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Taxonomic dependency of beta diversity components in benthic communities of bacteria, diatoms and chironomids along a water-depth gradient



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HIGHLIGHTS

GRAPHICAL ABSTRACT

- Beta diversity components are taxonomically dependent along waterdepth gradients.
- Bacteria show depth-decay in turnover, while diatoms or chironomids in nestedness.
- Uniqueness decrease towards deep water for bacteria, while increase for diatoms.
- Depth is most important for beta diversity components across three organisms.
- Biotic and abiotic factors explain beta diversity, while the latter more important.

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ABSTRACT

Community variation (i.e., beta diversity) along geographical gradients is a well-known ecological pattern, but the corresponding variation in beta diversity components (e.g., species turnover and nestedness) and underlying drivers remain poorly understood. Based on two alternative approaches (that is, the beta diversity partitioning proposed by Baselga and the Local Contributions to Beta Diversity (LCBD) partitioning proposed by Legendre), we examined the patterns of beta diversity components of lacustrine benthos, from bacteria to diatoms and chironomids, in the surface sediments along a 100-m water-depth gradient in Lugu Lake. We further quantified the relative importance of spatial, environmental and biotic variables in explaining water-depth patterns in beta diversity components with water-depth, showing a significant species turnover pattern for bacteria, while diatoms and chironomids showed significant nestedness. This dependency was also evident in the patterns of community

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Diatoms Local contributions to beta diversity Water depth uniqueness with water-depth because based on Legendre's framework, the LCBD decreased with water depth for bacteria whereas increased with depth for diatoms. The total beta diversity and species turnover of bacteria could be explained by the pure effects of spatial, environmental and biotic variables. A total of 26.8% and 23.6% of the nestedness component of diatoms and chironomids was explained by environmental variables, respectively, while species turnover was mostly related to spatial variables. Bacteria total LCBD and species replacement were driven only by environmental variables. For diatoms and chironomids, however, most of the total LCBD and its two components were explained by spatial variables, and biotic variables were most important for the diatom replacement component. Our findings provide insights into the mechanisms responsible for community organizations along water-depth gradients from the perspective of beta diversity components.

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1. Introduction

Understanding the variation in community composition (i.e., beta diversity) along environmental or spatial gradients is a central issue in ecology and conservation biology (da Silva et al., 2018a). Beta diversity connects local (i.e., alpha) and regional (i.e., gamma) diversity by measuring the amount of species dissimilarity between communities and plays an important role in revealing the various ecological processes for cross-scale biodiversity patterns (Maloufi et al., 2016). The beta diversity patterns along geographical or environmental gradients, such as elevation and latitude, have been extensively investigated (Qian and Wang, 2015; Teittinen et al., 2016). Nevertheless, to the best of our knowledge, few studies provide relevant information on beta diversity patterns along water-depth gradients, especially in terms of partitioning the beta diversity components.

Since the classical study of beta diversity by Whittaker (1960), several methods have been developed to measure the variations in species identities and richness through time or across space (Tuomisto, 2010; McGill et al., 2015). However, there is still no consensus on which beta diversity method is the most appropriate to address particular issues in ecology (Landeiro et al., 2018). In this context, Baselga (2010) further proposed a general framework for the partitioning of beta diversity. Based on the Sørensen dissimilarity index, beta diversity can be divided into the components of turnover (i.e., species replacement, where one species replaces another with no change in species richness) and nestedness (i.e., species richness differences due to species gain or loss) (Baselga, 2010). The mechanisms responsible for species turnover stem from environmental filtering, competition and historical events (Specziar et al., 2018). In contrast, nestedness differences originate from species thinning or from other ecological processes, such as human disturbance or physical barriers (Legendre, 2014). Partitioning beta diversity allows us to better understand the mechanisms that guide the structuring of biological communities across spatial scales and along environmental gradients and to make biodiversity conservation strategies more effective (Medeiros et al., 2016).

In a recent advance, Legendre and De Cáceres (2013) proposed a new metric called local contributions to beta diversity (LCBD), which is based on the total beta diversity estimated from a site-by-species abundance matrix or from a dissimilarity matrix. Ecologically, the LCBD is suitable for quantifying which sites contribute less (or more) to beta diversity than the mean and, thereby, for evaluating the degree of uniqueness of the each site in terms of community composition (Szabo et al., 2019). The LCBD can be also extended to the measure of sites' uniqueness in terms of species replacement (LCBD_{Repl}) and nestedness (LCBD_{Nes}) (Legendre, 2014; Castro et al., 2019). These metrics based on the Baselga's and Legendre's approaches are complementary, and considering multiple aspects of beta diversity could help researchers understand different aspects of ecosystem functioning as well as the general biodiversity patterns and underlying mechanisms (Legendre, 2014).

