Local and regional drivers of environmental changes in two subtropical montane ponds (central China) over the last two centuries

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HIGHLIGHTS

Primary producers of two subtropical montane ponds exhibited changes from the 1900s. The drainage versus seepage hydrologies of each pond were important modulators of primary production. Temperature and nitrogen deposition interacted with local catchment conditions to influence ecosystem response

Authors Contributions: XC and SM conceived and designed the study. XC, SM, JP, TZ, XB, and LZ collected and analysed the data. XC and SM wrote the manuscript.
Abstract: Central China, one of the Earth’s distinctive ecoregions due to its endemic subtropical biota, has been subjected to enhanced nitrogen deposition and climate warming during recent decades. However, the extent and timescale of ecological changes are largely unexplored. Multiproxy analyses (diatoms, photosynthetic pigments and geochemistry) of $^{210}$Pb-dated sediment cores from two shallow ponds within an alpine basin (central China) were used to investigate the response of primary producer communities to external stressors during the last two centuries. The study sites include one drainage pond and one seepage pond. Both ponds exhibited unambiguous changes in production and composition of photoautotrophs since the early 20th century, which are linked to climate warming, nitrogen deposition and local factors (e.g. lake morphometry, desiccation and macrophyte). Although primary producers responded to regional warming and nitrogen deposition, the ecological responses differed among ponds due to local factors. In the deeper seepage pond, light attenuation due to terrestrial organic matter input caused recent decreases in carotenoids and small fragilarioid taxa. In contrast, the co-occurrence of euterrestrial and tychoplanktonic diatoms in the shallower drainage pond was indicative of its hydrological instability. Our results indicate that subtropical montane ponds in the East Asian monsoon region appear to be strongly influenced by the combined effects of local (e.g. catchment-lake connectivity) and regional driving forces (e.g. warming and nitrogen deposition).

Keywords: diatom; pigment; nitrogen deposition; climate warming; lake morphometry; palaeolimnology
INTRODUCTION

Montane lakes are remote aquatic ecosystems characterized by prolonged ice cover, short growing seasons, dilute water chemistry and low primary production (Catalan and others 2013; Wolfe and others 2013). As such, montane lakes may act as sentinels for a variety of environmental stressors, such as climate warming, hydrological alteration, and nitrogen deposition (Moser and others 2019). Algae, the dominant primary producers in aquatic ecosystems, are of global significance for biogeochemical cycling, and are an invaluable bioindicators of ongoing global change due to their wide distribution, high diversity, and sensitivity to habitat alteration (Rühland and others 2015). Local and regional driving forces may induce shifts in primary producers of montane water bodies, with substantial implications for higher trophic levels and ecosystem structure and function (Catalan and others 2013; Rühland and others 2015; Hobbs and others 2016).

A number of processes have been proposed as contributors to observed changes in primary producer communities of alpine lakes. Firstly, the elevated inorganic nitrogen concentrations due to atmospheric deposition has increased primary production in lakes (Bergström and Jansson 2006). Secondly, climate warming is proposed to enhance primary production by prolonging the growing season (Rühland and others 2015). Thirdly, changes in local factors, such as catchment-lake hydrological connection, are important driving forces for shifts in primary producers (Hu and others 2018; Moorhouse and others 2018; Hadley and others 2019). For example, vegetation and soil development can increase the influx of terrestrial coloured dissolved organic matter (CDOM) to lakes (McGowan and others 2018a), imposing a dual effect on primary producers, via nutrients (positively) and light (negatively) (Bergström and Karlsson 2019). Due to the complexities of these processes, the ecological responses of small
and shallow montane lakes may vary spatially and temporally (Catalan and others 2013; Rühland and others 2015).

Present knowledge on the effects of multiple stressors on primary producers mainly derives from Arctic, European and North American montane lakes (Binford and others 1987; Caballero-Miranda 1996; Saros and others 2005; Catalan and others 2013; Rühland and others 2015; Hobbs and others 2016; Smol 2016; Moorhouse and others 2018), while there is a paucity of information on montane lakes in subtropical East Asia (Hu and others 2018; Wang and others 2020). Montane lakes are considered to be relatively pristine, nutrient-limited and seasonally frozen, and hence more sensitive to influxes of energy or mass from atmospheric changes (Vogt and others 2011; Smol 2016; Hadley and others 2019). Small and shallow lakes may show more pronounced biological responses to global environmental changes than deep lakes, due to their unique features of low water volumes and hydrological sensitivity resulting from high catchment: lake area ratios (Spaulding and others 2015; Rantala and others 2017; Giles and others 2018).

In monsoonal regions where rainfall patterns are generally intense and highly seasonal, the transfer of carbon and nutrients between the watershed and lake is likely to be highly efficient. However, the ecological responses of shallow lakes to eutrophication and hydrological changes are known to be complex because of strong benthic-pelagic interactions, which can result in distinctive macrophyte-dominated and turbid states (Squires and others 2002; Vadeboncoeur and others 2003; Scheffer and Jeppesen 2007). Long-term (millennial-scale) changes in lake level of montane lakes are associated with shifts in monsoonal cycles, and lake level variability has been linked to changes in ecosystem state in shallow lakes (REFS). Strong potential exists, therefore,
for abrupt ecosystem transitions in subtropical montane ponds which may be detectable in longer term records as recovered by palaeolimnology (Briddon and others 2020).

