



Impoundment intensity determines temporal patterns of hydrological fluctuation, carbon cycling and algal succession in a dammed lake of Southwest China

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ABSTRACT

Hydrological control of lakes has been increasingly practiced in many parts of the world, however, the long-term ecological impact of hydrological regulation and their dependence on lake impoundment intensity has been rarely examined. We combined a spatial survey of surface sediments with sediment core analyses to quantify the limnological changes over the last two centuries for an oligo-mesotrophic lake, which was dammed in 1957 and reinforced during 1987–1990, respectively. A water depth inference model constructed from surface sediment clay components was applied to a well-dated sediment core for water level reconstruction. The inferred water depth increased from 6.2 ± 0.9 m to 8.7 ± 1.7 m after dam construction and further to 13.6 ± 2.6 m after dam enforcement, resulting in an increase in the magnitude of water level fluctuation (WLF). Accordingly, bulk sediment C/N ratio and median grain size spiked in ~1957 and ~1990, respectively, reflecting a large input of terrestrial sources due to impoundment. With a consistent loss of littoral zone and benthic diatoms over time, a significant decrease in C/N ratio and an abrupt depletion of carbon isotopic signal suggested a shift of carbon transfer towards a pelagic pathway after ~1990. While there was a significant increase in algal production since ~1990, the accumulation rate of carbon and nitrogen burial displayed an accelerating drop since ~1957, reflecting a diluting effect derived from expanding water storage. Furthermore, there was a significant increase in both the ratio between inorganic and organic carbon fluxes and sediment burial of inorganic carbon, reflecting enhanced degradation and low storage of aquatic organic carbon in stratified deep waters since ~1990. Hydro-morphological variables were found to exert strong impact on diatom communities, with an increasing interplay with nutrient and climate variables over time. While there existed a significant shift of diatom composition in ~1960, species richness and community dissimilarity showed a significant decrease when water depth was raised to above ~10 m or the magnitude of WFL was above ~2 m. Thus, our sediment surveys provide evidence on the significant impact of lake regulation on hydro-morphology, carbon burial and ecological shift over time, as well as its stronger interaction with other forcing with increased impoundment intensity.

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1. Introduction

For the last few decades, hydrological manipulation has been increasingly practiced for irrigation, flood control, municipal water supply and hydropower generation globally (Schleiss and Boes, 2011). For example, > 90% of the major river basins were strongly

regulated across China, with a total storage capacity of reservoirs currently about two times higher than that of lakes (Yang and Lu, 2014). Meanwhile, the number of natural lakes that are converted to reservoirs has spiked over the last few decades and is projected to continue in the coming decade (Zarfl et al., 2015). At present, around 40% of inland water organic carbon is annually buried and stored in reservoirs which serve as an important sink for global carbon cycling (Mendonça et al., 2017). The environmental and ecological assessment of hydrological regulation has been predominantly derived from floodplain lakes and rivers (Van Geest

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et al., 2005). River flow regulation by dams has been widely found to alter the hydrological regime (Poff and Schmidt, 2016; Timpe and Kaplan, 2017), nutrient cycling (Maavara et al., 2015) and ecosystem structure (Kominoski et al., 2017). However, limnological succession and ecological processes can differ significantly between dammed rivers and regulated lakes (Hall et al., 1999). Thus far, understanding the environmental and ecological consequences of lake impoundment is often constrained by insufficient monitoring data that can cover the pre-damming period. Despite that few sediment-based studies have shown that water quality and community organization could be strongly altered with lake damming (Rühland et al., 2010; Elchysyn et al., 2018), the long-term role of lake regulation and their dependence on impoundment intensity have been rarely assessed from an integrated perspective on key ecological processes.

Hydrological regulation is known to alter lake hydro-morphology and habitat availability with significant ecological consequences (Leira and Cantonati, 2008). Anthropogenic conversion of a shallow lake into a deep system directly altered the morphology and typology of lake basin, which determine key limnological processes such as thermocline and habitat availability (Wetzel, 2001; Wantzen et al., 2008). An increase in water depth can shift the thermal regime from a mixed one to a stratified one, or enhance the stability of thermocline with a prolonged stratification (Nowlin et al., 2004). Habitat quantity and quality often vary with basin morphometry, generally showing a loss of littoral habitats and benthic producers with a shift towards a deeper system (Hellsten et al., 1996; Coops et al., 2003). Water level increase can further decrease both light penetration in deeper water and the proportion of sediment exposed to resuspension (Loiselle et al., 2005), posing a negative impact on benthic producers. A sustained increase in water level may adversely affect aquatic vegetation which predominantly colonize littoral zones (Howard-Williams et al., 1995; Middelboe and Markager, 1997), and can cause a shift towards a phytoplankton-dominated state due to the diminishing of macrophytes (Kong et al., 2017). Therefore, the increase in water depth beyond an threshold level can favor the pelagic pathway of trophic flow through decreasing habitat and resource availability for benthic producers (Devlin et al., 2013).

Dam-induced lake level increase can also strongly modulate biogeochemical processes and carbon cycling, through enhancing nutrient retention, dilution effect and bottom release (Forsberg et al., 1988; Zhao et al., 2013). Anthropogenic regulation can often increase water residential time and nutrient retention, leading to a reduction in their transfer to downstream environment (Erwin et al., 2011). It was estimated that >10% of global river nutrients (i.e. total phosphorus) was trapped in reservoirs in 2000 (Maavara et al., 2015). The lake-water nutrient concentration may also increase with higher water levels due to enhanced release of bottom sediment nutrients (Tang et al., 2015), however, an simultaneously increased water volume can also lead to the dilution of soluble nutrients (Yang and Yang, 2014). Meanwhile, the pattern of organic matter accumulation and carbon burial often varies significantly depending on lake size and typology (Chen et al., 2012), with the rate of organic carbon (OC) burial being greater in shallow water bodies of similar trophic status (Downing, 2010). It has been revealed that OC burial rate was > six times higher in reservoirs than that in lakes over a global scale (Mendonça et al., 2017). Furthermore, CO₂ efflux from reservoirs was around twice the magnitude of that from natural lakes, predominantly via the release from inorganic carbon storage (Cole et al., 2007). However, certainty in estimating reservoir carbon fluxes has been largely constrained by the scarcity of time-series data derived from dammed lakes or reservoirs. Therefore, it is crucial to refine the temporal shift in carbon burial in response to lake impoundment in the

upscaling of reservoir OC burial for estimating regional carbon cycling.

The variability of water level fluctuation (WLF), often dampened after damming when compared to the natural variability in non-regulated lakes, can play a significant role in altering ecological processes and ecosystem structure (Winter 2004; Mehran et al., 2017). The WLF can impact the sedimentation processes and biogeochemical cycling, through altering sediment transportation and accumulation (Håkanson, 1977; Furey et al., 2004). An increase in the WLF magnitude in deep lakes may significantly impact deep-water renewal and oxic conditions (Kaden et al., 2010). The magnitude of WLF was also found to affect the source of organic matter (OM) in seasonally flooded shallow lakes, with larger WLFs leading to increased OM input of allochthonous sources (Liang et al., 2016). Meanwhile, spatial surveys showed that both seasonal and long-term WLFs were significant in regulating community assembly in natural lakes (Casanova, 1994; Baastrup-Spohr et al., 2016). While the impact of WLF on lake biota was often restricted to littoral zones depending on the amplitude and frequency of WLF (Scheffer and Jeppesen, 2007; Evtimova and Donohue, 2016), field experiments showed that the WLF magnitude of < 1 m could significantly structure benthic producers (Evtimova and Donohue, 2014). Community diversity may also vary with the magnitude of WLF along an extended gradient of water depth (Aroviita and Hamalainen, 2008). Aquatic biodiversity was often found to vary depending on the magnitude of WLF, with higher species diversity under a moderate range of WLF (White et al., 2008) but with a loss of diversity under amplified WLF (Keddy and Reznicek, 1986; Aroviita and Hamalainen, 2008). Furthermore, the field survey revealed the strong interaction of lake depth and WLF in regulating the production and assemblages of lake biota (Evtimova and Donohue, 2016). Vertical mixing at the intermediate magnitude of WLF was also found to play an important role in structuring phytoplankton (Elliott et al., 2001). Therefore, it is essential to assess the long-term role of WLF in regulating ecosystem structure and diversity along an extended water depth gradient.

In the case of insufficient lake monitoring data, sediment records have been widely applied to track the history of lake-level and ecological changes (Last and Smol, 2001). For example, there could exist a strong mechanistic link between water depth and grain size component as recorded in surface sediments which can be applied in sediment sequences to quantify lake level changes over time (Xiao et al., 2015). Haixi Lake, an alpine rift lake located in Southwest China, experienced damming in 1957 and dam reinforcement in 1987–1990, respectively, showing a clear trend of increased water depth over the last few decades (WABD, 2012). Here, we combined the spatial and temporal surveys of lake sediments to reconstruct the variation in lake hydrology and to assess their role in altering limnological processes over the last two centuries. Specifically, we aim to (i) quantify the long-term trajectory in water levels and the WLF magnitude across different hydrological stages, (ii) identify the temporal shifts of habitat availability, carbon cycling and algal production, and (iii) evaluate the role of hydrological regulation in driving diatom community shift and diversity patterns, as well as their dependence on impoundment intensity.

