https://doi.org/10.1186/s13213-022-01707-2

Annals of Microbiology

ORIGINAL ARTICLE

Open Access

Warming changes the composition and diversity of fungal communities in permafrost

Yunbing Jiang[1], Libin Yang[1*], Song Wu[2*] and Tian Zhou[1]

Abstract

Purpose It is the data support and theoretical basis for the response mechanism of soil fungi to climate warming in permafrost areas in the Greater Xing'an Mountains.

Methods We collected permafrost from the Greater Xing'an Mountains for indoor simulation experiments and took the natural permafrost as the control (CK) and the test groups of 0 °C (T_1), 2 °C (T_2), and 4 °C (T_3) were set. Illumina MiSeq high-throughput sequencing technology was used to understand the changes in characteristics of fungal communities, and the correlations were analyzed combined with the soil physicochemical properties.

Results Compared with CK, the value of pH and the content of available potassium (AK) in the three warming treatment groups were significantly lower ($P < 0.05$), and the microbial biomass carbon (MBC) content was significantly higher ($P < 0.05$). The content of total nitrogen (TN) and available nitrogen (AN) in the T_1 and T_3 groups was significantly lower than that in the CK group ($P < 0.05$). A total of 11 phyla, 39 classes, 89 orders, 187 families, 361 genera, and 522 species were obtained through fungal sequencing and divided into 1463 amplicon sequence variants (ASVs). *Ascomycota* and *Dimorphospora* were the dominant phylum and genus, respectively, and there were differences in the response of relative abundance of various groups at the phylum and genus levels to warming. Warming significantly decreased the Sobs and ACE indexes of the treatment groups ($P < 0.05$), and the Shannon and Shannoneven indexes also showed a downward trend. Moreover, warming significantly changed the fungal beta diversity ($P < 0.01$), while the value of pH and the content of TN, MBC, and AK could significantly affect the community structure ($P <$ 0.05), and the correlation between fungi at different phyla levels and soil physicochemical properties was different.

Conclusions These results can provide a reference for further study on the changes in composition and structure of fungal communities and the influence factor in permafrost in the Greater Xing'an Mountains under the background of warming.

Keywords Fungal, Permafrost, Warming, Community structure, Soil physicochemical properties

*Correspondence:
Libin Yang
13664600518@139.com
Song Wu
wusong0927@126.com
[1] Key Laboratory of Biodiversity, Institute of Natural Resources and Ecology, Heilongjiang Academy of Sciences, Harbin 150040, China
[2] Science and Technology Innovation Center, Institute of Scientific and Technical Information of Heilongjiang Province, Harbin 150028, China

Introduction

Permafrost is an important part of the earth's cryosphere, which is widely distributed in high-latitude and high-altitude areas, covers 25% of the land surface mass of the earth, and stores approximately one-third of the global organic carbon (1330−1580 Pg) (Schuur et al. 2015). Monitoring data showed that global permafrost temperatures have increased by an average of 0.29 °C over the past 10 years, and the permafrost has

© The Author(s) 2023. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

also experienced significant degradation (Biskaborn et al. 2019). It is mainly manifested as the decrease of permafrost area (Luo et al. 2019; Zhao et al. 2019), the increase of active layer thickness (Screen and Simmonds 2010; Turetsky et al. 2020), and the gradual disappearance of the island and the discontinuous permafrost (Wu et al. 2010), which greatly threatens the stability of permafrost ecosystems. On the one hand, thawing of permafrost will not only lead to a large number of emissions of previously stored greenhouse gases but also accelerate the decomposition of soil organic matter by microorganisms, thus affecting the carbon budget balance of permafrost areas (Waldrop et al. 2010; Pautler et al. 2010), and may lead to the transformation of permafrost from carbon sink to carbon source. On the other hand, the hydrological process in cold regions (Wu et al. 2018a), the composition, and productivity of vegetation will also be affected by the thawing of frozen soil, which will lead to the transformation of ecosystems types, and eventually lead to a series of ecological environment problems (Baltzer et al. 2014).

Soil microorganisms play a key role in regulating the biogeochemical cycle of terrestrial ecosystems and take part in the process of organic matter decomposition and soil nutrient transformation (Guntinas et al. 2012; Ping et al. 2015). Despite the environmental stresses of low temperature, low water, and low nutrient in permafrost regions, there are still abundant microorganisms with unique genetic characteristics and physiological and biochemical adaptation mechanisms (Tripathi et al. 2018; Mackelprang et al. 2011). As the main decomposer of soil carbon, the change of fungal community composition may affect the stability of soil carbon in permafrost (Nguyen et al., 2016). In recent years, researchers have explored the diversity and distribution of soil fungi in permafrost regions such as the Arctic (Yang et al. 2017; Lipson et al. 2015), the Qinghai Tibet Plateau (Chen et al. 2017), and the Greater Xing'an Mountains (Sun et al. 2018). The evidence is that fungi have a certain resistance to changes in the external environment, and warming does not significantly affect the composition of fungal community (Penton et al., 2013). However, there are also different research results. For example, Wu et al. (2021) found that warming promoted the thawing of permafrost, resulting in a significant decrease in the abundance of deep soil fungi and significant changes of community composition and microbial functional structure. Chen et al. (2020) showed that warming not only significantly reduced the alpha diversity of fungi but also significantly changed the fungal community structure. It can be seen varied among relevant research results, and the response of permafrost fungi to warming needs further research and demonstration.

The permafrost is in the Greater Xing'an Mountains, which is located at the edge of southern of the permafrost belt in Eurasia. It remains the main distribution area of permafrost in middle and circumpolar latitudes in China, and the degradation of permafrost in this region was relatively significant in recent decades (Jin et al. 2007). Climate warming has caused the reverse succession of forest vegetation in this area, and the potential reactions such as ground temperature rise and hydrological change may affect the microbial ecological process in the whole area (Wei et al. 2010). At present, research on the composition and diversity of soil microbial community structure in the active layer of the area by warming has received more attention, but the study on the permafrost is little (Song et al. 2019; Dong et al. 2021). Jiang (2020) studied the effect of warming on the fungal abundance in permafrost, but the impact of warming on fungal diversity and community composition structure is still unknown. Therefore, we selected the permafrost soil in the Greater Xing'an Mountains as the research object and employed high-throughput sequencing technology to analyze changes in microbial community composition and structure along with warming treatments under laboratory incubation, analyzing the correlations and influencing factors between soil environmental factors and the composition and diversity of fungal communities, and discusses the mechanism of warming on permafrost fungi. It is expected to provide reference data and theoretical basis for the region to deal with climate warming and establish an accurate carbon cycle model.

Methods and materials

Study site

The sampling site was located in the Huzhong National Nature Reserve in the Greater Xing'an Mountains, Heilongjiang province, China (51°49′01″ N~51°49′1″ N, 122°59′33″ E~123°00′03″ E) (Fig. 1). This region belongs to the cold temperate continental monsoon climate, and it has an average annual temperature of −4 °C, a frost-free period of fewer than 80 days, and mean annual precipitation of 458.3 mm (Yang et al. 2022). Permafrost is widely distributed in this area, and the soil active layer thickness of different vegetation communities is around 55–88.9 cm. The soil is mainly brown coniferous forest soil, the dominant trees are *Larix gmelinii* and *Betula platyphylla*; the main shrubs include *Rhododendron dauricum*, *Ledum palustre*, and *Vaccinium uliginosum*, and *Maianthemum bifolium*, and *Sanguisorba officinalis* is the main herbal in this area.

