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Original Research

Land use and river-lake connectivity: Biodiversity determinants of lake ecosystems

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A B S T R A C T

Lake ecosystems confront escalating challenges to their stability and resilience, most intuitively leading to biodiversity loss, necessitating effective preservation strategies to safeguard aquatic environments. However, the complexity of ecological processes governing lake biodiversity under multi-stressor interactions remains an ongoing concern, primarily due to insufficient long-term bioindicator data, particularly concerning macroinvertebrate biodiversity. Here we utilize a unique, continuous, and *in situ* biomonitoring dataset spanning from 2011 to 2019 to investigate the spatio-temporal variation of macroinvertebrate communities. We assess the impact of four crucial environmental parameters on Lake Dongting and Lake Taihu, i.e., water quality, hydrology, climate change, and land use. These two systems are representative of lakes with Yangtze-connected and disconnected subtropical floodplains in China. We find an alarming trend of declining taxonomic and functional diversities among macroinvertebrate communities despite improvements in water quality. Primary contributing factors to this decline include persistent anthropogenic pressures, particularly alterations in human land use around the lakes, including intensified nutrient loads and reduced habitat heterogeneity. Notably, river-lake connectivity is pivotal in shaping differential responses to multiple stressors. Our results highlight a strong correlation between biodiversity alterations and land use within a 2–5 km radius and 0.05–2.5 km from the shorelines of Lakes Dongting and Taihu, respectively. These findings highlight the importance of implementing land buffer zones with specific spatial scales to enhance taxonomic and functional diversity, securing essential ecosystem services and enhancing the resilience of crucial lake ecosystems.

1. Introduction

Among the valuable biospheres in the world, the ecological significance and biotic health of lakes have historically been undervalued [1,2]. Lakes provide important ecosystem services and are sensitive to global environmental change and human activities. Although lakes account for 21% of terrestrial-aquatic ecosystems, they can store water resources nearly 90 times more than rivers, which is crucial in supporting the long-term maintenance of aquatic ecosystem balance and human economic activities [3]. The combination of natural stressors and multiple anthropogenic pressures has led to habitat degradation, with a concomitant loss of vital ecosystem services, the extinction of “keystone” species, and other adverse outcomes in lakes globally [4–7]. The relatively

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complex structure and function of undisturbed lake ecosystems contribute to the maintenance of ecological resistance and resilience [8], while after being driven by the interactions of multiple stressors over time, the biodiversity of lakes has been decreasing at an unprecedented rate [6,9]. Therefore, addressing the response patterns and main drivers of lake ecosystem and aquatic biodiversity, particularly focusing on multiple stressors, poses a major challenge in limnology and watershed ecology [10,11].

Research has shown that agricultural development and increased urbanization contribute to water quality degradation in lacustrine environments [12,13]. Over long periods, human activities have been the primary drivers of the ecological evolution in lake ecosystems [8,14,15]. Besides, man-made climate change will bring more extreme weather events, which can also cause biodiversity decline at different spatial scales [16,17]. In contrast, differences in hydrological connectivity at various scales of watersheds could affect the cycling of nutrients and the risk of eutrophication. Increased inputs of limiting nutrients, such as phosphorus (P), would lead to concomitant simplification of community structures and even extinctions of species, particularly in lakes with poorer river-lake connectivity [18]. Although each environmental factor exhibits distinct characteristics, aquatic communities in lakes usually respond to multiple factors in complicated ways, while these factors can also interact together in multiple, non-linear ways [19]. For example, expanding human construction could cause habitat fragmentation and reduced connectivity of lakes. Changes in regional physical conditions, such as reduced runoff depth and hydrologic flow rates, would produce significant enrichment of pollutants [20], thereby affecting the chemical conditions of lakes. Meanwhile, with the frequency of global climate events, the alternations of temperature and precipitation patterns would impact the structures and functions of local aquatic ecosystems by disrupting the status of hydrology and water quality [21]. Changes in physical and chemical factors transform aquatic habitats, ultimately acting on aquatic communities' absolute and relative compositions, affecting the biological integrity of lakes [22].

Based on taxonomic and functional diversity indices, diversities of macroinvertebrate communities are key indicators of lake ecosystems' health and services [16,23]. Taxonomic diversity reflects the structural composition of species and the uniformity of species distribution in the community. However, most studies have focused on the losses of species rather than quantifying the wider impacts of urbanization on the functioning of ecosystems, thus ignoring changes in trait-based functional diversity, usually related to shifts in ecosystem functioning [24]. Compared to assessing taxonomic diversity based on the absolute and relative numbers of taxa, methods to assess functional diversity combine biological and ecological indicators to better assess relationships between organisms along environmental gradients [25,26].

The middle and lower reaches of the Yangtze River basin constitute one of the world's richest freshwater biocontainment areas, with its complex climatic, geomorphological, and hydrological features nurturing distinctive lake-type basins [27]. Meanwhile, macroinvertebrate communities, with their high sensitivity, exhibit significant differences in species composition and functional structures across distinct lake morphologies. Due to the large and increasing population of humans and associated economic development over a long period, biological habitat has significantly deteriorated in the basins of these aquatic systems [28,29], resulting in considerable effects on the biodiversity of macroinvertebrate communities. It is of great concern that only two lakes are currently freely connected with the Yangtze River. Most lakes rely on confluences with smaller tributaries to maintain a certain hydrological cycle, which is smaller in volume than the river-connected lakes. This often results in higher nutrient concentrations and increased abundance of pollution-tolerant species [30,31]. Due to the relatively short period of biomonitoring of lakes in China, most studies mainly focus on environmental parameters such as water quality [32] and human activities [33] in lakes with similar characteristics. Therefore, it has been rarely studied to compare the evolution and response patterns of aquatic ecological conditions in multiple lake units with significant differences in geography and anthropogenic disturbance intensity.

This study selected Lakes Dongting and Taihu as representatives of the Yangtze-connected and disconnected lakes of subtropical floodplains in China. The unique continuous, *in situ* biomonitoring over the past nine years was combined with climate, hydrology, land use, and water quality data. The study aimed to (1) analyze the temporal trends of land use, climate change, hydrologic regime, water quality, and the taxonomic and functional diversity of macroinvertebrates in two lakes; (2) identify the main factors driving the changes in macroinvertebrate biodiversity; (3) further evaluate the impacts of land use changes in terrestrial ecosystems at different distances around the lake on macroinvertebrate communities. We hypothesized that the variation of macroinvertebrate biodiversity in Lake Dongting was strongly regulated by hydrological regime due to great inter- and intra-annual dynamics of hydrological variability. While in Yangtze-disconnected Lake Taihu with low water level variation, macroinvertebrate biodiversity was mainly related to human land use and associated environmental factors.

2. Materials and methods

2.1. Study area

The middle and lower Yangtze (MLY) basin (106°07′–121°47′ E, 24°30′–33°54′ N) (Fig. 1a) contains the most dense group of freshwater lakes in East Asia, with an average elevation above 50 m [27]. Lakes in this region are scattered over an area of about 20,000 km^2. Since 1940, more than 30% of the lake area in the middle and lower reaches of the Yangtze River has been “reclaimed” by diking and draining, converting it into terrestrial habitat for human activities, including agriculture and urban development. Lake Dongting (110°20′–114°14′ E, 27°98′–30°23′ N) [34] used to be the largest freshwater lake in China and later became the second largest lake due to reclamation. Since the construction of the Three Gorges Dam, the water level of Lake Dongting (Fig. 1b) has declined significantly, and the dry season has been prolonged. Besides, as the third largest freshwater lake in China, Lake Taihu (119°52′–120°36′ E, 30°55′–31°32′ N) (Fig. 1c) was more significantly disturbed by human activities and had significant hydrological differences compared with Lake Dongting, consequently lead to different water ecological conditions.

