



Linking pollution to biodiversity and ecosystem multifunctionality across benthic-pelagic habitats of a large eutrophic lake: A whole-ecosystem perspective

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ABSTRACT

Biodiversity loss is often an important driver of the deterioration of ecosystem functioning in freshwater ecosystems. However, it is far from clear how multiple ecosystem functions (i.e., ecosystem multifunctionality, EMF) relate to biodiversity across the benthic-pelagic habitats of entire ecosystems or how environmental stress such as eutrophication and heavy metals enrichment might regulate the biodiversity-EMF relationships. Here, we explored the biodiversity and EMF across benthic-pelagic habitats of the large eutrophic Lake Taihu in China, and further examined abiotic factors underlying the spatial variations in EMF and its relationships with biodiversity. In our results, EMF consistently showed positive relationships to the biodiversity of multiple taxonomic groups, such as benthic bacteria, bacterioplankton and phytoplankton. Both sediment heavy metals and total phosphorus significantly explained the spatial variations in the EMF, whereas the former were more important than the latter. Further, sediment heavy metals mediated EMF through the diversity of benthic bacteria and bacterioplankton, while nutrients such as phosphorus in both the sediments and overlaying water altered EMF via phytoplankton diversity. This indicates the importance of pollution in regulating the relationships between biodiversity and EMF in freshwater environments. Our findings provide evidence that freshwater biodiversity loss among phytoplankton and bacteria will likely weaken ecosystem functioning. Our results further suggest that abiotic factors such as heavy metals, beyond nutrient enrichment, may provide relatively earlier signals of impaired ecosystem functioning during eutrophication process.

1. Introduction

Increasing research has demonstrated that freshwater biodiversity loss can indeed exert significant impacts on ecosystem functioning and may hence threaten human welfare (Jackson et al., 2016). Evidence for this biodiversity-ecosystem functioning relationship in freshwater environments comes mostly from experimental or observational investigations testing how individual biodiversity affects a single ecosystem function such as primary productivity or organic degradation in a specific habitat (Ylla et al., 2013; Zimmerman and Cardinale, 2014; Zhang et al., 2017). However, it is urgent to examine biodiversity and ecosystem functioning from a whole-ecosystem perspective because natural ecosystems are defined by multitrophic organisms and multiple

functions (ecosystem multifunctionality, EMF) that work across various habitats and thus drive ecosystem circulation (Lopez-Rojo et al., 2019; Yuan et al., 2020). Moreover, links between biodiversity and human stressors may also modulate the forces driving the relationships between biodiversity and ecosystem functioning in freshwater environments (Rusak et al., 2004; Woodcock and Hury, 2005; Vinebrooke et al., 2009; McMahon et al., 2012).

Although biological processes occur extensively in freshwater pelagic and benthic habitats (Wang et al., 2020), it is unknown how the biodiversity across these two habitats jointly affects the suite of functions provided by the whole ecosystem. Most research on freshwater biodiversity-ecosystem functioning relationships focuses mainly on either pelagic (e.g., the positive relationship between phytoplankton

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diversity and biomass) (Zimmerman and Cardinale, 2014) or benthic (e.g., linear links between macroinvertebrate diversity and carbon and nitrogen cycling) (Cao et al., 2018) habitats. However, studies of marine environments show that understanding benthic-pelagic coupling processes and variability is important for quantifying the feedbacks of ecosystem functioning to changing anthropogenic pressures (Griffiths et al., 2017). A recent study of two freshwater lakes differing in trophic status also highlights the role of future changes to both sediments and lake waters in modifying sediment microbial communities and ecosystem functions (Orland et al., 2020). Further, increasing evidence shows that above- and belowground biodiversity jointly regulate EMF, such as in forest ecosystems (Jing et al., 2015; Yuan et al., 2020). Therefore, using integrative measures of biodiversity and EMF across benthic and pelagic habitats should increase our ability to predict the relationships between biodiversity and ecosystem functioning in freshwater environments.

In addition to biodiversity, environmental pressures derived from human activities can also directly (Mackintosh et al., 2016; Tiegs et al., 2019) or indirectly (Chadwick et al., 2006; McMahon et al., 2012; De Laender et al., 2016) affect ecosystem functions. Among the various human stressors that freshwater environments are suffering from, pollution such as nutrient and heavy metals enrichment are among the most urgent for supporting human welfare (Woodward et al., 2012; Beaumelle et al., 2020). For instance, from late May to early June 2007, a large cyanobacteria bloom covered an extensive area in Lake Taihu, causing a drinking water crisis in surrounding towns and cities; this event aroused global concern for the eutrophication, aquatic ecosystem safety and their importance for society (Qin et al., 2007). Severe eutrophication drives the imbalance of aquatic community structures (Richardson et al., 2007) and the deterioration of ecosystem functions such as litter decomposition (Woodward et al., 2012). Similarly, high contents of heavy metals such as zinc and lead cause the loss in decomposer diversity (Oguma and Klerks, 2017) and the declines in ecosystem functions including microbial respiration, primary and secondary production and litter breakdown (Carlisle and Clements, 2005; Peters et al., 2013). However, a knowledge gap in the relationships between biodiversity and ecosystem functioning under these pollution remain to be filled. As revealed by previous studies, it is debatable to what extent environmental pressures affect biodiversity-ecosystem functioning relationships. For instance, in a whole-lake experiment, although copepod richness and biomass show considerably positive relationships, such correlations shift to being negative or nonsignificant

when pH is controlled (Vinebrooke et al., 2009). A fungicide study using manipulative experiments demonstrates that contaminant-induced changes in freshwater ecosystem functions are driven by contaminant-induced declines in biodiversity (McMahon et al., 2012). Thus, to disentangle the mechanisms underlying biodiversity-ecosystem functioning relationships in freshwater environments, it is imperative to tease apart the effects of biodiversity and environmental pressures such as eutrophication and heavy metals enrichment on EMF variations.

Here, we studied spatial variations in the biodiversity of benthic bacteria, bacterioplankton and phytoplankton, and the multiple ecosystem processes associated with phytoplankton productivity and the biogeochemical cycling of carbon (C), nitrogen (N), phosphorus (P) and sulfur (S) in Lake Taihu (Fig. 1a). This lake has suffered from eutrophication since the 1990s (Liu and Wu, 2006), and there is great spatial heterogeneity in nutrient pollution, such as the varying pollution accumulations from the north to the south (Zhang et al., 2007). Thus, Lake Taihu could be considered as a natural laboratory well-fitting the studies on biodiversity-EMF relationships and their links to abiotic factors in lakes undergoing eutrophication. Specifically, we had two hypotheses: i) EMF is positively related to the diversity of autotrophic (phytoplankton) and heterotrophic (bacteria) organisms across benthic and pelagic habitats. ii) Pollution, such as sediment phosphorus and heavy metals, drive the spatial variations in EMF through modulating biodiversity.

