Differentiation of cognate bacterial communities in thermokarst landscapes: implications for ecological consequences of permafrost degradation

Running title: Bacterial communities in thermokarst landscape

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Abstract

Thermokarst processes likely result in new habitats harboring novel bacterial communities in degraded permafrost soil (PB), thermokarst lake sediments (SB), and lake water (WB). Our study aimed to investigate the paired PB, SB, and WB across the Qinghai-Tibet Plateau (QTP) by assessing the spatial pattern of diversity as well as assembly mechanisms of these bacterial communities. Each habitat had distinct bacterial assemblages, with lower alpha diversity and higher beta diversity in WB than in SB and PB. However, up to 41% of the OTUs were shared by PB, SB, and WB, suggesting that many taxa originate from the same sources via dispersal. SB and WB had reciprocal dispersal effects and both were correlated with PB. Dispersal limitation was the most dominant assembly process shaping PB and SB while homogeneous selection was the most dominant for WB. Bacterial communities of the three habitats correlated differently with environmental variables, but latitude, mean annual precipitation, and pH were the common factors associated with their beta diversity, while total phosphorus was the common factor associated with their assembly processes. Our results imply that thermokarst processes result in diverse habitats that have distinct bacterial communities that differ in diversity, assembly mechanisms, and environmental drivers.

Keywords: thermokarst; permafrost; bacteria, community assembly, Qinghai-Tibet Plateau

1 Introduction

Permafrost is an important landscape in high latitude and altitude regions, covering 15% of the land area of the Northern Hemisphere (Obu, 2021) and 40% of the Qinghai-Tibet Plateau (QTP) (Zou et al., 2017; Gao et al., 2021), and containing twice as much carbon as

is currently present in the atmosphere (Schuur et al., 2009; Hugelius et al., 2014; Mishra et al., 2021). Permafrost is highly sensitive to climate warming (Wu et al., 2007; Jorgenson et al., 2010; Biskaborn et al., 2019), which is expected to reduce 50-90% of permafrost cover by 2100 (Lawrence et al., 2012; Chadburn et al., 2017). As a result of ice-rich permafrost thaw, thermokarst lakes and ponds are formed (Kokelj and Jorgenson, 2013; Farquharson et al., 2016) and extensively distributed across the Arctic and sub-Arctic regions (de Jong et al., 2018) as well as the QTP (Niu et al., 2011; Luo et al., 2020). The initial sediment and water in thermokarst lakes originate from the melting of permafrost, and they are continuously replenished through the collapse of permafrost and precipitation (West and Plug, 2008; de Jong et al., 2018). Thus, thermokarst lake sediments and water, as well as the surrounding degraded permafrost soil, represent three distinct habitats derived from the original permafrost during the process of thermokarst formation (Figure 1). It is well known that thermokarst processes substantially influence regional hydrological, ecological, and biogeochemical processes (Chin et al., 2016; In'T Zandt et al., 2020; Manasypov et al., 2021) and initiate a strong positive climate feedback to global warming (Walter et al., 2006; Schuur et al., 2008; Schaefer et al., 2011; Anthony et al., 2018). However, the microbial differences and relationships among these distinct habitats in thermokarst landscapes are largely unknown.

Understanding microbes in thermokarst landscapes, and elsewhere, is important because microbial communities play pivotal roles in driving biogeochemical and ecological processes. To understand thermokarst microbial communities, we need to understand the assembly mechanisms structuring them, a central research topic in microbial ecology (Stegen et al., 2012; Nemergut et al., 2013; Zhou et al., 2014; Zhou and Ning, 2017). In

the assembly of microbial communities, both deterministic and stochastic processes occur simultaneously but with contributions that can vary (Chase, 2010; Zhou et al., 2013; Vellend et al., 2014; Makoto et al., 2019). Typically, deterministic processes place a strong emphasis on niche-based mechanisms, including ecological selection, environmental filtering, and biotic interactions (Zhou and Ning, 2017). Conversely, stochastic processes involve neutral mechanisms like random birth and death, unforeseen disturbance, probability-based dispersal, and ecological drift (Chave, 2004; Chase, 2010; Zhou et al., 2014). In various ecosystems or habitats, the significance of deterministic and stochastic processes can differ greatly and be shaped by a multitude of environmental factors (Tripathi et al., 2018; Aguilar and Sommaruga, 2020; Jiao and Lu, 2020; She et al., 2021). During thermokarst formation, vast areas of permafrost have been transformed to thermokarst lakes, leading to major changes in physicochemical environments as well as in biological communities of these regions. Thus, it is also expected that the microbial communities experience major changes in occupying degraded permafrost soil, thermokarst lake sediments, and lake water, and in doing so, display different assembly mechanisms (Figure 1).

Better understanding community assembly in these systems is important because thawing permafrost and thermokarst lakes are greenhouse gas emission hotspots (In'T Zandt et al., 2020; Mu et al., 2020; Elder et al., 2021). Close relationships between biogeochemical processes and microbial community assembly have been generally demonstrated (Bier et al., 2015; Graham et al., 2016; Le Moigne et al., 2020; Ren et al., 2022a). Assembly processes inevitably influence biogeochemical functions by shaping community diversity and composition (Graham et al., 2016; Leibold et al., 2017; Mori et al., 2018). For example,

dispersal (a stochastic process) can suppress biogeochemical functioning by increasing the proportion of maladapted taxa (Strickland et al., 2009; Nemergut et al., 2013; Graham and Stegen, 2017), while selection (a deterministic process) may have positive influence on biogeochemical function by facilitating locally adapted taxa (Graham et al., 2016). In particular, stochastic dispersal has been suggested to suppress the mineralization of organic carbon in soil and water (Le Moigne et al., 2020; Luan et al., 2020). Therefore, it is hypothesized that the relative influence of deterministic and stochastic processes on community assembly could impact the biogeochemical functions of microbial communities (Strickland et al., 2009; Nemergut et al., 2013; Pholchan et al., 2013; Graham and Stegen, 2017). Given the importance to understand how microbial community variations affect the biogeochemical cycles in permafrost and thermokarst landscapes, it is necessary to have a deeper understanding of the assembly mechanisms in shaping microbial communities that form following permafrost degradation.

In this paper we evaluated these ideas on the Qinghai-Tibet Plateau (QTP), which is known as the "Third Pole" of the Earth and is therefore uniquely positioned as an indicator of global change (Yao et al., 2012). Pronounced environmental changes in response to climate warming on the QTP have been observed and documented, especially in the past half century (Piao et al., 2012; Zhang et al., 2018; Ren et al., 2019a). Major changes are predicted to continue on the QTP and permafrost thawing is among the most prominent but little is known about the microbial communities in these rapidly emerging ecosystems. To fill this gap, we investigated water and sediment in thermokarst lakes across the QTP as well as permafrost soil around the lakes (Figure 1). Our aims were to (1) assess the spatial pattern of alpha and beta diversity of bacterial communities, and (2) evaluate the

community assembly mechanisms and environmental responses of the bacterial communities in degraded permafrost soil, as well as in the sediment and water of thermokarst lakes.