Lake Dongting is located in the northeastern part of Hunan province, with a surface area of 2691 km^2, a mean depth of 6.4 m, an average annual temperature, and precipitation of 17 °C and 1413 mm, respectively [35,36]. The northern outlet of the lake is directly connected to the Yangtze River. Due to seasonal hydrological changes (the water level varies regularly, with the dry water period mainly from December to March, the abundant water period from June to September, and the flat water period from April to May and October to November), it has been an important habitat with relatively great diversity of the macroinvertebrate community [37]. Lake Taihu, situated in the southern part of Jiangsu province, at the southern edge of the Yangtze River Delta, covers a surface area of 2338 km^2 with a mean water depth of 1.9 m. The average annual temperature ranges from 16–18 °C, and precipitation averages 1100–1150 mm. As one of the most urbanized regions in China,

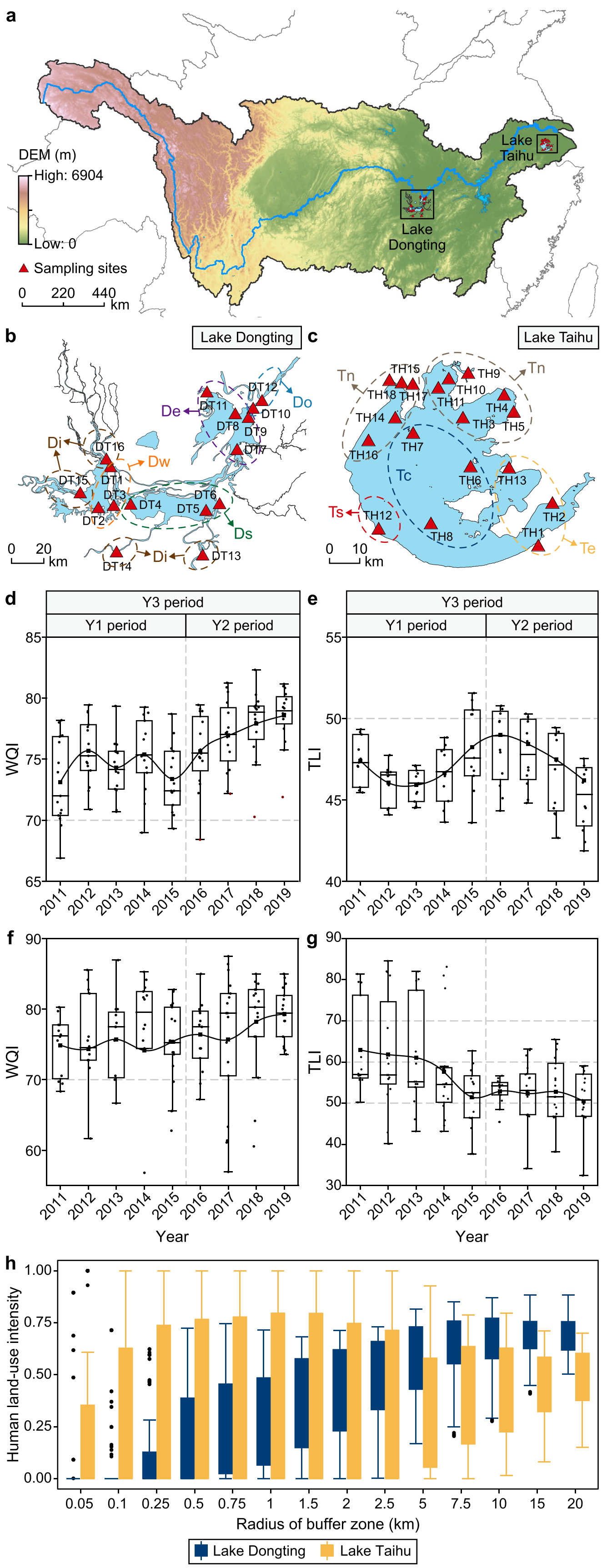

Fig. 1. **a**, The geographic location of Lake Dongting and Lake Taihu in the Yangtze River basin. **b**–**c**, The distribution and subdivisions of sampling sites in Lake Dongting (**b**) and Lake Taihu (**c**). In panel **b**, the subdivisions of Lake Dongting are mainly divided into Dw, Ds, De, Di, and Do, referring to the west, south, east, inlet, and outlet of Lake Dongting, respectively. In panel **c**, the subdivisions in Lake Taihu are divided into Tn, Tc, Te, and Ts, referring to the north, center, east, and south of Lake Taihu, respectively. **d**–**e**, Water quality index (**d**) and trophic level index (**e**) in Lake Dongting during Y1 (2011–2015), Y2 (2016–2019), and Y3 (2011–2019) periods. **f**–**g**, Water quality index (**f**) and trophic level index (**g**) in Lake Taihu during the Y1, Y2, and Y3 periods. The vertical gray dashed lines in panels **d**–**g** indicate the division of time Y3 into time Y1 and Y2 periods, respectively; the horizontal gray dashed lines indicate the thresholds for different classes of water quality or trophic status, the implications of which can be found in section 2.4.1. **h**, Variations of human land-use intensity in both lakes.

eutrophication in this lake continues to be serious, and the productivity and community structure of macroinvertebrate communities form the characteristics of urban lake taxa distribution [12]. These two lakes exhibited significant differences in their physical, chemical, and anthropogenic characteristics. It is noteworthy that the aquatic environments of both lakes have undergone considerable improvement since the “12th Five-Year Plan” (2011–2015) and “13th Five-Year Plan” (2016–2020) periods, the two major national plans implemented in China. However, increasing urbanization decreased aquatic biodiversity, and Lakes Dongting and Taihu habitat fragmentation has also raised significant concerns [12,32]. Sixteen sampling sites in five areas (west, south, east, inlet, and outlet) of Lake Dongting and eighteen sampling sites in four areas (north, center, east, and south) of Lake Taihu were established for aquatic ecological monitoring.

2.2. Macroinvertebrate sampling

In situ data on macroinvertebrate communities of Lakes Dongting and Taihu were from the Eco-Environment Monitoring Centre of Hunan Province in three seasons (March, June, September) and Jiangsu Province in three seasons (March, May, September) from 2011 to 2019 (Y1: 2011–2015; Y2: 2016–2019; Y3: 2011–2019), respectively. For each site, duplicate samples were collected using a Peterson grab (1/16 m^2 sampling area). Sediment samples were sieved through a 0.5 mm mesh screen and preserved in a 10% buffered formalin solution. The macroinvertebrates were identified to the lowest feasible taxonomic level (usually species or genera) and counted under a stereomicroscope or a microscope using regional keys [38–41].

2.3. Environmental data

Thirty-one major environmental parameters were classified into four categories according to their properties (Table S1): climate condition, land use, hydrological regimes, and water quality.

2.3.1. Climate condition variables

Mean annual temperature (MAT) and mean annual precipitation (MAP) were taken from a 30 km-resolution monthly temperature and precipitation data set of China from the National Earth System Science Data Center. We used ArcGIS 10.7 to extract the data from 34 sampling points in two lakes from 2011 to 2019.

2.3.2. Land use data

The data used in the analysis were based on classified land use status from 2011 to 2019, sourced from the School of Remote Sensing and Information Engineering, Wuhan University [42]. Distance buffers of each sampling site of 0.05, 0.1, 0.25, 0.5, 0.75, 1, 1.5, 2, 2.5, 5, 7.5, 10, 15, and 20 km were created by ArcGIS 10.7. The main land use types include cropland, forest, shrub, grassland, water, barren, impervious and wetland. Non-ecological land (NEL) was selected as the total proportion of cropland and impervious cover; meanwhile, ecological land (EL) [43] was calculated as the total proportion of forest, shrub, grassland, water, barren, and wetland.

