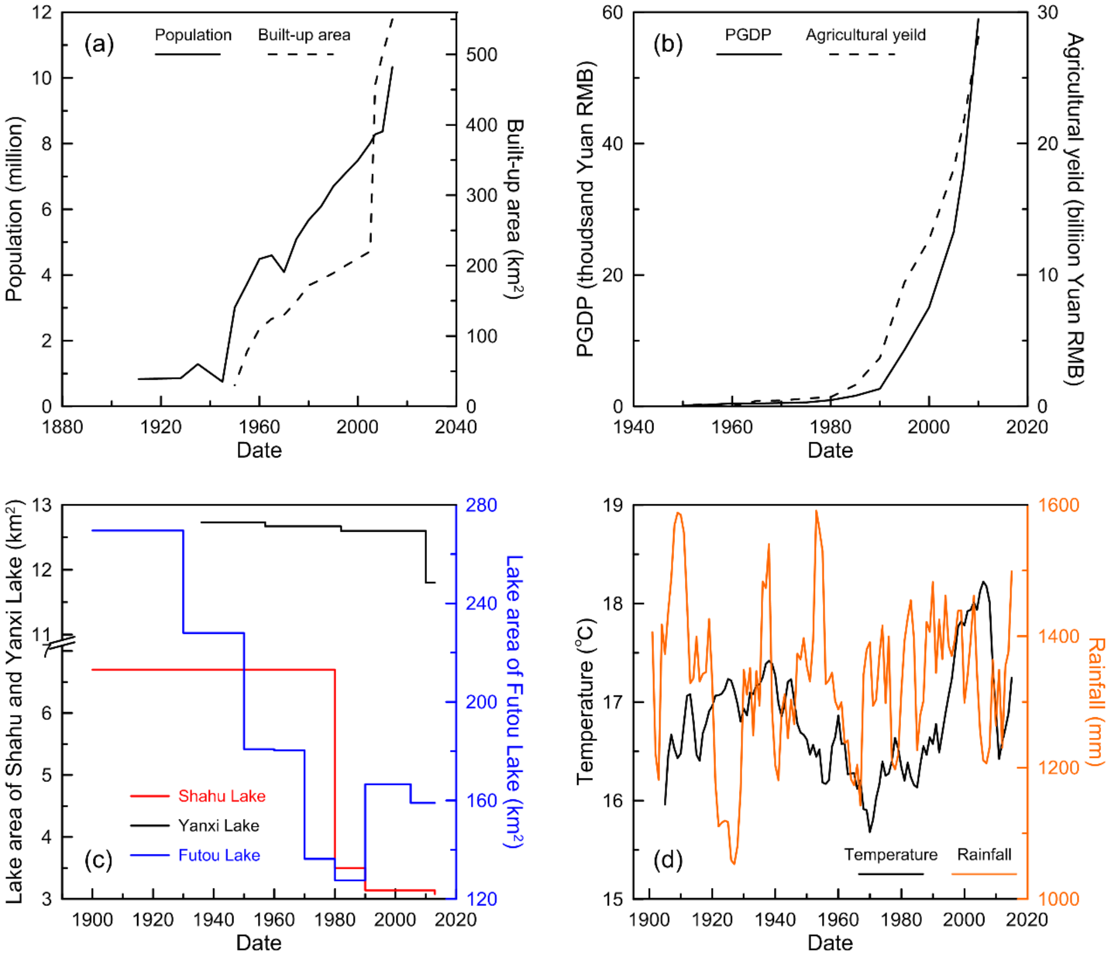


Figure 2 Historical (a, b, c) and climatic (d) records in Wuhan since early 20th century. Data of population, Per Capita GDP, build-up area and agricultural yield of Wuhan were cited from Bureau of Statistics of Hubei Province (2009, 2010-2014). Lake area data were cited from Zhang (2009).