Recently there has been increasing interest in environmental changes in montane lakes of China (Hu and others 2014; Chen and others 2018; Yan and others 2018; Kang and others 2019). In northern China, Chen and others (2018) found that rising primary production was consistent with enhanced nitrogen deposition in a montane lake after the 1980s. In contrast, the responses of algal communities to atmospheric deposition are more muted in alpine lakes of southwestern China, probably mediated by catchment processes (Hu and others 2014, 2018; Kang and others 2019). Algal communities of deeper stratified lakes shift mainly due to weak mixing and strong stratification caused by warming in both northern and southern China (Chen and others 2014; Yan and others 2018). For achieving a deeper understanding of the combined effects of local and regional driving forces, there is a necessity to decipher the response of primary producer communities across a broader geographic area. Central China, located in the East Asian monsoon region with synchronous changes in seasonal rainfall and temperature, displays a rapid warming trend of 1.5 °C/100 years during the last century (Wang and others 2009). In Central China, nitrogen deposition is dominated by wet deposition and demonstrates the world’s greatest increase rate (Ackerman and others 2019). The combination of local and regional drivers may cause substantial shifts in primary producer communities of montane lakes in central China.

In this study, we present fossil diatoms, preserved pigments and geochemical data (δ13C, δ15N, total organic carbon and total nitrogen) in sediment cores from two shallow but hydrologically different montane ponds (a seepage pond and a drainage pond with an outlet) in an alpine basin located in central China. Seepage ponds without surface outlets should enhance the accumulation of organic matter due to prolonged water
residence times, in comparison with drainage ponds (Spaulding and others 2015). We hypothesize that light attenuation due to enhanced CDOM accumulation in the slightly deeper seepage pond will inhibit the growth of some benthic algae, whereas primary producers (including macrophytes and phytobenthos) in the very shallow drainage pond would be free of light limitation and so probably more directly responsive to changing nutrient fluxes. The objectives of this study were to (1) investigate changes in primary producer communities of two montane ponds during the last two centuries; (2) evaluate potential effects of local (e.g. catchment-lake hydrological connectivity) and regional (e.g. climate warming, rainfall and nitrogen deposition) drivers on primary producer communities.

**MATERIALS AND METHODS**

**Study area**

Congping Basin (31°24′12″N, 110°03′25″E, 2080 m a.s.l.) is located in the Three Gorges Area (central China) that is a transition zone between the western mountains and the eastern plain of China (Fig. 1A). Bedrock within the basin is Triassic limestone, while the surrounding highlands feature Permian sandstone and sandy shale. The regional climate is strongly influenced by the subtropical monsoon, with cold, dry winters and cool, wet summers. There is a weather station at the nearby Dajiuhu Wetland (31°28′50″N, 110°00′09″E, 1758 m a.s.l.; 10 km away from Congping Basin). Mean annual air temperature is ~8°C, and mean annual precipitation is ~1700 mm at Dajiuhu weather station (Fig. 2a; Li and others 2019). According to the vertical lapse rate of temperature of 0.5 °C/100 m, air temperature at Congping would be ~1.5°C colder than at Dajiuhu. Mean monthly air temperature at Congping Basin is estimated to range from -6 °C to -2 °C between December and February (Fig. 2a), and hence water
bodies are ice-covered during the winter. Over the last century, temperature increased remarkably from the early 20th century, followed by a slight decrease until recent warming since the 1980s (Fig. 2b; Wang and others 2009). In contrast, seasonal precipitation displayed fluctuant trends over the last century, with an increasing trend in winter precipitation after 1980 (Fig. 2c). The mountains around the basin are characterized by montane conifers (e.g. *Pinus*, *Picea* and *Abies*), while the lowland vegetation within the basin is alpine meadow scattered with more than ten shallow ponds (Fig. 1B). The alpine meadow is dominated by *Carex*, *Allium* and *Sphagnum*. Surface soil in the basin is Alfisol, which is characterized by high proportions of SiO$_2$ (57%), Al$_2$O$_3$ (13%) and organic matter (18%, estimated by loss on ignition at 550°C), low contents of MgO (1.7%), CaO (0.6%) and Na$_2$O (0.8%), and relatively low pH (5.4) (Mo 2019).

These small ponds are developed from karst depressions, and there is no knowledge of these lakes drying within the last ~50 years. Humans have had relatively little direct effect on the landscape, with the exception of the expedition. Congping (CP) and Mulong (ML) ponds are selected as study sites (two unnamed ponds on published maps, Fig.1), and both of them are weakly-acidic, humic, oligotrophic, electrolyte-poor and fishless (Table 1). CP is a much shallower (20cm depth) drainage pond, covered with *Sparganium stoloniferum* (coverage of ~30%) with an outlet at the east, while ML is a deeper (1.5m depth) seepage pond with *Sphagnum* development around lake margins (Fig. 1).

