Taxonomic Dependency of Beta Diversity for Bacteria, Archaea and Fungi in a Semi-Arid Lake

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Abstract

Microbial beta diversity has been recently studied along the water depth in aquatic ecosystems, however its turnover and nestedness components remain elusive especially for multiple taxonomic groups. Based on the beta diversity partitioning developed by Baselga and Local Contributions to Beta Diversity (LCBD) partitioning by Legendre, we examined the water-depth variations in beta diversity components of bacteria, archaea and fungi in surface sediments of Hulun Lake, a semi-arid lake in northern China, and further explored the relative importance of environmental drivers underlying their patterns. We found that the relative abundances of *Proteobacteria*, *Chloroflexi*, *Euryarchaeota* and *Rozellomycota* increased towards deep water, while *Acidobacteria*, *Parvarchaeota* and *Chytridiomycota* decreased. For bacteria and archaea, there were significant ($P < 0.05$) decreasing water-depth patterns for LCBD and $LCBD_{Repl}$ (i.e., species replacement), while increasing patterns for total beta diversity and turnover, implying that total beta diversity and LCBD were dominated by species turnover or $LCBD_{Repl}$. Further, bacteria showed a strong correlation with archaea regarding LCBD, total beta diversity and turnover. Such parallel patterns among bacteria and archaea were underpinned by similar ecological processes like environmental selection. Total beta diversity and turnover were largely affected by sediment total nitrogen, while LCBD and $LCBD_{Repl}$ were mainly constrained by water NO_2^--N and NO_3^--N. For fungal community variation, no significant patterns were observed, which may be due to different drivers like water nitrogen or phosphorus. Taken together, our findings provide compelling evidences for disentangling the underlying mechanisms of community variation in multiple aquatic microbial taxonomic groups.

1. Introduction

Lake level or water depth of lakes, especially in arid regions, is vulnerable to global change largely since the accelerated decreasing winter ice cover and increasing surface temperature have been caused by climate warming [1]. Lake ecosystems support a global heritage of biodiversity and helps sustaining a variety of ecosystem functions [2]. Accordingly, understanding and disentangling the mechanisms of biodiversity variation are crucial to predict aquatic ecosystem responses to global climate changes [3]. As an essential biodiversity facet, beta diversity is well applied to reveal the patterns from local to global scales [4] in explaining the assembly mechanisms of community assemblages [5]. More generally, biological community variation along environmental gradients and the underlying drivers have been examined across temporal [6] and spatial scales [7], such as in mountain streams [8] and plateau lakes [9]. However, it is still relatively rare for addressing water-depth patterns of beta diversity and its components (i.e., turnover and nestedness) [10] across taxonomic groups, especially regarding aquatic microbes in semi-arid lakes.

Since the term “beta diversity” was introduced to describe biological community variations by Whittaker in 1960 [11], numerous methods have been proposed to disentangle its underlying mechanisms. In recent studies, for beta diversity, its partitioning components of turnover and nestedness mostly lie in the heart of discussion [12]. There are two alternative approaches for unraveling the variation in beta diversity

components, that is beta diversity partitioning developed by Baselga [10] and the Local Contributions to Beta Diversity (LCBD) partitioning by Legendre [13]. According to the Baselga's framework, beta diversity (i.e., Sørensen dissimilarity) can be partitioned into two components: species turnover and nestedness [10]. The former indicates that one species replaces another without changing species richness, while the latter refers to the richness differences attributable to species gain or loss [10]. More precisely, species turnover can effectively reflect species sorting via ecological processes like environmental selection or dispersal limitation, whereas nestedness is largely relevant to the dynamic processes of the ordered extinction-colonization [14]. In general, the ecological processes underpinning community assembly can be revealed by species turnover and nestedness [15], partitioning beta diversity may thus provide a better comprehension for the structuring of biological communities at spatial scales or along environmental gradients [16].

Unlike the Baselga's method [10], LCBD shows a shorter history of valuating variation in community composition and can substantially characterize the degree of community uniqueness [8, 17]. Based on the dissimilarity measures like Sørensen indices, total LCBD can be divided into the components of species replacement (i.e., $LCBD_{Repl}$) and nestedness (i.e., $LCBD_{Nes}$) [18]. The two partitioned components allow us to reveal the underlying mechanisms that guide the structuring of sites' uniqueness, largely facilitating the local biota to make corresponding conservation strategies. Ecologically, LCBD is often applied to quantify the relative contributions of individual sampling sites to overall beta diversity [13]. For example, in the subarctic ponds of Finland and Norway, the U-shaped elevational patterns in LCBD have been unraveled in bacterial communities, which provides novel perspectives for the complex biogeography patterns of microbial taxa [19]. Additionally, there exists different water-depth patterns in the total LCBD, $LCBD_{Repl}$ and $LCBD_{Nes}$ from bacteria, diatoms to chironomids in Lugu Lake, which is largely driven by different environmental factors, such as spatial or biotic variables [20]. Notably, LCBD and Sørensen coefficients can substantially provide crucial insights into the ecological processes driving the community assemblages [20, 21]. Therefore, coupling the two above approaches by Baselga and Legendre may pave a better way to examine the structuring of aquatic microbial communities.

Here, based on the Baselga's and Legendre's frameworks [10, 13], we partitioned the two beta diversity metrics Sørensen dissimilarity (i.e., total beta diversity) and LCBD into species turnover (or $LCBD_{Repl}$) and nestedness (or $LCBD_{Nes}$), and then examined the water-depth patterns in beta diversity components regarding bacteria, archaea and fungi in surface sediments of the semi-arid lake Hulun Lake in the Northern China. We primarily focused on the following three aims: First, we revealed the underlying mechanisms of variation in total beta diversity and LCBD from bacteria, archaea to fungi. Second, we investigated the cross-taxon congruence among the three microbial taxa regarding the above two metrics and their partitioning components. Third, we tested the relative importance of water and sediment variables on total beta diversity and LCBD across the three microbial taxa and evaluated how each driving factor influences the loss and replacement of species along the water-depth gradient.

2. Materials And Methods

2.1 Study area and field sampling

Hulun Lake (48°33' -49°20' N, 116°58' -117°48' E), also known as Dalai Lake, located in the west of Hulunbuir Prairie, is a shallow semi-arid lake in the Mongolian Plateau [22]. As the fifth largest freshwater lake in China, it has a surface area of 2,315 km^2, a perimeter of 447 km, a maximum depth of ~8.0 m, a mean depth of ~5.7 m, and the water storage capacity of 13.2 billion m^3 [23]. Hulun Lake, a historic and tectonic lake, showing an irregular or unique rectangular shape with the length of 93 km and the largest width of 41 km [23], lies in the semi-arid region of the middle temperate zone [24]. Accordingly, the lake is strongly affected by the temperate continental climate, displaying mean annual air temperature of -0.2°C, precipitation of 290 mm, and evaporation of 1,600 mm [25]. Additionally, its water supplies are mainly fed by direct surface runoff, rainfall and groundwater, and Kherlen River and Urson River provide the main source of water for this lake [23]. In the past 20 years, Hulun Lake has experienced dramatic water level fluctuations mainly resulting from variations in river runoff and evaporation associating with climate change [26]. To date, Hulun Lake is under meso-eutrophic with a documented history of severe eutrophication [27], such as cyanobacteria blooms [28].