2. Material and methods

2.1. Study area

Haixi Lake (locally called Haixihai), an alpine rift lake by origin with the altitude of 2130 m a.s.l., is located in northwest part of Yunnan Province, Southwest China (Fig. 1). The lake is a currently

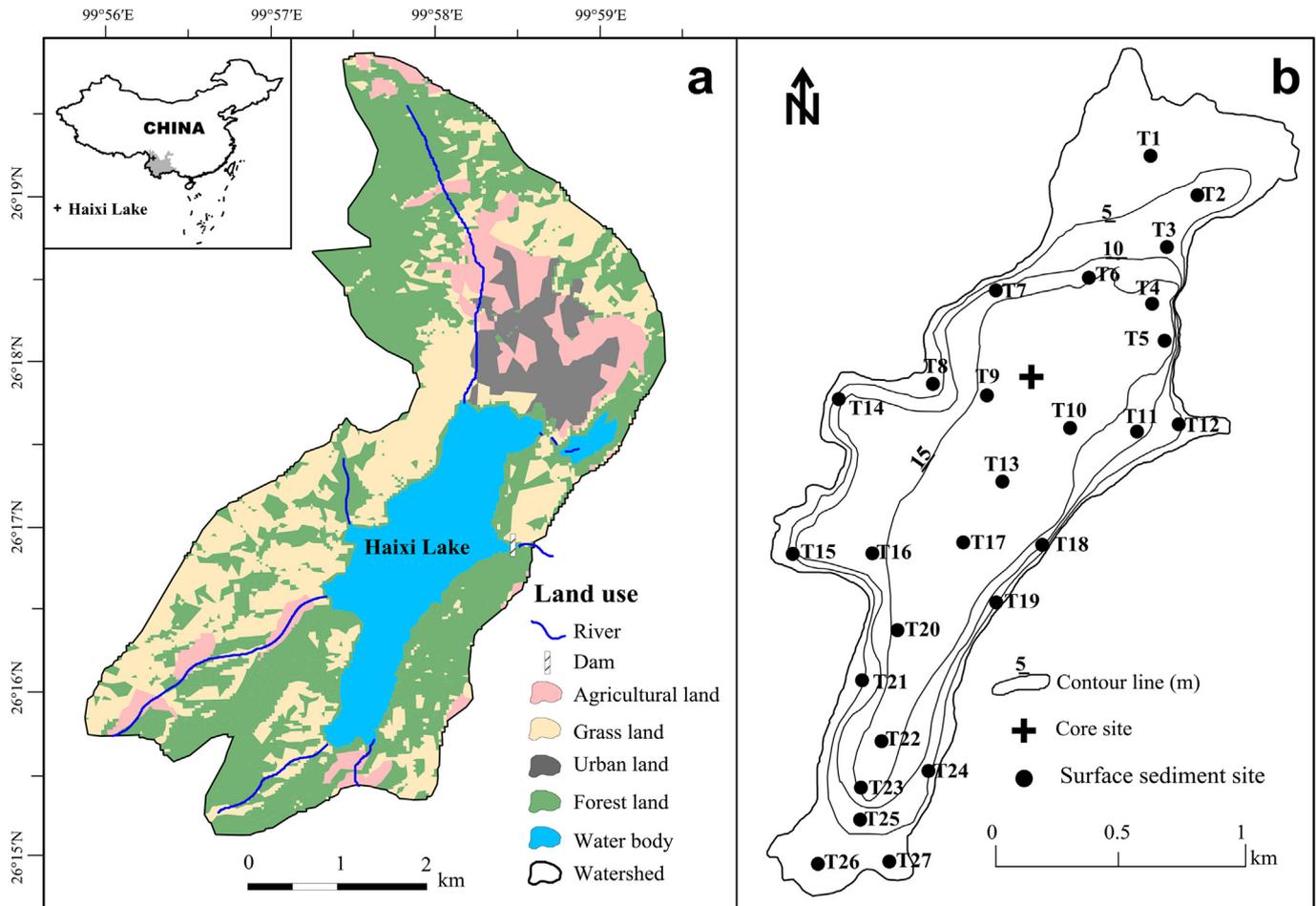


Fig. 1. Geographic map showing the site location and catchment land use of Haixi Lake (a); bathymetric map showing the sampling sites for surface sediment and down-core surveys, respectively (b). The maps were created in ArcMap 10.0 (ESRI®, USA).

a deep reservoir system with a maximum depth (Z_{\max}) of 18.5 m, a surface area of $\sim 3 \text{ km}^2$ and a watershed area of $\sim 23 \text{ km}^2$, respectively (Table 1). The lake is in-flown by a main river in the north and several streams from the west and south, respectively. Dominated by the Indian monsoon and influenced by Eastern Asian monsoon, the regional climate is characterized by distinct

wet and dry seasons. The annual mean precipitation is $\sim 1050 \text{ mm}$, with more than 70% rainfall occurring during the summer months of June to August, with an annual average temperature of about 15°C based on the monitoring data collected from the closest meteorological station of Dali during 1951–2013 ($\sim 77 \text{ km}$ southwest of Haixi Lake, 1990.5 m a.s.l.; Fig. S1). The regional climate was characterized by a clear warming trend since the 1980s and an overall decrease in annual mean precipitation over the last century (Fig. S1). The bedrock types in the watershed mainly include limestone, sandstone and mudstone, while the land use coverage is predominantly composed of forest and shrub lands (Fig. 1). The forested coverage, dominated by Yunnan pine (*Pinus yunnanensis*), is 42.9% while the brushwood, dominated by rhododendron (*Rhododendron coriaceum*), covered $\sim 25\%$ of the watershed (Table 1). There is a limited coverage of agriculture and urban lands (8.9% and 5.9%, respectively) within the catchment, with a small village of Baitayi located to the north of the lake with a population size of ~ 700 (Yang, 1996).

Haixi Lake is currently an oligo-mesotrophic, deep system due to its remote location and moderate catchment development. It was characterized by a Secchi disc depth, lake-water total phosphorus (TP) and total nitrogen (TN) concentrations of $\sim 2.7 \text{ m}$, $10.7 \mu\text{g L}^{-1}$ and $328 \mu\text{g L}^{-1}$, respectively, as measured in 2013 (Table 1). In this deep system with a mean depth (Z_{mean}) of $\sim 11.7 \text{ m}$, thermal stratification occurred during the summer with a surface water temperature of $\sim 22^\circ\text{C}$ and was totally mixed in winter with a water column temperature of $\sim 12^\circ\text{C}$ (Fig. S2).

Table 1
Summary of key limnological and catchment features of Haixi Lake.

Parameter	Value
Latitude ($^\circ\text{N}$)	$26^\circ 16' - 26^\circ 31'$
Longitude ($^\circ\text{E}$)	$99^\circ 57' - 99^\circ 59'$
Altitude (m)	2130
Lake area (km^2)	3.6
Catchment area (km^2)	22.97
Agricultural land (%)	8.9
Forest land (%)	42.9
Grass land (%)	25.0
Water body (%)	17.3
Urban land (%)	5.9
Maximum depth (m)	18.5
Mean Depth (m)	11.7
Macrophyte coverage (%)	22.4
pH (mean \pm 1SD)	7.9 ± 0.5
TN (mean \pm 1SD, $\mu\text{g L}^{-1}$)	328 ± 125
TP (mean \pm 1SD, $\mu\text{g L}^{-1}$)	10.7 ± 3.1
Chl. <i>a</i> (mean \pm 1SD, $\mu\text{g L}^{-1}$)	2.0 ± 1.1
Secchi disc depth (mean \pm 1SD, m)	2.7 ± 0.7

Haixi Lake was documented to experience pronounced lake regulation and drastic water level fluctuations since the 1950s (Fig. S3). The water levels were naturally constrained until a sluice was built on the outflow river with a height of 1.68 m in 1954, and a dam of 9.5 m height was built in 1957, with water level rising to ~6 m during 1958–1960 (Yang, 1996). In 1990, Haixi Lake became a middle-sized reservoir due to the installation of an enforced dam with a height of 21 m and three electric water pumping stations (WABD, 2012).

2.2. Lake surveys and sediment sampling

Limnological surveys of Haixi Lake were conducted in September 2013 and December 2015, respectively. Three sampling sites were selected for water chemistry sampling and limnological surveys. Lake-water temperature, turbidity, dissolved oxygen (DO), chlorophyll *a* and conductivity profiles were measured using a multi-parameter water quality meter YSI 6600 V2 (YSI® Co., USA). A total of 5 L surface water (0–1 m) per site was collected for water chemistry analysis following standard methods (SEPA, 2002) within 24 h after sampling. Furthermore, the Landsat images were collated and analyzed to extract the time series of lake surface area and catchment land use during 1987–2013 following the standard methods used in this study region (Wu et al., 2016).

Surface sediment samples (0–1 cm) were collected with a Renberg® gravity corer from 27 sites across the lake (Fig. 1). Parallel sediment cores were also collected from the deep basin of Haixi Lake in September 2013. A 37.5-cm long core (HXH-GC2), used in this study for multi-proxy analyses, was sectioned immediately in field at 0.5-cm intervals for the top 5 cm and at 1-cm intervals for the depth below 5 cm, respectively. The samples of the above core were stored at ~4 °C for lab processing before the samples were freeze-dried and stored in the dark to minimize degradation for pigment analysis.

2.3. Sediment analyses

The chronology profile of the short core was obtained by measuring ²¹⁰Pb_{ex} and ¹³⁷Cs radionuclide activities of sediment samples using the Canberra® well-detector gamma spectrometer (GCW3023). Sediment chronology sequence was established with the stratigraphic profile of unsupported ²¹⁰Pb_{ex} activities through applying the constant rate of supply (CRS) model. The stratigraphic profile of ¹³⁷Cs was independently used to verify the CRS model-inferred chronological sequence.