Variations in community compositions are mainly caused by the factors based on environmental conditions or geographical distances (Medeiros et al., 2016). For example, habitat filtering is the primary mechanism affecting species turnover in fish assemblages, whereas spatial connectivity can drive species nestedness (Pelaez and Pavanelli, 2019). For benthic diatoms, studies have shown that local environmental variables, such as total phosphorus and pH, may affect the LCBD, while chemical oxygen demand has effects on the $LCBD_{Repl}$ and LCBD_{Nes} components (Szabo et al., 2019). In freshwater ecosystems, the relative importance of environmental and spatial factors depends on the spatial scale as well as biological characteristics and traits (e.g., taxa, dispersal ability of the organisms, and dispersal vectors) (Yang et al., 2018; Pelaez and Pavanelli, 2019). In addition, biotic factors (e.g., species interactions) are well-known drivers of species assemblages at the local scale (Wisz et al., 2013; Coccia and Farina, 2019) and play an important role in the origin and maintenance of biodiversity (Schemske et al., 2009). For instance, biotic interactions can explain zooplankton species diversity in estuarine ecosystems (Sarker et al., 2018) and determine the spatial turnover of aquatic macrophyte assemblages (Boschilia et al., 2016). However, knowledge about how biotic interactions affect beta diversity along water-depth gradients, especially the components of beta diversity, is still limited.

To date, only a few studies have examined the partitioning of beta diversity among different taxonomic groups along water-depth gradients (Wagstaff et al., 2014), including unicellular and multicellular aquatic organisms. For multi-trophic groups such as bacteria, diatoms and macroinvertebrates, previous studies have shown that there are different elevational patterns in species diversity and underlying mechanisms (Wang et al., 2011). In this study, we hypothesize that the patterns in the beta diversity components along water-depth gradients would differ between organisms where: (1) Natural gradients (water-depth) result in species turnover of bacteria due to their short generation times, which allows enough time for species to evolve and adapt to every segment of the gradients. Moreover, bacteria show a high diversity in terms of energy and food resources, so there should be very different assemblages according to the availability of light and organic and inorganic matters at every depth layer. (2) Water-depth gradients result in the loss of specialist taxa of diatoms and chironomids due to the stratification of water, thus causing species nestedness. We thus took the water depth of Lugu Lake as a typical geographical gradient and employed the two abovementioned methods to partition the beta diversity of three taxonomic groups from the surface sediments: bacteria, diatoms and chironomids. We focused on three objectives. First, we explored the relationships between beta diversity and water depth across the three taxonomic groups by considering total beta diversity and its two components. Second, we examined patterns of community uniqueness based on water depth using the LCBD. Third, we evaluated the relative importance of the biotic, spatial and environmental factors underlying the patterns of beta diversity or the LCBD and its two components.

2. Materials and methods

2.1. Study region and field sampling

Lugu Lake $(27^{\circ}41'-27^{\circ}45'N, 100^{\circ}45'-100^{\circ}50'E)$ is located in Yunnan Province, on the southeastern margin of the Tibetan Plateau. It is one of the deepest plateau freshwater lakes in the region with a maximum

water depth of 93.5 m, a total water surface area of 50.5 km², and a catchment area of ~171.4 km². Lugu Lake is a warm temperate semi-enclosed plateau deep water lake and does not freeze all year round. The water temperature in winter is vertically homogeneous, while there is thermal stratification in the other seasons (Wen et al., 2016). The detailed procedures of the sample collection have been described in previous studies (Wang et al., 2012c). In brief, surface sediment samples (0–1 cm) were collected with a 6-cm diameter gravity core from 37 sites along a water-depth gradient of 0–93.5 m in August 2010. Sampling sites were recorded with GPS (Garmin eTrex Legend H). The surface sediments (~ 1 cm) from three cores were collected at each site and were then pooled together for the analyses of bacteria, diatoms and chironomids.

2.2. Community analyses

The community composition of the three taxa was examined according to the methods described in previous studies (Wang et al., 2012a; Wang et al., 2012c; Zhang et al., 2013). In brief, for bacteria, genomic DNA was extracted from the surface sediment samples using the phenol chloroform method as previously described (Zhou et al., 1996). We amplified the bacterial 16S rRNA genes using the 27F primer with the 454 Life Sciences 'A' sequencing adapter, and the modified 519R primer with a 8 bp barcode sequence and the 454 Life Sciences 'B' sequencing adapter (Hamady et al., 2008). Each sample was analysed with three replicates of PCR amplifications. Then, we checked the PCR products by electrophoresis and combined the replicates. The purified amplicons were pooled at equal molality and then sequenced using a Roche 454 FLX pyrosequencer (Roche, Switzerland).

