



## Effects of environmental factors on the distribution of microbial communities across soils and lake sediments in the Hoh Xil Nature Reserve of the Qinghai-Tibetan Plateau



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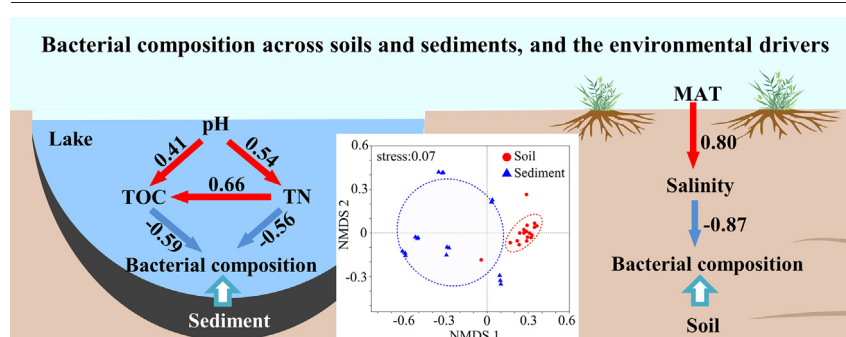
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### HIGHLIGHTS

- Soils and sediments had significant difference in bacterial diversity and composition.
- Heterogeneous selection dominated the bacterial distribution in soils and sediments.
- Bacterial composition in soils and sediments was driven by MAT, salinity, TOC, and TN.
- MAT significantly affected soil bacterial composition through changing soil salinity.
- TOC and TN had significant direct impact on sediment bacterial community composition.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Comparison of microbial community diversity and composition of terrestrial and aquatic ecosystems in undisturbed regions could expand our understanding on the mechanisms of microbial community assembly and ecosystem responses to environmental change. This study investigated the spatial distribution of bacterial community diversity and composition in the lakeshore soils and lake sediments from one of the best preserved nature reserves, Hoh Xil on the Qinghai-Tibetan Plateau, and explored the corresponding environmental drivers. A total of 36 sediment and soil samples were collected from six alpine lakes and the corresponding shore zones, and their bacterial community structure was identified by high-throughput 16S rRNA gene sequencing. Significant difference ( $p < 0.05$ ) in diversity and composition of bacterial communities between the soils and sediments was observed. Heterogeneous selection played a dominant role in shaping the spatial variations of bacterial communities between the soils and sediments. Results of canonical correspondence analysis showed that the difference in composition of bacterial communities at OTU level between the soils and sediments was mainly determined by the mean annual temperature, salinity, and contents of total organic carbon and total nitrogen. Structural equation modeling revealed that salinity played a significantly direct role in soil bacterial composition, while mean annual temperature indirectly affected the bacterial composition mainly through changing soil salinity. In contrast, the sediment bacterial composition was directly influenced primarily by the contents of total organic carbon and total nitrogen, while pH also had an important indirect effect on sediment bacterial composition. These results shed light on the distribution patterns of bacterial communities between lakeshore soils and lake sediments in high-altitude permafrost regions, and the major ecological processes and

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environmental drivers that shaped their bacterial communities, and provide insight into the mechanisms underlying microbial community assembly in such regions.

## 1. Introduction

Microbes play critical roles in the formation and degradation of organic matter and biogeochemical cycling of nutrient elements in both terrestrial (Fierer and Jackson, 2006; Joshi and Shekhawat, 2014) and aquatic ecosystems (Balci et al., 2012; Martins et al., 2011; Newton et al., 2011). Soils and lake sediments are the main place where microbes participate in the biogeochemical cycles in terrestrial and aquatic ecosystems, respectively. Observations of the spatial variations in microbial communities between soils and sediments could greatly enhance the understanding on community assembly (Monard et al., 2016; Wang et al., 2013) and the biogeochemical processes that maintain ecosystem functions (Chen et al., 2016; Wang et al., 2016), and help improve the predictions of ecosystem responses to environmental change. Previous studies have shown that the structure of microbial communities could differ substantially among habitat types (Lozupone and Knight, 2007; Wang et al., 2013), which provides the evidence for microbial biogeography. Wang et al. (2013) found that there were significant variations in phylogenetic dissimilarities among different habitat types, including stream biofilm, lake water, lake sediment, and soil, and the microbial communities showed strong habitat dependence through evolutionary adaptation. Obvious spatial variations in microbial communities were also observed between soils and sediments (Chen et al., 2016; Hollister et al., 2010; Wang et al., 2014). Nonetheless, several studies reported a large degree of overlap in microbial communities between soils and sediments (Monard et al., 2016; Wang et al., 2016). Therefore, the patterns of spatial distribution of microbial communities between soils and sediments remain controversial.

Understanding the mechanisms underlying the spatial variations in microbial communities has been a long-standing theme of ecological research (Anderson et al., 2011; Hubbell, 2001; Martiny et al., 2006). Both deterministic and stochastic processes were usually used to explain the microbial community assembly (Monard et al., 2016; Stegen et al., 2012; Wang et al., 2013). Deterministic processes assume that the community assembly is non-random and driven by environmental heterogeneity and biotic interactions, while stochastic processes include unpredictable disturbance, dispersal limitation, mass effect, and random birth-death events (Chase and Myers, 2011; Hubbell, 2001). It has been demonstrated that stochastic processes were the major determinant of some microbial systems (Caruso et al., 2011; Zhang et al., 2019), while increasing evidences have emerged for a dominant role of deterministic processes in shaping the patterns of microbial distribution across habitats (Lozupone and Knight, 2007; Mo et al., 2020; Wang et al., 2013). Despite these previous results, the relative contributions of deterministic and stochastic processes to microbial community assembly are still unclear, while investigations on local distribution of microbial communities across soils and lake sediments may help bridge this knowledge gap.

Environmental factors have crucial influence on the distribution of microbial communities in different ecosystems. Many studies reported that the microbial communities were determined by various environmental factors, such as pH (Tripathi et al., 2012; Xing et al., 2019; Xiong et al., 2012), contents of organic carbon (Yi et al., 2021), nitrogen, phosphorus, and potassium (Wang et al., 2016; Wang et al., 2020; Xing et al., 2019), and salinity (Lozupone and Knight, 2007). It has also been reported that climatic factors, such as mean annual temperature (MAT) and mean annual precipitation (MAP), also played a crucial role in the diversity and composition of microbial communities (Zheng et al., 2020). Obvious difference exists in the major environmental drivers of microbial communities between soils and lake sediments. For example, soil pH has been widely considered as the major driver of bacterial diversity and community composition across various terrestrial ecosystems (Fierer and Jackson, 2006; Tripathi et al., 2012). In contrast, several studies suggested that total organic carbon

and total nitrogen had more important influence than pH on the bacterial communities in the sediments of freshwater lakes (Bai et al., 2012; Gao et al., 2018; Zhang et al., 2015). Many studies observed that salinity played an important role in shaping the microbial communities in soils (Lozupone and Knight, 2007; Zhang et al., 2021), while it was also found to have a weaker effect on bacterial composition in lake sediments (Hollister et al., 2010; Xiong et al., 2012). In addition, MAT has been shown to have strong impact on microbial communities in soils (Vásquez-Dean et al., 2020; Zhao et al., 2021; Zheng et al., 2020) and sediments (Huang et al., 2017; Manirakiza et al., 2022). It is worth noting that these conclusions were drawn from studies on only soil or lake sediment samples, which were collected from different regions with distinct geographical and climatic characteristics. As a result, the environmental factors in different studies on the distribution of microbial communities in soils and lake sediments are not directly comparable. Investigations on the local distribution of microbial communities between lake sediments and adjacent lakeshore soils with significantly different physicochemical characteristics are necessary to obtain insight into the potential roles of various environmental factors in governing the assembly of microbial communities. Although a few studies have been carried out to gain insight into the distribution of microbial communities that inhabit soils and lake sediments from the same areas (Chen et al., 2016; Hollister et al., 2010; Wang et al., 2016), the specific impact of major environmental factors, such as temperature, pH, nutrient contents, and salinity, on the distribution of microbial communities across soils and lake sediments is still unclear.

