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**Macroinvertebrates and environmental responses to dredging and submerged
macrophytes transplantation**

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Abstract

1 Eutrophication of freshwater ecosystems is a major global problem, but restoration
2 can be difficult due to ongoing problems relating to water pollution, sedimentary
3 nutrient stores, and altered aquatic biodiversity. Mitigation of water quality stressors
4 is often conducted alongside transplantation of submerged macrophytes and
5 dredging, but knowledge of ecosystem response to post-dredging transplantation of
6 submerged macrophytes is limited.

2 Here, we report a long-term (2008-2018) in-situ monitoring study to evaluate the
3 effects of two different restoration measures: dredging only (Dredged) and dredging
4 with post-dredging transplantation of submerged macrophytes (Dredged with
5 macrophytes) conducted in five subtropical eutrophic lakes in Lake Taihu basin,
6 China. Water and sediment nutrients, bloom-forming algae *Microcystis*, and
7 macroinvertebrate were monitored every two years for each treatment and compared
8 with reference areas (Control) established in unrestored parts of the same lakes.

3 Dredging only decreased sediment nutrients (nitrogen, phosphorus, total carbon and
4 water total phosphorus significantly, however, this effect diminished about five
5 years later. Dredged with macrophytes had a stronger, longer-lasting positive effect
6 on water quality than Dredged alone. Disturbance caused by dredging (without
7 macrophytes transplantation) decreased the biomass of *Microcystis*, while
8 transplantation of submerged macrophytes shortly after dredging did not contribute
9 to the decreasing of *Microcystis* biomass. The biomass of *Microcystis* in Dredged
10 with macrophytes areas was always similar with Control over the period of our
11 monitoring.

4 A positive effect of submerged macrophytes transplantation post-dredging was
5 found for macroinvertebrate abundance and diversity: Dredged with macrophytes

45 areas had significantly higher macroinvertebrate biomass and richness than Dredged
46 areas after 9 years' recovery. Macroinvertebrate richness in Dredged with
47 macrophytes areas nearly doubled compared to Control; while Dredged areas were
48 just restored to Control levels.

49 5 Synthesis and applications. Our study provides an in-situ long-term field monitoring
50 with new findings about the benefits and caution of submerged macrophytes
51 transplantation post-dredging, and the effect of partial restoration, which could
52 inform eutrophic waterbody restoration schemes.

53 **Keywords:** Biodiversity; Eutrophication; Partial restoration; Beta-diversity;
54 *Microcystis*; Time-Series; Nutrients

1 Introduction

Dredging of deposited sediment is practiced around the world to enhance water conveyance and storage in flood prone areas and for commercial sand mining (Mohan et al., 2016). Dredging is also used for remediating nutrient pollution in shallow waterbodies (Riza et al., 2023); a practice that has become particularly popular in China (Liu et al., 2019). Previous studies have highlighted successful decreases of excess sediment N and P concentrations following dredging (Oldenborg and Steinman, 2019). However, where dredging is not complemented by reductions of external pollutant loadings, nutrients typically re-accumulate quickly in the lake sediment (Liu et al. (2016). Nonetheless, Li et al. (2021) reported that the internal P loading could be decreased successfully by transplanting submerged macrophytes in subtropical aquacultural lakes. This raises the possibility that restoration of eutrophic waters could be maintained and enhanced by the establishment of submerged macrophytes post-dredging.

Establishment of submerged macrophytes can provide essential and complex habitat for macroinvertebrates by offering protection from predators and a range of food sources (Wolters et al., 2019). A major impact of dredging is the profound alteration of benthic habitats and biodiversity. The colonization by macroinvertebrates of newly exposed surfaces after dredging typically takes months to several years depending on the type of organisms, local physical/chemical parameters, and metacommunity processes that influence dispersal (Wilber and Clarke, 2007). Whatley et al. (2014) noted that the decline of benthic invertebrate assemblages in eutrophic water was triggered by the deterioration in water quality and the loss of submerged macrophytes. In turn, benthic invertebrate assemblages can improve the physicochemical habitat

conditions of sediment-water interface through actions such as burrowing, playing central roles in nutrient cycling (Zhang et al., 2010), and linking benthic and pelagic food webs to support fishery production (Johannsson et al., 2000). Given many benthic macroinvertebrates are sediment-dwellers, they do not have the ability to escape from dredging and offer a good target group to assess the impacts and subsequent success of restoration (Zou et al., 2019).

Many studies demonstrated that aquatic submerged macrophytes have decreased rapidly worldwide because of eutrophication. In contrast, once their communities are established, submerged macrophytes improve water clarity and the stability of aquatic ecosystems via various buffer mechanisms (Bai et al., 2020). Therefore, aquatic macrophytes transplantation has been widely applied in the restoration of eutrophic waterbodies in China (Fang et al., 2016) and elsewhere (e.g., Hilt et al., 2006; Knopik and Newman, 2018). Nevertheless, the type and extent of the benefits offered by submerged macrophytes transplantation post-dredging as opposed to dredging only remains unclear.

Here, we present a long-term (2008-2018) monitoring study of five eutrophic shallow lakes in the Taihu basin, China, to investigate (i) the effects of dredging on sediment and water chemistry, *Microcystis* (bloom-forming algae) and community structure of benthic macroinvertebrates; (ii) the effects of submerged macrophytes transplantation post-dredging as a potential restoration measure compared to dredging only. We hypothesized that (H_i) dredging would decrease sediment and water nutrients by reducing internal loading after the removal of the nutrient-enriched sediment (Oldenburg and Steinman, 2019). We further expected that submerged macrophytes transplantation post-dredging would improve and consolidate these effects via the uptake and bioaccumulation of nutrients by the plants (Wang et al., 2021), and reduce

the risk of sediment resuspension (Zhu et al., 2015). We also expected that (H_{ii}) dredging would reduce the biomass of *Microcystis* due to disturbance as reported by Wan et al. (2021), while the transplantation of submerged macrophytes is expected to further limit *Microcystis* via light and nutrient competition and allelopathic influences (Amorim and Moura, 2020). Finally, we anticipated (H_{iii}) the transplantation of submerged macrophytes to accelerate the recovery of benthic macroinvertebrate communities impacted by dredging, due to the provision of improved habitats. The implications of our study could be considered in the management of eutrophic shallow lakes in subtropical regions.