The sequences were processed using the QIIME pipeline (v1.9.0) (Caporaso et al., 2010b). In brief, sequences longer than 200 bp were denoised with the Denoiser algorithm and clustered into operational taxonomic units (OTUs) at a 97% similarity level with the seed-based UCLUST algorithm (Edgar, 2010). After the chimeras were removed via the Chimera Slayer, representative sequences from each OTU were aligned to the Greengenes imputed core reference alignment using PyNAST (Caporaso et al., 2010a). The taxonomic identity of each representative sequence was determined using the RDP Classifier (Wang et al., 2007), and chloroplast and archaeal sequences were removed. We removed singletons before subsequent analyses, and the bacterial communities were rarefied at 1139 sequences to avoid the bias caused by the variation in abundance or sampling intensity. The generated sequences can be found in figshare (https://doi.org/10.6084/m9.figshare.8052788).

For the diatoms, the sediment samples were processed with 10% HCl to remove carbonates and 30% hydrogen peroxide to oxidize the organic matter (Berglund, 1986). Further, we identified and counted the diatom valves on an Olympus BX51 microscope with an oil immersion objective (magnification \times 1000). At least 500 diatom valves per slide were enumerated in each sample and diatoms were identified to species level if possible, primarily using standard European and North American references (Krammer and Lange-Bertalot, 1986; Metzeltin et al., 2009). Diatom concentration was calculated using the microsphere method and expressed as number of valves per gram of wet sediment in each sample (Battarbee and Kneen, 1982).

For the chironomids, the surface sediments were deflocculated in a warm water bath with 10% potassium hydroxide for 15 min and subsequently sieved through 212 and 90 μ m mesh sieves. The sieved residues were examined under a stereo-zoom microscope at \times 25. Each head capsule was mounted on a microscope slides in a solution of Hydromatrixs®. The chironomids were identified according to the literature (Oliver and Roussel, 1983; Brooks et al., 2007). The biomass of the chironomids was calculated as the count of the head capsules per gram of wet sediment.

2.3. Abiotic and biotic variables

For the abiotic variables, water depth, water temperature, pH, dissolved oxygen (DO) and conductivity were measured in the field using a YSI 650 multi-parameter display system with a 600XL probe. Additional chemical variables were measured in the laboratory using the water samples collected. For instance, total nitrogen (TN), total phosphorus (TP), HCO₃⁻, metal ions and silica were analysed using Water and Waste water Monitoring Methods (2002). Loss-on-ignition (LOI), grain size, porosity and water content of the surface sediments were also determined. The grain size was divided into five classes: <4 μ m (GSL4), 4–16 μ m (GS4–16), 16–32 μ m (GS4–16), 32–64 μ m (GS32–64) and >64 μ m (GLS64). Detailed measurement and calculation methods for these abiotic variables are described in a previous study (Wang et al., 2012c; Zhao et al., 2019).

For the biotic variables, we used the following factors: (1) the chlorophyll *a* of the bottom water and (II) the biomass and species richness of bacteria, diatoms and chironomids. For example, in explaining bacteria beta diversity components, we used biotic variables, that is, the chlorophyll *a* of the bottom water, the biomass and species richness of diatoms and chironomids.

2.4. Statistical analyses

First, we employed Baselga's (2010) approach to explore the waterdepth patterns of beta diversity and its two components (that is, species turnover and nestedness) for the three taxonomic groups. This method requires the calculation of three different dissimilarity matrices based on a species composition matrix as follows: (1) the total pairwise beta diversity was calculated with the Sørensen dissimilarity index; (2) species turnover was measured using the Simpson dissimilarity index; and (3) the nestedness index was estimated by subtracting the turnover component from the total beta diversity (Gutierrez-Canovas et al., 2013). Next, we calculated the water depth distances among the samples by Euclidean distance. The variations in beta diversity and its components for the three taxa were plotted against water-depth distances using a Gaussian generalized linear model. The significance was assessed by Mantel tests (999 permutations). The beta diversity indices were calculated with the presence-absence species data.

Second, to examine the changes in beta diversity across waterdepths, we divided the samples along the 100-m water-depth gradients into seven belts with an equal depth range of ~13 m, and calculated the beta diversity and its components for each belt. Then, the relationships between the mean water depth and beta diversity metrics of the seven belts were explored with linear and quadratic models. The best model was selected based on the lowest value of Akaike's information criterion (Yamaoka et al., 1978).

Third, the degree of ecological uniqueness of the three taxonomic groups in terms of community composition at each sampling site was estimated using the LCBD and its partitioned components, as proposed by Legendre (Legendre, 2014). We estimated LCBD via Sørensen-based indices of the Baselga's family, and partitioned the total beta diversity into replacement and nestedness components. We then computed the LCBD indices from the species replacement and nestedness matrices using the function '*LCBD.comp*'. We explored the relationships between the water depth and LCBD indices with linear and quadratic models, and the best model was selected based on the lowest value of Akaike's information criterion (Yamaoka et al., 1978).