Alpine ecosystems are highly vulnerable and sensitive to environmental change under global warming (Tang et al., 1986; Zheng et al., 2002). Changes in the microbial communities of alpine ecosystems are of great importance to global carbon and nitrogen feedbacks under climate warming (Chu et al., 2014; Ding et al., 2019; Peng et al., 2020). The structure of microbial communities in alpine terrestrial or aquatic ecosystem on various plateaus has been widely studied over the world (Fig. S1a), especially on the Qinghai-Tibetan Plateau in China (Fig. S1b). The Qinghai-Tibetan Plateau, the Earth's largest and highest plateau, contains several thousand saline-alkaline lakes and is also known as the "Asian water towers". This region is considered as the largest middle- and low-latitude permafrost and one of the most sensitive regions to global climate change in the world (Tang et al., 1986). It has been reported that global warming accelerated the thawing of permafrost and significantly changed the dynamics of alpine lakes (Liu et al., 2021b), which had important impact on microbial communities (Bischoff et al., 2014; Mackelprang et al., 2011; Nikrad et al., 2016; Wu et al., 2018). Although the structure of microbial communities in soils and sediments on the Qinghai-Tibetan Plateau has been extensively investigated (Fig. S1b and Table S1), most of the sites investigated were located in regions with various level of human disturbance, which could affect the niche selection of resident species through changing the deterministic and stochastic processes (Myers and Harms, 2011; Orrock and Fletcher, 2005), and thus alter the diversity and composition of indigenous microbiota. The Hoh Xil, located in the northeastern part of the Qinghai-Tibetan Plateau, is one of the coldest regions of the Qinghai-Tibetan Plateau. This region is covered with permafrost and contains a number of endorheic lakes (Liu et al., 2021b). Besides, the inaccessibility and the harsh climate have combined to keep Hoh Xil free from modern human influence and development. Therefore, the core zone of the Hoh Xil Nature Reserve, which is among the best preserved ecological environment in the world, is an ideal region to investigate the distribution of microbial communities across habitats, and explore the mechanisms underlying microbial community assembly in high-altitude permafrost regions.

Based on the above literature review, the spatial distribution of microbial communities between soils and lake sediments, and the mechanisms

underlying the assembly of microbial communities in these types of habitats are still not conclusive. The objective of this study was to investigate the spatial variations in diversity and composition of bacterial communities between lakeshore soils and lake sediments in high-altitude permafrost regions, and explore their environmental driving factors. The following hypotheses were examined: (1) significant difference exists in the structure of bacterial communities between soils and sediments; (2) deterministic processes play a dominant role in shaping the spatial distribution of bacterial communities in soils and sediments; (3) the difference in composition of bacterial communities between soils and sediments is mainly determined by MAT and salinity. A total of 36 lakeshore soil and lake sediment samples were collected from 12 sites located in the core zone of the Hoh Xil Nature Reserve on the Qinghai-Tibetan Plateau. The diversity and composition of bacterial communities in the soil and sediment samples were investigated based on 16S rRNA gene sequencing and their driving environmental factors were systematically analyzed to test the above hypotheses. The findings provide insight into the composition of microbial communities in soils and lake sediments in high-altitude permafrost regions of the Qinghai-Tibetan Plateau, and improve the understanding of microbial community assembly across habitats.

## 2. Materials and methods

### 2.1. Study area

The study area is located in the core zone of the Hoh Xil Nature Reserve in the northeastern part of the Qinghai-Tibetan Plateau in China (Fig. 1a). This reserve comprises extensive area of high mountains and steppes with an average elevation above 4600 m, where sub-zero average temperatures prevail all year-round. With alpine semi-arid continental climate, MAT, MAP, and mean annual wind speed of in Hoh Xil region are  $-4.72$  °C, 320.4 mm, and 4.31 m/s, respectively (Liu et al., 2019). The study area is dominated by alpine desert ecosystem, and is underlain by permafrost. Owing to the cold and dry climate, severe solar radiation, and intensive evapotranspiration, the vegetation type in the study area is mainly super-xerophytes (Shi et al., 2018). The areas of the lakes sampled were surveyed, while their water quality parameters, including temperature, salinity, chlorophyll-a concentration, blue-green algae concentration, turbidity, dissolved oxygen, fluorescent dissolved organic matter, and water clarity of Secchi depth, were measured *in situ* (Table S2), which have been reported in Liu et al. (2021a).

### 2.2. Sample collection and analysis

A total of six lakes ( $90^{\circ}10' - 92^{\circ}18'E$ ,  $34^{\circ}45' - 35^{\circ}55'N$ ), namely, Gorlushak Lake, Ulan Ul Lake, Xijir Ulan Lake, Lixi Oidaim Lake, Taiyang Lake, and Hoh Xil Lake, were sampled between October and November 2019, as part of the Second Tibetan Plateau Scientific Expedition and Research Program (Fig. 1b). Three surface sediment samples (0–10 cm) were collected from the bottom of each lake using a Peterson grab sampler. The depth of surface sediment sampling sites ranged from 10 to 51 m below water surface in the six lakes, as summarized in Table 1. Three surface soil samples (0–5 cm) were also randomly collected from three  $5\text{ m} \times 5\text{ m}$  quadrats at the shore of each lake, following the same procedure in our previous work (Wang et al., 2020). Each of the samples collected was mixed well with the extraneous materials (e.g., stones and root mats) removed, then stored in a cooler containing ice (the ambient temperature was far below 0 °C). When the samples were brought back to the laboratory, a portion of each sample was immediately stored at  $-20$  °C and processed for DNA extraction within one week. A portion of each sample was air-dried and passed through a 2 mm sieve to remove the stones and plant debris, and then used for measurement of the physicochemical properties.

Major physicochemical properties of the soil and sediment samples, including pH, total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), and electrical conductivity (EC), were measured. Specifically, the pH was measured in 1:5 mixture of dry

soil/sediment: water (Wang et al., 2020). The TOC content was measured using the method described in Wu et al. (2017b). The Kjeldahl digestion method was used to determine the TN content (Zhao et al., 2020). The contents of TK and TP were measured using the same methods reported in our previous work (Wang et al., 2020). The  $EC_{1:5}$  of the soils and sediments was measured directly with a conductivity meter according the method described in Lu (1999). The EC was used as a proxy for salinity (Corwin and Scudiero, 2020). The sample is deemed saline when the EC value is higher than 4 ms/cm (Nouri et al., 2017). The meteorological data (MAT and MAP) of sampling sites were extracted from the WorldClim database (Fick and Hijmans, 2017).

