Biodiversity patterns across taxonomic groups along a lake water-depth gradient: Effects of abiotic and biotic drivers

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HIGHLIGHTS

- Biodiversity show clear water-depth patterns, but distinct patterns for diatoms.
- Diatoms are U-shaped or hump-shaped, while decreasing for bacteria and chironomids.
- There is cross-taxon congruence among community compositions for the three taxa.
- Biotic attributes can explain diversity, although environmental filtering is pivotal.

GRAPHICAL ABSTRACT
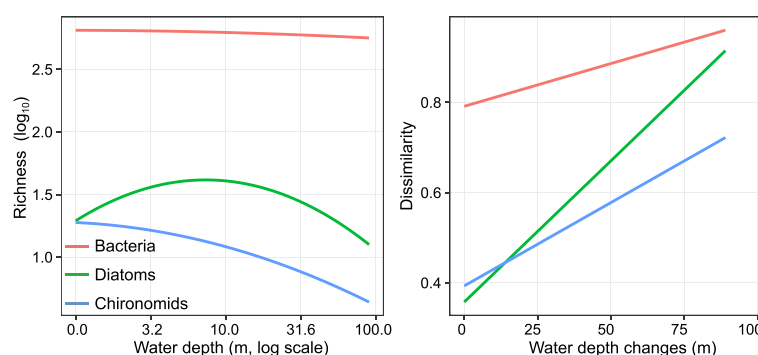
ARTICLE INFO

ABSTRACT

Understanding biodiversity patterns and the role of biotic attributes in governing these patterns remains one of the most important challenges in ecology. Here, taking water depth in Lake Lugu as a typical geographical gradient, we studied how these different taxa, that is bacteria, diatoms and chironomids, respond to the water depth and environmental gradients using molecular and morphological methods. We further evaluated the relative importance of water depth, environmental variables and biotic attributes in explaining biological characteristics, such as biomass, species richness, and community composition. The biomass of chironomids and the richness of bacteria and chironomids showed a nonlinearly decreasing pattern associated with increased water depth, while biomass and species richness of diatoms showed U-shaped and hump-shaped patterns, respectively. The three taxonomic groups all showed increasing dissimilarity with water depth changes, and there was clear cross-taxon congruence among the variations in community composition. Abiotic variables were pivotal in structuring biological characteristics; however, the biotic attributes also explained a unique portion of their variations. This suggests that biotic interactions significantly influenced the patterns of biomass, species richness, and community compositions along the water depth gradient for the three taxonomic groups studied. Our results provide

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Diatoms
Chironomids

new evidence that biotic attributes could help in predicting the biodiversity of aquatic communities along geographical gradients, such as water depth.

1. Introduction

Understanding the biogeographic patterns of biodiversity along geographical gradients, such as latitude, elevation, and water depth, is one of the most important goals in ecology (Gaston, 2000; Zintzen et al., 2017). Similar to the other geographical gradients, water depth shows complex variations in physical and chemical factors (Bryant et al., 2012), such as substrate type, temperature, light availability and nutrients, which provide strong environmental filtering of aquatic communities (Liu et al., 2018; Smith and Brown, 2002). Water depth is a major driver for species diversity and community composition (Brown et al., 2009; Rex et al., 2005), and thus unimodal and monotonically decreasing patterns for diversity are commonly reported along water depth gradients in marine environments (Levin et al., 2001; Rex, 1973). The literature on water-depth patterns in biodiversity mostly involves plankton and fish in marine and isolated water bodies (Smith and Brown, 2002), but benthic biofilm communities (e.g. bacteria) in lakes, important to aquatic ecosystem processes, have been less studied (Langenheder et al., 2017). Most studies regarding these community organizations report the patterns of species diversity along water depth gradients, and beta diversity is less considered. In addition, it is necessary to compare community patterns across biological groups of different trophic levels, such as microorganisms, animals and plants (Heino et al., 2014). Thus, the general patterns and driving mechanisms for aquatic assemblages along water depth gradients remain poorly understood. For example, are there general water-depth biodiversity patterns in aquatic ecosystems? What are the main influencing factors of water-depth biodiversity patterns for aquatic communities?

In addition to environmental filtering and spatial processes, biotic interactions are also important in structuring communities (Staniczenko et al., 2017; Wisz et al., 2013). Biotic interactions strongly affect the occurrence, biodiversity, and performance of species locally and thereby alter the community composition (Mod et al., 2016). For instance, facilitative interactions with cushion nurse plants change the plant community composition and increase their species richness along the high Andes of southern South America (Cavieres and Badano, 2009). Every species, no matter where it occurs, is connected to other species through complex interaction networks (Staniczenko et al., 2017). Biotic interactions can affect spatial patterns of species distribution through several mechanisms, such as competition, predation, mutualism and consumptive interactions (Faust and Raes, 2012; Worden et al., 2015). The biotic interactions across trophic levels may also promote biological congruence through selective predation, niche partitioning, or facilitation (Ozkan et al., 2014). Cross-taxon congruence and correlation patterns are thus increasingly used to predict biotic interactions. However, few studies show such biological congruence among assemblages for the prediction of species interactions in aquatic ecosystem (Corte et al., 2017).

Biotic interactions could have an important influence on community and ecosystem functioning (Lima-Mendez et al., 2015; Peoples and Frimpong, 2016), but the extent to which these interactions influence the biodiversity of communities remains poorly understood. For instance, in metacommunities, the relative importance of biotic attributes and abiotic variables is currently hotly debated. Compared to biotic attributes, abiotic variables could explain more variations in species diversity and community composition in aquatic environments such as in lakes (Alofs and Jackson, 2015; Langenheder et al., 2017) and streams (Astorga et al., 2011; Tonkin et al., 2018). However, biotic attributes, such as species diversity of other taxonomic groups, could be more important than environmental factors for explaining species diversity in streams (Johnson and Hering, 2010) or soil ecosystem (Carlson et al., 2010; Vandegehuchte et al., 2010). For example, abiotic factors such as water level fluctuation (Boschilia et al., 2008), substrate sizes (Astorga et al., 2014) and flow variability (Carbonell et al., 2011) are the primary factors in shaping stream species diversity, while biotic factors may play larger roles than abiotic factors in streams with low variability in flow regime such as spring-fed or larger mainstem rivers (Johnson and Hering, 2010). In predicting the abundance of plankton in marine environments, the random forest-based models that include biotic attributes, such as viral, prokaryotic, and eukaryotic abundance, are more accurate than those that use environmental variables (Lima-Mendez et al., 2015). Furthermore, biotic attributes have been used to predict the variations in diversity of fish (Peoples and Frimpong, 2016), invertebrates, and bacteria (Langenheder et al., 2017), but the role of biotic attributes in regulating the biomass and community compositions of multiple taxonomic groups remains relatively less studied.