To quantify the association of each component of beta diversity with the spatial, environmental and biotic matrices, we used a multiple regression on distance matrices (MRM) (Lichstein, 2007). Prior to the statistical analyses, all the abiotic and biotic variables were z-score standardized (i.e., mean = 0, SD = 1). For the 19 abovementioned metal ions, we applied principal component analysis (PCA) to reduce the dimensionality of the data and then used the first and second axes (i.e., PC1 and PC2) as additional environmental parameters. The variables related to PC1 were Mn and Ti, while PC2 was mainly associated with the variables Ti and Mn. The other measured variables, such as water depth, TN, TP, HCO3-, pH, DO, LOI, grain size, porosity, water content and conductivity, were used as environmental variables without a PCA step. Then, the statistical dependence between the explanatory variables was assessed using Pearson's correlation analyses, and the variables with high correlation coefficients (Pearson r > 0.7) were excluded from the models. The following three groups of explanatory variables were considered: spatial, environmental and biotic variable. A Euclidean distance matrix was calculated for spatial, each environmental and biotic variables. To reduce the effect of spurious relationships between the variables, we first ran the MRM test with all the selected variables in the non-redundant abiotic and biotic variable sets (Martiny et al., 2011). Then, we removed the non-significant variables from this initial MRM test and re-ran the test. The significance of the partial regression was tested 999 times by a matrix permutation.

The relationship between the LCBD indices and the selected variables was modelled using the random forest (RF) algorithm (Breiman, 2001) The environmental and biotic variables were the same as those in the MRM analysis except for the spatial variables, which were not included in the models. Then, an optimal number of 2000 trees was produced using cross-validation (Elith et al., 2008). The importance of each predictor variable was determined by its frequency of selection (for splitting) weighted by a measure of improvement of the model given each split and averaged across all the trees (contributions were scaled to sum to 100). To reduce the effect of spurious relationships between variables, we first ran the RF test with all the selected variables. Then, we removed the variable with the lowest contribution and re-ran the test until the lowest contribution of each variable was greater than 5%.

We performed variation partitioning analyses (Anderson and Cribble, 1998) to reveal the effects of the spatial, environmental and biotic variables on beta diversity, the LCBD and their components. All the significant environmental and biotic variables were selected by forward selection against the biological characteristics data with 9999 permutations for all three taxonomic groups.

These above analyses were performed in the R environment using the following packages, such as '*betapart*' V1.5.1 (Baselga et al., 2018), '*randomForestSRC*' V2.9.0 (Liaw and Wiener, 2002), '*vegan*' V2.5–4 (Borcard and Legendre, 2002), '*ecodist*' V2.0.1 (Goslee and Urban, 2007), and '*SpatialEpi*' V1.2.3 package (Kim and Wakefield, 2010).

3. Results

The relationships between the total beta diversity and water depth distance were consistently positive and significant (P < 0.05) for bacteria, diatoms and chironomids (Fig. 1a). The chironomids showed the strongest variation in total beta diversity along the water-depth gradient, with a slope of 0.0031, while the bacteria had the lowest slope at 0.0012. However, for the initial Sørensen dissimilarity, bacteria showed the highest value (0.84), and chironomids had the lowest value (0.35). Similar to the total beta diversity, bacteria showed positive and significant trends for the turnover component relative to the water depth changes, but the results were not significant for the nestedness component. For diatoms and chironomids, the nestedness component was significantly (P < 0.05) positively correlated with the water depth changes,



Fig. 1. The relationships between the variance in community compositions and water depth. The total beta diversity (a, d) was divided into two components, that is, turnover (b, e) and nestedness (c, f). The total beta diversity and its components across seven belts were linearly or quadratically modelled against the water-depth gradient, and the significant (P < 0.05) relations are shown as solid lines (d-f). Further, the local contributions to beta diversity (LCBD, g) were divided into species replacement (h) and nestedness (i). The normal Q-Q plot of the standardized residuals was shown in Fig. S4.

and the two groups had similar trends, with slopes of 0.0037 and 0.0038, respectively (Fig. 1b, c).

Consistent with the distributions of the three taxonomic groups along the water- depth gradient, the total beta diversity and their partitioned components showed similar patterns relative to environmental distance (Fig. S1). The exception was the nestedness component of diatoms and chironomids, which had different slopes (0.0076 and 0.0220, respectively; Fig. S1). Surprisingly, compared with the environmental conditions, the turnover components of diatoms and chironomids were more related to the spatial variables, while their nestedness components were not significantly (P>0.05) spatially structured (Fig. S2).

When viewed among water-depth belts, the Sørensen dissimilarity and turnover component of bacteria were higher in shallow water belts and showed significant decreasing trends towards deeper water (Fig. 1d, e). In contrast, the Sørensen dissimilarity and turnover component of diatoms showed increasing trends along the water-depth gradient (Fig. 1d, e). For chironomids, however, the Sørensen dissimilarity had higher variation in the intermediate water depth, while the nestedness component had higher variation in the deep-water belts (Fig. 1d, f). The changes of alpha and gamma diversity for each taxonomic group were similar along the water- depth belts (Fig. S3).