In June 2020, surface-sediment samples (0-5 cm) were collected from 19 sites of Hulun Lake (Fig. S1) using a stainless-steel grab sampler. At each sampling site, these surface sediments were fully stirred and homogenized, and then transferred to sterilized bottles. Meanwhile, 100 mL surface water was sampled within 50 cm. These sediment and water samples were transferred to laboratory at -18°C. Sediment samples were dried using a vacuum freeze dryer and then stored in -20°C before the physicochemical and biological analyses. Water depth was measured and recorded in situ.

2.2 Measuring the water or sediment properties

For environmental factors of surface water, temperature, dissolved oxygen (DO), pH, electrical conductivity (EC), secchi depth (SD) were measured in situ using a YSI 650 multi-parameter display system with a 600XL probe [20]. Additionally, NO_3^--N, NO_2^--N, NH_4^+-N, total nitrogen (TN), total phosphorus (TP) and PO_4^{3-}-P were determined based on the standard methods [29].

For sediment properties, we obtained pH, EC, water content (WC), grain size (GS), dissolved organic carbon (DOC), NO_2^--N, NO_3^--N, NH_4^+-N, PO_4^{3-}-P, TN, TP, and total carbon (TC). pH and EC were measured in situ. WC was measured by oven dry method and pycnometer method [30]. Sediment samples were first dissolved using ultrapure water and then filtrated with the 0.45 μm membrane to obtain the aqueous solution. NO_2^--N, NO_3^--N, NH_4^+-N, and PO_4^{3-}-P were then measured via the same methods as water samples [29]. DOC was extracted according to our previous studies [31], and measured by a total organic carbon analyzer (ET1020A, USA). The freeze-dried sediment samples were gound into fine powder and passed through a 100-mesh sieve for TC and TN analyses using an elemental analyzer (Flash EZ 1112 series, Italy), and for TP measurement using molybdenum blue colorimetry after acidification [32]. GS was divided into three classes: < 32 μm (GS32), 32-64 μm (GS32-64) and > 64 μm (GS64). Considering

multicollinearity between abiotic variables, GS32 was then selected as a representative of GS, and the detailed measurement or calculation methods for GS are described in a previous study [33].

2.3 Microbial communities

Briefly, as previously described [7, 9], the genomic DNA was extracted from 0.45 g of frozen sediments using the DNeasy Power Soil Kit (QIAGEN, Germany). Its quality was tested via NanoDrop One/OneC UV-Vis spectrophotometer (Thermo Fisher Scientific, USA). For bacteria and archaea, the 16S rRNA genes were amplified using the universal primers: 515F (5'-GTGYCAGCMGCCGCGGTAA-3') and 806R (5'-GGACTACNVGGGTWTCTAAT-3') [34, 35]. For fungi, we selected the gITS7F/ITS4R primer pair (gITS7F, GTGARTCATCGARTCTTTG, ITS4R, TCCTCCGCTTATTGATATGC) [36] to amplify the internal transcribed spacer 2 (ITS2) region of the rRNA gene. The 16S rRNA and ITS amplicons were pooled independently and sequenced using Illumina HiSeq 2500 platform (Illumina, San Diego, USA). For the obtained data, sequences analysis was then performed through Quantitative Insights into Microbial Ecology (QIIME) pipeline (v1.9.0) [37]. Based on the seed-based UCLUST algorithm, the sequences with $\geq$ 97% similarity were regarded as the same operational taxonomic units (OTUs) [38]. During the clustering, Singletons and Chimera sequence were excluded or removed by ChimeraSlayer [39]. For each representative sequence, the Greengenes database was applied to align taxonomic information via PyNAST [40]. More details are described in previous studies [41]. After taxonomic assignment, for the following analyses, the communities of bacteria, archaea and fungi were rarefied at 65,800, 200, 66,300 sequences, respectively. The raw data sequencing 16S rRNA and ITS genes have been submitted to the NCBI Sequence Read Archive database and are available under accession number SRR13611586 to SRR13611623.

2.4 Statistical analyses

For each microbial taxonomic group, we first explored the relationships between the relative abundances of their dominated phyla and water depth using linear and quadratic models. The water-depth patterns of the first three dominant phyla were visualized, such as *Proteobacteria*, *Chloroflexi* and *Acidobacteria* for bacteria, *Crenarchaeota*, *Euryarchaeota* and *Parvarchaeota* for archaea, and *Ascomycota*, *Rozellomycota* and *Chytridiomycota* for fungi. The better model was performed based on the lower value of Akaike's information criterion (AIC) [42].

Second, according to the Legendre's method [18], the Local Contributions to Beta Diversity (LCBD) and its components (i.e., $LCBD_{Repl}$ and $LCBD_{Nes}$) were performed to estimate the degree of ecological uniqueness regarding the community composition. The LCBD was examined using the Sørensen-based indices of the Baselga's family, and its indices were calculated via the function 'LCBD.comp' based on the species replacement or nestedness matrices [20]. The water-depth patterns of these LCBD indices were then explored using linear and quadratic models. Given the lowest value of AIC [42], we obtained the best model.

Third, as proposed by Baselga [10], we explored the depth-related patterns of the total beta diversity and its partitioned components such as species turnover and nestedness for the three taxonomic groups. Specifically, this method needs to be based on the multi-site different dissimilarity coefficients as follows:

(1) the total beta diversity was employed via the Sørensen coefficient, (2) the species turnover was computed using Simpson coefficient, and (3) the nestedness was calculated with nestedness coefficient [10, 43]. Moreover, the water depth difference was computed with the Euclidean distance. Analogous to LCBD, we then explored the relationship between the total beta diversity or its components and the water depth difference with linear and quadratic models. Mantel test (9,999 permutations) [44] was then performed to estimate the significance.

Further, we also explored the associations among bacteria, archaea and fungi using linear and quadratic models. For the three taxonomic groups, Pearson correlation was then applied to examine the associations between the environmental factors (i.e., water and sediment physiochemical properties) and the total LCBD or its components. Moreover, we performed Mantel test [44] to explore the relationships between the abiotic variables and the total beta diversity or its partitioned components. Further, the multicollinearity (Fig. S4) between all explanatory variables was evaluated using the function ‘varclus’ based on the R package Hmisc, and then one factor was selected from the variables having high correlation coefficients (Spearman $r > 0.7$) [45].