Particle size spectra of sediment samples (including both surface and down-core sediment samples) were measured using an automated laser optical particle-size analyser (Mastersizer, 2000; Malvern Instruments Limited, Malvern, UK). Briefly, ~0.3 g freeze-dried and disaggregated sediment for each sample was pre-treated with 10–20 mL of 10% H₂O₂ to remove organic matter. Around 10 mL of 10% HCl was then added and boiled to remove carbonates. Around 100 mL of deionized water was added and the sample solution was kept for 24 h to rinse acidic ions. The sample residue was dispersed with 10 mL of 0.05 mol L⁻¹ (NaPO₃)₆ on an ultrasonic vibrator for 10 min prior instrumental analysis. The sediment particle size was divided into the categories of clay (<2 μm), silt (2–63 μm) and sand (>63 μm), respectively.

Organic matter content was estimated for bulk sediments through the method of loss-on-ignition (% LOI550) at 550 °C for 3 h using a muffle furnace following the standard method (Heiri et al., 2001). Sedimentary chlorophyll *a* (Chl. *a*) concentration of the freeze-dried sediment samples was measured by the visible reflectance spectroscopy method, through a FOSS® NIR System model 6500 rapid content analyser (Michelutti et al., 2010). The

chlorophyll *a* (Chl. *a*) concentration was calculated with a unit of μg g⁻¹ per organic weight for each sample.

Pretreatment of the sediment samples were applied for carbon and nitrogen elemental and isotopic analyses following standard methods (Meyers et al., 2001). For the measurement of total organic carbon (TOC) and isotopic signals of organic matters, samples were acidified to remove inorganic carbon with high-purity HCl (10% by volume) until CO₂ release was invisible, and then were re-dried and rinsed until pH was 7. Approximately 10 mg of homogenized bulk sediment or organic sample in a tin capsule was combusted at 960 °C and measured using an elemental analyser (FLASH 2000) linked to a continuous flow mass spectrometer (MAT-253, Thermo Scientific, USA). C and N isotope ratios are expressed as per mil (‰) relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N₂ (AIR), respectively. The analytical precision was < ± 0.1‰ for isotopic data and < ± 1% for elemental data, respectively. Relative contents of C and N (% dry mass) and the ratio of carbon to nitrogen (C/N) were measured, with the deviation of TOC from total carbon (TC) calculated as total inorganic carbon (TIC) for each sediment sample.

Samples for diatom analysis were pretreated with HCl (10%) and H₂O₂ (30%) to remove carbonate and organic materials which can impede taxonomic identification, before being washed and mounted in Naphrax® (Brunel Microscopes Ltd., Wiltshire, UK) following the standard methods (Battarbee et al., 2001). Diatom identification and counting were performed under oil immersion at 1000 × magnification with phase contrast using a Leica® microscope (DM 2500). A minimum of 400 valves was counted for each sample along random transects. The diatom community data were expressed as percent abundance of the total sum in each sample. Diatom species were categorized into planktonic and benthic groups according to their habitat preferences (Round et al., 2007).

2.4. Numerical analysis

To infer the past lake water depth, we firstly developed a linear regression model between the clay components of 27 surface sediment samples and their water depths (Fig. 3). The performance of the water depth inference model was then evaluated through comparing the predicted values for sediment samples with the observed water depths (n = 13). Based on the water depth profile inferred for the sediment sequence, we defined the underwater area with water depth < 5 m as littoral zone, a threshold level for macrophyte growth as observed in field surveys of lakes from this study region (Li, 1980; Chu et al., 2014). Their percentage proportion of the total lake surface area were further calculated (Hellsten et al., 1996), through the application of ArcMap 10.0 (ESRI®, USA) using the high-resolution lake bathymetry (Fig. 3a).

Prior to statistical analyses, environmental variables were log-transformed and diatom percentage data were square-root transformed for normality, respectively (Borcard et al., 2011). Student t-test was used to test for the difference among samples from different time windows, and Pearson correlation or regression analysis was applied to examine the relationship between limnological variables. The method of constrained incremental sum of squares (CONISS) was applied to identify the significant biostratigraphic zones for diatom data with a broken-stick model (Grimm, 1987; Bennett, 1996). We conducted ordination analyses to define the temporal trajectories of diatom changes in sediment core samples. The detrended correspondence analysis (DCA) of diatom assemblages revealed a gradient length of 1.98 SD, indicating that the majority of the species displayed a linear response model along the latent environmental gradients and therefore linear methods are appropriate for ordination analyses of diatom data (ter Braak and Prentice, 1988). Principal components analysis (PCA) was

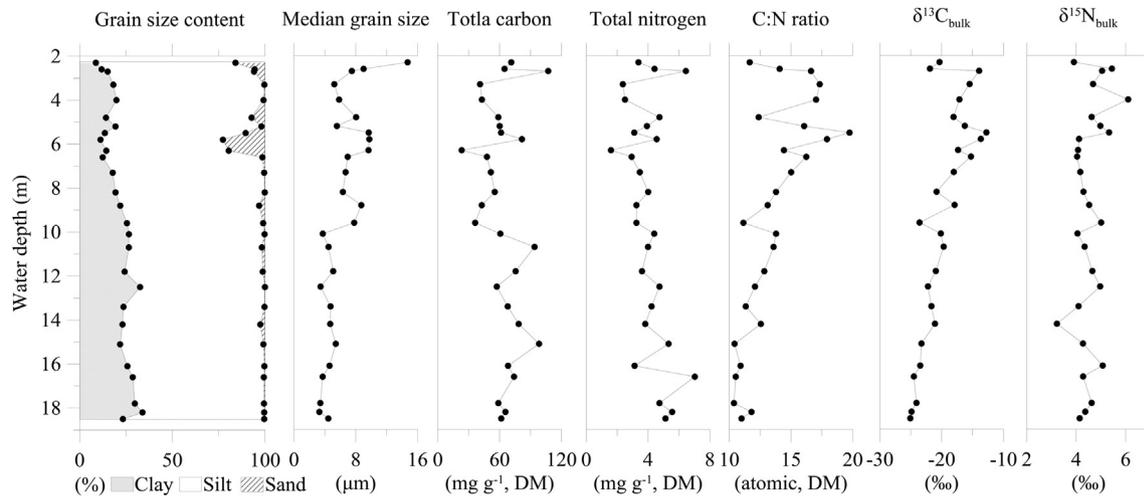


Fig. 2. Diagram showing the spatial distribution of grain size components, carbon and nitrogen contents, and stable isotope signatures in 27 surface sediment samples along the water depth gradient in Haixi Lake, respectively.

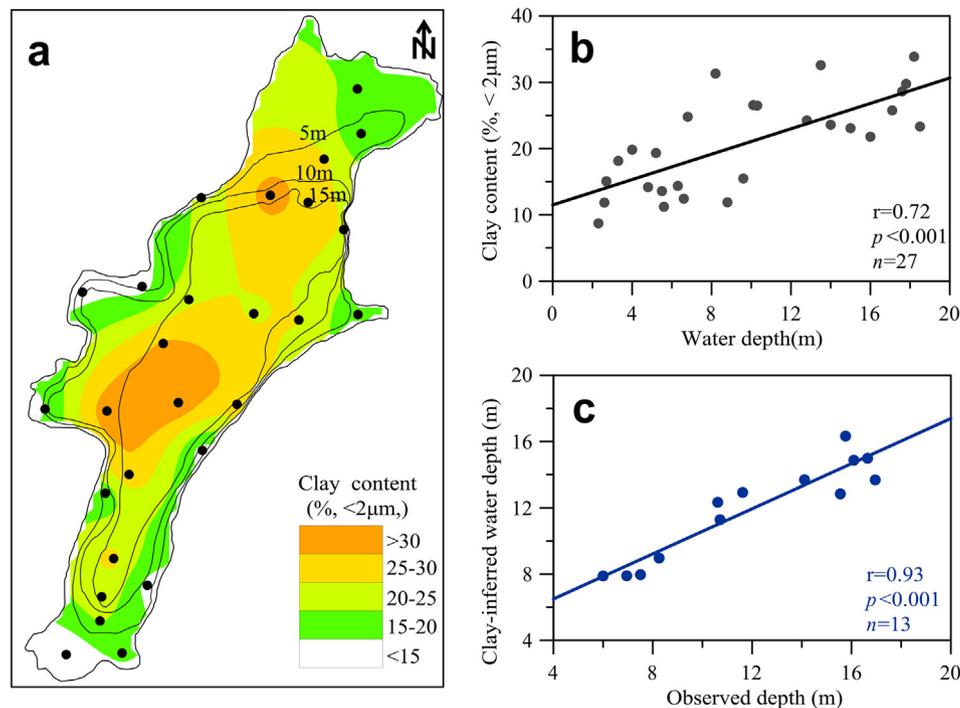


Fig. 3. Bathymetric map showing the spatial distribution of surface sediment clay components in 27 sites (a); scatter plots showing the relationship between water depth and surface sediment clay component (b), and the relationship between the observed and clay-inferred water depths covering the period of ~1958–2013 (c), respectively. The map was created in Suffer 12.0 (Golden software®, USA). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

applied to extract the major direction in diatom compositional changes. Furthermore, partial redundancy analysis (pRDA) and variation partitioning analysis (VPA) were conducted to identify the significant drivers for diatom community (Borcard et al., 2011), with Z-score transformation applied for environmental variables to take into account their different units. To reflect the regional climate gradient, tree-ring inferred temperature data for the last two centuries from this study region (Li et al., 2012a) were included in the above analyses due to their significant correlation with regional meteorological data ($P < 0.001$; Fig. S1).

