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RESEARCH ARTICLE

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Eutrophication modifies the relationships between multiple facets of macroinvertebrate beta diversity and geographic distance in freshwater lakes

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Abstract

Aim: Understanding the distance–decay relationship (DDR) has been considered important because it reflects a combination of several ecological processes such as dispersal limitation and environmental sorting. However, effects of human disturbances on DDR are poorly known, especially in freshwater lakes. This study is aimed to examine how anthropogenic eutrophication modified the relationships between three facets (taxonomic, functional and phylogenetic) of macroinvertebrate beta diversity and geographic and environmental distances across 30 freshwater lakes.

Location: The Yangtze River floodplain, China.

Methods: We used Mantel tests to examine the relationships between multiple facets of assemblage dissimilarities (overall beta diversity, replacement and richness difference components) and geographic and environmental distances. Distance-based redundancy analysis (dbRDA) and associated variation partitioning procedures were applied to explore the relative contributions of environmental and spatial factors on the three facets of beta diversity.

Results: We found that none of the three beta diversity facets was related to geographic distance, but all were significantly related to environmental distance, mainly mirroring eutrophication-related variables. Based on the variation partitioning approach, the macroinvertebrate assemblages examined were almost exclusively structured by environmental factors associated with eutrophication, while spatial variables had a negligible effect. Nevertheless, the different facets of beta diversity did not decrease (i.e., no homogenization trend) in lake groups showing the highest eutrophication levels, implying complex influences of anthropogenic disturbances in driving homogenization or differentiation in assemblage compositional dissimilarity.

Main Conclusions: Our findings suggested that the high degrees of eutrophication acted as an environmental filter to significantly modify the spatial distance–decay relationships, possibly via decreasing the importance of dispersal limitation in shaping macroinvertebrate assemblages in the studied lakes. Given the sensitivity of beta

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diversity patterns to eutrophication we found in this study, we recommend that the role of anthropogenic disturbances should be incorporated into research on general ecological patterns like the DDR.

KEYWORDS
environmental filtering, eutrophic distance, geographic distance, macroinvertebrates, multiple diversity facets, nutrient enrichment

1 | INTRODUCTION

Anthropogenic eutrophication caused by nutrient enrichment (through increasing inputs of nitrogen and phosphorus to ecosystems) has led to serious and widespread environmental degradation across the world (Rosset et al., 2014; Sala et al., 2000; Smith et al., 1999). Eutrophication is among the most severe threats to biodiversity and ecosystem functioning in aquatic environments, particularly in freshwater lakes (Donohue et al., 2009; Heino et al., 2021; Menezes et al., 2015). Anthropogenic eutrophication is generally associated with harmful algal blooms, oxygen depletion, habitat loss and substantial ecological degradation of ecosystem processes (Glibert & Burford, 2017; Schindler & Vallentyne, 2008). Not surprisingly, eutrophication may dramatically alter the community composition of various aquatic organisms, including bacteria, diatoms, zooplankton, macroinvertebrates and fishes, from local (alpha diversity) to regional scales (beta diversity) (Donohue et al., 2009; Ger et al., 2016; Li et al., 2022; Menezes et al., 2015; Zorzal-Almeida et al., 2021; Zuo et al., 2024).

In freshwater lentic ecosystems, empirical studies have consistently shown the detrimental effects of eutrophication on species richness and taxonomic beta diversity through a series of ecological processes, including decreasing habitat area and environmental heterogeneity. These changes have resulted in diminished regional species pools, disappearance of sensitive species, and increases in the prevalence of pollution-tolerant species (Chase, 2010; Donohue et al., 2009; Lougheed et al., 2008). However, limited attention has been given to other aspects of biodiversity (Jiang et al., 2022; Zhang, Cheng, Kong, et al., 2019), especially concerning multiple facets of beta diversity (Alahuhta et al., 2019; Zhang, Cheng, Li, et al., 2019). Interest in the functional and phylogenetic facets of beta diversity has been increasing in recent decades, because they may have distinct advantages over taxonomic approach (Heino & Tolonen, 2017a; Saito et al., 2015; Sobral et al., 2016) and provide important information complementing taxonomic diversity (Dross et al., 2017; Qin et al., 2016). For instance, functional diversity measures are assumed to be more strongly related to environmental gradients and thus should respond more directly to environmental stressors compared to taxonomic diversity measures (Diaz & Cabido, 2001; Villéger et al., 2008, 2017). Phylogenetic diversity indices are expected to reflect the imprints of evolutionary history on ecological communities as they measure the evolutionary relationships among species within communities (Graham & Fine, 2008; Morlon et al., 2011; Webb, 2000). Functional and phylogenetic diversity have been frequently evaluated at the alpha diversity level (Heino & Tolonen, 2017b; Villéger et al., 2008; Webb et al., 2002), whereas our current understanding of functional and phylogenetic beta diversity is still relatively limited (Graco-Roza et al., 2022; Heino & Tolonen, 2017a; Jiang et al., 2021; Rocha et al., 2019). Evaluating the responses of functional and phylogenetic beta diversity to eutrophication and other anthropogenic disturbances can potentially advance our understanding of how environmental stressors impact community assembly and ecosystem functioning.