Here, taking water depth in Lake Lugu as a typical geographical gradient, we simultaneously investigated the biomass, species richness, and community compositions of the three taxa, bacteria, diatoms and chironomids from surface sediments. We compared the water-depth patterns of the three taxonomic groups and explored the relative role of biotic attributes in explaining their biological characteristics, such as biomass, species richness and community composition. Lake Lugu, with a maximum depth of 93.5 m, provides an example system to study the biodiversity patterns along the water depth gradient with multiple taxonomic groups. By including bacteria, diatoms, and chironomids, we focused on three specific aims. First, we explored the water-depth patterns in the biological characteristics. Second, we investigated the cross-taxon congruence in the variation of community composition. Third, we evaluated the relative importance of water depth, environmental variables and biotic attributes in predicting these biological characteristics.

2. Materials and methods

2.1. Study area

Lake Lugu (27°41′–27°45′N, 100°45′–100°50′E), located in Yunnan Province, China, is a semiclosed deep-water lake. It has a surface area of 50.5 km², a maximum depth of 93.5 m, a mean depth of ~40.3 m, and an elevation of 2685 m. The detailed procedures for sample collection are described in a previous study (Wang et al., 2012b). In brief, we obtained the surface sediments (~1 cm) from 37 sites with various water depths for analyses of bacteria, diatoms and chironomids in August 2010. At each site, three sediment cores with a 6-cm diameter were retrieved for surface sediments. It should be noted that such surface sediment sampling may underestimate the chironomids in deeper layers, but it is a standard method for chironomids (Glew, 1991) which enables us to compare the communities along the water depth gradient. The sampling sites covered the whole lake area and were distributed along a water depth gradient of 0–93.5 m. The spatial characteristics of the lake ecosystem, such as high connectivity and a small area, enabled the species to disperse freely among sites.

2.2. Community analyses

Community analyses for the three taxonomic groups were performed according to previous studies (Wang et al., 2013; Wang et al.,

2012b; Zhang et al., 2013). Briefly, for bacteria, genomic DNA was extracted from surface sediment samples using the phenol chloroform method (Zhou et al., 1996). We amplified bacterial 16S rRNA genes in triplicate 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). PCRs with negative controls were run to ensure proper amplicons. We then combined and quantified the PCR products of triplicate reactions with PicoGreen and pooled the PCR products from samples sequenced at equal molality using a Roche 454 FLX pyrosequencer (Roche, Switzerland). All 16S rRNA pyrosequencing reads were analyzed using QIIME pipeline (v1.9.0) (Caporaso et al., 2010b). Sequences that were longer than 200 bp were denoised with the Denoiser algorithm (Reeder and Knight, 2010). Further, we clustered the sequences into OTUs at 97% pairwise identity with the seed-based UCLUST algorithm (Edgar, 2013). Chimeras were removed via Chimera Slayer (Haas et al., 2011), and representative sequences from each OTU were then aligned to the Greengenes imputed core reference alignment (DeSantis et al., 2006) using PyNAST (Caporaso et al., 2010a). We determined the taxonomic identity of each representative sequence using the RDP classifier (Wang et al., 2007) and removed chloroplast and archaeal sequences. Before the subsequent analyses, we removed singletons and the bacterial sequences were rarefied at 1,000 sequences to avoid the effects of the variation in abundance or sampling intensity in estimating biodiversity. The DNA concentration was determined using a spectrophotometer (Nanodrop 1000, Thermo Scientific) and used as the microbial biomass value for sediments.

For diatoms, the sediment samples were treated using standard procedures with 10% HCl to dissolve calcium carbonate and 30% H_2O_2 to oxidize organic matter (Berglund, 1986). Counts were conducted for diatom samples using an Olympus microscope with oil immersion objective (magnification × 1,000). At least 500 valves were counted per sample, and taxon biomass was expressed as diatom number per gram of wet sediment in each sample. Diatoms were identified at the species level or lower, primarily using standard European and North American references (Krammer and Lange-Bertalot, 1986-1991; Metzeltin et al., 2009).

For chironomids, surface sediments were deflocculated in 10% caustic potash in a water bath at 75 °C for 15 min, and then sieved at 212 and 90 μm. We then examined all chironomid residue using a stereo-zoom microscope at ×25, mounted head capsules on microscope slides in a solution of Hydromatrix and identified species according to the literature (Brooks et al., 2007; Oliver and Roussel, 1983). The biomass of chironomids was the count of head capsules per gram of wet sediment in each sample.

2.3. Abiotic variables and biotic attributes

We obtained abiotic and biotic variables for surface and bottom water, which were collected from the surface water at 0.5 m and bottom water near the sediment-water interface, respectively. For surface water, we measured temperature, conductivity, pH, chlorophyll-a, dissolved oxygen, total nitrogen, total phosphorus, HCO_3^- concentration, and silica. For bottom water, we analyzed temperature, conductivity, pH, chlorophyll-a, and dissolved oxygen. For surface sediments, we obtained total phosphorus, loss-on-ignition, porosity, water content, 19 metal ion concentrations (Al, Ba, Be, Ca, Co, Cr, Cu, Fe, Li, K, Mg, Mn, Na, Ni, Pb, Sr, Ti, V, and Zn), and grain size. The grain size was classified into 5 groups:<4 μm, 4–16 μm, 16–32 μm, 32–64 μm, and >64 μm. Detailed measurement and calculation methods for abiotic and biotic variables were described previously (Wang et al., 2007). For the above 19 metal ions, we applied principal component analysis (PCA) to reduce the dimensions, and then used the first and second axes (i.e., PC1 and PC2) as additional environmental parameters (Wang et al., 2012a). The remaining measured variables, such as total phosphorus and loss-

on-ignition of surface sediments, were used as environmental variables without a PCA step.

