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Ecosystem deterioration in the middle Yangtze floodplain lakes over the last two centuries: evidence from sedimentary pigments

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Highlights

- The middle Yangtze lakes have undergone unprecedented increases in algal production during the Anthropocene.
- Diazotrophic HABs are stimulated by P-enriched urban wastewater pollution.
- Agriculturally-derived N pollution favors non-N_2-fixing cyanobacteria
- Hydrological connections of lakes with the main channel mitigated against HABs occurrence.

Abstract:

Water quality of floodplain lakes in the Yangtze region which supports ca. 0.45 billion people is being severely compromised by nutrient pollution, climate change and dam installation resulting from intensive socio-economic development. However, due to a lack of long-term monitoring data, the onset and causes of ecosystem degradation are unclear. Here, we used chlorophyll and carotenoid pigments in dated sediment cores from six lakes spanning the region to reconstruct changes in algae and cyanobacterial HAB (harmful algal bloom) taxa alongside sedimentary nutrient flux measurements and historical archives. Sedimentary N fluxes are linked to changes in agriculture, while urbanization has had greater influences on P fluxes. Over the last 70 years algal and N_2-fixing HAB pigments increased markedly in lakes (Luhu, Wanghu) that are strongly influenced by urbanization/industrialization. Algal assemblages in two other lakes (Futou, Honghu) changed gradually and responded primarily to agriculture and associated N fluxes; diazotrophic HAB pigments were absent and the lakes retained macrophyte cover. Local dam installation had no discernible effect on pigment assemblages in three of the four lakes in the past 70 years, but in the two hydrologically-open lakes (Poyang, Dongting), increasing algal production was significantly related to the upstream installation of the Three Gorges Dam (TGD) and to urban/ industrial and agricultural stressors. Temperature only influenced phototrophs in the most degraded lakes (Luhu, Wanghu). This spatial and temporal overview identifies that nutrient pollution is the primary regional driver of lake phototrophs, but that diazotrophic HABs are stimulated by P-enriched urban wastewater pollution, and agriculturally-derived N pollution favors non-N_2-fixing cyanobacteria. Despite negative effects of the Three Gorges project, free connection to the river appears to help mitigate excess HABs in freely connected lakes. Management thus needs to be tailored appropriately to specific lake conditions and palaeolimnology can be valuable in identifying appropriate strategies.

Keywords: Anthropocene, algal production, HABs, hydrological modification, agriculture, urbanization, industrialization

1 Introduction

River floodplain ecosystems provide many benefits to society, but the services they provide are under threat from river regulation, land-use changes and pollution (Petsch et al., 2022). Floodplain lakes are dynamic systems, where primary productivity would naturally be sustained by periodic river flooding (Junk, 2005). In the Yangtze floodplain, this natural balance is being fundamentally altered by a combination of human socio-economic development and climate change (Dearing et al., 2012; Wang et al., 2016). Water quality in many Yangtze floodplain lakes is compromised by harmful algal blooms (HABs), turbid waters and loss of macrophytes (Xu et al., 2015; Dong et al., 2016; Song et al., 2021). Understanding the main drivers of water quality degradation is vital for effective remediation, but is particularly challenging in the Yangtze floodplain because of the diverse range of interacting stressors across a large, spatially heterogeneous and heavily modified floodplain.

Intensive nitrogen (N) and phosphorus (P) loading from fertilizer usage, aquaculture nutrient release and domestic and industrial sewage is causing eutrophication and ecological degradation of lakes all over the world (Conley et al., 2009; Waters et al., 2016; Wang et al., 2019; Wurtsbaugh et al., 2019), resulting in problems such as turbid waters, loss of aquatic macrophytes, reduced algal diversity (Dong et al., 2016; Chen et al., 2022) and associated reduction in ecosystem services (Janssen et al., 2021). In particular, the increased incidence of toxic HABs (i.e., cyanobacterial blooms) presents an emerging threat to human and ecosystem health (Taranu et al., 2015; Song et al., 2021). For example, HABs in Taihu Lake (lower Yangtze Basin) have compromised the regional drinking water source, and initiated major remediation work (Paerl et al., 2016). Although remote sensing has noted a rise in surface blooms (Zong et al., 2019), the onset and magnitude of algal blooms are unclear, especially in developing regions (Taranu et al., 2015). In addition, there is a long-running debate on whether N or P exerts overall control on HABs (Conley et al., 2009; Paerl et al., 2016; Schindler et al., 2012). Because the causes, and so the remediation options of HABs can differ among different lakes (e.g., Richardson et al., 2018), developing an understanding of how nutrient pollution and other drivers affect water quality is required.

Damming of rivers influences water flows and fluxes of sediments and nutrients on a global scale (Maavara et al., 2020). Reservoir formation from major damming projects on large rivers can degrade downstream water quality by mobilising bioavailable nutrients to exacerbate regional-scale eutrophication (Chen et al., 2020). However, dams which regulate single lakes also have localised consequences (Chen et al., 2016; Zeng et al., 2018). Periodic flooding can supply or remove nutrients, suspended particles and phytoplankton, thereby influencing turbidity, light availability and primary productivity in floodplain lakes (Tockner et al., 1999; Squires and Lesack, 2002; Richardson et al., 2018). Reducing (variability in) water retention time (WRT) by damming lake inflows can increase P retention in lakes and emphasize internal nutrient cycling processes (Vollenweider, 1976). WRT also influences HAB development because cyanobacteria compete well in lentic waters, whereas diatoms prefer well-flushed and lotic-influenced systems (Elliott, 2010; Liu et al., 2017). Since river connectivity (and WRT) plays a complex role which interacts with local hydrology, the effects of damming are likely to vary among lakes and need to be further explored (Cross et al., 2014; Olsson et al., 2022).

In addition to nutrients and hydrological regulation, climate change can also influence lake ecosystems (Lin et al., 2021). Together with atmospheric stilling, higher temperatures are increasing lake stratification in many lakes globally (Woolway et al., 2020). Bloom-forming cyanobacteria may have physiological advantages over eukaryotic algae under warmer conditions (Griffith and Gobler, 2020) and so warming appears to act synergistically with nutrients to exaggerate the extent and duration of HABs (Paerl and Paul, 2012; Lin et al., 2021). Rainfall variability can influence river discharge and lake flushing rates, affecting the seasonal development of algal communities (Cross et al., 2014; Richardson et al., 2019). Shifts in the hydrological balance of floodplain lakes can change phototrophic community composition (McGowan et al., 2011), but floodplain hydrology is naturally spatially heterogeneous, making lake responses to environmental stressors difficult to predict (Remmer et al., 2020). In the heavily-dammed mid-Yangtze region, it is not clear whether rainfall variability is able to exert a significant influence on floodplain ecosystems. Given the complexity of phytoplankton response to multiple stressors, developing an understanding of how nutrient pollution and other drivers affect floodplain lake ecosystems is required.

Typical in China, the mid-Yangtze region has experienced rapid socio-economic development and population growth, with key transition points including the establishment of the People's Republic of China in 1949 CE and the "reform and opening-up" policy for economic development in 1978 CE (Yu et al., 2019). Using palaeolimnology to reconstruct water quality changes and environmental drivers over long timescales offers important insights into floodplain lake dynamics that pre-date water quality monitoring records (Wolfe et al., 2008; Chen et al., 2016). As sedimentary biomarkers for phototrophic primary producers, including HABs, chlorophyll and carotenoid pigments are a reliable index to track the timing, nature and extent of water quality changes (McGowan, 2013). Since water quality monitoring was scarce in the Yangtze region before the 1980s, long-term sediment-based reconstructions of ecological change through the period of intensive change in comparison to earlier ecological baselines can inform restoration possibilities (Battarbee and Bennion, 2011). Also, when coupled with archival records of socio-economic and meteorological change, palaeolimnological records can help to infer the causes of lake ecosystem change (McGowan et al., 2012; Bunting et al., 2016). Palaeolimnological comparisons across landscapes provide a long-term overview of multi-lake dynamics that can help to extricate the regional and local drivers of change and provide focal points for management (Quinlan et al., 2002; Mills et al., 2017). In contrast to small lake districts where lake dynamics can be highly spatially organized (Kratz et al., 1997; Dixit et al., 2000; Leavitt et al., 2006), floodplain landscapes are generally more heterogenous (Wolfe et al., 2008; McGowan et al., 2011). Long-term comparisons across landscapes can identify commonalities and differences in lake responses to environmental drivers and ascertain whether regional versus local environmental drivers of change are most important (Moorhouse et al., 2018).