For bacteria, the total LCBD and its two components had significant (P < 0.05) correlations with the total beta diversity and species turnover (Table S1). The bacterial total LCBD showed a significant (P < 0.05) decreasing pattern with water depth, while the LCBD_{Nes} showed an increasing pattern (Fig. 1g, i). However, both the total LCBD and LCBD_{Nes} of diatoms increased towards deep water (Fig. 1h, i). For chironomids, there was no significant (P > 0.5) water depth pattern for any of the three components of LCBD (Fig. 1g, h, i).

In the MRM analyses, the water depth and spatial factors were important (P < 0.05) predictors of beta diversity and its two components for bacteria, diatoms and chironomids. The total beta diversity and species turnover of bacteria were also significantly (P < 0.05) correlated with other factors related to environmental variables, such as GSL4 and TP (Fig. 2a, Fig. S5a), and biotic variables, such as the biomass of diatoms and chironomids (Fig. 2a).

Based on the random forest analyses, the water depth was the most important variable in explaining the variations in the bacterial LCBD and its two components, followed by environmental factors, such as the first axes of the principal component analysis for the metal ions (PC1) (Fig. 2b). For diatoms, the environmental factors, such as porosity, GS4–16 and TP, had a great influence on the total LCBD and LCBD_{Repl} (Fig. 2b), and biotic factors, such as bacterial richness, were also important for the LCBD_{Repl} and LCBD_{Nes} (Fig. 2b, Fig. S5b). For chironomids, the total LCBD was best explained by SiO2, while GSL4 was the most important variable for the LCBD_{Repl} and LCBD_{Nes} (Fig. 2b).

In the variation partitioning analyses, the total beta diversity and species turnover of bacteria were explained by the pure effects of the spatial, environmental and biotic variables, although the total variation explained was the lowest for bacteria among the three taxonomic groups (Fig. 3a). For the turnover components, the pure effects of spatial variables accounted for a larger part of the variability in the community composition of diatoms and chironomids than that of the pure effects of the environmental variables, while the nestedness components of diatoms and chironomids were mainly explained by environmental variables (26.8% and 23.6%, respectively) (Fig. 3a, Table. S1).

We found that the variations in the bacterial total LCBD and $LCBD_{Repl}$ were strongly associated with environmental variables, while biotic variables dominated the variation in $LCBD_{Nes}$ (2.4%; Fig. 3b). For diatoms



Fig. 2. The spatial, environmental and biotic factors related to the variance in community composition, identified with multiple regression on distance matrices (a) and random forest (b). The total beta diversity (Total beta) was divided into turnover and nestedness (a). The local contributions to beta diversity (LCBD) were divided into species replacement ($LCBD_{Repl}$) and nestedness ($LCBD_{Nes}$) (b). For the environmental factors, we considered water depth (Depth), sediment porosity, grain size, the first axes of a principal component analysis for 19 metal ions (PC1), total phosphorus (TP.water), loss-on-ignition (LOI), the concentrations of HCO₃⁻ (HCO₃-water), dissolved oxygen (DO.bot), pH (pH.bot), SiO₂ (SiO₂-water) and total nitrogen (TN.water). The grain sizes were as follows: <4 μ m (GS4-16) and >64 μ m (GSL64). The biotic factors included the biomass of diatoms (Dia.bio) and chironomids (Chi.bio), species richness of bacteria (Bac.ric), and chlorophyll *a* (Chla.bot).



Fig. 3. The relative importance of the spatial, environmental and biotic variables in explaining the variance in community composition. The total beta diversity (Total beta) was divided into turnover and nestedness (a). The local contributions to beta diversity (LCBD) were divided into species replacement (LCBD_{Repl}) and nestedness (LCBD_{Nes}) (b). For simplicity, the pure effects of the three components in predicting beta diversity and its components are shown, but not the joint effects or unexplained variances. An alternative version of this figure showing the unique and shared variance of each group can be found in Supplementary Table S2 and S3.

and chironomids, the variations in total LCBD and LCBD_{Nes} were mainly explained by spatial variables (Fig. 3b). Interestingly, the pure effect of biotic variables was most important for the $LCBD_{Repl}$ of diatoms and explained 18.7% of the variation (Fig. 3b).

It should be noted that the shared fractions between spatial, environmental and biotic variables were also important for some beta diversity components. For instance, the shared fractions of spatial and environmental variables were important for the turnover components of diatoms and chironomids, albeit minor (Table S2). In addition, the shared fractions of spatial, environmental and biological variables were most important to the total LCBD and its two components of bacteria. For diatoms and chironomids, the variations in total LCBD and its two components were also explained by the shared fractions of spatial and environmental variables (Table S3). However, as our main focus is the pure effect of each driver component, we thus do not go further into the effects of shared components in order to keep the discussion clarified.