Then, the random forest model [46] was employed to examine the most important predictors of the LCBD and its two components from the water and sediment variables above. Notably, we applied cross-validation [47] to get the optimal number of 2,000 trees. The importance of a explanatory variable was valuated based on its frequency of selection (for splitting), weighted by a measure of improvement in the model given each split and averaged across all the trees (the contributions were scaled to sum to 100) [20].

Finally, we applied the multiple regression on distance matrices (MRM) [48] to estimate the relationships between the above environmental variables and each component of beta diversity for the three taxonomic groups. These variables were z-score standardized (i.e., mean = 0, SD = 1) before performing the statistical analyses. There were two groups of explanatory variables: water and sediment variables, which were calculated as a Euclidean distance matrix. Additionally, the spurious associations among the variables were excluded using the above function ‘varclus’ [45]. Then, the non-significant variables were removed from the initial MRM test and the test was further re-ran. The matrix permutation was performed 999 times to examine the significance of the partial regression [20]. These above analyses were implemented with the R packages vegan V2.5-4 [49], betapart V1.5.1 [50], ecodist V2.0.1 [51], Hmisc [52], and randomForestSRC V2.9.0 [53].

3. Results

3.1 Water-depth variations in the relative abundance of microbial dominant phyla

In general, there were different water-depth patterns in the relative abundance of the main phyla of bacterial, archaeal and fungal communities (Fig. 1). At the phylum level, the bacterial community was

dominated by the phyla *Proteobacteria*, *Chloroflexi* and *Acidobacteria*, comprising about 40%, 15% and 6%, respectively (Fig. S2a). The relative abundance of *Proteobacteria* and *Chloroflexi* significantly ($P < 0.05$) increased towards deep water (Fig. 1a, b), while *Acidobacteria* declined ($P < 0.001$) (Fig. 1c).

Regarding archaeal community, the dominant phyla were *Crenarchaeota* (40%), *Euryarchaeota* (40%) and *Parvarchaeota* (20%), which were mostly predominant in the whole lake (Fig. S2b). Notably, for the relative abundance, *Euryarchaeota* exhibited a significant ($P < 0.05$) increasing pattern along the water depth (Fig. 1e), whereas *Parvarchaeota* showed a decreasing pattern (Fig. 1f).

Additionally, fungal community was mainly composed of the phyla *Rozellomycota*, *Chytridiomycota* and *Ascomycota*, comprising about 41%, 28% and 18%, respectively (Fig. S2c). The relative abundance of *Rozellomycota* significantly ($P < 0.01$) increased with water depth (Fig. 1h), whilst that of *Chytridiomycota* decreased ($P < 0.05$) toward deep water (Fig. 1i).

3.2 Patterns and drivers of LCBD and its components along the water depth

The relationship between LCBDs (i.e., total LCBD, $LCBD_{Repl}$ and $LCBD_{Nes}$) and water depth was distinct among the three microbial groups. For total LCBD, the water depth pattern with a significant ($P < 0.05$) decrease was observed between bacteria and archaea (Fig. 2a). The latter had the stronger variation in total LCBD towards deep water, with a slope of -0.0043, whereas the former showed the lower slope at -0.0030 (Fig. 2a; Table S2). For $LCBD_{Repl}$, there was a significant ($P < 0.05$) decreasing pattern for archaea, while not significant for bacteria (Fig. 2b). Meanwhile, for $LCBD_{Nes}$, there was non-significant depth-related pattern for bacteria and archaea along the water-depth gradient (Fig. 2c). Note that such non-significant patterns were also observed for all of fungal LCBDs, including the total LCBD, $LCBD_{Repl}$ and $LCBD_{Nes}$ (Fig. 2a-c).

As expected, bacteria had a high positive correlation with archaea regarding the total LCBD (Pearson r = 0.58, $P < 0.01$) and $LCBD_{Repl}$ (r = 0.35, $P > 0.05$), although their correlation was not significant for $LCBD_{Repl}$ (Fig. 3a, b). Correspondingly, bacteria and archaea both showed consistent and non-significant correlations with fungi regarding the total LCBD and $LCBD_{Repl}$ (Fig. 3d, e, g, h). Likewise, for $LCBD_{Nes}$, there was still no significant correlation among all of the three taxonomic groups (Fig. 3c, f, i).

Further, the importance of each variable on the total LCBD, $LCBD_{Repl}$ and $LCBD_{Nes}$ varied substantially with the different microbial taxa. For instance, for bacteria, water NO_3^--N and sediment NH_4^+-N exerted great influences on the total LCBD, with the relative contribution of 16.12% and 14.87%, respectively, while water NO_2^--N was the most important variable explaining the variation in the $LCBD_{Repl}$ and $LCBD_{Nes}$ with the relative contribution of 33.15% and 90.61%, respectively (Fig. 5a). For archaea, the total LCBD and $LCBD_{Repl}$ were both well explained by water NO_3^--N and sediment TP, TN and NH_4^+-N, whereas the $LCBD_{Nes}$ was primarily affected by sediment NO_3^--N with the relative contributions of 14.87% (Fig. 5a).

Conversely, for fungal LCBDs, partial environmental factors showed certain influence (Fig. 5a) but no significant correlation (Fig. S3a).

3.3 Water-depth patterns and drivers of the total beta diversity and its components

Patterns in total beta diversity and its components along water depth difference were interesting across microbial taxonomic groups. For the total beta diversity, there were linearly positive and significant ($P < 0.05$) relationships with water depth changes for bacteria and archaea (Fig. 2d), and the latter changed faster than the former with the decay slopes of 0.0414 and 0.0253, respectively (Fig. 2d; Table S2). Similarly, for the turnover component, bacteria and archaea both showed significant ($P < 0.05$) increasing patterns with larger water-depth difference (Fig. 2e). Note that such water-depth decay patterns were not significant for nestedness components of bacterial and archaeal total beta diversity (Fig. 2f). In addition, for fungal community, there was still non-significant depth-related pattern for total beta diversity and the two partitioning components, which is similar to the LCBDs (Fig. 2d-f).

When viewed among the three microbial groups, intriguingly, there were cross-taxon congruence for the total beta diversity and its components. Accordingly, bacteria showed a strong positive correlation with archaea regarding total beta diversity (Mantel r = 0.64, $P < 0.001$, Fig. 4a) and the turnover component (Mantel r = 0.51, $P < 0.001$, Fig. 4b). Moreover, similar to the LCBD, fungi was still not significantly correlated with bacteria and archaea regarding total beta diversity (Fig. 4d, g) and the species turnover (Fig. 4e, h). For the nestedness component, there was still no significant correlation from bacteria, archaea to fungi, which is in line with the $LCBD_{Nes}$ (Fig. 4c, f, i).