We also applied regression models to explore the temporal variation of diatom species richness and community turnover (i.e. Jaccard's dissimilarity) along the gradients of water depth and WLF

amplitude, respectively. Break-point analysis using a two-segment piecewise linear regression were applied to estimate the timing of largest change in diatom diversity data along the depth gradient (Muggeo, 2003). All statistical analyses were performed in the packages of *vegan*, *rioja* and *segmented* in R software (RDCT, 2011).

3. Results

3.1. Spatial surveys of surface sediments

The basin-wide survey of surface sediments displayed a spatial pattern of grain size distribution over the gradient of water depth (Fig. 2). The sediment silt and sand components generally showed a

stable distribution with a median size of around 5 μm in deep waters (i.e. $Z_{\text{max}} > 10\text{ m}$). Both silt and sand percentages increased gradually and spiked along the littoral zones or near the mouth of inflowing river. With increasing water depth, the clay component increased significantly from 8.7% to 33.9%. The bulk sediment $\delta^{13}\text{C}$ signal varied between -26‰ and -14‰ with a clear trend of depletion towards the deeper water ($r = -0.74$, $P < 0.001$; Fig. 2). While the $\delta^{15}\text{N}$ signal of bulk sediments showed no clear correlation with water depth, littoral sites were generally more enriched in $\delta^{15}\text{N}$ signal than pelagic ones. The bulk sediment C/N ratio (mean $\pm 1\text{SD} = 15.0 \pm 2.3$) showed a decreasing trend with the increased water depth ($r = -0.33$, $P < 0.01$).

3.2. Construction of water level inference models

The surface sediment clay components displayed a clear concentric spatial pattern (Fig. 3a), showing a significant relationship with the water depth across the 27 sites ($r = 0.72$, $P < 0.001$; Fig. 3b). When compared to the water-level monitoring data during the period of ~ 1957 –2012 AD, our sediment clay-inferred water depth further showed a robust and significant correlation with the observed water depth ($r = 0.93$, $P < 0.001$, $n = 13$; Fig. 3c). Therefore, we applied this clay-inferred depth model into sediment samples for water depth reconstruction covering the whole core sequence (Fig. 4a).

3.3. History of water level and littoral zone changes

Excessive ^{210}Pb activities showed an exponential decline over the sediment sequence ($R^2 = 0.64$, $p < 0.001$, Fig. S4a), allowing for the construction of the CRS age model (Fig. S4b). The sediment bottom sample was estimated as ~ 1810 (Fig. S4c). Two peaks of ^{137}Cs at the sediment depths of 14.5 and 8.5 cm, with a CRS-estimated age of $\sim 1965.5 \pm 3.0$ and $\sim 1984.3 \pm 3.0$ AD, respectively, corresponded well with the widespread peaks of artificial radionuclide fallouts in 1963 and 1986 AD (Appleby, 2001), corroborating the reliability of our CRS model for Haixi Lake. The depth-age model showed a mean sedimentation rate of $0.28 \pm 0.10\text{ cm year}^{-1}$, with higher values occurring in ~ 1957 and ~ 1987 –1990 AD, respectively (Fig. S4d).

The sediment grain size components recorded drastic hydrological changes over the last two centuries (Fig. 4a). During the pre- ~ 1900 period, the grain size components modestly changed with a mean median size of $5.5 \pm 0.4\text{ }\mu\text{m}$ (1SD), with the clay and silt components varying in the range of 14.1–17.0% (mean = 15.7%) and 82.2–85.9% (mean = 84.2%), respectively. While the sand content remained consistently below 3% over the core, the clay component showed a clear increasing trend since ~ 1960 with a value above 20% with a synchronous decrease in the silt content. The median size spiked around ~ 1957 and ~ 1987 –1990, corresponding with the hydrological turbulent events due to lake damming and reservoir reinforcement, respectively.

Our clay-inferred water levels displayed a clear trajectory of increasing depth with strong fluctuations over the past two centuries (Fig. 5a). During ~ 1800 –1957 AD, the water depth had a moderate fluctuation ranging between 4.5 and 7.5 m (mean $\pm 1\text{SD} = 6.2 \pm 0.9\text{ m}$), suggesting a frequently mixed shallow lake. After ~ 1957 , there existed a dramatic increase of Z_{max} with remarkable fluctuations ($10.5 \pm 2.9\text{ m}$). More recently, the mean water level was significantly elevated from $8.7 \pm 1.7\text{ m}$ during ~ 1957 –1990 to $13.6 \pm 2.6\text{ m}$ after the enforcement of lake dam completed in 1990. With elevated water levels, there is a significant increase in the amplitude of WLF over the last two centuries ($r = 0.53$, $p < 0.001$). Simultaneously, the percentage coverage of littoral zone (i.e. water depth $< 5\text{ m}$) showed a shrinking trajectory

(Fig. 5b), decreasing from $83.6 \pm 13.8\%$ in ~ 1800 –1957 to $62.3 \pm 11.2\%$ and a further lower value ($44.8 \pm 9.2\%$) during ~ 1957 –1990 and ~ 1990 –2013, respectively.

3.4. Sedimentary profile of nutrient cycling and lake production

The sediment TN content consistently remained at a level of $1.6 \pm 0.2\text{ mg g}^{-1}$ before showing a moderate enrichment ($2.5 \pm 0.7\text{ mg g}^{-1}$) since ~ 1930 (Fig. 4a). In particular, there existed a clear increase in the bulk sediment TN ($2.9 \pm 0.8\text{ mg g}^{-1}$) after ~ 1990 . TC content remained at a stable and low level of $22.3 \pm 2.5\text{ mg g}^{-1}$ during ~ 1810 –1930, followed by a higher level of $41.0 \pm 7.4\text{ mg g}^{-1}$ up until ~ 1960 . After a strongly fluctuating variation, the TC level increased to a mean of $47.4 \pm 6.1\text{ mg g}^{-1}$ since ~ 1987 . Specifically, both TOC and TIC levels fluctuated with a low level in ~ 1800 –1920 and increased in ~ 1920 –1960 and ~ 1980 –1990, respectively (Fig. 4a). The decline in both TOC and TIC occurred shortly after ~ 1960 and ~ 1990 , while the decline of TOC after ~ 1990 ($12.2 \pm 3.9\text{ mg g}^{-1}$) contrasted to an increase in TIC towards a maximum over the core. Furthermore, there existed a significant negative relationship between TOC and inferred Z_{max} since ~ 1957 AD ($r = -0.58$, $p = 0.004$). After taking into account the sedimentation rate, the fluxes of both TN and TOC displayed an increasing trend prior to ~ 1957 AD, reaching a maximum of ~ 4 and $40\text{ mg cm}^{-2}\text{ a}^{-1}$, respectively, which were followed by a rapid decrease of both indicators to $< 1\text{ mg cm}^{-2}\text{ a}^{-1}$ towards core top (Fig. 5c and e).

The bulk sediment C/N ratio (Fig. 4a) varied significantly within the range of 12.7–22.3 with peak values found around ~ 1950 and ~ 1987 , with a strong decline occurring during the periods of around ~ 1890 –1930, ~ 1957 –1975, and ~ 1990 –2013, respectively. In comparison, sediment pigment data showed that Chl. *a* concentration varied in a direction opposite to those of C/N ratio and TOC over time, with an accelerating increase in algal production found after ~ 1990 (Fig. 5c). Furthermore, the algal production showed a positive correlation with both sediment TN ($r = 0.81$, $p < 0.001$) and inferred Z_{max} ($r = 0.87$, $p < 0.001$), but a negative relationship with TOC ($r = -0.31$, $p = 0.046$) and C/N ratio ($r = -0.53$, $p < 0.001$).

The $\delta^{13}\text{C}$ signal of bulk sediments ($\delta^{13}\text{C}_{\text{bulk}}$) showed a general trajectory of depletion with strong fluctuations over time (Fig. 4a). There existed a trend of enrichment from -20.5‰ in ~ 1810 to -17.3‰ in ~ 1836 AD, followed by a gradual decline to -20.7‰ in ~ 1930 AD, and then it moderately increased to -17.5‰ in 1996 before showing a unidirectional trend of depletion towards core top with a minimum value of -21.6‰ found in ~ 2010 AD. The $\delta^{13}\text{C}$ signal of organic matters ($\delta^{13}\text{C}_{\text{org}}$) displayed a consistently stable value (mean = $-26.7 \pm 0.67\text{‰}$) prior to ~ 1957 AD, and thereafter experienced a gradual decline (mean = $-28.5 \pm 2.0\text{‰}$) with an accelerating decrease towards -31‰ after ~ 1990 . Our sedimentary $\delta^{13}\text{C}_{\text{org}}$ signature was significantly and negatively correlated with water depth ($r = -0.77$, $p < 0.001$), sediment TN ($r = -0.73$, $p < 0.001$) and Chl. *a* concentration ($r = -0.86$, $p < 0.001$), respectively.

The bulk sediment and organic matter $\delta^{15}\text{N}$ records showed a synchronous and moderate change over time ($r = 0.466$, $p = 0.002$), with a decreasing trend during ~ 1810 –1904 followed by a period of slightly enriched signals during the last century (Fig. 4a). There also existed a moderate enrichment of $\delta^{15}\text{N}$ after the interval of ~ 1987 –1990 when both proxies were obviously diluted.