### 2.3. High throughput sequencing of 16S rRNA genes

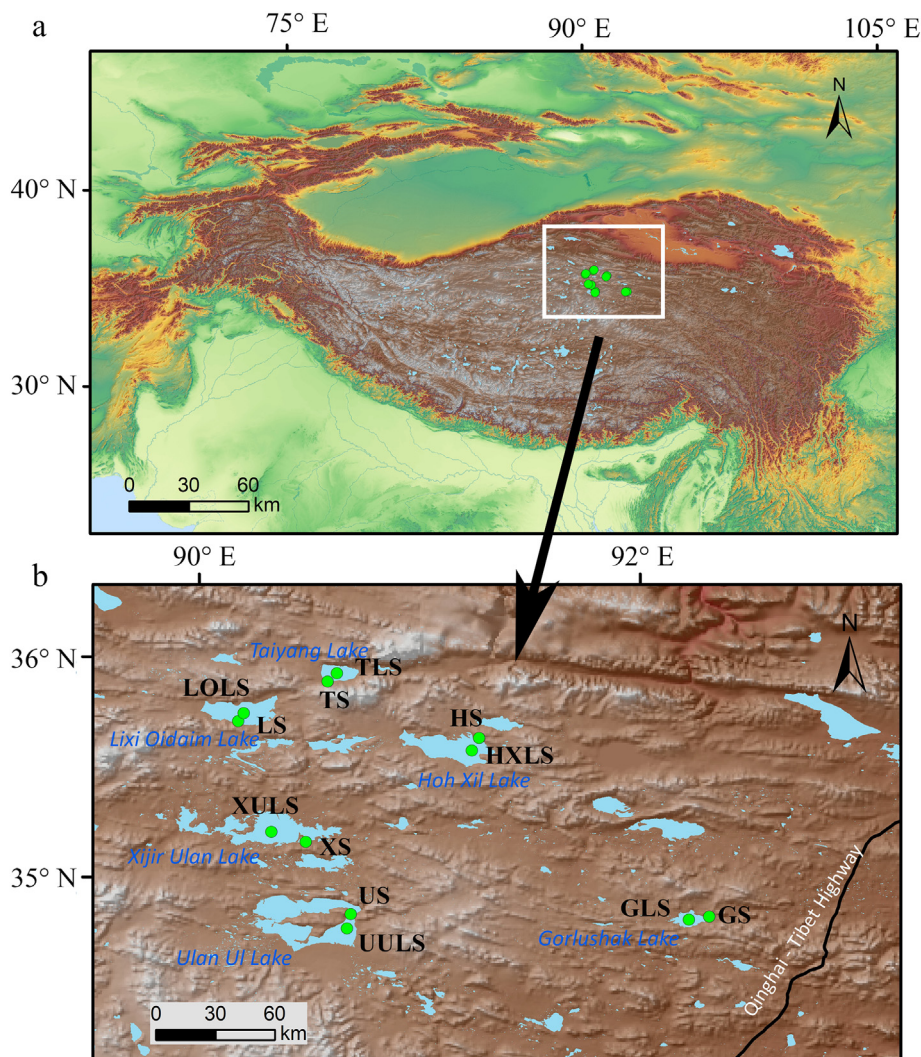
The total bacterial DNA in the soils and sediments was extracted from 0.5 g samples using a FastDNA Spin Kit (MP Biomedicals, USA), following the manufacturer's instructions. The V3-V4 region of the 16S rRNA genes was amplified using the primer sets of 338F (5'-ACTCCTACGGGAGGCA GCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') (Claesson et al., 2010; Wang et al., 2020). The PCR products were purified and quantified using an AxyPrep DNA Gel Extraction Kit and Quantus Fluorometer, respectively. A mixture of the purified amplicons was then sequenced on an Illumina MiSeq PE300 platform, according to the standard protocols at Majorbio in Shanghai, China. Raw sequence data were processed and analyzed using the QIIME pipeline (Caporaso et al., 2010). The UPARSE pipeline was used to cluster the operational taxonomic units (OTUs) at 97% sequence identity (Edgar, 2013). Each 16S rRNA gene sequence was aligned against the Silva database at a confidence threshold of 70% to obtain the taxonomy. The detailed procedures in DNA extraction, PCR amplification, and processing of the sequencing data were similar to those described in our previous work (Wang et al., 2020).

### 2.4. Analysis of bacterial community assembly

The  $\beta$ -nearest taxon index ( $\beta$ NTI) and Bray-Curtis-based Raup-Crick index ( $RC_{\text{bray}}$ ) were calculated to evaluate the relative contributions of deterministic and stochastic processes in governing the bacterial community assembly based on a null model theory (Chase and Myers, 2011; Stegen et al., 2012; Stegen et al., 2013). The bacterial community assembly is driven primarily by the deterministic and stochastic processes when  $|\beta$ NTI| > 2 and  $|\beta$ NTI| < 2, respectively (Stegen et al., 2013).  $\beta$ NTI values higher than +2 and lower than  $-2$  indicate the influence of heterogeneous selection and homogeneous selection, respectively, in deterministic processes (Dini-Andreote et al., 2015). In addition,  $\beta$ NTI in combination with modified  $RC_{\text{bray}}$  could be used to determine the influence of stochastic processes (Stegen et al., 2012; Stegen et al., 2013). Specifically,  $|\beta$ NTI| < 2 and  $|RC_{\text{bray}}| > 0.95$  suggest the community assembly is driven by homogenizing dispersal ( $RC_{\text{bray}} < -0.95$ ) or dispersal limitation ( $RC_{\text{bray}} > 0.95$ ). When  $|\beta$ NTI| is <2 but with a  $|RC_{\text{bray}}| < 0.95$ , the community assembly is governed by ecological drift.

### 2.5. Data analysis

The  $\alpha$ -diversity indices, including community diversity indices (Shannon index and Simpson index), community richness parameters (Chao 1 index and Ace index), and sequencing depth index (Good's coverage), were calculated using the Mothur software (Yi et al., 2021). The separation of bacterial community composition across soils and sediments was assessed by non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance of OTUs. The difference in bacterial community composition was also tested using the analysis of similarity (ANOSIM) (Ziegler et al., 2017). The canonical correspondence analysis (CCA) was applied to identify the effect of environmental factors on bacterial community composition at the OTU level in the soils and sediments. One-way analysis of variance (ANOVA) was conducted using the IBM SPSS Statistics (version 26.0).



**Fig. 1.** Sampling sites of the lakeshore soils and lake sediments in the core zone of Hoh Xil Nature Reserve on the Qinghai-Tibetan Plateau. GS, US, XS, LS, TS, and HS indicate the soil sampling sites at the lakeshores of Gurlushak Lake, Ulan Ul Lake, Xijir Ulan Lake, Lixi Oidaim Lake, Taiyang Lake, and Hoh Xil Lake, respectively; GLS, UOLS, XOLS, LOLS, TLS, and HXLS indicate the lake sediment sampling sites at Gurlushak Lake, Ulan Ul Lake, Xijir Ulan Lake, Lixi Oidaim Lake, Taiyang Lake, and Hoh Xil Lake, respectively.

Structural equation model (SEM) was used to test the direct and indirect effects of various environmental factors, including MAT, MAP, pH, salinity, TOC, and TN, on bacterial community composition in the soils, and in the sediments as well. An *a priori* model that showed the hypothesized interactions among the environmental factors, including MAT, MAP, pH, salinity, TOC, and TN, and bacterial composition was constructed based on current

knowledge. The scores of the first NMDS axis were used as the proxy for bacterial community composition (Xu et al., 2021). To simply the model, major physicochemical properties of the soils and sediments, including pH, salinity, TOC, and TN, were selected based on the results of CCA. The maximum-likelihood estimation method was used to fit the model. The  $\chi^2$  value, *p* value, root mean square error of approximation (RMSEA) test,

**Table 1**  
Summary of the conditions of the field sampling sites and the physical and chemical properties of the lakeshore soil and lake sediment samples.

Site	Sample type	Altitude (m)	Depth (m)	MAT (°C)	MAP (mm)	pH	EC (ms/cm)	TOC (g/kg)	TN (g/kg)	TP (g/kg)	TK (g/kg)
Gurlushak Lake	Soil	4766	-	-6.05	22.75	8.5 ± 0.05 cd	0.2 ± 0.02f	1.12 ± 0.50e	0.35 ± 0.06c	0.31 ± 0.01c	11.15 ± 0.21ef
	Sediment	4766	10.0	4	-	8.6 ± 0.09bcd	11.0 ± 0.3e	28.35 ± 3.31c	2.95 ± 0.39a	0.66 ± 0.08a	24.12 ± 2.44abc
Ulan Ul Lake	Soil	4837	-	-5.70	20.83	8.1 ± 0.25d	0.6 ± 0.04f	1.64 ± 0.56e	0.40 ± 0.05c	0.28 ± 0.02c	10.56 ± 0.46f
	Sediment	4867	40.7	4	-	9.4 ± 0.19a	19.5 ± 0.6c	38.23 ± 3.13b	2.50 ± 0.40a	0.49 ± 0.05b	15.82 ± 2.05def
Xijir Ulan Lake	Soil	4737	-	-5.95	19.25	8.9 ± 0.63abc	0.2 ± 0.02f	3.29 ± 2.06e	0.57 ± 0.05c	0.50 ± 0.07b	14.99 ± 1.08def
	Sediment	4746	11.8	4	-	8.5 ± 0.26 cd	32.2 ± 1.5b	14.52 ± 2.37d	1.62 ± 0.29b	0.50 ± 0.03b	23.79 ± 3.08bc
Lixi Oidaim Lake	Soil	4829	-	-7.22	18.33	8.3 ± 0.10 cd	0.2 ± 0.04f	4.80 ± 0.97e	0.72 ± 0.13c	0.53 ± 0.03ab	17.32 ± 0.96de
	Sediment	4803	38.0	4	-	8.3 ± 0.14 cd	37.6 ± 0.4a	2.65 ± 0.64e	0.77 ± 0.11c	0.52 ± 0.04b	26.42 ± 3.22ab
Taiyang Lake	Soil	4792	-	-7.74	18.33	8.4 ± 0.28 cd	0.1 ± 0.02f	6.12 ± 4.35de	0.68 ± 0.26c	0.65 ± 0.01a	18.41 ± 0.89 cd
	Sediment	4818	51.0	4	-	8.8 ± 0.34abcd	0.4 ± 0.2f	5.73 ± 0.28e	0.80 ± 0.10c	0.60 ± 0.04ab	30.45 ± 4.04a
Hoh Xil Lake	Soil	4753	-	-7.53	19.50	8.4 ± 0.15 cd	0.1 ± 0.01f	6.53 ± 2.69de	0.77 ± 0.22c	0.54 ± 0.06ab	19.33 ± 2.10 cd
	Sediment	4768	31.2	4	-	9.3 ± 0.16ab	14.1 ± 0.8d	55.14 ± 6.65a	2.83 ± 0.17a	0.50 ± 0.05b	17.25 ± 1.63de