**Sample collection and laboratory analysis**

Parallel sediment cores were retrieved from CP using a Russian corer in June 2016, and from ML using a Kajak gravity corer in September 2017, respectively. The gravity
The corer was most suitable for collecting short cores from soft sediments in the deeper ML Pond. The length of sediment cores collected from CP and ML was 50 cm and 33 cm, respectively. The sediment cores were sectioned immediately in field at 1-cm intervals. The samples were stored at <4 °C until analysis; pigment sub-samples were stored frozen at -20 °C prior to laboratory analysis. Sediment samples were analysed for radioactive isotopes (\(^{210}\)Pb, \(^{226}\)Ra and \(^{137}\)Cs), total organic carbon (TOC), total nitrogen (TN), carbon and nitrogen isotopes, particle size spectra, diatoms and pigments.

The radioactivities of \(^{210}\)Pb, \(^{226}\)Ra and \(^{137}\)Cs were measured at 2-cm intervals in ML and at 4-cm intervals in CP on a gamma spectrometer (Ortec HPGe GWL) following the procedures described in Appleby (2001). Following treatment with 10% HCl to remove carbonate, the samples were rinsed 3 times in distilled water and oven dried at 45°C. All dried samples were powdered in preparation for measurement of TOC, TN, \(\delta^{13}C\) and \(\delta^{15}N\). TOC and TN were measured by combustion with an elemental analyser (vario EL cube), with reference to standard samples (precision of ±0.1%). \(\delta^{13}C\) and \(\delta^{15}N\) of organic matter were determined using a Thermo Fisher Scientific stable isotope mass spectrometer (DELTA V advantage), with reference to standard samples (precision of ±0.3‰). TOC, TN, \(\delta^{13}C\) and \(\delta^{15}N\) were analysed at intervals of every 2-cm. Measured \(\delta^{13}C\) values were corrected for the Suess effect (the decrease in \(\delta^{13}C\) of the atmosphere due to the release of CO\(_2\) with low \(^{13}C\) content by fossil fuel burning) following the polynomial correction factor described by Neumann and others (2002).

Particle size spectra of samples were measured at 1-cm intervals using a Malven automated laser optical particle-size analyser (Mastersizer-3000) after the removal of carbonates by 10% HCl and organic matter by 30% H\(_2\)O\(_2\).

Diatom samples were treated with HCl (10%) and H\(_2\)O\(_2\) (30%) following the standard procedures (Battarbee and others 2001), and diatoms were counted using an
Olympus BX53 microscope with an oil immersion objective at 1000×. A minimum of 300 valves were counted in each sample. Diatom taxonomy mainly followed Krammer and Lange-Bertalot (1986-1991). For pigment analyses, freeze-dried weighed sediments (∼200 mg) were extracted in a mixture of acetone: methanol: water (80: 15: 5) by leaving in a -20 °C freezer for 24 h. Extracts were filtered with a 0.22-μm-pore PTFE filter, dried under N₂ gas, re-dissolved in an acetone: ion-pairing reagent: methanol mixture (70: 25: 5) and then injected into an Agilent 1200 series high-performance liquid chromatography unit. Pigments were identified and quantified based on their retention time and absorption spectra, compared with pigment standards (Leavitt and Hodgson 2001; McGowan 2013). To calculate pigment concentrations, chromatogram peak areas were calibrated using commercial standards (DHI Denmark). Linear regressions (r > 0.99) of mass pigment injected (as volume × concentration) and peak area were used for calibration (Leavitt and Hodgson 2001). Lutein and zeaxanthin did not separate in this study and so were reported here together. All concentrations were expressed as nmol g⁻¹ organic carbon.

**Data analysis**

Zonation schemes were developed for diatoms and pigments using the broken-stick model (Bennett 1996) using stratigraphically constrained cluster analysis (CONISS) in the Tilia program (Grimm 1991). Seasonal climate anomalies in the study area were collected from Atlas of Seasonal Temperature and Precipitation Anomalies over China (1880-2007) (Wang and others 2009). An early detrended correspondence analysis (DCA) showed that the gradient lengths of the diatom and pigment data from both ponds were less than 2 standard deviations, and hence principal component analysis (PCA) was used to summarise the major trends and a linear model (redundancy analysis,
RDA) was used to reveal the correlations between primary producer communities and explanatory variables. Considering the uncertainty of the $^{210}\text{Pb}$ chronologies prior to ca. 1850 and the timescale of available paleoclimate data, only data from ca. 1880 were used in the RDAs. In the RDAs, diatoms and pigments were used as response variables, and the explanatory factors included TOC, TN, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, anomalies in seasonal temperature and precipitation. Forward selection, with the false discovery rate correction and the Monte Carlo tests ($p<0.05$, $n=999$ unrestricted permutations) was used to reduce the explanatory factors to those correlating significantly with response variables. Ordination analyses were performed using CANOCO 5.0 (Šmilauer and Lepš 2014).

