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Vertical distribution patterns and drivers of soil bacterial communities across the continuous permafrost region of northeastern China

Baihui Ren[1,2], Yuanman Hu[2] and Rencang Bu[2*]

Abstract

Background: Soil microorganisms in the thawing permafrost play key roles in the maintenance of ecosystem function and regulation of biogeochemical cycles. However, our knowledge of patterns and drivers of permafrost microbial communities is limited in northeastern China. Therefore, we investigated the community structure of soil bacteria in the active, transition and permafrost layers based on 90 soil samples collected from 10 sites across the continuous permafrost region using high-throughput Illumina sequencing.

Results: Proteobacteria (31.59%), Acidobacteria (18.63%), Bacteroidetes (9.74%), Chloroflexi (7.01%) and Actinobacteria (6.92%) were the predominant phyla of the bacterial community in all soil layers; however, the relative abundances of the dominant bacterial taxa varied with soil depth. The bacterial community alpha-diversity based on the Shannon index and the phylogenetic diversity index both decreased significantly with depth across the transition from active layer to permafrost layer. Nonmetric multidimensional scaling analysis and permutation multivariate analysis of variance revealed that microbial community structures were significantly different among layers. Redundancy analysis and Spearman's correlation analysis showed that soil properties differed between layers such as soil nutrient content, temperature and moisture mainly drove the differentiation of bacterial communities.

Conclusions: Our results revealed significant differences in bacterial composition and diversity among soil layers. Our findings suggest that the heterogeneous environmental conditions between the three soil horizons had strong influences on microbial niche differentiation and further explained the variability of soil bacterial community structures. This effort to profile the vertical distribution of bacterial communities may enable better evaluations of changes in microbial dynamics in response to permafrost thaw, which would be beneficial to ecological conservation of permafrost ecosystems.

Keywords: Permafrost, Soil depth, Bacterial community structure, Soil properties, Illumina sequencing

Introduction

Permafrost is soil that remains continuously frozen for at least two years and underlies about 25% of terrestrial area in the Northern Hemisphere (Doherty et al. 2020). It is estimated that permafrost soil contains approximately 1300 Pg of carbon which is equal to half of the global soil organic carbon (Schuur et al. 2015; Zhou et al. 2020). During the past few decades, global warming has caused

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widespread permafrost thawing, which has induced a significant reduction of soil organic matter and the subsequent release of greenhouse gases (primarily carbon dioxide (CO_2) and methane (CH_4)) because of increased microbial activity, and potentially generate positive feedback to climate warming (Mackelprang et al. 2011; Graham et al. 2012; Heslop et al. 2019). Permafrost thaw has also led to the deepening of the active layer, which is the surface of permafrost that undergoes frequent environmental disturbances via seasonal freezing and thawing (Kim et al. 2016). Studies have reported that microbial biomass and metabolic activity were higher in the active layer of soil and decreased towards deeper soil layers (Frankfahle et al. 2014; Koyama et al. 2014). Even though deeper permafrost layer is considered to be an extreme environment with low temperature and nutrient availability, it is a relatively stable habitat for microbial communities (Jansson and Taş 2014). Transition layer refers to soil above the permafrost interface and is the boundary connecting the active layer and permafrost layer (Deng et al. 2015; Aksenov et al. 2021). Differences in physicochemical and biological properties imply that the factors shaping microbial communities may be different among soil layers and the composition and diversity of microbial communities in different layers changes in response to thawing (Mackelprang et al. 2011; Deng et al. 2015). Therefore, a better understanding of the changes in microbial communities in different soil layers and the factors that shape these communities is important to predict the potential microbial processes and permafrost ecosystem functions in a changing climate.

Soil depth profiles provide heterogeneous environmental conditions for microorganisms and therefore serve as a good model for predicting the variations in thawing permafrost. Investigations of the Tibetan Plateau and the Arctic have shown that microbial communities varied with soil depth, and that the abundance and diversity of soil microbial taxa declined with depth with the transition from the surface active layer to the underlying permafrost layer (Steven et al. 2008; Mackelprang et al. 2011; Frankfahle et al. 2014; Koyama et al. 2014; Taş et al. 2014; Wei et al. 2014; Deng et al. 2015; Hu et al. 2015, 2016; Frey et al. 2016). These studies revealed that the vertical distribution patterns of microbial communities were affected by corresponding soil properties such as soil nutrient availability and moisture content. Furthermore, recent studies have found that bacterial and fungal communities occurring in the active layer and permafrost respond differently to permafrost thaws at different depths (Wu et al. 2018; Sannino et al. 2021). However, most of these available studies of permafrost microbial communities included only one or a limited number of soil cores from each location. Studies focusing on shifts in microbial communities along soil depth profiles across multiple sampling sites over broad geographic scales are less affected by the heterogeneity of the soil ecosystems themselves and are statistically more confident (Deng et al. 2015; Chen et al. 2017). Hence, such studies are still needed to assess the spatial variability and dynamics of permafrost ecosystems in light of anticipated climate change.

Distributed in the southeast margin of the Eurasian cryolithozone, the latitudinal permafrost in northeastern China is sensitive to climate change and has experienced degradation owing to recent climate warming (Jin et al. 2007). Permafrost thaw in this region has resulted in substantial increases in the mean annual ground temperature and the depth of the active layer (Wei et al. 2011). Nevertheless, except for studies on the Sanjiang Plain (Zhou et al. 2017), in Mo-he (Dan et al. 2014), and along the China-Russia Crude Oil Pipeline (Yang et al. 2012), the microorganisms and distribution patterns of microbial communities in this unique permafrost soil remain relatively unexplored (Ren et al. 2018).