2.3.3. Hydrological variables

Hydrological connectivity is an essential factor affecting the material circulation of an aquatic ecosystem [44]. Changes in the flow rate of the inlet and outlet and the lake level can change concentrations of nutrients, organic matter, and the distribution and abundance of benthic communities [45]. The annual Runoff (Ra) of Lake Dongting was provided by the Dongting Lake Eco-Environment Monitoring Centre of Hunan Province. The annual runoff depth (RDa) and water level (WL) data for Lake Taihu were obtained by searching the Water Resources Bulletin of Taihu Basin and Southeastern Rivers from 2011 to 2019.

2.3.4. Water quality variables

Synoptically with macroinvertebrate sampling, 1 L depth-integrated water samples were collected at each site for water quality determination in the laboratory. Twenty-four physical, chemical, and heavy metal indicators were measured according to the Environmental Quality Standards for Surface Water (GB3838-2002) of China, including pH, permanganate index (COD_{Mn}), biochemical oxygen demand (BOD_5), chemical oxygen demand (COD), ammonia nitrogen (NH_3-N), total phosphorus (TP), total nitrogen (TN) and other associated parameters.

2.4. Statistical analysis

2.4.1. Biodiversity and water quality indices

Based on absolute and relative numbers of taxa and individuals, macroinvertebrate biodiversity was calculated as the annual mean number of macroinvertebrate species containing taxa abundance and richness. Taxonomic diversity was represented by Shannon-Wiener, Pielou, and Simpson indices [46]. Functional richness (FRis), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (RaoQ) were applied to characterize functional diversities of communities. Functional traits were in 40 categories belonging to nine groups (Table S2) [47–50], classified into four types: life history, morphology, ecology, and mobility. A discrete code was assigned to the category of each biological trait [48]. The ten indices of taxonomic and functional diversity were calculated by using the R packages "*vegan*" and "*FDiversity*" [51].

The water quality index (WQI) and comprehensive trophic level index (TLI) were selected to evaluate the lake's overall water quality and eutrophication level. Among them, eight water quality indexes, including pH, water temperature (WT), dissolved oxygen (DO), TN, NH_3-N, TP, COD_{Mn}, and BOD_5, were selected to calculate the WQI (equation (1)):

$$\mathrm{WQI} = \sum_{i=1}^{n}(C_i P_i) \Big/ \sum_{i=1}^{n}(\mathrm{P}_i) \tag{1}$$

where C_i is the value of water quality indicator i, which is mainly divided into 11 levels from 0 to 100 concerning the grading thresholds of each water quality indicator; P_i is the relative weight of water quality indicator I; and the division intervals of C_i, P_i, and WQI and their corresponding water quality conditions are referred to the literature [52,53]. Finally, the water quality conditions were classified into five grades according to the values of WQI, including "very good" for WQI >90, "good" for 70 < WQI ≤90, "medium" for 50 < WQI ≤70, "poor" for 25 ≤ WQI ≤50, and "very poor" for WQI <25.

TLI was calculated with five water quality indicators, including Chl.a, TP, TN, transparency (SD) and COD_{Mn} (equation (2)).

$$TLI\left(\sum\right) = \sum_{j=1}^{m} W_j \cdot TLI(j) \tag{2}$$

where W_j is the relevant weight normalized by the parameter j, with Chl.a as the baseline parameter; TLI(j) is the comprehensive trophic state index of the indicator j, and m is the number of evaluation indicators; where the calculation formula of W_j and TLI(j) refers to the literature [54]. Finally, it was classified into three trophic statuses according to the values of $TLI(\sum)$, including "Oligotrophic" ($TLI(\sum) < 30$), "mesotrophic" ($30 \le TLI(\sum) \le 50$), and "eutrophic" ($TLI(\sum) > 50$) status. Specifically, the "eutrophic" status can also be divided into three levels, "mild eutrophic" ($50 < TLI(\sum) \le 60$), "medium eutrophic" ($60 < TLI(\sum) \le 70$), and "hypertrophic" ($TLI(\sum) > 70$), respectively.

2.4.2. Spatio-temporal variation of ecological indicators

Multiple comparisons of independent indicators in several groups were tested using the Kruskal-Wallis (K–W) test; since the P value was significantly less than 0.05, there is a statistically significant difference between different groups, and there is no statistically significant otherwise. Then, the temporal stage variability of diversities of macroinvertebrate communities and environmental parameters were assessed by use of the Z and P values in the Mann-Kendall trend test (the R package "*trend*"), and significance (magnitude) was determined by the slope of the Theil-Sen regression (R package the "*deming*") [55]. Meanwhile, the dynamic evaluation method was introduced to analyze the degree of change in macroinvertebrate diversity during the study period [56] (equation (3)).

$$\mathrm{S} = \mathrm{Y}_n^{-1} \times (\mathrm{Y}_m - \mathrm{Y}_n) \times 100\% \tag{3}$$

where S refers to the macroinvertebrate biodiversity dynamic degree; Y_m and Y_n represent the biodiversity index at the start and end of the study period, respectively. The spatial pattern of macroinvertebrates was interpolated for each year using the inverse distance weighted (IDW) method created by ArcGIS 10.7. Furthermore, compositional similarities in community structures among distinct groups in Lakes Dongting and Taihu were analyzed by principal coordination analysis (PCoA) based on Bray-Curtis distance, and the significance was tested by PERMANOVA (the R package "*vegan*").

2.4.3. Identification of environmental drivers and their potential ecological response pathways

Principal component analysis (PCA) was first performed to quantify the relationship and major differences between environmental parameters. Then, the Mantel test and partial Mantel test (the R package "*vegan*" and "*linkET*") [57,58] were applied to examine the associations among macroinvertebrate communities and multiple environmental indicators by calculating Bray-Curtis distances of community data and Euclidean distances of physical and chemical factors between sampling sites. The taxonomic and functional diversity indices were divided into two categories to explore the relationship with each factor, which were determined using Mantel'r and Mantel'P.

To identify the key drivers of macroinvertebrate biodiversity, a random forest regression model (the R package "*randomForest*" and "*rfPermute*") [59] was constructed. The diversity of the macroinvertebrate community was selected as the dependent variable, and the environmental factors were selected as the independent variables; *ntree* was set to 500 and *nrep* to 1000. The greater the value of each factor weight, the greater the contribution of that environmental factor could be estimated.

Finally, a partial least squares path modeling (PLS-PM) (the "*plspm*" R package) [60] was implemented to analyze the influence pathways between the aquatic ecological status, which can use both observed (outer model) and latent (inner model) variables to evaluate the fitness of predictive models in the complex ecological factors. Not only can this model convey the causal relationship between observed variables, positive or negative correlation or no correlation, but it can also be used to characterize the contribution of latent variables to observed variables and overall model goodness of fit, which facilitates iterative operations to find the best linear predictive relationship [61].

2.4.4. Locally estimated scatterplot smoothing regression across multiple spatial extents

Based on constructing 14 buffers from 50 m to 20 km across multiple spatial extents of each sampling site, a correlation analysis was performed between the percentage of non-ecological land as the intensity of human activities and the macroinvertebrate biodiversity and nutrient level. Then, the absolute values of the correlation coefficients were used to fit the 14 buffer distances by the locally estimated scatterplot smoothing (LOESS) regression. The optimal control areas of the two lakes were determined and compared with the peak value of the mutation.

