



Anthropogenic eutrophication of shallow lakes: Is it occasional?

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ABSTRACT

Understanding and managing the susceptibility of lakes to anthropogenic eutrophication has been a primary goal of limnological research for decades. To achieve United Nations' Sustainable Development Goals, scientists have attempted to understand why shallow lakes appear to be prone to eutrophication and resistant to restoration. A rich data base of 1151 lakes (each $\geq 0.5 \text{ km}^2$) located within the Europe and the United States of America offers a rare opportunity to explore potential answers. Analysis of sites showed that lake depth integrated socio-ecological systems and reflected potential susceptibility to anthropogenic stressors, as well as lake productivity. In this study, lakes distributed in agricultural plain and densely populated lowland areas were generally shallow and subjected to intense human activities with high external nutrient inputs. In contrast, deep lakes frequently occurred in upland regions, dominated by natural landscapes with little anthropogenic nutrient input. Lake depth appeared to not only reflect external nutrient load to the lake, but also acted as an amplifier that increased shallow lake susceptibility to anthropogenic disturbance. Our findings suggest that shallow lakes are more susceptible to human forcing and their eutrophication may be not an occasional occurrence, and that societal expectations, policy goals, and management plans should reflect this observation.

1. Introduction

Despite covering $< 1\%$ of land area, lakes are key ecosystems that are disproportionately important to life on the continents (Dudgeon et al., 2006). From millions of years ago, lakes have provided essential and valuable ecosystem services in support of human existence and development, including water supplies (drinking, industry, irrigation), flood mitigation, fisheries, biodiversity, hydropower, transportation, recreation, and aesthetics (Ho and Goethals, 2019). However, human activities present a formidable threat to freshwater ecosystems that can transform aquatic ecosystems (Carpenter et al., 2011), in turn limiting the development and health of society (Foley et al., 2005). Unprecedented acceleration of industrialization, agriculture, urbanization, and population growth during the 20th century has increased nutrient influx, elevated primary production, degraded water quality, and reduced biodiversity in approximately 40% of the total number of lakes worldwide (Ho et al., 2019). Anthropogenic eutrophication has resulted in greatly increased occurrence of harmful algal blooms that threatens water security and the delivery of ecosystem services (Ho et al., 2019). Unfortunately, anthropogenic pressures and climate warming are expected to increase

further, such that the global occurrence of lakes with harmful algal blooms are expected to increase by over 20 percent by 2050 (UNESCO, 2014). Lakes are an important part of water resources (Goal #6) in the United Nations' Sustainable Development Goals (SDGs), while lake eutrophication poses a great threat to achieve the SDGs (Woolway et al., 2020). Therefore, there is a profound need to better understand the susceptibility of lakes to eutrophication to safeguard these systems for a sustainable future (Conley et al., 2009; Schindler, 1974; Paerl and Huisman, 2008).

Anthropogenic eutrophication of lake ecosystems is a widely acknowledged, but largely unresolved, global environmental problem that makes lake sustainability difficult to achieve (Ho et al., 2019). Management of lake eutrophication and harmful algae blooms remains unsuccessful in many regions (Birk et al., 2020), especially for large shallow lakes in North America (Okeechobee, Winnipeg, Erie, Champlain), Europe (Lough Neagh, Peipsi, Mälaren), and China (Taihu, Chaohu, Dianchi) (Bunting et al., 2016; Conley et al., 2009; Qin et al., 2019; Watson et al., 2016). It is well recognized that the prevalence of eutrophication varies with respect to watershed geology, climate, land use, landscape position, connectivity, and lake morphology, each of

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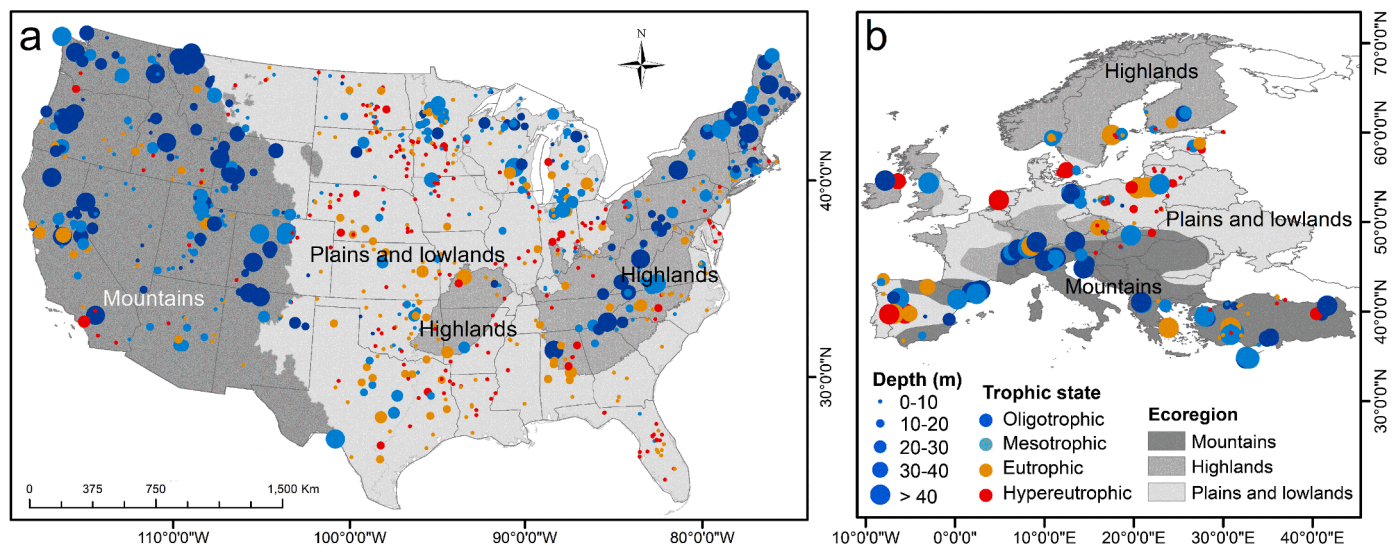