2 Material and methods

2.1 Study area

The Taihu Basin (30°07′-32°15′ N, 119°02′-121°58′ E) has a watershed of 36,895 km², accommodating 4.4% of the country's population (59.20 million) and accounting for 10.4% of China's gross domestic product (5418.8 billion RMB) in 2012 (Wu et al., 2018). To quantify the effect of ecological restorations and determine if responses could be generalized in space and time, five lakes (Dongjiu, Xijiu, Gehu, Yangcheng, Shanghu) were monitored over a ten-year period (2008-2018) throughout the basin (Fig. 1; Table 1). All lakes have been subject to the restoration of specific areas of the lake, which is a popular restoration practice in China. As a compromise solution between budgetary constraints and the improvement of water environment, some institutions opt to improve the aquatic environment as opposed to restoring the entire waterbody, especially for areas with public affluence such as proximity to parks or commercial public buildings.

2.2 Field sampling and data collection

An in-situ field monitoring study was used to assess the effect of partial restorations across the five lakes. Pre-dredging samples were collected in 2008 (August to October) before dredging took place in 2009 (January to February). The monitoring comprised three different areas (treatments) in each lake (Fig. 2): (1) a reference area comprising a non-dredged area without macrophyte cover located close to the dredged area (Control); (2) a Dredged area and (3) a dredged area with posterior transplantation of submerged macrophytes (Dredged with macrophytes). In each area, five sampling points were relatively evenly distributed. A buffer area of at least 300 m to avoid edge effects was maintained between each monitored area. Non-dredged areas with transplantation of submerged macrophytes were not available in our study, as this treatment was not implemented by the third parties (local institutions). Planting of submerged macrophytes without dredging was considered likely to fail due to the high probability that the accumulated eutrophic soft sediment on the lake beds, would lead to anchorage failure as submerged macrophytes tend to occupy relatively hard bottoms (Dong et al., 2017).

Dredged and Dredged with macrophytes areas were all subjected to suction dredging, with sediment removed to a depth of 0.5-0.8 m. Dredged with macrophytes areas had two native species of submerged macrophytes (*Vallisneria spiralis* and *Hydrilla verticillata* bought from local providers) transplanted one to two months after dredging with a density of 20-30 plants per m². Macrophytes were placed in bay areas of the lakes where they were less exposed to wave influence. There was no separation (enclosures) between Control, Dredged and Dredged with macrophytes within lake due to landscape requirements and the expectation for the future spread of submerged macrophytes to other parts of the lakes over time. Post-dredging repeated field

monitoring was carried out every two years from 2010 to 2018, August to October. The specific size of each monitoring area in each lake is noted in Table 1. Although the percentage of Dredged and Dredged with macrophytes areas in each lake was small (0.8%-18.8%, 0.3%-6.3% respectively), dredging or transplantation of macrophytes is difficult over the entire area of large lakes, due to complex physiochemical or hydrological conditions (such as depth and turbidity of water) and financial costs (Paerl, 2018).

Sediment and water chemistry

Surface sediment was collected from each sampling point using a 1/16 m² modified Peterson grab (three grabs per point) and sieved in situ through a 250- μ m mesh. Sieved replicates at each sampling point were combined, ground with a pestle and mortar, passed through a 2 mm sieve, stored in bottles before laboratory analysis. Phosphorus fractions in the sediment samples were determined using the sequential extraction procedure. Exchangeable phosphorus (Ex-P), aluminum-bound phosphorus (Al-P), iron-bound phosphorus (Fe-P), occluded inorganic phosphorus (Oc-P), and calcium-bound phosphorus (Ca-P) were extracted sequentially using NH₄Cl, NH₄F, NaOH, Na₂S₂O₄, H₂SO₄ solutions, respectively (Zhang et al., 2022). TP was determined by treating the sediment sample at 450 °C, followed by HCl extraction. Total carbon (Carbon) and total nitrogen (TN) were analysed with a C/N elemental analyser (Flash EA 1112, Thermo Fisher Scientific, Waltham, MA, USA).

Water samples were collected at a depth of 0.5 m at each sampling point, stored in acid-cleaned bottles (200 mL). TN, nitrate nitrogen (NO₃-N), ammonia nitrogen (NH₄⁺-N), orthophosphate (PO₄-P) and TP were then measured using an ultraviolet spectrophotometer (PhotoLab S12, WTW Company, Munich, Germany). NO₃-N and

NH₄⁺-N were determined from samples filtered by 0.45 µm Whatman GF/F filters (Whatman, Kent, Great Britain). Chemical oxygen demand (COD_{Cr}) was determined with the potassium dichromate method. All storage and chemical analysis were performed following national standard analytical methods for water and wastewater (National Environmental Protection Bureau, 2002).

Microcystis

To determine the biomass and density of *Microcystis* sp., 1 L of surface water was collected using a polymethyl methacrylate sampler at each sampling point and fixed with Lugol's iodine solution (1% final concentration), then concentrated to 50 mL (Huang et al., 1999). *Microcystis* cell numbers were counted from colonies and single cells using an inverted microscope (Olympus SZ-40, Olympus Corporation, Tokyo, Japan). *Microcystis* biomass (mg fresh weight/L) was estimated from its geometric cell volume, assuming a mean density of 1 mg/mm (Zhang et al., 2007). Cells of colonial *Microcystis* were separated using an ultrasonic device (JY88-II, Scientiz, Ningbo, Zhejiang, China) before enumeration.

Benthic macroinvertebrate

Benthic macroinvertebrates were sampled from the material retained on the sieve of the three Peterson grab samples collected per sampling point for the sediment sampling. The samples were preserved with 7% formalin solution and stored in a cool box for sorting and identification in the laboratory. Specimens were identified to the lowest feasible taxonomic level under a dissection microscope (Olympus® SZX10) using taxonomic keys (Morse et al., 1994; Wang, 2002). Macroinvertebrate biomass (wet mass) was then expressed by reference to the sediment area sampled (mg/m²).

2.3 Data analysis

Principal component analysis (PCA) was applied separately to sediment (Carbon, TP, TN, Oc-P, Ca-P, Fe-P, Ex-P, Al-P) and water (TN, TP, $\text{NH}_4^+\text{-N}$, COD_{Cr} , *Microcystis*) variables. Spearman Rank correlation analysis was performed to calculate the correlation coefficients which were detected by PCA. Sediment TP and Carbon, water TP and TN were selected accordingly to reduce multicollinearity and based on their contributions to the first two Principal Components (Figs 2 and S1). *Microcystis* biomass was also selected due to the importance of Cyanobacteria blooms in the Taihu basin. Taxonomic richness and Shannon-Wiener index were calculated as representative indices to describe the variation of macroinvertebrate community.