3. Results

3.1. Spatial and temporal variation of ecological status in Lakes Dongting and Taihu

3.1.1. Environmental factors and their interrelationships

The water quality of Lakes Dongting and Taihu has improved from 2011 to 2019 while cultural eutrophication still exists due to the increasing intensity of human activities (Fig. 1h). The score of WQI in Lake Dongting from 2011 to 2019 (Fig. 1d) was above 70 overall, indicating the water quality was at "good" level, while the score of WQI in a few sampling sites was between 50 and 70, indicating the "medium" water quality level. After 2015, the WQI rose significantly, reaching a maximum of 79.5 in 2019. In contrast, the score of WQI in Lake Taihu (Fig. 1f) was on a steady upward trend, while the eutrophication phenomenon was relatively serious (Fig. 1g). TLI scores between 50 and 90 exceeded 90% of the sampling sites from 2011 to 2014, dominated by mild, medium and hyper-eutrophic status. Then, after 2015, the TLI score stably decreased and remained at a mild eutrophic status overall.

During the study periods, the concentrations of water quality variables, such as TN, TP, and BOD_5, increased from 2011 to 2015 and decreased after 2015 (Table S3). As human activities intensified, the proportion of non-ecological land around Lake Dongting was growing slowly with an average of 45.97%, including 34.66% of cropland and 11.31% of impervious cover, significantly and positively correlated with TN, while negatively correlated with annual runoff (Fig. 2b).

Comparatively, results of the PCA showed that the 95% confidence interval of the environmental indicators in Lake Taihu exceeds that of Lake Dongting during the Y3 period, indicating a significant gradient in environmental factor variations, particularly pronounced in the north and south of the lake (Fig. 2a–c). The proportion of non-ecological land around the lake was heavily developed, taking up an average of 70%, which is higher than that in Lake Dongting. The temperature and precipitation increased yearly, while the TN, TP, COD, and NH_3–N concentrations decreased. Moreover, the annual water level and runoff depth showed similar trends, reaching the highest value in 2016 of 3.36 m and 612 mm, respectively (Fig. S1). Moreover, the ecological environment of Lake Taihu has been affected for the past nine years mainly by human activities, such as agricultural and industrial discharge (Fig. 2c). Additionally, it is noteworthy that during the Y2 period, the environmental gradient in Lake Dongting significantly increased compared to the Y1 period, particularly observed in the west and outlet of the lake (Fig. S3).

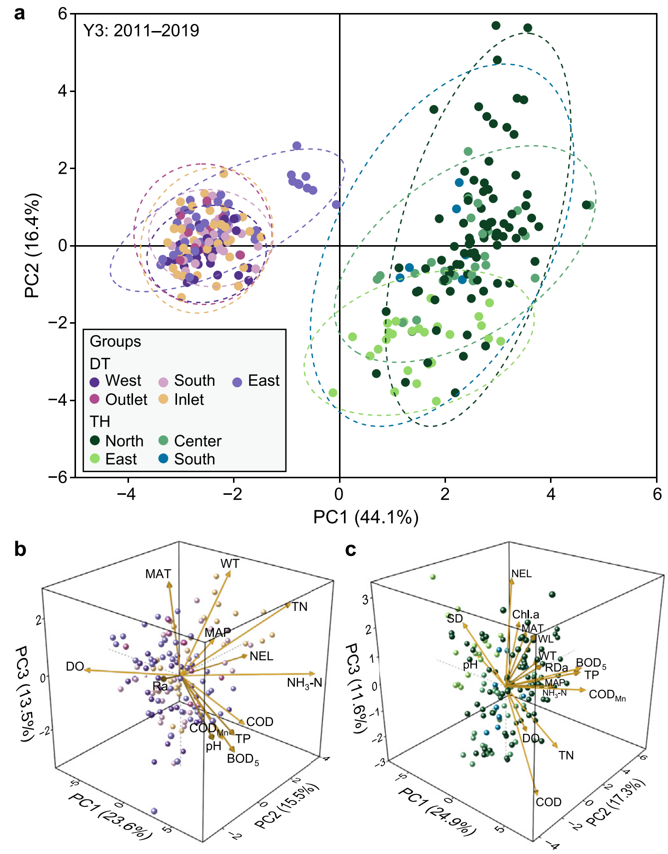

Fig. 2. The PCA of environmental factors in both two lakes (**a**), Lake Dongting (**b**), and Lake Taihu (**c**).

3.1.2. Structure and status of macroinvertebrate communities

During the past decade, the diversity of macroinvertebrate communities of Lakes Dongting and Taihu fluctuated significantly and differed in taxonomic composition and functional structure (Fig. 3, Figs. S2 and S4, Table S3). 115 and 112 taxa have been recorded in Lakes Dongting and Taihu, respectively. Although taxonomic richness was similar in both lakes, there were significant differences in taxonomic and functional composition, with abundant more sensitive species like *Mollusks*, which accounted for 41.7% of taxa in Lake Dongting (Fig. 3a), while a greater percentage of pollution-tolerant species like *Oligochaetes* (41.3%) and *Chironomids* (17.7%) were observed in Lake Taihu (Fig. 3b). In addition, *burrowers* in life habits and *gather-collectors* in feeding groups were highly distributed of the two lakes, but the relative abundance of *burrowers* (50.2%) and *gather-collectors* (57.3%) in Lake Taihu were significantly higher than those in Lake Dongting (38.2% and 53.4%, respectively).

Taxonomic abundance, richness, and evenness have decreased in Lake Dongting, while functional divergence has increased during the past decade (Fig. S2a). The overall dynamic index from 2011 to