Note: Values in the same column without shared lowercases letters indicate significant difference at *p* < 0.05 among the samples.

and goodness-of-fit index (GFI) were performed to assess the model fitness (Delgado-Baquerizo et al., 2016; Hooper et al., 2008). The criteria for a good fit, such as  $0 \leq \chi^2/df \leq 2$ ,  $0.05 < p \leq 1.00$ ,  $0 \leq RMSEA \leq 0.5$ , and  $0.95 \leq GFI \leq 1$ , were adopted according to the literature (Hooper et al., 2008; Xu et al., 2021). All SEM analyses were carried out using the IBM SPSS Amos 24.0.

### 3. Results

#### 3.1. Physicochemical properties of the lakeshore soils and lake sediments

The altitude of all sampling sites ranged from 4737 to 4867 m, and there was little variation for the MAT and MAP values among different sampling sites of lakeshore soils (Table 1). The MAT of lake sediment sampling sites was defaulted to 4 °C, which was higher than those of soil sampling sites (−7.7 to −5.7 °C). The pH values of soils and sediments were all above 8.0. The EC values of sediments were all above 4 ms/cm, except for the one from Taiyang Lake, and were much higher than those of the soils ( $p < 0.01$ ). Based on their pH and EC values, the soils could be identified as non-saline alkaline, while the sediments could be identified as saline alkali, with the exception of the sediment from Taiyang Lake. Overall, the pH, TOC, and TK values of the lakeshore soils were obviously lower than those of the corresponding lake sediments ( $p < 0.01$ ). Similarly, the contents of TN in soils were lower than those of the corresponding sediments ( $p < 0.01$ ), although their difference was small. Meanwhile, there was no significant difference for TP contents between the lakeshore soils and lake sediments ( $p > 0.05$ ).

#### 3.2. Diversity and composition of bacterial communities

A total of 9084 OTUs were identified across all soils and sediments (Fig. 2a). The number of OTUs in the soil and sediment samples ranged from 740 to 2423, with the lakeshore soils having more OTUs than the corresponding lake sediments ( $p < 0.01$ ). The Good's coverage ranged from 0.977 to 0.992, and showed no significant difference between the soils and sediments (Fig. 2b), indicating the sequencing depth was sufficient to

cover most bacteria. The rarefaction curves of Ace index, Chao 1 index, Shannon index, and Simpson index in all soil and sediment samples were saturated, suggesting the sequences sufficiently covered the bacterial community diversity (Fig. S2). The Chao 1 index ranged from 1073 to 3277 in the lakeshore soils, and from 891 to 2688 in the lake sediments (Fig. 2c). The Shannon index ranged from 4.67 to 6.73 in the lakeshore soils, and from 3.37 to 5.37 in the lake sediments (Fig. 2d). Besides, the Ace index and Simpson index were also calculated (Fig. S3). Overall, the Ace, Chao 1, Shannon, and Simpson indices consistently indicate that the lakeshore soils had significantly higher  $\alpha$ -diversity of bacterial communities than the lake sediments ( $p < 0.05$ ). It is worth noting that the uncertainty for some values on Fig. 2 was rather high, which resulted from the limited number of samples collected in the present study (collecting lake sediments under the harsh conditions of Hoh Xil had been particularly challenging). Nonetheless, statistically significant conclusions about the diversity of bacterial communities in the lakeshore soils and lake sediments could be drawn. The Venn diagram shows that only less than a quarter of the OTUs ( $n = 2745$ , 23%) were shared by the soils and sediments (Fig. 3a). About half of the OTUs ( $n = 1288$ , 45%) were shared by all lakeshore soils (Fig. S4a), while only few OTUs ( $n = 57$ , 1.7%) were shared by the lake sediments (Fig. S4b). Moreover, NMDS also showed significant difference in the composition of whole bacterial communities at OTU level between the soils and sediments (Fig. 3b; ANOSIM,  $r = 0.656$ ,  $p = 0.001$ ). These results revealed that there was significant difference in the diversity and composition of whole bacterial communities between the lakeshore soils and lake sediments.

The bacterial gene sequences of the 36 soil and sediment samples were clustered into 59 phyla, 130 classes, 363 orders, 663 families, 1327 genera, and 2742 species. Fig. 4 depicts the dominant bacterial taxa in the soils and sediments at the phylum (relative abundance >5%), class (top 10), and genus (top 10) levels. Overall, the phylum *Proteobacteria* was dominant in all samples, and its mean relative abundance was 14.63–36.62% and 16.79–33.71% in the soils and sediments, respectively (Fig. 4a). The relative abundance of phyla *Actinobacteria*, *Chloroflexi*, *Acidobacteria*, and *Gemmatimonadetes* in the soils was significantly higher than that in the sediments ( $p < 0.01$ ), while the relative abundance of phyla *Bacteroidetes*,