Fig. 1. The distribution of 1151 study lakes across the United States of America (a) and the Europe (b). According to U.S. EPA (Herlihy et al., 2008) and De Blij (1978), lakes are overlaid onto a background map detailing the three main ecoregions (plains and lowlands, mountains, and highlands). Lakes are categorized into four major trophic states: oligotrophic ($\text{Chl } a \leq 2 \mu\text{g L}^{-1}$), mesotrophic ($2 \mu\text{g L}^{-1} < \text{Chl } a \leq 7 \mu\text{g L}^{-1}$), eutrophic ($7 \mu\text{g L}^{-1} < \text{Chl } a \leq 30 \mu\text{g L}^{-1}$), and hypereutrophic ($\text{Chl } a > 30 \mu\text{g L}^{-1}$). The size classification of the circle indicates the maximum depth of the lakes.

which varies with lake district or ecoregion (Dolman et al., 2016; Heino et al., 2021). Hutchinson (1967) noted the difference of lake trophic state between upland and lowland. However, relatively little is known of how these factors interact, particularly at continental scales (Birk et al., 2020). In general, human activities increase with decreasing altitude, with plain and lowland areas being subject to intense agricultural activities, urban development, and population aggregation (Solheim et al., 2019). As the morphological characteristics of basins are largely determined by underlying geology and land forms, lakes in the plains and lowlands are often shallow (Scheffer and van Nes, 2007). As a result, it may be difficult to isolate the unique effects of basin morphology and human activities on lake trophic state and water quality in some lake regions (Hutchinson, 1967; Taranu and Gregory-Eaves, 2008). Further, many studies to date have focused on single lakes rather than landscape patterns of inland waters across continental scales (Moorhouse et al., 2018). Instead, a holistic understanding of lake eutrophication and improved lake management strategies requires freshwaters to be considered as part of an integrated socio-ecological system (Dearing et al., 2015; Schindler, 2006).

In this study, we analyzed 1151 lakes (Fig. 1) with area $\geq 0.5 \text{ km}^2$ located within the Europe (EU) and the United States of America (US) to identify how lake morphology and regional social-ecological systems interact to affect the susceptibility of lakes to anthropogenic eutrophication. Based on regional studies (Birk et al., 2020; Ho et al., 2019), we predicted that trophic state would be greatest in shallow lakes due to elevated rates of external and internal nutrient loading, particularly in areas with intensive human activities. Our goal was to develop a synthetic understanding of causes and correlates of lake eutrophication, with particular emphasis on evaluation of how physical features interact with social activities as controls of the eutrophication of lakes.

2. Materials and methods

2.1. Lake data

National lake surveys (NLA) of US were conducted during May to September in 2007 and 2012 by the Environmental Protection Agency of US (EPA) to provide an unbiased assessment of lake quality. Similarly, the EU Multi Lake Survey (EMLS) was conducted in the summer of 2015 across 27 countries to obtain a deeper insight into the dynamics of cyanobacteria across Europe (Mantzouki et al., 2018). In the current

study, very small lakes (area $< 0.5 \text{ km}^2$) were excluded from this analysis because small lakes are in generally shallow with small and diverse watersheds and wide distribution that could mask the causal mechanisms regulating these ecosystems. Accordingly, 215, 689, and 407 lakes were extracted in the EMLS, NLA 2007, and NLA 2012, respectively. The 162 US lakes surveyed in both 2007 and 2012 were used to quantify sub-decadal changes in lake trophic state and land use. Overall, 1151 lakes with area $\geq 0.5 \text{ km}^2$ were selected for the current study (Fig. 1).

2.2. Lake features

Survey parameters included lake morphometry (area, maximum depth), transparency (Secchi depth), nutrients (total nitrogen, TN; total phosphorus, TP; Ammonia), and algal abundance (as Chlorophyll *a*, $\text{Chl } a$), and cyanobacterial toxins (microcystins). The physical, chemical and biological variables of lakes were collected and analyzed in a fully standardized manner (detailed in Mantzouki et al. (2018) and <https://www.epa.gov/national-aquatic-resource-surveys/manuals-used-national-aquatic-resource-surveys#National%20Lakes%20Assessment>). Survey lakes included a wide range in area, depth, elevation, and trophic state (Table S1). Of these, 217 (18.9%) lakes were oligotrophic ($\text{Chl } a \leq 2 \mu\text{g L}^{-1}$), 360 (31.3%) were mesotrophic ($2 \mu\text{g L}^{-1} < \text{Chl } a \leq 7 \mu\text{g L}^{-1}$), and 306 (26.6%) were eutrophic ($7 \mu\text{g L}^{-1} < \text{Chl } a \leq 30 \mu\text{g L}^{-1}$), with a further 268 (23.3%) classified as hypereutrophic ($\text{Chl } a > 30 \mu\text{g L}^{-1}$) (Table S2).

2.3. Ecoregions

US and EU lakes were grouped into three main ecoregions (plains and lowlands, highlands, and mountains) as defined by US EPA (Herlihy et al., 2008) and De Blij (1978), respectively. In this database, 240 lakes (20.9%) are located in the highlands, 308 (26.8%) lakes are located in the mountains, and 603 lakes (52.3%) are located in the plains and lowlands (Table S2).

2.4. Land use and land cover

The NLA data set of 2007 and 2012 included land use and land cover data for each lake watershed, derived from the 2001 and 2006 National Land Cover Database (NLCD) (Fry et al., 2011; Homer et al., 2007), respectively. According to the methods of NLCD, Landsat images with a