The response of sediment and water nutrients, *Microcystis*, and macroinvertebrate community indices in the three areas across time were assessed by fitting generalized linear mixed models (GLMMs): with a Gamma distribution (log link) for sediment TP and Carbon, water TP and TN. Similarly, GLMMs were developed for macroinvertebrate biomass (Gaussian distribution with log link), richness (negative binomial distribution, Poisson family, log link), and *Microcystis* biomass (Gaussian family, log link). Shannon diversity of macroinvertebrates was not analysed further as it was significant positively correlated with richness. Time (continuous) and treatment (categorical) were included as fixed effects, and “LakeID/Treatment” was considered as a nested random effect for all models to account for replication within the same monitoring area. Interaction effects between time and treatment were included in all models. For the *Microcystis* biomass model, water TP, TN and sediment carbon were also added as fixed effects. *Microcystis* biomass were added 1 to deal with zero values before $\log_{10}$ transformation, and macroinvertebrate biomass were square root transformed + 1, to constrain the influence of extreme values. Time was introduced as a

quadratic term to account for non-linear responses to treatments over time. For each model, the most parsimonious model was selected based on Akaike's Information Criterion (AIC) scores (< 2 AIC units). For example, we had added “time * treatment * lake ID” as fixed term into all the models, while lake ID was deleted from the fixed term finally because no significant difference were detected, Model residuals were tested for compliance with model assumptions (Crawley, 2002).

Macroinvertebrate community structure in 2018 was further investigated to determine the long-term influence of the restoration treatments relative to Control. Variations of benthic macroinvertebrate community structure among treatments were visualized using non-metric multidimensional scaling (NMDS) based on the Bray–Curtis distance of Hellinger transformed density. Macroinvertebrate communities were then examined via the permutational homogeneity of dispersion (PERMDISP2) test for the analysis of multivariate homogeneity of group dispersions (variances); a multivariate analogue of Levene's test for homogeneity of variances (Anderson, 2006). Permutational multivariate analysis of variance (PERMANOVA) and analysis of similarities (ANOSIM) were then performed for pair-wise comparisons of macroinvertebrate communities among treatments. Similarity percentage (SIMPER) analysis was used to identify which taxa contributed the most to the average Bray-Curtis dissimilarity between the groups detected by ANOSIM and SIMPER. Indicator species of the three treatments were determined via multi-level pattern analysis (De Cáceres et al., 2010) to look at the association between species patterns and treatment across lakes.

Finally, beta diversity (BD_{total}) of macroinvertebrates between treatments over time and among lakes was calculated and decomposed into species richness difference (RichDif) and species replacement (Repl), using the Podani family decomposition (Legendre, 2014) with presence-absence data ($BD_{total} = RichDif + Repl$).

All data analysis and figures were completed using relevant functions from packages ‘vegan’ (Dixon, 2003), ‘indicspecies’ (De Cáceres et al., 2010), and ‘adespatial’ (Dray et al., 2017) in R v 4.0.1 (R Core Team 2020, <https://www.R-project.org/>). Temporal trends of beta diversity partitions for each treatment and lake were examined with the ‘ggplot2’ package (Wickham et al., 2016) using a loess smoother.

3 Results

3.1 Sediment and water chemistry

The PCA biplot (Fig. 3) and Spearman rank correlation analysis showed weak but significant positive correlation between sediment TP and Al-P ($\rho = 0.39$, $p < 0.001$). In contrast, sediment Carbon showed a much stronger positive correlation with TN ($\rho = 0.77$, $p < 0.001$). Furthermore, water TP was positively correlated with *Microcystis* cell density and biomass ($\rho = 0.52$, $p < 0.001$).

According to the results of GLMMs, both Dredged and Dredged with macrophytes were efficient at the initial reduction of sediment nutrients (Fig. 4a-b, Fig. S2, Table S2). Specifically, for Dredged areas, the concentrations of sediment TP and Carbon showed an initial period of rapid decline (2009-2012), then levelled off or even slightly increased during 2012-2018. Compared to Dredged areas, Dredged with macrophytes areas had similar trends (decreased first then increased slowly) over time, however Dredged with macrophytes areas tended to accumulated more nutrients in sediment, particularly Carbon. While for Control, the concentrations of Carbon decreased over the entire monitored period, TP initially increased then decreased after 2012 with an opposite pattern compared to Dredged or Dredged with macrophytes areas (Fig. 4a-b).

Although Dredged with macrophytes areas had significantly higher water TP concentrations than Dredged areas during the first few years after dredging and transplantation of macrophytes, Dredged with macrophytes areas showed lower water TP concentrations (0.04 ± 0.03 mg/L) than Dredged areas (0.05 ± 0.04 mg/L) in 2018, while water TP concentrations were 0.05 ± 0.07 pre-dredging for both Dredged and Dredged with macrophytes areas. Water TP concentrations of Dredged with macrophytes and Dredged areas therefore followed opposite trajectories over time, whereby Dredged with macrophytes areas initially increased then decreased, while Dredged areas first decreased then increased (Fig. 4c). Interestingly, in contrast to the overall trend of other nutrients, water TN concentrations increased over time for all treatments. Control areas continued to have lower TN values than the two dredged treatments (Dredged and Dredged with macrophytes) (Fig. 4d).

3.2 *Microcystis*

Spearman rank correlation analysis showed strong and significant positive correlation between *Microcystis* cell density and *Microcystis* biomass ($\rho = 0.89$, $p < 0.001$, respectively). The biomass of *Microcystis* decreased consistently over the duration of the monitored period in areas subjected to dredging only (Fig. 5a, Table S2, Fig. S3). This effect was not observed in Dredged with macrophytes areas, where the biomass of *Microcystis* was significantly higher than Dredged areas and did not show significant difference compared to Control areas over the period of our monitoring (Fig. 5a).

3.3 Benthic macroinvertebrates

The biomass and richness of macroinvertebrates decreased quickly after dredging (2009), particularly in areas which did not receive post-dredging transplantation of macrophytes (Dredged areas), but then started to increase after about 2014 for both Dredged and Dredged with macrophytes treatments (Fig. 5b-c, Table S2). Compared to Control, Dredged areas attained similar biomass and richness by the end of the monitoring (restored to pre-dredged community levels), while these indices were much higher than Control at Dredged with macrophytes; in particular, the richness indices almost doubled (Fig. 5b-c).

Macroinvertebrate community composition in 2018 showed clear differences between Dredged with macrophytes and Dredged, as well as Dredged with macrophytes and Control in the NMDS biplot (Fig. 6). These significant differences were confirmed by the results from ANOSIM and PERMANOVA (Table S3). No significant difference was detected between Dredged with macrophytes and Control. However, the p value of SIMPER results for the eight species contributing most to overall variation between Dredged and Dredged with macrophytes, Dredged with macrophytes and Control (cumulative contribution >60%), were > 0.05 (Table S4). Multi-level pattern analysis revealed three chironomids (*Microchironomus tabarui*, *Clinotanypus* sp., *Glyptotendipes* sp.) and one mussel (*Unio douglasiae*) to be associated strongly with Dredged with macrophytes in 2018 ($p < 0.05$). Additionally, the mussel *Anodonta woodiana* was associated strongly with both Dredged and Dredged with macrophytes ($p < 0.05$). Macroinvertebrate community variation of Dredged areas was significantly higher than Dredged with macrophytes areas in 2018 (Fig. S4 a). Similarly, Dredged with macrophytes areas showed significantly higher Shannon diversity and species

richness, while no considerable difference between Dredged and Control was detected (Fig. S4 b-c).