RESULTS

Lithology and chronology

Sediments in the CP core consisted of grey silty gyttja between 50 and 40 cm, yellow-grey gyttja between 40 and 22 cm, yellow gyttja with many plant remains in the uppermost 22 cm. Sediments in the ML core were mainly composed of black gyttja, with many plant remains in the bottom layers (below 26 cm). Sedimentary particle size spectra, i.e. clay (< 4 $\mu$m), silt (4 - 64 $\mu$m) and sand (> 64 $\mu$m), are shown in Fig. 3. Sediments were dominated by silt and clay in the drainage pond CP, and by silt and sand in ML, the seepage pond. Concentrations of excess $^{210}\text{Pb}$ ($^{210}\text{Pb}_{\text{ex}}$) were calculated by subtracting the $^{226}\text{Ra}$ supported $^{210}\text{Pb}$ concentrations from the total $^{210}\text{Pb}$ activities (Appleby 2001). The $^{210}\text{Pb}_{\text{ex}}$ profile is non-monotonic in both ponds (Fig. 3). One possible explanation is that hydrological changes due to monsoonal climate variability have influenced soil erosion and so sedimentation rates in these alpine ponds. Alterations in initial concentrations of $^{210}\text{Pb}$ and sedimentation rates indicate that both
the constant initial concentration (CIC) and constant flux constant sedimentation (CFCS) models fail to yield a reliable chronology (Appleby 2001). The constant rate of supply (CRS) allows changes in the initial concentrations and the sedimentation rates at different layers, and hence the CRS model yields more realistic results than the CIC and CFCS models (Appleby 2001). The $^{137}$Cs activities reached a peak at 11.5 cm in CP core (Fig. 3a) and at 12.5 cm in ML core (Fig. 3b), which can be assigned to the 1963 maximum atmospheric global fallout as a result of nuclear weapons testing (Appleby 2001). In order to improve the accuracy of the chronology, the $^{137}$Cs 1963 peak was used as an independent dated reference level. The final age-depth model was calculated using the CRS model, together with the $^{137}$Cs 1963 peak as a reference level.

Mass accumulation rate (MAR) in CP core increased to a peak around the 1880s, and reached consistently low rates from the 1970s onwards after a visible decrease between the 1880s and the 1970s. In contrast, MAR in ML core displayed a rising trend toward the core tops.

258

**Diatom stratigraphy**

Over 143 diatom taxa were identified from the two sediment cores, with a relatively high species richness of taxa which prefer oligotrophic conditions. The diatom assemblages were dominated by benthic taxa, such as *Staurosira construens* var. *venter* (Ehrenberg) Hamilton, *Navicula cryptotenella* Lange-Bertalot, *Sellaphora pupula* (Kützing) Mereschkowsky, and *Pinnularia microstauron* (Ehrenberg) Cleve, with frequent occurrences of *Aulacoseira alpigena* (Grunow) Krammer (Fig. 4). The two ponds had different taxonomic and temporal changes in diatom composition, in spite of their adjacent locations.
In CP, diatom assemblages were characterized by eutererestrial species before ca.1910 (Fig. 4a), such as *Hantzschia amphioxys* (Ehrenberg) Grunow and *Pinnularia borealis* Ehrenberg. The most pronounced changes occurred between 1910 and 1922, with the replacement of eutererestrial species by opportunistic species (i.e. *S. construens* var. *venter* and *Achnanthidium minutissimum* (Kützing) Czarnecki). Between 1922 and 1980, *A. alpigena*, *Cymbopleura naviculiformis* (Auerswald) Krammer, *Eunotia mucophila* (Lange-Bertalot et Nörpel) Lange-Bertalot increased gradually at the expense of a visible decrease in *S. construens* var. *venter*. The subdominant species *Gomphonema parvulum* (Kützing) Kützing and *S. pupula* increased to a peak at around 1930, and gradually decreased thereafter. After 1980, diatom communities were co-dominated by *S. construens* var. *venter* and *A. alpigena*, and remained relatively stable.

In ML, epiphytic or epipelic species were dominant throughout the record, including *S. construens* var. *venter*, *N. cryptotenella*, *S. pupula* and *P. microstauron* (Fig. 4b). After 1955, epiphytic diatoms increased towards the core tops, such as *Brachysira brebissonii* Ross, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt and *Eunotia exigua* (Brébisson) Rabenhorst. *S. construens* var. *venter* remained the dominant species, despite its recent decrease. The subdominant species *N. cryptotenella* increased to a peak at around 1963, followed by a gradual decrease.

**Pigment stratigraphy**

In CP, all pigments exhibited similar patterns with low concentrations before 1925. Thereafter they all began to increase, with further visible increases after 1960 (Fig. 5a). In ML, there were two obvious shifts in pigment composition (Fig. 5b). Before 1948, pigment composition was characterized by high concentrations of alloxanthin (cryptophytes), fucoxanthin and diatoxanthin (siliceous algae), lutein-zeaxanthin (from
plants, chlorophytes and cyanobacteria), pheophytin $b$ (plants and chlorophytes), pheophorbide $a$ (grazing or degradation of Chl $a$). Lutein-zeaxanthin increased to a peak between 1948 and 1980, concurrent with relatively stable concentrations of other pigments. Chl $a$ and Chl $b$ increased exponentially after 1980, with concurrent decreases in carotenoid pigments.