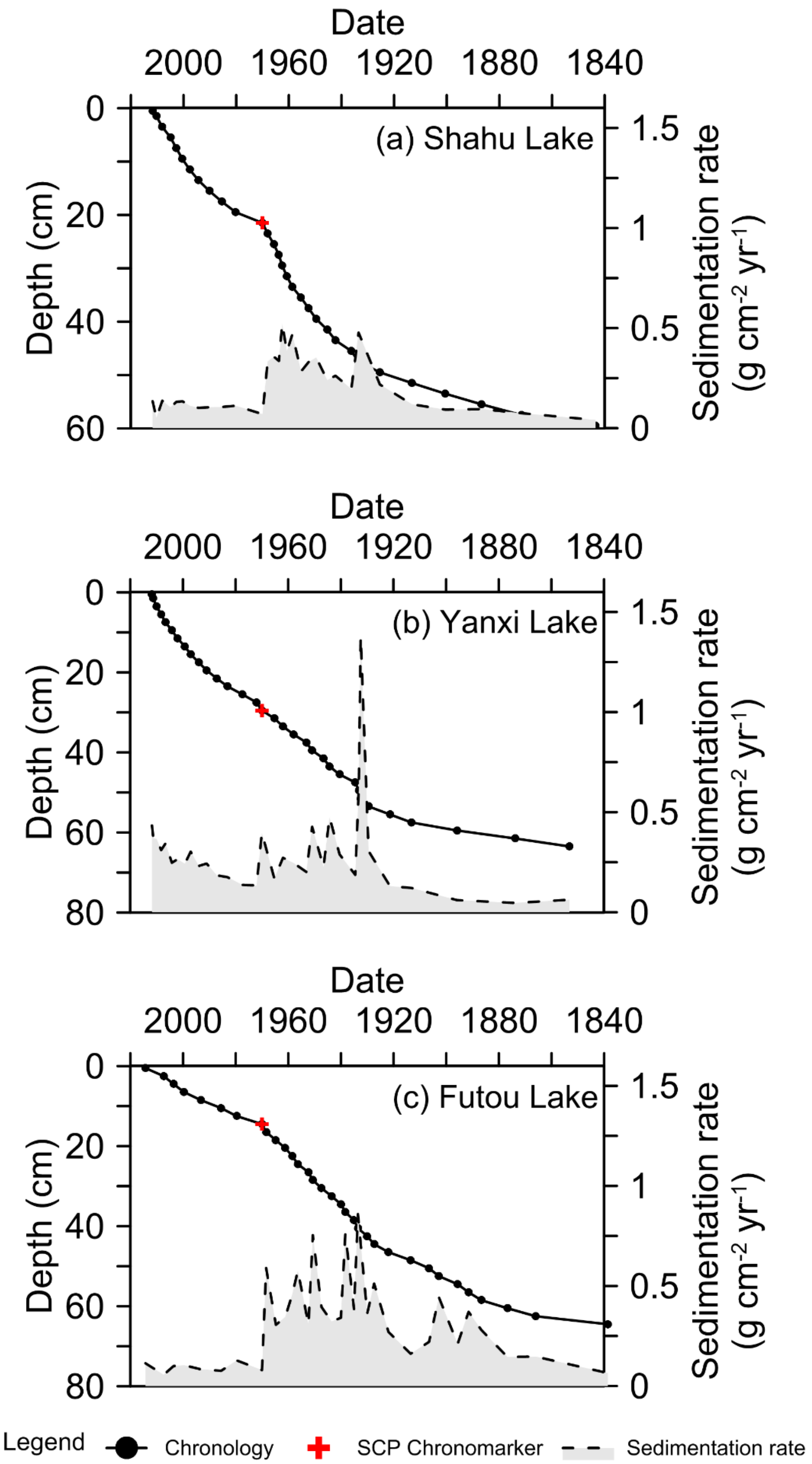