3.5. Diatom compositional changes

A total of 138 diatom taxa were identified over the sediment core, including 60 taxa with a maximum abundance of $\geq 1\%$, 14 of which occurred with a relative abundance of $\geq 5\%$ in at least one

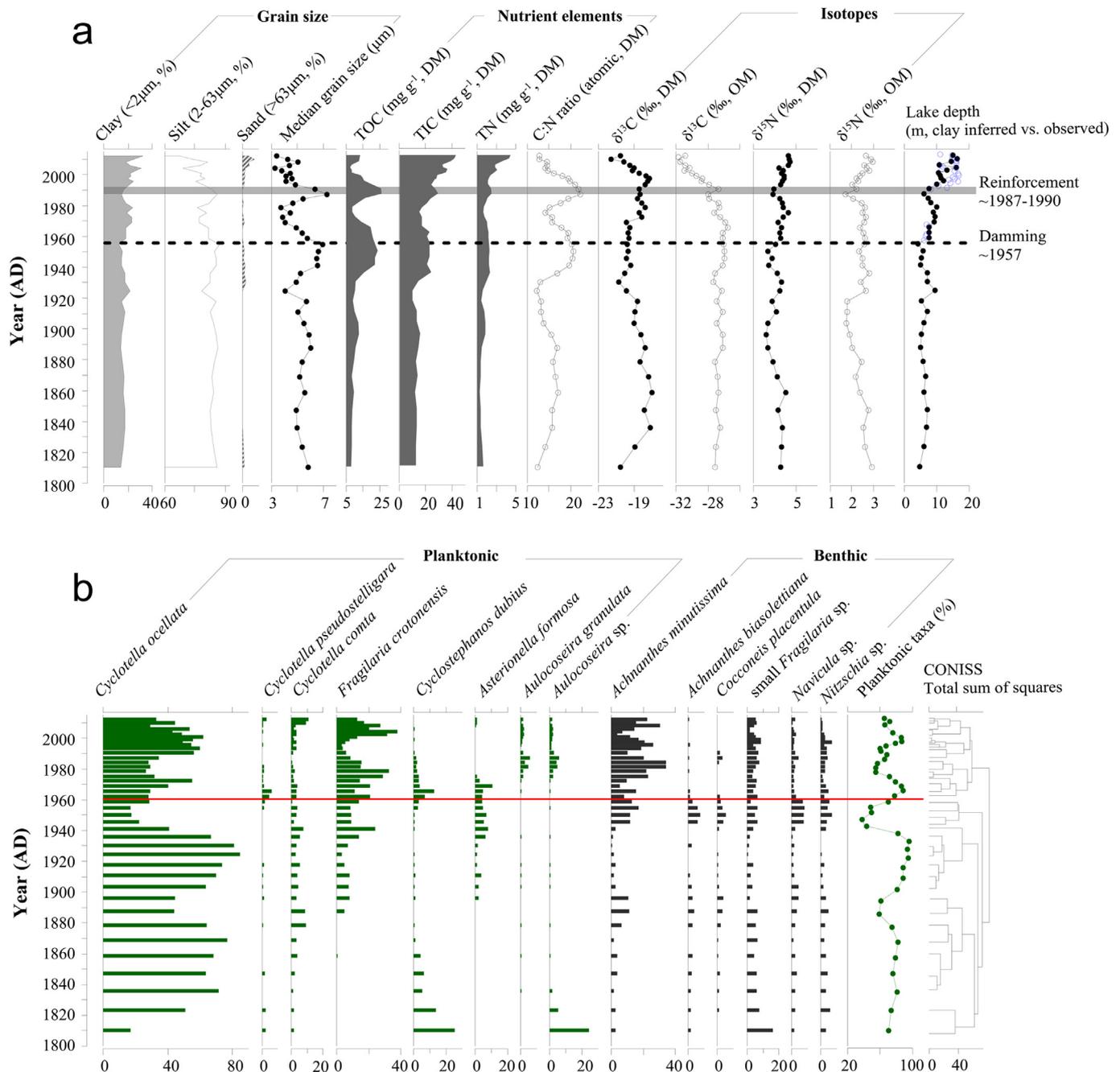


Fig. 4. Stratigraphic profiles showing the sediment records of grain size and geochemical variables (a) and diatom assemblages (b) over the past two centuries in Haixi Lake, respectively. In plot (a), the blue open circles represent the observational water depth data; the dashed line and dark grey shading indicate the damming event and reinforcement interval, respectively. The red line indicated the significant zonation defined by the CONISS analysis in plot (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sample. Diatom assemblages were generally dominated by planktonic taxa over the core (Fig. 4b), such as *Cyclotella ocellata* (16.9–84.2%), *Fragilaria crotonensis* (0–38.1%), *Cyclostephanos dubius* (0–25.5%), *C. comta* (1.7–9.0%). Benthic diatoms fluctuated within the range of ~4–62%, mainly including *Achnanthes minutissima* (1.6–30.3%), small *Fragilaria* spp. (0.9–15.9%), *Navicula* spp. (1.3–8.9%) and *Nitzschia* spp. (1.2–6.7%).

Diatom assemblages were characterized by strong fluctuations over the last two centuries, with a significant community shift found in ~1960 AD (Fig. 4b). During the period of ~1810–1880, the community was mainly composed of planktonic taxa ($56.1 \pm 8.6\%$)

with both *C. dubius* and *Aulocoseira* spp. decreasing from >20% to <5%, while *C. ocellata* increased rapidly from <20% to >60%. The benthic taxa showed moderate change ($26.3 \pm 8.6\%$) with a decrease of small *Fragilaria* spp. from ~20% to <5%. From ~1880 to 1930 AD, there was a strong community shift towards more planktonic taxa such as *C. ocellata* and *F. crotonensis*, with a decimation of benthic taxa, leading to a maximum in the planktonic:benthic ratio over the core. Shortly afterwards, planktonic taxa such as *C. ocellata* decreased considerably in ~1930–1957 when benthic taxa increased dramatically reaching a maximum of >50%. From ~1960, the community was characterized by frequent

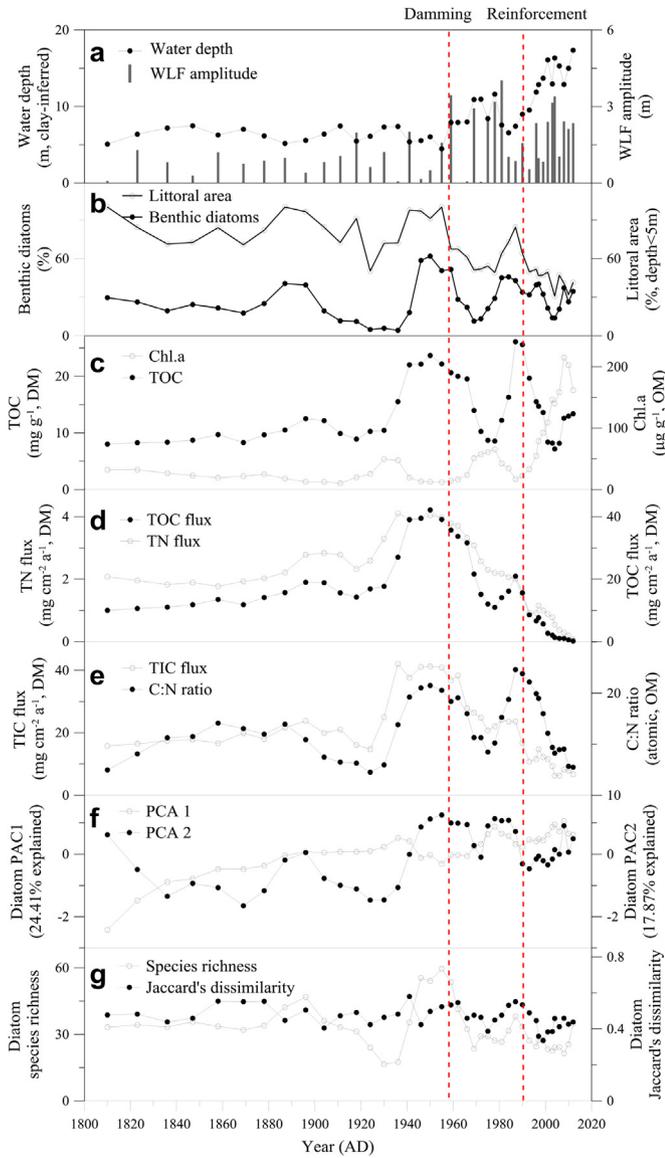


Fig. 5. Sediment-inferred time series showing the reconstructed water level and its variation (a), littoral area and relative abundance of benthic diatoms (b), algal production and TOC content (c), TOC and TN fluxes (d), TIC flux and C:N ratio (e), sample scores of the diatom PCA axes (f), diatom species richness and community shift (g) in Haixi Lake covering the last two centuries, respectively.

compositional shifts with a generally increased abundance of *C. ocellata*, *F. crotonensis* and *A. minutissima*. During the damming stage of 1960–1990, there exist a gradual increase in *F. crotonensis*, followed by a sub-dominance of *A. minutissima*, an increase in *A. granulata* and a loss of *C. dubius* and *A. formosa*. Over the reinforcement stage of ~1990–2013, the rapid increase in *C. ocellata* was followed by a spike in *F. crotonensis*, which was replaced by *A. minutissima* most recently.