2 Methods

2.1 Study area, field sampling, and chemical analysis

This work was conducted across the QTP in July 2021 (Figure S1). In total, 44 sites were investigated by collecting paired samples of lake water, lake sediment, and surrounding permafrost soil (Figure 1a) (Ren et al., 2022a). The sampling strategy and chemical analysis methods were described in detail in our previous publications (Ren et al., 2022a, b). For water sampling of each lake, surface water samples were collected at a depth of 0.3 to 0.5 m in three acid-clean bottles. For microbial analysis, 200 mL of water from each bottle was filtered using a 0.2-μm polycarbonate membrane filter (Whatman, UK) for DNA extraction. For each lake, three filters were combined into one composite sample for DNA extraction. The remaining water samples were transported to the lab for other physicochemical measurements. For sediment sampling, the top 15 cm of sediment was collected from 3 points. Sediment samples for microbial analysis were collected in a 45-mL sterile centrifuge tube, and the remaining samples were air-dried for analyzing physicochemical properties. For permafrost sampling, five topsoil cores were collected along three 25-m transects with increasing distances to the lake shore, respectively. The soils from one transects were homogenized. Soil samples for microbial analysis were stored in 45-mL sterile centrifuge tubes and the remaining soils were used for analyzing physicochemical properties. For each sampling site, pH, conductivity (Cond), organic carbon (DOC in water and SOC in sediment and soil), total nitrogen (TN), and total

phosphorus (TP) were measured according to our previous publications (Ren et al., 2022a, b). Moreover, the QTP climate dataset (Zhou, 2018) was obtained from the National Tibetan Plateau Data Center (https://data.tpdc.ac.cn/en/), and was utilized to extract the mean annual temperature (MAT) and mean annual precipitation (MAP) for each of the study sites.

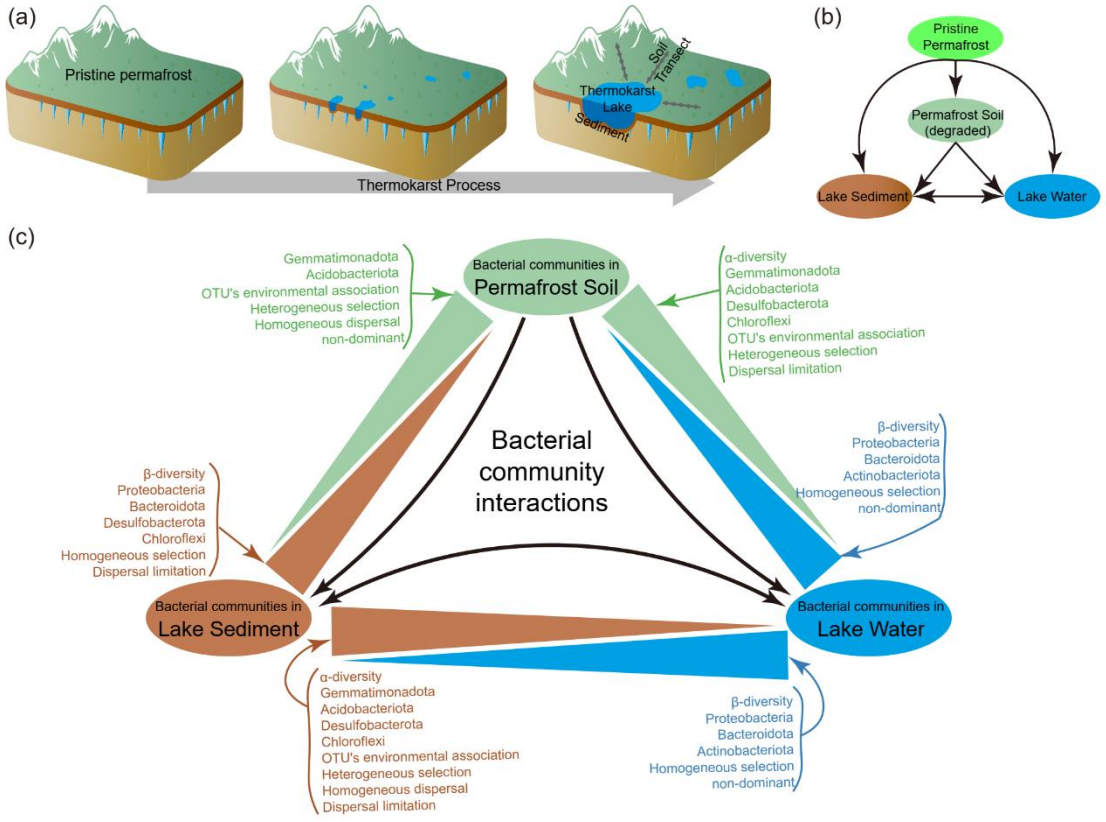

Figure 1 (a) The process of thermokarst lake formation in ice-rich permafrost (modified from Ren et al, 2022a). (b) A schematic view of the relationships between permafrost soil, lake sediment, and lake water. (c) Summary of the differences between distinct habitats of the bacterial communities in permafrost soil, lake sediment, and lake water.

2.2 DNA extraction, PCR, and sequencing

The Magen Hipure Soil DNA Kit (Magen, China) was used to extract DNA from soil (0.5 g frozen soil), sediment (0.5 g frozen sediment), and water (membrane filters by filtering 600 mL lake water) samples according to the manufacturer's protocols. Extraction blanks were routinely performed in parallel. The prokaryotic 16S rRNA gene's V3-V4 hypervariable regions were amplified using universal primers 343F-TACGGRAGGCAGCAG and 798R-AGGGTATCTAATCCT (Nossa et al., 2010). PCRs were conducted in 25 μl reaction mixture containing 2.5 μl of TransStart buffer, 2 μl of dNTPs, 1 μl of each primer, 0.5 μl of TransStart Taq DNA polymerase, and 20 ng template DNA. The PCR reactions were conducted on a thermal cycler (ABI GeneAmp® 9700, USA) using the followed procedure: initial denaturation at 94 ℃ for 5 min, 24 cycles of denaturation at 94 ℃ for 30 s followed by annealing at 56 ℃ for 30 s and extension at 72 ℃ for 20 s, and a final extension at 72 ℃ for 5 min. To reduce amplification bias, three individual PCR amplifications were performed for each sample and the triplicate PCR products were combined and purified. DNA libraries were verified on 2% agarose gels and quantified using a Qubit 4 Fluorometer (Thermo Fisher Scientific, Waltham, USA). Next generation sequencing of the amplicon products was conducted on an Illumina Miseq Platform (Illumina, San Diego, CA, USA). Automated cluster generation and 250/300 paired-end sequencing with dual reads were performed following the manufacturer's instructions. The forward and reverse reads were joined and assigned to samples based on barcode and truncated by cutting off the barcode and primer sequence. Raw sequences were trimmed of ambiguous bases and low-quality sequences (quality score lower than 20). After trimming, the paired-end reads were joined and de-noised using QIIME1.9.1

(Caporaso et al., 2010). The sequences were subjected to the following denoising criteria: sequences with ambiguous or homologous regions, as well as those below 200 bp in length, were excluded; sequences with at least 75% of bases having a quality score above Q20 were retained; and chimeric sequences were identified and eliminated. All sequences from extraction blanks were removed. The effective sequences were grouped into Operational Taxonomic Units (OTUs) using a 97% sequence similarity threshold and annotated the taxonomic classifications against the SILVA 138 database (released on 02-Nov-2020) (Quast et al., 2013). The singletons were removed, and the sequences were rarefied to the lowest number of sequences per sample (24,251 sequences) to eliminate the bias from the sampling effort.