It should be noted that the importance of water and sediment variables to total beta diversity and its partitioning components also varied across the three groups. For bacteria and archaea, sediment TN was the most important ($P < 0.05$) predictor of the total beta diversity and its turnover component (Fig. 5b). Additionally, the nestedness component of archaea was significantly ($P < 0.05$) negatively correlated with water NO_2^--N, with the linear coefficient of -0.5 (Fig. 5b). For fungi, total beta diversity and the nestedness component were mainly affected by water TP, while the turnover component was simply constrained by sediment NO_3^--N (Fig. 5b). However, there was no significant correlation between fungal total beta diversity and its components and each variable except for water PO_4^{3-}-P (Fig. S3b).

4. Discussion

Partitioning beta diversity is an effective way to unravel the response mechanism of organisms to climate change, especially in climate-sensitive arid regions [54]. Turnover and nestedness, showing different implications for biodiversity conservation [16], are often invoked to disentangle the spatial patterns of compositional beta diversity in biogeography and microbial ecology [12]. In the semi-arid Hulun Lake, we investigated the driving mechanisms of beta diversity and community uniqueness for bacteria, archaea and fungi towards deeper water based on the Baselga's [10] and Legendre's [18]

frameworks, respectively. Our results suggest that (1) the relative abundance of most dominant phyla had significant water-depth patterns across the three taxa. (2) For the LCBD and the total beta diversity and its turnover component, water-depth patterns were significantly observed for bacteria and archaea, but not for fungi. (3) There was a high correlation between bacteria and archaea regarding the LCBD, the total beta diversity and its turnover components. (4) The relative importance of water and sediment environmental factors on the LCBD, total beta diversity and their additive components was demonstrated to vary for the studied microbial taxonomic groups.

4.1 Water-depth patterns of the LCBD, total beta diversity and their partitioned components

For the total LCBD, we found that bacteria and archaea both showed significant decreasing patterns along the water depth, while fungi did not (Fig. 2a). Such variation may be relevant to sites with special ecological conditions like species combinations and environmental changes. Previous studies have shown that sites with high LCBD values not only have unique species combinations [55], but also indicate human interference or higher proportions of allochthonous species [56]. As the water level fluctuates, indeed, shallower sites are most likely the consequence of land flooding or mean annual precipitation and water evaporation, which largely changes the habitat environment of autochthonous species. Intriguingly, such variations are also observed for bacterial and archaeal communities in semi-arid grassland soils, which reveals that higher precipitation can effectively regulate microbial assemblies and strengthen their interactions in water-limited areas [57]. For $LCBD_{Repl}$, such decreasing water-depth patterns are also observed among bacteria and archaea, albeit not significant for bacteria (Fig. 2b). To our knowledge, this is the first study that such parallel patterns in LCBD and its components are observed across microbial taxonomical groups, implying that bacterial and archaeal community uniqueness may be affected by similar ecological progress [58, 59] such as environmental selection. Notably, when bacteria and archaea responded to the variation in water depth, fungi unexpectedly showed non-significant patterns towards deep water regarding LCBD, $LCBD_{Repl}$ and $LCBD_{Nes}$. During the historical events induced by drought, eukaryotic communities including protist and fungi generally present strong resilience in freshwater ecosystems [60]; that is, fungal assemblages in the dry sediment can effectively restore community structure after water refill. Compared to bacteria and archaea, there is thus lower proportions of allochthonous species (i.e., species gain or loss) for fungal communities in this semi-arid lake.

Previous studies have reported that species turnover is crucial for disentangling the underlying mechanism of beta diversity in aquatic ecosystem [61]. Likewise, for bacteria and archaea, our results indicated that the total beta diversity and its turnover component had consistent increasing patterns along water-depth difference (Fig. 2d, e), which largely consolidates the fact that species turnover contributes to the total beta diversity for aquatic microbial taxa. Moreover, such predominance is also observed in species of other lake environments. For instance, for bacterioplankton, turnover shows a higher contribution to total beta diversity than nestedness in the 25 shallow lakes of southern Brazil [62]. It should be noted that when considering some specific spatial factors such as geographical distance

between lakes, the predominance of bacterioplankton turnover may be replaced by nestedness [62]. In the Grand Galibier Massif of the French South-Western Alps, however, high turnover is exhibited in Crenarcheal, bacterial and fungal community distribution, which is greatly associated with plant species composition but not geographical distance [63]. Additionally, regarding nestedness, our studies showed no significant patterns for bacteria, archaea and fungi (Fig. 2f). In particular, for fungi, there was no significant depth-related pattern in total beta diversity and its two components. This may be because fungi has large difference with bacteria and archaea regarding biological characteristics, such as resilience and trophic position. Most importantly, nestedness is well applied to indicate dispersal limitation, while turnover can be as an indicator of species sorting based on environmental filters of microbial communities [62]. Accordingly, for the total beta diversity and turnover component, such parallel pattern between bacteria and archaea may be governed by similar ecological progress [58, 59] like environmental selection.

In addition, we found that there is a strong correlation between bacteria and archaea regarding the total beta diversity and its turnover component (Fig. 4a, b), which further underpins the above synchrony among bacteria and archaea toward deep water. As previously reported, such cross-taxon congruence can occur if different organisms covary in space regarding alpha or beta diversity [64]. Notably, such synchrony is also observed in macroorganisms. For example, in the Espinhaç Range and Mantiqueira Range of southeastern Brazil, total beta diversity of both galling insects and host plant show similar patterns along the elevational gradients, mainly driven by turnover rather than nestedness [65]. Intriguingly, for bacteria and archaea, such congruence is also found for the total LCBD (Fig. 3a). This may reflect the fact that beta diversity (including total beta diversity and LCBD) in semi-arid lake ecosystems is taxonomically dependent among bacteria and archaea. Our findings supported the conclusion that the total beta diversity of two high-dependent taxa is contributed by a similar component (i.e., turnover). It should be noted that, consistent with Yeh et al [19], no correlation was significantly detected between fungi and other microbial taxa, regardless of total beta diversity or LCBD. Conversely, in a arid inland river basin of northwest China, soil bacteria shows a high correlation with fungi for the total beta diversity and species turnover, and meanwhile, both of them respond sensitively to variations in such environmental variables and geographic distances [54]. Accordingly, compared to soil fungi, the relationship between sediment fungi and other taxa is more susceptible to climate change and environmental heterogeneity.