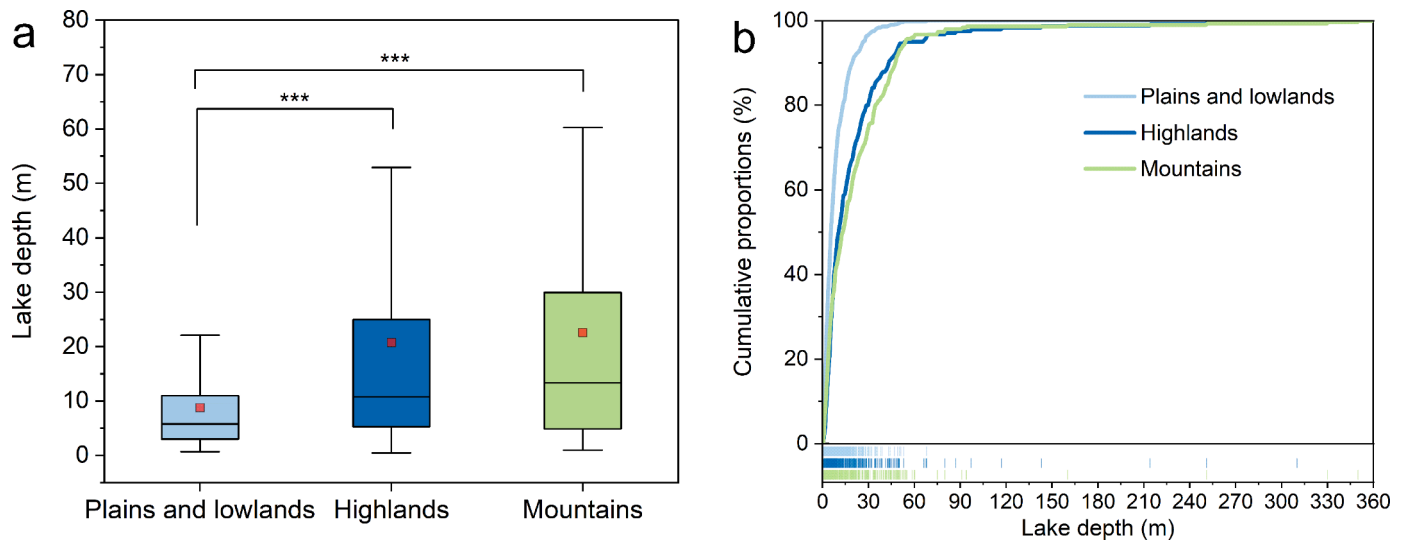


Fig. 2. The distribution (a) and cumulative proportions (b) of maximum lake depth in the three main ecoregions (plains and lowlands, highlands, and mountains). Red dots in the a indicate the mean of maximum lake depth. Statistical differences between ecoregions are shown on the basis of Mann-Whitney U test (*** $P < 0.001$).

spatial resolution of 30 m were obtained from the United States Geological Survey and were used to obtain lake area and land use data of each lake in the EMLS in the summer of 2015. The area and percentage of land use for each lake watershed was characterized for eight types, including developed, agriculture (planted/cultivated), water, barren, forest, shrubland, herbaceous, and wetlands. In the present study, land use is further divided into human land (developed, agriculture) and natural land (water, barren, forest, shrubland, herbaceous, wetlands).

2.5. Trophic state index

Key indicators of water quality are the concentrations of Chl *a* and nutrients (in particular TP and TN), as well as water transparency (Secchi depth). Accordingly, trophic state index (TSI) of Carlson (1977) can be calculated using each measure. In this paper, we calculated a mean value from all three TSI (Chl *a*, TP, and Secchi) and used that as our metric of trophic state at each lake. The TSI were calculated by

$$\text{TSI (Secchi)} = 10 \left(6 - \frac{\ln \text{Secchi}}{\ln 2} \right) \quad (1)$$

$$\text{TSI (TP)} = 10 \left(6 - \frac{\ln \frac{48}{\text{TP}}}{\ln 2} \right) \quad (2)$$

$$\text{TSI (Chl } a) = 10 \left(6 - \frac{2.04 - 0.68 \ln \text{Chl } a}{\ln 2} \right) \quad (3)$$

where *Secchi* is the depth of Secchi disk transparency (m), *TP* and *Chl a* are the concentrations of total phosphorus ($\mu\text{g L}^{-1}$) and Chlorophyll *a* ($\mu\text{g L}^{-1}$).

2.6. Statistical analysis

The decision tree-heatmaps is a new type of integrated visualization of decision trees and heatmaps, which provides a comprehensive data overview as well as model interpretation. This integration uncovers meaningful patterns among the predictive features and highlights the important elements of decision trees including feature splits and several leaf node characteristics such as prediction value, impurity and number of leaf samples. In this study, decision-tree heatmaps were used to predict the threshold of different trophic states based on the interactions

between ecoregion features, land use, and maximum lake depth using the package ‘treeheatr’ in R 4.0.4 (Le and Moore, 2021).

The relative (% cover) of each of eight land cover types was estimated for each lake and their distribution with lake depth was estimated using generalized additive model in the ‘mgcv’ package. Statistical differences of lake depth among ecoregions were examined with Mann-Whitney U test, because the distributions of lake depth were not normally distributed. Correlations among water depth, trophic state, nutrient input, and land use variables were explored with Spearman’s correlation coefficient using the package ‘stats’. Pearson’s Chi-Square test was used to evaluate correlations among lake depth, ecoregion, land use, and trophic state, and Cramer’s V coefficients were calculated to evaluate the magnitude of the correlation. All analyses performed in R 4.0.4 (R Core Team, 2021). The level of significance used for all tests was $P < 0.05$.

2.7. Data availability

The underlying data used for the analysis are openly accessible online. Specifically, the NLA data set is available at <https://www.epa.gov/national-aquatic-resource-surveys/nla>, and the data set of EU Multi Lake Survey is available at <https://portal.edirepository.org/nis/mapbrowse?packageid=edi.176.5>.

3. Results

3.1. Distribution of lake depth among ecoregions

Maximum lake depth ranged from 0.5 m to 350 m, with significant variation among ecoregions (Fig. 2). In general, lakes were significantly shallower in the plains and lowlands (8.8 ± 8.8 m) compared to the highlands (20.8 ± 33.4 m) and mountains (22.6 ± 35.1 m) (Fig. 2a, $P < 0.001$). Lakes located in the plain and lowland areas were generally shallow, while deep lakes were frequently distributed in the mountain and highland regions (Fig. 2b).