2.3 Analyses

Three α-diversity indices, including observed number of OTUs (OTU richness), Shannon diversity, and phylogenetic diversity (PD), were calculated using QIIME 1.9.1 (Caporaso et al., 2010). The “ses.mntd” function in the picante 1.8.2 package was used to calculate the standardized effect size measure of the mean nearest taxon distance (SES.MNTD) for assessing the phylogenetic clustering of bacterial communities (Kembel et al., 2010). The β-diversity was calculated as the Bray-Curtis distance based on the relative abundance of OTUs. In order to determine the habitat niche occupied by each taxon, we utilized the "spaa" package (Zhang, 2016) in R to calculate the Levin's niche width (Levins, 1968). The formula of niche breadth is $B_i = 1/\sum_1^n p_i^2$, where B_i represents the niche breadth of OTU_i across the communities, n is the total number of communities, and p_i is the proportion of OTU_i in each community. Differences in α-diversity and β-diversity among bacterial communities in different habitats, including permafrost soil bacterial communities (PB),

lake sediment bacterial communities (SB), and lake water bacterial communities (WB), were assessed using Wilcoxon rank-sum test. The relationships between taxonomic and environmental variables were assessed using Spearman correlation, and the P-values were corrected using the FDR method (Benjamini and Hochberg, 1995). Mantel tests were performed to examine the correlation between environmental variables and β-diversity. A Non-metric Multidimensional Scaling (NMDS) analysis was conducted to examine the distribution of PB, SB, and WB using the "metaMDS" function in the vegan 2.5-7 package based on the Bray-Curtis distance using the relative abundance of OTUs. (Oksanen et al., 2020). The distinctiveness of these communities was confirmed through a non-parametric statistical test (ANOSIM) using the "anosim" function in the vegan package. The habitat niche occupied by each species was estimated by calculating Levin's niche breadth (Levins, 1968) with the use of the spa 0.2.2 package (Zhang, 2016). Species with a broader niche breadth were distributed more evenly across a wider range of habitats, compared to those with a narrower niche breadth.

Structural equation modeling (SEM) was conducted to assess the relationships among location (including latitude, longitude, and elevation), climate (including mean annual temperature and mean annual precipitation), and physicochemical variables (including pH, conductivity, nutrients concentrations and stoichiometric ratios) of each habitat (permafrost soil, lake sediment, and lake water), as well as their bacterial communities (PB, SB, and WB). In model building, the SEM incorporated prior knowledges: (a) location and climate factors potentially influence all the studied bacterial communities, (b) physicochemical factor of each habitat potentially influences the corresponding bacterial communities, and (c) permafrost soil potentially influences thermokarst lake sediment and

water, while lake sediment and water interact with each other. In the SEM, location, climate, and physicochemical environments were reduced in dimensions by principal component analysis (PCA), respectively, using the "prcomp" function of the vegan package, and the first axis (PCA1) was used in SEM. For community structure, the first axis of NMDS was used. SEM was constructed using the lavaan package (Rosseel, 2012). The fit of SEM was assessed using standard indices, including chi-square (χ^2), goodness-of-fit index (GFI), comparative fit index (CFI), root mean square residual (RMR), and root mean squared error of approximation (RMSEA) (Hu and Bentler, 1999; Barrett, 2007).

Phylogenetic trees of bacteria were constructed in the R package ggtree 3.2.1 (Yu et al., 2017) using the top 1000 abundant OTUs in PB, SB, and WB, respectively. For each phylogenetic tree, a heatmap was built in the inner ring represents Spearman's correlation between OTUs and environmental variables. The middle ring was built to represent the frequency of the OTUs in our studied sites. The outer ring was built to represent the relative abundance of the OTUs.

A null model analysis was performed to investigate the processes shaping the assembly of bacterial communities in permafrost soil, lake sediment, and lake water using the R package picante 1.8.2 (Kembel et al., 2010). This analysis based on the calculation of the beta nearest taxon index (βNTI) to measure the extent of deterministic processes in shaping the phylogenetic composition of the communities, as well as a Bray–Curtis-based Raup-Crick matrix (RC_{Bray}) to assess the relative influences of stochastic processes (Stegen et al., 2013; Zhou and Ning, 2017). Because homogeneous selection results in communities that share greater phylogenetic similarity, the proportion of homogeneous selection was calculated as the fraction of pairwise comparisons with $\beta NTI < -2$. On the other hand,

heterogeneous selection, leading to communities with lesser phylogenetic similarity, was measured as the fraction of pairwise comparisons with βNTI > +2. Because homogeneous dispersal results in communities exhibiting greater taxonomic resemblance, the extent of its impact was measured as the proportion of pairwise comparisons with $-2 < \beta NTI < 2$ and $RC_{Bray} < -0.95$. Conversely, communities constrained by dispersal limitation display lesser taxonomic similarity, and the measure of dispersal limitation was derived from the fraction of pairwise comparisons with $-2 < \beta NTI < 2$ and $RC_{Bray} > 0.95$. Finally, the fraction of the pairwise comparisons with $-2 < \beta NTI < 2$ and $-0.95 < RC_{Bray} < 0.95$ was identified as "undominated". Mantel tests were conducted to test the relationships between environmental variables and βNTI.

All the statistical analyses were carried out in R 4.1.2 (R Core Team, 2020).

3 Results

3.1 General distribution patterns of α-diversity

After quality filtering, 3,201,132 high quality sequences were obtained and clustered into 9,361 OTUs, of which, 3870 OTUs were core OTUs shared by bacterial communities in permafrost soil, lake sediment, and lake water (Figure S2). Moreover, a large number of OTUs were shared by PB and SB (n=7053), of which, 16.4% were enriched in lake sediment and 19.3% were enriched in permafrost soil (Figure S2). However, a relatively small number of OTUs were shared by PB and WB (n=4007) and by SB and WB (n=4431), and only a very small proportion of OTUs were enriched in lake water (Figure S2). Bacterial communities had a significantly lower α-diversity in lake water than in lake sediment and permafrost soil (Figure 2a). α-diversity was not significantly different between PB and SB (Figure 2a). Correlation analyses showed that phylogenetic diversity

of PB was positively correlated with SOC, TN, and C:N:P ratios (Figure 2b). For SB, α-diversity indices were positively correlated with MAT, MAP, SOC, TN, C:P and N:P, while negatively correlated with latitude and pH (Figure 2b). For WB, α-diversity indices were negatively correlated with pH, and Shannon diversity was negatively correlated with DOC, TN, and C:P (Figure 2b).

PB and SB had a significantly greater phylogenetic diversity than WB (Figure 2a and Figure 3). The OTUs in PB had significantly higher frequency than that of SB and WB (Figure 3). The top 1000 abundant OTUs in PB were highly correlated with environmental variables, particularly with latitude, MAP, SOC, TN, TP, and C:N:P ratios (Figure 3a). The top 1000 abundant OTUs in SB were more commonly positively correlated with MAP, SOC, TN, and C:N:P ratios, but more commonly negatively correlated with latitude and pH (Figure 3b). The top 1000 abundant OTUs in WB had relatively fewer significant relationships with environmental variables in general, but were negatively correlated with latitude, conductivity, pH, DOC, TN, and C:N:P ratios, while more positively correlated with MAP (Figure 3c). In addition, WB had significantly higher SES.MNTD than PB and SB (Figure 3d), suggesting higher phylogenetic clustering of bacterial taxa in WB.

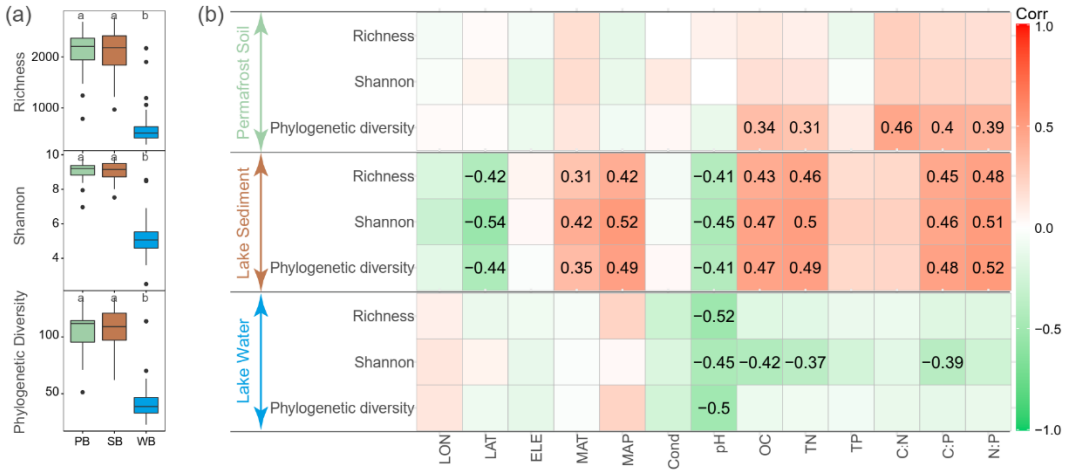

Figure 2 (a) Alpha diversity of bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB). The different low-case letters represent significant differences assessed using Wilcoxon rank-sum test. (b) Spearman correlations show the relationships between alpha diversity and environmental factors. The color represents the correlation coefficient, which is shown in number when the result is statistically significant ($p<0.05$).