2. Materials and methods

2.1. Study site and sampling

Lake Taihu ($30^{\circ}55'40''-31^{\circ}32'58''\text{N}$, $119^{\circ}52'32''-120^{\circ}36'10''\text{E}$), which is 68.5 km long from the north to the south and 34 km wide from the east to the west, is the third largest freshwater lake in China with a mean and maximum water depths of 1.9 m and 2.6 m, respectively. In June 2010, we visited 27 sites in Lake Taihu mainly from the north to the south (Fig. 1a). At each site, water temperature, conductivity and pH were monitored in situ using a multiparameter water quality detector (YSI Incorporated, Yellow Springs, OH, USA). Water samples from the upper 50-cm surface layer were collected by a 5-L Schindler sampler. To sample the phytoplankton community, 1-L of water was collected and preserved with acetic Lugol's solution. The sample was then sedimented for 48 h and concentrated to 50 mL by siphoning off the excess liquid. For the bacterioplankton community, 500-mL of water was sampled, from which the bacteria were aseptically collected using a 0.2- μm pore

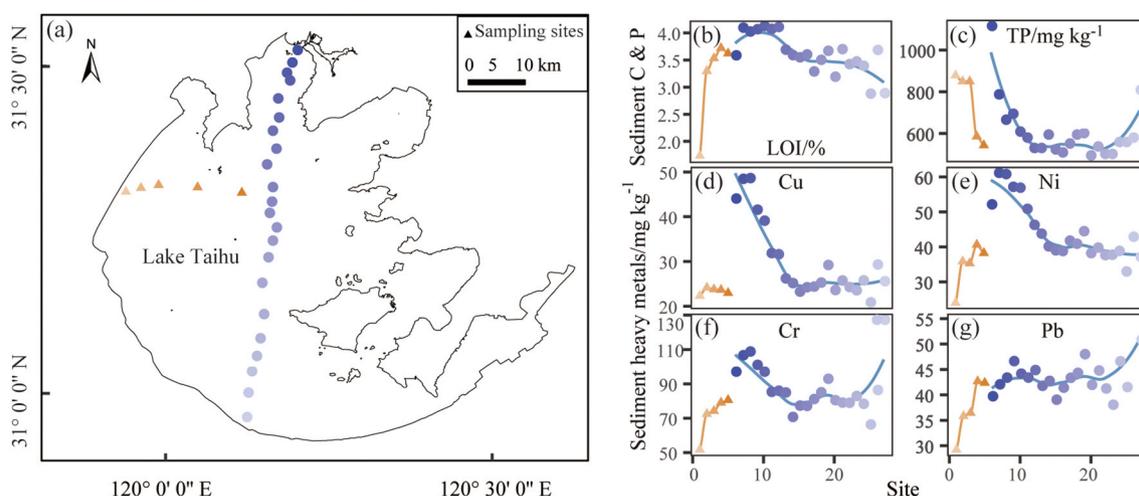


Fig. 1. Sampling map (a) and spatial variations of the main nutrients (b, c) and heavy metals (d–g) of Lake Taihu. For better visualization, we included only sediment loss-on-ignition (LOI) and total phosphorus (TP), and the sediment heavy metals (Cu, Ni, Cr and Pb). The blue circles and orange triangles represent the sampling sites from the northern to the southern area, and from the center to the western area of Lake Taihu, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

size isopore filter after being prefiltered with a 5- μm pore size isopore filter. Another 1-L of water was retained for laboratory chemical analyses.

We retrieved sediment cores using a Kajak-Brinkhurst sampler with 9 cm in diameter to obtain surface sediments, porewater and the whole cores for the biotic, abiotic and ecosystem function features. The surface sediments were obtained from the top 1 cm of the sediment cores in situ using a sterile spatula after discharging the overlaying water, and then the samples were placed in dark and separated into two subsamples: One subsample was used to immediately measure pH, Eh and temperature using a pH, Pt electrode and a thermometer, and was then stored in acid-rinsed polyethylene bags at 4 °C until physiochemical and enzyme analyses. The other subsample was stored in sterilized bottles at -20 °C for bacterial analysis. The porewater were extracted using 'Rhizon SMS' sampler (Rhizosphere Research Products, The Netherlands), which was proved effective and non-destructive for sediment porewater sampling (Song et al., 2003). Specifically, a small hole was drilled on the plexiglass sidewall 0.5 cm below sediment-water interface, and a Rhizon SMS suction sampler was inserted into the tube center. We immersed the suction samplers into deionised water bubbled with N₂, and then extracted ~6 mL porewater with an attached sterile syringe by inserting the samplers into sediment cores. Further, three intact sediment cores with overlaying water were transported to the laboratory after sealing plexiglass tube with rubber stoppers, and were incubated at 4 °C in a self-designed incubation system (Figs. S3, S4) without top rubber stoppers until the following measurement of whole-core ecosystem functions.

2.2. Physiochemical parameter measurements

For the pelagic habitat, the concentrations of dissolved inorganic nitrogen including nitrate (NO₃⁻), nitrite (NO₂⁻) and ammonium (NH₄⁺), and dissolved inorganic phosphorus (DIP) were measured using a continuous flow analyzer (Skalar SA 1000, Breda, The Netherlands). We measured the chromophoric dissolved organic matter (cDOM) concentration, represented by the absorption coefficients of cDOM (m⁻¹) at a wavelength of 355 nm (Bricaud et al., 1981).