Principal component analysis (PCA) of diatom data showed that the first two PCA axes were statistically significant and accounted for 24.41% and 17.87% of the total variance, respectively (Fig. S5). The samples covering the pre-~1957 AD period were predominantly located at the positive direction of axis 1, while the samples covering the stages of ~1957–1990 and ~1990–2013 AD were generally clustered at opposite directions along the axis 2 to the left side of axis 1. *A. minutissima* and *F. crotonensis* were strongly associated with axis 1, with planktonic species *C. ocellata* located at

the right side of this axis. Benthic species (i.e. *A. lanceolata* and *A. biasolettiana*) were strongly associated with axis 2, with planktonic species (i.e. *C. ocellata* and *F. crotonensis*) found at the opposite side of this axis.

3.6. Identifying limnological drivers for diatom changes

The diatom PCA axis scores were strongly correlated to environmental gradients related to lake hydrology, habitat availability and nutrients (Table S1). The diatom PCA axis 1 showed a significant correlation with water depth ($r = 0.59, p < 0.001$), TN ($r = 0.54, p < 0.001$) and Chl *a* concentration ($r = 0.53, p < 0.003$), respectively. The diatom PCA axis 2 showed a significant correlation with the proportion of benthic diatoms ($r = 0.67, p < 0.001$), littoral habitat area ($r = 0.34, p < 0.05$) and TC ($r = 0.47, p < 0.01$) over the core, respectively.

Variation partitioning results further indicated that the nutrient gradient (i.e. TN, TOC and C/N ratio) were found to be the most significant forcing of diatom changes, explaining 34.7% of the total variance over the last two centuries. Hydrological variables (clay-inferred water depth and littoral area) accounted for 20.9% of diatom changes, and shared a variance of 8.5% with nutrients. The climate gradient, as indicated by tree ring-reconstructed summer temperature, accounted for 6.6% of the diatom changes and the interaction among the three gradients accounted for 6.4% of diatom variation. Across the three hydrological stages over time (Fig. 6), both nutrients and climate independently played an increasing role with increased water depth, while the largest role of lake hydrology in driving diatoms (35.5%) was found in the stage of lake damming during ~1957–1990. Meanwhile, the interaction between lake hydrology and nutrients showed a gradual increase from 3.0% to 10.4%, and was also increasingly shared by the climate gradient.

Both diatom species richness and community dissimilarity showed a significant change along the gradients of water depth and the WLF amplitude over the last two centuries, respectively (Fig. 7a and b). Diatom species richness and community dissimilarity generally decreased at higher water levels, with a threshold water depth levels existing for both indices as identified by break-point analysis. Specifically, along the water depth gradient, species richness was decreased with a $Z_{max} > 10.8 \pm 2.2$ m to a lesser degree, while there was an accelerating decrease in community heterogeneity with a $Z_{max} > 9.0 \pm 1.7$ m. Furthermore, species richness and the degree of community dissimilarity were both higher with water level variation < 1.5 m, but decreased with a WLF amplitude > 2 m (Fig. 7c and d). Overall, there existed a significant unimodal response of both diatom species richness and community dissimilarity along the gradient of WLF amplitude ($p < 0.001, r^2 = 0.86$ and 0.69 , respectively).

4. Discussion

4.1. Hydrologic fluctuation and habitat changes

The significant correlation between the documented water levels and the depth predicted through a spatial survey confirmed the reliability of our inference models in reconstructing water level history for the last two centuries (Fig. 3 and Fig. S3). It has been recognized that the grain-size distribution of clastic deposits in lakes can provide pivotal information on hydrological changes (Håkanson, 1977; Liu et al., 2016). For example, the water level fluctuation was well reflected by the silt and clay components of both surface and core sediments in lithological surveys (Punning et al., 2006). Despite that sub-fossil indicators (such as diatoms) were widely applied to reconstruct the change of water depth within a lake or across lakes (Birks, 2012; Juggins and Birks, 2012),

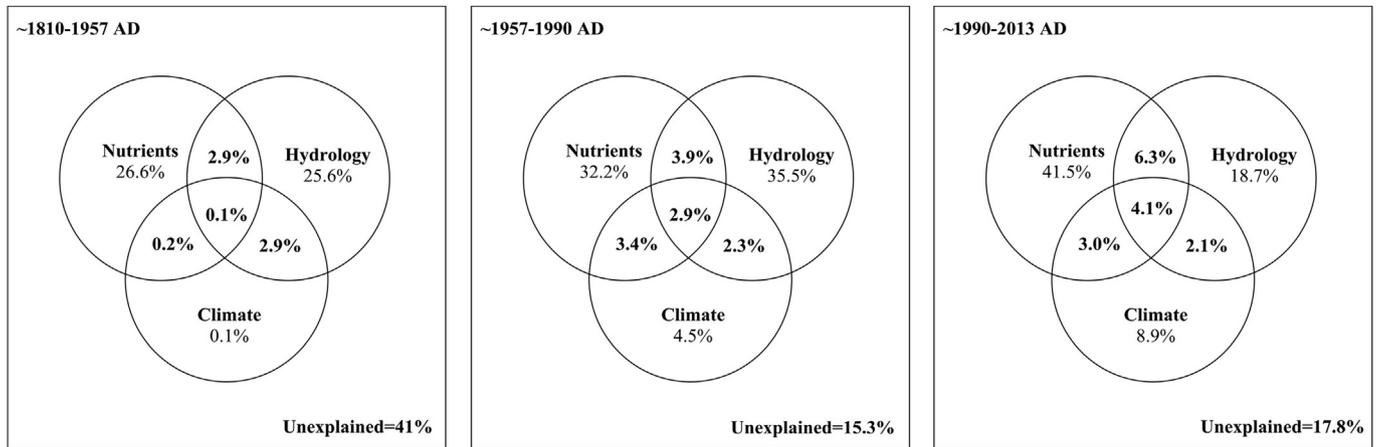


Fig. 6. Variance partitioning results with partial RDA analyses showing the minimum adequate models for diatoms changes during each of the three hydrological stages in Haixi Lake.

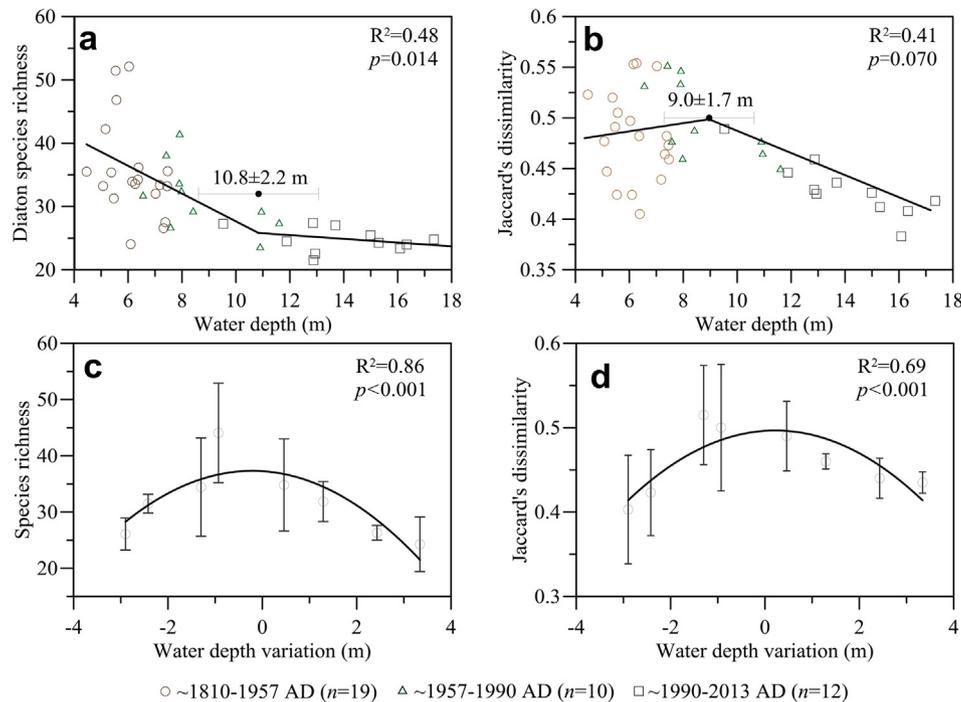


Fig. 7. Break-point analysis showing the segmented response curves of diatom species richness (a) and Jaccard's dissimilarity (b) along the gradient of water depth over the last two centuries in Haixi lake, respectively; regression analyses showing the unimodal-shaped curves for diatom species richness (c) and Jaccard's dissimilarity (d) in response to water depth variations, respectively.

the interplay of multiple environmental stressors have been identified to impede the performance of water depth inference models in quantifying hydrological fluctuation due to their synergistic impact on lake biota (Telford and Birks, 2005). In comparison, our application of sediment grain size is relatively straightforward in reflecting the lake level change due to the mechanistic link between hydrological fluctuation and sedimentation processes (López et al., 2016).

The two-century history of hydrological regime shifts reflected the conversion of a shallow lake to a deep-water reservoir as a result of lake damming in the context of regional climate change. The inferred mean water depth of Haixi Lake was consistently below 8 m with relatively limited variation (6.2 ± 0.9 m) when the lake was free flowing prior to 1957 (WABD, 2012). A decrease in

median grain size and a moderate increase in clay-inferred water depth (Fig. 4a) corresponded to a period of above-average regional precipitation over the period of 1910–1940 (Fig. S1), implying the impact of regional climate on natural hydrodynamics in this region (Chen et al., 2004). While there existed a regional warming trajectory during the last six decades, the occurrence of extreme drought around 2009–2013 led to a water level drop by > 3 m in Haixi, synchronous with regional shrinkage of large lakes (Lü et al., 2012; Wu et al., 2016). With the dam installment, the mean water level (8.7 ± 1.7 m) increased significantly with a spike in the sand component shortly after 1957. This was further followed by higher water levels (13.6 ± 2.6 m) after the dam was enforced in 1990 (WABD, 2012). Noticeably, the initiation of dam construction and enforcement in 1957 and 1987 corresponded to a lower than

average regional precipitation (Fig. S1), respectively. This may suggest that reduced water supply, in the context of increasing catchment demand, may have triggered hydrological regulation of lakes in this region as found in other areas (Hennig et al., 2013).