Measuring the decay in the between-community similarity along spatial or environmental distance (i.e., increasing assemblage dissimilarity with increasing distance) is a common approach to examine beta diversity (Nekola & White, 1999; Soininen et al., 2007). This distance–decay relationship (DDR) provides a robust descriptor of biodiversity distributions, as it reflects a combination of several ecological processes (e.g., dispersal limitation and environmental sorting) (Nekola & White, 1999). Examining and understanding such relationships can provide important implications for biodiversity management and conservation. Although many researchers have recognized that the distance–decay relationship may vary depending on specific ecological circumstances, only a few studies have evaluated the effects of eutrophication on the distance–decay relationship (Dai et al., 2017). Such studies are largely lacking in freshwater lentic ecosystems, being limited to microorganisms (Marquardt et al., 2017; Vilar et al., 2014). These studies highlight that eutrophication can significantly modify the distance–decay relationships of diatoms via attenuating the decay rates of assemblage similarity along geographic distance. For larger aquatic organisms, such as invertebrates and fish, there are no studies examining how eutrophication affects distance–decay relationships.

Benthic macroinvertebrates are a widespread and ecologically important group in aquatic ecosystems. Macroinvertebrates encompass a diverse range of taxonomic groups and functional traits and are widely employed as indicators of aquatic ecosystem conditions because of their sensitivity to anthropogenic stressors (Heino & Tolonen, 2017a; Morse et al., 2007). Numerous studies have shown the significant impacts of eutrophication on taxonomic, functional and phylogenetic structures of benthic macroinvertebrates (Ji et al., 2020; Jiang et al., 2019, 2022). Using data on lake macroinvertebrate assemblages, we examined how taxonomic, functional and phylogenetic facets of beta diversity and their components (overall dissimilarity, replacement and richness

components) varied along geographical and environmental distances among 30 freshwater lakes in the middle and lower reaches of the Yangtze River. These lakes have suffered from different environmental stressors (e.g., river–lake disconnection, water pollution and resource overexploitation) since the 1950s and show a distinct eutrophication gradient (from mesotrophic to strongly eutrophic lakes) (Le et al., 2010; Wang et al., 2014). Here, we (1) tested whether long-term eutrophication has modified the relationships between three facets of beta diversity and geographic or environmental distances and (2) estimated the degree to which environmental variables and spatial variables shape compositional heterogeneity in macroinvertebrate assemblage structure. Specifically, we proposed the following hypotheses: (1) eutrophication would significantly interfere the DDRs and result in the multifaceted beta diversity in the studied lakes being primarily structured by eutrophication-related environmental variables rather than spatial distance. (2) Similarly, due to the distinct eutrophication gradient, the relative importance of environmental factors would outweigh spatial factors on assemblage dissimilarities. (3) There would be homogenization of macroinvertebrate assemblages along eutrophication, measured based on different diversity facets, i.e., multiple facets of beta diversity decrease with increasing eutrophication.

2 | MATERIALS AND METHODS

2.1 | Study area and lake classifications

The macroinvertebrate and environmental datasets in the 30 lakes came from our previous publication (Jiang et al., 2022) in the Yangtze River floodplain. These lakes cover a narrow latitudinal range of 28°32′ to 31°28′ N and a wider longitudinal range of 111°51′ to 121°51′ E. The lake area ranges from 0.25 to 348.2 km^2 (on average 59.29 km^2). The 30 lakes were all disconnected (we excluded three connected lakes existing in previous publication) from the Yangtze River main stem by dams and sluice gates in the period from 1950s to1970s (Liu & Wang, 2010). Thereafter, these lakes have suffered from different levels of human disturbances (e.g., increased inputs of nutrients and pollutants, agricultural expansion, overfishing, pen culture in lake), resulting in a distinct eutrophication gradient (from mesotrophic, macrophyte-dominated state to a eutrophic, algae-dominated state) across these lakes (Jiang et al., 2022; Wang et al., 2014; Wang & Dou, 1998). The number of sampling sites ranged from 3 to 31 among the 30 lakes and was proportionable to the log-transformed lake area ($R^2 = .784$, $p < .001$, Figure S1).

We categorized the 30 lakes into three groups (macrophyte-dominated, macrophyte-algae transition and algae-dominated), using a disturbance score related to eutrophication, which was derived from measurements of aquatic vegetation coverage, total phosphate (TP) concentration and chlorophyll a (Chl *a*) (Table S1, see also Jiang et al., 2022). The classification of lakes resulted in 10 being macrophyte-dominated, 9 being macrophyte-algae transition and 11 being algae-dominated (Table S2).

2.2 | Macroinvertebrate sampling and environmental variable measurements

The macroinvertebrates sampling and environmental measurements of the studied lakes were carried out during the period of 1993 to 2010. At each lake, seasonal investigations were conducted across the entire lake area for a duration of one year. For macroinvertebrates, a modified Petersen grab (1/16 m^2) was used to take three quantitative bottom samples at each site of each investigation. The macroinvertebrates were sieved with a 500-μm sieve, then manually sorted from sediment and preserved in 10% formalin solution. In the laboratory, the macroinvertebrate specimen were identified to lowest possible taxonomic levels, typically genus and species.