The higher beta diversity between Dredged and Dredged with macrophytes after 2014 in Lake Dongjiu and Lake Xijiu was mainly due to the higher species richness difference. Total beta diversity between Dredged and Control was similar over time, but with different variations of species replacement and richness differences among lakes. For example, species replacement of Lake Gehu and Lake Yangcheng increased and then decreased after 2014, while the other three lakes decreased first and then generally increased since 2012. This phenomenon was not obvious between Dredged with macrophytes and Control. (Fig. 7)

4 Discussion

4.1 Sediment and water chemistry

Our long-term (2008-2018) in-situ field investigation confirmed that both Dredged and Dredged with macrophytes were efficient in decreasing of sediment nutrients (nitrogen, phosphorus, carbon) immediately after dredging, while areas Dredged with macrophytes tended to retain more nutrients in the sediment. However, the decreasing trend was lost after approximately five years post-dredging, becoming similar to Control by 2018. This indicates that, to have a long-lasting effect, dredging as a restoration tool should be applied every few years unless sources of pollution to freshwaters are also reduced. Liu et al. (2016) reported that environmental dredging reduced internal nitrogen and phosphorus loading for no more than three years if external pollution sources were not decreased. Clearly, external nutrient loadings were not eliminated within the Lake Taihu basin, although some restoration projects focusing on external nutrient reductions, such as sewage treatment inputs and the planting of

riparian buffer strips, were performed during the study period (Fu et al., 2021). This could have contributed to the decreasing trend of sediment TP and Carbon observed in Control, not just for Dredged and Dredged with macrophytes. On the other hand, Dredged with macrophytes improved water quality more than dredging only in the long run, especially for water TP. Even though water TP concentrations of Dredged with macrophytes and Dredged followed opposite trajectories over time. These findings are largely supported by Bai et al. (2020), who concluded that submerged macrophyte communities can govern water nutrients (TN, $\text{NH}_4^+\text{-N}$, TP), but enhance nutrient concentrations (TN, TP, organic matter) in sediment by decomposition.

Unlike previous studies (Bai et al., 2020), in our monitoring study, both Dredged and Dredged with macrophytes did not improve water TN. Compared to Control, Dredged and Dredged with macrophytes areas were exposed to more anthropogenic disturbances by being located close to a park or commercial public buildings. Additional reasons for this phenomenon could be that Dredged and Dredged with macrophytes areas were too small in each lake to modify the water quality at the lake level. In particular, surface runoff after rainfall events on August and September in the Taihu basin often carry high TN concentrations (ranging from 1.2 - 2.83 mg/L) from diffuse pollution sources (Li et al., 2017). This in line with the finding that even though the water quality at in the Taihu basin has, in general, improved over the last decade, water TN concentrations still exceed 2 mg/L (Qin et al., 2019).

4.2 *Microcystis*

Transplantation of submerged macrophytes immediately after dredging (one to two months) did not decrease *Microcystis* biomass. This contrasts with previous studies which demonstrated that restored submerged macrophytes could inhibit phytoplankton growth and decrease the risk of algal blooms (Zeng et al., 2017). Specifically, in our

study, *Microcystis* biomass in Dredged with macrophytes areas showed no difference to Control by the end of our monitoring (2010-2018). Biomass of *Microcystis* showed strong positive relationships with TP concentrations of water in our study, which is consistent with the findings in Lake Taihu from 2005 to 2014 by Su et al. (2015), suggesting phosphorus limitation of *Microcystis* growth. Even though Dredged with macrophytes areas showed a tendency to have lower water TP concentrations compared to Dredged in 2018, water TP concentrations in Dredged with macrophytes areas first increased after transplantation of macrophytes post-dredging, then decreased after 2012 but always higher or similar with Dredged areas later. Further, compared to dredging only, transplantation of submerged macrophytes may have improved water clarity and lifted the light limitation of *Microcystis* (Brookes and Ganf, 2001).

A series of indirect effects could also account for the higher *Microcystis* biomass in Dredged with macrophytes areas. For example, compared to Dredged, Dredged with macrophytes usually located in bays less exposed to the influence of waves and with relatively lower depth of water, to provide a more suitable environment for the living of submerged macrophytes (Dong et al., 2017). *Microcystis* can aggregate and form blooms on the water surface which are then pushed by wind-generated waves. Thus, lake edges or bays can typically function as accumulation zones from the open lake area (Tan et al., 2009). In addition, it is likely that a proportion of the newly transplanted submerged macrophytes had failed to establish at the beginning, leading to decomposition and additional P inputs (Min et al., 2019). However, the survival ratio of transplanted submerged macrophytes was not recorded in this study. The area of submerged macrophytes transplantation in each lake could have also been too small to have any immediate effect. The reestablishment of submerged macrophyte communities in these lakes will require more time to have the ability to compete with algae such as

Microcystis. However, our results do demonstrate that dredging as a disturbance could be useful to mitigate cyanobacterial blooms (Wan et al., 2021), as Dredged areas showed continuous reductions of *Microcystis* biomass when compared to Control.

4.3 Benthic macroinvertebrates

Compared to dredging only, Dredged with macrophytes was shown to considerably improve benthic macroinvertebrates biomass and diversity recovery. Specifically, compared to Control, Dredged areas just attained similar abundance and richness by the end of our monitoring (2018), while the biomass of macroinvertebrate at Dredged with macrophytes areas was much higher than Control, and richness almost doubled. Biomass and richness of macroinvertebrates in Dredged with macrophytes areas were always higher than Dredged after transplantation of macrophytes post-dredging. Notably, the biomass and richness of macroinvertebrates in Dredged with macrophytes areas were significantly higher than Control until 2018 and 2016, respectively. This implies a prolonged period of recovery after dredging even with macrophyte transplantations, most likely due to organism dispersal limitations restricting colonization of restored habitats. A possible explanation for the eventually higher biomass and richness is that submerged macrophyte beds provide refuge against predation (e.g. fish) due to extensive plant substrate, with plants also supporting species with a wider range of ecological habitat needs (Walker et al., 2013).