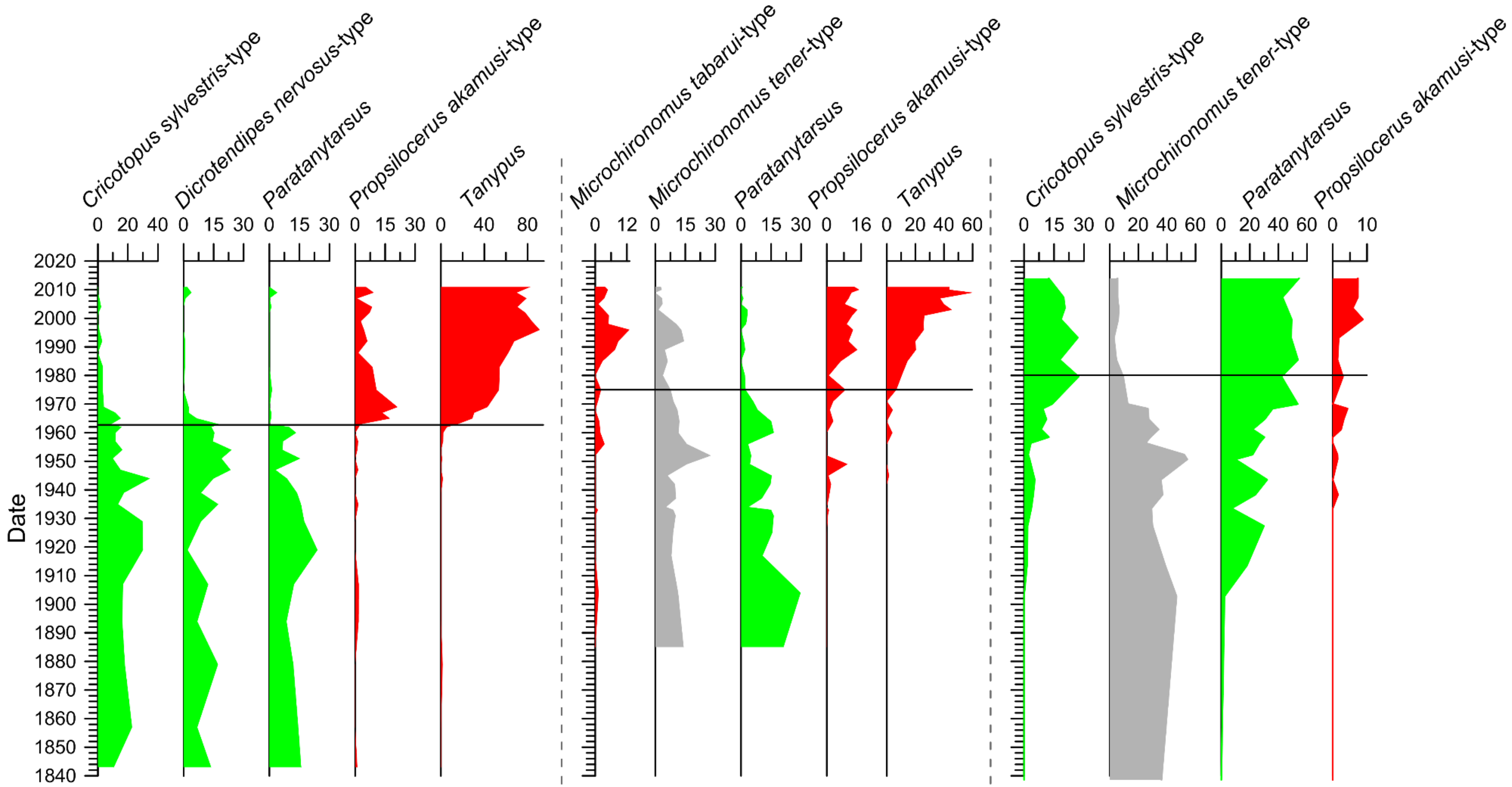