For the benthic habitat, the porewater samples were filtered using a 0.45- μm cellulose acetate membrane, and then diluted twice for the analyses of dissolved inorganic nitrogen (NO₃⁻, NO₂⁻ and NH₄⁺) and phosphorus (DIP), following the methods described for the analysis of overlying water. Water content in surface sediments was determined by weight loss after drying at 105 °C for 24 h and sediment porosity was calculated according to previous literature (Crusius and Anderson, 1991). Loss-on-ignition (LOI) was measured with the ignition method (Heiri et al., 2001). The remaining surface sediment samples were freeze-dried for measurement of grain size, total phosphorus (TP) and heavy metals. The grain size of surface sediments was measured with a Mastersizer-2000 laser diffraction particle size analyzer (Malvern Instruments Ltd., UK). TP was analyzed using the peroxodisulfate oxidation and molybdate reaction methodology (Ebina et al., 1983). To more comprehensively profile the spatial variations in pollution conditions, we also examined the heavy metals including Cu, Zn, Ni, Cr, Pb, Ba, Co, Fe, Mn, Sr, Ti and V using inductively coupled plasma-atomic emission spectrometry (ICP-AES) (Dahlquist and Knoll, 1978). We compared the mean values of main heavy metals in our study with those of the geochemical background around Lake Taihu (Zhu et al., 2005) and along the banks of China lakes (Tao, 1983), and with those in 110 lakes in China during the past 10 years (Xu et al., 2017). The geoaccumulation index (I_{geo}) (Müller, 1969) was calculated to evaluate the anthropogenic influence levels of metal concentrations by classifying the contamination into seven grades in Lake Taihu in 2010, and during 2014–2018 and in lakes in China (Yang et al., 2020).

2.3. Phytoplankton and bacterial community analyses

For the phytoplankton community, species identification and biomass calculation were performed following morphological methods (Hu and Wei, 2006). Phytoplankton analyses were conducted under 400 \times magnification using a microscope (Olympus B \times 41, Tokyo, Japan).

For the bacterial communities in water and sediments, the details of DNA extraction, high-throughput sequencing, bioinformatic analyses, and sequence deposits are described in a previous study (Wang et al., 2013). In brief, genomic DNA in water and sediments was extracted using the phenol chloroform method. The primers Bac27F (5'-AGA GTT TGG ATC MTG GCT CAG-3') and Univ1492R (5'-CGG TTA CCT TGT TAC GAC TT-3') were used to amplify the bacterial 16S ribosomal RNA gene by polymerase chain reactions with three replicates per sample, and then the replicates were mixed. The purified amplicons were pooled in equimolar amounts and sequenced using a Roche 454 FLX pyrosequencer. Then, the sequences generated from pyrosequencing were processed using the QIIME pipeline (Quantitative Insights into Microbial Ecology, v1.2) (Caporaso et al., 2010a). Briefly, the sequences were denoised using a Denoiser algorithm (Reeder and Knight, 2010), and clustered into operational taxonomic units (OTUs) at $\geq 97\%$ pairwise similarity using the seed-based UCLUST algorithm (Edgar, 2010). The representative sequences from each OTU were aligned to the Greengenes imputed core reference alignment (DeSantis et al., 2006) using PyNAST (Caporaso et al., 2010b) after chimeras were removed by ChimeraSlayer (Haas et al., 2011). After removing gaps and hypervariable regions using a Lane mask, the alignments were then used to construct an approximately maximum-likelihood phylogenetic tree based on Jukes-Cantor distance using FastTree (Price et al., 2010). Finally, the taxonomic identity of each representative sequence was determined by a naive Bayesian model using the RDP classifier (Wang et al., 2007).

2.4. Ecosystem function measurements

We measured 15 ecosystem functions associated with carbon, nitrogen, phosphorus and sulfur cycling in pelagic and benthic habitats (Table S1). For carbon storage, we included the biomass of four main phytoplankton phyla such as Cyanophyta, Bacillariophyta, Cryptophyta, and Chlorophyta, and the sediment microbial biomass represented by DNA concentration. For carbon degradation, we included the sediment organic hydrolysis rates and the respiration rates. The organic hydrolysis rates were measured using fluorescein diacetate hydrolase activity (FDA) followed the methods described in previous literature (Schnurer and Rosswall, 1982). The respiration rates were represented by oxygen consumption quantified with the slopes of oxygen microprofile across diffusion boundary layer at 24 °C, and the whole ecosystem respiration at the three temperature levels (that is, 5, 8 and 24 °C). The slopes of oxygen microprofile characterizes the oxygen consumption across the sediment-water interface where intensive respiration takes place (Rasmussen and Jørgensen, 1992). Since macrofauna such as Tubificidae is rich in Lake Taihu especially at the northern and eastern bays (Wang et al., 2009), oxygen consumption based on oxygen microprofile might underestimate the effects of macrofauna disturbance (Kim and Kim, 2007; Wang, 2008). Therefore, we included the whole ecosystem respiration as an integration of oxygen consumptions by diffusion, bioturbation and benthic faunal respiration (Rasmussen and Jørgensen, 1992; Wang, 2008). We decided to measure the whole ecosystem respiration under three temperatures by elevating the temperature from 4 to 24 °C because of the temperature sensitivity of whole ecosystem such as diffusion boundary layer and macrobenthos (Wang, 2008). The low temperature of 5 or 8 °C will minimize the effects of disturbance of macrobenthos on diffusion boundary layer and the obtained results will be more relevant to the respiration of microbes, and reflect a different but complementary scenario to the in-situ conditions. The schematics (Figs. S1, S3), photos (Figs. S2, S4) and the measurement procedures for oxygen microprofile and whole ecosystem respirations are detailed in

the supplementary materials.

For the nitrogen cycle, we used the surface sediments to determine the potential denitrification rate according to the modified acetylene inhibition technique (Zhong et al., 2020). It should note to the readers that the acetylene inhibition technique may be flawed. For instance, acetylene may not completely inhibit the reduction of N_2O to N_2 by sediment denitrifiers (Qin et al., 2012) and may inhibit NO_3^- production by nitrifiers (Seitzinger et al., 1993). For phosphorus and sulfur mineralization, we measured the alkaline phosphatase activities in the overlying water, sediment porewater and surface sediments, and the arylsulfatase activity in the surface sediments by following the methods described in previous literature (Hadas and Pinkas, 1997). These ecosystem functions are summarized in Table S1.

2.5. Calculating biodiversity and ecosystem multifunctionality

Shannon diversity, which encompasses both species richness and evenness, was used to characterize the diversity of benthic bacteria, bacterioplankton and phytoplankton. Ecosystem biodiversity and functioning are inherently multidimensional, and multidiversity (MD) and ecosystem multifunctionality (EMF) are thus used to indicate the simultaneous performances of multiple taxonomic groups and functions (Allan et al., 2014; Manning et al., 2018). MD and EMF research can generate an integrative understanding of ecosystem features (Allan et al., 2014; Manning et al., 2018). To measure MD and EMF, we used a synthetic approach to collapse multiple taxonomic diversity values and ecosystem functions, respectively, into a single metric; that is, we calculated Z-scores for all the variables evaluated, and MD (Allan et al., 2014) or EMF (Maestre et al., 2012c) were the averaged Z-scores of all the biodiversity values or ecosystem functions measured for each site.