Here we investigate six shallow floodplain lakes spanning the middle Yangtze floodplain, including the two largest floodplain lakes in China, to determine how socio-economic drivers, damming and climate change have influenced nutrient fluxes and communities of primary producers (including HABs). We aimed to (1) determine how and when lake phototrophic communities (including HABs) and nutrient fluxes have changed across the lakes in the region over the past ca. 200 years; (2) quantify how socio-economic drivers including agricultural changes, urban/industrial development, climate and dam installation have influenced nutrient fluxes and algal communities in the lakes over the past 70 years (the duration of the historical datasets); and (3) identify which drivers should be targeted for lake management.

2 Materials and methods

2.1 Study area

The Yangtze River, known as the "mother river of China", has a total length of ca. 6300 km and is the longest river in Asia and third longest in the world (Milliman and Farnsworth, 2013). Originating from the Tibetan Plateau in Western China, the Yangtze River flows through the deep rocky canyons in the upper reaches and then meanders in the vast plain in the middle and lower reaches before entering the East China Sea (Figure 1a). The middle Yangtze, between the cities of Yichang and Hukou, is characterized by a sub-tropical monsoon climate, with a mean annual temperature of 13-20 $^{\circ}$C and an annual precipitation of 800-1600 mm (Wang et al., 2016). The geological setting combined with the seasonally variable monsoonal climate make this area susceptible to flooding (Chen et al., 2001) with the formation of thousands of floodplain lakes. This study focuses on six large (40-3000 km^2) freshwater lakes spanning the Middle Yangtze Basin, including the largest (Poyang Lake) and second largest (Dongting Lake) freshwater lakes in China by area (Table 1; Supplementary Information). Two of the lakes (Dongting and Poyang) are freely and directly connected with the Yangtze River and are dominated by diatoms (Liu et al., 2017), while the others (Honghu, Futou, Luhu and Wanghu) are indirectly connected with the Yangtze River via tributaries and hydrologically restricted by local dam construction (Zeng et al., 2022) (Figure 1b). For the four hydrologically restricted lakes, two have abundant macrophyte cover (Futou and Honghu) (Song et al., 2016; Liu et al., 2020) while Luhu and Wanghu are frequently featuring cyanobacterial HABs (Rao et al., 2018; Zong et al., 2019) (Figure 1c).

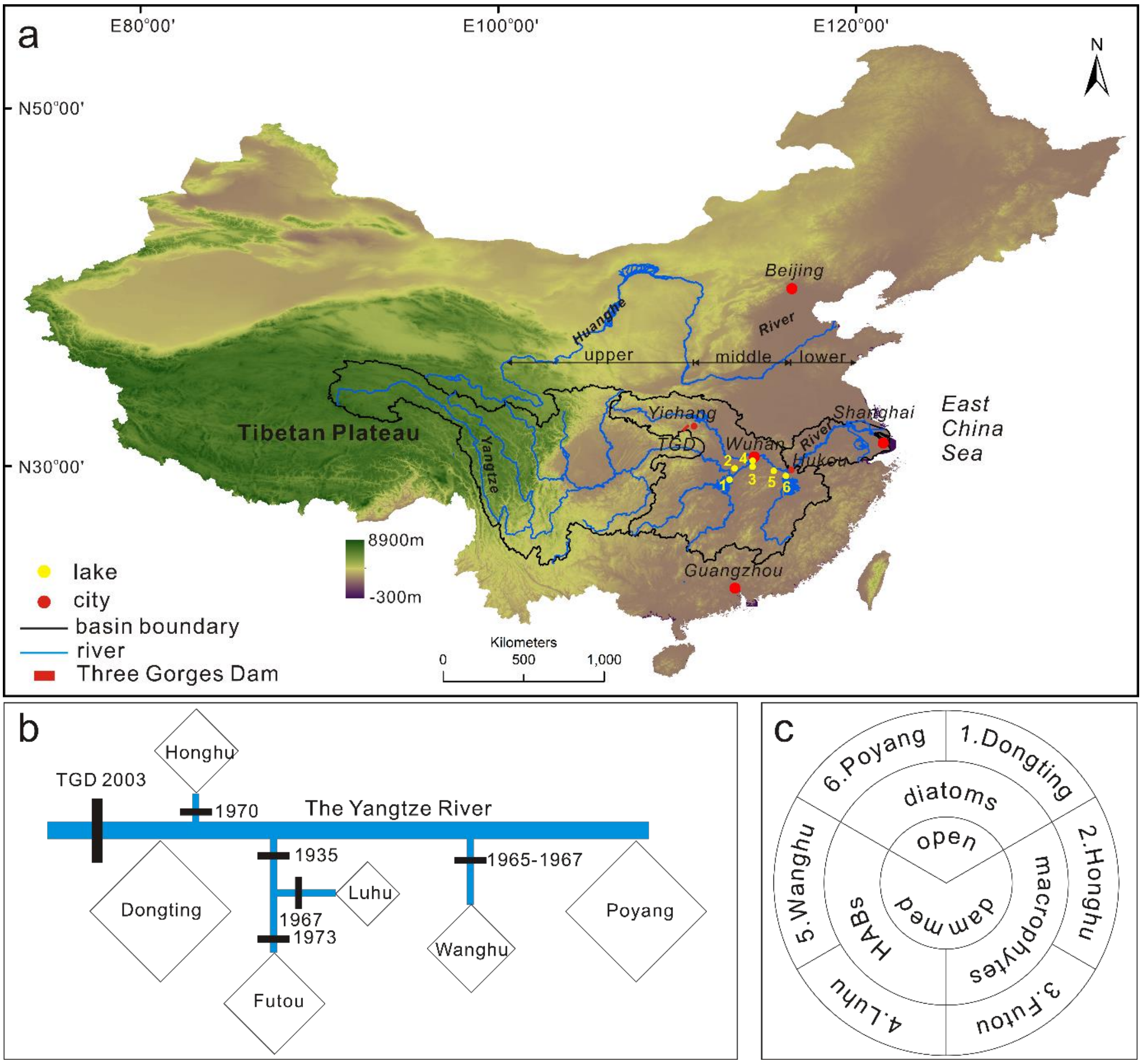

Figure 1 (a) Location of the Yangtze Basin and the study lakes in mainland China (1=Dongting Lake, 2=Honghu Lake, 3=Futou Lake, 4=Luhu Lake, 5=Wanghu Lake, 6=Poyang Lake) with insets showing (b) the hydrological setting (the size of the squares reflects the relative surface area of each lake) and (c) the hydrological conditions and ecological features of the lakes.

Table 1 Location and water chemistry of the study lakes

Site	1 Dongting	2 Honghu	3 Futou	4 Luhu	5 Wanghu	6 Poyang
Latitude (N)	28°44’-29°35’	29°38’-29°59’	29°55’-30°07’	30°12’-30°17’	29°51’-29°54’	28°24’-29°46’
Longitude (E)	111°53’-113°05’	113°11’-113°28’	114°09’-114°20’	114°9.5’-114°15’	115°20’-115°25’	115°49’-116°46’
Administrative location	Hunan	Jingzhou	Wuhan/Xianning	Wuhan	Huangshi	Jiangxi
Administrative area (km^2)	211,855	14,069	9,178	8,494	4,583	166,900
Mean lake depth (m)	6.4	1.9	2.9	2.7	3.6	5.1
Lake area (km^2)	2500	344	115	40	42	2933
Sampling date	2017	2015	2014	2016	2016	2016
Hydrology	Open	Dammed	Dammed	Dammed	Dammed	Open
TP (µg/L)	53.6	8.0	37.4	68.2	223.5	27.2
TN (mg/L)	0.17	0.17	0.20	0.33	0.44	0.29
Water TN/TP ratio	7.02	47.05	11.84	10.71	4.36	23.61
Dominant phytoplankton	Bacillariophytes ~50%[1]	Bacillariophytes 93.72% [2]	Cyanobacteria 34.1% Bacillariophytes 31.6% Euglenophytes 21.6%[3]	Chlorophytes 43.5% Cyanobacteria 41.8%[4]	Cyanobacteria 39.67% Bacillariophytes 23.6% Chlorophytes 20.5%[5]	Bacillariophytes>50%[1]

Water samples for TN and TP were collected and analyzed in June 2017. Longitude and latitude of lakes are from Google Earth. Dominant phytoplankton groups summarised based on [1] Liu et al., 2017; [2] Deng et al., 2010; [3] Gong et al., 2009; [4] Rao et al., 2018; and [5] Hubei Wildlife Trust, 2005

2.2 Historical archives and climate data

Historical archives for agriculturally-related metrics (rural population, grain and aquaculture production, N and P fertilizer use) and urbanization/industrialization-related metrics (urban population, concrete and electricity production, the total length of roads and the number of vehicles) were collected for each catchment from local Chinese reports (Supporting Information Table S1; Figure S1). Data before the foundation of the People's Republic of China were rarely recorded and poorly curated, and so only historical archives from 1949 CE to 2016 CE were used in this study.