Figure 3 Age-depth models for the sedimentary cores collected from Shahu (a), Yanxi (b) and Futou (c) Lake, with sedimentation rates shown.



(a) Shahu Lake (b) Yanxi Lake (c) Futou Lake

Figure 4 Dominant chironomid species in sediment cores collected from Shahu (a) and Yanxi (b) and Futou (c) Lake. Green color represents macrophyte-related or clear water taxa, whereas the red colored taxa favour more eutrophic conditions.

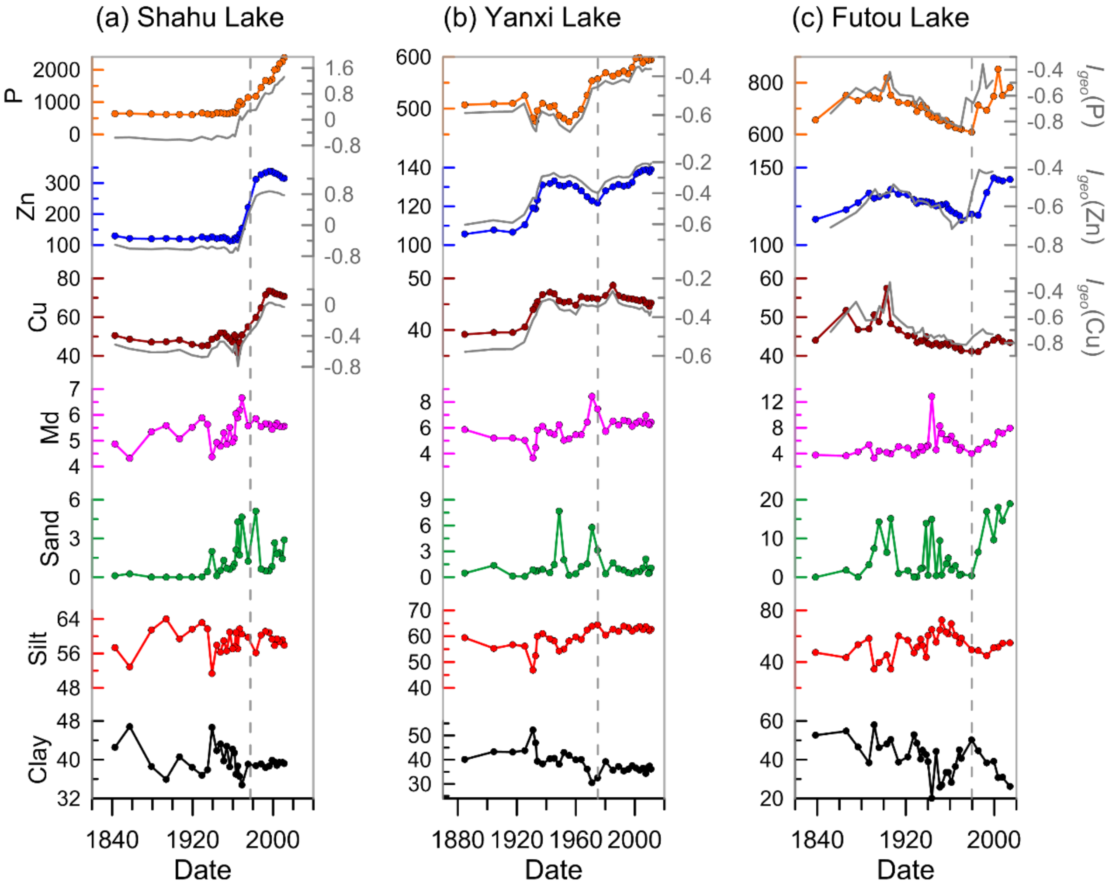


Figure 5 Particle size spectra, elemental contents and geoaccumulation index (*solid grey* line) in the sediment cores collected from Shahu (a) and Yanxi (b) and Futou (c) Lake. Units of vertical axis are % for clay, silt and sand, μm for median grain size (Md), and mg/kg for Cu, Zn and P. Dotted lines represent abrupt shift point in chironomid assemblages for each lake.