The composition of benthic macroinvertebrate communities differed significantly between Dredged and Dredged with macrophytes, Dredged with macrophytes and Control at the end of the monitoring in 2018. Specifically, IndicSpecies analysis revealed three species of chironomids (*Microchironomus tabarui*, *Clinotanypus* sp., *Glyptotendipes* sp.) and one mussel (*Unio douglasiae*) were strongly associated with Dredged with macrophytes areas in 2018. This reflects that strong association of

chironomids with submerged macrophyte communities (Grzybkowska et al., 2020) as they provide important niches and protection from predators (van Oosterhout et al., 2020). This also highlights the success of macrophytes transplantation in Dredged with macrophytes areas, as the chironomids are submerged macrophyte associated taxa (Brodersen et al., 2001). Additionally, a bivalve mussel (*Anodonta woodiana*) was highly associated with both Dredged and Dredged with macrophytes ($p < 0.05$). *Anodonta woodiana* is a native and common filter-feeding mussel across the Taihu basin (Bian et al., 2009), and often reintroduced as a part of efforts to restore eutrophic lakes as they can decrease the biomass of pelagic algae (Zhang et al., 2014).

The five lakes in our study can be categorized into two groups by the different variation trend of beta diversity partitions of macroinvertebrates across time between Dredged and Control: one group is Lake Gehu and Lake Yangcheng, the other is Lake Dongjiu, Lake Xijiu and Lake Shanghu (Fig. 7). Specifically, species replacement of Lake Gehu and Lake Yangcheng between Dredged and Control: first increased then decreased after 2014, while species replacement of the other three lakes first decreased then gradually increased since 2012. Possible reasons could be that compared to other three lakes, Lake Gehu and Lake Yangcheng with significantly larger water surface area and higher environmental heterogeneity, resulting in high beta diversity driven by species turnover (López - Delgado et al., 2020).

4.3 Implications for aquatic ecosystem management

Our long-term in-situ monitoring study demonstrates that partial restorations (such as dredging and transplantation of macrophyte) without separation at large lakes can have positive effects on the ecological environment recovery, although the effect could vanish over time where source pollutants are not controlled sufficiently. Specifically, dredging only can significantly decrease nutrients (nitrogen, phosphorus, carbon) in

sediment and water, but the effect can be lost approximately five years later. We confirmed that dredging only disturbance could decrease *Microcystis* biomass and cell density, while transplantation of submerged macrophytes shortly post-dredging could not decrease *Microcystis* biomass, although other lake characteristics could not be ruled out. Our results suggest that lake managers should always consider submerged macrophyte transplantation, as multiple benefits can accrue via significant decreases in nutrient concentrations plus the recovery of benthic macroinvertebrate communities destroyed by dredging.

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Figure legends

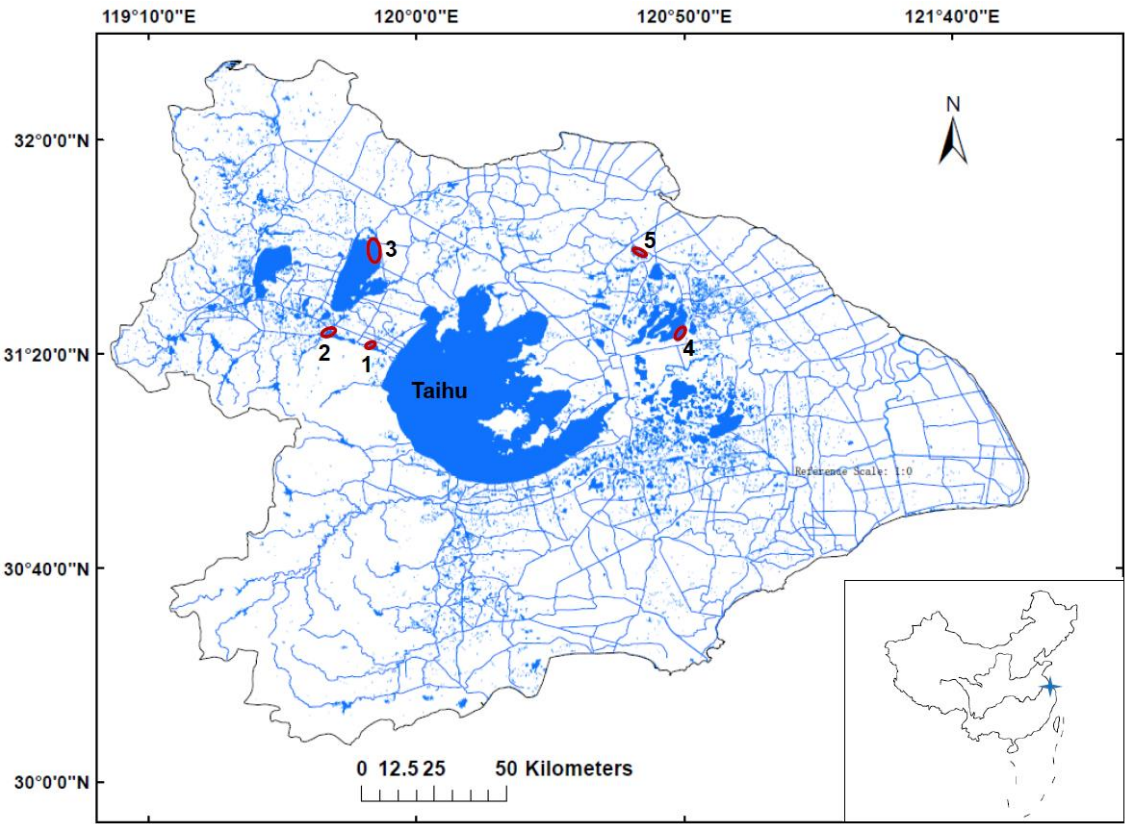
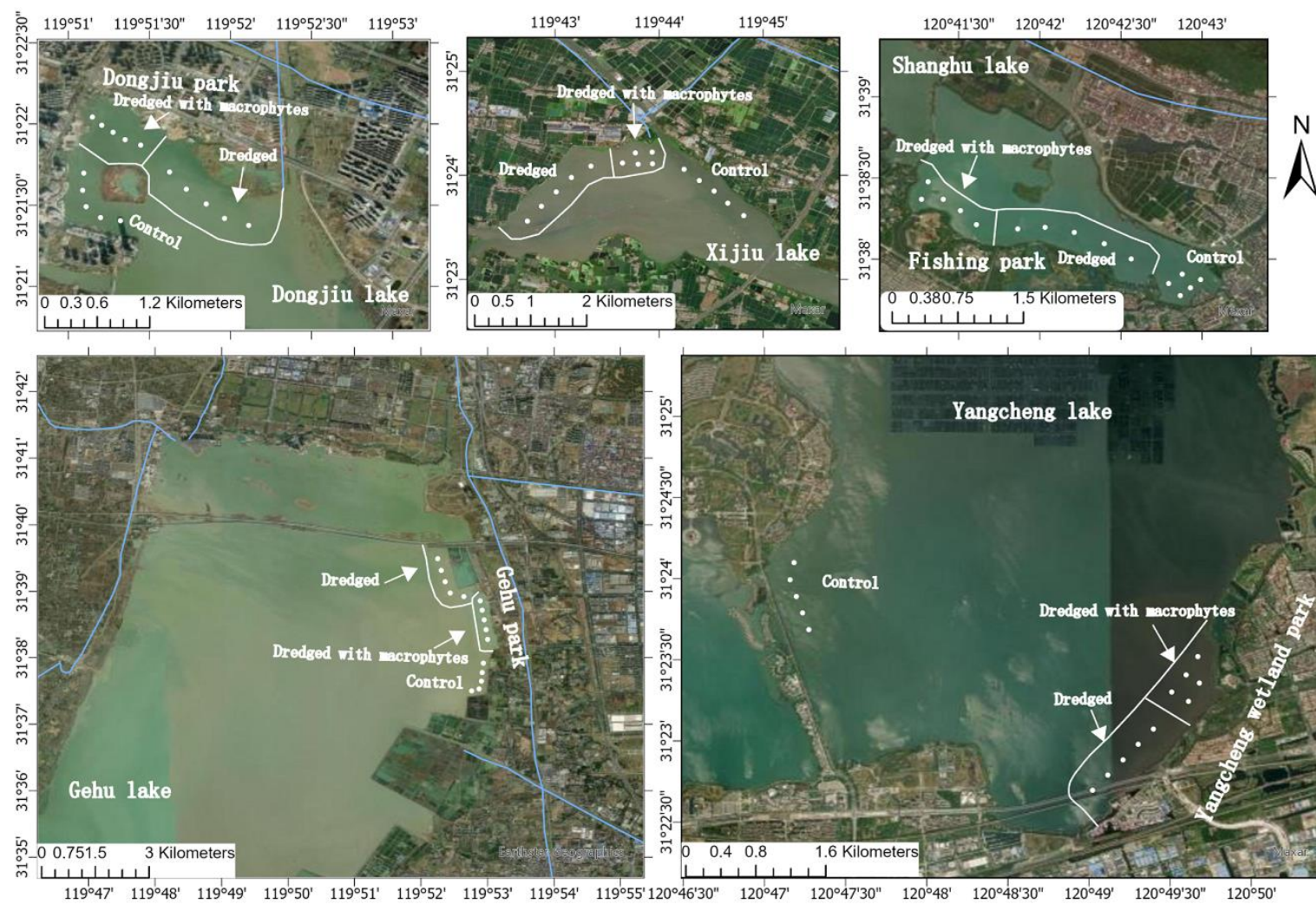