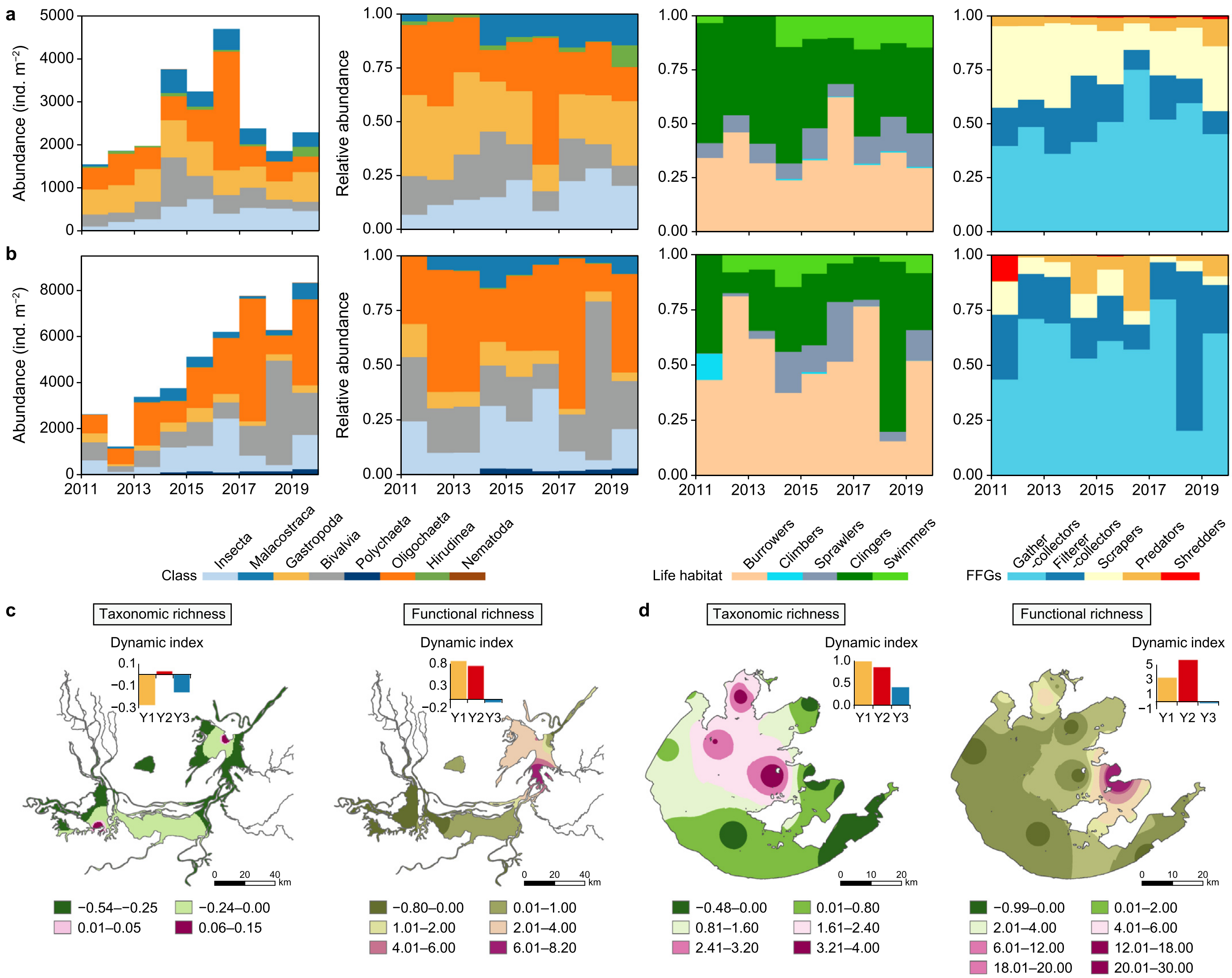

Fig. 3. **a**–**b**, Taxonomic composition of macroinvertebrates and relative abundance of life habitat and functional feeding groups (FFGs) in Lake Dongting (**a**) and Lake Taihu (**b**). **c**–**d**, Dynamic taxonomic and functional richness change in Lake Dongting (**c**) and Lake Taihu (**d**). Dynamic index refers to the degree of change in the study area over some time. Positive numbers indicate growth, and negative numbers indicate decline.

2019 of taxonomic and functional richness ($S_{Y3} = -0.27$ and -0.06) both decreased slightly, with the most obvious changes showed in the east and outlet of the lake (Fig. 3c, Fig. S5), which were mostly related to disturbance by human activities [62]. In Lake Taihu, abundance of macroinvertebrates increased in a stepwise fashion from 2011 to 2017, declined significantly after 2017, and increased again until 2019 (Fig. S2b). The overall dynamic index showed different variation trends with increasing taxonomic richness ($S_{Y3} = 0.41$) and decreasing functional richness ($S_{Y3} = -0.16$) from 2011 to 2019. Moreover, taxonomic richness in Lake Taihu exhibited more extreme values in the south-eastern and northern areas, while functional richness in the western and central areas decreased and then increased again (Fig. 3d, Fig. S6).

PCoA and PERMANOVA showed that the taxonomic composition of macroinvertebrates among five areas of Lake Dongting (west, south, east, inlet, and outlet) ($R^2 = 0.025$, $P = 0.001$) and four areas of Lake Taihu (north, center, south, and east) ($R^2 = 0.079$, $P = 0.001$) were significantly different during Y3 periods (Fig. 4). Similarly, the spatial difference of taxonomic groups at Y1 and Y2 periods were still significant in both two lakes (Fig. S7). Although the water quality of the two lakes improved with decreases in concentrations of parameters, such as TN, TP, NH_3–N, and BOD_5 (Table S3), the taxonomic groups showed significantly different compositions during the study period, based on the composition and relative abundance of functional traits processed, such as the life habitat and functional feeding groups, macroinvertebrates in the Lake Taihu were facing more serious homogenization than Lake Dongting (Fig. 3, Fig. S4). The ecological stability in both lakes was significantly less.

3.2. Identification of major drivers and response pathways

The results of the Mantel test showed that the environmental indicators of the two lakes were strongly correlated mainly with taxonomic and functional richness (Figs. S8 and S9). Therefore, random forest regression analysis was conducted by selecting taxonomic richness and functional richness as dependent variables, respectively (Fig. 5). It is revealed that the variables of land use, hydrology, and nutrient level indicators contributed significantly to changes in taxonomic diversity. In Lake Dongting, with taxonomic

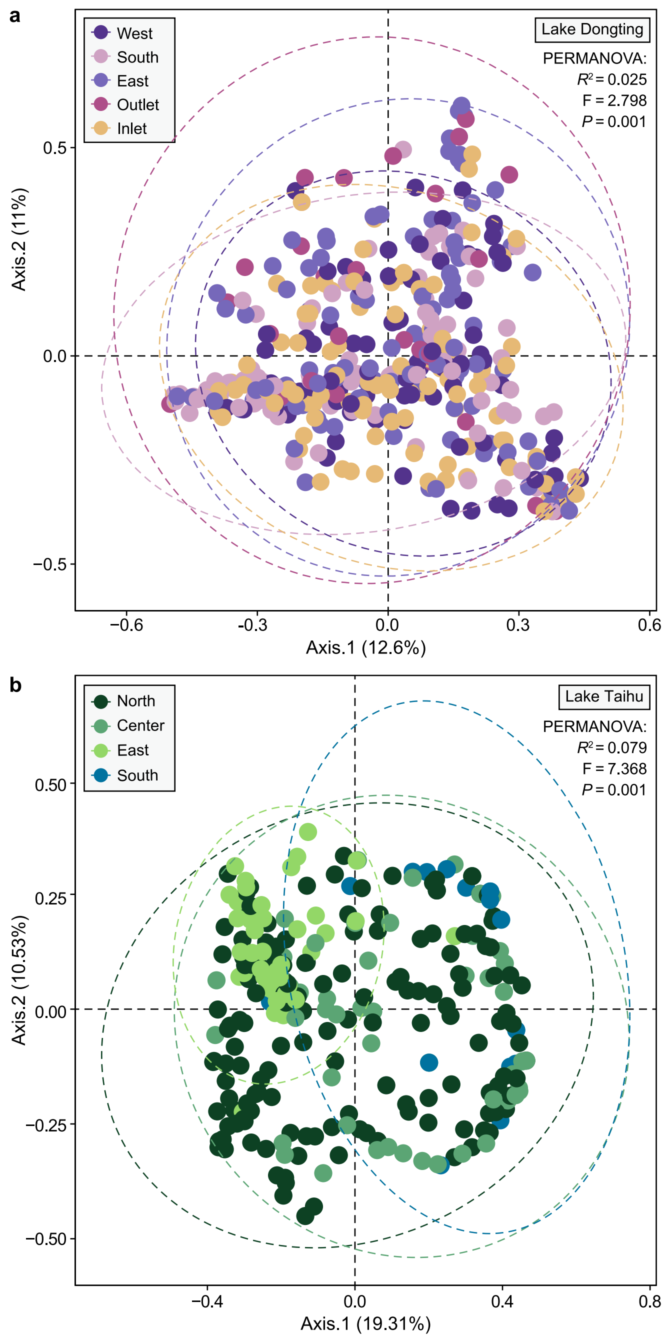

Fig. 4. Spatial differences in macroinvertebrate taxonomic groups in Lake Dongting (**a**) and Lake Taihu (**b**).