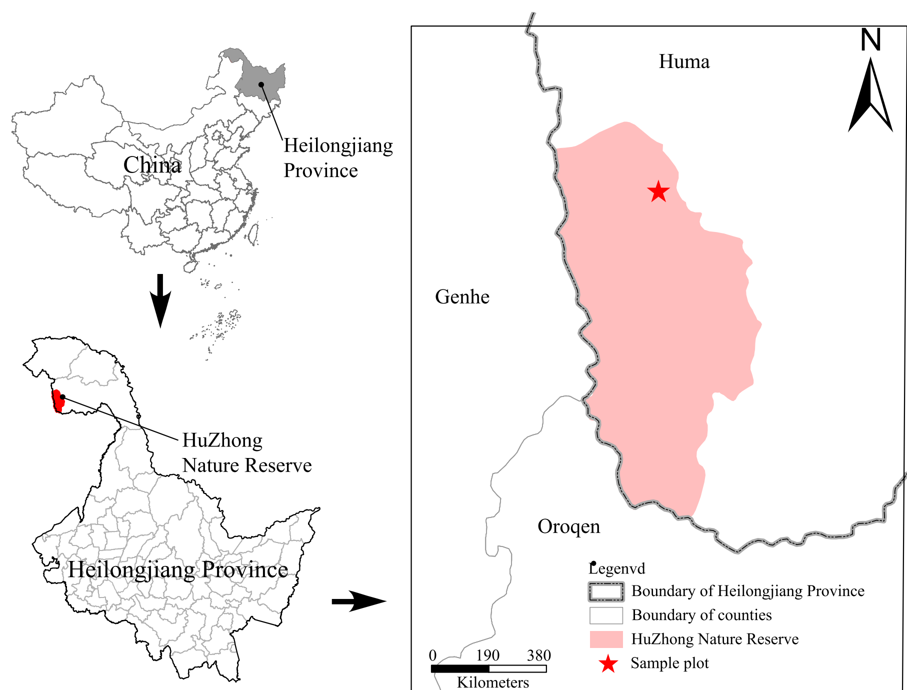

Fig. 1 Map of the field sampling sites on the Greater Xing'an Mountains

Soil sampling and experimental warming experimental design

Specially, we select the region with better site conditions and delimit three quadrats of 20 m × 20 m, which is from in the fixed monitoring sample plot of 500 m × 500 m. Soil samples were collected from 80 to 100 cm, belonging to the permafrost layer, which used a drill with a diameter of 20 cm (the measured average temperature is −2 °C). The soil samples were packed in sterile bags for freezing treatment, transported back to the laboratory, and then stored at −20 °C until the warming experiment was started.

Compared with the current temperature, the Sixth IPCC Assessment Report predicts that the temperature may rise as high as 2.2–4.6 °C by the end of this century (IPCC. 2021). −2 °C is the temperature of pristine soil, 0 °C is the critical temperature of permafrost thaw, 2 °C is the melting temperature (the temperature that can be reached by the end of this century, to simulate the melting temperature of frozen soil), and 4 °C is used to simulate a more intense melting state. Therefore, the test control group is −2 °C (CK), and the simulated warming test group is 0 °C (T_1), 2 °C (T_2), and 4 °C (T_3), respectively. Before the warming experiment, the obtained soil sample was cut into segments and then mixed with equality to form a composite sample. Test soil samples (equal to 100 g of dry soil) collected from the composite sample were cultured in a 1000 mL sterile wide-mouth bottle, and per culture at 0 °C, 2 °C, and 4 °C for 3 days, and then anaerobic culture for 15 days, with 3 repetitions for each treatment (Jiang. 2020). After the warming experiment, the soil was taken out and mixed evenly at the same temperature. Part of the pristine soils and test soils was transferred to polyethylene bags and then quickly frozen in liquid nitrogen for microbial community analysis. The other part was used for the determination of soil physicochemical properties.

Soil physical and chemical analyses

The soil pH (1:10 soil:water ratio) was measured using soil suspensions with a pH probe (PB-10, Sartorius, Germany) (Kim et al. 2014). Microbial biomass carbon (MBC) was determined using the chloroform fumigation-extraction method (Shang et al. 2016). The content of total nitrogen (TN) was examined using an elemental analyzer (Elementar Vario EL III, Hanau, Germany) (Hu et al. 2015). The soil organic carbon (SOC) content was measured using a TOC analyzer (Vario TOC cube, elementary) (Wu et al. 2018b). The available phosphorus (AP) content was determined based on the sodium bicarbonate extraction-molybdenum antimony into colorimetric method (Ade et al. 2018). The available nitrogen (AN) content was determined by the alkali hydrolysis diffusion method (Ade et al. 2018). The available potassium

(AK) content was analyzed by the ammonium acetate extraction-flame photometric method (Ade et al. 2018).

DNA extraction, amplification, and MiSeq sequencing

The total DNA was extracted from 0.5 g of each soil samples using a PowerMax® Soil DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, CA, USA) according to the manufacturer's instructions. DNA samples were examined on a 1% agarose gel and quantified using NanoDrop 2000 spectrophotometers (Thermo Fisher Scientific, Wilmington, DE, USA). For fungi, the gene fragments (ITS1) were amplified by using primer ITS1F (5′-CTT GGTCATTTAGAGGAAGTAA-3′) and ITS2R (5′-GCT GCGTTCTTCATCGATGC-3′) (White et al. 1990; Gardes and Bruns 1993). PCR conditions were an initial denaturation of 95 °C for 3 min, 30 cycles of 94 °C for 45 s, 55 °C for 45 s, and 72 °C for 30 s, followed by an extension at 72 °C for 8 min. PCRs were performed with 4 μL 5 × *TransStart* FastPfu buffer, 2 μL 2.5 mM deoxynucleoside triphosphates (dNTPs), 0.8 μL of each primer (5 μM), 0.4 μL (2.5 u/μL) *TransStart* FastPfu DNA polymerase, 10 ng of extracted DNA, and finally using ddH_2O to make up 20 μL. Every sample for 3 replicates. After mixing the amplicons of the same sample, used 2% agarose gel to recover, purified by the Kit (Axygen Biosciences, Union City, CA, USA), and then detected and quantify the recovered products by Quantus™ Fluorometer (Promega, USA). Finally, after the establishment of library preparation, amplicons were subjected to paired-end sequencing on the Illumina MiSeq sequencing platform using PE300 chemical at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The raw sequences were uploaded to the NCBI Sequence Read Archive database under submission number PRJNA894101.

Bioinformatic and statistical analyses

Raw fastq files were quality filtered by fastp (https://github.com/OpenGene/fastp, v0.19.6) (Chen et al. 2018) and merged by FLASH (https://ccb.jhu.edu/software/FLASH/index.shtml, v1.2.7) (Magoc and Salzberg, 2011) with the following criteria: (1) the reads were truncated at any site receiving an average quality score < 20 over a 50 bp sliding window. (2) Sequences whose overlap being longer than 10 bp were merged according to their overlap with mismatch no more than 2 bp. (3) Sequences of each sample were separated according to barcodes (exactly matching) and primers (allowing 2 nucleotide mismatching), and reads containing ambiguous bases were removed. Then, the DADA2 (Divisive Amplicon Denoising Algorithm 2) plug-in unit in the QIIME 2 (https://qiime2.org, v2022.2) process is used to denoise the optimized sequence after quality control splicing and obtained the amplicon sequence variants (ASVs) (Bolyen et al. 2019). Based on unite8.0/its_fungi (http://unite.ut.ee/, v8.0) species annotation database, we used the Naive Bayes classifier in Qiime2 for species taxonomic analysis of ASVs.

First, the alpha diversity index was analyzed using Mothur (https://www.mothur.org/wiki/Download_mothur, v1.30.2). We employed one-way ANOVAs with an LSD test to analyze the effects of warming on the soil physicochemical properties, the relative abundance of fungal domain phyla and genus, and the variations of fungal alpha diversity (Coverage, ACE, Sobs, Shannon, and Shannoneven indexes).

Second, the community composition of fungal was visualized by principal coordinate analysis (PCoA) based on the Bray-Curtis dissimilarity matrices, and the permutational multivariate analysis of variance (ADONIS) and multi-response permutation procedures (MRPP) were performed to test whether the warming of permafrost had significant effects on fungal communities (Chen et al. 2020).