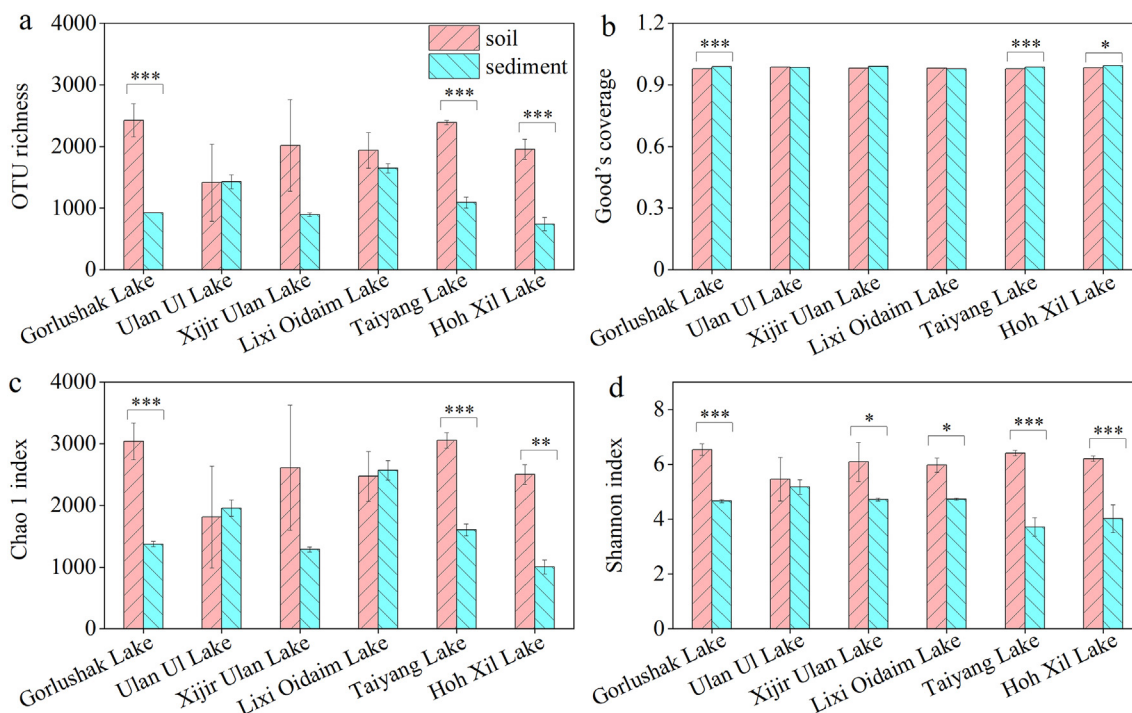
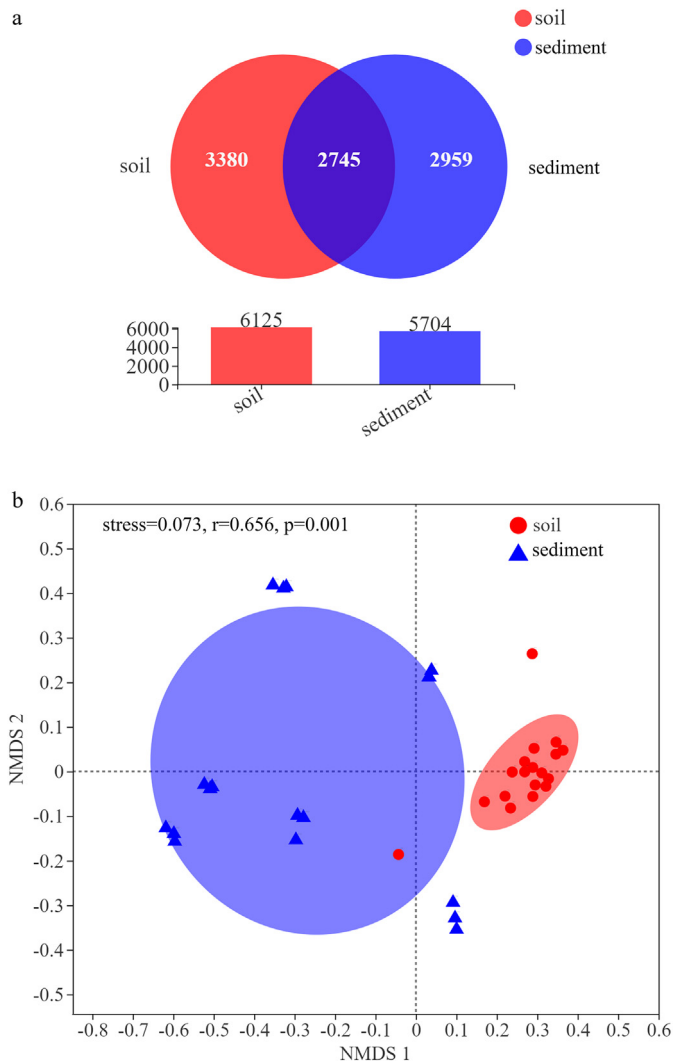


Fig. 2. OTU richness and  $\alpha$ -diversity indices of bacterial communities in the lakeshore soils and lake sediments: (a) Observed OTUs; (b) Good's coverage; (c) Chao 1 index; and (d) Shannon index. \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ .



**Fig. 3.** Comparison of the bacterial composition at OTU level between the lakeshore soils and lake sediments: (a) Venn diagram displaying the degree of overlap of bacterial OTUs; and (b) comparison of bacterial composition at OTU level by NMDS.

*Firmicutes*, *Deinococcus-Thermus*, and *Epsilonbacteraeota* in the soils was significantly lower than that in the sediments ( $p < 0.05$ ) (Fig. S5a). These results indicate that the dominant phyla were *Proteobacteria*, *Actinobacteria*, *Chloroflexi*, *Acidobacteria*, and *Gemmatimonadetes* in the lakeshore soils, but *Proteobacteria*, *Bacteroidetes*, *Firmicutes*, *Deinococcus-Thermus*, and *Epsilonbacteraeota* in the lake sediments. Fig. 4b shows the relative abundance of the top 10 shared classes in the soils and sediments. The most dominant classes were *Actinobacteria*, *Alphaproteobacteria*, *Chloroflexia*, *Subgroup\_6*, and *Gemmatimonadetes* in the soils, but *Bacteroidia*, *Gammaproteobacteria*, *Deltaproteobacteria*, and *Deinococci* in the sediments based on the difference in their relative abundance (Fig. S5b). At genus level, soil bacterial communities were mainly composed of *norank\_f\_JG30-KF-CM45*, *norank\_f\_norank\_o\_norank\_c\_Subgroup\_6*, *Rubrobacter*, and *norank\_f\_67-14*, while the sediment bacterial communities were dominated by genera *Truepera*, *Sulfurimonas*, *norank\_f\_Bacteroidetes\_BD2-2*, and *norank\_f\_E6aC02* (Fig. 4c and Fig. S5c). LEfSe analysis was conducted to identify the specific taxon that best characterizes each biological category with an LDA threshold of 2.0. As shown on Fig. S6, the soils and sediments had 11 and 6 abundant bacteria clades,

respectively, indicating these specific taxa may be the potential biomarkers for the lakeshore soils and lake sediments, respectively. These results revealed that there was significant difference in the dominant bacterial taxa based on their relative abundance between the soils and sediments.

### 3.3. Assembly of bacterial communities

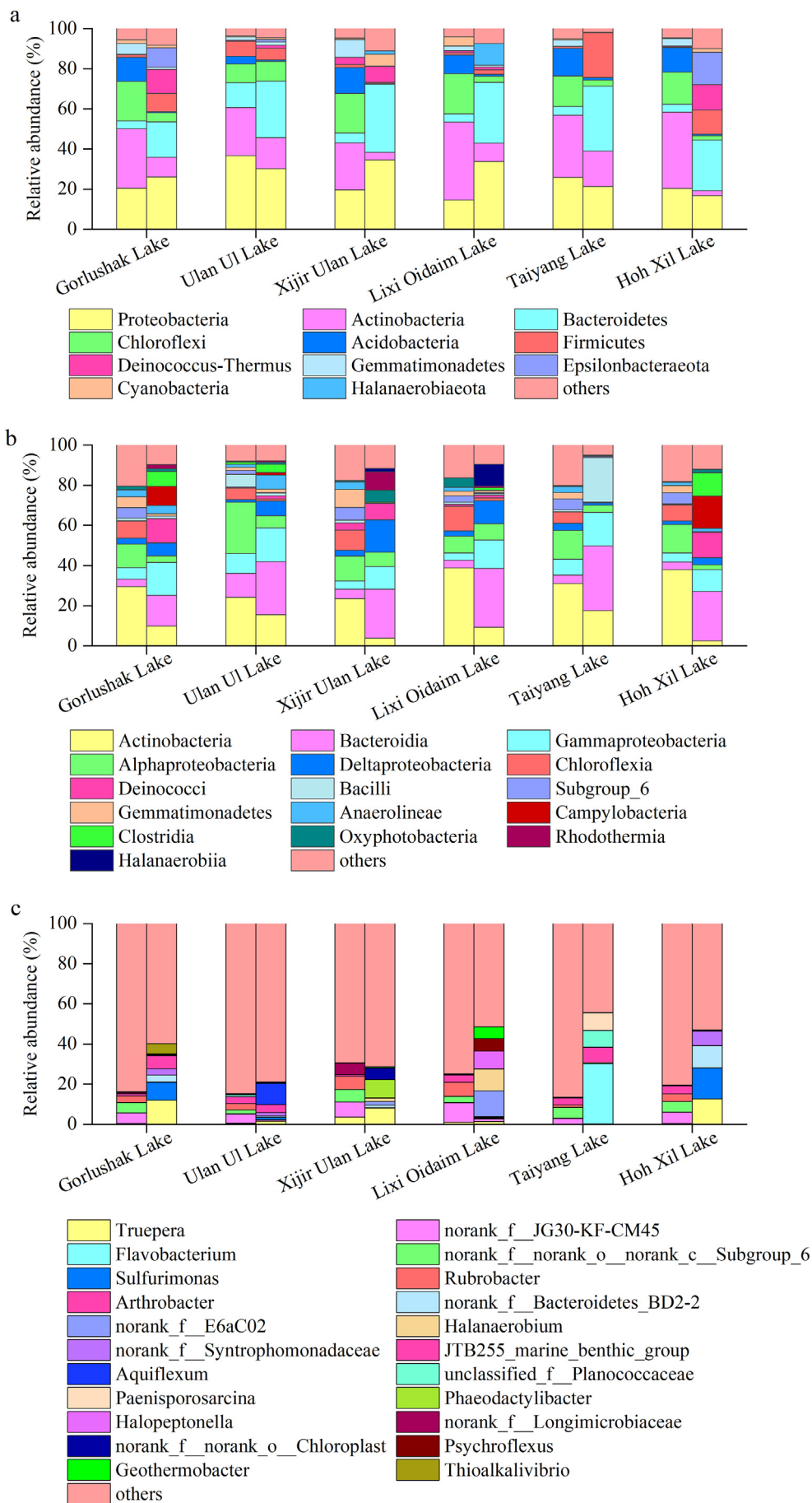
$\beta$ NTI was used to quantify the relative contributions of deterministic and stochastic processes in the assembly of bacterial communities in the soils, the sediments, and between these two types of habitats by null modeling approaches. Although both the deterministic (homogeneous and heterogeneous selection) and stochastic processes (homogenizing dispersal, dispersal limitation, and ecological drift) played roles in bacterial community assembly, according to the  $\beta$ NTI values (Fig. S7), their relative contributions were different across the habitats (Fig. 5). Specifically, stochastic processes, mainly ecological drift (47.1%) and dispersal limitation (30.7%), played a dominant role in the assembly of bacterial communities in the soils (Fig. 5a), while the assembly of bacterial communities in the sediments was mostly affected by dispersal limitation (46.4%) and heterogeneous selection (42.5%) (Fig. 5b). Heterogeneous selection, however, accounted for approximately 78.4% of the bacterial community assembly between the lakeshore soils and lake sediments (Fig. 5c), indicating it was a major determinant of the deterministic processes in shaping the spatial distribution of bacterial communities between these two types of habitats.