Climate variables were collected from the Climatic Research Unit dataset (CRU TS 4.02) of the University of East Anglia (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/ge/) (Harris et al., 2014). In this dataset, global climate datasets are constructed at 0.5° latitude/longitude resolution based on monthly observations at meteorological stations across the world since 1900 CE. Mean annual temperature and total annual rainfall in each catchment were collected at the nearest grid in this study.

2.3 Sediment coring

Sediment cores of < 1m in length were collected using a gravity corer in each lake between 2014 CE and 2017 CE, maintaining the water-sediment interfaces. Cores were collected at the centre of the four relatively smaller lakes (Honghu, Futou, Luhu and Wanghu). In the two large lakes (Poyang and Dongting), sediment cores were collected from areas where previous investigations had indicated good sedimentation and so the potential for a reliable chronology (Xiang et al., 2002). Sediment cores were sectioned at 1-cm intervals with subsamples stored in sealed bags at – 20 ˚C for pigment analyses and 4 ˚C for dating.

2.4 Chronology

Sediment cores were dated using ^{210}Pb and ^{137}Cs. The ^{210}Pb activities for dating the sediment cores from Honghu, Luhu, Wanghu and Poyang are from Chen et al. (2019). The ^{210}Pb activities in the sediment core from Futou Lake are previously published in Zeng et al. (2018). ^{210}Pb and ^{137}Cs in the Dongting Lake sediment core were published in Zeng et al. (2022). Chronologies of the sediment cores were established using excess ^{210}Pb with a constant rate of supply (CRS) model and dry mass accumulation rate (DMARs) were calculated (Chen et al., 2019; Zeng et al., 2022). For sediment beyond the detection limit of ^{210}Pb dating (i.e., older than ca. 150 years), dates were extrapolated using a linear model from the last two or three samples with measurable excess ^{210}Pb. As extrapolated chronologies are less reliable, we limited the temporal span of the data presented to that after 1800 CE.

2.5 TN and TP fluxes

Total phosphorus (TP) in sediment cores from Honghu, Luhu, Wanghu and Poyang are from Ji (2020). TP in the Dongting sediment core was analysed using inductively coupled plasma-atomic emission spectrometry (ICP-AES) at the Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences. Total nitrogen (TN) in sediment cores from Dongting, Honghu, Luhu, Wanghu and Poyang were analysed using a Costech Elemental Analyser (EA) and on-line VG TripleTrap and Optima dual-inlet mass spectrometer at the British Geological Survey. TN and TP data in the Futou sediment core are from Zeng (2016). Sedimentary TN and TP fluxes were calculated by multiplying DMARs with the content of TN and TP respectively.

2.6 Pigments

Chlorophyll and carotenoid pigments in core samples were analysed using a high performance liquid chromatography (HPLC) comprised of an Agilent 1200 series quaternary pump, autosampler, ODS Hypersil column (250 × 4.6 mm; 5 μm particle size) and photo-diode array (PDA) detector after being extracted from sediments and dried under N_2 gas (Chen et al., 2001). Firstly, freeze-dried sediments were weighted into vials for extraction (~ 0.2 g in the top 20 cm and ~ 1.0 g below 20 cm due to low pigment concentrations). Then, 5 ml extraction solvent (acetone: methanol: deionised water 80: 15: 5) were added into the vials to extract the pigments. During extraction, the vials were kept in a freezer at –4°C for 12 hours. After that, the samples were filtered through a 0.22 μm PTFE syringe filter, followed by drying under N_2 gas. Subsequently, the samples were dissolved in injection solvent, a mixture of acetone (70%), ion-pairing reagent (25%) and methanol (5%). Samples were transferred into HPLC vials and set up for running in the HPLC to separate different pigments. The solvent streams (the mobile phase) passing through (> 20 kPa; flow rate of 1 ml min^{-1}) the separation column were a modified version of Chen et al. (2001), where the composition of Solvent A (80% methanol: 20% 0.5 M ammonium acetate), Solvent B (90% acetonitrile: 10% de-ionised water) and Solvent C (100% HPLC-grade ethyl acetate) are changed with time over a 52-minute sequence. Pigment chromatographic peaks were calibrated using commercial standards from DHI (Denmark) with concentrations expressed as nanomole pigment per gram organic carbon (nmol g^{-1} TOC). TOC (total organic carbon) was analysed using a Costech Elemental Analyser (EA) and on-line VG TripleTrap and Optima dual-inlet mass spectrometer at the British Geological Survey (Zeng et al., 2022). Thirteen pigments including those from total algae (chlorophyll *a* and its derivatives phaeophorbide *a*, pheophytin *a* and pyropheophytin *a*, and β-carotene), chlorophytes (chlorophyll *b* and its derivatives pheophytin *b* and pheophytin *b*'), cryptophytes (alloxanthin), siliceous algae (diatoxanthin), N_2-fixing cyanobacteria (aphanizophyll), colonial cyanobacteria (canthaxanthin) and chlorophytes/cyanobacteria (lutein-zeaxanthin) were reported in all six lakes with the exception of Futou Lake where aphanizophyll was not detected (Supporting information Figure S3a-f).

2.7 Numerical analyses

To eliminate differences in units or scales of measurements and provide an integrated metric that emphasizes and identifies the timings of changes, the historical archive datasets were each standardized using Z-scores. Indicators of agriculture (rural population, grain production, N fertilizers, P fertilizers and aquaculture production) and urbanization/industrialization (urban population, electricity and concrete production, number of vehicles and length of roads) were then each summed to be used as proxies for agricultural (Z-agriculture) and urban/industrial (Z-urban) development in each lake catchment.

As the gradient length assessed by a detrended correspondence analysis was less than 2 standard deviations, principal component analysis (PCA) was used to summarize sedimentary pigments. To investigate pigment changes on a common scale among different lakes, a single PCA was performed using log(x+1)-transformed pigment data from all six lakes to summarize and simplify the pigment dataset. PCA was conducted using the "*vegan 2.5-4*" package (Oksanen et al., 2019). Because PCA axis 1 represented a gradient of abundance in most pigments, the Mann-Kendall trend coefficients of the

PCA axis 1 scores were analysed using the "*Kendall version 2.2*" package (McLeod, 2011) to evaluate whether primary production increased over time in these middle Yangtze floodplain lakes. To assess periods of major change in the catchment, agricultural and industrial "drivers" and pigment "responses", GAMs were fitted to time series of Z-agriculture, Z-urban and pigment PCA axis 1 using the *gamm()* function with the "*mgcv*" (version 1.8.31) package. The first derivatives were calculated to detect the timing of significant changes in each lake and catchment using the "*gratia*" package (Simpson, 2020).

In order to disentangle the relative importance of different environmental variables (i.e., urbanization/industrialization, agriculture, climate and hydrology) on pigment (algal community) composition since the 1950s CE in each lake, hierarchical partitioning analysis was used via the *rdacca.hp()* function with the "*rdacca.hp*" package as this analysis can deal with high collinearity among the environmental variables (Lai et al., 2022). The response variables were the log(x+1)-transformed pigment datasets. Environmental drivers in the analysis included Z-agriculture and Z-urban, climate variables (mean annual temperature, total annual rainfall) and dam construction (as 1/0 dummy variable). For the two open lakes (Dongting and Poyang), dam construction refers to the installation of the TGD in 2003; for the other lakes (Honghu, Futou, Luhu and Wanghu) only local dams constructed after 1949 CE were included in the analysis. The relationship between nutrient fluxes (sedimentary TN and TP fluxes) and algal production (pigment PCA axis 1) in each individual lake (Supporting Information Figure S4) since the 1850s CE were investigated using linear regression analysis. All statistics were performed in R (R Core Team, 2020).

3 Results

3.1 Historical archives

Z-agriculture and Z-urban indicate that changes in agriculture preceded those in urbanization/industrialization in all lake catchments (Figure 2a, b). There was a period of sustained agricultural growth between 1949 CE and the mid-1990s CE (slope = ~ 0.25) in all six catchments with the exception of a hiatus in growth between 1955 CE and the early 1960s CE associated with the Great Famine (Dearing et al., 2012), and followed by a reduction in growth rate afterwards (slope = ~ 0.15), associated with rural depopulation as people moved into cities (Figure 2a) (Yang, 2013). Z-urban increased exponentially with a slow and significant increase starting around the 1980s CE associated with the release of the "reform and opening up" policy (Dearing et al., 2012), which accelerated in all catchments in the early 2000s CE (Figure 2b).

Total annual precipitation fluctuated at around 1350 mm in all the catchments with no overall directional trend through time (Figure 2c). Mean annual surface temperatures fluctuated around ~ 16.2 °C in the Wanghu catchment and ~17.0 °C in other catchments before the 1990s CE, followed by a significant increase between the 1990s and ~ 2000 CE (Figure 2d).