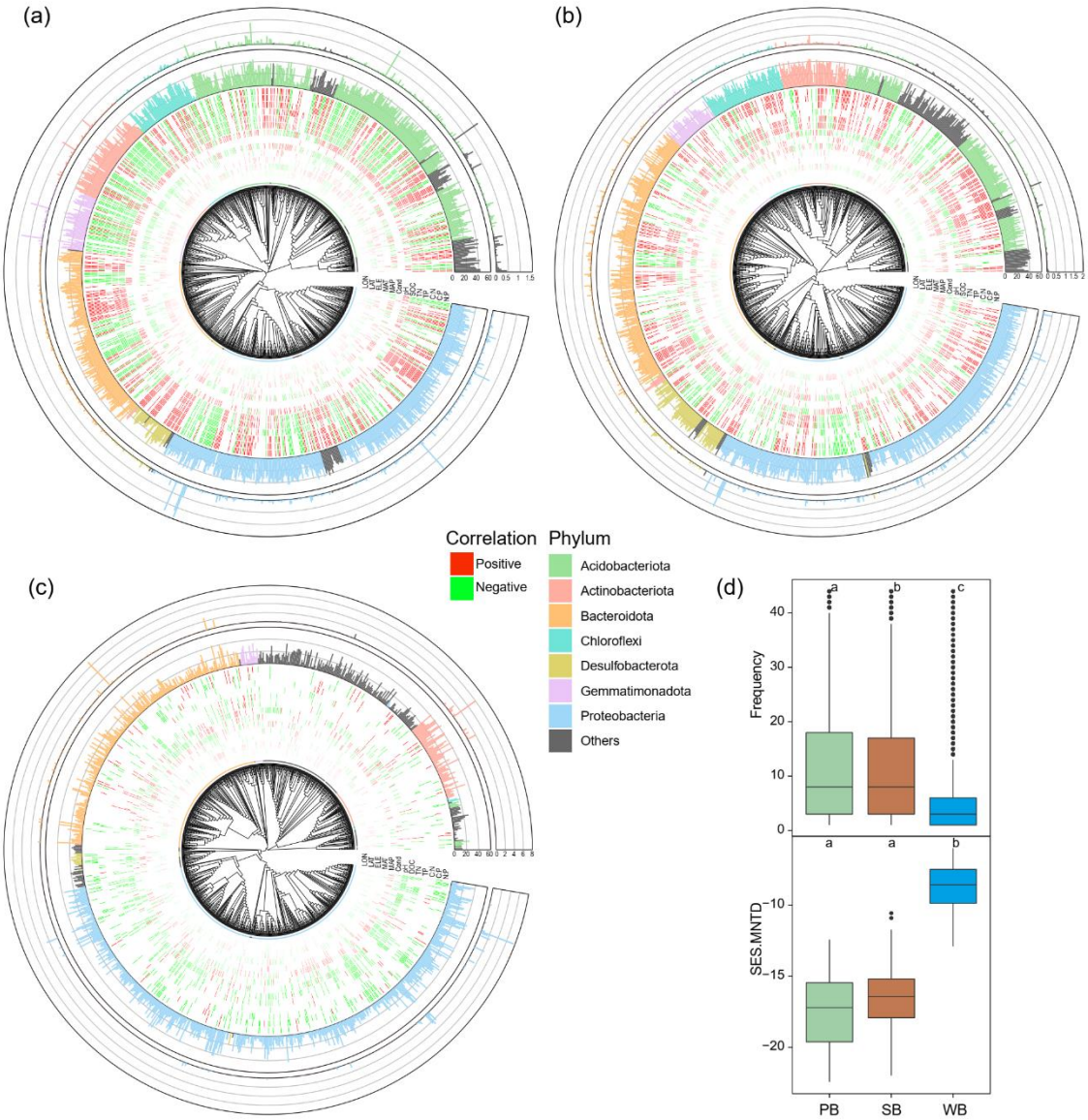

Figure 3 Phylogenetic tree of the top 1000 OTUs in bacterial communities in (a) permafrost soil, (b) lake sediment, and (c) lake water. Tree tips are colored by major phylum. The inner ring of the heatmap represents spearman's correlation between OTUs and environmental variables. Only significant ($p<0.05$) results are shown. The middle ring represents the frequency of the OTUs in our studied sites. The outer ring represents the relative abundance of the OTUs. (d) Boxplots showing differences of OTU's frequency and SES.MNTD values among bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB). The different lower-case letters represent significant differences assessed using Wilcoxon rank-sum test.

3.2 Community composition and β-diversity patterns

PB were dominated by Proteobacteria (30.4%), Acidobacteriota (25.3%), Bacteroidota (11.4%), Actinobacteriota (6.8%), Chloroflexi (5.2%), and Gemmatimonadota (5.2%) (Figure 4a). SB were dominated by Proteobacteria (35.2%), Bacteroidota (20.0%), Acidobacteriota (11.3%), Desulfobacterota (6.4%), Chloroflexi (6.3%), and Actinobacteriota (5.8%) (Figure 4a). WB were dominated by Proteobacteria (46.9%), Bacteroidota (29.2%), and Actinobacteriota (17.4%) (Figure 4a). While Proteobacteria were predominant in all three habitat types, these dominant phyla had significantly different relative abundances among these habitats. Proteobacteria and Bacteroidota had a significantly higher relative abundance in WB than in SB and PB (Figure 4a). The relative abundance of Actinobacteriota was the highest in WB but was not significantly different between PB and SB (Figure 4a). Gemmatimonadota and Acidobacteriota were significantly enriched in PB than in SB and WB. Desulfobacterota and Chloroflexi were significantly enriched in SB than in PB and WB (Figure 4a).

These phyla responded differently to environmental variables (Figure 4b). For example, Actinobacteriota and Gemmatimonadota in PB and Actinobacteriota and Desulfobacterota in SB were negatively correlated with nutrient concentrations and ratios, while Desulfobacterota in PB and Acidobacteriota in SB were positively correlated with nutrient concentrations and ratios (Figure 4b). pH frequently correlated with taxa in various taxonomic groups across all three habitats (Figure 4b)

Nonmetric multidimensional scaling (NMDS) analysis along with non-parametric statistical tests showed that bacteria in different habitats formed distinct communities (Figure 5a). The extent of difference was larger for WB vs PB (β=0.98; R_{ANOSIM} = 0.989, P<0.001) than the differences for WB vs SB (β=0.96; R_{ANOSIM} = 0.967, P<0.001). There was the least dissimilarity between PB and SB (β=0.81; R_{ANOSIM} = 0.384, P<0.001). The fitted SEM model showed that PB had direct effects on SB and WB, and the latter two had reciprocal effects on each other (Figure 5b). In addition, location, climate, and permafrost soil physicochemical environments had direct effects on PB. Climate had direct effects on SB while lake water physicochemical environments had direct effects on WB (Figure 5b).