Therefore, in this study, we analyzed the vertical distribution patterns and drivers of bacterial communities in different soil layers in the continuous permafrost region of northeastern China. A total of 90 samples collected from 10 sites across the whole region were used to characterize the microbial communities by high-throughput Illumina sequencing. In agreement with previous studies, we hypothesized a decrease in both the number and genetic diversity of bacteria with the increase in soil depth. We further hypothesized that soil chemical-physical properties would have substantial influences on the diversity and composition of the bacterial communities due to stratified soil abiotic conditions of different soil layers. To test these hypotheses, we aimed to determine: (1) the differences in the composition and diversity of bacterial community along the vertical depth, and (2) the main factors driving the distribution of the bacterial community in the permafrost soil.

Materials and methods

Soil sampling and analysis

The soils at 10 sites in the continuous permafrost region of northeastern China were sampled during August 2015 (Fig. 1). The active layer thickness of the study sites we chosen were measured using a steel probe to reach the freezing solid and were all approximately 50 cm. At each site, three randomly selected 2 m × 2 m plots within an area of 20 m × 20 m were selected as replicates. In each plot, five 70 cm soil cores were collected, and soil samples were collected from three depth intervals representing the active layer (0–20 cm, refers to the surface thawed soil at the time of sampling within the organic horizon),

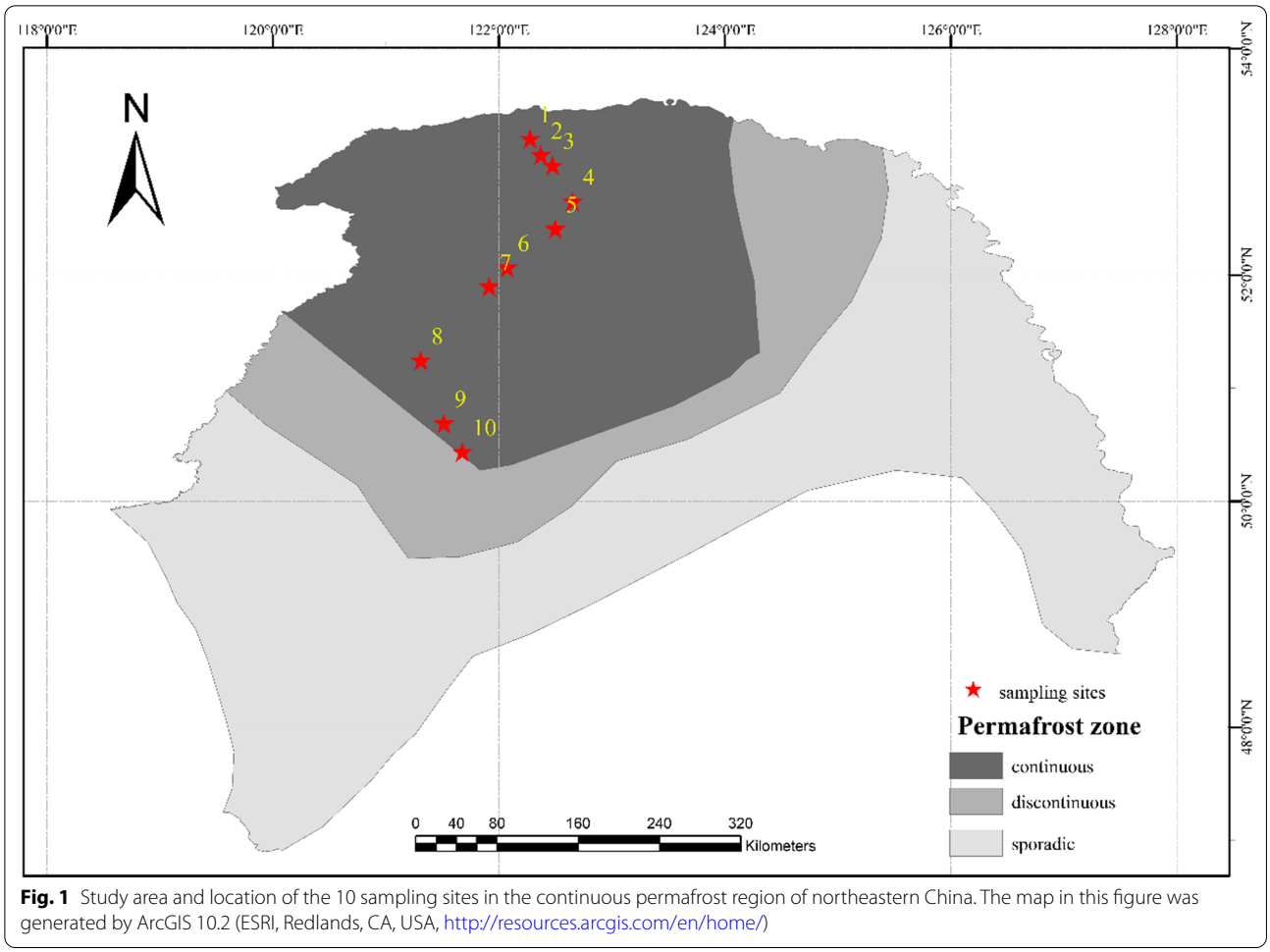


Fig. 1 Study area and location of the 10 sampling sites in the continuous permafrost region of northeastern China. The map in this figure was generated by ArcGIS 10.2 (ESRI, Redlands, CA, USA, http://resources.arcgis.com/en/home/)

the transition layer (20–50 cm, contains soil within the seasonally thawed mineral horizon, that is above the permafrost interface) and the permafrost layer (50–70 cm, refers to soil at or below the permafrost interface). The five subsamples from each depth within the same plot were pooled into a single soil sample, resulting in 90 soil samples (10 sites × 3 plots × 3 layers). Soil moisture, temperature and salinity were synchronously measured using an in-situ soil testing device (TZS-PHW-4, China). The soil samples were immediately transported to the laboratory while stored on ice. After being sieved through a 2 mm standard mesh, the soils were divided into two portions. One portion was stored at 4 °C for analysis of soil properties, and the other was stored at − 80 °C for microbial analyses (All permafrost layer soil were stored at − 80 °C).