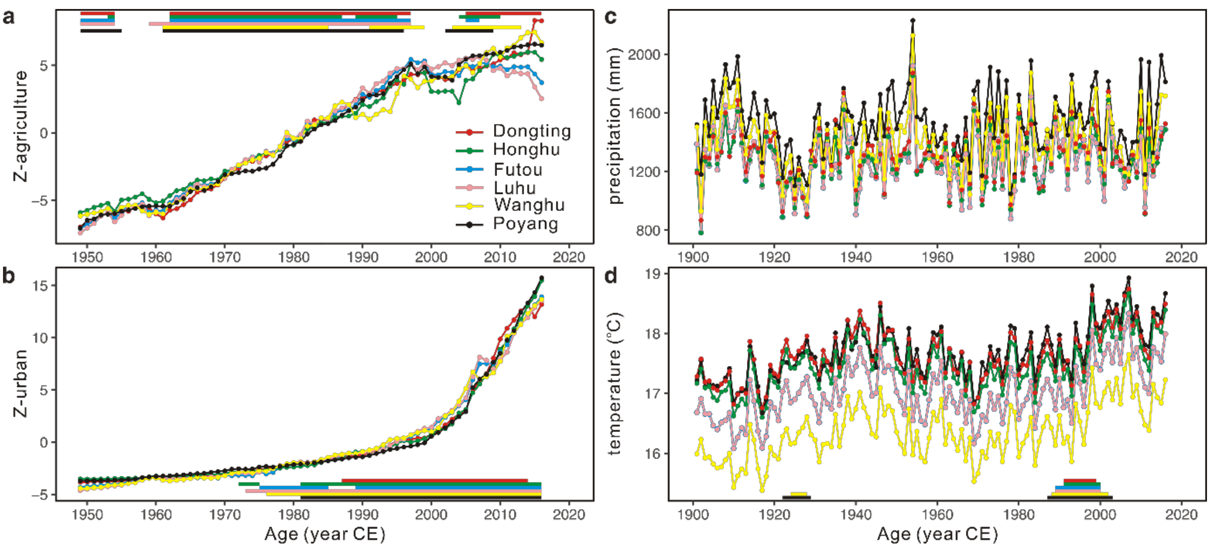

Figure 2 Summarized Z-scores of agricultural (a) and industrial/urban (b) drivers and total annual rainfall (c) and mean annual temperature (d) in each catchment. The horizontal bars in (a), (b) and (d) indicate the period when the first derivatives of the fitted GAMs values were significantly larger than 0, indicating periods of significant change.

3.2 Sedimentary TN and TP fluxes

Fluxes of N and P increased markedly in all lakes, relative to fluxes before ~ the 1950s CE (Figure 3). Between the 1950s and 2010s CE, TN fluxes were highly variable but increased from < 0.05 g cm^{-2} $year^{-1}$ to > 0.10 g cm^{-2} $year^{-1}$ (Figure 3). TP fluxes also increased since the 1950s CE, but temporal trends differed among lakes (Figure 3). Before the 1950s CE, sedimentary TP fluxes in the lakes were generally low (~ 0.01 g cm^{-2} $year^{-1}$). Since then, TP fluxes increased to ca. 0.04 g cm^{-2} $year^{-1}$ by the

1980s CE, followed by a decrease in Dongting, Honghu and Futou Lakes. However, TP fluxes continued to increase in Luhu, Wanghu and Poyang Lakes from 1950 CE onwards. In the 2010s CE, sedimentary TP fluxes were more than 0.025 g cm^{-2} year^{-1} in Dongting, Luhu, Wanghu and Poyang Lakes, which was ca. 2-fold of that in Honghu and Futou Lakes (~ 0.01 g cm^{-2} year^{-1}) (Figure 3). Overall, there was a more marked increase in TN fluxes in the upstream lakes relative to the downstream lakes where TP increased more prominently.

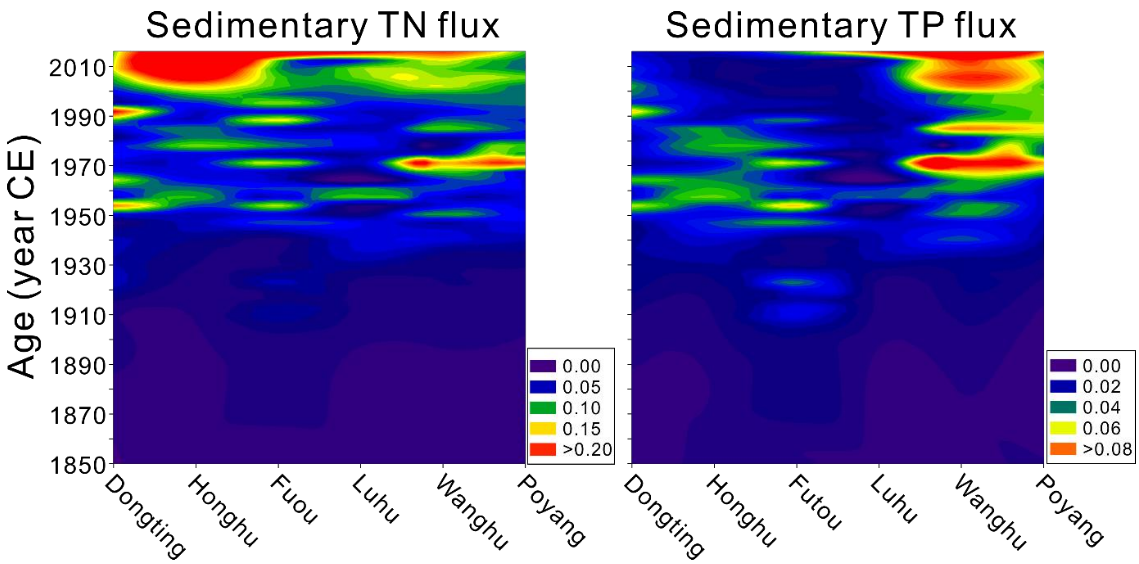

Figure 3 Sedimentary TN and TP fluxes in six lakes of the middle Yangtze floodplain. (unit: g cm^{-2} year^{-1}).

3.3 Summarising pigment trends in the lakes

Biomarker pigments from siliceous algae, cryptophytes, cyanobacteria and chlorophytes were present in all the lakes (Figure 4, Figure S4). When the pigment assemblages from all six lake cores were ordinated together, the first PCA axis (PCA axis 1, 74.8% variance) was significantly negatively correlated with all pigments ($R < -0.38$, $p < 0.001$). PCA axis 1 of pigments was therefore inferred to indicate overall algal (pigment) production in the lakes. The second PCA axis explained a further 11.8 % of the variance and was significantly correlated with aphanizophyll from HAB-forming cyanobacteria ($R = 0.61$, $p < 0.001$) (Figure 4). Trajectories of change were greatest in pigment assemblages from Luhu and Wanghu Lakes, and in the large open drainage lakes (Dongting, Poyang). Pigments in these four lakes moved towards negative PCA axis 2 scores (Figure 4), indicating the appearances of aphanizophyll after ~ 2000 CE (Figure 5; Supporting information Figure S3a-f). Aphanizophyll was not detected in significant quantities in the other macrophyte-dominated lakes (Futou, Honghu) and algal (pigment) change was also less pronounced in these sites.

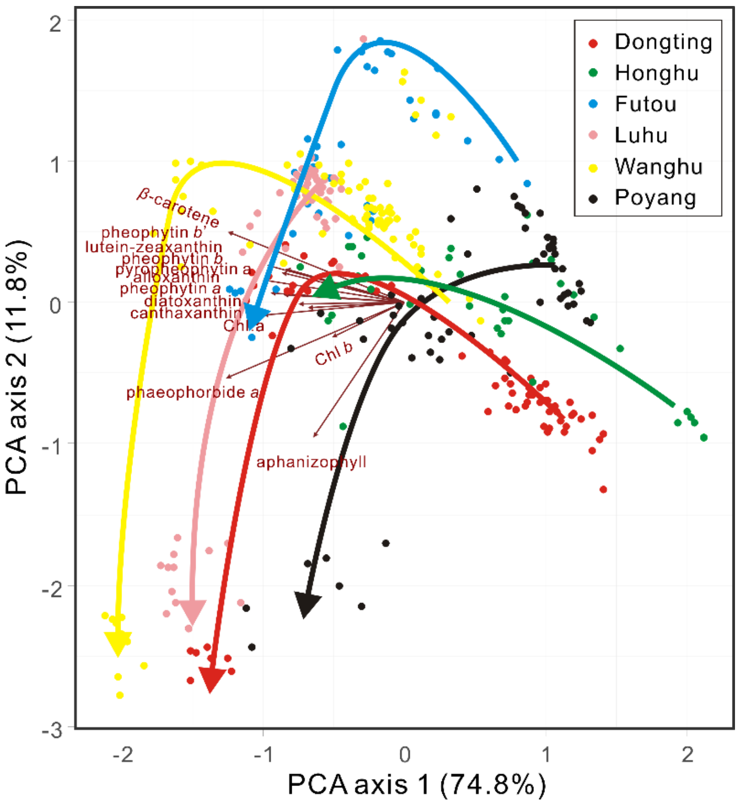

Figure 4 Biplot of PCA of sedimentary pigments from all six lakes. The coloured arrows indicate the trajectory from samples of older age to younger age.