Fig. 1. General location of study area in each lake (shown in red circle), in relation to its location in China (inset panel). Lakes 1, Dongjiu; 2, Xijiu; 3, Gehu; 4, Yangcheng; 5, Shanghu.



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623 Fig. 2. Sketched spatial structure of three treatments and sampling sites (shown in white point) in each lake.

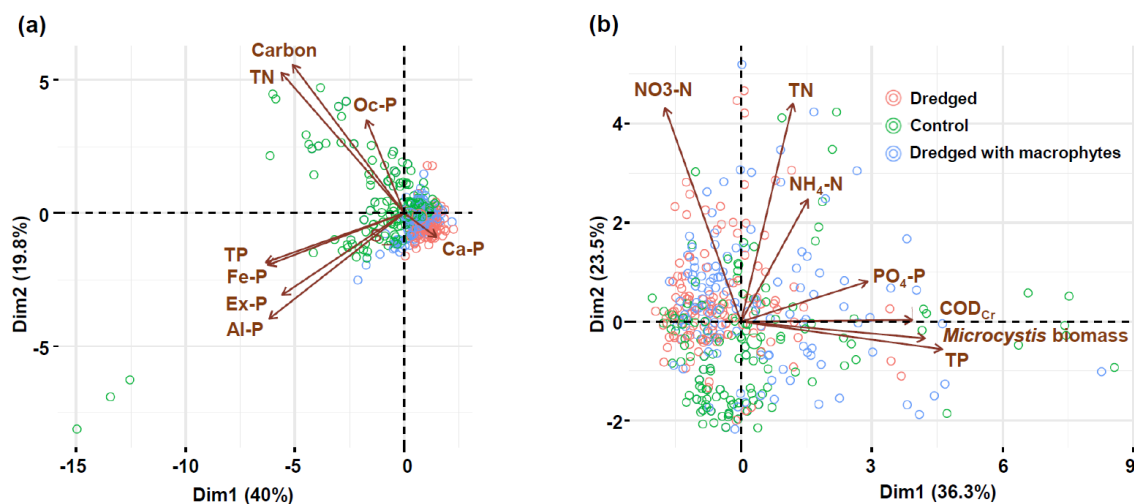


Fig. 3. The principal component analysis (PCA) first two dimensions biplot of (a) sediment indices and (b) water quality indices. The length of the arrows is proportional to the loading score of the variable on each principal component.