Soil texture was measured using a particle size analyzer (Malvern Instruments, Malvern, UK) and classified by the universal criteria of soil particle size (clay < 0.002 mm, silt 0.02–0.002 mm, sand > 0.02 mm). Soil pH was determined by suspending soil in a 1:2.5 (w/v) aqueous solution and then analyzed by a pH electrode (Kalra 1995). Soil total nitrogen content (TN) and total carbon content (TC) were measured with an element analyzer (EL III, Elementar, Germany). The mass ratio of soil carbon:nitrogen (C/N) was calculated based on the TC and TN. The Mo-Sb anti-spectrophotometry method was used to measure soil total phosphorus content (TP) after digestion of the samples with concentrated $HClO_4$–H_2SO_4. Soil total organic carbon (TOC) was determined by the $K_2Cr_2O_7$ oxidation method as described in Walkley (1947). Soil available phosphorus (AP) was extracted with 0.5 M $NaHCO_3$ and measured using a colorimetric method. Soil available N (AN) was measured using a continuous flow analyzer (SAN++, Skakar, Breda, Holland) after extraction with 2 M KCl (soil to water ratio of 1:5).

DNA extraction, amplification and sequencing

Genomic DNA of each soil sample was isolated using the PowerSoil DNA Isolation Kit (MO BIO, USA) according to the manufacturer's instructions. The extracted DNA was qualitatively evaluated by agarose gel electrophoresis

and the concentration was determined using a Nanodrop 2000 (Thermo, USA). To amplify the V4 hypervariable region of the 16S rRNA gene, we used the 515F (5′-GTG CCAGCMGCCGCGGTAA-3′) and 909R (5′-CCCCGY CAATTCMTTTRA GT-3′) primers with unique barcodes. The PCR amplification process was performed as previously described (Gibson et al. 2014), after which the products were purified using an AxyPrepDNA Gel Extraction Kit (AXYGEN, California, USA). The resultant PCR products were then combined at equimolar concentrations before being sequenced using the Illumina Miseq platform at the Chengdu Institute of Biology, Chinese Academy of Sciences.

Processing of sequencing data

The obtained raw sequence data were analyzed using the Quantitative Insights into Microbial Ecology (QIIME) pipeline (QIIME v.1.8.0; http://www.qiime.org). Paired-end reads with at least a 50-bp overlap and < 5% mismatches were combined using FLASH (version 1.0.0). A threshold of average quality scores > 30 over 5-bp window size was used to trim the unqualified sequences using BTRIM (version 1.0.0; Kong 2011). Any joined sequences with ambiguous bases and lengths < 200 bp were discarded. After trimming of ambiguous bases, joined sequences with lengths between 240 and 260 bp were subjected to chimera removal by U-Chime (Edgar et al. 2011). The resultant high-quality sequences were clustered into operational taxonomic units (OTUs) at the level of 97% similarity using UCLUST (Edgar 2010). Sequences were subsequently aligned using the PyNAST software, after which OTUs were classified against the 13_8 Greengenes database and taxonomic assignments were based on their respective taxonomy files (Werner et al. 2012). A taxon filtering script provided by QIIME was applied to separate the OTU tables of individual microbial taxa, which were then used to analyze the abundance of specific taxa. The community compositions were then described by the relative abundance of sequences that were assigned to each taxon. To compute the alpha diversity, we calculated the Shannon diversity index and the phylogenetic diversity index (Faith 1992). Beta-diversity metrics were introduced by the unweighted UniFrac distance (Lozupone and Knight 2005). All the diversity calculations were performed in QIIME.

Statistical analyses

One-way analysis of variance (ANOVA) followed by Tukey's post-hoc HSD (Honest Significant Difference) was performed to identify differences in soil properties, the relative abundance of the major microbial phyla, Shannon index and phylogenetic diversity index among the three different soil layers. The relationships between the Shannon index and phylogenetic diversity index with soil physicochemical factors were tested by Spearman's correlation analysis. All analyses were conducted using the SPSS 20.0 software (IBM Co., Armonk, NY, USA).

A permutation multivariate analysis of variance (PERMANOVA) was conducted to identify significant differences in community composition variance among soil layers. Venn diagrams for graphical descriptions of unique and shared bacterial genera between different soil layers were calculated using the "VennDiagram" package in R (Team RDC 2016). Nonmetric multidimensional scaling (NMDS) analysis based on the unweighted UniFrac distance matrix was conducted to identify variations in bacterial communities among soil layers using the nmds.py script in QIIME. Redundancy analysis (RDA) was employed to measure the effects of environmental variables on bacterial community structures in the CANOCO 4.5 software (Microcomputer Power, Ithaca, NY, USA). A Monte Carlo test (999 permutations) based on the RDA was used to assess the effects of each variable. We implemented a variation partitioning analysis to assess the relative importance of each factor (Distance factor: Latitude, Longitude; Environment factor: Temperature, Moisture, Salinity, TC, TN, TP, C/N, TOC, AN, AP, pH, Clay, Silt and Sand; Depth factor) in explaining the microbial community compositions with the "vegan" package in R.

Results

Soil physicochemical characterization

In general, soil properties changed with depth (Table 1). Soil temperature decreased sharply with depth, dropping from 6.27 °C in the active layer to −0.45 °C in the permafrost layer. The TC, TN and TP contents were all highest in the active layer. TC contents decreased significantly with depth and TN and TP contents decreased significantly from active layer to transition layer. Nevertheless, soil moisture and AP greatly increased with depth, reaching their maximum values in the permafrost layer. The soil was acidic, but the pH values did not vary significantly by depth. The distribution of clay, silt and sand did not vary significantly with depth. However, the soil salinity, C/N ratio, TOC content and AN value did not show obvious changes among depths.