GAM analyses identified the periods of most significant change in pigment PCA axis 1 (algal production) and indicated that lakes fell into two categories: in the first group of lakes, algal assemblages shifted abruptly around 1979-1982 CE (Luhu, Wanghu, Donting, Poyang), whereas the second group (Honghu, Futou) changed more gradually and the change started earlier (1952 CE and 1932 CE respectively) (Figure 5). Mann-Kendall coefficients (tau) of pigment PCA axis 1 indicated an increase in algal production (decrease in pigment PCA axis 1) in all of the lakes over the last two centuries (tau ≤ 0.37; $p < 0.001$), but a more consistent increase in the second group of lakes which changed more gradually (Figure 5).

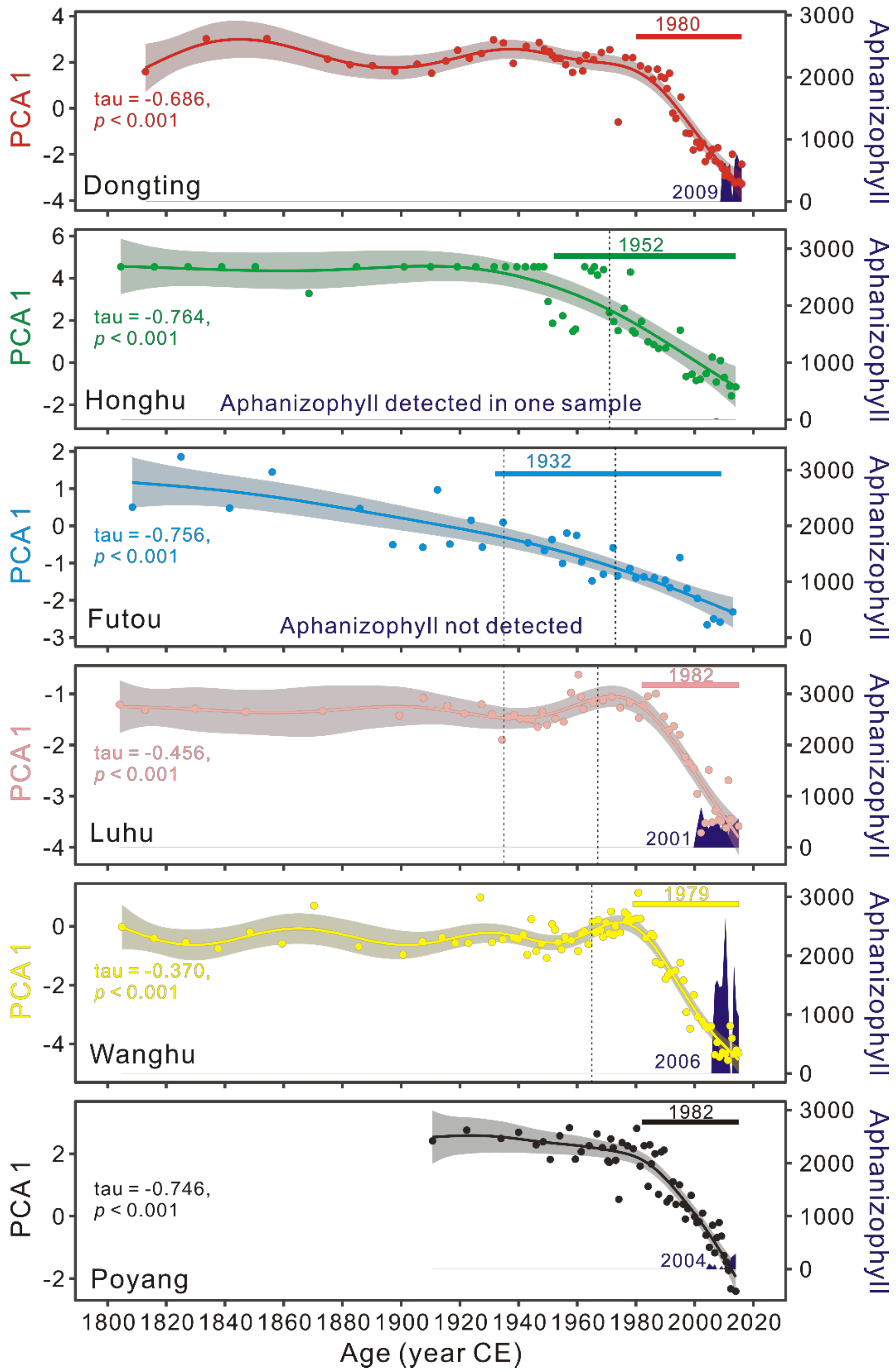

Figure 5 Observed and GAM fitted values for all-lake pigment PCA axis 1 scores (the band is the 95% pointwise confidence interval on the fitted values). The horizontal lines show the period when the first derivative of pigment PCA axis 1 is significantly different from 0, with the year indicating the start of the period. The vertical dashed lines indicate the date of local dam construction. tau is the MK coefficient values and p is the significance level. Aphanizophyll concentrations are indicated in purple, alongside the timing of this pigment first appearance in each lake.

Hierarchical partitioning analysis was used to investigate changes since 1949 CE and showed that the environmental variables (i.e., urbanization/industrialization, agriculture, precipitation, temperature, damming) explained ~ 65% (adj. $R^2 = 0.58$ to 0.71) of the variance in algal community composition of the six studied lakes. Human activities (agriculture and urbanization/industrialization) accounted for more than 57% of the total explained variances (Figure 6). Urban and industrial activities had the greatest effect on Luhu Lake (53.5%, $p < 0.01$), followed by Wanghu (42.2%, $p < 0.01$), Poyang (36.6%, $p < 0.01$), Dongting (35.0%, $p < 0.01$), Futou (34.6%, $p < 0.05$) and Honghu (22.3%, $p > 0.05$) (Figure 6). In contrast, agricultural activities had the greatest effect on algal community in Honghu (35.0%, $p < 0.05$), followed by Futou (32.4%, $p < 0.01$), Dongting (31.3%, $p < 0.05$), Wanghu (30.5%, $p < 0.01$), Poyang (29.4%, $p < 0.05$) and Luhu (17.6%, $p > 0.05$). While there are no local dams installed at the hydrologically open lakes (Dongting and Poyang), the TGD operation has changed river flows entering the lakes since 2003 CE. In these two lakes, the construction of the TGD also explained significant ($p < 0.05$) amounts of the variance in algal community composition, accounting for 24.5% and 24.9% of the total explained variance, respectively. In Luhu and Wanghu Lakes, temperature rather than damming explained significant ($p < 0.05$) amount of the variances in algal community composition and accounted for 25.0% and 25.2% of the total explained variances, respectively.