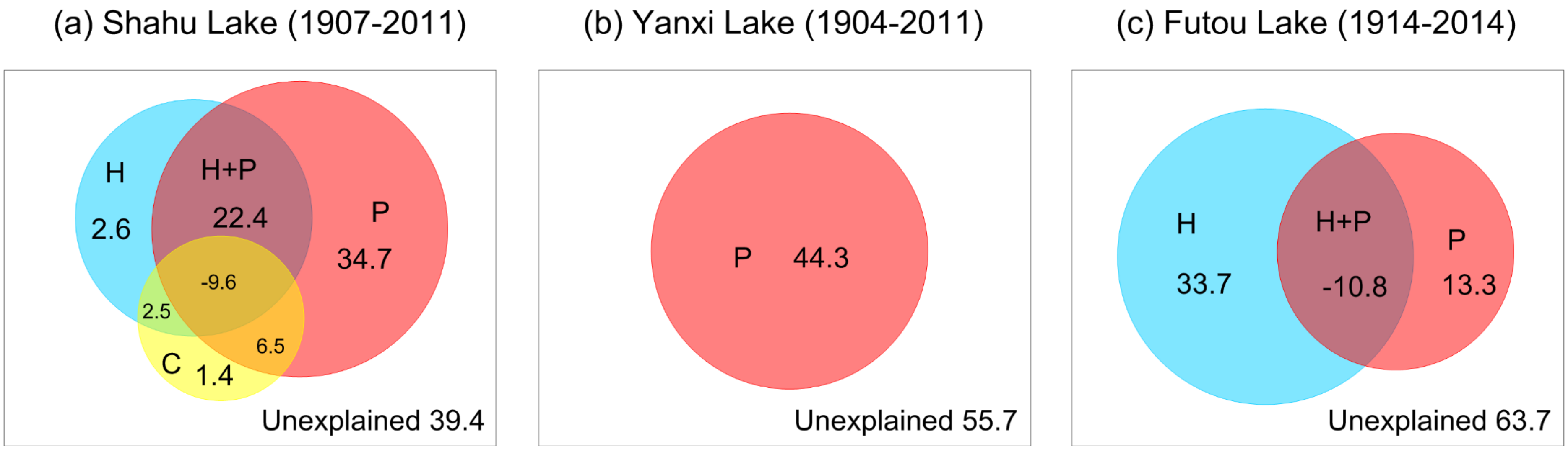


Figure 6 Effects of anthropogenic pollution (P), hydrological (H) and climate (C) change on chironomid communities for Shahu (a), Yanxi (b) and Futou (c) Lake using variance partitioning analysis.