richness as the dependent variable, the overall explanatory rate of the variance (R^2) of the environmental indicators explored was 44.17, with annual runoff contributing 25.56%, followed by non-ecological land with 18.89%. Moreover, the overall R^2 was only 23.41 when taking functional richness as the dependent variable, with ecological land (12.95%, $P < 0.01$) and non-ecological land (12.52%, $P < 0.01$) contributing the most. In Lake Taihu, land use and nutrients were the dominant indicators affecting taxonomic and functional richness, with cumulative impacts of 36.97% and 24.74% on taxonomic richness and 40.58% and 25.70% on functional

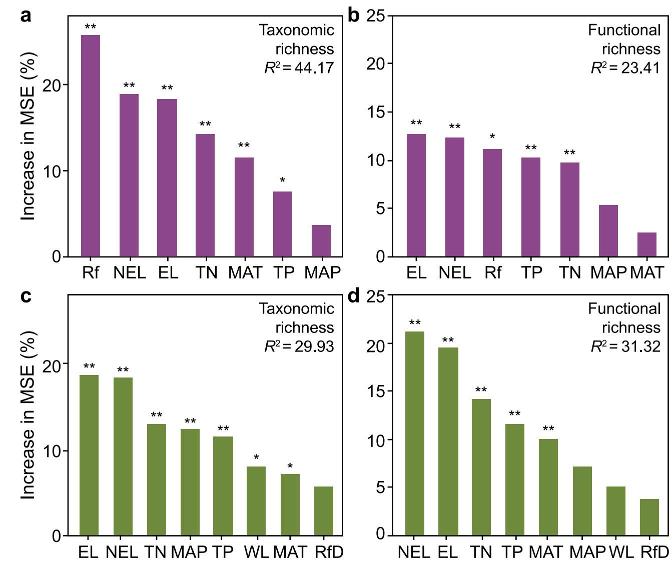

Fig. 5. Potential drivers of variation in ecological response at Lakes Dongting and Taihu. **a**–**b**, Importance of four variables (land use, climate, hydrology, and water quality) affecting the macroinvertebrate taxonomic (**a**) and functional richness (**b**) in Lake Dongting. **c**–**d**, Importance of four variables affecting taxonomic (**c**) and functional richness (**d**) in Lake Taihu. The importance of predictor variables in the four panels was measured as the "percentage increase in mean square error (increase in MSE (%)) in the random forest model, where higher MSE% values indicate more important predictors. R^2 indicates the overall explanation of variance in the response variables, taxonomic and functional richness, by the predictor variables. $^*P < 0.05$, $^{**}P < 0.01$.

richness, respectively.

Structural relationships between the environmental indicators and diversities of macroinvertebrate communities were also investigated [63,64]. It was found that anthropogenic inputs of nutrients, such as nitrogen (N) and phosphorus (P), can more directly affect macroinvertebrates than construction activities [13,65], such as damming [66]. Thus, TN and TP can be important linkages between external environmental factors and macroinvertebrate biodiversity. Finally, the latent variables were delineated, and the causal relationships between the factors were initially constructed for PLS-PM simulations.

The response relationships in the two lakes were significantly different (Fig. 6), mainly in terms of the differences in water-land connectivity and the intensity of human construction activities. As a Yangtze river-connected lake, changes in hydrological regimes can directly affect macroinvertebrate taxonomic and functional diversity in Lake Dongting (Fig. 6a), with coefficients of 0.40 ($P < 0.05$) and −0.1, respectively. Besides, the main pathway affecting the water's ecological status involves the construction of non-ecological land, which directly changes nutrient concentrations with a coefficient of 0.28 ($P < 0.05$). This change leads to habitat fragmentation, indicated by a coefficient of −0.43 ($P < 0.05$), and finally indirectly affects benthic taxonomic diversity.

Lake Taihu differs from Lake Dongting in that the macroinvertebrate community is significantly less affected by hydrological regimes than non-ecological land (Fig. 6b). There were mainly two influencing pathways in Lake Taihu: First, land use, climate and hydrological processes acted synergistically on TN (path coefficients of 0.10, 0.09 and −0.21, respectively). The path coefficient of land use construction on TP was 0.17, which indirectly influenced benthic communities with a cumulative influence of 0.28. Secondly, non-ecological land directly impacts macroinvertebrate

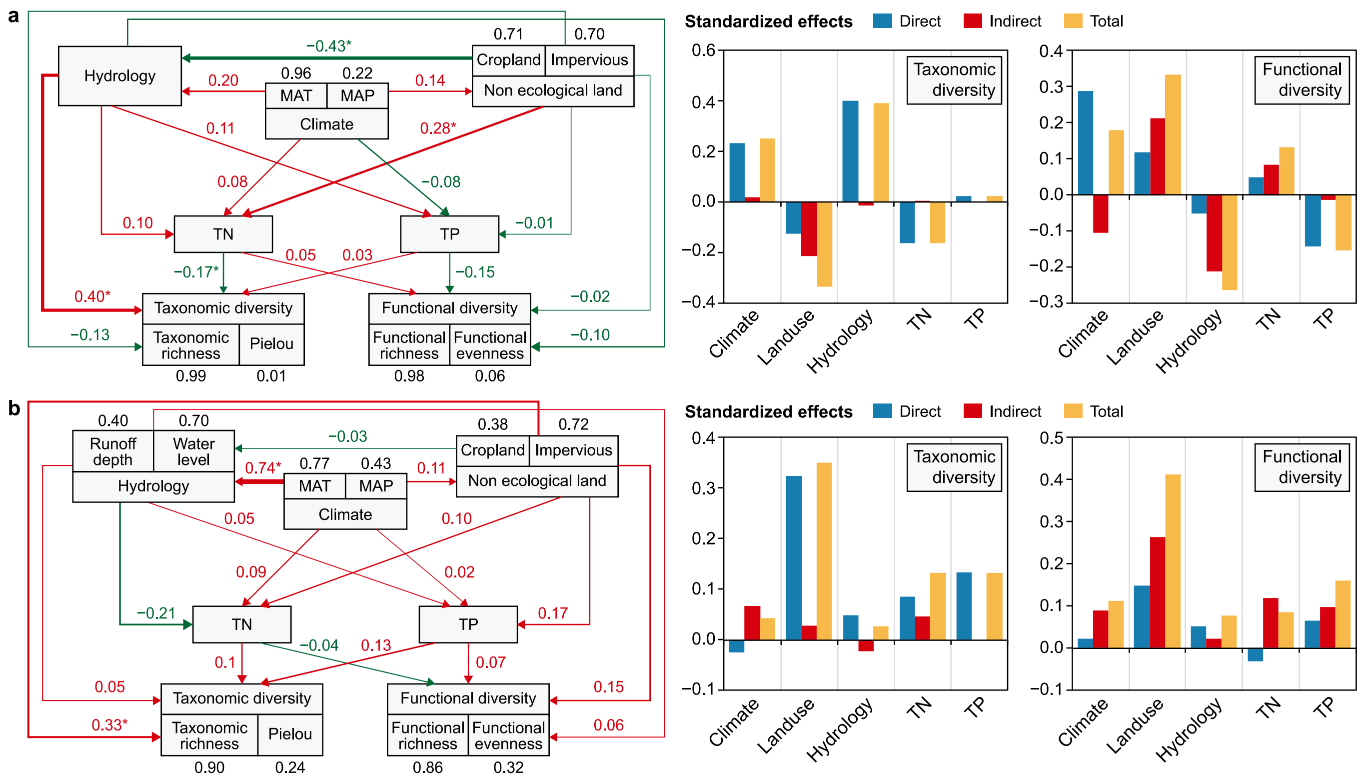

Fig. 6. The influencing pathways between multiple stressors and macroinvertebrate biodiversity in Lake Dongting (**a**) and Lake Taihu (**b**).

biodiversity (path coefficients of 0.33, $P < 0.05$).