4.2 Environmental determinants of the LCBD, total beta diversity and their components

Previous studies have shown that eutrophication and climate change are two processes promoting the proliferation or expansion of algal blooms [66]. Similarly, for bacteria and archaea, we found that variations in total LCBD and $LCBD_{Repl}$ were greatly contributed by the water factors such as NO_3^--N or NO_2^--N (Fig. 5a), which may be also related to the eutrophication and the local climates. Hulun Lake, as a large hypereutrophic steppe lake, has clearly shown that microbial taxa such as bacteria and archaea frequently participate in the cycling of carbon, nitrogen and phosphorus in aquatic ecosystem [67]. Over

the past few years, however, the warming and drying climate has gradually accelerated the shrinking of water area and the decrease of water level in Hulun Lake [68]. These climate changes have constantly caused the variations in water or sediment factors, and further driven the site uniqueness of microbial communities. The resulting water depth variation has a nonnegligible effect on determining environmental factors in lacustrine ecosystems [20]. For example, in Lake Azul of São Miguel Island, environmental variables such as light intensity, nutrient availability or disturbance regimes vary largely with water depth, and thereby resulted in the distinct distribution of biological assemblages [69]. Considering the vertical variations of light, nutrients and other physical context, water depth is well accepted to be a better determinant driving the site uniqueness of bacterial and diatom communities in Lugu Lake [20]. Consistent with this, for bacteria and archaea, our results revealed a strong negative correlation between water depth and the total LCBD or $LCBD_{Repl}$ (Fig. S3a), implying that the drivers of bacterial and archaeal community uniqueness could be substantially constrained by water depth. In addition, climate change has a profound impact on the terrestrial input of inorganic nutrients and organic matter in aquatic ecosystems, thereby increasing the rate of eutrophication for water bodies [70]. In particular, drought, as an extreme hydrologic event, will accelerate the occurrence of eutrophication when nutrients are overenriched [71, 72]. As noted above, the uniqueness of bacterial and archaeal communities may be predominantly caused by eutrophication and climatic change.

Contrary to the LCBD, our findings revealed that bacterial and archaeal total beta diversity and turnover component were mainly influenced by sediment factors like TN rather than water factors (Fig. 5b). As such, the observed total beta diversity and species turnover may be associated with the trophic status or nutrient supply. Although numerous nutrients and organic matters are stored in sediments of lakes and wetlands [73], much less is known about the effect of nutrients on the total beta diversity and its components across microbial taxa. In the shallow lakes of the southern Brazil, high species turnover is observed in bacterioplankton, strongly conditioned by environmental factors such as TN and total dissolved nitrogen [62]. Additionally, nutrients, including water NH_4^+-N, NO_3^--N and NO_2^--N, show great direct effects on bacterial species turnover in aquatic microcosms, and such turnover rates do not decrease with lower temperatures [74]. Admittedly, nutrient status is closely related to the sustainability of lake ecosystems, and meanwhile, the growths of aquatic organisms are largely governed by nitrogen concentrations such as TN, NO_3^--N, NO_2^--N and NH_4^+-N [75]. Collectively, the total beta diversity and species turnover of bacteria and archaea were well explained by sediment TN, even after accounting for the water variables.

Regarding the LCBD, total beta diversity and their components, fungi have almost nonsignificant water-depth patterns and drivers (Fig. 2; Fig. 5), which may be related to its resilience in response to climate disturbances (e.g., precipitation or drought). As noted above, fungal assemblages in the dry sediment can effectively restore community structure after water refill [60]. Indeed, fungi is more drought-tolerant than bacteria since its hyphae can effectively obtain water from the water-filled micropores [76]. Based on such nonsignificant strong contribution from water factors like TP and TN (Fig. 5), we speculated that

fungal communities may be relevant to the trophic status or nutrient supply of lake water, possibly disturbed by precipitation or drought.

4.3 Perspectives

To better clarify these studies, there are three main perspectives for the interpretation. First, historical legacies may be the key factor underlying the water-depth patterns in beta diversity. As proposed by Cardoso [77], the observed patterns of biodiversity cannot be fully explained without considering the effects of historical factors, which can be reflected in the case of the invertebrate taxa [78] and diatoms [79] in the Orinoco river basin. In the Neotropical region, the distinct river forms and riparian ecosystems are shaped by past geological and climatic events, namely Andean uplifts and glacier retreats, which greatly affects the evolution of ecosystem and biological succession [80]. Hulun Lake, having experienced the processes of swamping, drying, and sharp increase or decrease of water level, is constantly evolving between saline, brackish and freshwater lakes owing to the high evaporation [81]. With special geographical location of high latitude, Hulun Lake shows a half-year frozen period and its salinity is 300-400 mg L^{-1} higher than that of unfrozen status [81]. Under the interplay of natural factors and anthropogenic activities [23], Hulun Lake shows a long history documenting the frequent outbreaks of severe eutrophication [27], such as the cyanobacteria bloom [28], which largely influences the nutrient status of this lake. Due to the historical legacies, nutrients [82] and salinity [83] have crucial roles in shaping microbial structure in aquatic ecosystems. Therefore, for microbial taxa, such water-depth pattern in beta diversity may be affected by historical factors.

Second, climate is a pivotal driver of biodiversity patterns [84], which is widely observed in bacterial biogeographic patterns in arid and semi-arid grasslands [85, 86]. Hulun Lake, as a semi-arid lake, affected by the temperate continental climate [25], is exceptionally fragile and suffers frequently from extreme climatic phenomena such as dramatic drought and low temperatures. Notably, drought intensification and precipitation alterations can effectively drive the turnover of composition structures, which is well known in the case of soil microbiome [87] and stream invertebrates [88]. Moreover, species turnover is also considered as the legacy of climatic or geological events [89]. For example, for the microbenthic communities in the Paraíba do Norte or Mamanguape estuaries, beta diversity is individually affected by species turnover in dry season, while turnover and nestedness in wet season [16]. Furthermore, in response to temperature changes, organisms evolving in temperate zones generally have stronger thermal adaptations and dispersal capabilities than that in tropical regions [90]. Accordingly, compared to tropical zones, species turnover is often lower in temperate regions [91]. Even so, our results reveal that bacterial and archaeal total beta diversity were mainly explained by species turnover (Fig. 2), implying that microbial communities may be relatively sensitive to climate change. Given that the role of climatic variation and dispersal ability on species turnover plays key importance [92], patterns in microbial beta diversity may be substantially relevant to climate changes.

Third, similar patterns are underpinned by equivalent ecological processes [58]. Such processes, including drift, selection and dispersal, governs the turnover of biological community composition in space [93]. Simultaneously, turnover can replace species via environmental selection and historical or spatial

restriction [94], and its predominance can evaluate beta diversity across different taxa, type of dispersal or trophic position [12]. In our studies, the total beta diversity (Fig. 2d) and turnover (Fig. 2e) of bacteria and archaea consistently increased with the water depth difference, implying that their parallel patterns are supported by similar processes like environmental selection. Note that the same patterns are not only observed in total beta diversity and turnover, but also in LCBD and $LCBD_{Repl}$. Thus, for bacteria and archaea, consistent patterns in LCBD and $LCBD_{Repl}$ are also theoretically governed by same ecological processes such as environmental filtering. From macro-organisms to microbes, whether it is regional or local variation in community structures, such parallel patterns are dictated by similar processes [59]. Thereby, parallel patterns can serve as a powerful tool for understanding the forces driving species turnover or replacement across taxonomic groups, even after accounting for the absence of theoretical derivations.