Furthermore, we measured several environmental variables concurrently with the macroinvertebrate sampling. First, we measured water depth (in centimetres), transparency (in centimetres using a Secchi disk), and aquatic vegetation coverage (%, using 1 m × 1 m grid and the percentage was estimated into 11 levels, i.e., 0: 0%, 1: 1%–10% and 11: 91%–100%, based on a subdivided frame) at each site in the field. Then, water samples were obtained from each site for laboratory analysis within the following 24 h. The collected samples were used to measure pH, conductivity (μs/cm), chlorophyll *a* (Chl *a*, mg/L), permanganate index (COD_{Mn}, mg/L), ammonium nitrogen (NH_4-N, mg/L), nitrate nitrogen (NO_3-N, mg/L), total nitrogen (TN, mg/L), PO_4-P (mg/L) and total phosphorus (TP, mg/L). To represent the overall environmental characteristics of each lake, we calculated the average values of the environmental variables across all sampling occasions, encompassing all sites and sampling times sites within the lake. Finally, lake area of each lake were obtained following Wang and Dou (1998).

The field measurement of submerged vegetation coverage within 1 m × 1 m quadrats was conducted. In each quadrat, the coverage (C) was determined using a subdivided frame and 11 coverage levels (coverage rates of 10%), i.e., 0 (0%), 1 (1%–10%) and 11 (91%–100%).

2.3 | Calculation of three facets of beta diversity

Before calculating the beta diversity, a macroinvertebrate abundance dataset was compiled. The percentage of total macroinvertebrate density for each taxon was averaged across all sampling occasions, encompassing all sites and sampling times, for each lake. We used Sorensen dissimilarity index to represent taxonomic, functional and phylogenetic beta diversity of macroinvertebrate assemblages. Additionally, we decomposed each facet of beta diversity into its replacement (β_{repl}) and richness difference components (β_{rich})

(Cardoso et al., 2015). It has been long known that beta diversity can be attributed to two basic processes, i.e., the species turnover or replacement (linked to environmental filtering and spatial and historical constraints) and species richness differences (reflecting the non-random process of species loss or gain along environmental gradients) among assemblages (Harrison et al., 1992; Qian et al., 2005). The decomposition approach has strong implications for the understanding of biotic patterns and their causes and has gained increasing attention during recent decades (Cai et al., 2019; Cardoso et al., 2014; Heino & Tolonen, 2017a). There are two widely used approaches for partitioning beta diversity, namely POD framework (Podani & Schmera, 2011) and BAS framework (Baselga, 2010), and here we chose the POD framework because the BAS framework may lead to overestimated replacement component and underestimated richness difference component (Schmera et al., 2020).

First, we used the function "beta" in the R package BAT (Cardoso et al., 2015) to calculate the taxonomic dissimilarities based on lakes-by-species data. This allowed us to get overall dissimilarity (β_{total}) and its replacement (β_{repl}) and richness difference (β_{rich}) components.

Second, we selected 10 functional traits (i.e., maximal size, body form, exoskeleton, life habit, functional feeding group, respiration, dispersal ability, fertilization mode, oviposition mode and sexual maturity) for the calculation of functional beta diversity of macroinvertebrate assemblages (Table S3). To obtain the trait information for each taxon, we referred to relevant books (Brinkhurst, 1986; Liu et al., 1979; Morse et al., 1994), articles (e.g., Poff et al., 2006; Usseglio-Polatera et al., 2000) as well as an Internet database (MolluscaBase, 2021). Upon application of the BAT package, computations of functional and phylogenetic beta diversities are based on a tree structure (e.g., hclust or phylo object), necessitating the inclusion of the root path in the calculations. Therefore, before the calculation of functional dissimilarities, Gower distance was used to calculate inter-species trait distances with the function "gowdis" in package FD (Laliberté et al., 2014). Then, we used the "hclust" function in the package stats to produce a functional tree. Finally, using the lakes-by-species matrix and the functional tree in combination, we derived three functional dissimilarity matrices (i.e., functional β_{total}, β_{repl} and β_{rich}) similar to the taxonomic community dissimilarities between lakes.

Third, we utilized Linnaean taxonomic hierarchies as a surrogate for true phylogeny to calculate phylogenetic dissimilarities, because true phylogenetic information for macroinvertebrate species in the studied region was unavailable. Although taxonomic classification only reflects the evolutionary relationships among species to a certain extent, and thus may lead to an imprecise calculation of true phylogenetic diversity, this approach has been considered a reasonable approximation of true phylogenetic diversity when real phylogenetic information is lacking (e.g., Cai et al., 2019; Heino & Tolonen, 2017a; Jiang et al., 2021; Rocha et al., 2019). We employed six taxonomic levels in the present study, i.e., species, genus, family, order, class and phylum. Prior to calculating phylogenetic beta diversity, we constructed taxonomic distances between different species using the function "taxa2dist" in the package vegan. Afterwards, a hierarchical clustering procedure was used to produce the Linnaean taxonomic tree. Finally, the lakes-by-species matrix and the Linnaean taxonomic tree were used in combination for the calculation of phylogenetic dissimilarities between lakes.

We also calculated the three facets of multiple-site overall beta diversity and their replacement and richness difference components using the function "beta.multi" in the R package BAT. In this study, we calculated dissimilarity indices based on presence/absence data rather than abundance-based data, because using proportional abundance data would cause that abundance difference component cannot vary between sites (the summed abundance of taxa for each community is standardized to 100%). Furthermore, we used Bray-Curtis index to calculate the three facets of abundance-based overall beta diversity and found their values (Table S4), the relationships between overall dissimilarity and spatial and environmental distances (Figures S2 and S3) and the dbRDA results (Table S5) were quite similar to those based on presence/absence data.