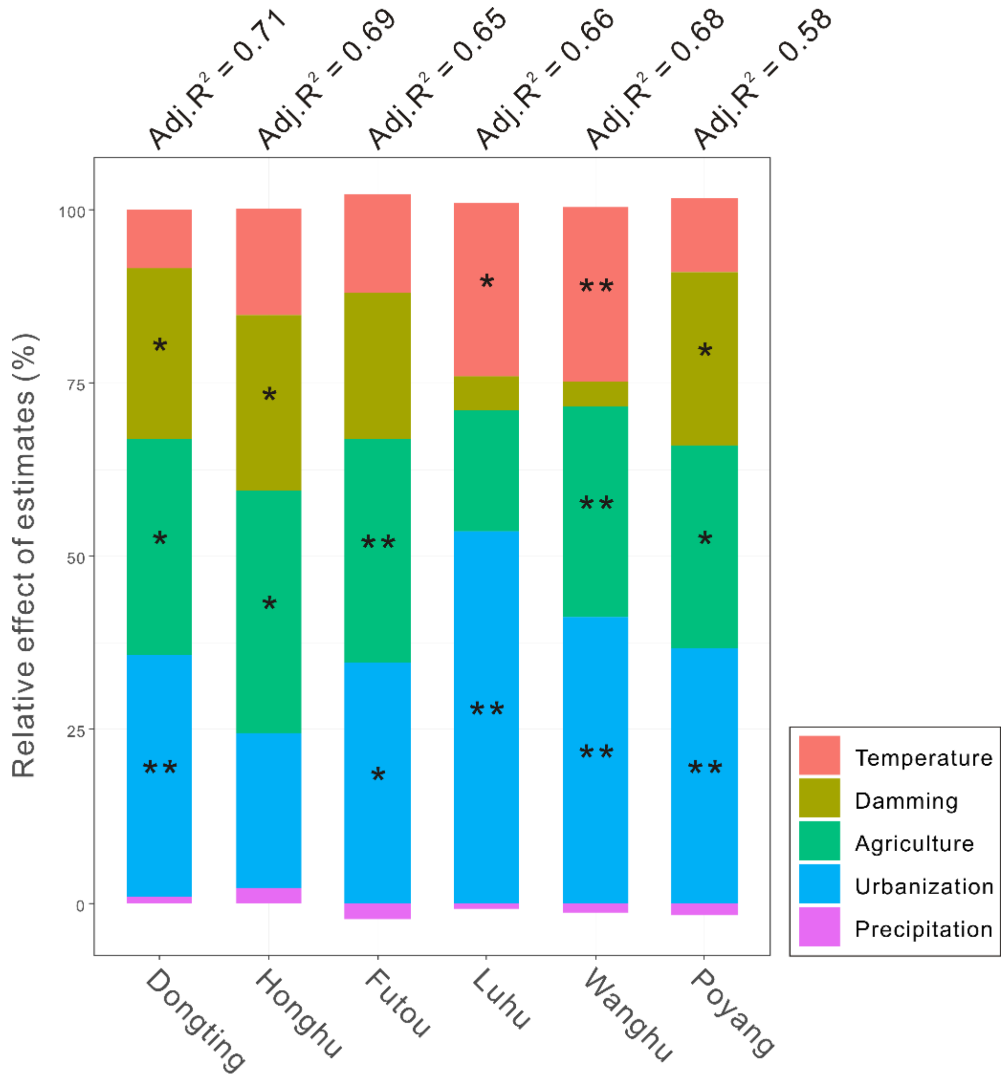

Figure 6 Relative importance of each individual environmental variable calculated by hierarchical partitioning in estimating algal assemblage change (sedimentary pigments) after 1949 CE in the study lakes. Adj. R^2 indicates the total variance explained by the explanatory variables. Significance level of the explanatory variables were based on permutation test based on 999 randomizations. ** < 0.01; * < 0.05

Regression analysis showed that relationships between PCA axis 1 (algal production) and sedimentary TN and TP fluxes since the ~1850s CE differed among lakes (Figure 7). In Dongting, Honghu and Futou Lakes, the first PCA axis of pigments was significantly correlated with TN but not with TP flux. In Luhu and Wanghu Lakes, both TN and TP fluxes were significantly correlated with pigment PCA axis 1. In Poyang Lake, there was no significant correlation between TN and TP fluxes and PCA axis 1 of pigments.

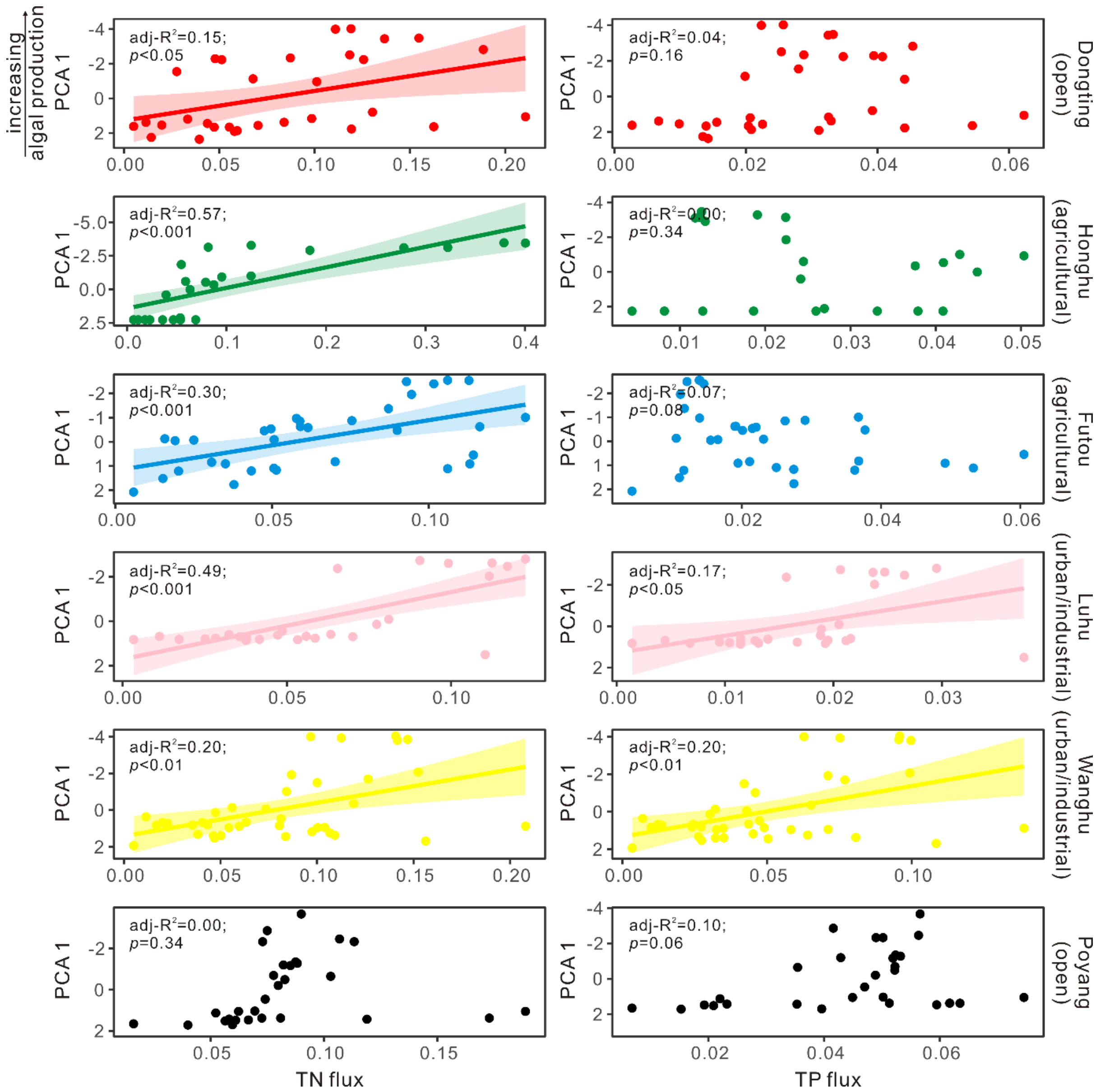

Figure 7 Linear regression between the first PCA axis of pigments (indicated algal production) and TN (left) and TP (right) fluxes (unit: g cm^{-2} yr^{-1}) to each lake (since ~ 1850 CE). The shaded bands surrounding the fitted lines indicate the 95 % confidence intervals.

4 Discussion

Many Yangtze floodplain lakes have undergone environmental degradation and declines in ecosystem services associated with extensive and intensive social-economic development since the 1950s CE (Dearing et al., 2012; Dong et al., 2016; Kattel et al., 2016; Zhang et al., 2018). However, because water quality monitoring and remote sensing records mostly began around the 1980s CE in China (Zong et al., 2019), the timing, trajectories and causes of changes in primary producer communities, including HABs are unclear. Using chlorophyll and carotenoid pigments as a proxy for phototrophic algae and cyanobacteria we reveal significant increases in production and shifts in pigment composition across all six lakes which span the mid-Yangtze region (Figure 5; Figure S4). Shifts in phototrophic pigments began during the 20th century, i.e. pigment concentrations increased relative to organic carbon in the sediments, indicating either an increase in phototroph production or pigment burial in the lakes, or both. The changes concur with observed increases in surface cyanobacterial blooms (Zong et al., 2019; Song et al., 2021), and shifts in diatom assemblages indicating more eutrophic waters (Yang et al., 2008; Dong et al., 2016). Hence, pigment assemblage shifts appear to faithfully reflect significant water quality degradation and increased HAB incidences (increases in aphanizophyll and canthaxanthin), reflecting broader changes in ecosystem functioning across this region. This change, observed from the 1930s CE onwards, far exceed the "baselines" of the 19th century (Figure S4), demonstrating that shifts in primary producers were unprecedented in recent history.

Unlike some watersheds where eutrophication intensity of lakes is spatially ordered (Quinlan et al., 2002; Moorhouse et al., 2018), the timing and patterns of phototroph changes were not apparently organized by watershed position across this large and hydrologically-complex mid-Yangtze region (Lin et al., 2021; Huang et al., 2022). Changes in pigment assemblages of two lakes were more gradual and occurred earlier (Futou in 1932 CE and Honghu in 1952 CE) than the other four where significant shifts happened around 1980 CE (Figure 5). This suggests localised stressors which differed among each sub-catchment, were driving pigment variability. Comparing the pigment records with dam installation dates, as well as meteorological and archival records documenting socio-economic development activities since 1949 CE provides further insights into the reasons for these major water quality declines.