WB had a higher β-diversity than SB and PB, suggesting that bacterial communities were more spatially heterogeneous in lake water than in lake sediment and permafrost soil (Figure 5c). Taxa in PB had higher habitat niche breadths than taxa in SB and WB (Figure 5d). We estimated the distance decay relationship of bacterial community similarity. Significant distance-decay relationships were observed for all communities but the fitness values were relatively low (Figure S3), indicating weak decay of community similarity with geographic distance in thermokarst landscape. We also explored the main environmental variables that influence the variations of the bacterial communities (Figure

6). β-diversities of PB, SB, and WB were all significantly correlated with latitude, MAP, and pH (Figure 6). In addition, β-diversity of PB was also significantly correlated with all the other environmental variables except MAT and conductivity. β-diversity of SB was also significantly correlated with conductivity and C:N (Figure 6). β-diversity of WB was also significantly correlated with elevation, MAT, conductivity, DOC, TN, and TP (Figure 6). The results suggested that the compositional variation among PB, SB, and WB was differentially structured by spatial, climatic, and physicochemical variables.

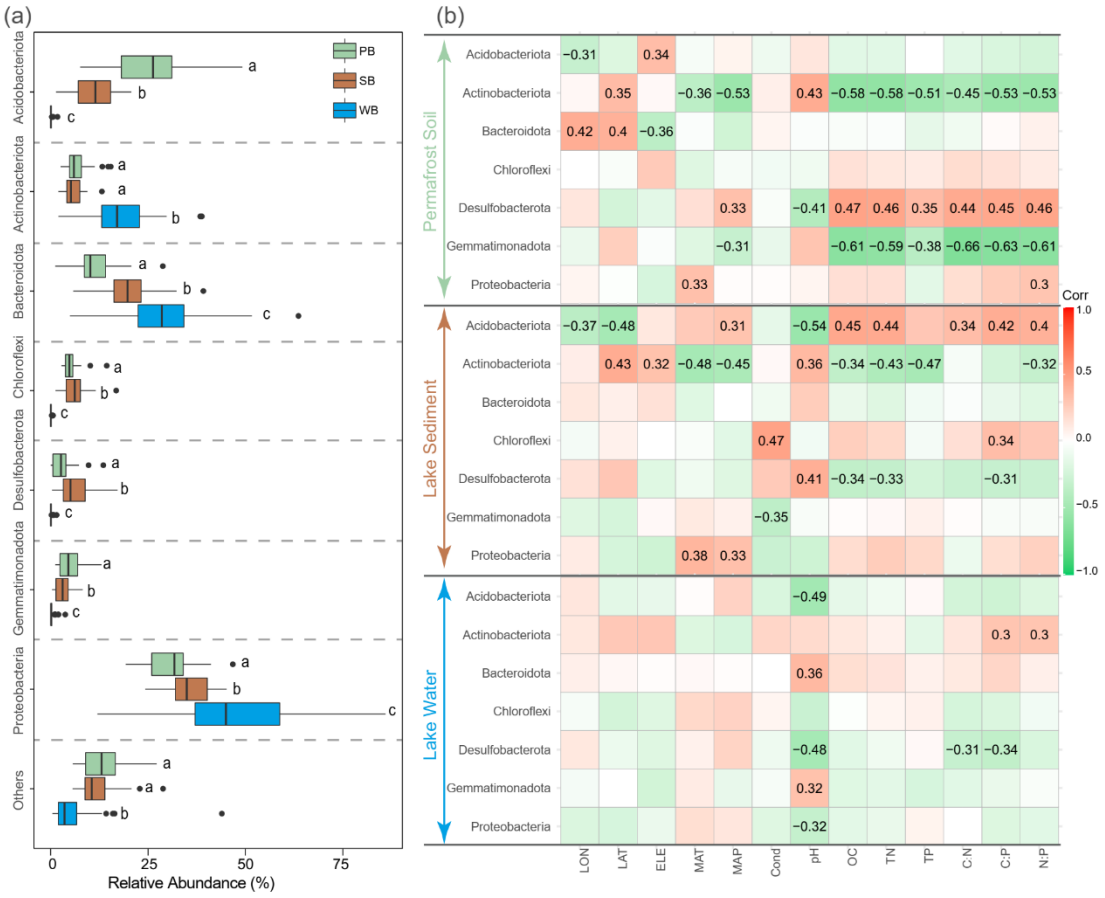

Figure 4 (a) Relative abundances of major phyla in bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB). The different low-case letters represent significant differences assessed using Wilcoxon rank-sum test. (b) Spearman correlations

337 show the relationships between the relative abundance of major phyla and environmental
338 factors. The color represents the correlation coefficient, which shown in number when the
339 result is significant ($p<0.05$).

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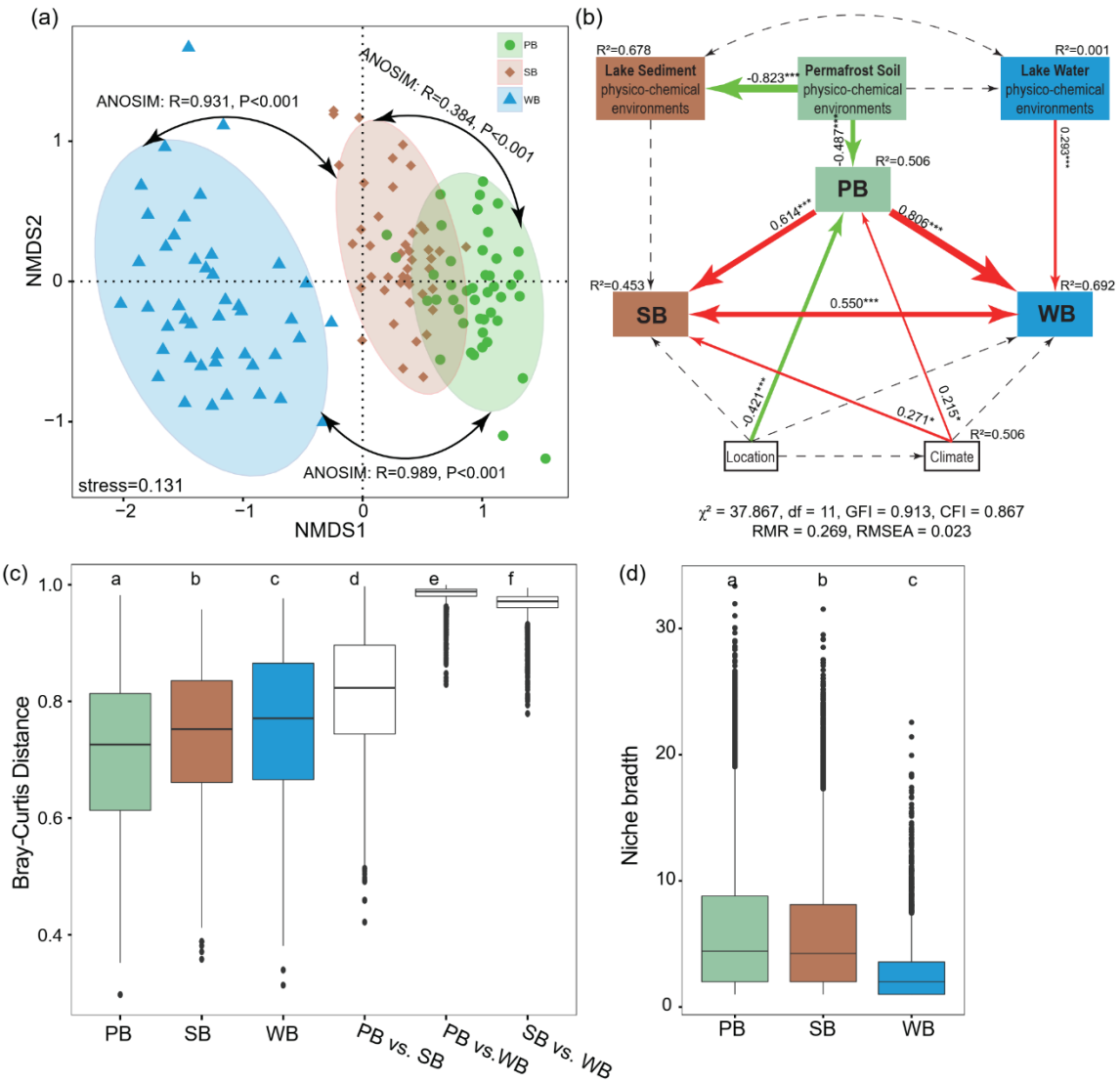