5. Conclusions

Overall, based on the Baselga's and Legendre's approaches, our studies provide evidence that beta diversity including total beta diversity and LCBD was taxonomically dependent across microbial taxa in a semi-arid lake. There were significant water-depth patterns in total beta diversity, LCBD and their components for bacteria and archaea but not for fungi. For both of bacteria and archaea, the total beta diversity attributed to species turnover, and LCBD was predominated by $LCBD_{Repl}$. Moreover, there was a spatial synchrony between bacteria and archaea regarding total beta diversity, species turnover, LCBD and $LCBD_{Repl}$. Such parallel patterns are largely underpinned by similar ecological process like environmental selection. For instance, the total beta diversity and species turnover were better explained by sediment factors such as total nitrogen, while LCBD and $LCBD_{Repl}$ were strongly affected by water factors like NO_2^--N or NO_3^--N. In addition, for fungi, there was no significant pattern in each beta diversity index toward deep water, which may be due to different drivers like water nitrogen or phosphorus. To date, studies partitioning beta diversity across multiple taxonomic groups are still relatively lacking in aquatic ecosystems. We encourage future studies to confirm our findings by comparing the associations among the multiple taxonomic groups in other aquatic ecosystems or under other climatic conditions.

Declarations

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Author Contributions Haijun Yuan — wrote the paper and analyzed data, Weizhen Zhang — wrote the paper, conducted field sampling and experimental work, Huaqun Yin — performed research and and contributed new methods or models, Runyu Zhang — contributed substantially to manuscript drafting, Jianjun Wang — conceived the idea and designed the experiments. All of the authors assisted in writing the manuscript, discussed the results, and commented on the manuscript.

Data Availability The raw data sequencing 16S rRNA and ITS genes have been submitted to the NCBI Sequence Read Archive database and are available under accession number SRR13611586 to SRR13611623.

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Figures

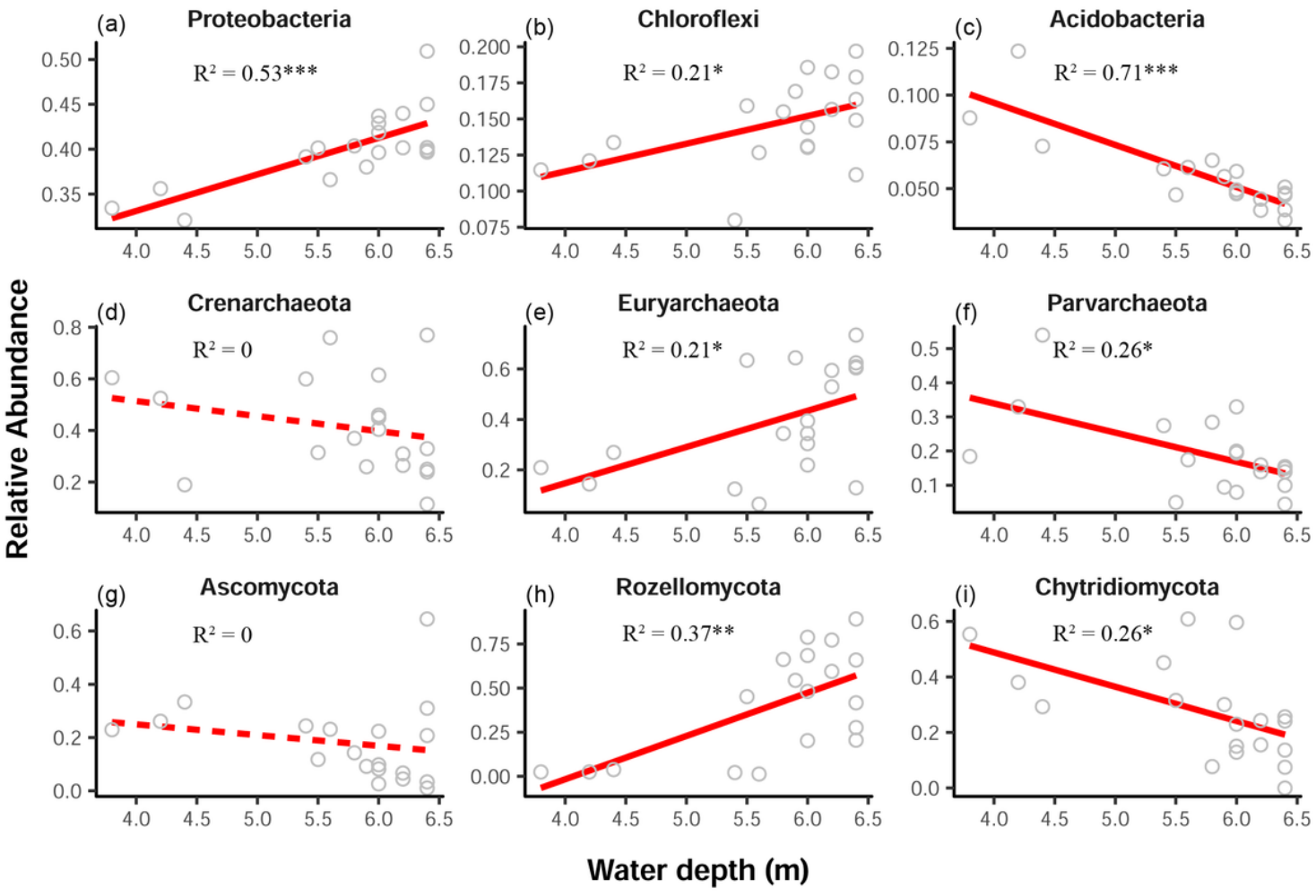

Figure 1

Relative abundance of the dominant bacterial (a-c), archaeal (d-f) and fungal (g-i) phyla along the water-depth gradient. The relationships between the water depth and relative abundance were modeled using linear and quadratic models, and the best model was selected based on the lowest value of Akaike's information criterion. Solid and dashed lines denote the significant and non-significant relationships, respectively. *P ≤ 0.05, **P < 0.01, ***P < 0.001.

Figure 2

Water-depth patterns of LCBD and total beta diversity and their components for bacteria, archaea and fungi. We considered two metrics for the variance in community compositions, that is the local contributions to beta diversity (LCBD, a) and the total beta diversity (d). The LCBD (a) was divided into species replacement (b) and nestedness (c), and the total beta diversity (d) was partitioned into turnover (e) and nestedness (f). These metrics and components were linearly or quadratically modelled against the water depth or water depth distance, and solid and dashed lines indicate the significant and non-significant relationships, respectively. More details on these models are listed in Table S2.