3.2. Relationships among lake depth, land use, and trophic state

Watersheds of shallow lakes were composed mainly of human-influenced land use types, while watersheds of deep lakes were frequently dominated by natural land use (Fig. 3a). In this analysis, the percentage of developed, agriculture, water, herbaceous, and wetlands

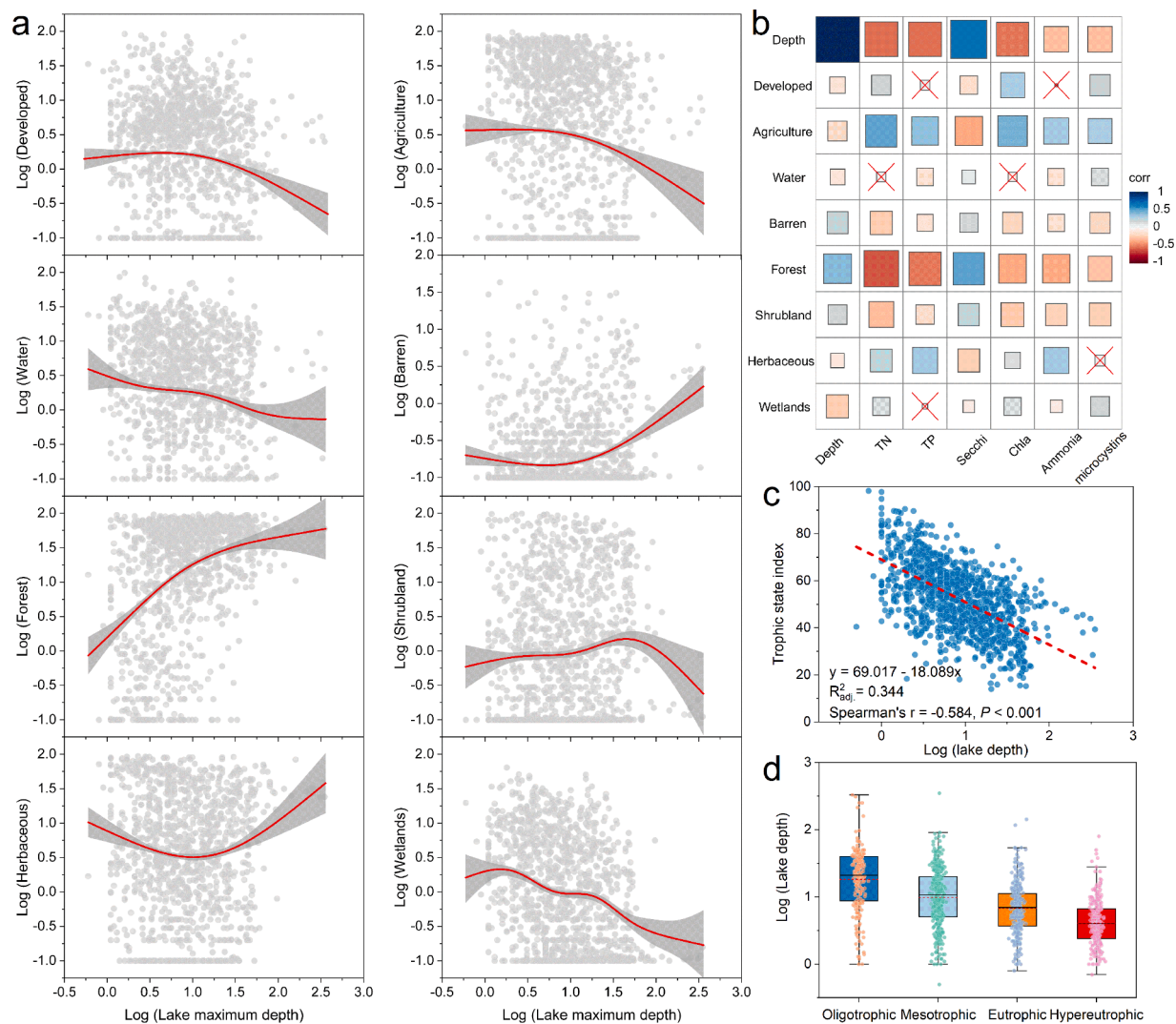


Fig. 3. The relationships among land use, lake depth, and trophic state. **a**, the percentage of land cover for developed, agriculture, water, barren, forest, shrubland, herbaceous, and wetlands varies with lake maximum depth. The red line is a generalized additive model regression, and grey shading represents pointwise 95% confidence interval of the fitted values. The data were \log_{10} -transformed prior to analysis. **b**, pairwise correlations among land use, maximum lake depth (depth), trophic state (TN, TP, secchi, Chl *a*, and Ammonia), and microcystins are explored with Spearman's correlation coefficient. The color gradient indicates the correlation coefficients (corr), and the square without cross indicate the correlations are significant ($P < 0.05$). **c**, the relationships between maximum lake depth and trophic state index. Lake depth was \log_{10} -transformed prior to analysis. **d**, the distributions of maximum lake depth in four lake trophic categories. Red dotted lines indicate the mean of maximum lake depth.

exhibited a significant decreasing trend with increasing maximum lake depth, while the opposite was observed for barren, forest, and shrubland covers (Fig. 3a and b, $P < 0.05$). Human land use was correlated negatively with lake depth (Spearman's $r = -0.21$, $P < 0.001$), while it was opposite for natural land use (Spearman's $r = 0.2$, $P < 0.001$, Fig. S1). In particular, forest ($34.5\% \pm 28.5\%$) and agriculture ($21.5\% \pm 23.7\%$) were the two predominant land types, both of which were correlated strongly to lake depth (Fig. 3b, $P < 0.001$). Lake productivity and microcystins showed a consistent negative correlation with the percentage of natural land use, yet were correlated positively with human land (Fig. 3b, $P < 0.05$).

Eutrophic conditions were mainly concentrated in shallow lakes (Fig. 3c and d). According to the TP, Chl *a*, and Secchi depth indices, the trophic state index of lakes showed a significant decreasing trend with increasing depth (Fig. 3c, Spearman's $r = -0.584$, $P < 0.001$). Furthermore, based on the lake trophic categories, lake depth varied widely in both the oligotrophic and mesotrophic lake categories, whereas eutrophic and hypereutrophic lakes were frequently confined to shallow water depths (Fig. 3d).

3.3. Variations of land use and trophic state with lake depth from 2007 to 2012

Based on the 162 lakes surveyed in both NLA 2007 and NLA 2012, the variations in land use and trophic state between 2007 and 2012 mainly distributed in shallow lakes, while there were few marked variations in deep lakes (Fig. 4). From 2007 to 2012, the average percentage of natural land decreased $0.06\% \pm 2.5\%$ overall, whereas human-influenced land use increased $0.05\% \pm 2.5\%$. These variations mainly occurred in shallow lake catchments, while deep basins were relatively unchanged (Fig. 4a). Moreover, from 2007 to 2012, the values of TN, TP, Secchi, and Chl *a* increased $0.07 \pm 0.56 \text{ mg L}^{-1}$, $0.008 \pm 0.21 \text{ mg L}^{-1}$, $0.09 \pm 1.37 \text{ m}$, and $0.55 \pm 24.7 \text{ } \mu\text{g L}^{-1}$, respectively (Table S3). Similar to land use, the variations of TN, TP, and Chl *a* generally occurred in shallow lakes, but deep lakes remain stable (Fig. 4b). Overall, lakes in the plain and lowland areas exhibited intensified eutrophication (as Chl *a*), whereas water quality mainly improved in highland and mountain ecoregions (Table S3).