Third, the db-RDA (distance-based redundancy analysis) was used to reveal the effects of soil physicochemical properties on the composition of the fungal community, and the Monte Carlo test was used to reveal the significance of the impact of soil factors on the fungal community (Liu et al. 2020). Furthermore, to further understand the impact of soil physicochemical properties on soil fungal communities, Heatmap analysis was completed at the phyla level of fungal combined with the Pearson correlation coefficient. In this study, SPSS (v25.0) was used to complete one-way ANOVA, origin was used to draw the abundance different chart, and the rest was completed by VEGAN package of R (R-3.3.1) on the free online platform of Majorbio Cloud Platform (www.majorbio.com)

Results

Warming effects on soil physicochemical properties

According to Table 1, most soil parameters were significantly different from the CK after warming. The value of pH, and the content of AK in T_1, T_2, and T_3, was significantly lower than those in CK ($P < 0.05$). The content of TN and AN in T_1 and T_3 was significantly lower than those in CK ($P < 0.05$). However, the content of MBC in T_1, T_2, and T_3 was significantly higher than in CK ($P < 0.05$). There was no significant difference in the content of SOC and AP among all treatments ($P > 0.05$).

Fungal community composition and distribution characteristics

A total of 421,226 optimized sequences were obtained, with an average length of about 270 bp. After being flattened by the minimum number of sample sequences, 317,376 optimized sequences were obtained, with 26,448

Table 1 Physicochemical properties of soil samples in different temperatures

Treatments	TN (g/kg)	SOC (g/kg)	MBC (mg/kg)	AN (mg/kg)	AK (mg/kg)	AP (mg/kg)	pH
CK	2.59 ± 0.00a	61.72 ± 0.82a	50.77 ± 0.22d	82.72 ± 1.35a	129.15 ± 0.65a	80.13 ± 0.63a	4.58 ± 0.00a
T_1	2.51 ± 0.00c	60.06 ± 0.41a	73.00 ± 0.00b	77.99 ± 0.91b	116.35 ± 1.20c	79.83 ± 0.56a	4.52 ± 0.01b
T_2	2.58 ± 0.00a	60.92 ± 0.00a	75.60 ± 0.00a	79.80 ± 1.65ab	121.82 ± 1.18b	82.12 ± 0.43a	4.50 ± 0.00c
T_3	2.54 ± 0.01b	59.78 ± 0.87a	68.40 ± 0.15c	76.83 ± 0.71b	123.44 ± 0.81b	81.52 ± 1.21a	4.46 ± 0.00d

The results are reported as mean value ± standard error (n = 3). Different letters in each column indicate significant differences among the four temperature treatments (P < 0.05, ANOVA). CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C. *TN* total nitrogen, *SOC* soil organic carbon, *MBC* Microbial biomass carbon, *AN* Available nitrogen, *AK* Available potassium, *AP* Available phosphorous

sequences per sample, and 1463 ASVs were obtained from all samples through denoise the optimized sequence finally. Figure 2 presented the total number ASVs under different treatments was CK > T_1 > T_2 > T_3, which were 626, 584, 531, and 447, respectively. There were 128 ASVs in each treatment, and the number of unique ASVs was T_1 > CK > T_2 > T_3, which were 332, 322, 241, and 196, respectively.

For fungal taxonomic identification, the detected ASVs were classified into 11 phyla, 39 classes, 89 orders, 187 families, 462 genera, and 522 species. Figure 3 showed the most abundant fungal phylum in four treatments was *Ascomycota* (80.47–90.09%). Other phyla include *unclassified_k__Fungi* (2.21−9.43%), *Basidiomycota* (3.87−7.01%), *Mortierellomycota* (0.57–2.39%), and *Rozellomycota* (0.15−3.9%). Particularly, the relative abundance of *Ascomycete* increased with the increase of temperature and in T_2 and T_3 were significantly higher than T_1 and CK (P < 0.05). The relative abundance of *unclassified_k__Fungi* decreased with the increase in temperature (P < 0.05). There were significant differences in *Mortierellomycota* among each treatment, and the relative abundance of each treatment was CK > T_3 > T_1 > T_2 (P < 0.05).

Figure 4 illustrated that the dominant fungal genus was *Dimorphospora* (12.28−47.51%) in each treatments, followed by *unclassified_o__Helotiales* (9.75−34.22%), *Pseudeurotium* (5.54−11.45%), *Gyoerffyella* (1.58−17.21%), *Meliniomyces* (1.18−16.56%), *unclassified_k__Fungi* (2.21−9.43%), *unclassified_f__Hyaloscyphaceae* (2.86−8.18%), and *unclassified_c__Microbotryomycetes* (1.57−2.02%). In particular, *Dimorphospora* has the highest relative abundance in T_1 and the lowest in T_2, which is significantly different from CK and T_2 (P < 0.05). The relative abundance of *unclassified_o__Helotiales*, *Pseudeurotium*, and *unclassified_k__Fungi* was significant differences in each treatment (P < 0.05).

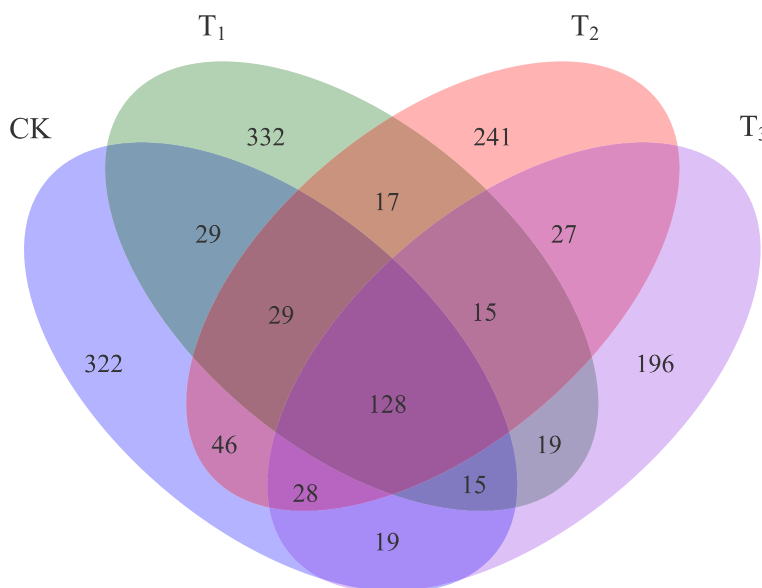

Fig. 2 Venn diagram of amplicon sequence variants (ASVs) of fungal community in permafrost in different temperatures. CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C

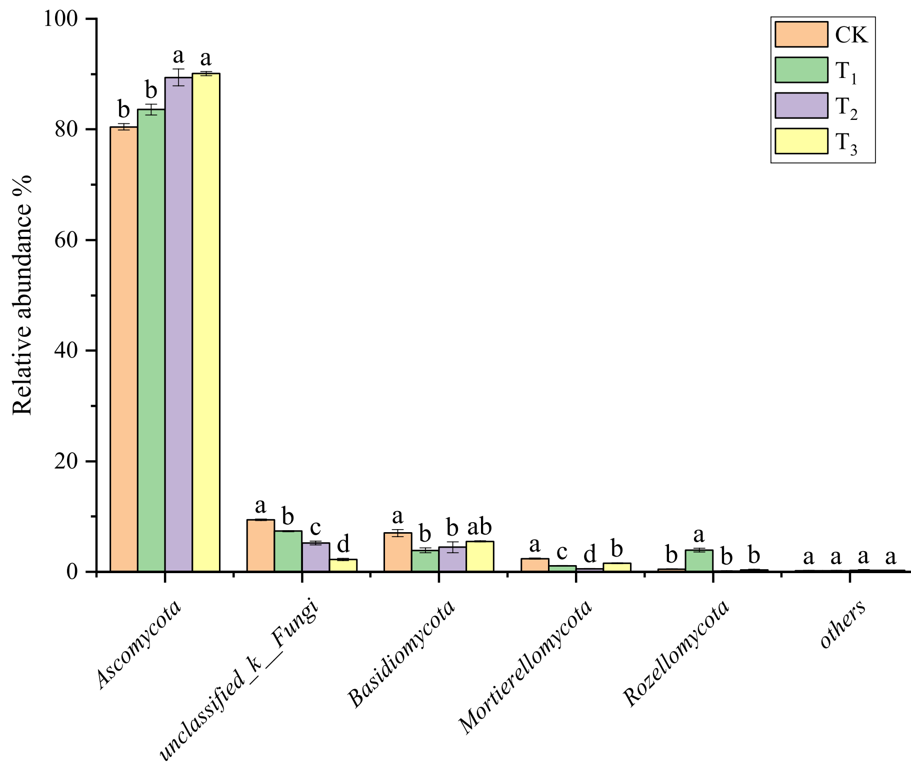

Fig. 3 Relative abundance differences of fungal at phyla level in different temperatures. CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C