Vertical distribution of soil bacterial communities

High-throughput Illumina sequencing yielded a total of 934,181 high-quality 16S rRNA gene sequences across all examined samples. The sequences were binned into 185,574 OTUs belonging to 63 phyla at 97% sequence identity. The microbial community composition was profiled according to their relative abundance at the phylum

Table 1 Soil physical and chemical properties along soil depth

Soil depth layer	Temperature (°C)	Moisture (%)	Salinity (mS cm^{-1})	TC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	C/N	TOC (g kg^{-1})	AN (mg kg^{-1})	AP (mg kg^{-1})	pH	Clay (%)	Silt (%)	Sand (%)
Active layer ($n=30$)	6.27 (0.31)^{a}	41.22 (2.86)^{a}	0.05 (0.005)	183.87 (11.70)^{a}	9.40 (0.59)^{a}	2.90 (0.22)^{a}	19.67 (0.43)	33.62 (1.15)	1157.59 (80.80)	16.18 (1.73)^{a}	5.21 (0.11)	1.31 (0.13)	19.74 (1.46)	78.95 (1.59)
Transition layer ($n=30$)	2.43 (0.16)^{b}	81.24 (3.82)^{b}	0.06 (0.01)	128.00 (10.80)^{b}	6.37 (0.57)^{b}	2.20 (0.16)^{b}	23.45 (2.86)	30.28 (1.31)	955.01 (61.17)	17.15 (1.95)^{a}	5.13 (0.12)	1.70 (0.16)	24.21 (1.70)	74.09 (1.86)
Permafrost layer ($n=30$)	−0.45 (0.05)^{c}	75.58 (4.91)^{b}	0.07 (0.01)	92.81 (7.41)^{c}	5.00 (0.43)^{b}	2.08 (0.09)^{b}	20.46 (2.19)	31.08 (1.31)	1053.30 (103.30)	24.19 (3.27)^{b}	5.17 (0.11)	1.84 (0.24)	25.03 (2.43)	73.14 (2.66)

The values indicate means and standard error (in parentheses). The differences in soil properties among soil depth layers were analyzed using a one-way analysis of variance. Means significantly different ($P<0.05$, Tukey's HSD) are indicated with superscript contrasting letters

TC, soil total carbon; TN, soil total nitrogen; TP, soil total phosphorus; C/N, soil C:N; TOC: soil total organic carbon; AN: soil available nitrogen; AP, soil available phosphorus

level (Fig. 2). Among those taxa examined, Proteobacteria (31.59%), Acidobacteria (18.63%), Bacteroidetes (9.74%), Chloroflexi (7.01%) and Actinobacteria (6.92%) were dominant, and these phyla accounted for > 70.95% of the bacterial sequences from all soils. Each sample also contained a number of sequences that could not be classified (5.19%), even at the phylum level. Although most bacterial groups were present in all samples, the relative abundances of the dominant bacterial taxa varied among soil depths. Overall, the abundance of Proteobacteria and Planctomycetes decreased significantly with soil depth, whereas Chloroflexi, Verrucomicrobia, Gemmatimonadetes, Crenarchaeota, Chlorobi and Firmicutes increased with depth.

The number of detected genera also varied across the three soil layers (Fig. 3). For example, a total of 957 genera were detected in the active layer, 910 in the transition layer and 872 in the permafrost layer. Overall, 132 unique genera were detected in the active layer, 56 in the transition layer and 58 in the permafrost layer. When the three soil layers were compared, we found that they shared 722 genera.

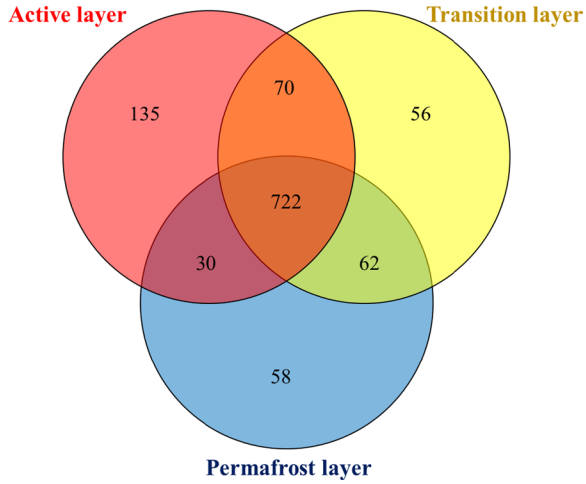
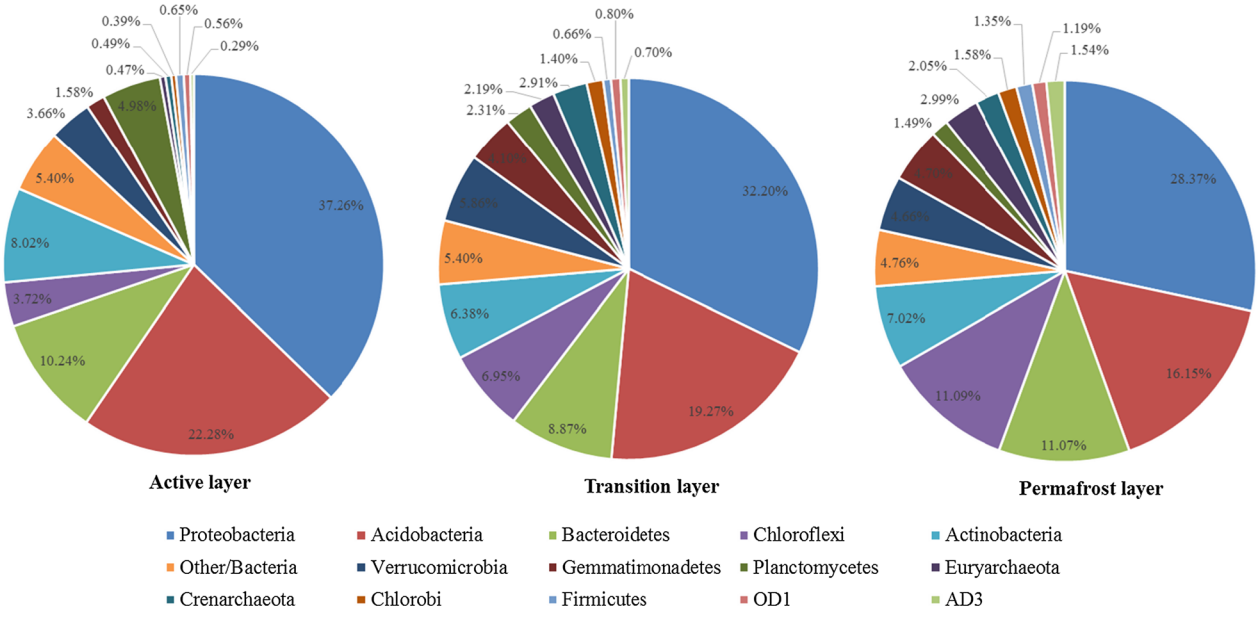