### 3.4. Environmental drivers of bacterial composition

To better understand the importance of the deterministic factors in microbial community assembly, CCA was carried out to determine the influence of major environmental factors on the composition of bacterial communities at OTU level. As shown on Fig. 6, the first and second ordination axes of CCA explained 12.47% and 11.08% of the variance of bacterial composition in the soils and sediments, respectively. Contents of TOC and TN were the crucial factors controlling the distribution of bacterial composition in the soils and sediments, while MAT and salinity also played important roles. When the effects of environmental factors on the bacterial composition in the soils and sediments were analyzed separately, salinity and pH were found to be the crucial factors affecting the soil bacterial community composition, while salinity and contents of TOC and TN played more important roles than the other factors in shaping the sediment bacterial community (Fig. S8). Fig. S9 also indicates that the relative abundance of dominant phyla, classes, and genera in the soils and sediments was strongly correlated with environmental factors, and there was obvious difference in the relationship between the soils and sediments. These results suggest that the bacterial community composition was affected by different environmental factors in the lakeshore soils and lake sediments.

Based on the *a priori* model (Fig. S10), SEM was further applied to identify the direct and indirect effects of major environmental factors, including MAP, MAT, pH, salinity, TOC, and TN, on the composition of bacterial communities in the lakeshore soils and lake sediments, respectively (Fig. 7). The results of SEM indicate that MAT and salinity were the most important factors controlling the soil bacterial community composition, while TOC and TN strongly influenced the composition of sediment bacterial communities (Fig. 7a, b). Specifically, salinity had a key direct effect on soil bacterial composition (standardized coefficient =  $-0.87$ ,  $p < 0.05$ ), while MAT could indirectly influence soil bacterial composition (standardized coefficient =  $-0.78$ ) through its impact on soil salinity. Compared with that in the lakeshore soils, the bacterial composition in the lake sediments was significantly directly affected by the contents of TOC (standardized coefficient =  $-0.59$ ,  $p < 0.01$ ) and TN (standardized coefficient =  $-0.56$ ,  $p < 0.01$ ), but had no significant relationship with

**Fig. 4.** Relative abundance of the dominant bacteria in the lakeshore soils (left column) and lake sediments (right column) of different lakes at phylum (a), class (b), and genus (c) levels.



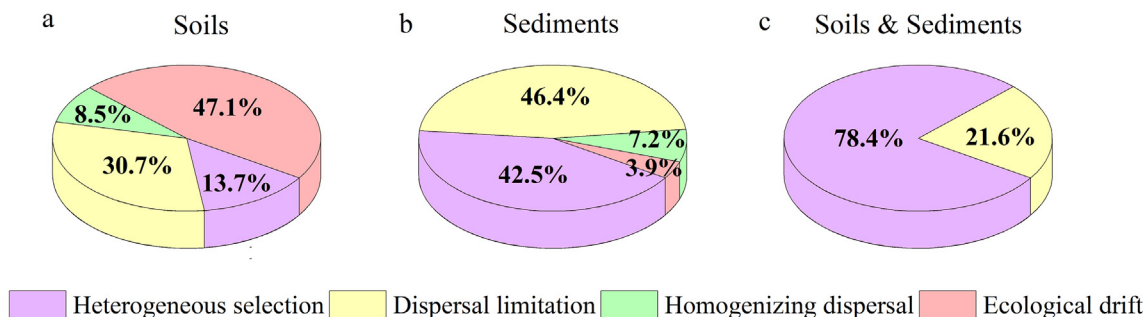


Fig. 5. Relative contributions of different ecological processes to bacterial community assembly within the lakeshore soils (a) and the lake sediments (b), and between the lakeshore soils and lake sediments (c).

MAT and salinity ( $p > 0.05$ ). Besides, pH also had an important indirect effect on the sediment bacterial composition (standardized coefficient =  $-0.76$ ) by affecting TOC and TN contents. When both the direct and indirect influence was considered, salinity was the key driving factor for the soil bacterial community composition (total coefficient =  $-0.65$ ), whereas TN was the key driving factor for the sediment bacterial composition (total coefficient =  $-0.95$ ) (Fig. 7c, d). MAT was the second most important driving factor for the soil bacterial composition (total coefficient =  $-0.51$ ), while TOC was the second one for the sediment bacterial composition (total coefficient =  $-0.59$ ). Combined, environmental factors accounted for 43 and 88% of the variation in the bacterial community composition in the lakeshore soils and lake sediments, respectively.

#### 4. Discussion

##### 4.1. Spatial variations in the diversity and composition of bacterial communities

Soil is an open ecosystem, in which bacterial communities are influenced by a variety of environmental factors, such as soil properties, climate conditions, vegetation, and other accidental vectors (Green and Bohannon, 2006). In contrast, lake sediment is isolated by lake water, which buffers the weather fluctuations and disturbance from the terrestrial environment. Higher bacterial diversity was observed in the lakeshore soils than in lake sediments in the present study, which is consistent with the findings of studies conducted in other regions (Hollister et al., 2010;

Lozupone and Knight, 2007; Torsvik et al., 2002). This could result from the combined actions of multiple factors. Terrestrial ecosystem, with changing environmental conditions and great resource availability, creates more opportunity for the establishment of new species and accumulation of large numbers of mutations than aquatic ecosystem (Torsvik et al., 2002). Compared with sediments, the intermittent environmental disturbance that occurs frequently in soils, such as coldness/heat, drought/wet, and freezing/thawing, can also ensure that microbes contain a mixture of different succession stages (Connell, 1978). Besides, a more open ecosystem is also beneficial for gene transfer and recombination (Torsvik et al., 2002), thereby increasing the microbial diversity.