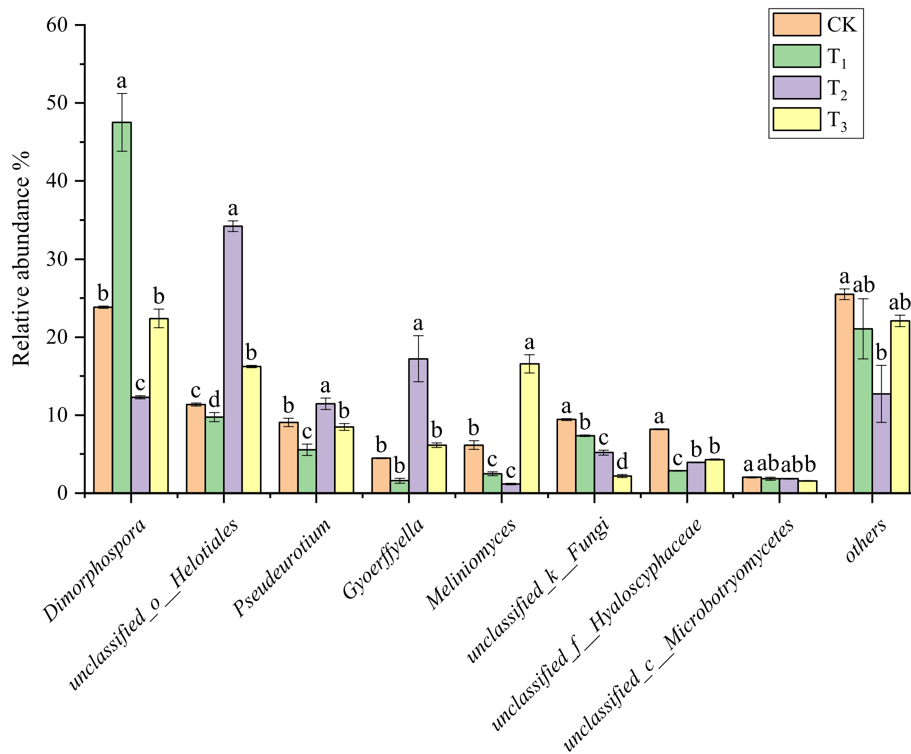

Fig. 4 Relative abundance differences of fungal at genera level in different temperatures. CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C

Table 2 Fungal alpha diversity index in different temperatures

Treatments	Coverage	Sobs	ACE	Shannon	Shannoneven
CK	0.9991 ± 0.0006a	296.6667 ± 10.1050a	315.3579 ± 7.4249a	3.4584 ± 0.0882a	0.6075 ± 0.0121a
T_1	0.9996 ± 0.0002a	266.0000 ± 16.8226b	270.5325 ± 14.0582b	2.7153 ± 0.2162b	0.4859 ± 0.0333b
T_2	0.9994 ± 0.0002a	241.3333 ± 15.4308bc	247.7954 ± 12.9505bc	2.6733 ± 0.2547b	0.4867 ± 0.0405b
T_3	0.9998 ± 0.0000a	214.0000 ± 11.5326c	215.0334 ± 11.2055c	3.0149 ± 0.0530ab	0.5621 ± 0.0041ab

The results were reported as mean value ± standard error ($n = 3$). Different letters in each column indicate significant differences among the four temperature treatments ($P < 0.05$, ANOVA). CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C

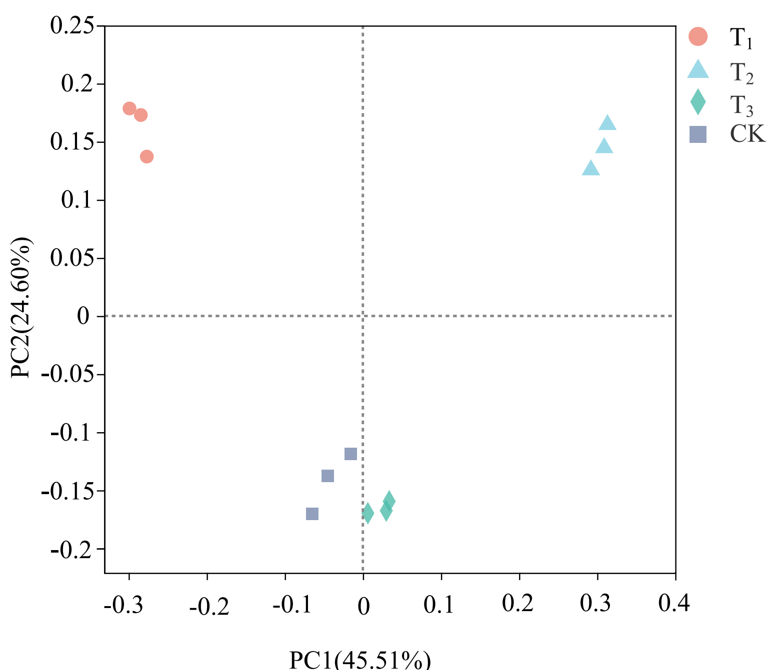

Fig. 5 Principal coordinates analysis (PCoA) of soil fungal community structure in different temperatures. CK, −2 °C; T_1, 0 °C; T_2, 2 °C; T_3, 4 °C

Warming changes the fungal community alpha diversity

As listed in Table 2, the coverage index of each group exceeded 0.99, suggesting that the sequencing results could reflect the real situation of fungi in the sample. After warming treatment, fungal alpha diversity decreased in three warming groups. Specifically, both the observed fungal Sobs and ACE diversity indexes in warming treatments (T_1, T_2, and T_3) were significantly lower than in CK ($P < 0.05$). In addition, Shannon and Shannoneven indexes were the highest in CK and significantly higher than T_1 and T_2 ($P < 0.05$), whereas there was no significant difference with T_3 ($P > 0.05$).

Associations of fungal beta diversity with environmental variables

PCoA showed that the distance among repeated samples in each group is small, indicating that the repeatability of samples was well and the little difference within those groups (Fig. 5). The explanation of PC1 and PC2 was 45.51% and 24.60%, respectively, with a total cumulative contribution of 70.11%. Furthermore, we found that the fungal community structure of each treatment group was well separated in Fig. 5. Combined with the Adonis and MRPP results from Table 3, it is confirmed that the

Table 3 Significance tests of the fungal microbial community structure in the four temperatures

Datasets	Adonis		MRPP	
	R^2	P	A	P
All groups	0.8230	**0.001*****	0.68	**0.001*****

Adonis, permutational multivariate analysis of variance (PERMANOVA); MRPP, multi-response permutation procedures. Significant differences were denoted in bold ($P < 0.05$) and marked with an * sign, *$0.01 < P \leq 0.05$, **$0.001 < P \leq 0.01$, ***$P \leq 0.001$

fungal beta diversity differed significantly among each treatment (P=0.001) .