Geochemistry records

The changing TOC and TN contents are accompanied by significant variations in the isotopic composition of organic matter (Fig. 6). Sedimentary $\delta^{15}$N values became significantly lighter towards the sediment surface in the two lakes, i.e. from 0.3‰ to -1.5‰ in ML and from 6.4‰ to 1.6‰ in CP. Sedimentary TN showed a linear increase in both lakes after the 1900s, especially a recent acceleration since the 1980s. The Suess-corrected $\delta^{13}$C changed in the opposite directions in the two lakes, i.e. an increase in ML but a decrease in CP. TOC gradually increased by ca. 10% in CP, whereas it decreased slightly before the 1970s, followed by a rebound in ML. The molar ratios of carbon to nitrogen (C/N) ranged from 11 to 20 in both lakes. C/N ratios in CP were variable, but generally increased before 1960 and decreased thereafter; while the ratios were more stable and exhibited a gradual decrease in ML.

Multivariate analysis

In CP, diatom PCA 1 and pigment PCA 1 captured 47% and 81% of the total variance in diatoms and pigments, respectively. Diatom PCA 1 represented a shift from euterestrical (e.g. H. amphioxys and P. borealis) to aquatic taxa, while all the pigment types were positively correlated with pigment PCA 1. In ML, diatom PCA 1 and pigment PCA 1 explained 64% and 40% of the total variance in diatoms and pigments,
respectively. Diatom PCA 1 was most strongly correlated with changes in small fragilarioid and moss-attached taxa, while pigment PCA 1 in ML was positively correlated with changes in chlorophylls. Diatom and pigment PCA 1 sample scores of the two lakes displayed obvious changes from the early 1900s, broadly corresponding to the $\delta^{15}N$ depletion in the two sediment cores, the nitrate enrichment in the Himalayan ice core (Thompson and others 2000), the rising nitrogen content and the $\delta^{15}N$ (NO$_3^-$) depletion in the Greenland ice core (Geng and others 2014) (Fig. 7). In the RDA analyses of environment-diatom and -pigment correlations at CP and ML ponds, both diatom and pigment assemblages were significantly correlated with seasonal temperature and $\delta^{15}N$ but not with changes in total annual rainfall (Fig. 8).

DISCUSSION

The Congping basin receives water from the surrounding mountains (local relief ca. 300m) and is an interconnected mosaic of alpine meadows, wetlands and ponds. Such heterogeneity is driven by localised conditions across the basin and is important in supporting terrestrial and aquatic biodiversity of this region (Chen and others 2012). Our results indicate different conditions in water bodies located within a few hundred metres of one another. Although primary producers responded to the same regional drivers of nitrogen deposition and warming, the ecological consequences differed among ponds (Fig. 9). Differences in hydrological setting, water depth and macrophyte communities between the drainage and seepage ponds are useful in helping to understand the divergent ecological responses.

Lake-specific factors
Before the 1900s, high abundances of euterrestrial diatom species (e.g. *H. amphioxys* and *P. borealis*) were concomitant with occasional occurrence of tychoplanktonic species (i.e. *A. alpigena*) in the very shallow drainage pond CP, suggesting that it was ephemeral (seasonally dried out) during the dry season (winter), with episodic flooding and water-level rises in the wet season (summer). The near absence of pigments apart from alteration products of chlorophylls *a* and *b* (pheophytin *a* and *b*) corroborates the idea of seasonal desiccation because exposure to oxygen and light accelerates pigment degradation (Leavitt and Hodgson 2001). A seasonally desiccated wetland would most likely be dominated by wetland plants such as sedges, rushes and mosses which produce chlorophylls *a* and *b*, consistent with the pheo-pigments recorded. Due to water table drawdown in the dry season and wind-driven mixing, kinetic isotope fraction during protein hydrolysis likely contributed to the $^{15}$N-enrichment in oxic conditions (Lehmann and others 2002) before the 1900s. Our evidence suggests, therefore, that there were pronounced hydrological changes in CP, the drainage pond, from ephemeral to more permanently inundated after the 1900s, leading to a rise in the production and preservation of algae-derived carotenoids more commonly associated with shallow freshwater communities (McGowan 2013).