A strong variation in littoral habitats due to pronounced lake regulation can be an important ecological implication in structuring littoral communities (Schindler and Scheuerell, 2002). As the undulation of littoral area was strongly linked with the underwater morphometry (Dearing, 1997), a consistent loss in littoral zones has been widely found in lakes that were converted to deeper reservoirs (Hellsten and Riihimäki, 1996). In Haixi Lake, ~90% of the modern macrophyte coverage was located in a water depth of < 5 m, and the littoral area (i.e. water depth < 5 m) has displayed a significant loss with increased water depth (Fig. S7). Similarly, an increase of water level by 1.7 m due to the installation of a sluice led to a swift drop of submerged vegetation coverage from 25 to 30% to < 2% in a large shallow lake of Eastern China (Kong et al., 2017). Conversely, the water level drop after a sustained period of high waters may not lead to the recovery of submerged vegetation in shallow lakes (Havens et al., 2005).

4.2. Biogeochemical cycling in response to hydrological regulation

The artificially extended gradient of water depth in Haixi Lake has significantly impacted nutrient cycling over time. The consistently low concentrations of TN (Fig. 4) suggested that the lake was nutrient-poor during the period of ~1800–1957, reflecting low nutrient loadings from the catchment that were often found in this region (Ni and Wang, 2015). A moderate increase in sediment TN since the 1930s corresponded with an expanding population and agricultural development as recorded in other lakes of this study region (Li et al., 2007). A further increase of bulk TN concentration occurred around the period of 1990–2013 (Fig. 4a) may be related to the moderate expansion of agricultural land and associated nutrient input since the 1980s (Fig. S6), as well as a prolonged water residence time and reduced flow velocity after the construction of hydropower dams (Kawara et al., 1998). In contrast, the accumulation rate of sediment TN displayed a long-term and significant decrease since ~1957, possibly reflecting the dilution effect of increased water storage as there was a doubled increase in lake volume from $2.1 \times 10^6 \text{ m}^3$ in 1957 to $>4.0 \times 10^6 \text{ m}^3$ for the last two decades (Fig. S3). This dilution effect has clearly been found to exist in designing water-level management for dammed lakes and reservoirs of North America (Christensen and Maki, 2015).

Lake level fluctuation is well documented to alter the carbon cycling and biogeochemical processes (Piovano et al., 2004; Woszczyk et al., 2014). In consistent with the depth-related spatial distribution across the lake basin (Fig. 2), sediment TOC concentration and C/N ratio experienced a remarkable decrease with raised water levels over time (Fig. 5). The lowest C/N ratios in recent deposits reflect a greater contribution of algae-derived organic matters that are high in nitrogen-rich proteins and lipids, as lake expansion was often associated with a decrease in C/N ratio (Korosi et al., 2017). The relatively large values of C/N ratio and TIC flux during ~1840–1900 indicated a high input of catchment-derived allochthonous materials (Fig. 5e), while the peak values in the C/N ratio and carbon fluxes occurred around ~1940–1957 when a minimum level of lake depth (~5 m) was found for the last two centuries (Fig. 5e). Furthermore, our results displayed that the burial and accumulation rate of OC are closely related to the gradient of water depth and associated limnological properties over time. Noticeably, the accumulation rate of TOC displayed a consistent decrease since the damming in 1957, with significantly lower fluxes observed for the dam enforcement stage than those during the pre-damming stage (Fig. 5d). This temporal pattern contrasted

strongly with an increasing rate of OC burial for northern lakes driven by regional warming and atmospheric deposition (Heathcote et al., 2015), as well as a regional increase in TOC storage in lakes across China due to intensifying land use (Wang et al., 2015).

Our results may well reflect the role of lake depth in determining carbon burial processes as higher storage rates were often found in shallow lakes (Downing, 2010). It has been estimated that the sediment OC burial could be more than doubled increased in reservoirs than that in natural lakes during the last few decades due to the consistent increase in the number of reservoirs (Cole et al., 2007). While there existed an overall increase in sediment carbon burial rate after lake damming in 1957 (Fig. 8), our results also showed that the TOC flux was significantly reduced with higher water levels ($r = -0.58$, $p < 0.01$), with a significant drop in the sediment carbon fluxes during the dam reinforcement stage. Simultaneously, there was a significant decrease in both C/N ratio and littoral habitats after 1990, reflecting the increased carbon utilization via aquatic carbon dioxide fixation (Baastrup-Spohr et al., 2016). When compared to land-derived OC, these aquatic organic matters are characterized by high degradation rates and low sediment storage, potentially causing stronger water-atmosphere exchange of greenhouse gases (Mendonça et al., 2017). Despite that the sediment content and flux of TOC displayed a temporal trajectory that generally followed those of TIC (Figs. 4a and 5), the ratio between TIC and TOC fluxes was significantly elevated during the enforcement stage when compared to the previous two stages (Fig. 8). This can partly be due to enhanced mineralization rate of OC and their transformation to inorganic carbon in stratified and anoxic waters with increasing water depth (Clayer et al., 2016), as well as warmer climate during the last few decades (Gudasz et al., 2010). As the various forms of inorganic carbon can easily release CO_2 (Bade, 2009), the monitoring results have shown that greenhouse gas efflux to the atmosphere in reservoirs was about twice the magnitude of that in natural lakes (St. Louis et al., 2000). Therefore, the increased impoundment intensity and dominance of aquatic organic matters has significantly reduced sediment OC storage in our lake in the context of regional warming, which more recently served as a new inorganic carbon source allowing for stronger greenhouse gas emission.

4.3. Temporal patterns of algal production and community shift

The concurrent increase in Chl. *a* and TN concentrations suggested a greater lake production over time due to enhanced nutrient cycling and hydrological retention (Kaushal and Binford, 1999; Meyers, 2003). For example, the algal production increased with rising water levels and expanded euphotic zone, which was also reflected in a declining C/N ratio. The $\delta^{13}\text{C}_{\text{organic}}$ signal was significantly depleted with increasing impoundment intensity (Fig. 4a), inferring the increased input of autochthonous sources such as phytoplankton (Meyers and Ishiwatari, 1993). Meanwhile, there was a lack of significant link between sediment TN and Chl. *a* during ~1810–1990 when lake level was below 10 m (Fig. 5). This contrasting pattern in the nutrient-biomass relationship among hydrological stages may well reflect the difference of hydrological processes such as mixing and flushing. This was evident in a multi-basin lake where sediment resuspension and nutrient release in shallow basins decoupled the nutrient-biomass relationship (Zhang et al., 2013). Under the more nitrogen-rich conditions, as was the case for Haixi Lake (Table 1), moderate nutrient enrichment can enhance autochthonous OM with enriched $\delta^{15}\text{N}$ signal because of the dominance of non- N_2 fixing algae which discriminated against lighter isotopic signals (Meyers, 1997). Thus, along the extended water depth gradient in Haixi Lake, the stratigraphic