2.4 | Data analysis

To assess the relationships between three facets of assemblage dissimilarities and geographic and environmental distances (for testing hypothesis 1), we conducted Mantel tests using Pearson's correlation coefficient. These tests involved 999 permutations to determine the statistical significance of the correlation (Nekola & White, 1999). The geographic distance between any two lakes was measured according to the overland (Euclidean) distance. Principal coordinates of neighbour matrices (PCNM) were explored to obtain spatial variables based on the between-lake Euclidean distance. Here, we generated 5 vectors of principal coordinates of neighbour matrices (PCNM) with positive eigenvalues to represent the spatial variables, using the "pcnm" function within the package *vegan* (PCNM, Borcard & Legendre, 2002). For environmental distance, we chose five water quality variables, i.e., TN, TP, Chl *a*, transparency and COD_{Mn} and standardized them to bring their mean value to 0 and standard deviation to 1, prior computing distance matrix based on Euclidean distance. These five variables were considered as important indicators of trophic status of freshwater lakes (Carlson, 1977). We also examined the relationships between dissimilarities and geographic and environmental distance for each lake group separately.

To explore the relative importance of environmental and spatial variables on three types of assemblage dissimilarities, we performed distance-based redundancy analysis (dbRDA) and associated variation partitioning procedures (Legendre & Legendre, 2012) (testing hypotheses 2 and 3). To select significant explanatory variables for each model of assemblage dissimilarities, we used the function "ordiR2step" and adopted forward selection procedure with 1000 permutations. Variation partitioning was applied to disentangle the unique and shared contributions of environmental and spatial

variables on assemblage dissimilarities. The dbRDA was conducted using the "dbrda" function, and the variation partitioning analysis was performed using the "varpart" function, both within the R package *vegan*. All analyses of this study were carried out in R (R Developement Core Team, 2022).

3 | RESULTS

3.1 | Variations in the three facets of beta diversity among studied lakes

Between-lake dissimilarities of macroinvertebrate assemblages differed considerably among different diversity facets (Table 1). Across all 30 lakes, the multiple-site overall taxonomic beta diversity (0.741) was equally contributed by the replacement (0.370) and richness difference (0.371) components. For the functional and phylogenetic dissimilarities, multiple-site overall beta diversity and its two components were all lower than their taxonomic counterparts, with mean values 0.368 for functional β_{total}, and 0.579 for phylogenetic β_{total}, respectively. Similar to taxonomic β_{total}, phylogenetic β_{total} also showed nearly balanced contributions of the replacement (0.267) and richness difference (0.311) components. Instead, functional β_{total} was mainly contributed by its richness difference (0.243) component, whereas replacement was less important (0.125) (Table 1).

For the three lake groups, we found that taxonomic and phylogenetic dissimilarities differed only slightly among different lake groups, although the algal-dominated lake group generally showed the highest values of β_{total} based on each of the three facets. The structure of three facets of beta diversity (relative contributions of replacement and richness difference components) was quite similar among different facets (Table 1).

3.2 | The relationships between dissimilarities and geographical and environmental distances

Examining the relationships between three facets of dissimilarities and two distance matrices, we found that none of the facets of beta diversity and their replacement and richness difference components correlated with geographic distance (Figure 1). In contrast, most of the dissimilarities were positively related to environmental distance (Figure 2). When examining such relationships for each lake group seperately, significantly positive correlations between assemblage dissimilarities and geographic distance were only observed in the macrophyte-dominated lakes, but not in the more disturbed macrophyte-algal transition and algal-dominated lakes (Figure S4). We also observed negative dissimilarity-geographic distance correlations for functional and phylogenetic β_{total} in algal-dominated lakes (Figure S4). Moreover, the relationships between assemblage dissimilarities and environmental distance were generally significant only in the group of macrophyte-algal transition lakes (Figure S5).

Forward selection indicated that different sets of environmental factors were significant predictors of the three facets of dissimilarities, whereas spatial variables were important in two dbRDA models only (taxonomic and functional β_{total}) (Table 2). The environmental variables related to the degree of eutrophication (e.g., nitrogen and phosphorus concentrations, Chl *a* and COD_{Mn}) were frequently identified as significant variables in affecting variation in the three facets of beta diversity (Table 2). According to the variation partitioning analysis, the total amount of explained variation ranged from 17.8% to 41.6% across the other dissimilarity matrices, being almost solely attributable to environmental variables. Even for the taxonomic and functional β_{total}, the variation explained by spatial variables was much less than that attributable to environmental variables (Figure 3).

TABLE 1 Taxonomic, phylogenetic and functional multiple-site overall beta diversity (β_{total}) and their respective replacement (β_{repl}) and richness difference (β_{rich}) components of macroinvertebrate assemblages in the studied lakes, calculated with the "beta.multi" function in the R package BAT.