In Fig. 6, the result of db-RDA showed that CAP1 and CAP2 explained 29.04% and 21.06%, respectively, and the two axes explained 50.10% of the differences in fungal community structure in permafrost under warming conditions. We found that fungal communities in CK and T_3 were positively correlated with MBC and AP whereas negatively correlated with SOC, AN, and pH content. The fungal community of T_1 was positively correlated with SOC, TN, AK, AN, and pH content but negatively correlated with AP and MBC content. The fungal community of T_2 was positively correlated with MBC and pH content, but negatively correlated with AP, TN, AK, SOC, and AN content. As seen in Table 4, the Monte Carlo test revealed that the value of pH, TN, MBC, and AK content has significant effects on the fungal community (P < 0.05).

Figure 7 and Table 5 show that *Ascomycota* was significantly negatively correlated with AN (P < 0.05) and pH (P < 0.001) but positively correlated with MBC and AP (P < 0.05). *Basidiomycota* was significantly negatively correlated with MBC (P < 0.01), while it was opposite with AK (P < 0.01). *Mortierellomycota* was significantly negatively correlated with MBC (P < 0.0001) but positively correlated with AK (P < 0.01) and pH (P < 0.05). In addition, *Rozellomycota* was only significantly negatively correlated with TN and AK (P < 0.05), while *unclassified_k__Fungi* was positively correlated with AN (P < 0.05) and pH (P < 0.001).

Table 4 Significance tests between soil physicochemical properties and fungal community structures

Soil factors	r^2	P
TN	0.6285	**0.017***
SOC	0.2412	0.348
MBC	0.9906	**0.001*****
AN	0.4020	0.104
AK	0.8998	**0.001*****
AP	0.4439	0.084
pH	0.7766	**0.002****

Significant differences were denoted in bold (P < 0.05) and marked with an * sign, *0.01 < P ≤ 0.05, **0.001 < P ≤ 0.01, ***P ≤ 0.001

Discussion

Warming altered soil physicochemical properties

It is common knowledge that warming can alter the soil physicochemical properties such as soil temperature, humidity, and nutrient (Wang et al. 2019). In this study, we found that pH decreased significantly, which was different from the research of the warming of frozen soil active layer (Wu 2021). This phenomenon may be due to differences in soil state, microbial community structure, and diversity between permafrost and active layers, resulting in changes in microbial metabolic processes after the thawing of permafrost (Messan et al. 2020). Coolen and Orsi (2015) found that thawing of frozen soil was conducive to the expression of acetylated genes, and acetylated bacteria may be a potential source of acetic

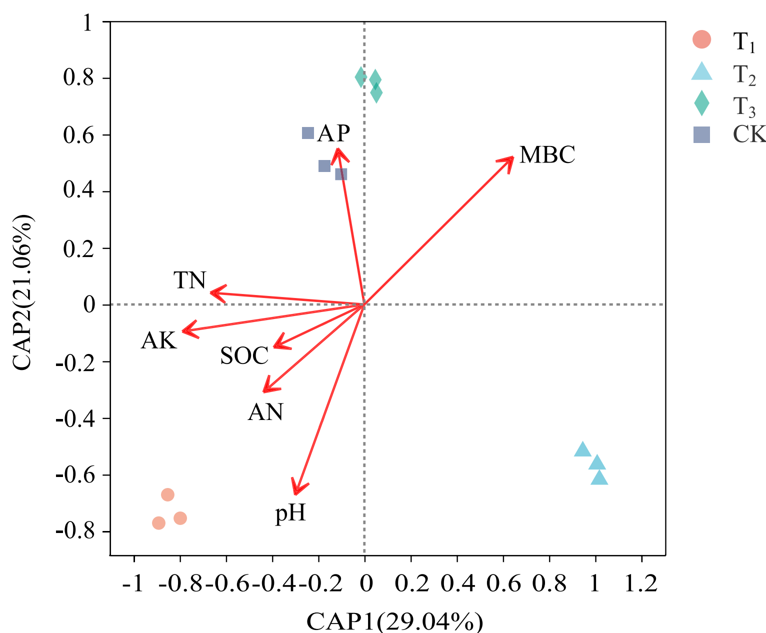

Fig. 6 Distance-based redundancy analysis (db-RDA) of soil physicochemical properties and fungal community structure

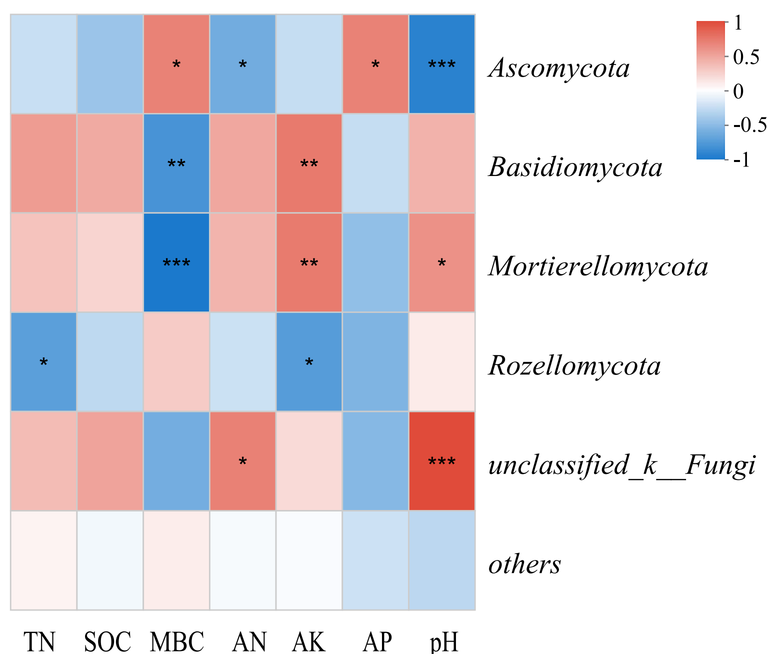

Fig. 7 Correlation heatmap of fungal phyla and soil physicochemical properties. Note: the *x*-axis and *y*-axis are soil environmental and species respectively. The *R*-value is shown in different colors in the figure. If the *P*-value is less than 0.05, it is marked with an * sign, *0.01 < $P \leq 0.05$, **0.001 < $P \leq 0.01$, ***$P \leq 0.001$

Table 5 Correlation analysis of dominant fungal phyla and soil physicochemical properties

Phyla	TN	SOC	MBC	AN	AK	AP	pH
Ascomycota	0.4886	0.1854	**0.0171***	**0.0476***	0.4672	**0.0170***	**0.0001*****
Basidiomycota	0.0731	0.1358	**0.0044****	0.1185	**0.0090****	0.4598	0.1777
Mortierellomycota	0.2988	0.4649	**0.0000*****	0.1887	**0.0098****	0.1425	**0.0438***
Rozellomycota	**0.0157***	0.4052	0.3698	0.5180	**0.0116***	0.0792	0.7230
unclassified_k__Fungi	0.2440	0.1027	0.0507	**0.0161***	0.5254	0.0999	**0.0000*****
others	0.8279	0.8908	0.7439	0.9243	0.9557	0.5209	0.3889

TN Total nitrogen, *SOC* Soil organic carbon, *MBC* Microbial biomass carbon, *AN* Available nitrogen, *AK* Available potassium, *AP* Available phosphorous. Significant differences were denoted in bold ($P < 0.05$) and marked with an * sign, *0.01 < $P \leq 0.05$, **0.001 < $P \leq 0.01$, ***$P \leq 0.001$

acid. With the increase of temperature, it may lead to the accumulation of acidic metabolites and then change the soil pH. The results showed a significant increase in MBC content after warming, which is similar to the results of a meta-analysis (Zhang et al. 2015), indicating that microbes in a colder environment are extremely sensitive to warming, and it will change the microbial biomass in soil. In addition, as the driving force of soil organic matter degradation and transformation, soil MBC can be used to characterize the changes of soil carbon and nitrogen nutrients (Anderson 2003). Therefore, with the absence of exogenous carbon and nitrogen, the increase of MBC content means an increase of microbial biomass, while the increase in nutrient consumption will lead to a decrease of SOC, TN, and AN content (Wu 2021). Studies also suggested that the increase of temperature promotes the increase of soil microbial biomass, which may promote the metabolism of enzymes, induce the increase of soil respiration, and ultimately lead to the loss of soil SOC (Li et al. 2020). However, there was no significant difference in the SOC content among the groups in this study, which may be caused by the short culture cycle and the total consumption of SOC by microorganisms in each group. The difference was that the AK content in the warming treatment groups decreased significantly, and the AN content in the T_1 and T_3 was significantly lower than that in the CK. The main reason may be that the warming increased the microbial activity, then

accelerated the utilization of soil nutrients, and led to the decrease of soil nutrient content in the end (Fang et al. 2020; Peng et al. 2019).