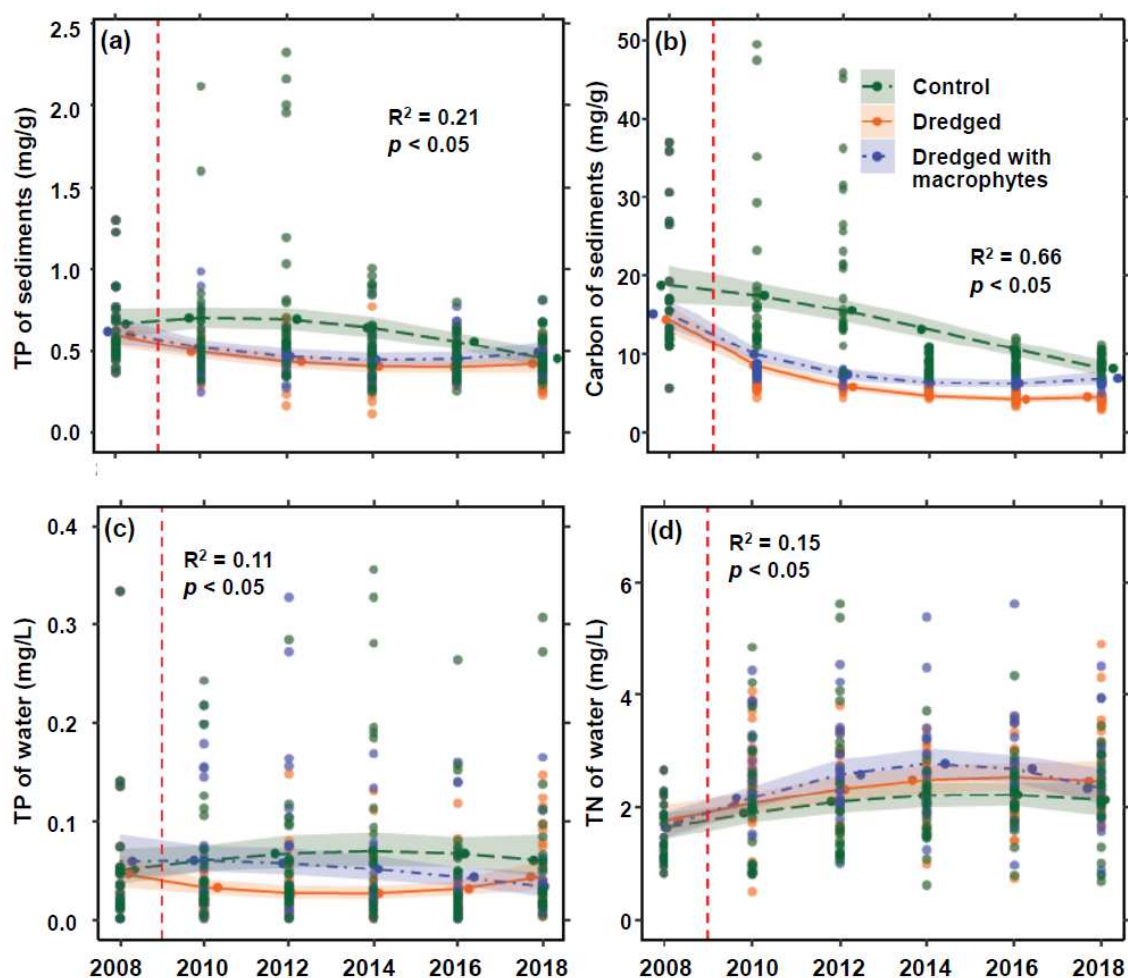


Fig. 4. Marginal effects of the indices of (a, b) sediment and (c, d) water nutrients over the monitored years. Red dashed lines denote the year of the dredging intervention and subsequent transplantation of submerged macrophytes.

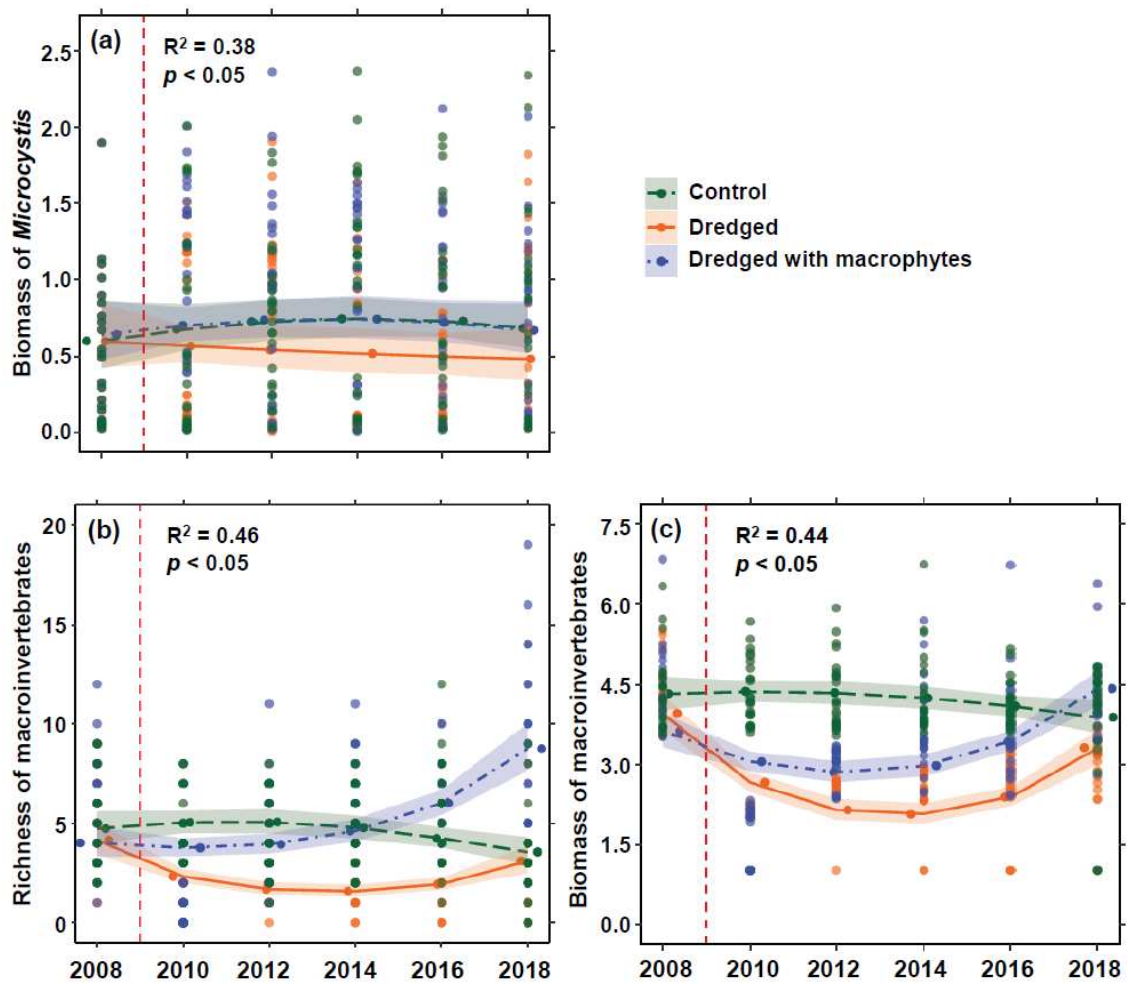


Fig. 5. Marginal effects of (a) *Microcystis* biomass and (b, c) benthic macroinvertebrate communities over the monitored years. The red dashed lines denote the year of the dredging intervention and subsequent transplantation of submerged macrophytes.