The pronounced increase in temperature at this time (Fig. 2b) could be associated with this shift in hydrology. Warmer temperatures can promote the development of vegetation and soil, which could act as giant sponges retaining moisture during the rainy season and steadily supplying water to the ponds during the dry season (Giles and others 2018). This could buffer against increased evapotranspiration caused by higher temperatures. Vegetation growth may also restrict drainage pathways, increasing the residence time of the pond, indicating the potential for localised geomorphic effects within the basin (Gurnell 2014). Local changes in hydrology most likely explain the
non-significant relationship between rainfall and pigment responses (Fig. 8). Rising abundance of *A. alpigena* in CP after the 1930s indicated an increase in water depth (Fig. 4); in particular, the subdominance of *A. alpigena* and low C/N ratios after the 1980s indicated a status of permanent inundation during the ice-free season. Hydrological changes were also evidenced by an increase in coarse particles (Fig. 3). The coarsening grain size may indicate fine suspended particles would be washed out, as rising water levels caused water discharge through the outlet (Fig. 1).

In contrast to CP, the deeper seepage pond ML displayed clear decreases in carotenoid pigments and small fragilarioid taxa (i.e. *S. construens* var. *venter*) after the 1980s (Figs. 4 and 5). Recent changes in diatom assemblages were significantly correlated with higher $\delta^{13}$C (Fig. 8b), suggestive of a linkage to carbon cycling. The ranges of Suess-corrected $\delta^{13}$C (between -29.7‰ and -25.7‰) and C/N ratios (from 11 to 20) in both ponds are within the range of allochthonous soil organic matter (Meyers and Teranes 2001) and C3 plants (e.g. *Carex* and *Sphagnum*) in the nearby Dajiuhu Wetland ($\delta^{13}$C ranging from -29.3‰ to -22.8‰; Liu and others 2018), suggesting that organic matter is mainly sourced from terrigenous inputs, with some contributions from algae. In ML, an increase in $\delta^{13}$C after the early 1900s may imply that littoral *Sphagnum* made a larger contribution to the carbon pool, since *Sphagnum* mosses have relatively heavier $\delta^{13}$C values than other plants (e.g. *Juncus*, *Polytrichum* and *Sanguisorba*) (Liu and others 2018).

Continuous inputs of CDOM attenuate light and may restrict light penetration and inhibit benthic primary productivity (McGowan and others 2018a; Bergström and Karlsson 2019). Higher sedimentary TN and TOC contents in the seepage pond ML may suggest enhanced organic matter accumulation (Fig. 6). Shallowing of the euphotic zone due to terrestrial CDOM inputs, may thus have impeded the growth of benthic
algae beneath the euphotic zone (Fig. 9). This is consistent with recent decreases in fossil carotenoids and small fragilarioid species after 1955. After 1980, changes to more diverse periphytic taxa that are associated with littoral habitats and mossy substrates (e.g. Brachysira, Frustulia and Eunotia species) (Chen and others 2016), are inferred to reflect increased littoral habitat availability with longer growing seasons. Such shifts were not observed in CP because CDOM additions could not have a significant effect on light attenuation at the bottom of such a shallow pond (20cm depth).

Differences among the pond diatom assemblages are consistent with the hydrological characteristics. For example, A. minutissimum and the planktonic A. alpigena successively increased in the drainage pond CP since water level increased, and are common in snowmelt-fed Swiss alpine basins, whereas T. flocculosa was present in the seepage pond ML and may be more common in lakes which are disconnected from riverine influence (Robinson and Kawecka 2005). The diatom assemblages of both ponds were dominated by benthic taxa, including some motile species (e.g. N. cryptotenella, S. pupula, P. microstauron and A. minutissimum) that can migrate within biofilms (McGowan and others 2018b). Migration of motile diatoms enables the avoidance of unfavourable conditions (e.g. desiccation, excessive light exposure, grazing and nutrient limitation), to maximise overall fitness and productivity of the biofilm (Consalvey and others 2004).

Nutrients may be delivered in pulses to lake margins during snowmelt, which may offer benthic diatoms living at lake margins a competitive advantage over planktonic taxa in these seasonally frozen ponds (McGowan and other 2018b). However, in this region summer monsoon rains deliver the majority of rainfall, supplying benthic diatoms with a regular supply of catchment-delivered nutrients (Hu and others 2018). The majority of the benthic taxa in both ponds would be considered epipelic or
periphytic species, suggesting that shifts in the diatom assemblages in the ponds were not strongly associated with changes in macrophyte abundance (Scheffer and Jeppesen 2007), but instead driven by changes in water level and nutrients in the drainage pond CP where light was not limiting, and water browning and seasonal water level fluctuations in the seepage pond ML where the relative availability of benthic: pelagic habitat was regulated by light limitation.