Effects of warming and soil physical and chemical factors on the structure and diversity of soil fungal community

This study found that *Ascomycota* was the dominant fungal phyla of permafrost; the relative abundance from CK to T_3 was 80.47%, 83.58%, 89.38%, and 90.09%, which is similar to the previous research results (Wang et al. 2016; Cheng et al. 2020). ANOVA analysis showed that warming affected the relative abundance of fungi at phyla and genus levels, but different species showed different degrees of influence, which may be related to the different adaptability and sensitivity of different species to temperature (Balser and Wixon, 2009). It has been reported that changes in the soil environment caused by the thawing of permafrost will alter the microbial community (Patzner et al. 2021; Kluge et al. 2021). Similar to these conclusions, our results revealed that fungal communities were mainly related to pH, TN, MBC, and AK content, which showed that the composition, structure, and diversity of soil fungi in permafrost were affected by carbon, nitrogen, and other nutrients (Zhang et al. 2014). Specifically, AN was significantly negatively correlated with *Ascomycota* but significantly positively correlated with *unclassified_k__Fungi*. AK was positively correlated with *Basidiomycota* and *Mortierellomycota* but negatively correlated with *Rozellomycota*. pH was significantly negatively correlated with *Ascomycota* but significantly positively with *Mortierellomycota* and *unclassified_k__Fungi*. Thus, it can be seen that the correlation and significance between different fungi and soil physical and chemical factors were different, which is probably caused by the different utilization preference of different nutrient elements among different fungi (Yang et al. 2022). On the whole, pH has the most significant effect on the fungal community at the phylum level, and it is speculated that pH plays a major role in constructing the fungal community structure in permafrost. However, at present, the research on the driving mechanism of pH on permafrost microbial has mostly focused on the study of bacteria communities, and many studies believed that pH was the key factor in bacterial community structure (Chu et al. 2010; Kim et al. 2014). On the contrary, there were few studies on the impact of permafrost soil fungal. Although a few studies have found that pH can affect the structure of fungal communities (Jiang et al. 2021), little is known about whether pH has a significant driving contribution to permafrost fungal communities on different scales.

In this study, the index of richness, diversity, and evenness of fungal alpha diversity was decreased after warming, which is similar to the research results on the warming of permafrost in the Tibet Plateau (Chen et al. 2020), alpine meadow (Yao et al. 2021), and lakeside wetland (Zhang et al. 2021). These studies have confirmed the high sensitivity of soil microbial to temperature. Early results showed that rare fungi were psychrophilic, cold tolerant, and extremely sensitive to environmental fluctuations lived in permafrost for a long time, and warming stress may inhibit or even kill this temperature-sensitive flora and then reduce alpha diversity (Ren 2018). At the same time, warming also intensified the nutrient competition between soil microbial communities. The higher the abundance of the dominant microbial community, the stronger the inhibition effect on the growth and reproduction of vulnerable microbial such as rare species (Jousset et al. 2017).

It is worth noting that AK is significantly correlated with the beta diversity of permafrost fungal communities in this study. Yao et al. (2017) believed that the soil fungal community structure was closely related to the physicochemical properties of AK, and Li and Yan (2019) also found a significant correlation between AK and soil fungal community structure, and those results confirmed the importance of AK to the soil fungal community. At present, studies have found that AK has a significant correlation with the beta diversity of permafrost bacteria (Wang et al. 2020), but it has not been identified as the key factor affecting beta diversity, and relevant studies rarely involved the impact on permafrost soil fungal communities. Can this be used as a reference for future research indicators? Therefore, considering the spatial heterogeneity of global permafrost, whether the succession of microbial communities in different regions and the driving factors of beta diversity are similar under the condition of climate warming still need further study.

Conclusion

Our findings showed that simulated warming changed the soil physicochemical properties of permafrost in the Greater Xing'an Mountains and reduced the Sobs, ACE, Shannon, and Shannoneven indexes of fungal communities. *Ascomycota* and *Dimorphospora* were the dominant phylum and genus, respectively, but there were differences in the response of fungal groups at different levels to warming. In addition, fungal communities were significantly correlated with pH, TN, MBC, and AK, while the correlations between different fungal phyla and soil physicochemical properties were different. In short, permafrost warming can lead to changes in soil physicochemical properties and fungal community structure and diversity, which also highlights the need to study global warming on environmental changes in permafrost regions and understand microbial ecology.

Acknowledgements
The author(s) would like to thank all editors and reviewers for their comments and suggestions and support from the staff at the Heilongjiang Huzhong National Nature Reserve.

Authors' contributions
All authors listed have made a substantial, direct, and intellectual contribution to the work and have read and agreed to the published version of the manuscript. The authors read and approved the final manuscript.

Funding
This research was financially supported by The Financial Special Project of Heilongjiang Province (ZNJZ2020ZR01), The Special Project of the Central Government to Guide Local Science and Technology Development (ZY20B15), and The Key Laboratory of Forest Plant Ecology, Ministry of Education (K2020A02).

Availability of data and materials
Relevant data materials involved in the study can be directly contacted with the corresponding authors.

Declarations

Ethics approval and consent to participate
The article did not involve any research that violated ethical norms, and all participants agreed to publish the paper.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Received: 16 August 2022 Accepted: 30 November 2022
Published online: 03 February 2023