Fig. 3 Venn diagram showing the number of unique and overlapping genera between different soil layers

The bacterial community alpha-diversity based on the Shannon index and the phylogenetic diversity index both decreased significantly with soil depth (Fig. 4). Non-metric multidimensional scaling (NMDS) analysis was



Soil depth layer	Proteobacteria	Chloroflexi	Verrucomicrobia	Gemmatimonadetes	Planctomycetes	Crenarchaeota	Chlorobi	Firmicutes
active layer	a	a	a	a	a	a	a	a
transition layer	b	a	b	ab	b	b	b	a
permafrost layer	b	b	ab	b	c	b	b	b

Fig. 2 Relative abundance of dominant microbial phyla in different soil layers. The differences in relative abundance for each phyla among soil layers were analyzed using a one-way analysis of variance. Values of microbial phyla significantly different ($P < 0.05$, Tukey's HSD) are shown in the table with contrasting letters

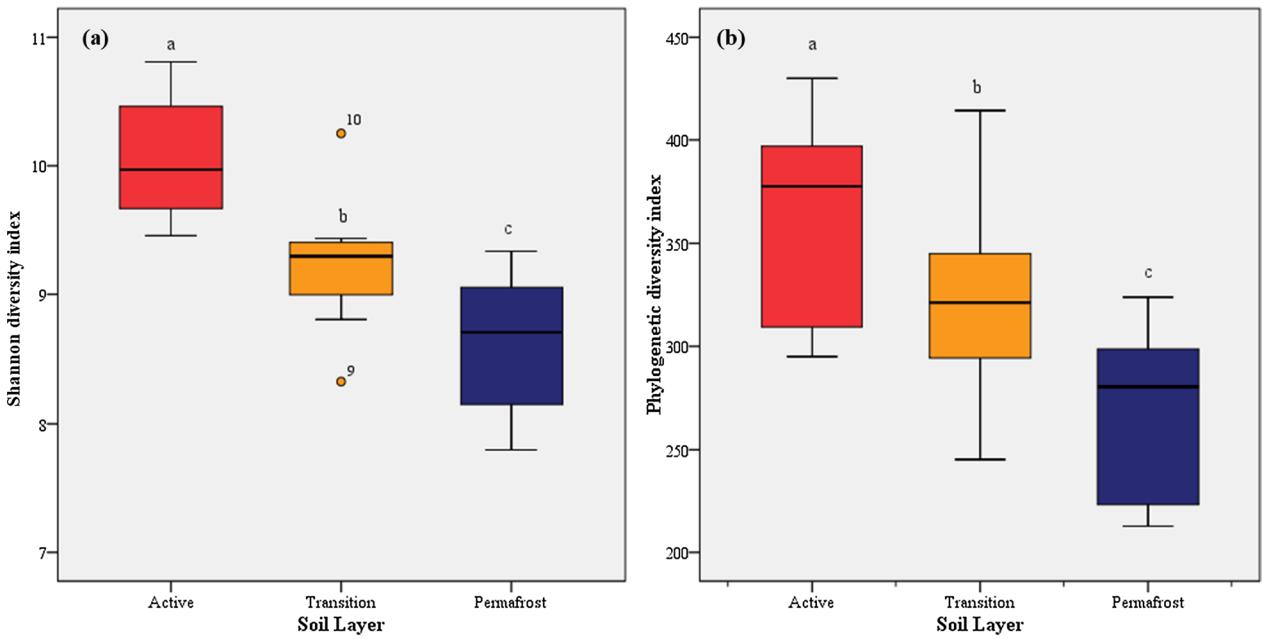


Fig. 4 Box plot based on diversity analysis of soil microbes along soil layers as characterized by (**a**) Shannon diversity index and (**b**) Phylogenetic diversity index

performed to illustrate the bacterial community variance (beta-diversity) along soil layers (Fig. 5). Communities from the same soil layer tended to cluster together. Moreover, a PERMAVONA test based on the unweighted UniFrac distance matrix was performed to further test the significance of differences in microbial community composition between soil layers, and the results indicated that the composition of bacterial communities varied significantly among layers (PERMANOVA, $P < 0.01$).