3.3. *Spatial thresholds of the effects of land use on macroinvertebrate biodiversity*

Results of LOESS regression showed the response of ecological status in Lake Taihu to human land use is more sensitive than that in Lake Dongting (Fig. 7). Lake Taihu exhibits stronger anthropogenic disturbances than Lake Dongting, particularly within a 5 km radius (Fig. 7a and b). Additionally, significant differences in land use intensity exist within their respective buffer zones ($P < 0.001$). Concentrations of nutrients in Lake Dongting were significantly influenced by non-ecological land from 2 to 5 km, while taxonomic diversity was most associated at a spatial range of 2 km (0.37, $P < 0.01$) and functional diversity reached the peak correlation coefficient at 5 km (0.38, $P < 0.01$) (Fig. S10a, Fig. 7c). Moreover, correlation coefficients for concentrations of key nutrients in Lake Taihu were greater, ranging from 0.05 to 2.5 km, while taxonomic and functional diversity exhibited the greatest correlation coefficients within 1.5 km of human land use, with coefficients of 0.37 ($P < 0.01$) and 0.41 ($P < 0.01$), respectively (Fig. S10b, Fig. 7d).

4. Discussion

4.1. *Multiple environmental stressors intricately contribute to a complex landscape of biological diversity*

In the past decade, there has been a significant transformation in both eutrophication and overall water quality conditions, particularly during the “13th Five-Year Plan” period. Coincidentally, in April 2015, the Action Plan for Prevention and Control of Water Pollution ("10-Point Water Plan”) was promulgated by the Chinese government in response to the severe water pollution and other issues [67], clear provisions were made for funding and pollution control in the basin, which is consistent with the performance of water quality changes in both two lakes.

However, compositions of macroinvertebrate communities exhibited considerable complexity, often subject to the combined constraints of various environmental indicators. Influenced by the Yangtze River and its tributaries and regulated by the Three Gorges Reservoir, non-ecological land in Lake Dongting closely correlates with TN, displaying a significant negative association with annual runoff [66]. In Lake Taihu, human land use significantly correlates with TN and TP but not with annual mean water level or runoff depth, primarily due to substantial artificial regulation impacting Lake Taihu's water level [13]. Moreover, lakes' depth and hydraulic residence time could exert important effects on nutrient cycling [65,68]. Human activities and river-lake connectivity would also increase the sensitivity among environmental factors in lakes [69,70].

The unique hydrological conditions of Lake Dongting lead to a heterogeneous substrate composition [71], which can support more functional taxa and positively contribute to the macroinvertebrate community. Conversely, an increase in human footprint can cause bio-homogenization of the lake [72]. Previous studies have found that long-term eutrophication reduces the survival of sensitive benthic organisms [37,73]. With the proximity of a large range of human disturbance, the aquatic habitat in Lake Taihu has been more severely damaged, emphasizing the importance of controlling the main driving factors within lake ecosystems.

The intricate relationship of multiple indicators has resulted in varying degrees of decline in functional diversity and diminished resilience of ecosystem functions in Lakes Dongting and Taihu. The relationship between species and environmental stressors is not linearly responsive, which depends on species classification by

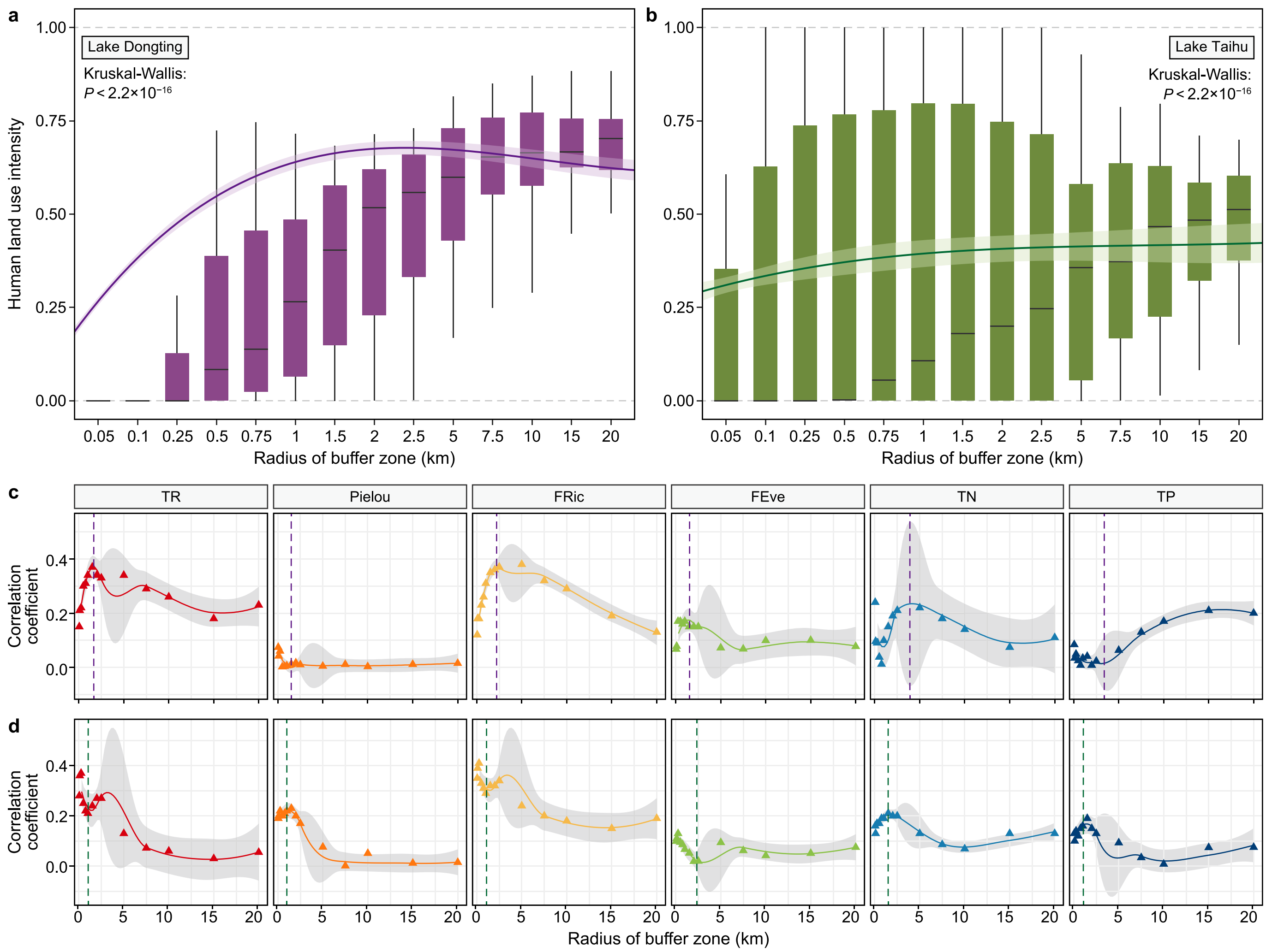

Fig. 7. **a**–**b**, Human land-use intensity across multiple spatial scales in Lake Dongting (**a**) and Lake Taihu (**b**). **c**–**d**, Effects on biodiversity and nutrients at different buffer zones in Lake Dongting (**c**) and Lake Taihu (**d**). The vertical purple and green dashed lines indicate the spatial ranges of human land use intensity where the ecological indicators show significant mutations in Lake Dongting and Lake Taihu, respectively.

community composition [74] but also on the inclusion of functional traits [75]. This provides information on the key biological mechanisms driving community mutations and how biome function is most affected by environmental stressors, ultimately refining the underlying driving processes among ecological status.