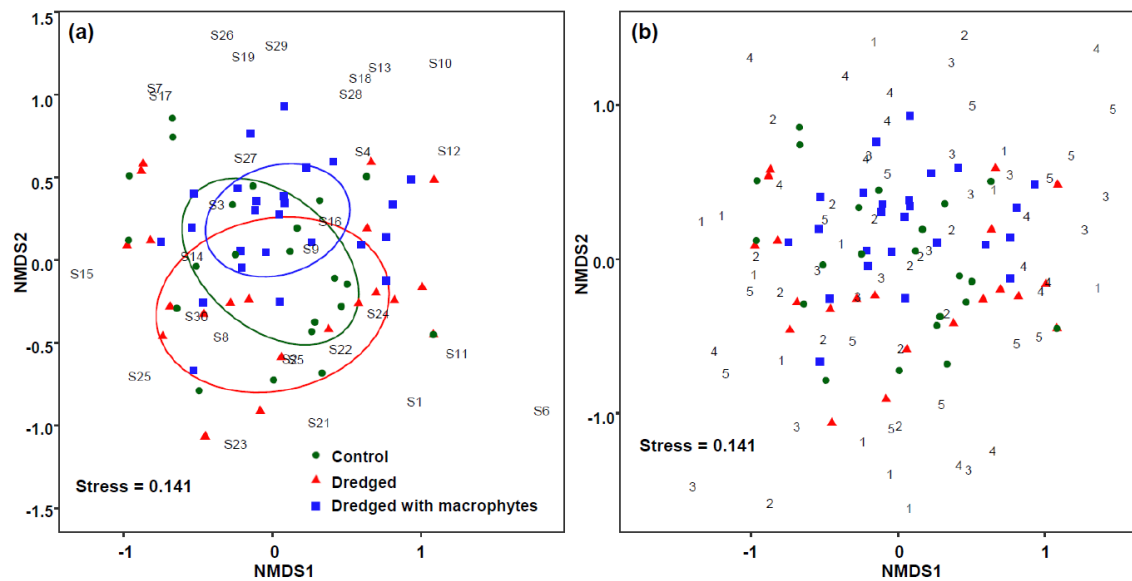


Fig. 6. Non-metric multidimensional scaling (NMDS) biplots of benthic macroinvertebrate communities in the three treatments (Dredged, Dredged macrophytes, Control) in 2018, with indication of (a) the individual taxa (denoted by S, show 50% ellipses) and (b) investigated five lakes (1, Dongjiu; 2, Xijiu; 3, Gehu; 4, Yangcheng; 5, Shanghu). Abbreviations for species name see Table S5.

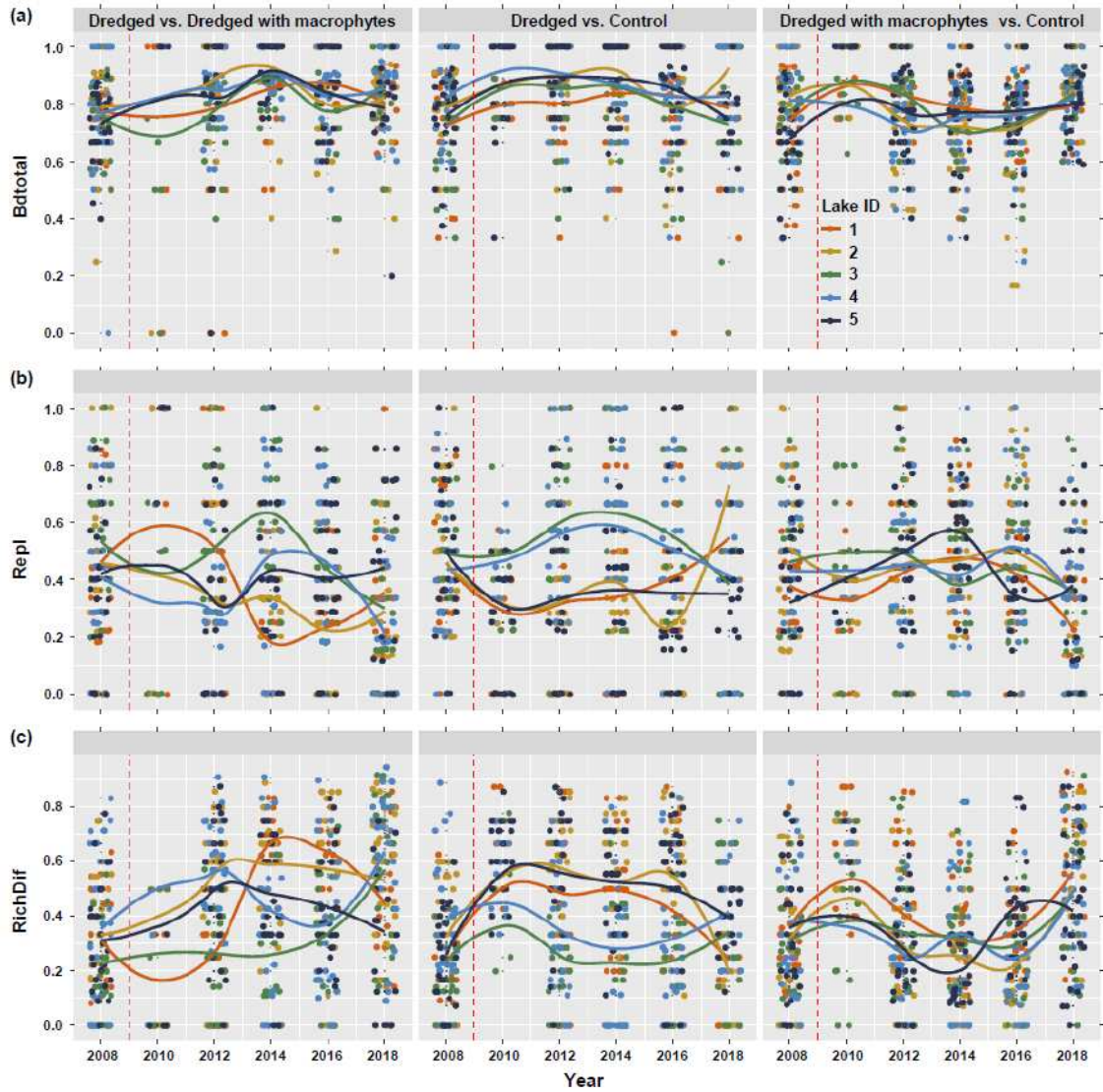


Fig. 7. Temporal variation of beta diversity components for macroinvertebrates between different treatments from 2008-2018. Red dashed line denotes dredging intervention and submerged macrophytes transplantation post dredging. $BD_{total} = RichDif + Repl$, BD_{total} , total beta diversity; $Repl$, replacement; $RichDif$, species richness difference. Lake ID: 1, Dongjiu; 2, Xijiu; 3, Gehu; 4, Yangcheng; 5, Shanghu.

Table legends

Table 1. Contextual information for the five lakes. Longitude and latitude represent the center location of the entire monitored area in each lake.

No.	Lake name	Longitude	Latitude	Mean water depth (m)	Surface water area (km ²)	Dredging area (km ²)	Planting area (km ²)
1	Dongjiu	119°51′	31°21′	1.85	8	1.5	0.5
2	Xijiu	119°43′	31°24′	1.79	12.4	2.0	0.5
3	Gehu	119°52′	31°39′	1.27	160	1.5	0.5
4	Yangcheng	120°49′	31°22′	1.8	119.8	1.0	0.4
5	Shanghu	120°41′	31°38′	2.8	8.2	0.9	0.3