	All lakes	Macrophyte-dominated	Macrophyte-algal	Algal-dominated
Taxonomic				
β_{total}	0.741 (100%)	0.694 (100%)	0.726 (100%)	0.733 (100%)
β_{repl}	0.370 (49.9%)	0.395 (56.9%)	0.354 (48.8%)	0.384 (52.4%)
β_{rich}	0.371 (50.1%)	0.299 (43.1%)	0.372 (51.2%)	0.349 (47.6%)
Functional				
β_{total}	0.368 (100%)	0.296 (100%)	0.336 (100%)	0.397 (100%)
β_{repl}	0.125 (34.0%)	0.118 (39.9%)	0.145 (43.2%)	0.145 (36.5%)
β_{rich}	0.243 (66.0%)	0.178 (60.1%)	0.191 (56.8%)	0.252 (63.5%)
Phylogenetic				
β_{total}	0.579 (100%)	0.535 (100%)	0.555 (100%)	0.569 (100%)
β_{repl}	0.267 (46.2%)	0.293 (54.8%)	0.271 (48.8%)	0.274 (48.2%)
β_{rich}	0.311 (53.8%)	0.242 (100%)	0.284 (51.2%)	0.295 (51.8%)

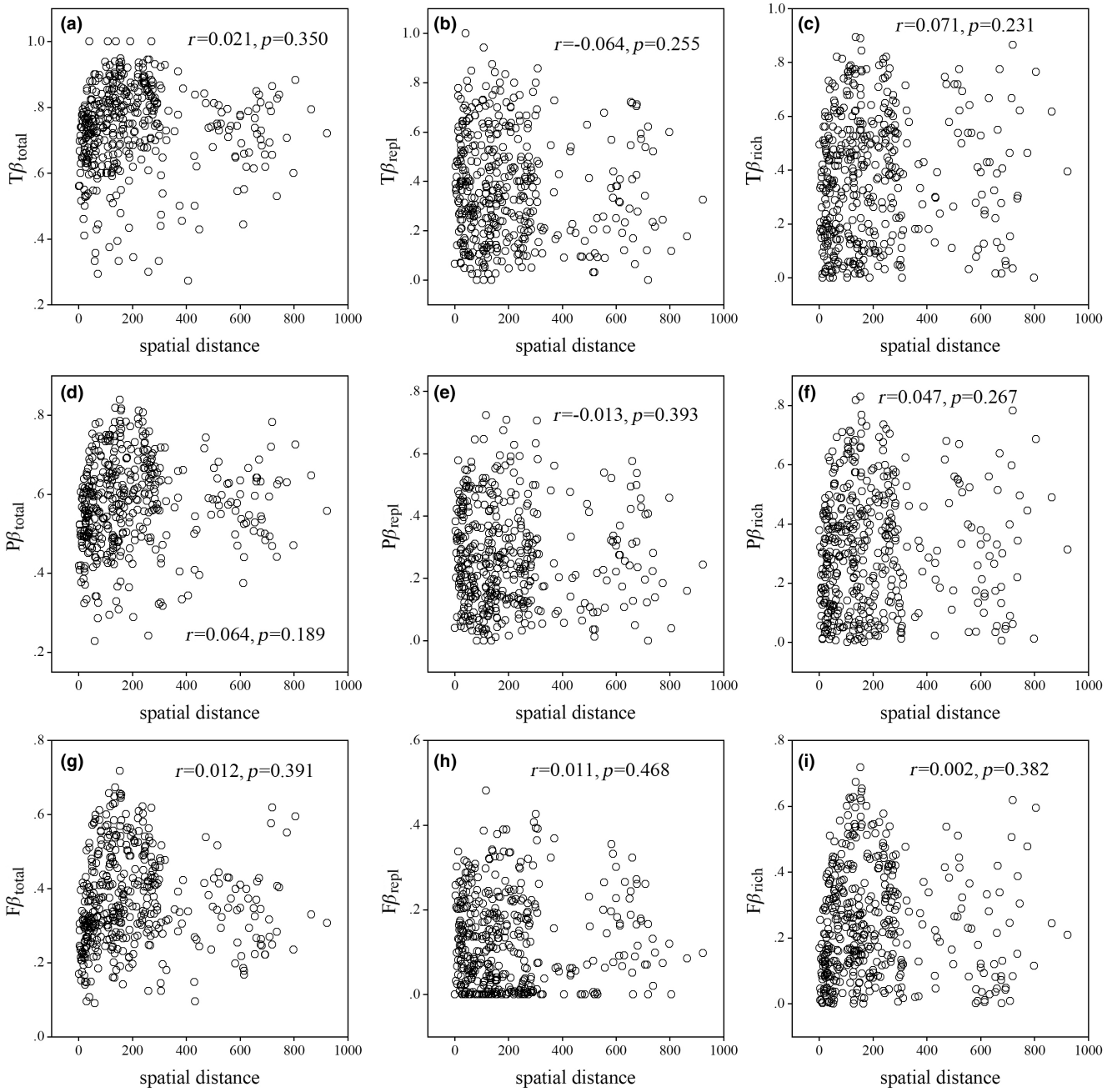

FIGURE 1 Relationship between taxonomic (a–c), phylogenetic (d–f) and functional (g–i) of dissimilarities and spatial distance (km) among the 30 studied lakes. The Pearson correlation (*r*) and significance (*p*-value) of Mantel tests are also provided in each panel.