2.6. Statistical analyses

To reduce the dimensions of the environmental variables, we derived the first and second axes (that is, Sed.metal.comp1 and Sed.metal.comp2) from the principal component analysis (PCA) of the 12 surface sediment heavy metals which were Z-score transformed in advance (Legendre and Legendre, 2012). We performed Pearson correlation analyses to determine the relationships among abiotic factors, and between single ecosystem functions and abiotic factors or biodiversity. Further, we fitted ordinary least squares (OLS) regressions for the effects of biodiversity on EMF. Random forest (RF) analysis (Breiman, 2001) was used to quantify the relative contributions of abiotic factors to each biodiversity metric, and the relative contributions of abiotic factors and MD to EMF. There was a significantly high correlation (Pearson $r = 0.828$) between Sed.metal.comp2 and sediment TP, which were the two main explanatory variables for EMF variations; therefore, we fitted partial linear regressions to separately identify the relative contributions of Sed.metal.comp2 and sediment TP to EMF.

To further determine the role of abiotic factors in linking biodiversity and EMF, we performed partial correlation and structural equation model (SEM) analyses (Grace et al., 2012). In the partial correlation analyses, the effects of biodiversity on EMF were quantified with the coefficients of correlation analysis or partial correlation analysis by accounting for abiotic factors which were important for EMF variations according to RF analysis. In the SEMs, all the initial input variables were Z-score transformed to allow comparisons among the explanatory variables. The biotic factors were the synthetic diversity index MD or the single diversity of the three groups of organisms, and the abiotic factors included the variables associated with three environmental modules: the water column, surface sediments and porewater. The composite variables in each environmental module were selected based on the multiple stepwise regressions of the EMF. The final model met the model fit criteria, with a nonsignificant χ^2 test ($\chi^2 < 2$, $p > 0.05$), a high comparative fit index (CFI > 0.95) and a nonsignificant root mean square error of approximation (RMSEA < 0.05 , $p > 0.05$) (Grace et al.,

2010). ANOVA was used to test the overall significance of the SEM models. After the SEM analyses, we derived the standardized effects (standardized coefficient, β) of the explanatory variables on EMF from the SEMs to infer the direct and indirect effects of abiotic factors and biodiversity on EMF.

The statistical analyses, including the Pearson correlation analyses, partial correlation analyses, OLS regressions (and PCA), partial linear regressions, RF and SEM, were performed in R version 3.6.1 by using the Hmisc V.4.3-0, ggml V.2.3, Stats V3.6.1, asbio V.1.6-3, randomForest V2.9.2 (Breiman, 2001) and lavaan V.0.6-5 (Rosseel, 2012) packages, respectively.

3. Results

3.1. Spatial variations in nutrients and heavy metals

Across our sampling sites, which covered nearly the whole lake, there was a clear spatial heterogeneity in pollution loading such as that from nutrients and heavy metals (Fig. 1, S5). The contents of organic matters in both surface sediments (LOI, Fig. 1b) and overlying water (cDOM, Fig. S5) decreased from the north to the south of the lake. For phosphorus, the sediment TP was higher in the north bay and along the west coast than in the center and south of the lake (Fig. 1c), while the DIP in the overlying water was higher in the lake center (Fig. S5). The mean value of the sediment TP reached 633.3 mg kg^{-1} (Table S2). For the heavy metals, both the first and second PCA axes of the 12 heavy metals (that is, Sed.metal.comp1 and Sed.metal.comp2) depicted U-shaped trends from the north to the south of the lake (Fig. S5). Sed.metal.comp1 and Sed.metal.comp2 accounted for 48.2% and 24.1% of the variations in all the measured heavy metals, respectively (Fig. S6). The first three metals represented by Sed.metal.comp1 were Pb, Fe and Cr, while Ti, Zn and Cu were represented by Sed.metal.comp2. Specifically, single heavy metals showed various spatial patterns (Fig. S6). For example, Cu, Ni and Zn decreased substantially from the north of the lake to its center, followed by a minor variation in the south (Fig. 1de, S5). From north to south, Cr and Fe followed U-shaped patterns (Fig. 1f, S5), while Pb had no clear spatial pattern (Fig. 1e). The mean contents of main sediment heavy metals such as Cr, Ni, Cu, Zn and Pb were above those of the reported geochemical background and those of other lakes in China especially for Cr and Pb, and were generally at uncontaminated to moderately contaminated levels (Table S3). Moreover, investigations in northern Lake Taihu during 2014–2018 show a trend towards moderate to heavy contamination levels in heavy metals including Cr, Ni, Cu, Zn and Pb (Table S3).

3.2. Relationships between biodiversity and EMF

There were significant correlations between diversity and single ecosystem functions such as the C, N, P, and S cycling processes. For instance, the Shannon diversity of benthic bacteria and bacterioplankton was significantly ($p < 0.001$) positively correlated with the pelagic features including the biomass of Chlorophyta and Cryptophyta, and with the benthic functions including sediment denitrification, alkaline phosphatase activities and arylsulfatase activity ($p < 0.05$, Fig. S7). The Shannon diversity of phytoplankton also showed significant ($p < 0.05$) positive correlations with the biomass of Chlorophyta and Cryptophyta (Fig. S7).

Further, ecosystem multifunctionality significantly ($p < 0.01$) correlated with the Shannon diversity values of benthic bacteria, bacterioplankton and phytoplankton, with the explained variations of 26.6%, 26% and 18.4%, respectively (Fig. 2a–c). The multidiversity significantly explained 49.2% of the spatial variations in EMF ($p < 0.001$, Fig. 2d).