Distinctive difference in the composition of bacterial communities between the lakeshore soils and lake sediments was also observed, which could be attributed to the ecological roles of relevant bacterial taxa. Widely distributed in nature, *Actinobacteria* plays an important role in organic matter decomposition and humus formation (Goodfellow and Williams, 1983; Lechevalier and Lechevalier, 1967). Members of *Actinobacteria* can survive well under drought conditions through spore formation (Gao and Gupta, 2005), which may be a contributor of their dominance in the dry soils in Hoh Xil Nature Reserve on the Qinghai-Tibetan Plateau. Both *Chloroflexi* and *Acidobacteria* are oligotrophic bacteria, and they prefer to live in nutrient-poor environment (Dai et al., 2019; Eo and Park, 2016; Ye et al., 2022). Therefore, they could survive better in the low-fertility desert soils compared with nutrient-rich lake sediments in Hoh Xil. Besides, *Acidobacteria* is ubiquitous in the environment and participates in nutrient cycling, while its relative abundance is significantly negatively correlated with the water content (Chen et al., 2016; Zeglin et al., 2011). Thus, the relatively high abundance of *Acidobacteria* in the lakeshore soils could also partially result from their rather low water contents. Moreover, the relative abundance of several other dominant taxa was significantly higher in the lake sediments than in the lakeshore soils. *Bacteroidetes* and *Firmicutes* are involved in carbon and nitrogen metabolism (Fernández-Gómez et al., 2013), and their relative abundance has been found to be positively correlated with the contents of TOC and TN (Bai et al., 2012; Wu et al., 2017b). Most members of *Deinococcus-Thermus* belong to extremophilic bacteria and usually possess extraordinary biological adaptations because of their tolerance to ultraviolet radiation and high temperatures (Chaudhari et al., 2020; Theodorakopoulos et al., 2013). The greater relative abundance of phylum *Deinococcus-Thermus* and its genus *Truepera* in the lake sediments probably resulted from the warmer temperatures at the bottom of lakes. Furthermore, some unique endemic taxa were also found in the lakeshore soils and lake sediments, respectively, which supports the key role of environmental factors in shaping microbial communities, as described by the classic microbiological tenet ‘everything is everywhere, but, the environment selects’ (Baas-Becking, 1934). Although virtually all microbial life is distributed all over the world, most of the microbial species always exist latently in a given environment (Wit and Bouvier, 2006). Terrestrial and aquatic ecosystems with distinct characteristics may select for particular bacterial taxa (Chen et al., 2016). These taxa can be potential biomarkers for the soils and sediments, and further study is necessary to better understand their specific roles in the biogeochemical processes.

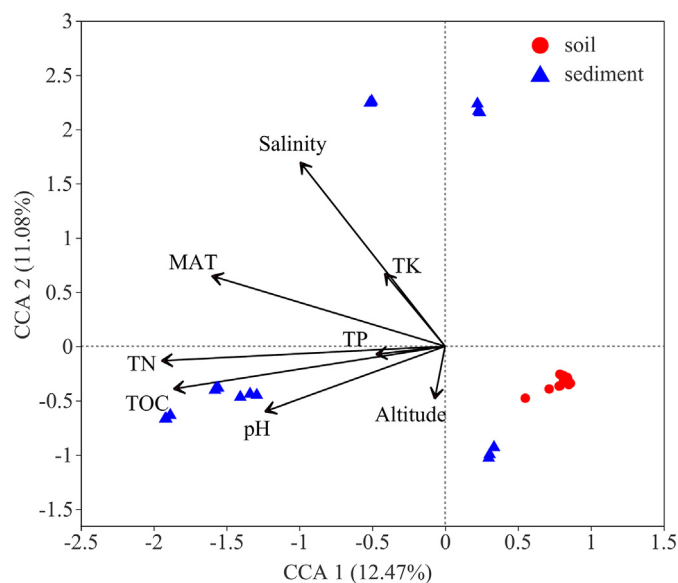


Fig. 6. Relationship of the bacterial community composition in the lakeshore soils and lake sediments with the major environmental factors revealed by CCA at OTU level.



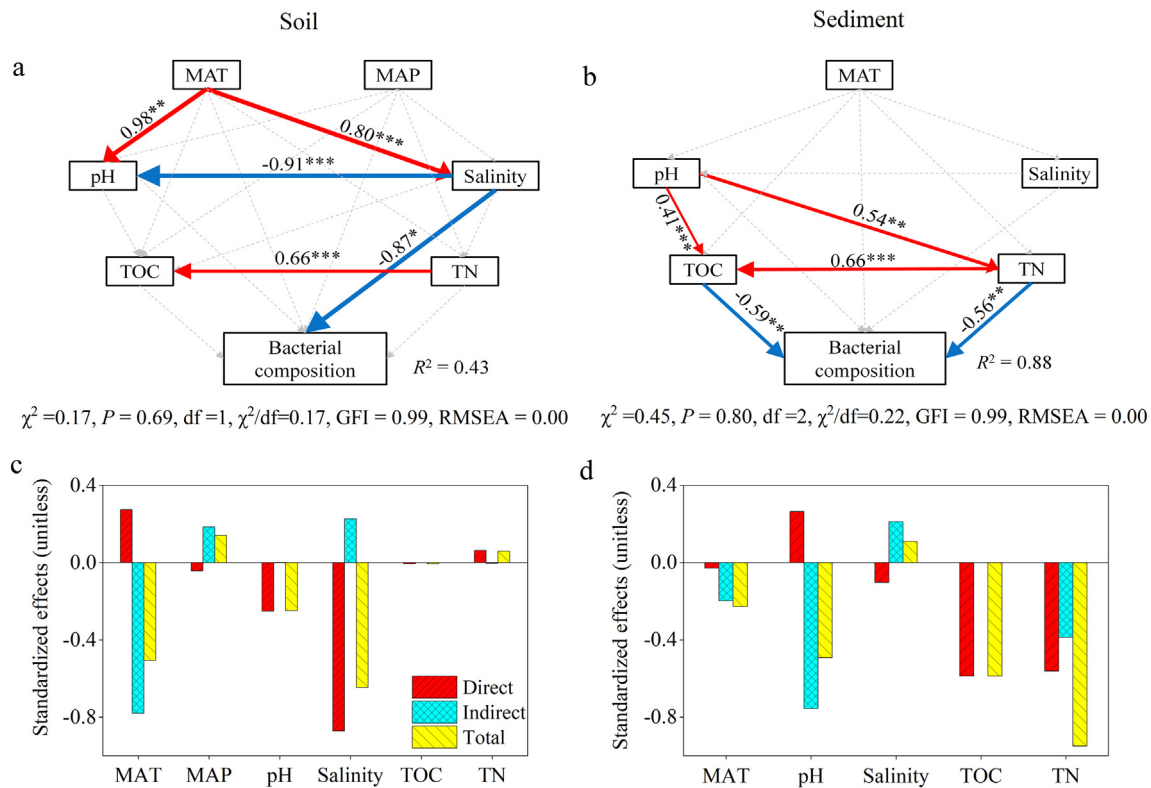


Fig. 7. Direct and indirect effects of environmental factors on the bacterial composition of (a) lakeshore soils and (b) lake sediments revealed by SEM; and the standardized direct, indirect, and total effects of these factors in (c) lakeshore soils and (d) lake sediments derived from the SEM. Red arrow indicates positive relationship, while blue one indicates negative relationship; solid arrow indicates a significant effect, while dashed one indicates a non-significant effect; arrow width denotes the strength of standardized path coefficient;  $R^2$  value indicates the variance explained by the model; \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ .

Although both deterministic and stochastic processes control the microbial community assembly (Stegen et al., 2012; Stegen et al., 2013), it is generally accepted that the distribution of bacterial communities across distinct habitats is governed by different contributions of the ecological processes (Caruso et al., 2011; Hanson et al., 2012; Wang et al., 2013; Yu et al., 2022). We observed that the assembly of bacterial communities in the soils was governed primarily by ecological drift. It has been demonstrated that the stochastic processes may overwhelm the deterministic ones within the habitats with less selective strength (Ofiteru et al., 2010; Wang et al., 2013). Ecological drift can act alone through probabilistic factors and become substantial enough to over-ride deterministic processes in shaping bacterial communities in open systems (Orrock and Watling, 2010). Both dispersal limitation and heterogeneous selection were found to play important roles in the assembly of bacterial communities in the sediments in the present study. Different lakes are isolated in physical distribution, and have discrete boundaries and high heterogeneity in physicochemical properties, causing covariant influence of geographic distance and environmental filtration on the sediment microbial communities in aquatic ecosystems (He et al., 2022). It is notable that heterogeneous selection had more important impact on bacterial community assembly across the soils and the lake sediments in the present study. These findings provide further support for the dominant role of deterministic processes in microbial distribution among different habitats proposed in previous investigations (Monard et al., 2016; Wang et al., 2013; Zhang et al., 2021). The geological difference between the soils and lake sediments leads to partition of resources and emergence of new niches, contributing to the dominance of habitat specialization through evolutionary adaptation (Torsvik et al., 2002). Besides, the steep gradients of environmental factors between the soils and lake sediments, such as ambient temperature and substrate concentrations, also cause changes in the relative abundance of microbial communities (Torsvik et al., 2002; Wang et al., 2013). Generally,

these results suggest that the relative contributions of deterministic and stochastic processes to the spatial distribution of bacterial communities depend on the habitat types and local environmental conditions, and heterogeneous selection played a key role in shaping the bacterial community assembly among distinct habitats.

#### 4.2. Environmental factors driving the distribution of bacterial communities

Salinity is an environmental factor that can have important impact on microbial communities (Lozupone and Knight, 2007). Salinity has been reported to have significant impact on microbial biomass, respiration, growth, carbon-use efficiency, enzyme activities, microbial community structure, and fungal-to-bacterial balance (Rath and Rousk, 2015). High salinity causes cells to lose water, resulting in high osmotic stress and even cell death (Munns, 2002; Rath and Rousk, 2015). High salinity also has adverse influence on soil physical properties, leading to an indirect effect on soil microbial communities (Warrence et al., 2002). Excess salt can cause soil swelling and dispersion by separating and expanding clay particles during the wetting and drying processes (Mohanty et al., 2015; Nouri et al., 2017). The dispersion of soil causes a hard surface layer and further decreases the permeability, and water and nutrient uptake (Nouri et al., 2017; Warren et al., 2002), thus destroying the microbial communities (Rath and Rousk, 2015). Despite of its significant influence on soil microbial communities, salinity was observed to have a rather weak effect on the bacterial composition in the lake sediments. Similar results have been reported in previous studies on microbial communities in saline-alkaline lakes (Hollister et al., 2010; Xiong et al., 2012). That is, the bacterial communities in lake sediments are less sensitive to salinity than those in soils.

Plenty of studies have shown that pH can alter the diversity, composition, and richness of microbial communities through directly or

indirectly influencing the nutrient availability, organic carbon, and cationic metal solubility (Brady and Weil, 2007; Lauber et al., 2009; Liu et al., 2015). pH can also directly change the competitive outcome and influence the net growth of individual tax on, and thus imposes a physiological constraint on microbes (Lauber et al., 2009). The results of SEM in the present study show that pH influenced the bacterial community composition through changing TOC and TN contents in the lake sediments. While pH played a role in shaping the bacterial communities of the lakeshore soils and lake sediments, it was not the most important driver that determined the difference in bacterial composition between the soils and sediments. This could be explained by the fact that the pH gradient of the soil and sediment sampling sites was not substantially different.

TN and TOC were found as the major factors responsible for the difference in bacterial community composition between the soils and sediments. As some of the most important nutrients in terrestrial and aquatic ecosystems, TN and TOC play essential roles in microbial growth and reproduction, and other metabolism processes as well (Wu et al., 2017a). According to the SEM results, TN had direct negative influence on bacterial community composition in the lake sediments, perhaps because nitrogen-fixing microorganisms, whose growth are promoted by TN (Mirza et al., 2014), were not among the dominant microbial species. TN also had an indirect effect on sediment bacterial composition through changing soil organic carbon with a positive relationship. Previous studies have reported that nitrogen enrichment could reduce bacterial richness (Freedman et al., 2015; Ling et al., 2017; Wang et al., 2018; Zeng et al., 2016; Zhang et al., 2018). Nitrogen enrichment could inhibit the activity of enzymes that break down complex carbon (Sinsabaugh et al., 2005) and promote the accumulation of stable organic matter (Guo et al., 2017), reducing the availability of carbon to microbes. Besides, the direct incorporation of nitrogen and organic carbon could also produce heterocyclic forms of nitrogen (Thorn and Mikita, 1992) or phenolic compounds polymerized by nitrogen bridges (Nommik and Vahtras, 1982), which are highly resistant to decomposers, thus reduce organic matter decomposition and enhance carbon sequestration (Janssens et al., 2010). Moreover, bacteria have been reported to be primarily responsible for decomposing labile substrates (Boer et al., 2005), and are generally considered to be the fast carbon cycling regulators (Rinnan and Bååth, 2009). With the easily degradable organic carbon in the sediments converted into CO<sub>2</sub> and CH<sub>4</sub> by microorganisms, the remaining organic carbon is mainly refractory after a long period of geochemical cycling (Gudasz et al., 2015), which is not favorable for bacteria, particularly under anoxic conditions (Alcocer et al., 2021). This can explain the significant negative effect of TOC on sediment bacterial composition observed in the present study. In contrast, TN and TOC were not found to have important influence on bacterial composition in the lakeshore soils, which is attributed to the much lower TN and TOC contents in the soils than in the sediments. TK content also affected the composition of bacterial communities, especially in the sediments, which may be attributed to the presence of potassium-solubilizing bacteria, as the solubility and availability of potassium are known to affect the selection of specific bacteria associated with potassium (Miransari, 2013).

There was significant difference in the temperature between the lakeshore soils and the lake sediments. Temperature not only influences microbial respiration (Gudasz et al., 2015; Xu et al., 2021), but also exerts a strong selective pressure on microbial communities (McHugh et al., 2017). MAT was also found to have an indirect effect on the composition of soil bacterial communities through altering soil salinity in the present study. In contrast, as the temperature of all lake sediments was defaulted to 4 °C in the present study, its impact on the sediment bacterial composition, even if existed, could not be identified. MAP is also well known to be an important factor influencing soil bacterial communities through affecting the availability, transport, and uptake of nutrients, as well as soil physicochemical properties (Wang et al., 2020; Wu et al., 2018; Zhang et al., 2014; Zhang et al., 2013). However, MAP was found to have no significant impact on the soil bacterial community in the present study, partially because of the very low MAP and extremely poor water retention

capacity of the desert soil in the Hoh Xil region, which has cold and dry climate and poor vegetation.

## 5. Conclusions

The findings of the present study yield insight into the spatial variations in diversity and composition of bacterial communities in the lakeshore soils and lake sediments from the core zone of Hoh Xil Nature Reserve on the Qinghai-Tibetan Plateau. Heterogeneous selection mainly determined the distribution patterns of bacterial communities between the soils and the sediments. Furthermore, MAT, salinity, and contents of TOC and TN were the major deterministic factors that drove the difference in bacterial composition between the soils and the sediments. These results help bridge the knowledge gap on the spatial distribution of bacterial communities in soils and sediments in high-altitude permafrost regions, providing evidence of biogeographical patterns for microorganisms across habitats. They also highlight the different influence of deterministic and stochastic processes on microbial community assembly among distinct habitats, and improve the understanding on the responses of microbial communities to environmental change.

## CRediT authorship contribution statement

**Xiaojie Wang:** Conceptualization, Data curation, Methodology, Writing – original draft, Writing – review & editing. **Yuxuan Ren:** Data curation, Visualization. **Zhiqiang Yu:** Project administration, Supervision. **Guofeng Shen:** Project administration, Funding acquisition, Resources. **Hefa Cheng:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Shu Tao:** Project administration, Funding acquisition, Resources.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.156148>.

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