References
Ade LJ, Hu L, Zi HB, Wang CT, Lerdau M, Dong SK (2018) Effect of snowpack on the soil bacteria of alpine meadows in the Qinghai-Tibetan Plateau of China. Catena 164:13–22. https://doi.org/10.1016/j.catena.2018.01.004
Anderson T (2003) Microbial eco-physiological indicators to asses soil quality. Agric Ecosyst Environ 98(1-3):285–293. https://doi.org/10.1016/S0167-8809(03)00088-4
Balser TC, Wixon DL (2009) Investigating biological control over soil carbon temperature sensitivity. Global Change Biol 15(12):2935–2949. https://doi.org/10.1111/j.1365-2486.2009.01946.x
Baltzer JL, Veness T, Chasmer LE, Sniderhan AE, Quinton WL (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. GCB Bioenergy 20(3):824–834. https://doi.org/10.1111/gcb.12349
Biskaborn BK, Smith SL, Noetzli J, Matthes H, Vieira G, Streletskiy DA, Schoeneich P, Romanovsky VE et al (2019) Permafrost is warming at a global scale. Nat Commun 10:264. https://doi.org/10.1038/s41467-018-08240-4
Bolyen E, Rideout JR, Dillon MR, Bokulich NA, Abnet CC, Al-Ghalith GA, Alexander H, Alm EJ et al (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. Nat Biotechnol 37(8):852–857. https://doi.org/10.1038/s41587-019-0209-9
Chen SF, Zhou YQ, Chen YR, Gu J (2018) fastp: an ultra-fast all-in-one FASTQ preprocessor. Bioinformatics 34(17):884–890. https://doi.org/10.1093/bioinformatics/bty560
Chen YL, Deng Y, Ding JZ, Hu HW, Xu TL, Li F, Yang GB, Yang YH (2017) Distinct microbial communities in the active and permafrost layers on the Tibetan Plateau. Mol Ecol 26(23):6608–6620. https://doi.org/10.1111/mec.14396
Chen YL, Liu FT, Kang LY, Zhang DY, Kou D, Mao C, Qin AQ, Zhang QW et al (2020) Large-scale evidence for microbial response and associated carbon release after permafrost thaw. GCB Bioenergy 27(14):3218–3229. https://doi.org/10.1111/gcb.15487
Cheng JM, Yang YF, Yuan MTM, Gao Q, Wu LY, Qin ZY, Shi ZJ, Schuur EAG et al (2020) Winter warming rapidly increases carbon degradation capacities of fungal communities in tundra soil: potential consequences on carbon stability. Mol Ecol 30(4):926–937. https://doi.org/10.1111/mec.15773
Chu HY, Fierer N, Lauber CL, Caporaso JG, Knight R, Grogan P (2010) Soil bacterial diversity in the Arctic is not fundamentally different from that found in other biomes. Environ Microbiol 12(11):2998–3006. https://doi.org/10.1111/j.1462-2920.2010.02277.x
Coolen MJL, Orsi WD (2015) The transcriptional response of microbial communities in thawing Alaskan permafrost soils. Frontiers in Microbiology 6:197. https://doi.org/10.3389/fmicb.2015.00197
Dong XF, Liu C, Ma DL, Wu YF, Man HR, Wu XW, Li M, Zang SY (2021) Organic carbon mineralization and bacterial community of active layer soils response to short-term warming in the Great Hing'an Mountains of Northeast China. Frontiers in Microbiology 12:802213. https://doi.org/10.3389/fmicb.2021.802213
Fang X, Zhou GY, Qu C, Huang WJ, Zhang DQ, Li YL, Yi ZG, Liu JX (2020) Translocating subtropical forest soils to a warmer region alters microbial communities and increases the decomposition of mineral-associated organic carbon. Soil Biol Biochem 142:107707. https://doi.org/10.1016/j.soilbio.2020.107707
Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes--application to the identification of mycorrhizae and rusts. Mol Ecol 2(2):113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x
Guntinas ME, Leiros MC, Trasar-Cepeda C, Gil-Sotres F (2012) Effects of moisture and temperature on net soil nitrogen mineralization: a laboratory study. Eur J Soil Biol 48:73–80. https://doi.org/10.1016/j.ejsobi.2011.07.015
Hu WG, Zhang Q, Li DY, Cheng G, Mu J, Wu QB, Niu F, An LZ et al (2015) Diversity and community structure of fungi through a permafrost core profile from the Qinghai-Tibet Plateau of China. J Basic Microbiol 54(12):1331–1341. https://doi.org/10.1002/jobm.201400232
IPCC (2021) 2021: summary for policymakers. In: climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge and New York (In Press)
Jiang L (2020) Effects of increasing temperature on soil carbon and nitrogen transformation and its microbial mechanisms in a peatland of the Great Hing'an Mountains. Dissertation, Northeast Institute of Geography and Agroecology, Chinese Academy of Science
Jiang L, Song YY, Sun L, Ma XY, Wang XW, Song CC, Hou AX, Wang LL (2021) Distribution of carbon and nitrogen cycle microbes along permafrost peatland profile in Northeast China. Environ Prog Sustainable Energy 40(5):e13707. https://doi.org/10.1002/ep.13707
Jin HJ, Yu QH, Lii LZ, Guo DX, He RX, Yu SP, Sun GY, Li YW (2007) Degradation of permafrost in the Xing'anling Mountains, northeastern China. Permafrost Periglacial Processes 18(3):245–258. https://doi.org/10.1002/ppp.589
Jousset A, Bienhold C, Chatzinotas A, Gallien L, Gobet A, Kurm V, Kusesl K, Rillig MC et al (2017) Where less may be more: how the rare biosphere pulls ecosystems strings. ISME J 11(4):853–862. https://doi.org/10.1038/ismej.2016.174
Kim HM, Jung JY, Yergeau E, Hwang CY, Hinzman L, Nam S, Hong SG, Kim OS et al (2014) Bacterial community structure and soil properties of a subarctic tundra soil in Council. Alaska. FEMS Microbiol Ecol 89(2):465–475. https://doi.org/10.1111/1574-6941.12362
Kluge M, Wauthy M, Clemmensen KE, Wurzbacher C, Hawkes JA, Einarsdottir K, Rautio M, Stenlid J et al (2021) Declining fungal diversity in Arctic freshwaters along a permafrost thaw gradient. GCB Bioenergy 27(22):5889–5906. https://doi.org/10.1111/gcb.15852
Li F, Peng YF, Chen LY, Yang GB, Abbott BW, Zhang DY, Kang K, Wang GQ et al (2020) Warming alters surface soil organic matter composition despite unchanged carbon stocks in a Tibetan permafrost ecosystem. Funct Ecol 34(4):911–922. https://doi.org/10.1111/1365-2435.13489
Li M, Yan W (2019) Effects of altitude on rhizosphere fungal community structure of Pinus tabulaeformis in Wula Mountain. China. Mygosystema 38(11):1992–2006. https://doi.org/10.13346/j.mycosystema.190243
Lipson DA, Raab TK, Parker M, Kelley ST, Brislawn CJ, Jansson J (2015) Changes in microbial communities along redox gradients in polygonized Arctic wet tundra soils. Environ Microbiol Rep 7(4):649–657. https://doi.org/10.1111/1758-2229.12301
Liu FT, Kou D, Chen YL, Xue K, Ernakovich JG, Chen LY, Yang GB, Yang YH (2020) Altered microbial structure and function after thermokarst formation. GCB Bioenergy 27(4):823–835. https://doi.org/10.1111/gcb.15438