4.1 Consequences of socio-economic development during the Anthropocene

The summarised archival data shows an earlier and more gradual rise in agricultural intensity across the region since 1949 CE (Figure 2a), than urban-industrial activities which increased significantly and exponentially after ~ 1980 CE (Figure 2b). Although trends in the archival indices were similar across the region (Figure 2), the intensity of agricultural versus urban/industrial pressures differed among the sub-catchments (Figure S1). This resulted in contrasting timings of phototrophic responses among the lakes, and consequently the strength of relationship between urbanization/industrialization versus agricultural activities also differed (Figure 8). Agricultural activities explained more of the pigment assemblage variance in Honghu and Futou lakes than urban/industrial indicators (Figure 8); major increases in algal production started from the ~ 1940s CE (Figure 5), consistent with the gradual intensification of agriculture (Figure 2). In contrast, the timing of significant algal production increases in Luhu, Wanghu, Dongting and Poyang lakes was coincident with the exponential rise of urban and industrial indicators (~ 1980 CE); these indicators explained higher amounts of the variance in the sedimentary pigments than agricultural indicators (Figure 8).

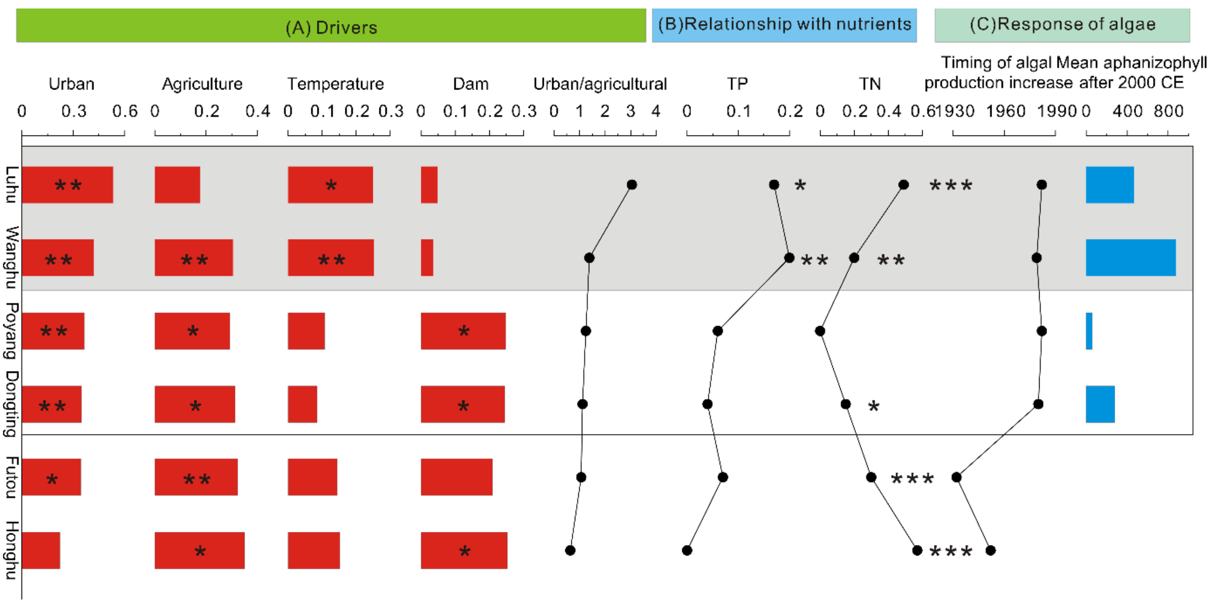

Figure 8 Comparison of (A) the relative importance of drivers calculated by hierarchical partitioning, (B) the R^2 values between pigment PCA axis 1 and sedimentary nutrient fluxes, and (C) the response of algae among the lakes. Number of * indicates the significance level, *** <0.001; ** < 0.01; * < 0.05

The rise in sedimentary nutrient (TN, TP) fluxes after ~ 1950 CE demonstrate how socio-economic development has increased nutrient loads into aquatic systems across the region. Agricultural use of synthetic fertilizers has significantly enhanced N loading in China (Yu et al., 2019) and we found that 55% of the variance in sedimentary TN flux was explained by agricultural proxies, of which, aquaculture products were a more important driver of sedimentary N than grain production (Supporting Information Figure S2). China is the biggest freshwater aquaculture producer in the world (FAO, 2020), with Hubei Province in the mid-Yangtze being a hotspot for aquaculture nutrient release (Wang et al., 2019). Inefficient use of fish feeds can lead to N accumulation in lake sediments (Legaspi et al., 2015). Grain production (mainly rice in this region) was also a significant explanatory variable for sedimentary TN fluxes, indicating that fertilizer runoff is another source of N pollution to lakes.

P is a component of most agricultural fertilizers, but P wastes associated with human consumption in China shifted from rural to urban areas as cities expanded (Liu et al., 2016) when P-laden wastewaters were released into waters via sewage systems (Tong et al., 2017). Accordingly, the largest amount (26.7%) of the variance in sedimentary TP flux was explained by concrete production, a summary indicator of urban growth (Supporting Information Figure S2) (Huang et al., 2018). Our results indicate that this rapid urbanization had major implications for P loading in these lakes, but that agricultural fertilizers also significantly contributed to P loading (Supporting Information Figure S2). Interestingly, the elevated P fluxes between 1950 and 1980 CE in the upstream lake sediments (Figure 3) prior to the period of urban expansion, likely record the period of maximum P fertilizer use before price controls were imposed on fertilizers by the Chinese government in the 1980s CE (Liu et al., 2016).

There were obvious spatial and temporal differences in nutrient fluxes among lakes, which altered how lake phototrophs responded (Figure 3, Figure 7, Figure 8). N accumulation rates rose markedly in Honghu and Futou lake sediments in the 2000 CE, but only reached similar levels in Luhu and Wanghu lakes in the last 5 years. Moreover, PCA axis 1 (an indicator of phototrophic changes) was solely related with sedimentary TN fluxes in Honghu and Futou lakes ($p < 0.001$), whereas there were significant relationships between pigment PCA axis 1 and both sedimentary TN and TP fluxes in Luhu and Wanghu lakes ($p < 0.05$) (Figure 8). Since 2008 CE, wastewater treatment has increased the TN/TP ratio in

Chinese freshwaters due to improved P removal (Tong et al., 2020). It seems likely that this shift explains both the later rise in N fluxes in urbanized Luhu and Wanghu Lakes, and significant phototroph responses to changes in both N and P fluxes, due to the shifting balance of delivery in these elements in the urbanized catchments. Overall, our data support the idea that, in agricultural landscapes, lake water quality and algal production are more likely to be influenced by excessive N pollution (e.g., Moss et al., 1994), while N and P pollution drives water quality declines in urbanized catchments.

4.2 The effects of dam installation

Construction of the TGD explained a significant amount of the variance in sedimentary pigments from the two hydrologically open lakes (Dongting and Poyang). The dam was installed upstream of all lakes in 2003 CE as part of the TGD project and so the lakes remained hydrologically open to the river. However, the reduction in Yangtze River flows led to a decline in the water exchange ratio (e.g., between Dongting Lake and the Yangtze River of ~ 35%; Li et al., 2013) and likely promoted the retention and sedimentation of nutrients and phototrophs, as registered by the increasing sedimentary nutrient fluxes and pigment concentrations in the early 1980s CE (Figure 5) (McGowan et al., 2011). It is also possible that the impoundment of the TGD upstream increased nutrient bio-availability in riverine waters (Chen et al., 2020) which, in synergy with the rapidly increasing nutrient loads from socio-economic development, fuelled elevated algal production. Together, the modification of physical (WRT) and chemical (nutrients) properties likely combined to trigger the huge increase in primary producer pigment assemblages after the ~ 1980s CE in Dongting and Poyang Lakes.

The lakes with open hydrological connections to the Yangtze River had insignificant (Poyang Lake, $p >$ 0.05) or weaker (Dongting Lake) relationships between algal production and nutrient fluxes when compared with the four locally-dammed lakes (Figure 7). The highly variable hydrological conditions and water levels in open lakes likely influence this relationship through periodic removal of algal biomass via wash-out interspersed with periods of accumulation and deposition (Tockner et al., 1999; Elliott, 2010; Richardson et al., 2019) with complex cycling of N and P sedimentation processes (Pan et al., 2009; Liu et al., 2017). For example, periodic flooding and drawdown in open lakes may accelerate the release of P from sediments (Attygalla et al., 2016).