For biotic attributes, bacteria, diatoms, and chironomids were sorted and identified to the lowest possible taxonomic level. To explain the biological characteristics of the three taxonomic groups, we used the following biotic attributes as predictor variables: (i) chlorophyll-a levels of the surface and bottom water; (ii) biomass of microbe, diatoms and chironomids, and species richness of bacteria, diatoms and chironomids; (iii) the first two axes of non-metric multidimensional scaling analyses (nMDS) using Bray-Curtis dissimilarity for the three taxa. For example, in explaining bacterial characteristics, we used 10 biotic variables, that is chlorophyll-a levels of the surface and bottom water, and the biomass, species richness and the first two axes of nMDS of the other taxonomic groups.

2.4. Statistical analyses

First, the relationships between water depth and biomass or species richness were explored with linear and quadratic models with log_{10}-transformation. The better model was selected based on the lower value of Akaike's information criterion (Yamaoka et al., 1978).

Second, we studied the water-depth patterns of beta diversity for the three taxonomic groups and the cross-taxon congruence between different taxonomic groups. We quantified the variation in beta diversity (Tuomisto and Ruokolainen, 2006) using the matrices based on Bray-Curtis dissimilarity to examine the dissimilarity in community composition between pairwise sites for the three taxa. The water-depth distance was measured as the Euclidean distance without a log_{10}-transformation. Then, the variations in beta diversity of the three taxa were plotted against the changes in water-depth distance and taxonomic beta diversity of the other taxonomic groups. This distance-decay relationship (which measures how dissimilarity decays with increasing distance between pairwise sites) was analyzed using a Gaussian generalized linear model, and the significance was determined using Mantel tests (Pearson's correlation) on 9,999 permutations.

Third, we used a random forest model (Feld et al., 2016) to identify the most important predictors of biomass, species richness, and community compositions for bacteria, diatoms and chironomids. The first axis of the nMDS for the three taxonomic groups was used to represent their community composition. NMDS attempts to represent the set of objects along a predetermined number of axes while preserving the ordering relationship between them (Legendre and Legendre, 2012). The following explanatory variables were considered: water depth, environmental variables, and biotic attributes. Statistical dependence between the explanatory variables was assessed using Pearson's rank correlation coefficients, and variables with high correlation coefficients (Pearson $r >$ 0.7) were excluded from the models. Then, an optimal number of 2,000 trees was produced using cross-validation (Elith et al., 2008). The importance of a 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 trees (contributions were scaled to sum to 100).

Finally, we partitioned the variation in biological characteristics into water depth, environment variables and biotic attributes using linear model (Anderson and Gribble, 1998; Borcard et al., 1992). By generating models with the three explanatory matrices, we estimated the proportions of variation in the biological characteristics of bacteria, diatoms and chironomids explained by the three components. The abiotic variables and biotic attributes were the same as those in the random forest analysis. All significant environmental variables and biotic attributes were selected by forward selection against the biological characteristics data with 9,999 permutations for all three taxa. The community composition was Hellinger-transformed with relative abundance square-rooted, as this transformation makes complex data with numerous zero values more suitable for the analysis with linear methods (Legendre and Gallagher, 2001). All statistical analyses were conducted

with *vegan* V2.5–5 (Oksanen et al., 2013), *packfor* V0.0–8 (Dray et al., 2009) and *randomForestSRC* V2.9.0 (Ishwaran and Kogalur, 2014) in the R environment.

3. Results

The relationships between water depth and biomass or species richness were all significant ($P < 0.05$) for bacteria, diatoms and chironomids. The biomass of chironomids and the richness of bacteria and chironomids all showed a nonlinearly decreasing pattern with deeper water (Fig. 1c, d and f). The microbial biomass increased slightly at 0 to 2 m, but then declined with increasing depth (Fig. 1a). For diatoms, however, the biomass showed a U-shaped pattern along the water depth gradient, reaching a minimum at ~18 m, and species richness exhibited a hump-shaped pattern with a peak at ~18 m (Fig. 1b, e).

For all three taxonomic groups, the Bray-Curtis dissimilarity was positively and significantly ($P < 0.05$) related to the changes in water depth (Fig. 2a–c), showing distance-decay relationships with water depth. Such relationships were the strongest for diatoms ($r = 0.48$, $P = 0.001$), followed by bacteria ($r = 0.41$, $P = 0.001$) and then chironomids ($r = 0.39$, $P = 0.001$). For initial dissimilarity, bacteria showed the highest value of 0.79, and diatoms had the lowest value at 0.36. However, bacteria consistently showed the lowest turnover rate with a slope of 0.0019, and diatoms had the highest turnover rate at 0.0063. There were also significant ($P < 0.05$) and positive relationships among these community compositions (Fig. 2d–f), indicating a strong cross-taxon congruence. Diatoms and chironomids showed the highest congruence ($r = 0.71$, $P = 0.001$), followed by bacteria and diatoms ($r = 0.69$, $P = 0.001$) and then bacteria and chironomids ($r = 0.65$, $P = 0.001$). The correlations among their biomass and species richness of the three taxonomic groups were all generally significant ($P < 0.05$), except for the correlation of biomass or species richness between bacteria and diatoms (Fig. S1a, d).

In the random forest and redundancy analyses, for all three taxonomic groups, biotic attributes were selected as significant predictors of the biomass, species richness and community composition (Fig. 3, Fig. S2). In addition, water depth was the most important predictor for the biological characteristics of bacteria, diatoms and chironomids (Fig. 3, Fig. S2, Fig. S3). Environmental variables, such as dissolved oxygen and the pH of bottom water, were also important for these

biological characteristics (Fig. 3). Similar drivers were confirmed for community composition based random forest on the first axis of principal coordinate analyses (Fig. S5).

In variation partitioning analyses, abiotic environmental filtering was the main driver for biological characteristics of the three taxonomic groups, and the pure effect of environment was significant ($P < 0.05$) for their variation (Fig. 4). A lower fraction of variations in the three biological characteristics could be explained by water depth, whereas the shared variation between environmental variables and water depth was substantial, especially for community composition of chironomids (67%) (Fig. 4f). In general, the pure effects of biotic variables accounted for around 1–3% variations of the three biological characteristics for each taxonomic group, except for diatom biomass. For chironomids, the pure effects of biotic attributes were important, albeit minor. Biotic attributes explained 1%, 1% and 3% of the variation in biomass, species richness and community composition, respectively, whereas the shared fraction between environmental variables and biotic attributes was high (8%–13%, Fig. 4c, f and i). For diatoms, biotic attributes were important and explained 21% of the variation in diatom biomass, which was larger than that explained by environmental variables (19%) or water depth (11%) (Fig. 4b). However, pure biotic attributes could not explain the variations in bacterial characteristics (Fig. 4a, d and g).