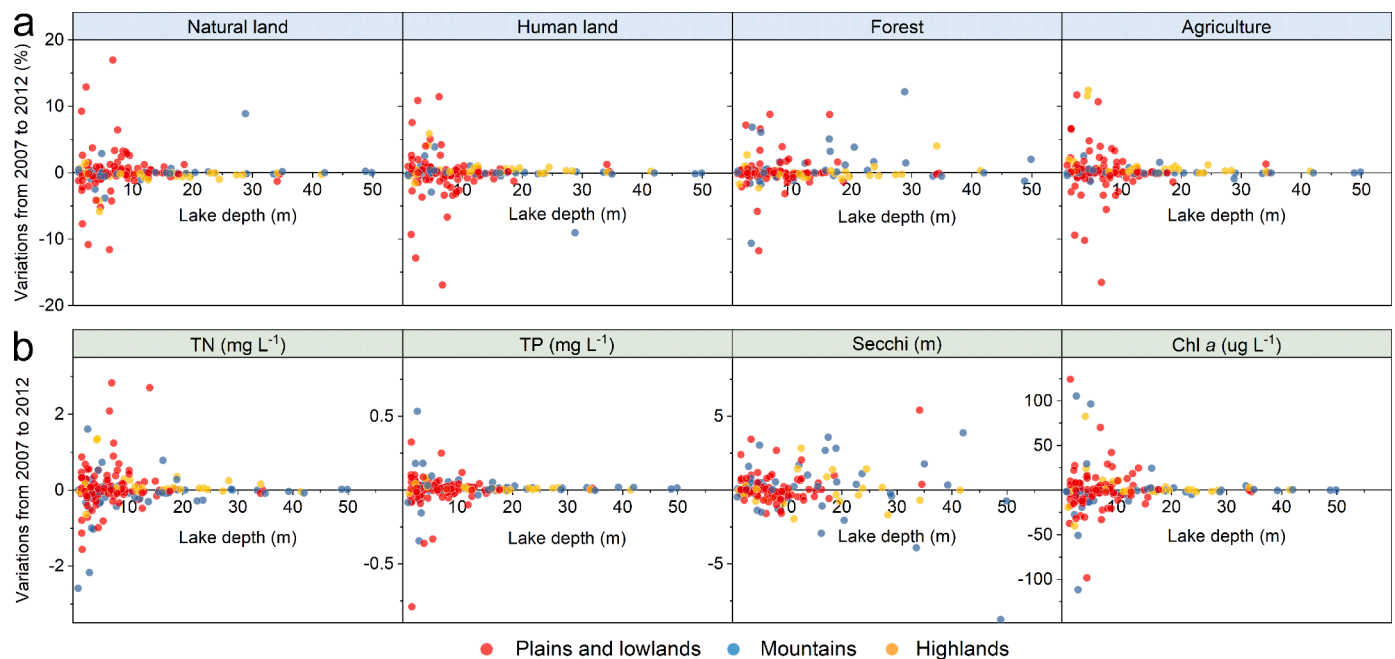


Fig. 4. Variations of land use (a) and lake trophic state (b) from 2007 to 2012 along with maximum lake depth based on the 162 common lakes between the NLA 2007 and NLA 2012. Lakes are categorized into three ecoregions (plains and lowlands, mountains, and highlands).

3.4. Relationships among lake depth, ecoregion, land use, and trophic state

Decision-tree heatmap analysis demonstrated that water depth was closely related to ecoregion and land use, likely reflecting an intrinsic relationship between water depth and lake productivity (Fig. 5a). For example, lakes were eutrophic or hypereutrophic if their maximum depth was ≤ 13.8 m unless located in natural landscape of highland and mountain ecoregions (Fig. 5a). In contrast, oligotrophic or mesotrophic lakes were routinely deeper than 13.8 m, especially > 34.1 m, irrespective of ecoregion or land use within the lake catchment (Fig. 5a). Correlation analysis revealed a significant association among lake depth, ecoregion, land use, and trophic state (Table 1, χ^2 test, $P < 0.001$).

80.6% lakes in the plains and lowlands were ≤ 13.8 m, while deeper lakes were more common in the highland (41.2%) and mountain (50.7%) regions (Fig 5b). Similarly, 83.3% lakes in human-dominated watersheds were ≤ 13.8 m, while lake depth varied widely in nature-dominated landscapes (Fig 5b). As well, 63.2% of the lakes ≤ 13.8 m were eutrophic or hypereutrophic, whereas only 19.8% of lakes > 13.8 m depth were highly productive (Fig 5b). Furthermore, 44.6% of ≤ 13.8 m lakes located in the mountain and highland areas and dominated by natural land were eutrophic and hypereutrophic compared to only 10.5% in lakes > 13.8 m deep (Fig 5b). However, 33.3% of > 13.8 m lakes in the plains and lowland regions and human-dominant land were eutrophic compared to 82.8% of shallow lakes (≤ 13.8 m, Fig 5b). Accordingly, although human land use in watersheds influences all lakes, lake depth can act as a ‘filter’ that modifies lake response to disturbance, with greater influence of land use on water quality in shallow lakes.

4. Discussion

A better understanding of the dynamic relationships between lake depth, social, and environmental phenomena is necessary to improve lake management strategies (Dearing et al., 2015). Randomized, unequal probability surveys conducted by the US EPA and EMLS provide unbiased estimates of lake eutrophication and allows us to infer the

causal relationships between lake trophic state and environmental conditions needed to advance the restoration and protection of lakes (Stoddard et al., 2016). Our analysis suggests that lake depth is linked to the ecoregion and land use of lake ecosystems, which largely determines the intensity of human activities and, consequently, lake productivity. This information may help clarify why shallow lakes are prone to eutrophication and improve lake management strategies for a sustainable future.