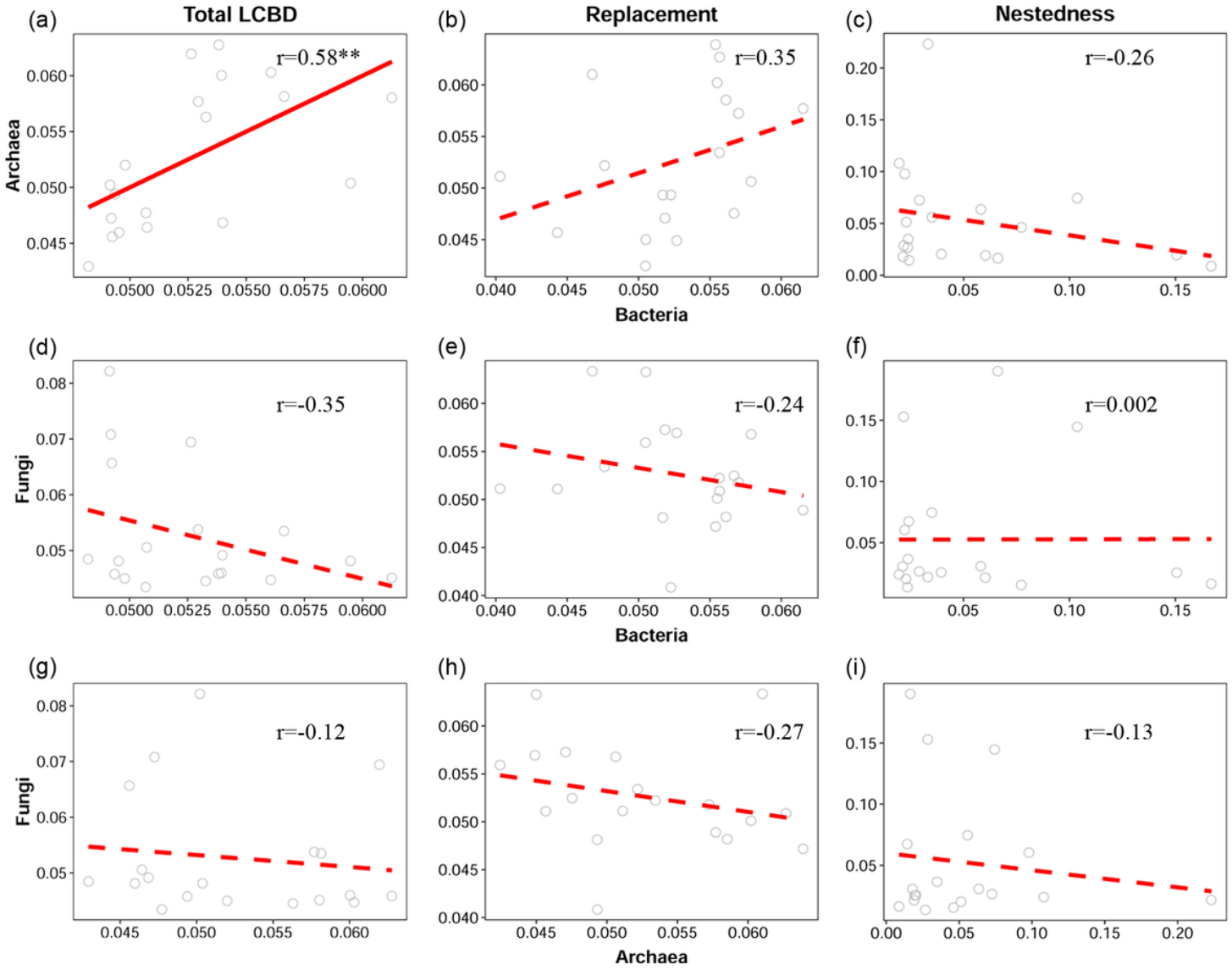

Figure 3

Correlation between bacteria, archaea and fungi regarding the total LCBD and its two components. For the total LCBD (a, d, g), species replacement (b, e, h) and nestedness (c, f, i), the relationships between bacteria, archaea and fungi were modeled with linear and quadratic models, and the best model was selected based on the lowest value of Akaike's information criterion. The solid and dashed lines indicate the significant and non-significant relationships, respectively. *P ≤ 0.05, **P < 0.01, ***P < 0.001.