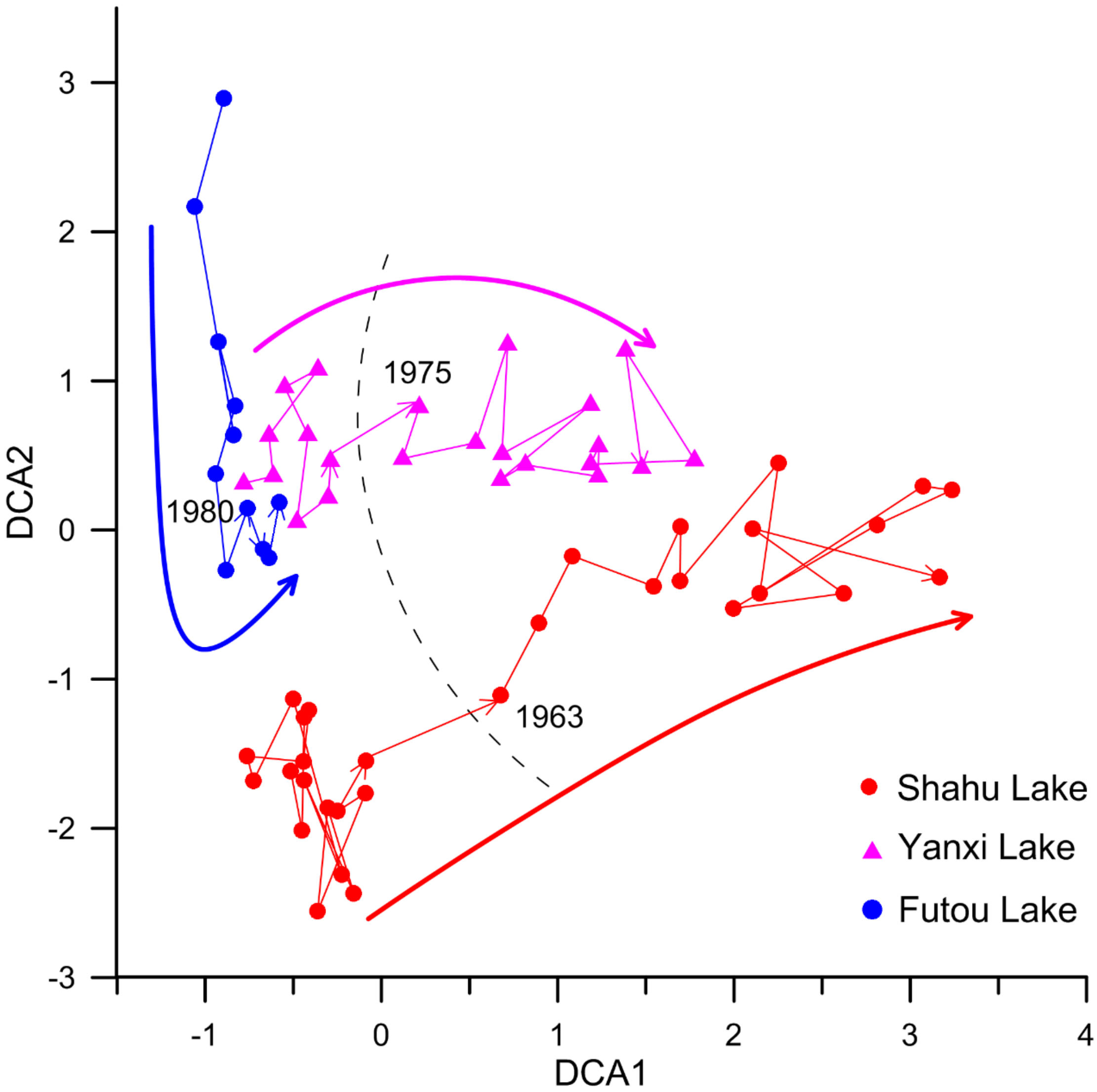


Figure 7 Diagram of DCA1 *vs* DCA2 for integrated chironomids in all three lakes.

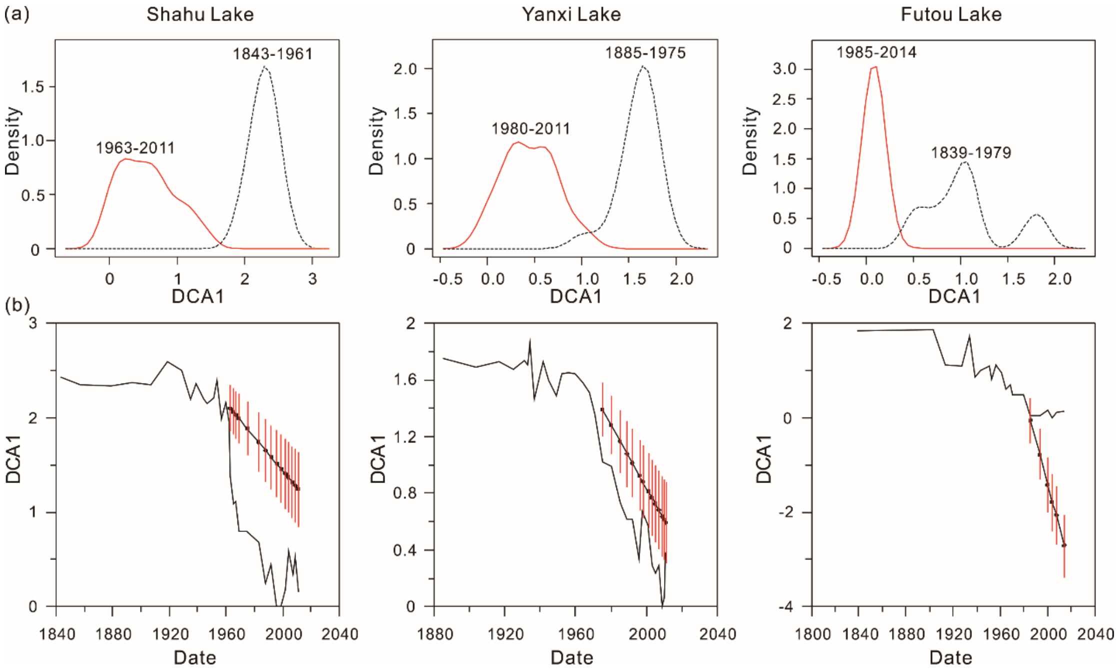


Figure 8 Evidence of bistability between before and after the tipping points in three lakes. The results are based on (a) Gaussian kernel density estimation and (b) autoregressive integrated moving average (ARIMA) model.

***conflict of Interest Statement**

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

*Credit Author Statement

Author contributions

Yanmin Cao conceptualized, wrote and revised the original draft.

Peter Langdon and Xu Chen were mainly responsible for revision and improvement of the manuscript.

Chunling Huang completed sample treatments and collected historical data in this manuscript.

Yi Yan, Jia Yang and Linghan Zeng helped the improvement of figures and revision of the manuscript.