4. Discussion

The assessment of beta diversity is a central topic in biogeography and ecology. Studies have shown that the beta diversity of biological communities is composed by two main components, i.e., species turnover and nestedness, which have different implications for biodiversity conservation (Medeiros et al., 2016). In this study, we explored the driving mechanisms of beta diversity in bacteria, diatoms and chironomids based on two methods of beta diversity partitioning: beta diversity based on Baselga's framework (Baselga, 2010) and community uniqueness based on Legendre's framework (Legendre, 2014). We revealed that water-depth patterns in beta diversity were taxonomically dependent. There was also a taxonomic dependency of community uniqueness patterns for the three benthic groups along water-depth gradients. Further, the importance of the three variables (that is, spatial, environmental and biotic) to beta diversity and its components varied across the three groups. Compared with the biotic variables, the abiotic conditions explained more of the variation in the community composition.

Previous studies have shown that species turnover is the most important component contributing to beta diversity in all waterbody types (Epele et al., 2019). However, our results provided evidence that beta diversity in lake ecosystems was taxonomically dependent across bacteria, diatoms and chironomids. Our findings supported the

conclusion that the contribution of particular beta diversity components to total beta diversity varied substantially among the studied different organism taxa. The bacteria showed a significant species turnover pattern, while that of diatoms and chironominds showed significant nestedness. This may be because the three taxonomic groups have large differences in their main characteristics, such as body size, trophic position and dispersal ability (Soininen et al., 2007; Wang et al., 2012b). In addition, sedimentation and taphonomic processes may also enforce the spatial distribution of subfossil assemblages, but certain taxa may be more strongly affected by these processes than others (Raposeiro et al., 2018). Another important factor to explain the difference in the spatial distribution of diatoms or chironomids, but not bacteria, within a lake basin could be the variability of mesohabitats along the depth gradient, as the diversity changes of lake mesohabitats habitats would increase beta-diversity with depth distance (Pla-Rabes and Catalan, 2018). The high spatial turnover of bacteria also suggests a role for evolutionary adaptation to environmental circumstances within depth bands (Wagstaff et al., 2014). For diatoms and chironomids, beta diversity was mainly caused by nestedness components, which is inconsistent with previous studies. In small-sized spring fens, chironomid metacommunities are more influenced by species turnover than by nestedness (Radkova et al., 2014). Our result inconsistency with Radkova et al. (2014) could be related that they sampled relevant mesohabitats instead a sample that is integrating all the site habitats heterogeneity as it is a surface sediment samples in our study. The turnover component of chironomids was shown to be slightly more important than the nestedness component in lake, wetland and stream network (Specziar et al., 2018), which would increase the turnover of beta-diversity by comparing quite different environments (lotic and lentic). These findings are likely to be dependent on the habitat types. Lugu Lake, which we studied in this research, is a small deep lake, and the light, temperature and dissolved oxygen concentration gradually decrease with the water depth (Zhang et al., 2013). Such depth-related environmental changes may be tolerated by only a few species, and therefore, these deep regions could support nestedness-related beta diversity of chironomids.

In addition to the findings described above, which were detected by the traditional decomposition method of beta diversity proposed by Baselga (2010), we further quantified the community uniqueness of the three taxonomic groups using the LCBD, an approach developed by Legendre (2014). Similarly, we found that the patterns of community uniqueness with water depth were taxonomically dependent for the three benthic microbial groups. For instance, the total LCBD of the bacteria showed a significant decreasing pattern along the water-depth gradient, while the total LCBD and LCBD_{Nes} of the diatoms increased towards deep water. However, for chironomids, the three components of the LCBD had no significant patterns along the water-depth gradient. The contributions of the sampling sites to beta diversity can indicate the ecological uniqueness of each sampling site in terms of community composition and provide valuable information on the level of habitat degradation of these sites (Sor et al., 2018). Sites with higher LCBD values exhibit substantial dissimilarity in species compositions and may have high or low species richness (Qiao et al., 2015; Kong et al., 2017; Wang et al., 2019). Higher LCBD_{Repl} values reflect sites with higher species replacement in relation to the typical communities. On the other hand, sites with high $LCBD_{Nes}$ are those with very low or high species richness. The high LCBD index values may be the result of special ecological conditions, which should be given more attention in terms of conservation (Legendre, 2014).

Our results reveal that water depth had the greatest explanatory power for beta diversity and its components of the three taxonomic groups. Additionally, water depth was also the most important variable for determining the community uniqueness which was indicated by the diatom LCBD_{Nes} and the three components of the bacterial LCBD. Water depth has a crucial role in determining environmental factors in lakes, such as light intensity, nutrient availability and disturbance regimes, all of which have been shown to influence the distribution of biological assemblages (Raposeiro et al., 2018). Water depth was an important determinant for the diatom community composition, consistent with a previous study of stream by Virtanen and Soininen (2012), and may be related to light conditions. Light is an important factor for both diatoms and chironomids. For instance, diatoms are directly affected by light, because it can be a limiting factor for photosynthesis at low intensities (Cantonati et al., 2009) or at high intensities due to photoinhibition (Saunders et al., 2016). In a lake with similar maximum depth, the main source of variation in the diatom composition were depth, substrate type as these variables encapsulate the main sources of environmental variability (light, nutrients and physical context) that are relevant for diatom communities in lakes (Pla-Rabes and Catalan, 2018). Other depth associated factors include turbidity, wave action, water-level fluctuation and temperature, all of which can modulate the effects of light on benthic algal communities (Cantonati et al., 2009; Yang and Flower, 2012). Chironomids avoid light and predators by hiding under stones or burying themselves in sediments (Armitage et al., 2012). Compared with the changes in beta diversity along with a geographical distance, studying beta diversity along depth gradient increases the complexity of interpretation. There are significant changes in mesohabitats heterogeneity and relevant environmental factors along the depth gradients (light, nutrients, oxygen, habitat diversity), which are not always necessarily linear (i.e. the presence of a summer thermocline) that could interplay to explain betadiversity patterns.