4. Discussion

One of the longstanding goals of ecology is to explain the distribution patterns of biodiversity. Many studies usually only use the environmental and spatial variables to construct models explaining community distribution and diversity. Much less is known, however, about the role of biotic attributes on the variations in community structures. To the best of our knowledge, this is the first study in revealing the water-depth patterns for multiple taxonomic groups and the biotic effect on biological communities along a water depth gradient. We further explored the relative importance of water depth, environmental variables and biotic attributes in explaining the patterns of biological characteristics, such as biomass, species richness and community composition, among bacteria, diatoms and chironomids. We found that (1) there were predictable water-depth patterns for biological characteristics across the three taxonomic groups, but the patterns for diatoms were distinct from those of bacteria and chironomids. (2) There was
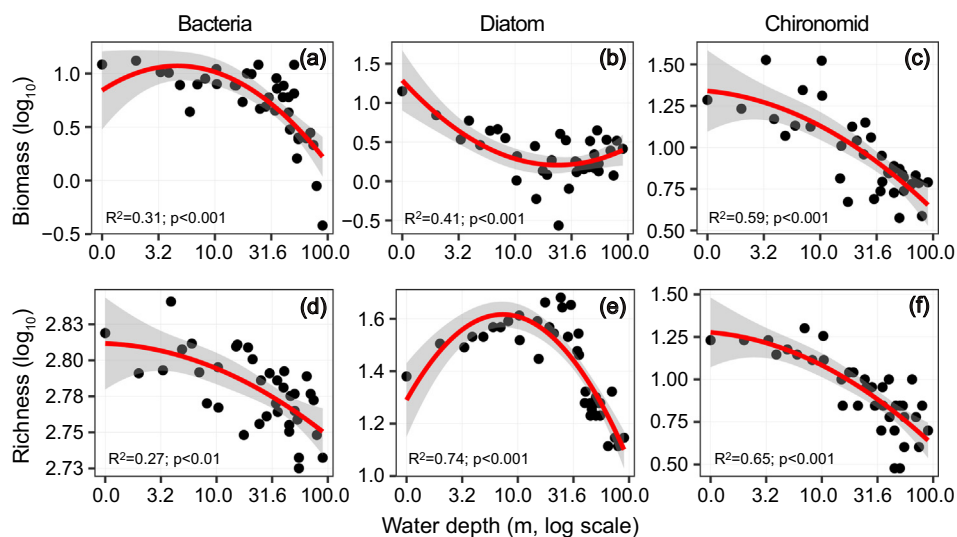

Fig. 1. Water-depth biodiversity patterns for bacteria, diatoms and chironomids. For each taxonomic group, we considered two biological characteristics: biomass (a–c) and species richness (d–f). The left column (a, d) shows the relationships between water depth and bacterial biological characteristics, except for microbial biomass (a). The middle (b, e) and right (c, f) columns show the relationships between water depth and biological characteristics of diatoms and chironomids, respectively. The relationships between water depth and biodiversity were modeled with linear and quadratic models. The better model was selected based on the lower value of Akaike's information criterion. For better visualization, biomass, species richness and water depth were $\log_{10}$ transformed.
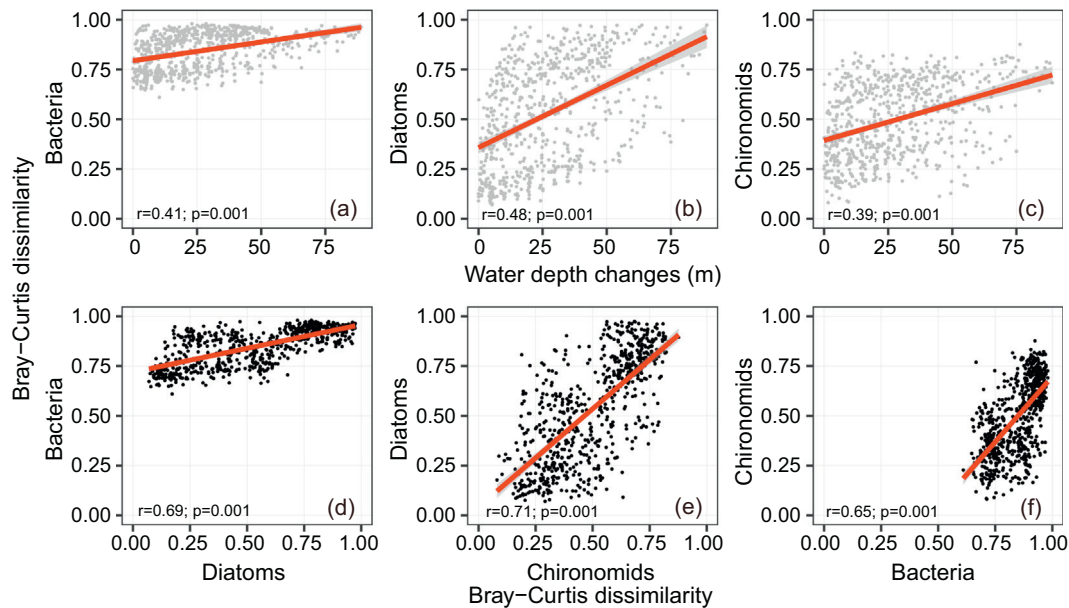
Fig. 2. The relationships among the community dissimilarities and water depth. The upper panels show the relationships of the changes in water depth and the dissimilarity of community compositions for bacteria, diatoms and chironomids. The lower panels illustrate the relationships of the dissimilarity of community compositions among the three taxonomic groups. The regressions of linear relationships, based on the Gaussian generalized linear model, are shown with solid lines. Mantel tests were used to examine the correlations among community dissimilarities and the changes in water depth with 9,999 permutations.

significant congruence among the variations in community compositions for the three taxonomic groups. (3) Although environmental variables showed pivotal roles for biological characteristics, biotic attributes had nonnegligible and significant influences.