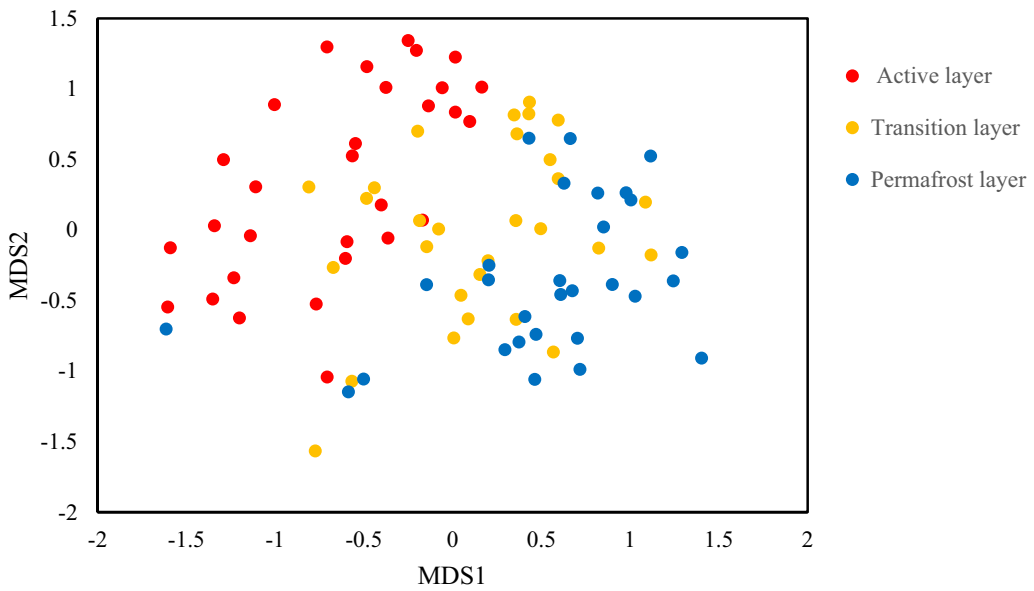


Fig. 5 Nonmetric multidimensional scaling (NMDS) analysis (Stress = 0.08) using the unweighted UniFrac as the distances measure showing the dissimilarities among bacterial communities from the three soil layers: active (red), transition (yellow), and permafrost (blue)

Relationships between bacterial communities and environmental properties

The relative importance of each individual environmental variable on bacterial community composition was measured by redundancy analysis (Fig. 6). The first and second axis of the RDA explained 49.4% and 31.2% of the variance in the bacterial community, respectively. Of all soil properties examined, soil temperature (27.8%), TC (16.7%), TN (13.9%), TP (11.1%), soil moisture (8.3%) and clay content (5.6%) were the most significant factors underlying the variations in the bacterial community composition. Moreover, RDA ordination revealed distinct differences in bacterial community composition between soil layers. Bacterial communities of the active layer soils tended to be distributed in environments with high soil temperature and high TC, TN and TP contents, whereas bacterial communities of the permafrost layer soils were more concentrated in areas with high soil moisture and high clay content.

The effects of soil physicochemical factors on bacterial diversity were tested by Spearman's correlation analysis (Table 2). The Shannon index was significantly positively correlated with soil temperature, TC, TN, TP, AN and sand content and negatively correlated with soil moisture, salinity, clay and silt content. The phylogenetic diversity index was significantly positively correlated with soil temperature, TC, TN, TP, AN, pH and sand content and negatively correlated with soil clay and silt content.

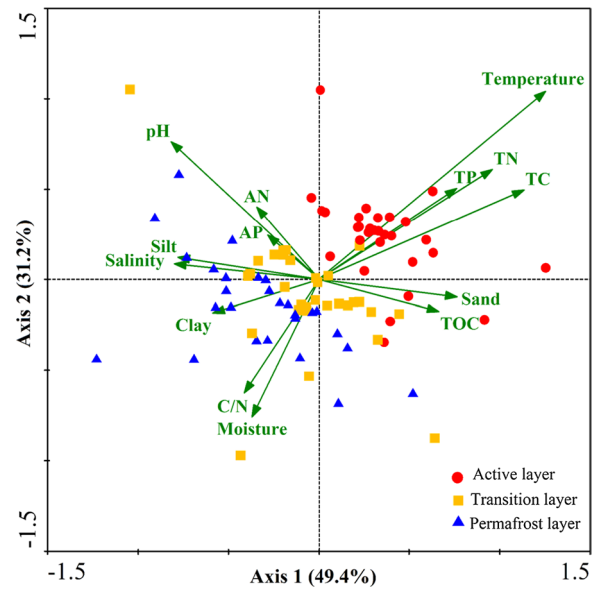


Fig. 6 Redundancy analysis based on the microbial community structures and environmental factors. (TC, soil total carbon; TN, soil total nitrogen; TP, soil total phosphorus; C/N, soil C:N; TOC: soil total organic carbon; AN: soil available nitrogen; AP, soil available phosphorus)

A variance partitioning analysis was carried out to assess the relative contributions of distance factor, environment factor and depth factor to microbial community composition (Fig. 7). The combination of these variables explained 45.92% of the observed variation in soil microbial community composition. Environmental factors explained the largest fraction of the variation (31.52%), with a pure effect of 17.59%. Depth factor and distance factor explained 21.22% and 4.59% of the variation, respectively.

Discussion

To our knowledge, this study provides a comprehensive comparison of patterns and drivers of bacterial communities among soil depth layers across the continuous permafrost region of Northeastern China. The dominant bacterial taxa phyla of Proteobacteria and Chloroflexi exhibited obvious changes in their relative abundance with soil depths (Fig. 2). The higher abundance of Proteobacteria and Planctomycetes in the active layer could be related to their preference for carbon- and nutrient-rich environments (higher TC, TN in the active layer, Table 1). This is in agreement with the studies in the Arctic (Saul et al. 2005) and on the Qinghai-Tibet Plateau (Zhang et al. 2017) reported that the predominant Proteobacteria comprised a higher percentage of the total bacterial population in carbon-rich soils. An important driver of species' ecological functions differentiation is nutrient availability, leading to a spectrum of microbial lifestyles: at opposite ends, copiotrophs dominate in environments with greater nutritional opportunities, whereas oligotrophs prevalent in chronic starvation environments (Koch, 2001; Norris et al. 2021). The subdivision of Betaproteobacteria has been proposed as copiotrophs that prefer nutrient-rich environments (Fierer et al. 2007). Planctomycetes have large genomes that show features of copiotrophs based on genomic insight (Lauro et al. 2009). In the present study, Oligotrophic and anaerobic-like bacteria of Chloroflexi were more abundant in permafrost layers with relatively lower nutrient availability and higher soil moisture content (Table 1). This result is generally agreed with Fierer et al. (2012) reporting a decrease in relative abundance of Chloroflexi after N addition. Moreover, Chloroflexi were found to be well adapted to survive in a water-saturated permafrost wetland of Lake Namco (Yun et al. 2014). Because of their ability to resist long-term exposure to low temperatures and limited nutrient availability, Gemmatimonadetes, Chlorobi and the spore-forming Firmicutes have frequently been detected in deeper soil and permafrost (Debruyn et al. 2011; Wilhelmroland et al. 2011; Jansson and Taş 2014; Deng et al. 2015; Schostag et al. 2015). The observed abundance patterns could be related to the different