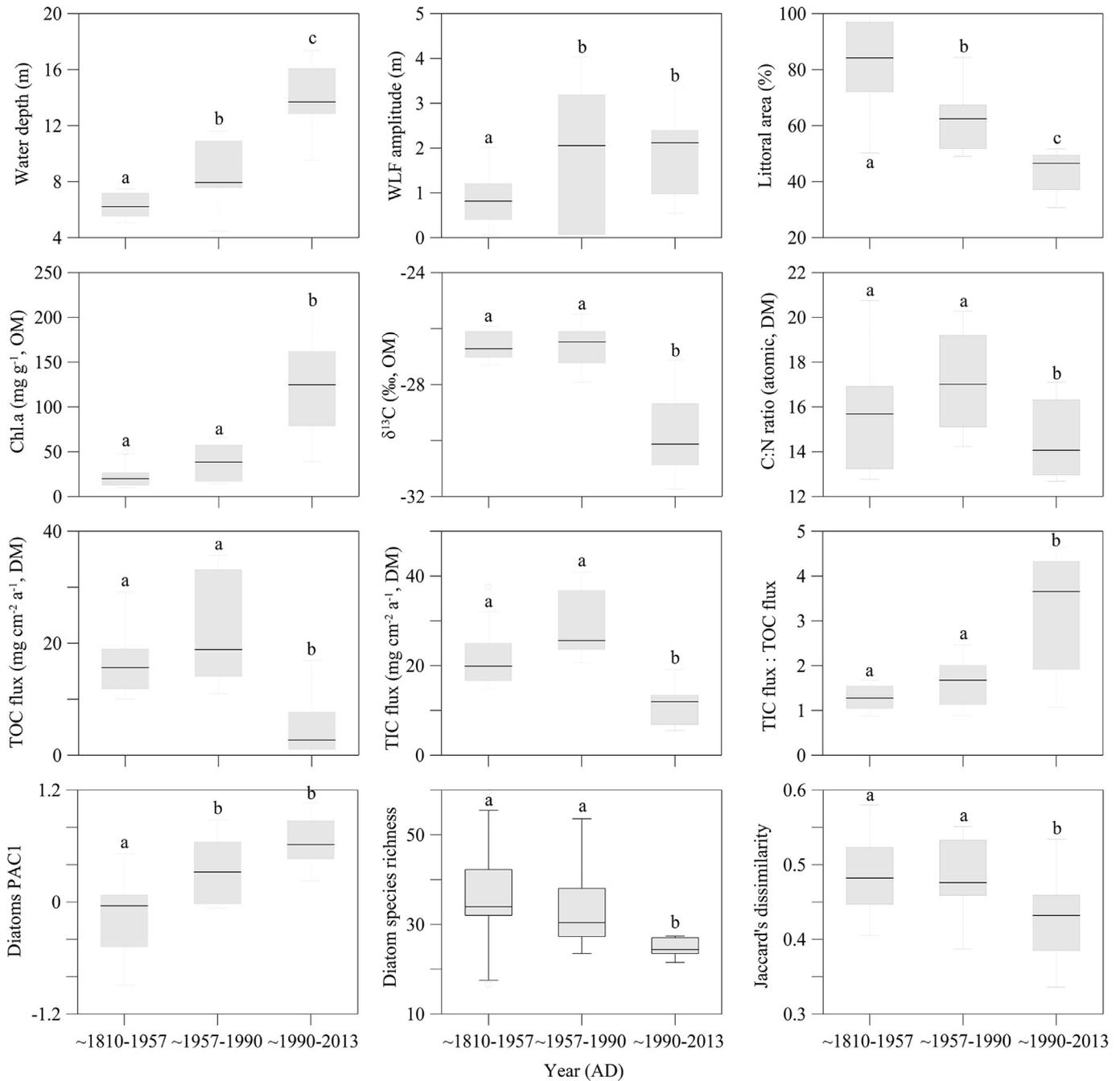


Fig. 8. Boxplots showing the comparison in lake hydro-morphology (inferred-water depth, WLF amplitude and littoral area; first row), lake production (Chl.a, $\delta^{13}\text{C}_{\text{organic}}$ and C:N ratio; second row), carbon fluxes (TOC flux, TIC flux and their ratio; third row) and diatom changes (sample score of diatom PCA axis 1, species richness and Jaccard's dissimilarity; fourth row) among the pre-disturbance (~1810–1957), post-damming (~1957–1990) and post-reinforcement (~1990–2013) stages, respectively. The significance test was based on Student's t-test with different letters indicating a significant difference between groups ($p < 0.05$).

changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals of OM over the past two centuries may have been a result of increasing autochthonous OM (Furey et al., 2004).

Diatom community shift was well reflective of water level increase and enhanced thermal stratification. During the pre-disturbance stage of ~1830–1930, the dominance of the small and planktonic *Cyclotella ocellata* (i.e. > 50%) suggested the existence of a turbulent and nutrient-poor shallow system (Soylu et al., 2007). With a continuous increase in water level from ~1957, this species typically predated other sub-dominant species during the temporal community succession, confirming its high sensitivity to

the change of thermal regime (Cremer and Wagner, 2003; Padišák et al., 2009). Our modern surveys (Fig. S1) showed the existence of thermal stratification in summer with raised water levels (Kling, 1988), which would favor small, fast-growing planktonic diatoms such as *Cyclotella* (Smol et al., 2005). Furthermore, regional climate has warmed markedly in recent decades (Fig. S1), often leading to a longer and stronger thermal stability (Wilhelm and Adrian, 2008). Similarly, the abundance of small *Cyclotella* was strongly linked with mean air temperature ($r = 0.58$, $p = 0.007$) for the last six decades in Haixi Lake.

Diatom assemblages were also characterized by response to the

damming-related changes in nutrients, benthic habitats and hydrological fluctuation (Fig. 5). Our sediment records revealed a synchronous change of *F. crotonensis* with TN ($r = 0.469$, $p = 0.002$), which was an indicator species in N-rich waters (Macintyre et al., 2009). Similarly, *C. comta* displayed a gradual increase after ~1980 with elevated TN as found in other studies (Chen et al., 2012). The loss of littoral zones also likely played a role in structuring diatom assemblages, leading to a gradual decrease in benthic diatoms (Fig. 5b). Furthermore, a moderate increase in *A. granulata* was consistent with a significant increase in the magnitude of WLF since ~1960, as this species is characterized by high sinking rates and competitive advantage in turbulent waters (Vieira et al., 2008). Noticeably, *A. minutissima*, the subdominant benthic diatoms over the core, was found to be more abundant after ~1957. This species was known to grow favorably not only in the littoral zones (Laird et al., 2011), but also can proliferate as epilithon over a long depth gradient (i.e. up to ~24 m) in oligotrophic lakes with frequent water level fluctuation (Cantonati et al., 2009).

4.4. Ecological shifts along the impoundment intensity gradient

Water depth and associated hydrological variables showed a stronger impact on diatom communities during the damming stage, when compared to the pre-disturbance and reinforcement stages (Fig. 6). The loss in littoral habitats may have been triggered by lake damming (Geest et al., 2005; Li et al., 2007; Wang et al., 2015), leading to a significant decrease in diatom species richness in Haixi Lake, as found in spatial surveys of lake biota such as zooplankton (Gal et al., 2013) and fish (Langer et al., 2017). Furthermore, the break-point analysis suggested a threshold depth of ~10.8 m for diatom species richness, which was consistent with the spatial surveys with a threshold depth of ~9.0 m found in temperate lakes (Laird et al., 2010). This water depth-dependence of biodiversity patterns was also obvious in deeper lakes with stronger thermal resistance to water mixing (Longhi and Beisner, 2010). Similarly, there existed a significant decrease in community dissimilarity with the lake depth raised above ~9 m (Fig. 7b), suggesting a higher degree of community stability and stronger ecological resistance to external stressors in this deep-water environment (Wantzen et al., 2008). Accordingly, a shift from benthic to planktonic pathway of energy flow was evidenced in the significant increase in algal production and a clear depletion of $\delta^{13}\text{C}_{\text{organic}}$ signals during the enforcement stage of this oligo-mesotrophic lake (Fig. 8). Comparably, this pattern was often found in shallow lakes with a regime shift to an algae-dominated state with the loss of macrophytes due to eutrophication (Torres et al., 2012). Meanwhile, there existed a significant decrease in the reconstructed littoral area (% < 5 m depth) that was strongly linked with macrophyte growth in response to expanding water depth over the last two centuries (Fig. S7b). While water level control has been found to enhance the role of nutrients in causing regime shifts in shallow lakes (Kong et al., 2017), the expanded gradient of water depth alone may have shifted the ecological regime towards a phytoplankton-dominated state in Haixi Lake after ~1990.

Our results also revealed that WLFs can influence biodiversity under the theoretical framework of intermediate disturbance hypothesis. Modern surveys have shown that an intermediate level of hydrological disturbance could enhance the degree of community shift for aquatic biota such as macrophyte and phytoplankton (Elliott et al., 2001; White et al., 2008; Li et al., 2012b). Both diatom species richness and the degree of community shift was found to be higher under a moderate amplitude of water levels (i.e. < 2 m) in Haixi Lake over time (Fig. 7c and d), corresponding well with experimental results (Casanova, 1994; Evtimova and Donohue, 2014). Similarly, an increased amplitude of WLF (i.e. > 2 m/

month) in subtropical reservoirs played a negative impact on algal production (Yang et al., 2016) and significantly affected phytoplankton structure (Yang et al., 2017). While dam enforcement further deepened water levels and significantly altered limnological processes, the amplitude of WLF after 1990 remained similar as that found for the damming stage (Fig. 8). This may suggest an independent role of WLF magnitude in affecting community stability, despite that the interaction between water depth and WLF may exist in shallow lakes (Evtimova and Donohue, 2016). While our sediment records were characterized by capturing an integrated signal of WLF and ecological changes beyond the seasonal variability, long-term monitoring data revealed that the annual mean variation in WLF was often greater than the monthly fluctuation (Evtimova and Donohue, 2016). Therefore, an implication for reservoir management derived from our study is that there may exist a threshold level for both water depth and the amplitude of WLF, beyond which community stability and ecological state will be significantly altered over time with detrimental effects on biodiversity.

5. Conclusions

In consistent with the documented events of hydrological regulation, our sediment records revealed a two-century history of a significant increase in lake levels with increasing impoundment intensity. Along an expanded gradient of lake depth, a gradual loss of littoral zone and benthic diatoms over the last few decades was consistent with a significant depletion of $\delta^{13}\text{C}_{\text{organic}}$ signal, suggesting a dominance of pelagic trophic pathway and autochthonous source in aquatic organic carbon transfer after ~1990. Despite that there was a significant increase in the algal production since ~1990, the accumulation rate of TOC displayed an accelerating decrease since ~1957, reflecting a dilution effect derived from expanding water storage. With a significant shift in lake ecological state after the dam enforcement, the enhanced inorganic carbon burial, coupled with strong degradation and low storage of aquatic organic matters, can allow for stronger emission of greenhouse gases from this deep-water reservoir. While hydro-morphological fluctuation impacted diatom community shift, a further increase in water depth during the dam enforcement stage has significantly decreased diatom biodiversity and community heterogeneity when a threshold level in water depth or the WLF amplitude was reached. Meanwhile, the nutrient and climate forcing showed an increasing interaction with hydrological variables in structuring diatom changes across the three hydrological stages. Therefore, lake impoundment not only significantly regulated hydrological regime, carbon cycling and algal shift over time, but also enhanced the ecological role of nutrient and climate forcing with increasing impoundment intensity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.watres.2018.10.032>.

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