4.2. *Human expansion induces biodiversity homogenization and alters aquatic element response pathways*

Growing anthropogenic pressures poses a direct threat to the integrity of biological habitats [28]. It has been predicted that nearly a quarter of simulated species will lose more than 10% of their habitat by 2051 [76]. Changes in lake macroinvertebrate communities' structure and functional traits are largely influenced by human land use and hydrological regimes [45,77]. The varying responses of lake ecosystems to non-ecological land use are most likely regulated by hydrological connectivity [20,44]. Furthermore, it was also found that nutrients contributed more significantly to the diversity of the macroinvertebrate community than did climatic conditions in both lakes.

As human influence grows, the benthic community structure in both lakes tends to be gradually singular, and the diversity of functional categories has decreased, consistent with several previous findings [72,78]. The construction of human land use leads to the fragmentation of lake habitats, reducing connectivity, affecting hydrological processes, and altering regional physical and chemical conditions. This further influences changes in aquatic organisms and habitats, directly or indirectly impacting the spatiotemporal distribution patterns of aquatic ecosystems [22,79]. The reduction in runoff depth and flow velocity results in significant pollutant enrichment in the discharged water into lake areas [20].

As a Yangtze river-connected lake [18], hydrological variables significantly influenced the ecological condition of Lake Dongting. The primary pathways of influencing benthic communities' response primarily are manifested in three distinct categories: (1) non-ecological land use primarily affects the variation of TN, indirectly impacting the taxonomic diversity of benthic organisms; (2) the construction of non-ecological land can directly lead to habitat fragmentation in Dongting Lake; (3) changes in hydrological connectivity can also directly influence benthic organisms, thereby reducing taxonomic richness and evenness. In contrast, land use variables contributed most to Lake Taihu. Two main pathways may affect benthic communities and functions: (1) Non-ecological land use, in conjunction with hydrological and climatic factors, jointly influence TN and TP levels, thereby altering the composition of benthic communities; (2) Non-ecological land use under human disturbance directly exerts a significant impact on benthic organism diversity. The dense urban development with developed industries around Lake Taihu has severely altered the habitat of macroinvertebrates [33], directly leading to a decrease in taxonomic richness, an increase in the abundance of pollution-tolerant species, and functional homogenization.

4.3. Strategically planning land use at various scales is crucial for lake and aquatic ecosystem health

The response pathways exhibit discernible variations among distinct lake regions. Studies have shown that habitat heterogeneity and biodiversity correlate positively [80]. Increasing anthropogenic disturbance has led to dramatic changes in lake geomorphology, resulting in habitat fragmentation and destruction of river-lake connectivity, which has caused a decline in macroinvertebrate biodiversity. Therefore, controlling the intensity of human development and construction within a specific spatial threshold is necessary.

Research in other countries focuses predominantly on multi-scale watersheds, whereas studies in China often center on a single scale. Within these investigations, distinct land use types exhibit significant biological responses. Cropland and impervious cover were negatively correlated with taxonomic and functional richness in Lake Dongting. However, they exhibited a positive correlation with taxonomic and functional richness in Lake Taihu, which can be attributed to a significantly greater abundance of *Oligochaetes* species. The expansion of non-ecological land stimulates the growth of pollution-tolerant species, reflecting a decline in the community hierarchy of the lake ecosystem and an increasing trend in pollution levels.

The construction and development of agricultural land, as well as the establishment of impervious, all influence the status of the lake ecosystem [81,82]. Numerous studies have found that changes in community assemblages, taxonomic diversity, and biological integrity of various trophic levels, such as primary producers and primary and secondary consumers, are influenced by human land use activities [72]. Rivers are affected by human activities to a larger radius than lakes. The abundance and richness of fish in the mainstem of the Yangtze River responded significantly to human land use within 5 km of the river bank, both upstream and downstream [83]. However, the diversity of the macroinvertebrate community in lakes can be closely associated with human land use at a smaller scale than in rivers.

Meanwhile, due to complex biological response relationships and long-term disturbance caused by high-intensity human activities [84,85], the aquatic ecological response of isolated lakes tends to be more sensitive concerning land development than connected lakes. Specifically, the benthic community of Lake Dongting, along with nutrient levels, is notably influenced by cultivated land and impermeable layers within the spatial range of 2−5 km. Conversely, the impact of non-ecological land use on the aquatic ecological condition of Lake Taihu is predominantly within the spatial range of 0.05−2.5 km. Therefore, in developing protection and restoration measures for lakes suffering from eutrophication and declining aquatic biodiversity, attention should be paid to managing and improving land use patterns in surrounding terrestrial ecosystems, especially in lakeshore zones.

5. Limitations

Long-term urbanization, agriculture, and other human activities can considerably impact the health and integrity of aquatic organisms in affected watersheds. The findings of this study are generally consistent with those previously published on drivers of the structure and function of aquatic ecosystems [72]. However, the processes of response to anthropogenic disturbances are not identical and may exhibit extreme differences for lakes in different environmental contexts. Due to the lack of long-term historical biomonitoring data, the results reported here have the following limitations: First, it was not possible to analyze the seasonal aquatic ecological conditions of Lakes Dongting and Taihu with hydrological characteristics. Secondly, this study focused solely on macroinvertebrate communities' structure and functional composition, excluding other communities. Third, the analysis was limited to the spatial and temporal patterns of physical, chemical, and biological elements at the macro-level, omitting other micropollutants, such as neonicotinoid pesticides (NEOs) and organophosphorus pesticides (OPPs). At the same time, the complete response-driven analysis of lake ecosystems remains uncertain due to the absence of a longitudinal series of aquatic survey data [19], leading to a mismatch between environmental and aquatic variables on temporal and spatial scales.

6. Conclusions and perspective

Human land use has been identified as the primary factor impacting lake ecosystems. Additionally, variations in river-lake connectivity directly influence the differing responses to multiple stressors across various lakes. Although the health status of aquatic communities in Lakes Dongting and Taihu are driven by multiple factors, land use dominates over climate change and hydrological alteration for lake ecosystems with river-lake barriers. In contrast, the influence of hydrological conditions is more intuitive for better river-lake connectivity lakes. Accordingly, to protect lake basins with low ecological stability and resilience, rational planning of construction activities on non-ecological land is crucial for effective watershed protection and restoration.

Simultaneous monitoring of *in situ* aquatic organisms and the aquatic environment at long-term scales is beneficial for understanding the response mechanisms of aquatic ecological conditions under multiple stressors. Although the water quality of Lakes Dongting and Taihu has significantly improved in the past decade, the macroinvertebrate community structure still tends to be homogenized, and the ecological stability has become significantly weakened — outcomes contrary to those expected from water environment management. Future research extends beyond nutrients to include the status of the biological communities. Applying biodiversity metrics on a spatial scale can enable managers to more effectively target interventions to enhance lake health.

CRediT authorship contribution statement

Huiyu Xie: Investigation, Conceptualization, Data Curation, Methodology, Writing - Original Draft, Software. **Yu Ma:** Investigation, Software. **Xiaowei Jin:** Conceptualization, Funding Acquisition, Methodology, Supervision, Writing - Review & Editing. **Shiqi Jia:** Investigation. **Xu Zhao:** Investigation. **Xianfu Zhao:** Supervision, Writing - Review & Editing. **Yongjiu Cai:** Supervision, Writing - Review & Editing. **Jian Xu:** Supervision, Writing - Review & Editing. **Fengchang Wu:** Funding Acquisition, Supervision. **John P. Giesy:** Supervision, Writing - Review & Editing.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ese.2024.100434.

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