The ecoregional characteristics of lake watersheds provide an important basis predicting the trophic state of lakes, largely reflecting the underlying climatic, soil, topographical, and hydrological characteristics (Tang et al., 2020). Generally, in plain and lowland areas, the terrain is flat and soil is naturally fertile, with a well-developed drainage system that is consequently subject to agricultural activities and urban development (Heino et al., 2021; Read et al., 2015; Solheim et al., 2019). Since the start of the 20th century, the global expansion of agricultural activities and urbanization associated with widespread socio-economic development is occurring in plain and lowland ecoregions, resulting in marked changes in land cover and enhanced anthropogenic nutrient inputs (Beaver et al., 2014). In contrast, steep slopes and poor soil development in upland regions usually make lake watersheds unsuitable for agriculture and urban development (Aranguren-Riano et al., 2018). Indeed, agricultural land use of lakes is dominant in the plains and lowlands ($30.4 \pm 25.3\%$) but not upland regions (highlands $14.7 \pm 16.4\%$, mountains $9.3 \pm 17.5\%$), while forests are the main land cover at higher elevations (highlands $59.3 \pm 20.9\%$, mountains $41.4 \pm 28.2\%$) than occur in plains and lowlands ($21.2 \pm 23.0\%$, Fig S2). Moreover, compared to the lakes situated in upland regions, the water temperature of lakes is generally higher in plain and lowland regions, which could provide a favorable environment for cyanobacteria (Paerl and Huisman, 2008).

Agriculture is one of the most important drivers of lake eutrophication at a global scale (Nielsen et al., 2012), contributing 84% of the P discharged into US surface waters (Carpenter et al., 1998). However, watersheds dominated by forest and natural vegetation generally export lower amounts of allochthonous material to surface waters (Nobre et al., 2020). Consistent with these patterns, in this study, 67.0% of lakes in plains and lowlands were eutrophic, while only 27.6% of lakes in the

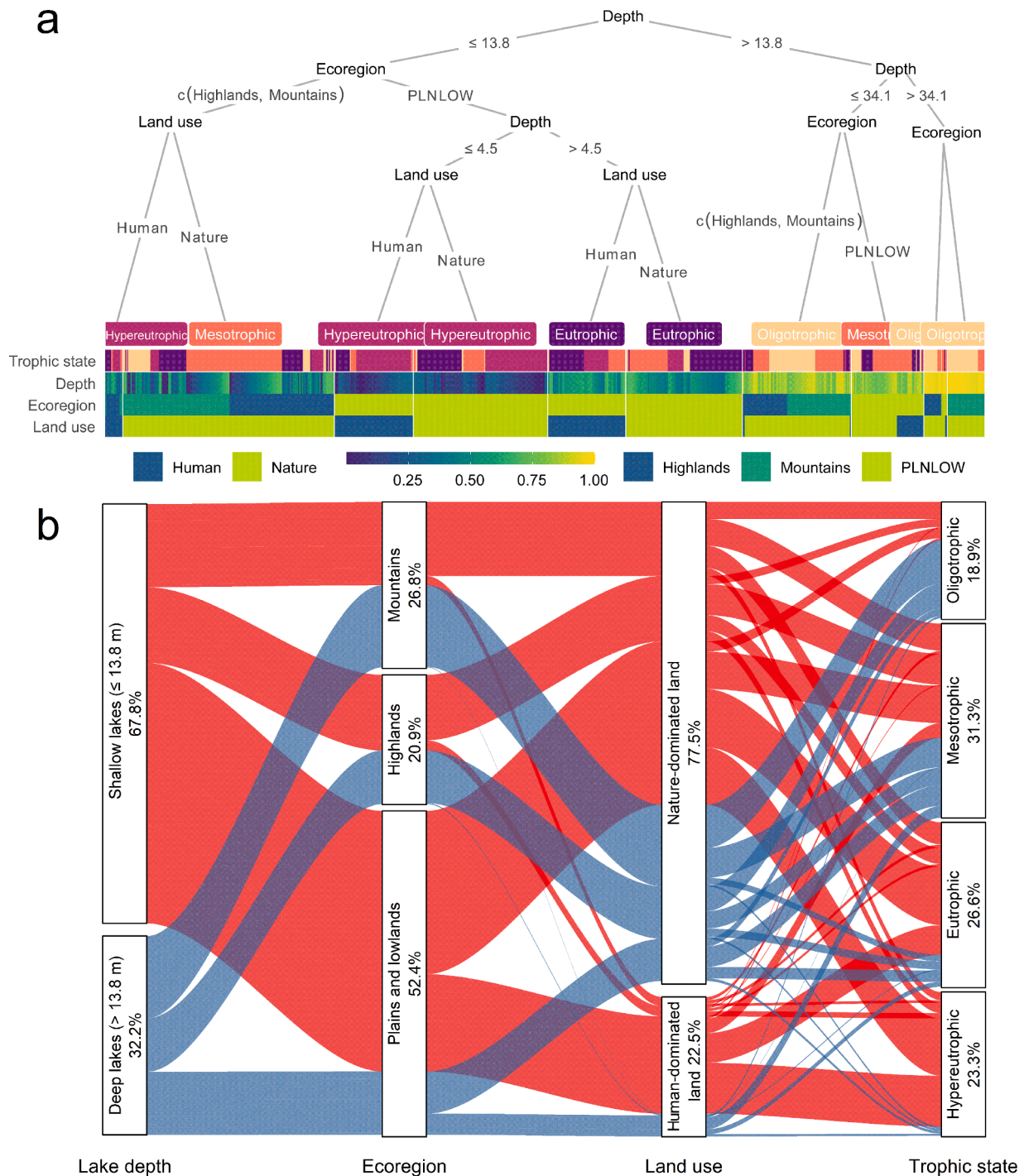


Fig. 5. The relationships among lake depth, ecoregion, land use, and trophic state. a, a decision tree-heatmap for predicting the threshold of different trophic lakes based on the three ecoregions (plains and lowlands [PLNLOW], highlands, and mountains), land use (nature- and human-dominated land), trophic state (oligotrophic, mesotrophic, eutrophic, and hypereutrophic), and maximum lake depth. The tree and heatmap give us an approximation of the proportion of samples per leaf and the model's confidence in its classification of samples in each leaf. The colors present the categories of land use, ecoregions, and trophic state, and the color bar present the relative value of maximum lake depth. b, the synchronous distribution of shallow (≤ 13.8 m) and deep (> 13.8 m) lakes in the differential ecoregions, land use categories, and trophic states.