**The linkage to climate variability**

Pigment and diatom data were significantly correlated with seasonal temperature, but not with rainfall in both ponds (Fig. 8), suggesting that climate warming stimulates changes in primary producer communities. In shallow water bodies, light penetration to the bottom allows the development of complex benthic communities which respond to warming differently (Spaulding and others 2015). The increasing primary production (inferred from chlorophylls and their derivatives) in both ponds in the early 1900s was compatible with a persistent rise in regional temperature between 1900 and 1920 (Figs. 5 and 7). The shortened ice-cover duration under warmer climate is an important factor influencing the growth of primary producers in the study ponds (Fig. 9). Firstly, a longer ice-free season would enhance the terrestrial-aquatic linkage (i.e. runoff and nutrients from land to lake). Secondly, a longer growing season allows more time for the development of primary producer communities, including macrophytes which provide substrates for epiphytes, thus accelerating annual biomass accumulation (Rühland and others 2015). Taken together, warming-related processes may promote primary production of the study ponds, indicated by rising pigment concentrations in the early 1900s.
Seasonal precipitation was not significantly correlated with pigments and diatoms of both ponds, indicating that precipitation effects were probably mediated by local hydrological factors. For example, groundwater is an important component of the water cycle in limestone areas, and there are lags between rainfall and groundwater recharge which may have been particularly important in the seepage lake (ML). In contrast, it appears that local vegetation development might have influenced the drainage of CP and increased the complexity of the relationship between rainfall and ecological response. For example, lower rainfall before the 1900s probably caused periodic desiccation, subsequently increasing phosphorus availability by mineralization processes of inorganic and organic phosphorus in lake sediment (Reddy and other 2005). An increasing supply of soluble phosphorus would facilitate the growth of eutrophic species (e.g. *C. naviculiformis*, *G. parvulum*, *Stauroneis phoenicenteron* Nitzsch) (cf. Van Dam and others 1994) in CP Pond (Fig. 4a). In addition, an increase in winter rainfall after the 1980s (Fig. 2c) would provide habitats suited to small fragilarioid taxa that can compete well under ice during the winter (Laing and Smol 2000; Lotter and Bigler 2000). This explanation probably accounted for the proliferation of *S. construens* var. *venter* in the upper strata of CP core (Fig. 4a).

### The linkage to nitrogen enrichment

Sediment $\delta^{15}$N has declined progressively in both lakes since the early 20th century, and, despite considerable local heterogeneity and ecological complexity in these ponds, this trend parallels the records of nitrogen deposition observed in other remote Northern Hemisphere lakes (Holtgrieve and others 2011), a Himalayan ice core (Thompson and others 2000), and the Greenland Ice Sheet (Geng and others 2014) (Fig. 7). Although fertilizer use was limited before 1950, inputs from animal manure from the fast-growing
animal stocks, and human excreta from the expanding population have increased during the early 20th century (Bouwman and others 2013). Average nitrogen deposition rates over forests in East Asia have increased from less than 2 kg N ha\(^{-1}\) yr\(^{-1}\) in the mid-19th century to more than 3 kg N ha\(^{-1}\) yr\(^{-1}\) in the mid-20th century (Wang and others 2017).

Remote montane lakes are often N-limited, which renders them susceptible to the enrichment effects of nitrogen deposition (Bergström and Jansson 2006; Baron and others 2011). Enhanced nitrogen deposition elicits mesotrophic species as N-deposition rates cross a critical load (Saros and others 2011).

Carotenoids (e.g. lutein-zeaxanthin) increased gradually in both ponds from the 1920s (Fig. 5), suggesting that rising N inputs may have caused nutrient enrichment with higher primary production. Meanwhile, synchronous increases in chlorophylls and their derivatives (e.g. Chl \(a\) and pheophytin \(a\)) implied that nutrient enrichment might also promote the growth of macrophytes that contain chlorophylls and their derivatives (McGowan 2013). However, gradual decreases in carotenoids in the seepage pond ML after the 1980s indicated that algal growth might be inhibited by local factors (Fig. 9). Meanwhile, nutrient inputs promoted the development of aquatic plants in the littoral zone, probably accounting for rising concentrations of chlorophylls and their derivatives in ML Pond (McGowan 2013). Although most dominant diatom taxa in both ponds are thought to use inorganic forms of nitrogen, some taxa that can utilise organically bound nitrogen increased obviously after the early-1900s (Tuchman and others 2006), such as the increase of \(E.\ mucophila\), \(S.\ pupula\) and \(C.\ naviculiformis\) in CP, and the expansion of \(E.\ exigua\) and \(E.\ bilunaris\) in ML.

**CONCLUSIONS**
This study investigates the response of primary producer communities to local and regional driving forces in two subtropical montane ponds (central China) during the last two centuries. Climate warming and nitrogen deposition have altered biomass and community composition of primary producers, probably mediated by local factors (e.g. lake morphometry and catchment-lake connections). Further warming and nitrogen deposition would possibly increase autotrophic biomass (especially nitrophilous taxa) in these subtropical montane ponds, probably influencing ecosystem structure and function through aquatic food web. The effects of warming and nitrogen deposition on primary producers are mainly deduced from correlational statistical analyses, and previous knowledge of the autoecology of dominant taxa. In order to disentangle the effects of warming and nitrogen deposition, further seasonal monitoring of primary producers are needed in the study region. Therefore, it is essential to conduct palaeolimnological and seasonal monitoring studies in order to track the ecological responses of subtropical montane lakes to changes in local and regional drivers over subtropical East Asia.

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TABLE AND FIGURE CAPTIONS

Table 1 Summaries of environmental conditions in the two study ponds.