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342 Figure 5 (a) Non-metric multidimensional scaling (NMDS) ordination showing the
343 distribution of bacterial communities in permafrost soil (PB), lake sediment (SB), and lake
344 water (WB). The differences between these communities are confirmed by the non-

parametric statistical test (ANOSIM). (b) Structural equation modeling analysis depicting the relationships between location (including latitude, longitude, and elevation), climate (including mean annual temperature and mean annual precipitation), physicochemical environments (pH, conductivity, nutrients concentrations and stoichiometric ratios) of each habitat. Solid and dashed arrows represent the significant and nonsignificant relationships, respectively. Red and green arrows represent positive and negative relationships, respectively. Significant path coefficients are shown adjacent to the path with *, **, and *** denoting the significant level of $p<0.05$, $p<0.01$, and $p<0.001$, respectively. (c) β-diversities within and between PB, SB, and WB. (d) Habitat niche breadth of the bacterial communities.

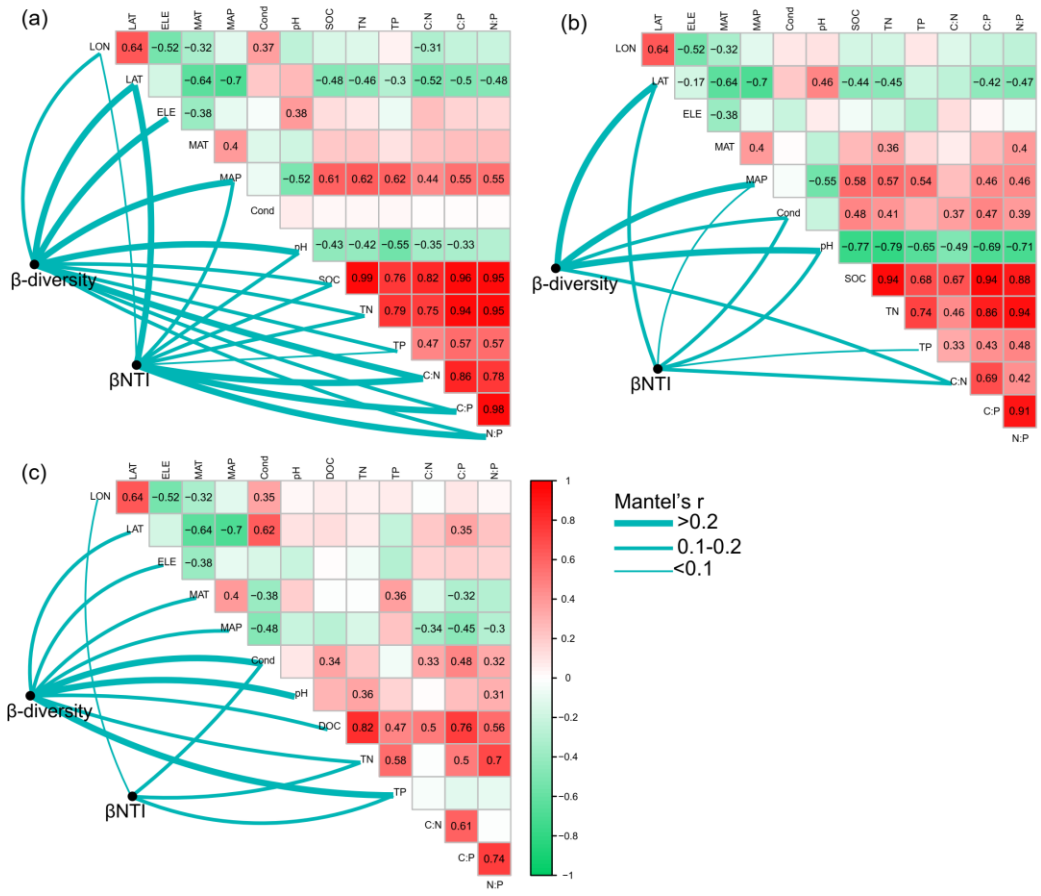

Figure 6 Pairwise correlations between environmental variables as well as the Mantel tests between environmental variables and β-diversity and beta nearest taxon index (βNTI) for (a) bacterial communities in permafrost soil, (b) bacterial communities in lake sediment, and (c) bacterial communities in lake water. β-diversity was calculated as Bray-Curtis distance. The lines denote significant relationships while the line width represents the Mantel's r statistic. Pairwise correlations between environmental variables are shown in color gradient matrix. The color represents Pearson's correlation coefficient, which shown in number when the result is significant ($p<0.05$). The abbreviations of the environmental variables are explained in the Methods section.

3.3 Assembly processes

To explore the mechanisms underlining the observed distribution patterns, a null-model-based framework was employed to quantify the deviation of phylogenetic turnover. PB had significantly higher βNTI than SB and WB (Figure 7a). Deterministic processes contributed 51.3%, 41.2%, and 44.9% to community variations for the bacterial communities in permafrost soil, lake sediment, and lake water, respectively (Figure 7b). In particular, the results showed that homogeneous selection contributed a larger fraction to the assembly of the WB (44.8%), followed by SB (35.2%) and PB (29.7%) (Figure 7b). Heterogeneous selection influenced PB (21.6%) more than SB (6.0%) and WB (0.1%). Dispersal limitation contributed a larger fraction to SB (57.2%) than to PB (45%) and WB (37.5%).

The relationships between βNTI and major environmental variables were used to estimate changes in the relative influences of deterministic and stochastic assembly processes. Mantel tests showed that the assembly processes of bacterial communities in permafrost soil, lake sediment, and lake water had similarities and differences in the responses to environmental variables (Figure 6). Particularly, differences of TP were significantly associated with βNTI of PB, SB, and WB, implying that an increasing divergence of TP could contribute to a shift from homogeneous selection to heterogeneous selection in the assembly of bacterial communities in the QTP thermokarst landscape. Moreover, βNTI of PB was also significantly associated with other environmental variables, except elevation, MAT, and conductivity. βNTI of SB was also significantly associated with latitude, MAP, conductivity, pH, and C:N, while βNTI of WB was significantly associated with longitude, conductivity, and TN.

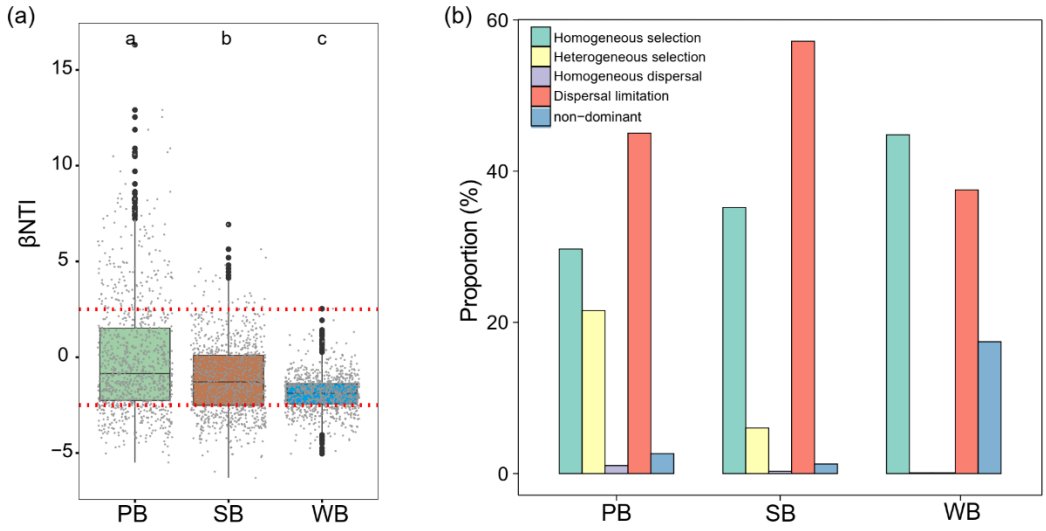

Figure 7 (a) The values of βNTI with horizontal dashed red lines indicate upper and lower significance thresholds at βNTI = +2 and −2, respectively in the three habitat types. (b) The contribution of deterministic (homogeneous and heterogeneous selection) and stochastic (dispersal limitations and homogenizing dispersal) processes to turnover in the assembly of bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB). "Non-dominant" indicates that the fraction was not dominated by any single process.