4 | DISCUSSION

Our study showed that eutrophication exerted significant effects on the relationships between taxonomic, functional and phylogenetic beta diversity of macroinvertebrates and geographic distance in the studied lakes. In other words, we did not find any significant correlations between the three facets of assemblage dissimilarities and geographic distance but detected significant correlations only between assemblage dissimilarities and environmental distance associated with eutrophication. Such findings support our first hypothesis and indicate that anthropogenic eutrophication was so serious that it modified the assumed distance decay of similarity (or increasing dissimilarity along spatial distance), which is a widespread phenomenon found for various organism groups and ecosystems (Nekola & White, 1999; Qian & Ricklefs, 2012; Soininen et al., 2007). The analysis for the three individual lake groups also confirmed this assumption, however; the increase in dissimilarities along geographic distance only occurred in mesotrophic macrophyte-dominated lakes, but not in the more eutrophic transition and algal-dominated lakes (Figure S1). The significant impacts of eutrophication on the distance–decay relationships were expected, as increasing number of studies have shown that increasing eutrophication profoundly

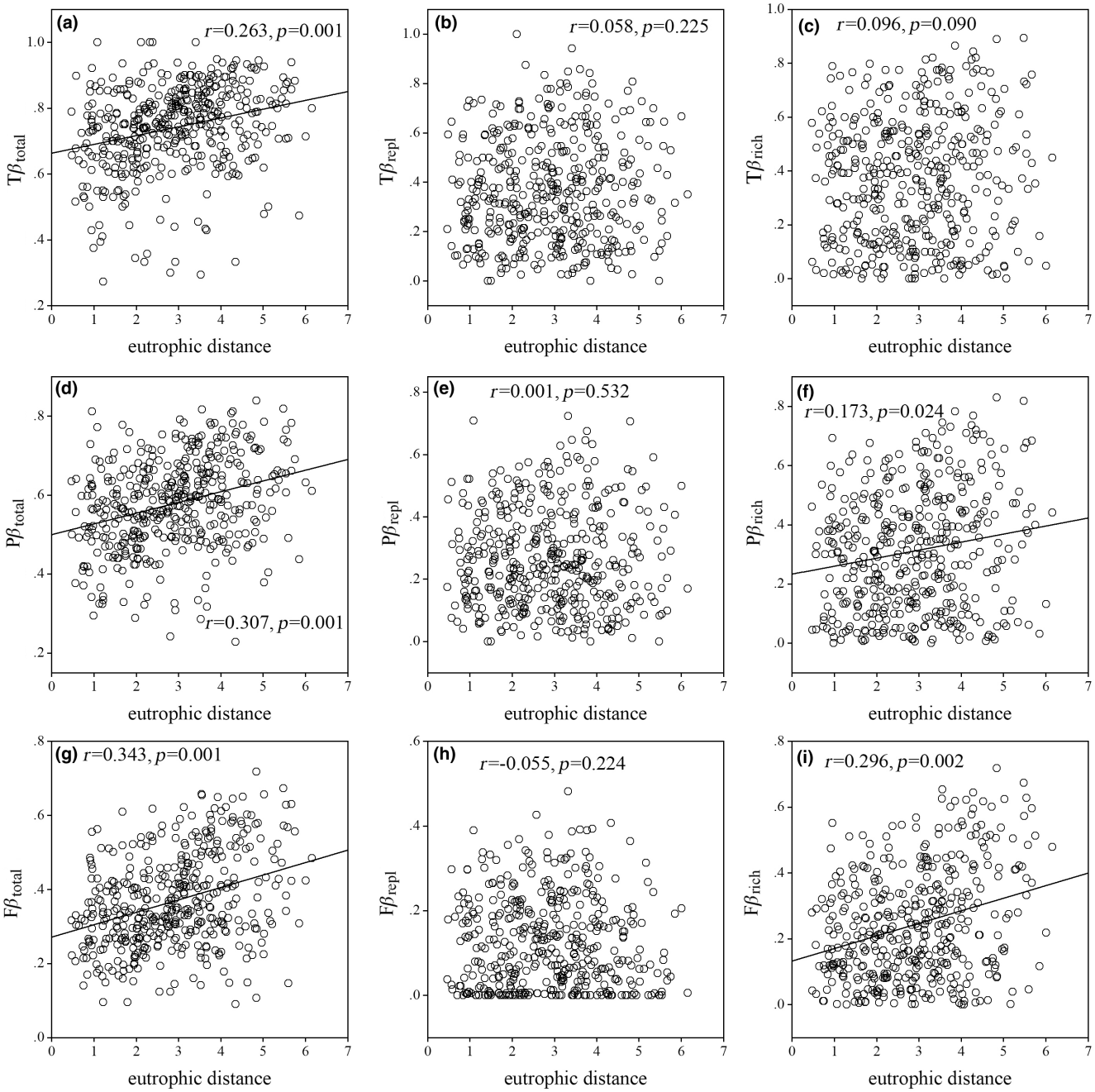

FIGURE 2 Relationship between taxonomic (a–c), phylogenetic (d–f) and functional (g–i) of dissimilarities and environmental distance associated with eutrophication distance among the 30 studied lakes. The Pearson correlation (*r*) and significance (*p*-value) of Mantel tests are also shown in each panel. Only the significant regression lines are shown.