4.1. Water-depth patterns in biological characteristics

For biomass and species richness, there are predictable patterns along the water depth gradient in Lake Lugu. The water-depth patterns of bacteria have rarely been reported for lakes. We found significantly decreasing patterns for bacterial richness and chironomid biomass and richness at greater water depths, and U-shaped and hump-shaped patterns for biomass and species richness of diatoms, respectively, along the water depth gradient. The decreasing and unimodal patterns for diversity are consistent with the taxonomic groups of other habitats, such as marine environments (Brown et al., 2009). For instance, monotonously decreasing patterns in the diversity of microbial communities were found in the eastern tropical South Pacific (Bryant et al., 2012). In the northeast Pacific Ocean, plankton biomass and zooplankton diversity declined exponentially with water depth and the diversity of pelagic fish reached a peak at <200 m in depth (Smith and Brown, 2002). In contrast, the diversity of copepod increased with depth in Worth Lake in Canada (Kosobokova et al., 2010).

In contrast to biomass and species richness, beta diversity along water depth gradients is less studied. As expected, bacteria, diatoms and chironomids all showed significant distance-decay relationships along the water depth gradient, that is, that community dissimilarity significantly increased with changes in water depth. This is in line with the results of a recent review of spatial distance-decay relationships for micro- and macroorganisms (Hanson et al., 2012; Nekola and White, 1999), for example, the similarity of the fish community decreased with the differences of water depth (Zintzen et al., 2017).

Interestingly, we found that for bacteria, the initial dissimilarity along the water depth gradient was higher, but the turnover rate along the water depth gradient was lower than those for diatoms or chironomids. Regarding the initial dissimilarity, bacteria can respond more intensively to small-scale changes in local environments and thus can have higher dissimilarity among neighboring communities than can diatoms or chironomids. Diatom assemblages showed the lowest initial

dissimilarity among the three taxonomic groups along the water depth gradient. This difference might be because diatoms and bacteria were more affected by water conditions and sediment characteristics (Haglund et al., 2003), respectively, and the water conditions were more homogenized within smaller scales than sediments. For distance-decay relationships, diatoms showed the highest turnover rate. The distance-decay relationship can result from a decrease in environmental consistency with distance (e.g. water depth gradients in our study) (Nekola and White, 1999). The lowest turnover rate of bacteria may be due to the following: (1) the initial dissimilarity within short distances was highest for bacteria and thus the dissimilarity is less likely to change that much along the water depth gradient, and (2) diatom communities may be the most sensitive to the changes in water depth, while bacteria are affected more by other local environment variables, such as organic matter (Wang et al., 2012a).

For the above three biological characteristics, we showed direct evidence that water depth was the main driver, resulting in predictable patterns along the water depth gradient. The relative contribution of depth was the highest in the three taxonomic groups, which is consistent with previous studies that showed water depth had important effects on the species diversity and community composition (Brown et al., 2009; Bryant et al., 2012; Liu et al., 2018). For instance, depth is the main factor leading to the separation of surface and deep-water communities in marine and lake environments (Brown et al., 2009; Gushulak et al., 2017; Haglund et al., 2003; Kosobokova et al., 2010). Although the water-depth patterns of communities have been widely studied in aquatic systems in recent years, most studies have focused on marine environments (Bryant et al., 2012; Smith and Brown, 2002; Wang et al., 2013), meaning lake ecosystems, such as lake sediments, are less explored (Haglund et al., 2003). Compared to water columns, the sediment environments are more stable and have less stochastic processes affecting biotic communities. The biotic communities in sediments are less exposed to ambient environmental variations, such as water movement and air temperature, than those in water columns, and sediment assemblages are less affected by stochastic processes compared to free-living communities (Wang et al., 2016). In sediments of aquatic ecosystems, deterministic processes have more influence on the microbial communities than those in the overlying water (Wang et al., 2013). We may thus expect that biomass and diversity patterns
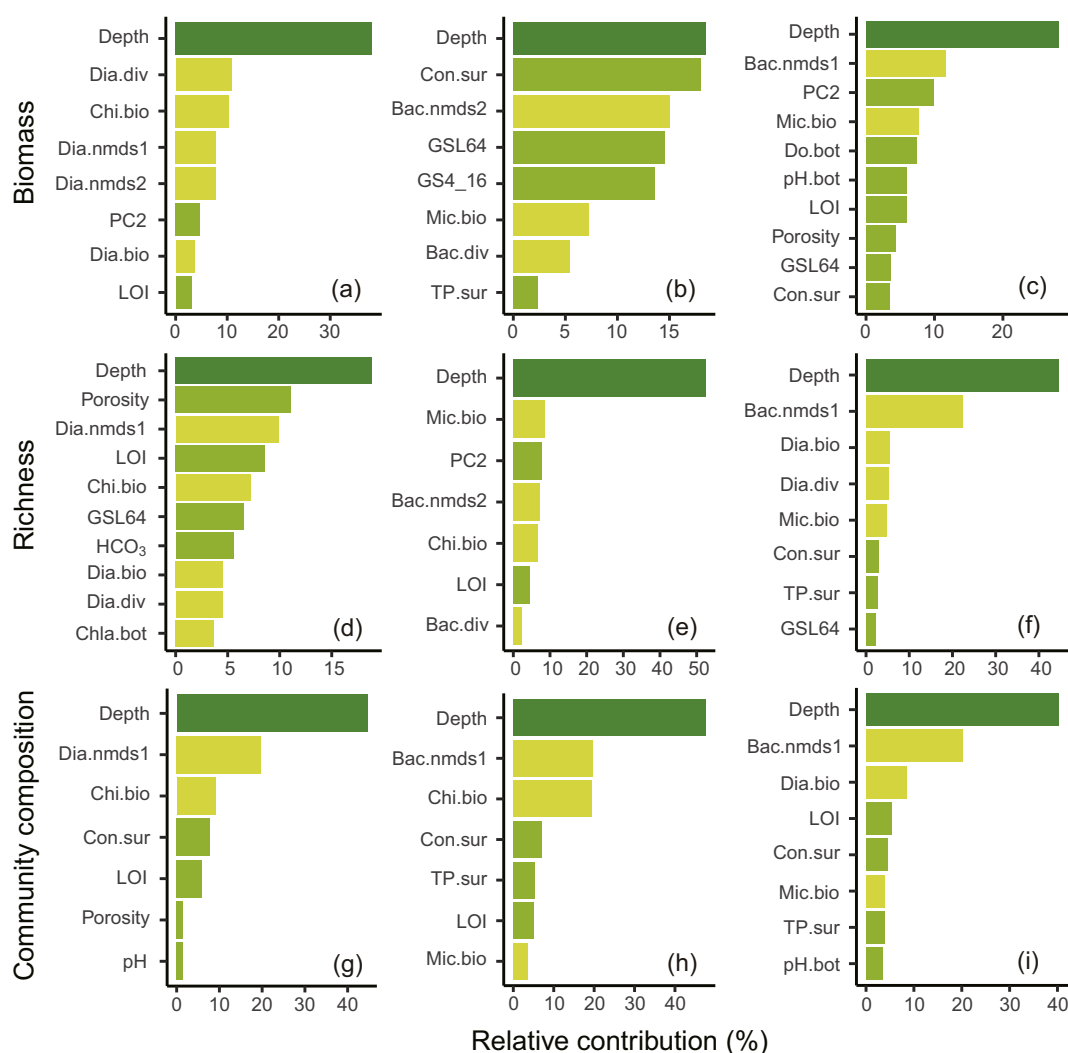
Fig. 3. The abiotic and biotic variables explaining the biodiversity of bacteria, diatoms and chironomids. The biodiversity metrics are biomass, species richness, and community composition. Random forest analysis aimed to identify the important predictors of biological characteristics, such as biomass, species richness and community composition of the three taxonomic groups. The left column (a, d, and g) represents the mean values of relative variable importance for bacterial biological characteristics except for microbial biomass (a). The middle (b, e, and h) and right (c, f, and i) columns represent the mean values of the relative variable importance for biological characteristics of diatoms and chironomids, respectively. Predictors include water depth, environmental variables and biotic attributes. For surface water, total phosphorus (TP.sur), conductivity (Con.sur) and concentration of HCO_3^- (HCO_3) were included in the models. For bottom water, we obtained dissolved oxygen (DO.bot), pH (pH.bot) and chlorophyll-a (Chla.bot) values. In surface sediment, porosity, loss-on-ignition (LOI), grain size, PC1 and PC2 were considered in the models. PC1 and PC2 represent the first and second axes of principal component analysis for 19 metal ions of sediments, such as Al, Ba, Be and Ca. The grain size was classified into five groups:<4 μm (GSL4), 4–16 μm, 16–32 μm, 32–64 μm, and >64 μm (GSL64). Biotic attributes included biomass of microbe (Mic.bio), diatoms (Dia.bio) and chironomids (Chi.bio), species richness of bacteria (Bac.div), diatoms (Dia.div) and chironomids and the first two axes of separate nonmetric multidimensional scaling analyses (nMDSs) for bacteria (Bac.nmds1, Bac.nmds2) and diatoms (Dia.nmds1, Dia.nmds2).