Table 2 Correlation matrix for microbial richness and environmental variables as revealed by Spearman Correlation analysis

	SDI	PDI	Temperature	Moisture	Salinity	TC	TN	TP	C/N	TOC	AN	AP	pH	Clay	Silt	Sand
SDI	1.000															
PDI	0.936**	1.000														
Temperature	0.619**	0.499**	1.000													
Moisture	−0.216*	−0.105	−0.563**	1.000												
Salinity	−0.218*	−0.158	−0.016	−0.126	1.000											
TC	0.532**	0.477**	0.636**	−0.198	−0.229*	1.000										
TN	0.530**	0.474**	0.638**	−0.278**	−0.131	0.937**	1.000									
TP	0.414**	0.355**	0.382**	−0.175	−0.240*	0.342**	0.308**	1.000								
C/N	0.059	0.046	0.015	0.151	−0.507**	0.182	−0.114	0.012	1.000							
TOC	0.099	−0.009	0.039	−0.150	−0.165	0.246*	0.183	0.149	0.149	1.000						
AN	0.280**	0.246*	0.300**	−0.150	−0.005	0.493**	0.588**	0.163	−0.338**	−0.044	1.000					
AP	−0.119	−0.129	−0.227*	0.265*	−0.028	−0.322**	−0.364**	0.269*	0.045	−0.017	−0.382**	1.000				
pH	0.168	0.211*	0.249*	−0.234*	0.399**	0.145	0.268*	−0.126	−0.457**	−0.294**	0.470**	−0.450**	1.000			
Clay	−0.278**	−0.296**	−0.222*	0.220*	−0.047	−0.478**	−0.582**	−0.035	0.232*	−0.093	−0.494**	0.659**	−0.445**	1.000		
Silt	−0.281**	−0.282**	−0.207	0.272*	0.007	−0.377**	−0.484**	−0.022	0.148	−0.097	−0.392**	0.634**	−0.340**	0.944**	1.000	
Sand	0.281**	0.283**	0.210*	−0.270*	−0.003	0.388**	0.497**	0.023	−0.160	0.093	0.407**	−0.641**	0.356**	−0.955**	−0.999**	1.000

* Significant at $P < 0.05$. **: Significant at $P < 0.01$

SDI, Shannon diversity index; PDI, Phylogenetic diversity index; TC, soil total carbon; TN, soil total nitrogen; TP, soil total phosphorus; C/N, soil C:N; TOC: soil total organic carbon; AN, soil available nitrogen; AP, soil available phosphorus

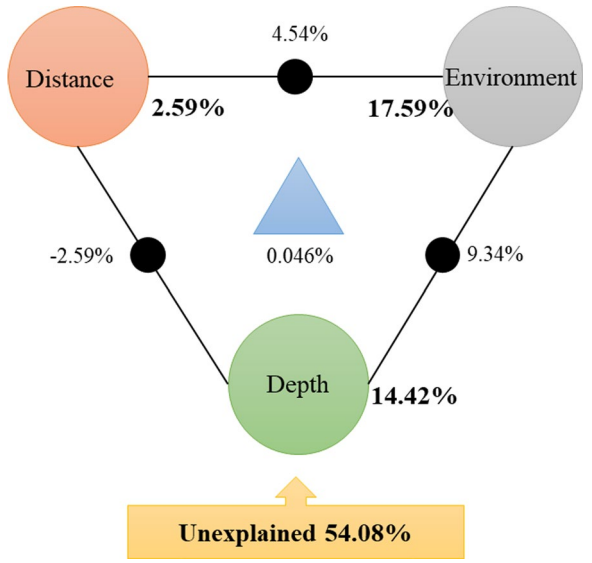


Fig. 7 Variation partitioning analysis showing the percentages of variance in bacterial communities explained by Distance (Latitude, Longitude), Environment (Temperature, Moisture, Salinity, TC, TN, TP, C/N, TOC, AN, AP, pH, Clay, Silt and Sand) and Depth. Each diagram represents the variation partitioned into the relative effects of each factor or a combination of factors

resource availability of each bacterial group and suggest a close association with the corresponding soil conditions. Marked changes in soil parameters with depth have been found in this study (Table 1) and also in studies of other permafrost regions (Wu et al. 2012, 2017a; Dörfer et al. 2013), and such variations in soil properties are expected to influence the composition and diversity of bacterial communities inhabiting soils at different depths.

Our results showed that bacterial community structure and diversity showed obvious variations with soil depth in the studied region (Figs. 3, 4 and 5). Previous studies have indicated that microbial abundance and diversity were highest in the surface active layer soil and declined towards deeper layers to underlying permafrost soil (Yergeau et al. 2010; Wilhelmroland et al. 2011; Frankfahle et al. 2014; Koyama et al. 2014; Taş et al. 2014; Deng et al. 2015; Kim et al. 2016), and microbial community structures were significantly different between the active layer and the permafrost layer on the Tibetan Plateau (Hu et al. 2015, 2016) and in the Arctic (Steven et al. 2008; Mackelprang et al. 2011). Different environmental properties between soil depth layers could be responsible for the observed differences in microbial communities. The near-surface active layer experiences seasonal thawing and freezing and larger environmental fluctuations than permafrost, providing more probabilities for the growth of micro-organisms (Deng et al. 2015). In contrast, deeper soil layers are characterized by restraining factors of low temperature and limited oxygen and nutrient contents, which causes environmental stress to indigenous microorganisms and makes the layers less hospitable for microbial communities (Jansson and Taş 2014). Our results implied that the heterogeneous habitats might cause niche separation and subsequent variations in microbial communities between horizons.