upland areas were eutrophic (Table S2). As a result of limited land suitable for future agricultural expansion, yet a growing human population, fertilization and disturbance of plain and lowland regions is likely to intensify on a global basis (Tilman, 1999; Laurance et al., 2014). For example, according to NLCD, 1.77% of land cover was mapped as changed from 2006 to 2011 of the continental United States, which mainly occurred in the plains and lowlands of southeastern United States

(Homer et al., 2015). The largest net losses occurred in the forest classes ($-31,038 \text{ km}^2$), while the land use of developed classes and cultivated crop increased $7,631 \text{ km}^2$ and 696 km^2 , respectively (Homer et al., 2015). Indeed, according to the NLA 2012, the proportion of lakes in the most disturbed condition for TP were mainly (80%) located in the Northern Plains as compared to the Western Mountains (17%), while the Southern Plains exhibited the highest proportion of disturbed condition

Table 1

Summary of Pearson's Chi-square test and Cramer's V coefficient among depth, ecoregion, land use, and trophic state of lake ecosystems. $n = 1151$ lakes. The values indicate the correlation coefficient (Cramer's V), which reveal a significant association among lake depth, ecoregion, land use, and trophic state. Statistical significance is indicated by *** $P < 0.001$.

	Depth	Ecoregion	Land use	Trophic state
Depth	1	0.297***	0.251***	0.460***
Ecoregion		1	0.447***	0.309***
Land use			1	0.233***
Trophic state				1

(41.6%) based on Chl *a* analysis, in sharp contrast to the low proportion disturbed (only 0.7%) in the Western Mountain ecoregion (USEPA, 2016). Together, these patterns suggest that lakes in the plain and lowland areas are both generally shallow and more susceptible to human activities, whereas deep lakes are distributed mainly in mountain and highland regions with little anthropogenic nutrient input.

Although external nutrient inputs are the main determinants of lake eutrophication, effects of allochthonous nutrients will also be modified by in-lake biogeochemical processes such as sedimentation, export, and sedimentary exchange—all factors which vary strongly with water depth (Qin et al., 2020). The susceptibility of lakes to anthropogenic eutrophication and water quality degradation may be more pronounced

in shallow lakes (Richardson et al., 2018). Eutrophic shallow lakes generally have high catchment area to lake area (or volume) ratios and short water residence times, which are particularly sensitive to anthropogenic forcing (Tammelin and Kauppila, 2018). Further, in shallow lakes, strong water-sediment interactions are more common and sediment is more prone to resuspension (Fig. S3), leading to elevated internal nutrient loading and higher productivity (Havens and James, 2005). In contrast, deep lakes have a greater ability to dilute nutrients exported from watersheds (Fig. S4) and may exhibit a slower response to eutrophication and other pollutants (Liu et al., 2010). Deep lakes also lose a greater proportion of nutrients through sedimentation due to generally longer water residence times and lower turbulence at depth (Brooks et al., 2014; Vollenweider, 1975). Not surprisingly, the ratio of epilimnetic sediment-to-lake volume ratio is a parameter that predicts the retention and cycling of internal nutrients and generally decreases with increasing depth (Qin et al., 2020; Read et al., 2015). In the present study, the threshold of lake depth occurred at 13.8 m based on the interactions between ecoregion features, land use, and trophic state (Fig. 5a). In addition, according to our analysis, although watershed land use influences all lakes, lake depth can act as a 'filter' that modifies lake response to disturbance (Fig. 5b), with greater influence of land use on water quality in shallow lakes (Blenckner, 2005; Leavitt et al., 2009; Tammelin and Kauppila, 2018; Taranu and Gregory-Eaves, 2008). Therefore, many shallow lakes have shifted between stable states from