in sediments would be more consistent and stable than those in water columns.

4.2. Cross-taxon congruence along the water depth gradient

There was clear cross-taxon congruence in community variations among the three taxonomic groups, which is supported by the significant correlations among their beta diversities. This is consistent with the significant correlations between the species richness of chironomids and bacteria or diatoms. The congruence of community variations was strongest between diatoms and chironomids, and weakest between bacteria and chironomids. Such cross-taxon congruence was previously reported in producer-consumer relationships. For example, the richness and composition of phyto- and zooplankton are significantly congruent in lakes of Danish (Ozkan et al., 2014). Cross-taxon congruence can occur when the diversity or community composition of different biological groups spatially covary (Rooney et al., 2015). One taxonomic community may provide an indication of general trends in biodiversity and underlying processes of the other biotic components (Bilton et al., 2006). Such a nonrandom congruence may be caused by similar abiotic environments and trophic interactions.

A similar response to abiotic environments, such as microenvironments, may result in the strong congruence among various taxonomic groups (Johnson and Hering, 2010; Ozkan et al., 2014). In Lake Lugu, bacterial and chironomid richness both showed positive relationships with the temperature of bottom water, but not with that of surface water (Fig. S4). Temperature is usually the main environmental factor affecting biodiversity and community composition in aquatic ecosystems (Berger et al., 2010; Soininen et al., 2016; Straile and Adrian, 2010). The diversity of different taxa will be correlated if they respond to the same environmental processes or different environmental variables that covary. For instance, the abundance of macrofaunal and nematode assemblages in marine sediments showed congruent decreasing patterns with higher percentages of coarse sands (Corte et al., 2017).
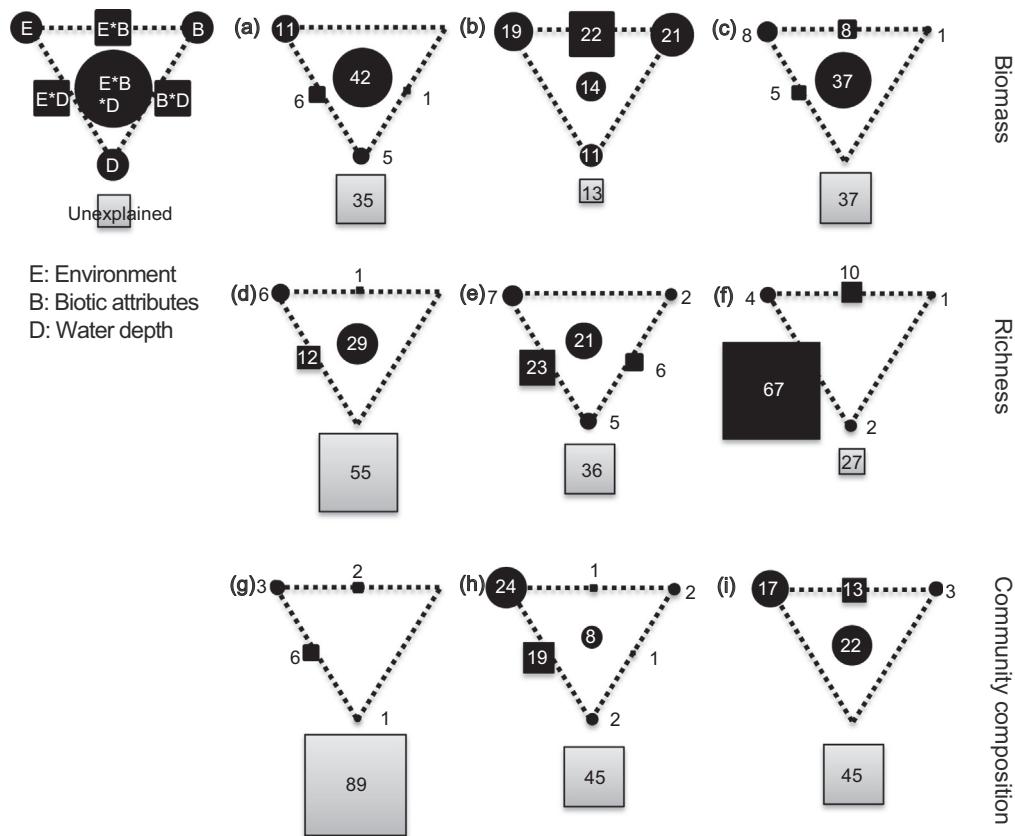
Fig. 4. The relative importance of water depth (D), environmental factors (E) and biotic attributes (B) in explaining biological characteristics. The left-top panel is the general outline. The pure variation explained by each factor is represented by the edges of the triangle. The sides and middle of the triangles indicate the percentages of variation explained by interactions of two or all factors, respectively. For the other penels, the left columns (a, d and g) are bacterial biological characteristics except for microbial biomass (a). The middle (b, e and h) and right (c, f and i) columns are for biological characteristics of diatoms and chironomids, respectively. Unique and shared variances of each factor for explaining the biomass (a–c), species richness (d–f) and community compositions (g–i) for bacteria, diatoms and chironomids are depicted, and geometric areas are proportional to the respective percentages of explained variation. The selected variables are shown in Table S1. The statistical significance was determined according to Monte Carlo permutation test (9,999, $P < 0.01$). The values are the adjusted coefficient of determination (adjusted R^2) and negative variance components are not shown.