Our results suggested that nutrient contents of TC, TN and TP had the greatest influence on both soil microbial community compositions (Fig. 6) and diversity patterns (Table 2) in the permafrost region of northeastern China. Previous studies have indicated that nutrient availability was strongly correlated with microbial mineralization and subsequently caused shifts in the bacterial community structure (Koyama et al. 2014; Siciliano et al. 2014; Deng et al. 2015). The predominant bacterial diversity in the active layer soil could be explained by their pre-adaption for the rapid metabolism of highly available nutrients (Fierer et al. 2003). Soil nutrient availability could also influence microbial communities via effects on the root exudates of plant communities (Millard and Singh 2010). Carbon and nitrogen concentrations were found to be related to microbial community compositions in permafrost affected soils on the Tibetan Plateau (Zhang et al. 2014). Significant correlations between microbial biomass and soil carbon contents with depth were also observed in terrestrial soils (Rumpel and Kögel-Knabner 2011; Eilers et al. 2012). Soil nitrogen levels played important roles both in the community structure of dominant bacteria and nitrogen-cycling communities in soils of the high Arctic and Antarctica (Walker et al. 2008; Ganzert et al. 2011). Moreover, phosphorus was reported to be an important growth-limiting soil nutrient affecting microbial community development and thus regulating microbial community structures (Siciliano et al. 2014; He et al. 2016). Soil microbial biomass increased in response to the addition of P in various soil environments (Griffiths et al. 2012; Liu et al. 2013). TP contents were highest in the active layer, whereas AP contents were highest in the permafrost layer in our study (Table 1). However, AP seemed to have no obvious effect on microbial richness (Table 2) and community structures (Fig. 6), suggesting that the form of phosphorus may play important roles in influencing microbial communities.

In the present study, soil temperature was found to be one of the main factors explaining the patterns observed in the bacterial community structure (Fig. 6), which was consistent with the results of earlier studies that identified temperature gradients along different soil depths as one of the primary environmental variables driving soil microbial community structure in other permafrost affected areas (Wagner et al. 2005; Yergeau et al. 2012). In accordance with many previous

studies conducted in the Tibetan Plateau (Zhang et al. 2013; Yun et al. 2014), as well as in the Arctic and Antarctica (Fell et al. 2006; Bridge and Newsham 2009; Glanville et al. 2012; Lee et al. 2013; Steven et al. 2013), soil moisture was also found to make a great contribution to differentiation of bacterial community structure (Fig. 6). Soil moisture has been found to have important effects on soil respiration and oxygen availability (Wang et al. 2008; Yang et al. 2012), which influence bacterial community composition, especially that of carbon and nitrogen cycling bacteria (Høj et al. 2006; Zhang et al. 2013). The associated redox potential and anaerobic soil conditions in permafrost layers with high soil moisture have been shown to limit the diversity of bacterial community. Kim et al. (2008) found that short-term drought could lead to a dramatic decrease in gene abundance of the microbial community associated with greenhouse gas emissions. Interacting with other soil parameters, soil texture was shown to be an important factor influencing bacterial communities (Wu et al. 2017b). Although numerous studies have emphasized the importance of soil pH in driving soil microbial community structure (Chong et al. 2009, 2010; Feng et al. 2014; Siciliano et al. 2014), soil pH had no significant effect on the patterns of bacterial communities in our study. The low variability in pH among soil layers, which was not comparable to the influence of variables such as soil nutrient contents, temperature and moisture that spanned greater ranges, may explain this discrepancy with previous studies. Moreover, with 54.08% of unexplained variation in microbial community composition showed by variation partitioning analysis (Fig. 7), a more detailed consideration of a diverse set of environmental parameters is required in determining order to better understand the factors that drive microbial community structures in future studies.

According to the observed trend of climate warming, permafrost will thaw with the increase of ground temperature. And that will result in the enhancement of microbial activity and diversity, since soil temperature was positively correlated with microbial richness (Table 2). Besides, Planctomycetes and Proteobacteria, which showed higher abundance in the active layer (Fig. 2), are abundant in nitrogen-fixing populations involved in nitrogen cycling (Delmont et al. 2018). All of this could bring about huge positive feedback to the greenhouse effect and accelerate climate warming. Nevertheless, further research is required to reveal the detailed dynamics of carbon and nitrogen cycling with the corresponding measurement of microbial biomass and functional attributes of microbial communities in these changing permafrost habitats.

Conclusions

This study provides a comprehensive comparison of patterns and drivers of bacterial communities among different soil layers in the continuous permafrost region of northeastern China. Our results revealed significant differences in bacterial composition and diversity among the active layer, transition layer and permafrost layer. Our findings suggest that the heterogeneous environmental conditions between the three soil horizons had strong influences on microbial niche differentiation and further implied that soil nutrient contents, temperature and moisture predominantly explained the variability of soil bacterial community structures. This study improves our understanding of microbial ecology in this unique permafrost area, which is of great importance in assessment of spatial changes in permafrost ecosystems under current climate warming.

Abbreviations

SDI: Shannon diversity index; PDI: Phylogenetic diversity index; TC: Soil total carbon; TN: Soil total nitrogen; TP: Soil total phosphorus; C/N: Soil C:N; TOC: Soil total organic carbon; AN: Soil available nitrogen; AP: Soil available phosphorus; ANOVA: One-way analysis of variance; QIIME: Quantitative Insights into Microbial Ecology; OTUs: Operational taxonomic units; PERMANOVA: Permutation multivariate analysis of variance; NMDS: Nonmetric multidimensional scaling; RDA: Redundancy analysis.

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Authors' contributions

BR, YH and RB designed this study; BR performed the laboratory analysis and wrote the paper. All authors read and approve the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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