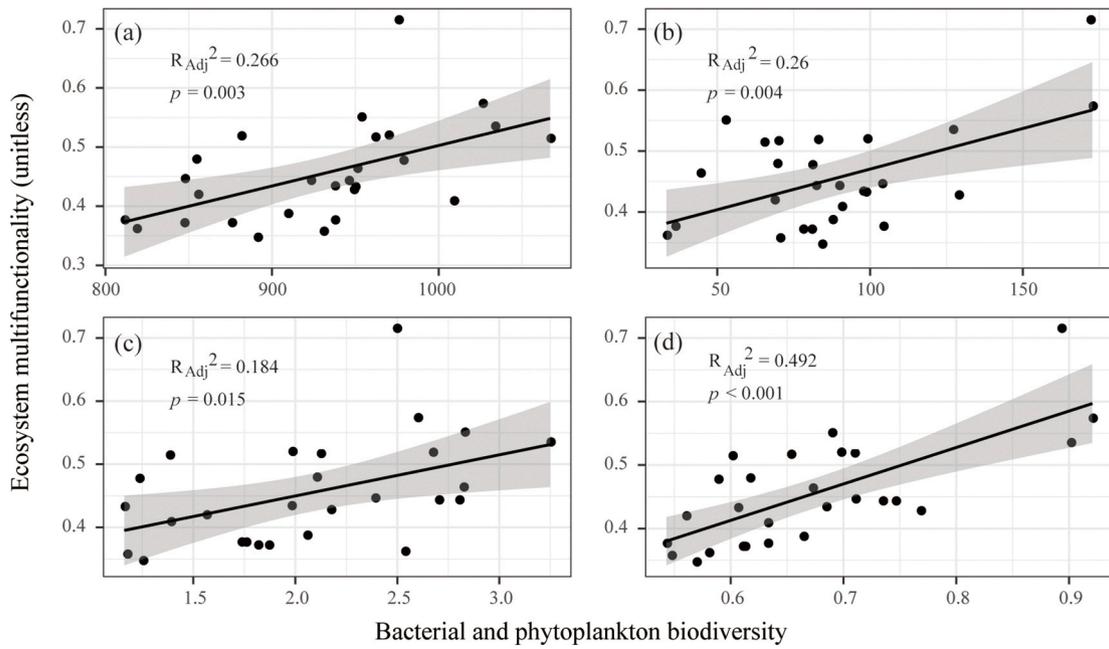


Fig. 2. Relationships between biodiversity and ecosystem multifunctionality (EMF). The biodiversity values include the Shannon diversity for the benthic bacteria (a), bacterioplankton (b) and phytoplankton (c), and the multidiversity of these three taxonomic groups (d). The lines represent the fitted ordinary least squares (OLS) regressions, with 95% confidence intervals indicated by the shaded areas. The p and adjusted R^2 values of the OLS regressions are shown.

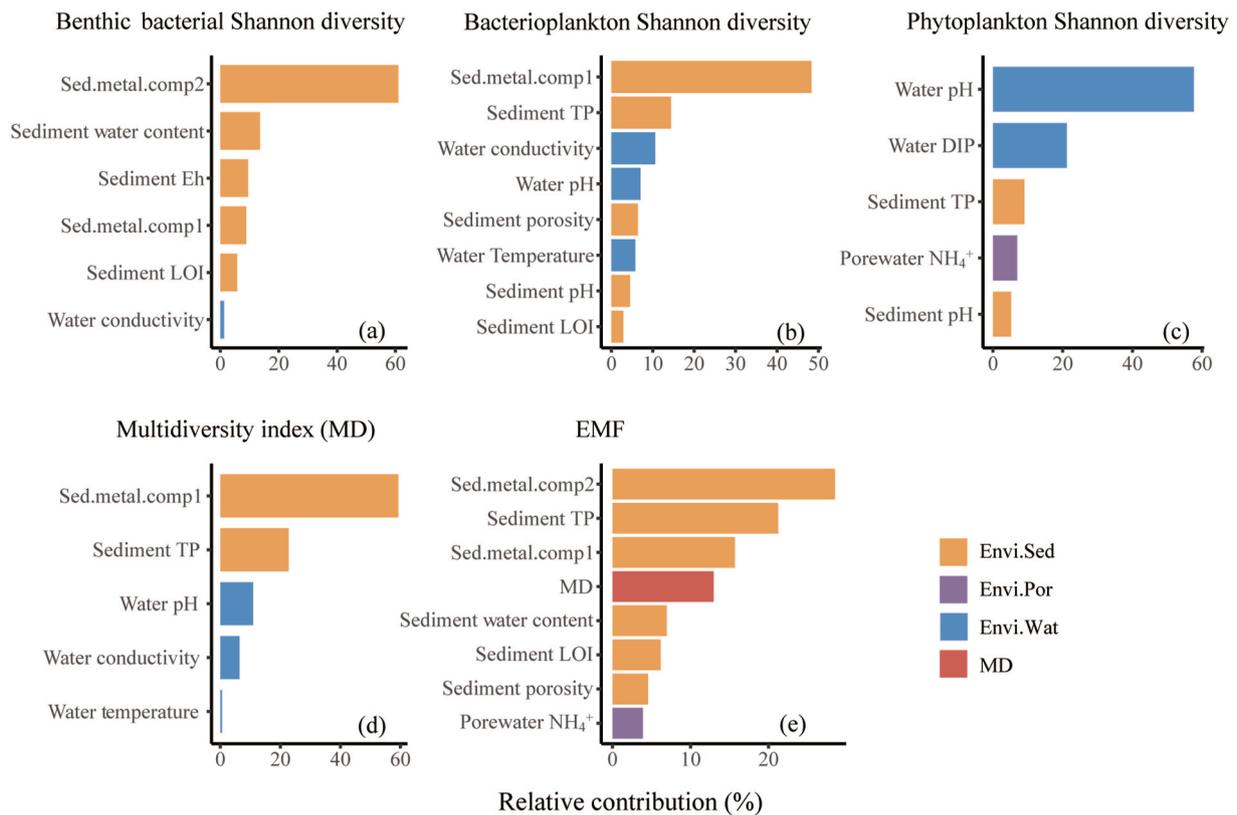


Fig. 3. Relative importance of abiotic factors on biodiversity and of abiotic and biotic factors on ecosystem multifunctionality (EMF, e). The biodiversity values include the Shannon diversity for the benthic bacteria (a), bacterioplankton (b), phytoplankton (c), and the multidiversity (MD, d). Env.Wat, Env.Por and Envi.Sed: the abiotic explanatory factors in the water column, porewater and surface sediments, respectively. LOI: loss-on-ignition of sediments. Sed.metal.comp1 and Sed.metal.comp2: the first and second axes, respectively, of the principal component analysis of 12 heavy metals. TP: total phosphorus. DIP: dissolved inorganic phosphorus.