affects the assemblage compositional heterogeneity of aquatic macroinvertebrates (Donohue et al., 2009; Zhang, Cheng, Li, et al., 2019) and other aquatic organisms (Li et al., 2022; Lougheed et al., 2008; Menezes et al., 2015). Our findings also parallel with several recent studies assessing the effects of eutrophication on the taxonomic distance–decay patterns of diatom communities (Marquardt et al., 2017; Vilar et al., 2014), which highlighted that beta diversity in eutrophic areas was not controlled by spatial distance but only by eutrophication-related environmental variables. When the degree of anthropogenic disturbance increases, environmental selection would be assumed to become more important in structuring biological communities via filtering out intolerant species (Chase, 2007). This is also the case in the studied lakes, as high levels of eutrophication and associated habitat degradation (e.g., increase in turbidity, reduction in macrophyte cover and deterioration of water quality) have caused the disappearance of many sensitive species (e.g., mayflies, caddisflies and plant-associated snails) and have left almost a non-random subset of tolerant species (e.g., tubificid worms and chironomid midges) (Jiang et al., 2013, 2022). In other words, the severe eutrophication we observed here actually served as an

TABLE 2 Results of distanced-based redundancy analyses (dbRDA), showing the significant environmental and spatial variables and their cumulative adj. R^2 values on taxonomic (T), functional (F) and phylogenetic (P) overall dissimilarity (β_{total}) and their replacement (β_{repl}) and richness difference (β_{rich}) components.

	Selected variables	Adj. R^2	*F*	*p*
Tβ_{total}				
Spatial	PCNM5	.027	1.793	.043
Environmental	Chl *a*, NH_4-N, pH, depth	.194	1.878	.026
Tβ_{repl}				
Spatial	None			
Environmental	NO_3-N, TN, NH_4-N, transparency	.416	4.148	.043
Tβ_{rich}				
Spatial	None			
Environmental	vegetation coverage, PO_4-P	.275	5.104	.018
Fβ_{total}				
Spatial	PCNM5	.068	3.115	.017
Environmental	Chl *a*, NO_3-N, vegetation coverage, PO_4-P	.295	2.523	.028
Fβ_{repl}				
Spatial	None			
Environmental	Conductivity, NH_4-N, water depth	.342	4.636	.039
Fβ_{rich}				
Spatial	None			
Environmental	Chl *a*, PO_4-P	.400	6.687	.006
Pβ_{total}				
Spatial	None			
Environmental	Chl *a*, pH, NH_4-N	.178	2.170	.017
Pβ_{repl}				
Spatial	None			
Environmental	NO_3-N, TN, NH_4-N	.278	4.646	.019
Pβ_{rich}				
Spatial	None			
Environmental	Vegetation coverage, PO_4-P	.345	6.144	.008

Abbreviation: Adj.R^2, cumulative adjusted.

environmental filter, thereby modifying the spatial distance–decay relationships of macroinvertebrate assemblages, possibly via reducing the importance of dispersal limitation in shaping macroinvertebrate assemblages (Heino, 2013).

The environmental filtering effects associated with eutrophication were certainly not only important for the taxonomic facet (e.g., the loss of certain species) but also for the functional (e.g., loss of certain species traits) and phylogenetic (e.g., loss of distinct evolutionary lineages) facets. Functional compositions are usually pertinent to changing taxonomic composition across various spatial and temporal scales, as the species loss or gain leading to taxonomic homogenization or differentiation are closely associated to the traits possessed by these species (Brice et al., 2017; Villéger et al., 2014). Previous publications in the studied region also showed that the loss of species caused by eutrophication is associated with the loss of certain traits (e.g., large size, scrapers and aerial active dispersal mode), which have significantly altered the functional trait structure of lake macroinvertebrate assemblages (Jiang et al., 2022; Zhang, Cheng, Kong, et al., 2019). For the phylogenetic facet, nutrient enrichment led to significant decline or near-absence of species belonging to sensitive lineages. These lineages include species from the orders Ephemeroptera and Trichoptera, as well as several families or orders within the phylum Arthropoda (Zhang et al., 2020). Therefore, it is reasonable to observe that the functional and phylogenetic dissimilarities were also controlled by the eutrophication gradient rather than spatial distances between lakes.

The dbRDA and associated variation partitioning analyses also confirmed the effects of eutrophication on the assemblage-geographic distance relationships. Except for taxonomic and functional overall beta diversity, no spatial variables were important in affecting all facets of macroinvertebrate dissimilarities. The results support mostly our second hypothesis. Indeed, the intensity and extent of anthropogenic disturbances played an important role in determining the relative contribution of environmental and spatial