Cross-taxon congruence can also be promoted by trophic interactions, such as competition, predation and facilitation (Englund et al., 2009; Greve et al., 2012). Diversity of higher trophic levels can be promoted by a diverse producer community via enabling niche partitioning (Tilman et al., 1982) or simply through productivity effects. For instance, bacterial abundance and community composition were directly related to the community composition of algae (Grossart et al., 2005). In turn, due to predation, the distribution of consumers can constrain distributions or range limits of producers, such as plants (Wisz et al., 2013). As chironomids are consumers of diatoms, the predation of chironomid larvae can influence diatom assemblages in lakes.

4.3. Abiotic variables and biotic attributes in explaining water-depth patterns

For the three taxonomic groups, environmental factors showed strong effects on biomass, species richness and community composition, which is in line with the view that species are filtered by environmental factors and are more productive in suitable conditions (Alofs and Jackson, 2015; Cottenie, 2005; Heino et al., 2014). In general, the pure effect of biotic attributes or water depth was lower than that of environmental variables for the three biological characteristics of each taxonomic group. This finding reflects that environmental variables play a strong role in determining species diversity and community composition (Fierer et al., 2007; Tuomisto et al., 2003). For instance, environmental variables, such as pH and temperature, were the primary drivers for the community composition of bacteria in lakes in northern Europe (Lindstrom et al., 2005). In Canadian lakes, dissolved organic

carbon and total phosphorus of water are the important environmental variables for bacterial community composition and zooplankton abundance, respectively (Beisner et al., 2006).

Among biotic and abiotic variables considered, water depth was the most important factor for aquatic assemblages, which is consistent with previous studies. For instance, water depth explained a significant and substantial proportion of the variation in chironomid communities along the water depth gradient (Kurek and Cwynar, 2008). Bacterial abundance decreased toward deep sediment depths in Lake Erken (Haglund et al., 2003). The pure effect of water depth was, however, low, while it was substantial for the joint effects of environmental variables and water depth (Fig. 4f). This indicated that water depth is a multi-proxy variable and affects the biological communities by interplaying with other covaried explanatory factors (Fig. 5). For instance, physicochemical factors, such as temperature, light and nutrient levels, may be the actual causes of water-depth patterns for aquatic community (Engels and Cwynar, 2011; Gushulak et al., 2017; Jamieson et al., 2010; Laird et al., 2010). Thermocline, a rapid decrease in temperature along water depth, separates the mixed layer or epilimnion from the cooler bottom layer or hypolimnion (Mazumder et al., 1990). In Lake Lugu, the thermocline depth varied from 10 m in summer to 17.5 m in autumn, which agrees largely with the abrupt changes in the biomass and species richness of diatoms at 18 m based on quadratic models. This consistency indicates that thermocline depth may affect the biomass and diversity of benthic diatoms (Wang et al., 2018), which is also reported for plankton communities (Berger et al., 2006; Longhi and Beisner, 2009). Plankton assemblages could be influenced by thermocline depth through sedimentation losses and nutrient
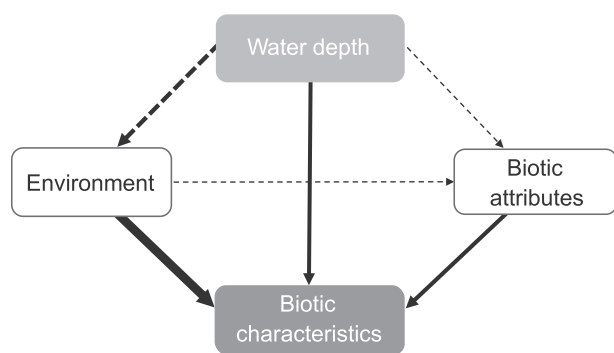
Fig. 5. The conceptual model for the explanation of biological characteristics along water depth gradients. Three main drivers were considered for biomass, species richness and community compositions: water depth, environmental variables and biotic attributes. The direct and indirect effects of these variables are shown as solid and dotted lines, respectively. Line width indicates the relative importance of these variables for biological characteristics.

availability, and thus the biomass of diatoms peaks near the metalimnion, where colder and denser water prevents their sinking (Reynolds, 1984). With the deepening of thermocline, the biomass of zooplankton (Gauthier et al., 2014) and phytoplankton (Cantin et al., 2011) shows increased and unimodal responses, respectively.