4 Discussion

4.1 Alpha diversity and community composition

Thermokarst lakes are known to have sediments that derive from the permafrost soil and are constantly replenished by the collapse of nearby permafrost (Payette et al., 2004; West and Plug, 2008; Veremeeva et al., 2021). This suggests that permafrost soil and lake sediments are likely to have high levels of similarity in bacterial diversity and community composition. Thus, there is no doubt that permafrost soil, lake sediments, and lake water should share a certain number of bacteria. Indeed, our study showed that 41% OTUs were shared among PB, SB, and WB, while 75% OTUs were shared between PB and SB.

Additionally, our prior research has shown that there are close correlations between the abiotic features of the two environments (Ren et al., 2022b). However, despite these similarities and connections, we found substantial differences in the bacterial communities of permafrost soil and lake sediments. As proposed by the Baas-Becking hypothesis (Baas-Becking, 1934), environmental selection is partially responsible for variation in microbial communities, which are also shaped by other ecological processes, such as diversification and dispersal limitation. In our study, alpha diversity and the dominant phyla found in PB and SB responded differently to various environmental variables. In addition, there were significant differences in composition and structure among PB, SB, and WB, while the dissimilarities between PB and SB were the lowest.

Bacterial communities in lake water had significantly lower alpha diversity as well as distinct community composition and structure in comparison to bacterial communities in permafrost soil and lake sediment. However, PB and SB had direct influence on WB. For thermokarst lakes, the water first originates from the thawing of the ice-rich permafrost and the lake is then fed by precipitation-derived and permafrost-derived water (Yang et al., 2016a; Narancic et al., 2017; Wan et al., 2019). Microorganisms present in lake water have a diverse range of sources, including terrestrial inputs and other sources such as bacteria distributed with the atmosphere, associated with plants and animals, and carried by migratory birds and animals (Ruiz-Gonzalez et al., 2015). Thus, there was a relatively small proportion of OTUs shared between permafrost soil and lake water, as well as between lake sediment and water, and only a few shared OTUs were enriched in lake water. It is a well-established fact that different habitats often support distinct microbial communities (Fierer et al., 2012; Hugerth et al., 2015; Louca et al., 2016). The contrast in bacterial

community composition between lake sediments and water has been extensively documented (Briee et al., 2007; Gough and Stahl, 2011; Yang et al., 2016b; Ren et al., 2017). In addition, sediment generally harbor a higher species-level diversity of bacteria compared to lake water (Lozupone and Knight, 2007; Ren et al., 2019b). For example, in a permafrost thaw pond of Andes, it was also found that water samples had lower alpha diversity than lake sediment and permafrost samples (Aszalós et al., 2020). Permafrost soil and lake sediment may provide more habitat heterogeneity for bacterial taxa than the water column, supported by our observation that the bacterial taxa had higher niche breadth in permafrost soil and lake sediment than in lake water. Moreover, in hydrologically connected terrestrial-aquatic ecosystems, bacterial communities can present distinct but directional spatial structure driven by terrestrial recruited taxa (Ruiz-Gonzalez et al., 2015). Thus, these community similarities between distinct bacterial habitats might be the result of common bacterial source (original permafrost) and the differences are likely caused by subsequent environmental selection, colonization from multiple other bacterial sources, and distinct assembly mechanisms.

Despite connections driven by dispersal, distinct thermokarst habitats had different bacterial community composition, as seen in previous work (Ottoni et al., 2022). All the dominant phyla were significantly different in relative abundance among PB, SB, and WB. In this study, Proteobacteria, Bacteroidota, Actinobacteriota, Gemmatimonadota, Acidobacteriota, Desulfobacterota, and Chloroflexi dominated bacterial communities in permafrost soil and/or thermokarst lakes despite high variabilities. Similar dominance of these taxa has also been found in permafrost and thermokarst landscapes in other areas (Aszalós et al., 2020; Belov et al., 2020; Wu et al., 2022). The most commonly reported

bacterial groups in permafrost environments include members of Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Firmicutes, and Chloroflexi (Steven et al., 2009; Altshuler et al., 2017; Ottoni et al., 2022), as observed in our samples.

4.2 Beta diversity and assembly processes

In our studied regions across the QTP, PB, SB, and WB all had a high beta diversity (average values > 0.7), with WB showing the highest, suggesting that bacterial communities shifted substantially across the large spatial scale of our sampling. Moreover, beta diversities of PB, SB, and WB were significantly correlated with each other, further suggesting that the bacteria in different habitats had a considerable proportion of members from the same source, the original pristine permafrost soil. The significantly lower mean SES.MNTD for PB indicate that bacterial communities in permafrost soil were more closely phylogenetically clustered and suffered stronger environmental filtering than those in lake sediment and water (Langenheder et al., 2017), consistent with the observation that PB had lower beta diversity than SB and WB. SES.MNTD is sensitive to changes in lineage close to the phylogenetic tips (Kembel et al., 2010). The higher SES.MNTD observed for SB and WB suggest the possibility that the bacteria in lake sediment and water exhibit a substantial divergence in the co-occurring species, and thermokarst lakes have experienced colonization by bacterial species originating from distinct clades or lineages from external sources following permafrost thaw (Webb et al., 2002; Stegen et al., 2013).

The structure of bacterial communities can vary across spatiotemporal scales and different habitats (Ren et al., 2017; Aguilar and Sommaruga, 2020; Pearman et al., 2020). A key objective in the field of microbial ecology is to determine the relative influence of stochastic and deterministic processes in shaping the assembly of communities (Stegen et

al., 2013; Zhou and Ning, 2017). In this study, bacterial communities in lake water displayed a higher influence of homogeneous selection but lower influence of heterogeneous selection compared to those in lake sediments and permafrost soil. Long-term changes in thermokarst lakes result in homogenized habitats and consequently strong homogenous selection on bacterial communities (Ning et al., 2019). In contrast, permafrost soil is a highly heterogeneous environment across spatial scales (Etzelmüller, 2013; Nitzbon et al., 2021), creating a wide range of habitats which can impose strong heterogeneous selection pressures on bacterial communities. Furthermore, permafrost soil is characterized by limited nutrient availability due to the frozen state of organic matters (Beermann et al., 2017; Zhang et al., 2023), while lake water offers a more diverse and abundant array of dissolved organic compounds and nutrients. As a result, bacterial communities in permafrost soil might be more sensitive to variations in resource availability, rendering them more strongly influenced by heterogeneous selection. In addition, dispersal limitation contributed a larger fraction to SB (57.2%) than to PB (45%) and WB (37.5%). The dispersal of microorganisms is often considered as a passive process that results in community variation and turnover coupled with the function of environmental filtering (Cline and Zak, 2014; Stegen et al., 2015; Custer et al., 2022). The high dispersal limitation of microbial communities in thermokarst lakes may be attributed to several factors. These include the isolated nature of thermokarst lakes, which are endorheic and therefore have limited connectivity, as well as the strong restriction on microbial dispersal and the presence of strong environmental filtering processes. Additionally, the prolonged frozen phase of thermokarst lakes and permafrost soil restrict the movement of microorganisms (Vargas Medrano, 2019; Vigneron et al., 2019).