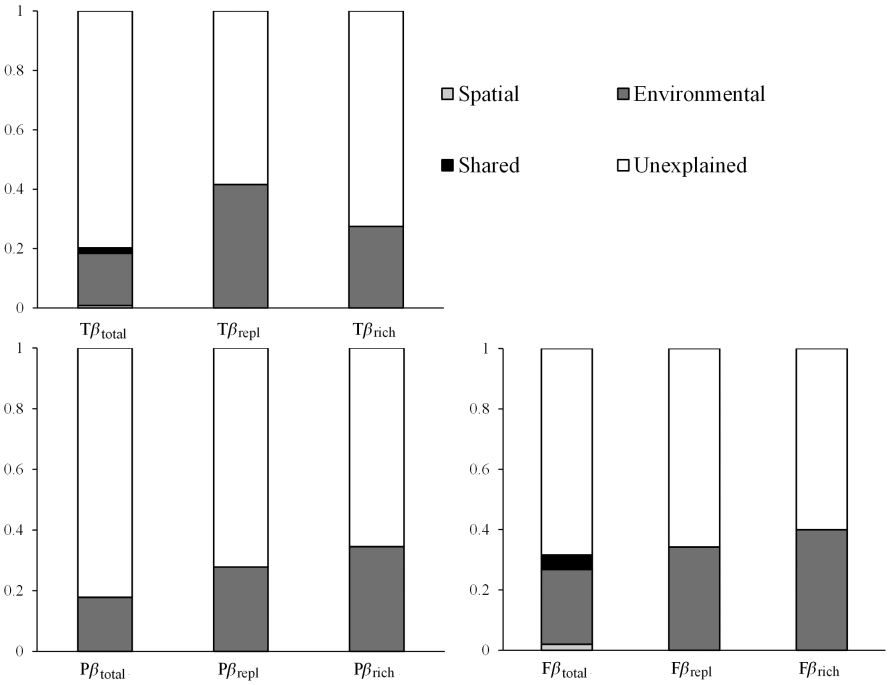

FIGURE 3 Results of variation partitioning analysis, showing the percentage variation in the three facets of beta diversity attributed to environmental factors, shared fraction (Shared), spatial factors and unexplained variation (unexplained).

factors on assemblage compositional variations (Costa et al., 2009). The high degree of disturbance in the studied lakes caused a strong eutrophication-related environmental gradient, for which variation in three facets of beta diversity was mainly explained by environmental filtering.

Somewhat suprisingly, we did not detect significant homogenization (i.e., decrease in beta diversity) of macroinvertebrate assemblages in the groups of more eutrophic lakes (Table 1). In contrast, the three facets of multiple-site beta diversity were highest in the most eutrophic algal-dominated lakes, especially in the case of functional beta diversity. These findings did not support the third hypothesis and were inconsistent with a recent study conducted in the same region, which indicated that nutrient enrichment led to taxonomic and functional homogenization of macroinvertebrate assemblages in most eutrophic lakes (Zhang, Cheng, Li, et al., 2019). Although eutrophication increases the importance of environmental filtering and decreases the effects of random processes in structuring biotic communities, the increase (differentiation) or decrease (homogenization) in compositional dissimilarity depends on complex mechanisms (Rolls et al., 2023), including initial ecological conditions, the magnitude and uniformity of disturbances and the sensitivity or tolerance of individual taxa (Chalcraft et al., 2008; Gutiérrez-Cánovas et al., 2013; Hawkins et al., 2015). In our study, despite the higher levels of nutrient concentrations, the algal-dominated (i.e., most eutrophic) lakes showed broader ranges of eutrophication-related water quality (i.e., transparency, TN, TP and Chl *a* and COD_{Mn}) than the macrophyte-dominated (or least eutrophic) lakes (Table S6) and showed a larger gradient of eutrophication (Figure S5, the environmental distance between algal-dominated lakes were larger than that between macrophyte-dominated lakes). Another probable reason for the slightly increasing beta diversity along the eutrophication gradient may be associated with the different dispersal modes of invertebrates dominant in different lake groups. Most taxa (e.g., tubificid worms and chironomid midges) in eutrophic lakes had generally weak dispersal ability, whereas the macrophyte-dominated lakes supported more taxa (e.g., mayflies, caddisflies and beetles) with strong dispersal ability. These differences in dispersal ability may also contribute to the observed beta diversity patterns (Li et al., 2021; Liu et al., 2022). Our results implied that different facets of beta diversity are controlled by different factors, which probably have diverse effects on assemblage composition. Hence, it is necessary to consider the factors driving the variation in diversity patterns across freshwater ecosystems and how different facets and components of diversity respond to different types and extents of anthropogenic disturbances (Hawkins et al., 2015).

5 | CONCLUSION

Overall, our study indicated that the anthropogenic eutrophication influenced the relationships between the three facets (i.e., taxonomic, functional and phylogenetic) of beta diversity of macroinvertebrate assemblages and geographic or environmental distances in the Yangtze River floodplain lakes. The high degrees of eutrophication affected the a priori assumptions of distance–decay relationships of assemblage similarity based on the three facets of beta diversity. The macroinvertebrate assemblages examined were almost exclusively structured by environmental factors (mainly associated with eutrophication), with a negligible importance of spatial factors. Our results highlight that increasing anthropogenic disturbances would significantly increase the importance of environmental factors in structuring ecological communities. Nevertheless,

the effects of anthropogenic disturbance on the distance–decay relationships have mostly been ignored in previous studies (e.g., Baselga & Gómez-Rodríguez, 2021; Nekola & White, 1999; Soininen et al., 2007), which have typically considered the effects of organism characteristics (e.g., differences in body size, dispersal ability and taxonomic group) (Graco-Roza et al., 2022). Given the sensitivity of distance–decay relationships of macroinvertebrate assemblages to eutrophication detected in the present study, focusing on the distance–decay relationships solely from the perspective of organismal characteristics may result in inadequate interpretations of the ecological processes driving assemblage turnover and variation along ecological gradients. Therefore, we recommend that the role of anthropogenic disturbances should be better incorporated into freshwater biodiversity research (e.g., Agra et al., 2021), because doing so can enhance our understanding of the drivers of spatial patterns of beta diversity.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to report.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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