Environmental selection and dispersal limitation are considered the two main ecological processes that control the biogeographic patterns of beta diversity (Tang et al., 2012; Wang et al., 2017; Zorzal-Almeida et al., 2017). Biotic interactions may also have an important impact on microbial beta diversity (Langenheder et al., 2017). For bacteria, species turnover almost entirely dominated the total beta diversity rather than nestedness, implying that the total beta diversity of bacteria may mainly arise from the species turnover component. Furthermore, the responses of the total beta diversity to the biotic, environmental and spatial variables were highly consistent with those of species turnover. Habitat heterogeneity has previously been shown to structure beta diversity for oceanic bacteria to a global extent (Zinger et al., 2011). Both the spatial and environmental factors significantly affected the composition and biodiversity of the benthic bacteria (Sun et al., 2011). Furthermore, the biotic variables, such as the biomass of diatoms and chironomids, were significantly correlated with the total beta diversity and species turnover of bacteria. Chironomid larvae feed mainly on bacteria (Pinder, 1986), while the growth and physiological status of diatoms largely determine the community structure of bacteria (Grossart et al., 2005). However, the relative effects of these processes on the patterns of microbial beta diversity might vary across taxa.

Similarly, for diatoms and chironomids, abiotic environmental heterogeneity and the spatial variables were the main two predictors of total beta diversity. Biotic factors, such as chironomid biomass and bacterial richness, were also significantly correlated with the total beta diversity of diatoms. This could be because the bacterial backbone (including extracellular polymeric substances) is likely viscoelastic (Stoodley et al., 1999), providing ample opportunity for diatoms to colonize (Besemer et al., 2007). Chironomids larval predation can affect diatom communities through a cascading effect (Mieczan et al., 2015). The turnover and nestedness components of beta diversity are influenced by different ecological processes and thus generally relate to different environmental and spatial attributes (Boieiro et al., 2013; Lewis et al., 2016; Gianuca et al., 2017; Specziar et al., 2018). For the decomposed components of diatom and chironomid beta diversity, the spatial variables can explain most of the variation in turnover, while nestedness was more related to the environmental variables. Spatial isolation by habitat differentiation may result in species turnover due to the long-term evolutionary processes of speciation and extinction, which creates differences among local habitat species pools (Leprieur et al., 2011; Gianuca et al., 2017). The importance of the spatial variables to the turnover component of beta diversity may also potentially reflect the influence of other unmeasured environmental factors, such as the seasonal variations in photic zone depth, the extension of mixing layer, and the slope of bottom. For instance, the slope of bottom can condition LOI, grain size, and other variables, which can influence the biological communities in lakes (Rossi et al., 2010; Zhao et al., 2019).

For the total LCBD and LCBD_{Repl} of bacterial communities, the environmental variables, such as water depth and metal ion concentrations, were found to be the only influential variables. The solubility and mobility of metals in lake sediments are related to redox potential, which is a key component to explain changes in bacterial communities (Miao et al., 2006; Frindte et al., 2015). As the LCBD represents the uniqueness of sites based on community variation, the environmental variables can be correlated with the LCBD values (Tonkin et al., 2016; da Silva et al., 2018b). This result may indicate that species-sorting processes are important. Barriers to bacterial dispersal are overcome by the high connectivity and small spatial scale of our studied lake, reinforcing the role of species sorting in the bacterial community composition (Lima et al., 2016). On the other hand, smaller species with better dispersal abilities are likely driven by habitat heterogeneity because they might be able to respond more sensitively to minor environmental differences (Hajek et al., 2011; De Bie et al., 2012; Szabo et al., 2019). However, some reports targeting beta diversity assessments showed that the LCBD was not well determined by local environmental characteristics, for instance, in the case of stream invertebrates (Tonkin et al., 2016).