Figure 1 Maps showing the location of study sites in Asia (A) and local topography (B), and photos of Congping (C) and Mulong (D) ponds. The inserted maps in Figure B show local topography of Congping (the upper) and Mulong (the lower). Congping is dominated by *Sparganium stoloniferum*, with coverage of ~30%. Maps A and B have been modified from the maps downloaded from http://www.lib.utexas.edu/maps/asia.html and Google Earth, respectively.

Figure 2 Mean monthly temperature and precipitation between 2016 and 2017 (a) at Dajiuhu Wetland (31°28′50″N, 110°00′09″E, 1758 m a.s.l.; 10 km away from Congping Basin). Mean monthly temperature at Congping (blue line) was calculated based on the vertical lapse rate of temperature of 0.5°C/100 m. Anomalies in seasonal temperature (b) and precipitation (c) in the study area since 1880 were sourced from Wang and others (2009).

Figure 3 Particle size spectra and chronology of sediment cores in Congping (a) and Mulong (b), with mass accumulation rate (MAR, orange line) shown.

Figure 4 Diatom assemblages in Congping (a) and Mulong (b).

Figure 5 Fossil pigment diagrams of Congping (a) and Mulong (b).

Figure 6 Multiple proxies in sediment cores collected from Congping (a) and Mulong (b). Original and Suess effect corrected δ¹³C values are indicated by filled circles and open squares, respectively.

Figure 7 Synthesis of sedimentary records (a-f) with (g) δ¹⁵N (NO₃⁻) and (h) nitrate concentration from the Summit, Greenland ice core (Geng and others 2014), (i) nitrate concentration from the Himalayan ice core (Thompson and others 2000), (j)
winter temperature anomalies based on reconstruction (Wang and others 2009).

Diatom PCA1 sample scores, pigment PCA1 sample scores, and δ¹⁵N in Congping (a, c, e) and Mulong (b, d, f) are shown.

**Figure 8** Biplots of redundancy analyses, main diatom species and significant variables in CP (a) and ML (b), pigments and significant variables in CP (c) and ML (d).

Diatom species abbreviations: Bra bre: *B. brebissonii*, Cym gra: *Cymbella gracilis*, Enc ces: *Encyonopsis cesatii*, Eun bil: *E. bilunaris*, Eun exi: *E. exigua*, Eun muc: *E. mucophila*, Fru rho: *Frustulia rhomboidea*, Gom par: *G. parvulum*, Han amp: *H. amphioxys*, Nav cry: *N. cryptotenella*, Nei amp: *Neidium ampliatum*, Pin bor: *P. borealis*, Pin mic: *P. microstauron*, Pin vir: *Pinnularia viridis*, Sel pup: *S. pupula*, Sta ven: *S. construens* var. *venter*, Sta pho: *Stauroneis phoenicenteron*, Tab flo: *Tabellaria flocculosa*.

**Figure 9** Schematic diagram of some possible effects of climate warming and nitrogen deposition on primary producer communities. Effects of nitrogen deposition and warming either inhibit (-) or stimulate (+) response variables.
|                        | Congping       | Mulong         | Congping       | Mulong         |
|------------------------|----------------|----------------|----------------|----------------|
| **Sampling date**      | June 2016      | June 2016      | Sep. 2017      | Sep. 2017      |
| **Latitude (N)**       | 31°24′13.58″   | 31°24′10.03″   | 31°24′13.58″   | 31°24′10.03″   |
| **Longitude(E)**       | 110°03′35.83″  | 110°03′17.89″  | 110°03′35.83″  | 110°03′17.89″  |
| **Altitude (m a.s.l.)**| 2073           | 2078           | 2073           | 2078           |
| **Water depth (m)**    | 0.2            | 1.5            | 0.2            | 1.5            |
| **Secchi depth (m)**   | 0.2            | 0.5            | 0.2            | 0.5            |
| **Area (m²)**          | 360            | 380            | 360            | 380            |
| **pH**                 | 6.17           | 5.17           | 6.43           | 5.83           |
| **Conductivity (μS cm⁻¹)** | 12         | 9              | 23             | 12             |
| **PO₄³⁻ (μg L⁻¹)**     | 4              | 2              | 3              | 2              |
| **DOC (mg L⁻¹)**       | 18.0           | 12.3           | n.a.           | n.a.           |
| **NO₃⁻ (μg L⁻¹)**      | 73             | 22             | 115            | 25             |
| **K⁺ (mg L⁻¹)**        | 0.4            | -              | 1.39           | 0.13           |
| **Ca²⁺ (mg L⁻¹)**      | 1.04           | 0.86           | 1.22           | 0.69           |
|          |        |        |        |        |
|----------|--------|--------|--------|--------|
| Na⁺ (mg L⁻¹) | 0.71   | 0.26   | 0.78   | 0.07   |
| Mg²⁺ (mg L⁻¹) | 0.27   | 0.19   | 0.25   | 0.12   |
| Si (mg L⁻¹)   | 0.17   | 0.43   | 0.87   | 0.52   |

-The value was below detection limit. n.a. Environmental factors were not measured.
Figure 1
Figure 2
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8
Figure 9