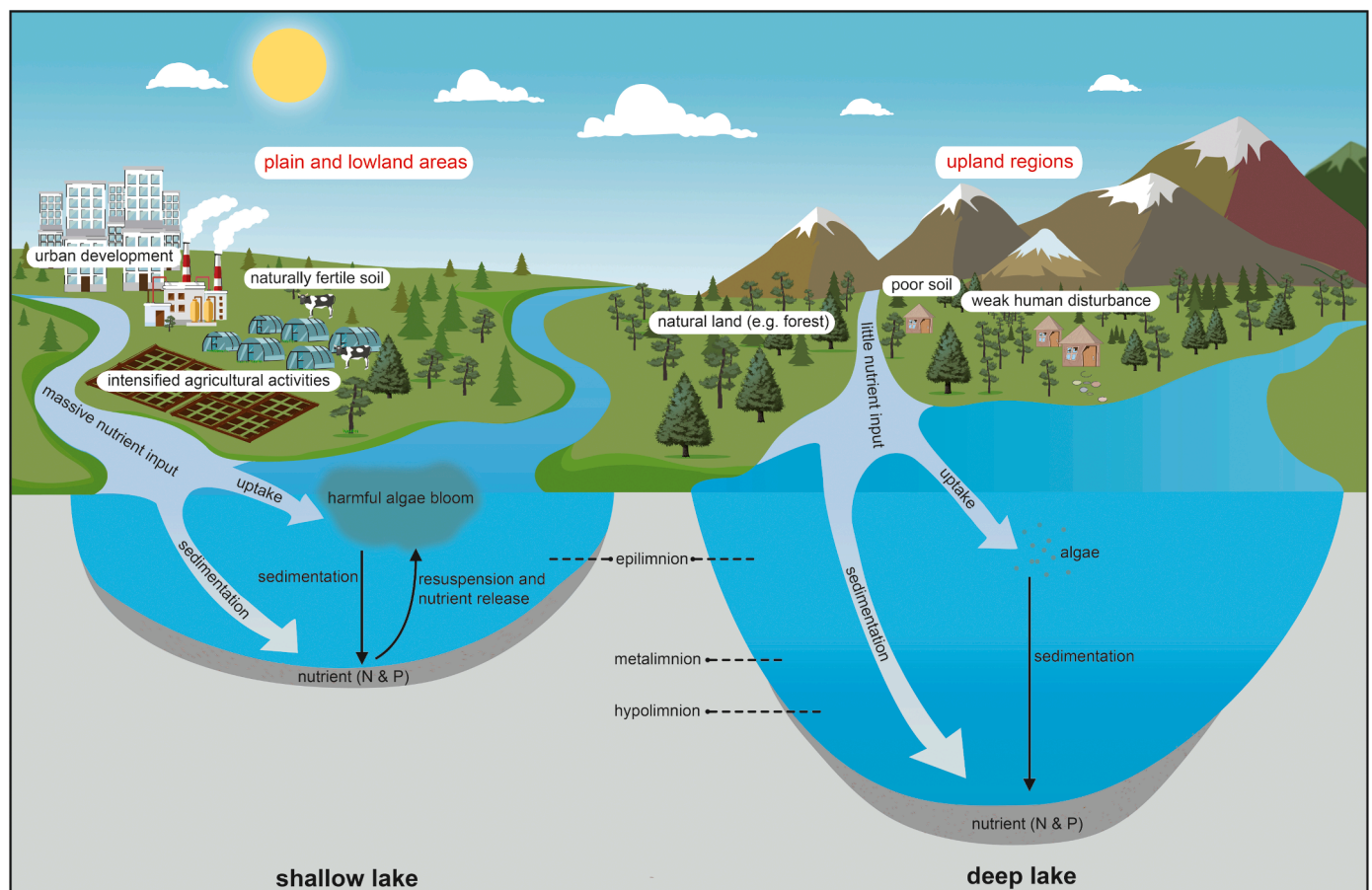


Fig. 6. Lake depth relates the effects of external nutrient input and in-lake biogeochemical processes to regulate the productivity of lake ecosystems. Generally, shallow lakes lie in naturally fertile plain and lowland regions, where they are exposed to strong anthropogenic disturbances (agriculture and urban development) and are predisposed to receiving large quantities of nutrients due to extensive drainage networks. In contrast, deep lakes are frequently concentrated in poor upland regions (mountains and highlands) with mainly natural land cover (e.g., forest and shrubland), low degrees of human disturbance, and limited nutrient input. Compared to deep lakes, shallow basins often have a small volume and weak capacity to dilute input nutrients resulting in high sensitivity to anthropogenic forcing. In addition, strong water-sediment interactions are more common and sediment is more prone to resuspension in shallow lakes, leading to elevated internal nutrient loading and higher productivity. Collectively, shallow lakes in agricultural or populated regions may be particularly susceptible to eutrophication and their eutrophication may be not an occasional occurrence.

clear state (macrophyte dominant) to turbid state (phytoplankton dominant) as a result of anthropogenic or natural drivers (Janssen et al., 2021). The alternative stable states in shallow lakes may further promote the nutrients release from macrophyte and sediment to increase the trophic state, affecting key supporting, provisioning, regulating, and cultural ecosystem services supplied by lakes (Scheffer and van Nes, 2007).

Our analyses suggest that lake depth correlates the effects of socio-economic development and natural landscape features to regulate the susceptibility of lakes to anthropogenic stressors (Fig. 6). In the future, increased agricultural production to meet demands for food and energy will intensify both point and diffuse sources nutrients (Carpenter et al., 2007; Tomer et al., 2013). Many shallow lakes already exhibit eutrophic conditions, yet lie in watersheds where further eutrophication may be an inevitable rather than an occasional occurrence. Consistent with this hypothesis, eutrophication is extensively studied in many large relatively-shallow lakes (e.g., Okeechobee, Winnipeg, and Erie) yet continues to be the central factor reducing water quality despite intensive management (Bunting et al., 2016; Michalak et al., 2013; Zhang et al., 2011). These lakes display many features typical of shallow freshwater ecosystem, including lowland location, high agricultural land use, and symptoms of recently-accelerated eutrophication (Havens and James, 2005). Similar patterns are also seen for other lakes in the basin of Rivers Havel and Spree (Germany) (Schönfelder and Steinberg, 2004) and the middle and lower reaches Yangtze River basin in China (e.g., lakes Taihu and Chaohu) (Dearing et al., 2012). These lakes lie in watersheds where rapid population growth and cultivation during the past 70 years has favoured eutrophication (Schönfelder and Steinberg, 2004; Wang et al., 2014).

Unlike natural lake ontogeny which leads to slow gradual changes as lakes infill, human activities have greatly accelerated water eutrophication by altering external and internal nutrient supplies (Carpenter et al., 1998). We propose that lakes now exist as coupled socio-ecological systems in which water depth integrates economic, societal and ecological factors related to lake production (Heino et al., 2021). In fact, the susceptibility of lake to anthropogenic eutrophication, and consequently the risk of water quality issues, is not the same for all lakes. Our findings suggest that shallow lakes are more susceptible to human forcing and are predisposed to receiving large quantities of nutrients. In addition, in shallow lakes, even though external nutrient inputs have been controlled, nutrients stored in the sediments can be continuously released to support high phytoplankton populations (Qin et al., 2020). Accordingly, special attention should be given to shallow lakes that are at high risk of waters quality degradation (Borics et al., 2013), yet may be more resistant to restoration compared to deep lakes (Martin et al., 2011; Tammelin and Kaupila, 2018). These findings could enhance our understanding of why the efforts in controlling lake eutrophication have failed in a number of shallow lakes, but are often effective in deep lakes (Schindler et al., 2016). This study convinces stakeholders to continue to invest in nutrient reductions, despite slow rates of recovery in eutrophic shallow lakes. Overall, societal expectations, policy goals, and management plans should reflect this observation.

5. Conclusion

Lake eutrophication is a great international concern because of its economic and ecological consequences. Our findings demonstrate that lake depth correlates socio-ecological systems, as well as lake susceptibility to potential anthropogenic stressors, and that shallow lakes exhibit disproportionately degraded water quality and trophic state. Accordingly, freshwater management will become increasingly necessary for shallow lakes. This information may help clarify why shallow lakes are prone to eutrophication and why some efforts to control eutrophication have resulted in frustratingly slow or modest effects in shallow productive lakes. This study helps set realistic goals and adjusts community

expectations to advance the protection and restoration of lakes globally. It may be a challenge that convincing stakeholders continue to invest in nutrient reductions without evidence of rapid improvement, but it is necessary for long-term water quality improvement. We hope that these findings will increase understanding for limnologists, stakeholders, and managers.

Contributions

J.Z. designed the research, conducted data analysis, created figures and wrote the draft of the paper; P.L. contributed to research design, data compilation, analysis and manuscript preparation; Y.Z. conducted data analysis and created Fig. 1; B.Q. proposed the idea and helped prepare the manuscript.

Declaration of Competing Interest

The authors declare no competing financial interest.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2022.118728.

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