3.3. Factors affecting biodiversity and EMF

We used random forest modeling to identify the most important predictors of biodiversity and EMF (Fig. 3). Sed.metal.comp2 and sediment water content accounted for 60.98% and 13.56% of the spatial variations in Shannon diversity of benthic bacteria, respectively (Fig. 3a). For bacterioplankton, Sed.metal.comp1 and sediment TP accounted for 48.34% and 14.4% of the variations, respectively (Fig. 3b). For phytoplankton, water pH contributed the most to Shannon diversity (57.7%), followed by water DIP (21.2%), sediment TP (9.0%) and porewater NH_4^+ (7.0%) (Fig. 3c). When the diversity of the three taxonomic groups was integrated into MD, Sed.metal.comp1 was the most important variable (59.3%), followed by sediment TP (22.8%) and water pH (11.0%) (Fig. 3d).

For the spatial variations in EMF, we found that Sed.metal.comp2 had the greatest relative contribution (28.5%), followed by sediment TP (21.2%), Sed.metal.comp1 (15.7%), MD (13.0%), sediment water content (7.0%), sediment LOI (6.2%), sediment porosity (4.6%) and porewater NH_4^+ (3.9%) (Fig. 3e). Specifically, sediment TP was positively correlated with the ecosystem processes associated with the cycling of sediment carbon (i.e., respiration rates and the absolute value of SOP), nitrogen (i.e., denitrification), phosphorus (i.e., alkaline phosphatase activities) and sulfur (i.e., arylsulfatase activity) (Fig. S8, $p < 0.05$). Among the sediment heavy metals, V, Fe, Co, Ba, Pb, Cr and Ni were negatively correlated with the biomass of Chlorophyta, Bacillariophyta, and Cryptophyta (Fig. S8, $p < 0.05$). Ni, Zn and Cu were positively correlated with phosphorus and sulfur cycling, while V, Ti, Fe, Co and Pb were negatively correlated with carbon and nitrogen cycling (Fig. S8, $p < 0.05$). Since Sed.metal.comp2 was highly correlated with sediment TP (Fig. S9), we fitted partial linear regressions to disentangle their pure effects on EMF and found that Sed.metal.comp2 and sediment TP exclusively accounted for 17.0% (Fig. 4b, $p < 0.05$) and 1.8% (Fig. 4a, $p > 0.05$) of the variation in EMF, respectively. Overall, heavy metal composition (e.g., Sed.metal.comp2) was the best single predictor of EMF among all the measured explanatory variables.

3.4. Abiotic factors mediated the links between biodiversity and EMF

The partial correlation analyses showed that Shannon diversity exerted no significant effects ($p > 0.05$) on EMF for the bacterioplankton and phytoplankton communities when controlling for porewater NH_4^+ and sediment TP, respectively (Table 1). After controlling for Sed.metal.comp2, the relative influence of the benthic bacterial diversity on EMF

decreased, with coefficients from 0.543 ($p < 0.01$) to 0.406 ($p < 0.05$) (Table 1). According to the SEM analyses, we built two best-fit models that accounted for 80.7% and 82.9% of the variations in EMF. In both models, we selected abiotic exploratory variables including Sed.metal.comp1, Sed.metal.comp2 and sediment water content, thus creating a composite variable for sediment environment (i.e., Env.Sed); water conductivity and NO_2^- for the water environment (i.e., Env.Wat); and porewater DIP for the porewater environment (i.e., Env.Por) (Fig. 5a, S10a). The first model showed that Env.Sed impacted EMF directly ($\beta = 0.487$), and indirectly via Env.Wat ($\beta = 0.452$), Env.Por ($\beta = 0.584$) and MD ($\beta = 0.404$). Env.Wat indirectly affected EMF via MD ($\beta = 0.457$). The second model further revealed the significant effects of Env.Sed on the benthic bacterial diversity ($\beta = 0.58$), and the effects of Env.Wat on the diversity of phytoplankton ($\beta = 0.488$) and bacterioplankton ($\beta = 0.398$). Overall, the composite variable Env.Sed substantially contributed to the variations in EMF in both the first (50.34%, Fig. 5b) and second (46.97%, Fig. S10b) models. The total relative contributions of biodiversity to EMF were similar between the first (20.65%, Fig. 5b) and the second (26.45%, Fig. S10b) models.

4. Discussion

Using a whole-ecosystem perspective, we considered ecosystem functions by accounting for the C, N, P, and S cycling in both benthic and pelagic habitats in Lake Taihu, and showed the positive effects of the biodiversity of the bacterial and phytoplankton communities on ecosystem multifunctionality. For bacteria, elements of pelagic ecosystems like phytoplankton biomass or algal derived extracellular material can support for the growth of particular bacterioplankton (Hornak et al., 2017), which might account for the close links between phytoplankton biomass and bacterioplankton. In pelagic-benthic coupling processes, positive bacterial diversity-EMF relationships could be attributed to the fact that single ecosystem functions associated with C, N, P, or S metabolisms were significantly promoted by the diversity of bacterioplankton or benthic bacteria (Fig. S7). Our findings were consistent with both the results of experimental studies and field observations reported in previous literature (Wagg et al., 2014; Zhang et al., 2017; Luo et al., 2018; Zheng et al., 2019). For example, in a microcosm experiment with a manipulated soil microorganism diversity gradient, litter decomposition and N turnover decline with reduced soil biodiversity (Wagg et al., 2014). Enzyme activities related to C, N, P, and S cycling are positively affected by microbial diversity in agriculture (Luo et al., 2018; Zheng et al., 2019) and river sediments (Zhang et al., 2017).