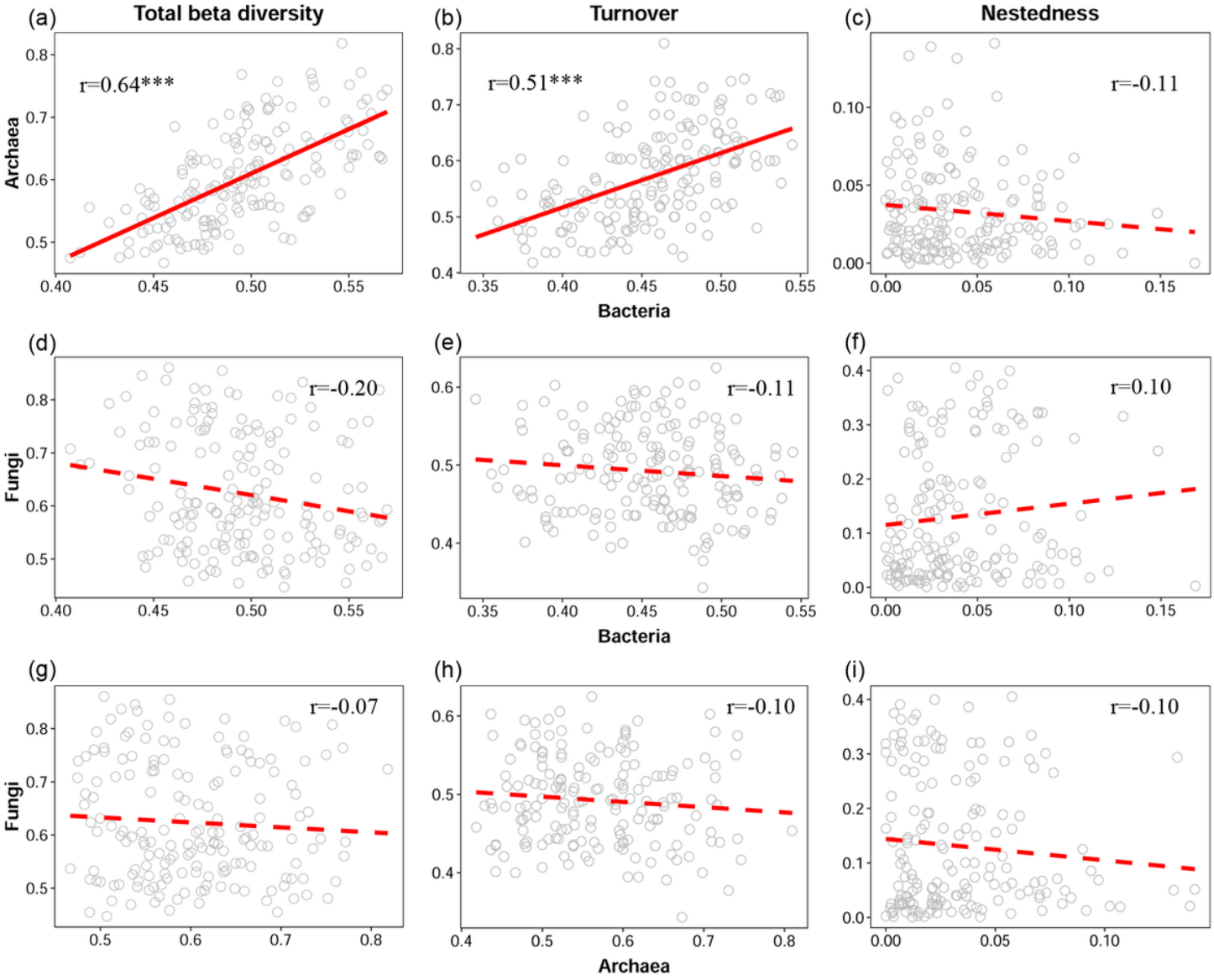

Figure 4

Correlation between bacteria, archaea and fungi regarding the total beta diversity and its two components. For the total beta diversity (a, d, g), turnover (b, e, h) and nestedness (c, f, i), the relationships between bacteria, archaea and fungi were modeled using linear and quadratic models, and the best model was selected based on the lowest value of Akaike's information criterion. The solid and dashed lines indicate the significant and non-significant relationships, respectively. *P ≤ 0.05, **P < 0.01, ***P < 0.001.

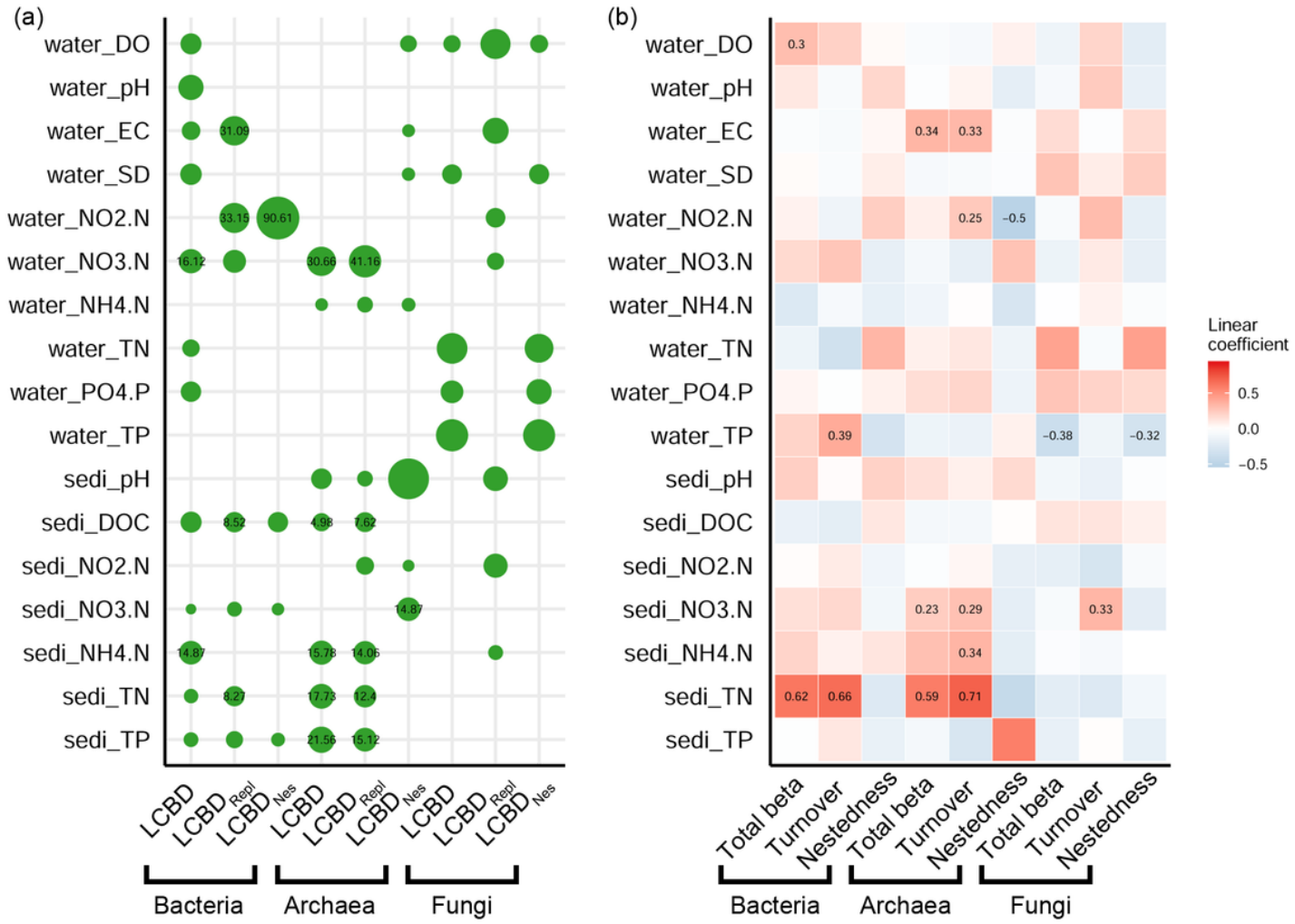

Figure 5

The water and sediment factors related to the variance in community composition. The local contributions to beta diversity (LCBD) are divided into species replacement (i.e., LCBDRepl) and nestedness (i.e., LCBDNes), and the total beta diversity (Total beta) is partitioned into turnover and nestedness. Random forest analysis (a) was applied to show the relative contributions of the water and sediment factors in explaining the LCBD and its two components. The multiple regression on distance matrices (b) was performed to explain the total beta diversity and its partitioned two components via these abiotic variables. The size of the circle and the numerical value indicate the relative contribution, and the color or the numerical value denote the linear coefficients. Moreover, the presence of these numerical values also indicates the significant ($P < 0.05$) relationship. The abbreviations of these variables are listed in Table S1.

Supplementary Files

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- SupplementaryInformation.docx