For diatoms and chironomids, our results showed that the variations in the LCBD and its partitioned components were mainly affected by spatial variables, indicating that the LCBD of these taxonomic groups was spatially structured across the sampling sites. The impact of environmental gradients on species distributions are generally spatially distributed, so the LCBD values might be related to spatial variables (da Silva et al., 2018b). This is consistent with previous studies, which showed that ecological uniqueness in lake diatom communities was pronouncedly connected to the spatial isolation caused by environmental differences or barriers (Vilmi et al., 2017), and may depend on the organismal groups or ecosystem types studied. For example, when studying urban pond ecosystems, no significant spatial structural features are found in the ecological uniqueness of aquatic insect communities (Heino and Gronroos, 2017). The uniqueness may have implications for the future sampling of diatoms and chironomids, as they are strongly related to spatial factors.

Nevertheless, there are some caveats for the interpretation of our results. First, taphonomic processes may interfere with the observed water-depth patterns in beta diversity. A sediment sample assemblage accumulates the organisms that grow on the sampled site, but also the organisms that arrive from other lake locations due to taphonomic processes. For bacteria, they could grow elsewhere such as both trophogenic and tropholytic lake zones. Although taphonomy will also affect the assemblage recovered for each sediment sample, it is expected to be a minor issue. For diatoms, they grow in the trophogenic zone where there is enough light for their growth. However, due to taphonomy processes, a sediment assemblage includes diatoms from different lake habitats so that a sediment sample contains the planktonic life forms that do not growth in the epipedon. Hence, the samples from the trophogenic zone (that is, photic zone) contain diatoms frustules that are growing nearby the sampling site, but also frustules arrive from other lake habitats. However, in the tropholytic zone the frustules should come from other lake habitats due to a burial system. For chironomids, the same rationale as diatoms could be applied. However, chironomids could survive and grow in deep sediments if there is enough oxygen, which is a function of redox potential. Some chironomid species are adapted to low oxygen conditions, which could partly explain the observed turnover and nestedness patterns. However, the effects of taphonomic processes may be minimized because we considered not only the contemporary environments (that is, overlying water variables, including TN, TP HCO3- and pH), but also long-term environments (that is, sediment variables such as metal variables) in explaining the observed beta diversity patterns. Thus, although our findings provide a systematic comparison of such contrasting organisms in one-piece study, future studies are encouraged to apply beta diversity approaches for both morden ecology and paleolimnology to intertwine and synthesize the ecological knowledges of the current and past.

Second, the changes in alpha and gamma diversity may also affect the observed patterns in beta-diversity metrics (Chase et al., 2011; Kraft et al. 2011), which is among the challenging theoretical and empirical studies. We however focused on the empirical impact of spatial, environmental and biological effects on beta diversity and thus left the above theoretical effects less touched. In addition, thermal stratification of lakes has been considered as the most important limnological feature of deep lake ecosystems affecting both the chemical heterogeneity of the water column and the composition of lake biota (Borics et al., 2015). For instance, thermal stratification possibly causes the distinctive distribution and the shift of the major bacterial groups in the deep Lake Nam Co. Phylum Actinobacteria is usually considered to be common and often numerically important components in freshwater lakes, and occupy the metalimnion and hypolimnion (Liu et al., 2016). Strong stratification may create dispersal barriers (Baltar and Aristegui, 2017), thus influence the vertical beta diversity through spatial effects. Moreover, stratification can enhance physicochemical dissimilarity among water layers and thus affects vertical beta diversity through environmental heterogeneity (Boucher et al., 2006; Cheng et al., 2020). Regarding such unique lake stratification characteristics, alpha and gamma diversity are encouraged to be included in future theoretical studies for better explaining the observed patterns in beta diversity.

5. Conclusions

In summary, our results indicated that the differences in beta diversity due to water depth variation were dependent on the studied groups, which is supported consistently by Baselga's framework and Legendre's approach. The environmental and spatial processes accounted for most of the variation in the patterns of beta diversity components, and biotic variables also explained a unique portion of the variation. The large values of the LCBD may be associated with sampling sites that have high conservation value or, perhaps, species-poor and degraded sites that need restoration and should receive more attention in a conservation context (da Silva et al., 2019). To date, the beta diversity partitioning of multiple benthic taxonomic groups in lake systems, especially bacteria, has been little studied, and our study provides a first view of the beta diversity decomposition of contrasting benthic communities, comprising bacteria, diatoms and chironomids along water-depth gradients. Further studies are encouraged to investigate the underlying mechanisms of beta diversity of other different benthic communities along different geographical gradients. The effects of alpha and gamma diversity are challenging theoretical studies and encourages inclusion in future theoretical studies to better explain the observed patterns in beta diversity.

CRediT authorship contribution statement

Kaiyuan Wu: Writing - original draft. Wenqian Zhao: Formal analysis. Xiaoying Cheng: Conceptualization. Jianjun Wang: Conceptualization, Investigation, Formal analysis, Writing.

Declaration of competing interest

The authors declare no conflict of interest.

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Author contribution

JW conceived the idea. JW provided physiochemical and biological data and performed the bioinformatic analyses. WZ performed the data analyses. KW wrote the first draft of the manuscript. KW and JW finished the manuscript with the contributions of the other co-authors. All the authors contributed substantially to the study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2020.140462.

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