4.3 The influence of climate

The amount of rainfall had no apparent effect on lake phototroph composition, but temperature was significantly correlated with Luhu and Wanghu Lake pigment assemblages (Figure 6). These two lakes are located within an area where air temperature is lower (mean value $\leq 17\ ^{\circ}C$) than other lakes (mean value > 17.5 $^{\circ}C$) (Figure 2d). It is plausible that long-term temperature increases have a greater effect on phototrophs at this lower temperature range. For example, warmer temperatures can modify phototrophic assemblages by providing a physiological advantage for cyanobacteria (Griffith and Gobler, 2020), and enhancing sedimentary nutrient release (Tong et al., 2020). The response to temperature in these lakes which are significantly influenced by nutrient loading indicates that, at this temperature range, and over decadal timescales, temperature appears to act synergistically with nutrient loading to influence phototrophic responses (Lin et al., 2021).

Temperature was not a significant driver of algal community changes in Dongting, Poyang, Honghu and Futou Lakes (Figure 6). While this lack of response could be attributed to the influence of the free hydrological setting in Dongting and Poyang Lakes (see above), we interpret that the dense aquatic macrophyte coverage in Honghu and Futou Lakes helped to buffer the phototrophic response (Song et al., 2016; Zeng et al., 2018). Macrophytes may supress phytoplankton production and HABs through several mechanisms according to the aquatic stable state hypothesis (Scheffer et al., 1993): by competing with phytoplankton for nutrients, by providing refuge to zooplankton which feed on phytoplankton and by limiting sediment resuspension and hence nutrient release (Timms and Moss, 1984; Jeppesen et al., 1998). We therefore hypothesize that the so-called “buffer mechanisms” associated with macrophyte cover helped to limit phototrophic production in Futou and Honghu Lakes (Figure 5, Table 1).

4.4 HABs

The sedimentary records of HAB indicators confirm remote sensing observations of widespread rises in surface bloom coverage on lake surfaces across the middle-Yangtze region since the 2000s CE (Zong et al., 2019). Carotenoids from cyanobacteria including canthaxanthin and zeaxanthin started to rise in all lakes prior to the appearance of aphanizophyll (from N_2-fixing cyanobacteria) during the 2000s CE (Figure S4, Figure 5). Of the lakes studied here, Wanghu Lake has the highest concentrations of aphanizophyll and also shows sustained elevated cyanobacterial bloom coverage since the 2000s CE in remote sensing records (Zong et al., 2019). Remote sensing also detected surface blooms in Poyang Lake (since 1990 CE), and Dongting, Futou and Luhu Lakes during the 2000s CE (Figure S4, Figure 5). While there is broad agreement on the rise in prevalence of HABs throughout the region, in contrast to remote sensing, our pigment analyses provide a continuous, long-term record of cyanobacteria, that also integrates phytoplankton from surface and deeper waters. N_2-fixing cyanobacteria pigments (aphanizophyll) were almost entirely undetectable in Futou and Honghu Lakes where nitrogen pollution was not intensive. Since other cyanobacterial biomarkers were also present in these lakes (Supplementary Information), we infer that non-N_2-fixing cyanobacteria were likely to be prevalent at these sites (e.g., *Microcystis* spp.) (Figure 3). Higher supply of N relative to P increases the likelihood that N remains replete later in the growth season when cyanobacteria blooms mostly occur (Xu et al., 2015). An excess supply of N means that N_2-fixing cyanobacterial taxa (e.g., *Anabaena* spp., *Aphanizomenon* spp.) are likely outcompeted by other cyanobacterial HAB-forming taxa (e.g., *Microcystis* spp) (Paerl et al 2016; Finlay et al., 2010; Liu et al., 2019). Our analyses suggest that expansion of urban/industrial activities after 2000 CE exacerbated P pollution in Luhu, Wanghu, Poyang and Dongting Lakes (sedimentary TN/TP flux < 10 after 2000 CE), resulting in the prevalence of N_2-fixing cyanobacteria (Schindler et al., 2008; Paerl et al., 2016). In contrast, Honghu and Futou Lakes which are more significantly influenced by agricultural N (sedimentary TN/TP flux > 15 after 2000 CE) (Figure 3), supported mainly non-N_2-fixing cyanobacteria.

The prevalence of HABs could also be increased by longer lake water retention times from damming which give a competitive advantage to slow-growing cyanobacteria (O'Neil et al., 2012). WRTs in Poyang Lake and Dongting Lake are approximately 30 and 29 days, respectively, which is about a sixth of that in the hydrologically-isolated lakes (~ 190 days in Honghu) (Wang and Dou, 1998). The production (Poyang) and duration (Dongting) of N_2-fixing HABs pigments (aphanizophyll) were lower in the hydrologically open lakes than the restricted-drainage lakes (Wanghu and Luhu) (Figure 8).

Phytoplankton surveys confirm that the dominant phytoplankton was cyanobacteria (e.g., *Anabaena* spp., *Aphamizomenon* spp.) in Wanghu and Luhu Lakes (Hubei Wildlife Trust, 2005; Rao et al., 2018), with a comparatively low biomass of diazotrophic cyanobacteria in Dongting and Poyang Lakes (Liu et al., 2017; Liu et al., 2019).

As observed in Taihu Lake in the lower Yangtze basin (Lin et al., 2021), warming can promote algal production and HABs by advancing the maximum growth rate and extending the growth season (Paerl et al., 2012), amplifying the physiological advantage of cyanobacteria (Griffith and Gobler, 2020), and enhancing sedimentary nutrient release (Tong et al., 2020). Mean annual temperature increased by ~ 0.4 $^{\circ}$C between 1950-1980 CE and 1981-2016 CE in the Luhu and Wanghu catchments and this proved to be important in exacerbating the expansion of HABs (Figure 2).

5 Conclusions

This study emphasizes the pervasive role of agrarian and urban social-economic development in enhancing nutrient delivery to lakes beyond 19th century baselines which led to significant increases in algal production in the middle Yangtze floodplain lakes. Algal community shifts associated with agricultural changes started earlier (~ 1940s CE) than those prompted by urban development (~ 1980 CE), but the degree of algal community change was greater when lakes were influenced by urban change. Urbanization and industrialization particularly exacerbated P fluxes into these lakes to a greater degree than agricultural activities, leading to the proliferation of N_2-fixing HAB-forming taxa. In contrast, lakes with algal communities that were influenced most by agricultural change retained macrophyte coverage and this appeared to be important in buffering against major shifts in algal communities. Management should prioritise protecting lakes that have retained macrophytes from further nutrient inputs, through agricultural management of aquaculture and cropland N, and avoiding further inputs of urban wastewaters.

The maintenance of an open hydrological connection with the river appears to also be important in influencing algal community composition and hence, water quality. Although the large and hydrologically-connected lakes (Dongting and Poyang) showed evidence of significant algal community change, the quantity of cyanobacterial HAB indicators was lower than in other lakes where HABs increased and algal communities responded less strongly to increasing nutrient fluxes. Therefore, the maintenance of connectivity of these lakes to the Yangtze River should be a priority.

Our results indicate that future climate change is unlikely to have a greater effect on these lakes than current nutrient inputs and damming. In none of our lakes did phototrophs respond to variability in annual rainfall, but it is possible that projected future shifts in seasonal distribution of rainfall could prove to be important. Temperature had significant effects on phototroph communities in two of the lakes (Wanghu, Luhu) that were the most degraded. In these lakes, macrophyte community coverage is now lacking, suggesting that macrophyte cover is key in supporting resilience in shallow lakes. Our analyses indicate that temperature may have exacerbated the HAB issues at these lakes, and that temperature effects may be more pronounced in lakes at the lower range of temperatures in this region. Therefore, reduction of nutrient inputs is important as a way of mitigating the effects of increasing temperature. Further, the results of our analysis suggest that local damming of these lakes had a limited effect on algal communities relative to nutrient reduction and so remediation measures such as active hydrological management of dams are unlikely to be effective in the face of such severe eutrophication cases.

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Declaration of competing interest

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

Authorship contribution statement

Linghan Zeng: Funding acquisition, Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft. **George E. A. Swann:** Visualization, Writing – review & editing, Supervision. **Melanie J. Leng**: Data curation, Writing – review & editing. **Xu Chen:** Funding acquisition, Data curation, Writing – review & editing. **Jing Ji**: Data curation, Writing – review & editing. **Xianyu Huang:** Funding acquisition, Writing – review & editing. **Suzanne McGowan:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing, Supervision.

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Declare of interest

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

Authorship contribution statement

Linghan Zeng: Funding acquisition, Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft. **George E. A. Swann:** Visualization, Writing – review & editing, Supervision. **Melanie J. Leng**: Data curation, Writing – review & editing. **Xu Chen:** Funding acquisition, Data curation, Writing – review & editing. **Jing Ji**: Data curation, Writing – review & editing. **Xianyu Huang:** Funding acquisition, Writing – review & editing. **Suzanne McGowan:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing, Supervision.