Biotic interactions, however, had nonnegligible and significant influences on the biological characteristics of the three taxonomic groups, especially for chironomids and diatoms (Fig. 5). This is consistent with previous studies that have shown biotic interactions influence species distributions, promote assemblages of species and thus also potentially alter biodiversity patterns (Alofs and Jackson, 2015; Lima-Mendez et al., 2015; Wisz et al., 2013). For example, approximately 48% of the variance in fish diversity is related to the diversity of invertebrates, macrophytes and diatoms in European streams (Johnson and Hering, 2010). In lakes of northeastern Finland, biotic attributes, such as algal biomass and species richness of macroinvertebrate communities, have a significant, albeit minor, effect and could explain a unique proportion of variation in bacterial phylogenetic diversity (Langenheder et al., 2017).

For chironomids, biotic interactions were likely the important limiting factors to community biological characteristics. More specifically, a unique variation in their biological characteristics could be explained by the biotic attributes, such as biomass and richness of diatoms, microbial biomass and bacterial community composition. Among these biotic attributes, the most important one was the bacterial community composition, suggesting that bacteria could be important in determining of chironomid diversity and community composition. Bacteria in the environment can be fed by chironomid larval, furthermore, bacteria can chemically modify detritus to render it usable by chironomids or can supply particular substances essential for growth (Pinder, 1986). In addition, the biomass and species richness of diatoms were also important biotic attributes for chironomid richness and community composition, which indicates that the top-down control of producer communities is strong in lakes (Shurin et al., 2002; Wisz et al., 2013). Thus, chironomid biological characteristics along the water depth gradient could be a function of bacterial and diatom biotic attributes.

For diatoms, a high proportion of variation in its biological characteristics could be explained by bacterial community composition and chironomid biomass. For instance, the two biotic attributes explained 16.3% and 16.0% of the variation in diatom community composition, respectively, which is higher than that of environmental variables (Fig. 3h). This may reveal that biotic attributes were relatively important for diatom communities. The bacterial community composition was generally the most important biotic attribute for the biomass and community composition of diatoms, indicating that biotic interactions with bacteria can be one of the main factors driving diatom aggregation (Bruckner et al., 2011; Gardes et al., 2011). Bacteria can provide

inorganic nutrients to producers through mineralization and bacterial metabolic products may also affect algae communities (Cole, 1982). Furthermore, bacteria can control algal communities by inhibiting the growth of diatoms or by active lysis of algal cells (Paul and Pohnert, 2011). Chironomid biomass was also related to the species richness and community composition of diatoms, which indicates the important effects of predation on lower trophic levels (Mieczan et al., 2015; Shurin et al., 2002). For example, the species richness of diatoms increased toward higher chironomid richness in our study (Fig. S1). Predation of chironomid larvae could stimulate diatom production through excretion and further influence diatom communities via a cascading effect (Pagano et al., 2010). In addition, bioturbation of chironomid larvae may enhance mineralization processes and inorganic nutrient efflux by the oxygenation of sediment influences (Lohrer et al., 2004; Ståhl-Delbanco and Hansson, 2001), which contributes to the nutrient supply for primary producers, such as diatoms.

Nevertheless, there are some caveats for the interpretation of our results. First, abiotic environmental gradients could generate spurious correlations between the communities. For example, if there was irradiance at the bottom, the diatoms in sediments would be composed of both benthic species growing at sediments and planktonic species settling to the bottom (Lange et al., 2011). Then, higher species richness is expected in this zone, which is consistent with the abrupt decrease of diatom richness at 40 m (Fig. 1e). Likewise, a higher primary production of benthic and planktonic diatoms can provide greater carbon availability for bacteria and chironomids, which finally explains their higher biomass with abrupt changes at 40 and 15 m, respectively (Fig. 1a, c). Therefore, the explanatory variable for diatoms could be the light, and for bacteria and chironomids would be the primary production conditioned by light. Such relationships could be interpreted as a biotic explanation of diatom community or as that the causal explanatory variable is the light.

Second, some abiotic variables are highly correlated or difficult to measure, which increases the difficulty in statistically exploring the pure effects of abiotic factors on the water-depth patterns in biodiversity. Further, the observed biodiversity pattern could be also explained by other unmeasured ecologically important environmental variables, such as the depth of photic zone (Pla-Rabés and Catalan, 2018), the extension of mixing layer and the slope of the bottom. For instance, the slope of the bottom can condition loss-on-ignition, grain size, and other variables, which can influence the biological communities in lakes (Rossi et al., 2010). Such abiotic variables are encouraged to be included in future studies for better explaining the observed patterns in biomass and biodiversity.

5. Conclusion

Overall, we found predictable water-depth patterns in the biomass, species richness, and beta-diversity at multiple biological levels, from tiny bacteria to relatively large chironomid fly larvae. These results are expected for significant declines in biomass and species richness with depth for bacteria and chironomids, but are surprising for diatom biomass and richness peaking at intermediate depths. The water-depth patterns in diatom biomass and species richness were distinct from those of bacteria and chironomids. Although the number of taxonomic groups included here was relatively limited, our findings can be regarded as be the first study to synthesize and compare the water-depth patterns in biological characteristics for multiple taxonomic groups. For bacteria, the initial dissimilarity along the water depth gradient was higher, but turnover rate was lower than those of diatoms or chironomids. Water depth was the main driver for biomass, species richness and turnover of the three taxonomic groups. Furthermore, there was significantly strong congruence among these taxa, especially between diatoms and chironomids. We also provided new evidence for the important role of biotic attributes in explaining the variations in multiple taxonomic communities in aquatic ecosystems. Such

information suggests that biotic attributes could help in predicting the biodiversity of aquatic communities along geographical gradients. Further studies are encouraged to investigate and quantify the relative importance of biotic attributes among different community assembly processes along geographical gradients.

Author contributions

JW conceived the idea. JW, XY, QW, EZ and ZN provided physiochemical and biological data. JW performed the bioinformatic analyses. WZ led the statistical analyses with the contributions from AH and JW. WZ wrote the first draft of the manuscript. WZ, JW and AH finished the manuscript with the contributions from HD, JS and LZ. All authors contributed to the intellectual development of this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.05.381.

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