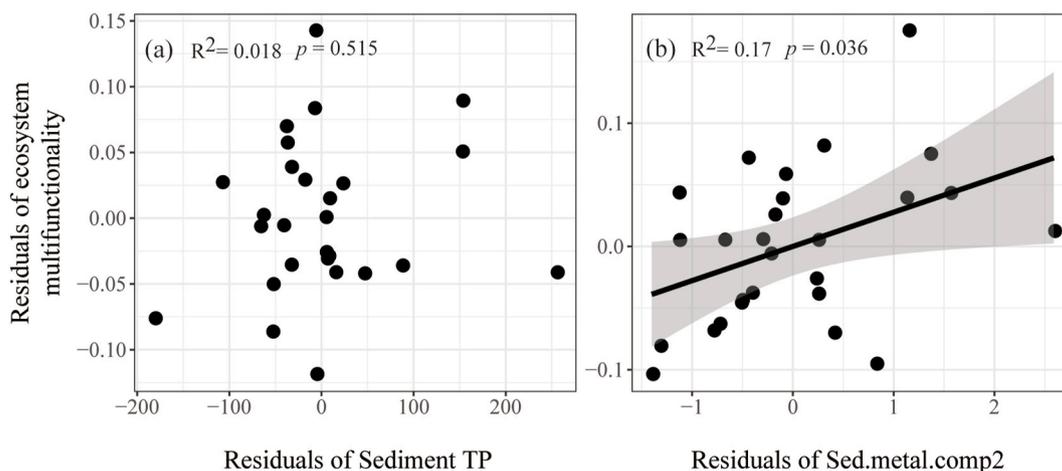


Fig. 4. The relative effects of sediment total phosphorus (TP, a) and heavy metals (b) on ecosystem multifunctionality (EMF). The variable of heavy metals was represented by the second axis (i.e., Sed.metal.comp2) of the principal component analysis of 12 heavy metals. The line was fitted according to partial linear regressions, and only the significant ($p < 0.05$) regression line is shown with 95% confidence intervals indicated by the shaded areas. The R^2 value denotes the partitioning variance explained by sediment TP or Sed.metal.comp2.

Table 1

The effects of diversity on ecosystem multifunctionality. The effects were quantified with the coefficients of the correlation analyses and also the partial correlation analyses after accounting for abiotic factors. These abiotic factors were confirmed to be important in explaining the EMF variations by random forest analysis. LOI: loss-on-ignition of sediment. Sed.metal.comp1 and Sed.metal.comp2: the first and second axes, respectively, of the principal component analysis of 12 heavy metals.

Controlling for	Effect of			
	Benthic bacterial Shannon diversity	Bacterioplankton Shannon diversity	Phytoplankton Shannon diversity	MD
None	0.543**	0.537**	0.464*	0.715***
Sed.metal.comp2	0.406*	0.526*	0.572**	0.758***
Sediment total phosphorus	0.501**	0.441*	0.33^{NS}	0.609***
Sed.metal.comp1	0.558**	0.43**	0.418*	0.668***
Sediment water content	0.598**	0.512**	0.465*	0.703***
Sediment LOI	0.621***	0.474*	0.471*	0.691***
Sediment porosity	0.566**	0.537**	0.483*	0.732***
Porewater NH4 ⁺	0.598**	0.327^{NS}	0.519**	0.65***

NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Values in bold highlight the abiotic factors having the greatest impact on the relationships between biodiversity and ecosystem multifunctionality.

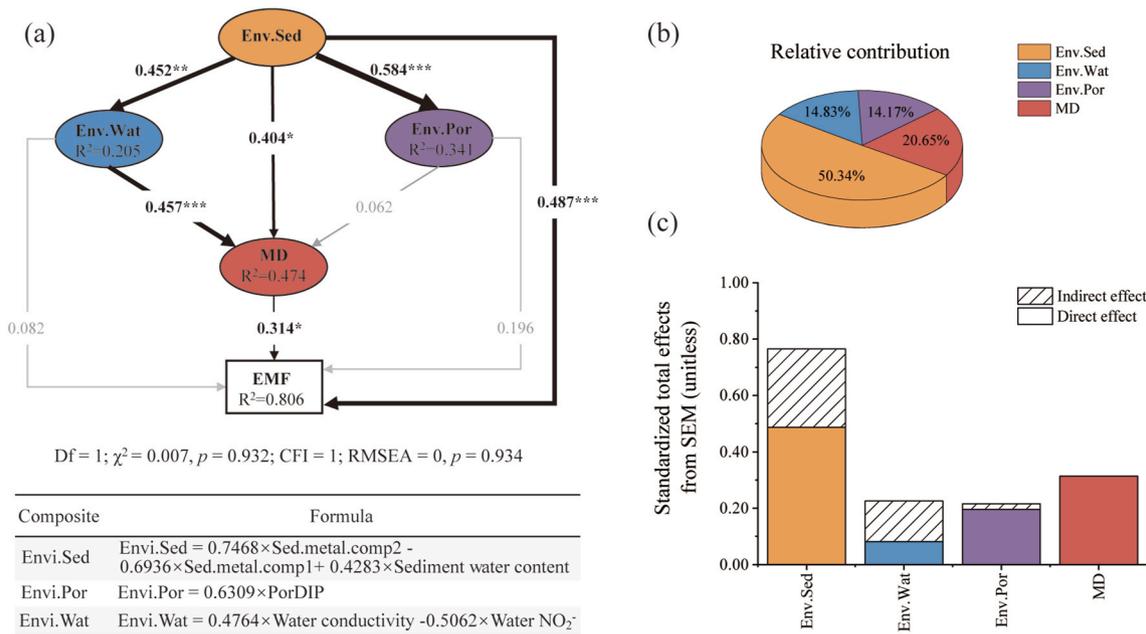


Fig. 5. Structural equation models (SEM) of ecosystem multifunctionality (EMF). (a) Best-fit model depicting the effects of three abiotic environmental composite variables and biodiversity on EMF. The three environmental composite variables, Env.Wat, Env.Por and Env.Sed, represent the abiotic explanatory factors in the water column, porewater and surface sediments, respectively. The biodiversity is represented in terms of multidiversity (MD) which is the averaged z-score for the Shannon diversity of the benthic bacteria, bacterioplankton and phytoplankton. In the model diagram, the R² indicates the proportion of variance explained for the model variables. The black and gray arrows represent significant (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) and nonsignificant ($p > 0.05$) effects, respectively. The arrow widths and accompanying values denote standardized path coefficients. We show the SEM model formula for each environmental module below the model diagram. Details for the initial variables in each abiotic environmental module are listed in Table S2. In the model formula, Sed.metal.comp1 and Sed.metal.comp2 are the first and second axes, respectively, of the principal component analysis of 12 sediment heavy metals. PorDIP is the dissolved inorganic phosphorus in the porewater. (b) The relative contributions of Env.Wat, Env.Por, Env.Sed, and MD to EMF. (c) The direct and indirect effects of Env.Wat, Env.Por, Env.Sed, and MD on EMF. The solid colored bars represent direct effects whereas the patterned bars show indirect effects.