Furthermore, geographical barriers, exemplified by prominent mountain ranges like the Tanggula Mountains, Kunlun Mountains, Nyenchen Tanglha Mountains, and Bayan Har Mountains, serve as impediments to the dispersal of both macro- and microorganisms (Wan et al., 2016; Yu et al., 2019; Ren et al., 2022c). Particularly in lake sediment, where bacterial communities are more isolated over distances and will not disperse as far as those in lake water and permafrost soil, resulting in stronger influence of dispersal limitation (Martiny et al., 2006; Xiong et al., 2012). Although the "everything is everywhere" hypothesis suggests that many microorganisms have a cosmopolitan distribution, their slow mobility allows for the development of regional phylogenetic differences and the emergence of specialized, endemic taxa in isolated habitats, resulting in a low likelihood of microorganisms dispersing to suitable distant sites (Telford et al., 2006). Therefore, dispersal processes in this thermokarst landscape may be restricted by the lack of hydrological connection, limited movement of water, short duration since thawing, and strong environmental filtering, contributing to the observed high dispersal limitation in the studied permafrost soil and thermokarst lakes. This inference is supported by many previous studies showing that dispersal limitation plays a major role in structuring microbial communities in lakes (Telford et al., 2006). Strong dispersal limitation for bacterial communities in permafrost has also been documented across an Alaskan boreal forest landscape (Bottos et al., 2018).

4.3 Environmental influences

Understanding how environmental factors shape bacterial communities is a crucial aspect in the field of microbial ecology (Fierer and Jackson, 2006; Pla-Rabes et al., 2011). In our study, bacterial communities were differentially correlated with various measured

environmental variables. In our data, pH was consistently identified as a strong correlate of microbial community structure and diversity, as is often observed in terrestrial and aquatic ecosystems worldwide (Fierer and Jackson, 2006; Xiong et al., 2012). While such correlations between pH and bacterial communities have been widely found, the regulation mechanisms still remain unknown (Malard and Pearce, 2018). Moreover, the influences of pH are often species- and location-specific (Malard and Pearce, 2018; Egelberg et al., 2021). In this study, pH had significantly negative relationships with alpha diversity of bacterial communities in lake sediment and water, and had negative or positive correlations with some phyla. Moreover, differences in pH might drive community variation observed between PB, SB, and WB, and shift community assembly processes for PB and SB. Moreover, with permafrost degrading and thermokarst developing, nutrient status will be strongly altered in permafrost areas. Organic carbon and nutrient stocks in permafrost are decreasing (Turetsky et al., 2020; Wu et al., 2021) and thermokarst lakes are developing, leading to dynamic environmental change (Luo et al., 2015; Vucic et al., 2020). These environmental disruptions likely impose strong influences on bacterial communities in thermokarst landscapes. Our study showed that nutrient (C, N, and P) concentrations and stoichiometric ratios were strongly related to alpha diversity (particularly for SB) and community variation and assembly (particularly for PB). High organic matter content, for instance, has been shown to support diverse and complex microbial communities (Garrido-Benavent et al., 2020; Ren and Gao, 2022). The role of nutrient availability in shaping bacterial communities has also been well established (Torsvik et al., 2002; Lee et al., 2017; Zhou et al., 2020). For example, Actinobacteria and Gemmatimonadota have a negative, while Gemmatimonadota has a positive relationship with organic carbon and nutrients in

permafrost (Romanowicz and Kling, 2022; Fu et al., 2023), in line with our results. The fact that different bacterial phyla exhibited varied responses to changes in organic carbon and nutrient further emphasizes the intricate interplay between microorganisms and their environment. Due to their ecological strategies, metabolic features, and environmental preferences, bacteria in permafrost respond differentially to nutrient status and other stressors, driving adaptive changes in community composition and function (Mackelprang et al., 2017). In addition, compared to permafrost soil and lake water, lake sediment can exhibit more stable physicochemical conditions. However, permafrost soil and lake water experience more dynamic and extreme environmental changes, which drive the bacterial communities. The results of SEM also in line with bacterial community assembly that deterministic processes had stronger influences on PB and WB than on SB. In addition, thermokarst lakes have sediment directly formed from permafrost soil, and thus, permafrost soil environments and bacterial communities had strong associations with that of lake sediment.

In addition to physicochemical environments, location and climate were also suggested to influence bacterial communities in distinct habitats. On the QTP in particular, air temperature and precipitation are increasing in most regions (Xu et al., 2008; Lu et al., 2018). Warming and altered precipitation regimes under climate change have been demonstrated to affect alpha diversity and composition of stream microbial communities at continental scales (Picazo et al., 2020). Our study indicates that location (particularly latitude) and climate (particularly MAP) factors are important in shifting bacterial communities in thermokarst landscapes. Particularly for bacterial communities in permafrost soil, location and climate have been evidenced as strong factors in shaping

567 microbial communities (Taş et al., 2018; Barbato et al., 2022). Understanding large-scale
568 pattern of bacterial communities is increasingly important to offer insights into the impacts
569 of climate change (Picazo et al., 2020; Ren et al., 2021). As global climate changes, QTP
570 is getting warmer and more humid (Xu et al., 2008; Lu et al., 2018). Therefore, significant
571 alterations to the physical, chemical, and biological properties of thermokarst lakes on the
572 QTP can be expected in the coming decades. Based on "space-for-time" substitution, our
573 study serves as a foundation for predicting the potential impact of climate change on
574 bacterial communities in thermokarst landscapes.

575 **5 Conclusion**

576 In this study, we investigated bacterial communities in paired water and sediment samples
577 in thermokarst lakes as well as permafrost soil around the lakes across the QTP. esults
578 showed that each habitat had distinct bacterial assemblages, with lower alpha diversity in
579 lake water and higher beta diversity in lake sediment and permafrost soil. There was
580 considerable overlap in OTUs across habitats. Bacterial communities in permafrost soil
581 and lake sediment were influenced by dispersal limitation, while those in lake water were
582 driven by homogeneous selection. Environmental variables, including latitude, mean
583 annual precipitation, and pH, affected bacterial community variations in all habitats. The
584 study highlights the unique bacterial communities and ecological impacts of permafrost
585 degradation in diverse habitats created by thermokarst processes.

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Data availability statement:

Raw sequences were uploaded to the China National Center for Bioinformation (PRJCA009850, CRA007082).

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The authors declare no competing interests.

Author's contributions:

Z.R. designed the study, did the analyses, and prepared the manuscript, performed the field work and laboratory work. All the authors prepared the manuscript.

Ethics approval statement:

Not applicable

Permission to reproduce material from other sources:

Not applicable

Originality-Significance Statement:

This is our original study and not submitted to elsewhere

Supplementary Information

Figure S1 Map of the 44 sampling sites of permafrost soil and thermokarst lakes across the Qinghai-Tibet Plateau. The distribution of the permafrost was cited from Zou et al., 2017. This map was cited from Ren et al, 2022a.

Figure S2 (a) Venn diagram showing the unique and shared OTUs among distinct bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB). (b) The volcano plot showing the shared OTUs that significantly (t-test, $P < 0.05$) enriched in a certain habitat. The volcano plot was constructed using $\log_2$ (fold change) on x-axis and $-\log_{10}$ (p-values of t-test) on y-axis.

Figure S3 Distance-decay curves showing community similarity of bacterial communities in permafrost soil (PB), lake sediment (SB), and lake water (WB) against geographic distances between sampling sites. Solid lines denote the ordinary least-squares linear regressions.

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