Luo J, Yin GA, Niu FJ, Lin ZJ, Liu MH (2019) High spatial resolution modeling of climate change impacts on permafrost thermal conditions for the Beiluhe Basin. Qinghai-Tibet Plateau. Remote Sens 11(11):1294. https://doi.org/10.3390/rs11111294
Mackelprang R, Waldrop MP, DeAngelis KM, David MM, Chavarria KL, Blazewicz SJ, Rubin EM, Jansson JK (2011) Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. Nature 480(7377):368–371. https://doi.org/10.1038/nature10576
Magoc T, Salzberg SL (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. Bioinformatics 27(21):2957–2963. https://doi.org/10.1093/bioinformatics/btr507
Messan KS, Jones RM, Doherty SJ, Foley K, Douglas TA, Barbato RA (2020) The role of changing temperature in microbial metabolic processes during permafrost thaw. PLoS One 15(4):e0232169. https://doi.org/10.1371/journal.pone.0232169
Nguyen NH, Song ZW, Bates ST, Branco S, Tedersoo L, Menke J, Schilling JS, Kennedy PG (2016) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Soil 20:147–171. https://doi.org/10.5194/soil-1-147-2015
Patzner MS, Mueller CW, Malusova M, Baur M, Nikeleit V, Scholten T, Hoeschen C, Byrne JM et al (2021) Iron mineral dissolution releases iron and associated organic carbon during permafrost thaw. Nat Commun 11(1):6329. https://doi.org/10.1038/s41467-020-20102-6
Pautler BG, Simpson AJ, Mcnally DJ, Lamoureux SF, Simpson MJ (2010) Arctic permafrost active layer detachments stimulate microbial activity and degradation of soil organic matter. Environ Sci Technol 44(11):4076–4082. https://doi.org/10.1021/es903685j
Peng YF, Peng ZP, Zeng XT, Houx JH (2019) Effects of nitrogen-phosphorus imbalance on plant biomass production: a global perspective. Plant Soil 436(1-2):245–252. https://doi.org/10.1007/s11104-018-03927-5
Penton CR, St Lous D, Cole JR, Luo YQ, Wu LY, Schuur EAG, Zhou JZ, Tiedje JM (2013) Fungal diversity in permafrost and tallgrass prairie soils under experimental warming conditions. Appl Environ Microbiol 79(22):7063–7072. https://doi.org/10.1128/AEM.01702-13
Ping CL, Jastrow JD, Jorgenson MT, Michaelson GJ, Shur YL (2015) Permafrost soils and carbon cycling. Soil 1(1):147–171. https://doi.org/10.5194/soil-1-147-2015
Ren JS (2018) Effects of warming on soil microorganisms in the permafrost peatland of the Great Hing'an Mountains. Dissertation, Northeast Institute of Geography and Agroecology Chinese Academy of Sciences
Schuur EAG, McGuire AD, Schaedel C, Grosse G, Harden JW, Hayes DJ, Hugelius G, Koven CD et al (2015) Climate change and the permafrost carbon feedback. Nature 520(7546):171–179. https://doi.org/10.1038/nature14338
Screen JA, Simmonds I (2010) The central role of diminishing sea ice in recent Arctic temperature amplification. Nature 464(7293):1334–1337. https://doi.org/10.1038/nature09051
Shang W, Wu XD, Zhao L, Yue GY, Zhao YH, Qiao YP, Li YQ (2016) Seasonal variations in labile soil organic matter fractions in permafrost soils with different vegetation types in the Central Qinghai-Tibet Plateau. Catena 137:670–678. https://doi.org/10.1016/j.catena.2015.07.012
Song YY, Song CC, Ren JS, Ma XY, Tan WW, Wang XW, Gao JL, Hou AX (2019) Short-term response of the soil microbial abundances and enzyme activities to experimental warming in a boreal peatland in Northeast China. Sustainability 11(3):590. https://doi.org/10.3390/su11030590
Sun HZ, Ma DL, Zang SY, Wu XW (2018) Characteristics of soil microbial community structure under different forest types of permafrost regions in the Greater Khingan Mountains. J Glaciol Geocryol 40(5):1028–1036. https://doi.org/10.7522/j.issn.1000-0240.2018.0112
Tripathi BM, Kim M, Kim Y, Byun E, Yang JW, Ahn J, Lee YK (2018) Variations in bacterial and archaeal communities along depth profiles of Alaskan soil cores. Sci Rep 8:504. https://doi.org/10.1038/s41598-017-18777-x
Turetsky MR, Abbott BW, Jones MC, Anthony KW, Olefeldt D, Schuur EAG, Grosse G, Kuhry P et al (2020) Carbon release through abrupt permafrost thaw. Nat Geosci 13(2):138–143. https://doi.org/10.1038/s41561-019-0526-0
Waldrop MP, Wickland KP, White R, Berhe AA, Harden JW, Romanovsky VE (2010) Molecular investigations into a globally important carbon pool: permafrost-protected carbon in Alaskan soils. GCB Bioenergy 16(9):2543–2554. https://doi.org/10.1111/j.1365-2486.2009.02141.x
Wang H, Liu S, Schnidlbacher A, Wang JX, Yang YJ, Song ZC, You YM, Shi ZM (2019) Experimental warming reduced topsoil carbon content and increased soil bacterial diversity in a subtropical planted forest. Soil Biol Biochem 133:155–164. https://doi.org/10.1016/j.soilbio.2019.03.004
Wang XJ, Zhang ZC, Yu ZQ, Shen GF, Cheng HF, Tao S (2020) Composition and diversity of soil microbial communities in the alpine wetland and alpine forest ecosystems on the Tibetan Plateau. Sci Total Environ 747:141358. https://doi.org/10.1016/j.scitotenv.2020.141358
Wang YF, Wei SP, Cui HP, Su X, Zhu YH, Lu ZQ, Li LP, Zhang S et al (2016) Distribution and diversity of microbial community along a vertical permafrost profile, Qinghai-Tibetan Plateau. Microbiology China 43(9):1902–1917. https://doi.org/10.13344/j.microbiol.china.151074
Wei Z, Jin HJ, Zhang JM, Yu SP, Han XJ, Ji YJ, He RX, Chang XL (2010) Prediction of permafrost changes in Northeastern China under a changing climate. Scientia Sinica (Terrae) 41(1):74–84. https://doi.org/10.1007/s11430-010-4109-6
White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Academic Press, New York
Wu JC, Sheng Y, Wu QB, Wen Z (2010) Processes and modes of permafrost degradation on the Qinghai-Tibet Plateau. Sci China Earth Sci 53(1):150–158. https://doi.org/10.1007/s11430-009-0198-5
Wu LW, Yang F, Feng JJ, Tao XY, Qi Q, Wang C, Schuur EAG, Bracho R et al (2021) Permafrost thaw with warming reduces microbial metabolic capacities in subsurface soils. Mol Ecol. 31(5):1403–1415. https://doi.org/10.1111/mec.16319
Wu P, Liang SH, Wang XS, Feng YQ, Mckenzie JM (2018a) A new assessment of hydrological change in the source region of the Yellow River. Water 10(7):877. https://doi.org/10.3390/w10070877
Wu XD, Zhao L, Liu GM, Xu HY, Zhang XL, Ding YJ (2018b) Effects of permafrost thaw-subsidence on soil bacterial communities in the southern Qinghai-Tibetan Plateau. Appl Soil Ecol 128:81–88. https://doi.org/10.1016/j.apsoil.2018.04.007
Wu YF (2021) Effects of warming and exogenous nitrogen addition on soil physical and chemical properties and enzyme activities in active layer of permafrost in Daxing'an mountains. Dissertation,. Harbin Normal University
Yang LB, Jiang YB, Zhou T, Cui FX, Zhu DG, Xu F (2022) Effects of litter fall on soil fungal diversity under snow cover in the Greater Xing'an Mountains. Res Environ Sci 35(4):1037–1044. https://doi.org/10.13198/j.issn.1001-6929.2021.12.12
Yang ZM, Yang SH, Van Nostrand JD, Zhou JZ, Fang W, Qi Q, Liu YR, Wullschleger SD et al (2017) Microbial community and functional gene changes in Arctic tundra soils in a microcosm warming experiment. Front Microbiol 8:1741. https://doi.org/10.3389/fmicb.2017.01741
Yao Q, Liu JJ, Yu ZH, Li YS, Jin J, Liu XB, Wang GH (2017) Three years of biochar amendment alters soil physiochemical properties and fungal community composition in a black soil of Northeast China. Soil Biol Biochem 110:56–67. https://doi.org/10.1016/j.soilbio.2017.03.005
Yao ST, Lu GX, Deng Y, Dang Y, Wang YC, Zhang HJ, Yan HL (2021) Effects of simulated warming on soil fungal community composition and diversity. Ecol Environ Sci 30(7):1404–1411. https://doi.org/10.16258/j.cnki.1674-5906.2021.07.009
Zhang N, Chen KL, Wang HS, Yang Y (2021) Effect of simulated warming on soil microorganism of bird island in Qinghai Lake. Microbiol China 48(3):722–732. https://doi.org/10.13344/j.microbiol.china.200494
Zhang XF, Xu SJ, Li CM, Zhao L, Feng HY, Yue GY, Ren ZW, Cheng GD (2014) The soil carbon/nitrogen ratio and moisture affect microbial community structures in alkaline permafrost-affected soils with different vegetation types on the Tibetan Plateau. Res Microbiol 165(2):128–139. https://doi.org/10.1016/j.resmic.2014.01.002
Zhang XZ, Shen ZX, Fu G (2015) A meta-analysis of the effects of experimental warming on soil carbon and nitrogen dynamics on the Tibetan Plateau. Appl Soil Ecol 87:32–38. https://doi.org/10.1016/j.apsoil.2014.11.012
Zhao DS, Wu SH (2019) Projected changes in permafrost active layer thickness over the Qinghai-Tibet Plateau under climate change. Water Resour Res 55(9):7860–7875. https://doi.org/10.1029/2019WR024969

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.