For phytoplankton, there was also a positive diversity-EMF relationship. Such a result for primary producers is consistent with the single-function literature on the classical relationships in biodiversity-ecosystem functioning; that is, the phytoplankton diversity-biomass relationship is consistently positive in both experiments and natural ecosystems (Zimmerman and Cardinale, 2014). In previous literature, however, the relationships between primary producers and EMF are rarely reported for freshwater environments, and are mostly available for terrestrial environments where plant diversity shows positive (Jing et al., 2015; Lundholm, 2015) or no (Schuldt et al., 2018; Hu et al., 2020; Yuan et al., 2020) effects on EMF. Future studies are encouraged to consider more aspects to untangle the universal relationships in aquatic environments regarding the following aspects. (1) The number of ecosystem functions measured. In a grassland biodiversity experiment

based on 82 indicator variables of ecosystem functions, the effects of plant biodiversity on EMF were stronger when more functions were included (Meyer et al., 2018). (2) The identity of ecosystem functions included. Since different ecosystem functions may positively or negatively correlate with each other, the identity of the ecosystem functions included also alters the strength of the effects of biodiversity on EMF (Meyer et al., 2018). (3) The biodiversity attributes considered. Biodiversity encompasses multiple attributes such as taxonomic, phylogenetic and functional diversity, and community composition. While species richness tends to promote multifunctionality, this effect is largely modulated by community composition and spatial patterns (Maestre et al., 2012), and could even be enhanced by three-fold when phylogenetic and functional diversity are also considered (Le Bagousse-Pinguet et al., 2019). Therefore, identifying the effects of

comprehensive biodiversity attributes is encouraged in future studies to better predict EMF.

Somewhat inconsistent with our hypothesis, we found that heavy metals were better predictors and drivers of the spatial variations in EMF than sediment TP, although the latter was also important. This following may explain this phenomenon. Firstly, eutrophication and heavy metal pollution tend to co-occur in aquatic ecosystems due to human interferences, such as the discharge of domestic, industrial and agricultural sewage and recreational activities (Li et al., 2014; Li et al., 2018; Yang et al., 2020). In our results, sediment TP and heavy metals (e.g., Sed.metal.comp2) in Lake Taihu showed similar spatial distribution patterns (Fig. 1c, S5). Secondly, Fe can promote phosphorus deposition by forming the relatively stable iron-bound phosphorus in sediments (Meng, 2005; Cesbron et al., 2014). Thirdly, ecosystem functioning might be more sensitive to heavy metals than to phosphorus loading. We found that in contrast to the promoting effects of total phosphorus on ecosystem functions such as C, N, P and S cycling, heavy metals such as Fe, Co, Pb, Cr and Ni were negatively related to phytoplankton biomass and C and N cycling (Fig. S8). Consistently, there are negative effects of high heavy metal concentrations on ecosystem processes (Ferreira et al., 2016), such as the inhibition effects of Cr on algal photosynthesis (Arun et al., 2014) and the negative influences of Pb on microbial enzyme activities and respiration (Chan and Dean, 1988). Notably, in January 2017, the concentration of soluble Cr in overlaying water of a northern bay in Lake Taihu exceeded the criteria continuous concentration for Cr (III) (threshold value: $74 \mu\text{g L}^{-1}$; Environmental Protection Agency, 2006), and the threshold values of drinking ($10 \mu\text{g L}^{-1}$) and fisheries ($100 \mu\text{g L}^{-1}$) water quality standards for DGT-labile Cr(VI) and total Cr respectively (Administration of Environmental Protection of China, 2002), resulting from the high mobility of sediment Cr (Fan et al., 2019). Our findings underscore the potential of heavy metal loading to impair ecosystem functioning in eutrophic aquatic ecosystems, and indicate that heavy metal loading and probably other abiotic factors not monitored in this study can be deemed as earlier signals than nutrient loading of destroyed ecosystem functioning and services in eutrophic waterbodies. This is of great significance to the monitoring and management of the health of aquatic ecosystems undergoing eutrophication.

We further found that heavy metal and nutrient loadings also mediated the associations between biodiversity and ecosystem functioning. Phytoplankton biomass was promoted by sediment TP and porewater NH_4^+ , meanwhile phytoplankton diversity was mostly influenced by nutrient status including water phosphate, sediment TP and porewater NH_4^+ . This might partly explain the significant correlations between the phytoplankton diversity and biomass (Fig. S7). Similarly, sediment heavy metals dominated the spatial variations in EMF and in the diversity of the benthic bacteria and bacterioplankton, which could explain the high correlations between the bacterial diversity and EMF. In previous studies, the links between biodiversity and ecosystem multifunctionality have been increasingly, though still rarely, proven to be mediated by climate change and human disturbances, such as the mean annual precipitation and temperature changes in alpine grasslands (Jing et al., 2015), long-term fertilization management in agricultural soils (Luo et al., 2018), nutrient and herbivore alterations in estuarine tidal flats (Alberti et al., 2017) and dredging of river sediments (Zhang et al., 2017). Our study thus provided new evidence for the regulating effects of human disturbances (i.e., eutrophication) on lake ecosystem multifunctionality. We further proposed to build an earlier warning strategy for impaired freshwater environments using heavy metals or other abiotic signals needed for further discovery and to reduce these anthropogenic disturbances to sustain aquatic biodiversity and maintain ecosystem functioning. It should be noted that our above findings were obtained from a single lake (that is Lake Taihu) and could further be supported by cross-comparing multiple lakes using the similar whole-ecosystem investigations as shown in this study in order to provide compelling theoretical guidance and evidences for aquatic biodiversity conservation and lake management in the future.

5. Conclusion

This study revealed that the diversity of both phytoplankton and bacteria promoted ecosystem multifunctionality in freshwater benthic-pelagic ecosystems. We showed that in the eutrophic Lake Taihu, heavy metal and phosphorus loadings were of pivotal importance in explaining ecosystem multifunctionality, with the former having greater predatory power. Unexpectedly, we further found that such pollution loading mediated the links between biodiversity and ecosystem multifunctionality. Our findings advance the key ecological topic of the relationships between biodiversity and ecosystem multifunctionality in freshwater environments, which has been previously reported mainly in terrestrial ecosystems, and further emphasize the significance of protecting freshwater biodiversity from human disturbances in order to sustain aquatic ecosystem functioning. Earlier warning signals for impaired ecosystem, such as heavy metals, should be identified for the future management of aquatic ecosystems undergoing eutrophication.

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.envpol.2021.117501>.

Credit author contribution statement

Weizhen Zhang: Investigation, Software, Formal analysis, Visualization, Writing – original draft. **Ji Shen:** Resources, Writing – review & editing. **Jianjun Wang:** Supervision, Conceptualization, Resources, Writing – review & editing, Data curation, Funding acquisition.

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