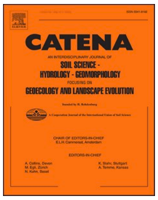
Catena 249 (2025) 108694

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena



Permafrost as a source of mineral weathering bacteria: Implications of active layer thickening on James Ross Island, Antarctica

Lenka Micenková [a,*], Martin Kadlec [b], Ivana Mašlaňová [a], Ivo Sedláček [c], Pavel Švec [c], Vojtěch Kovařovic [a], Roman Pantůček [a], Michaela Kňažková [b], Daniel Nývlt [b], Filip Hrbáček [b]

[a] *Department of Experimental Biology, Division of Genetics and Molecular Biology, Faculty of Science, Masaryk University, Kotlářská 2, Brno 611 37, Czech Republic*

[b] *Department of Geography, Faculty of Science, Masaryk University, Kotlářská 2, Brno 611 37, Czech Republic*

[c] *Department of Experimental Biology, Czech Collection of Microorganisms, Faculty of Science, Masaryk University, Kamenice 5, Brno 625 00, Czech Republic*

ARTICLE INFO

Keywords:
Antarctica
James Ross Island
Soil
Geology
Microbiome

ABSTRACT

Studying permafrost in Antarctica provides insights into climate history, soil and rock structure, and a unique biodiversity with potential impact on ecosystems. Although a great deal of effort has been devoted to the microbiological composition of permafrost soils, the objective pursued in this study is, for the first time, to examine soil and rock samples collected from a 350 cm deep core drilled near the Johann Gregor Mendel Czech Antarctic Station on the Ulu Peninsula of James Ross Island, to study the effect of geochemical properties on microbial composition and diversity and *vice versa*. We collected samples from the profile starting on the ground surface down to 350 cm depth and correlated information from metagenomic 16S rRNA gene analysis and geochemical data. The 80-cm-thick active layer had a distinct bacterial composition different from the *Pseudomonadota*-rich permafrost layer, with *Actinomycetota*, *Acidobacteriota*, *Chloroflexota*, and *Verrucomicrobiota* being the prevalent phyla. Throughout the core, the higher bacterial diversity was positively associated with the sand fraction and intensive weathering. The highest identified diversity in the deepest part of the active layer (transient active layer) suggests that the bacteria here have been gradually cryopreserved, possibly accumulating from the upper layers. In summary, the identified interface between the active layer and permafrost, as well as the transition within the permafrost from Holocene marine sediments to underlying Cretaceous sedimentary rocks (deeper than ~ 260 cm), had the greatest influence on the bacterial composition. Decadal records of soil temperature and active layer thickness predict more significant interactions in the future between bacterial communities in the current active layer and mineral weathering bacteria that are typical of permafrost.

1. Introduction

Permafrost, one of the key components of the earth's cryosphere, covers about 11 % of the world's land area (Obu, 2021). It is typically associated with ground ice and contains one of the least known soil microbial communities, where microbiota live in an ice-enclosed environment (Xue et al., 2019).

Despite being a hostile environment, permafrost harbours a diverse and active microbial community (Altshuler et al., 2017). Although most of our understanding of permafrost microbiology has been derived from cultivation experiments, recent developments in sequencing methods have revealed the enormous diversity of bacterial populations in Antarctica, which play an important role in weathering soil minerals and understanding the initial formation of soil. Typical microbial mechanisms involved in the breakdown and transformation of minerals are e.g., oxidation, oxidoreduction or organic acid production (Altshuler et al., 2007; Meier et al., 2019; Alekseev et al. 2020; Garrido-Benavent et al., 2020; Horrocks et al., 2020; Díaz-Puente et al., 2021; Dziurzynski et al., 2023).

The relationship between biotic and abiotic components in permafrost environments continues to be a major topic of ecosystem research. Combined geochemical and metagenomic data from sites around the northern hemisphere, including the United States, Canada, Russia, Sweden, and Spitsbergen, have shown that bacterial biodiversity in permafrost varies with pH, latitude, soil depth, ice content, and age of the deposit (Burkert et al., 2019; Liang et al. 2019; Waldrop et al., 2023). However, there has been a limited number of studies focusing on the polar environment that combine geochemical and microbiological

---

[*] Corresponding author at: Department of Experimental Biology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic.
E-mail address: lenka.micenkova@sci.muni.cz (L. Micenková).

https://doi.org/10.1016/j.catena.2024.108694
Received 18 December 2023; Received in revised form 18 December 2024; Accepted 24 December 2024

approaches in Antarctica (Wynn-Williams, 1990; Ganzert et al., 2011; Bajerski and Wagner, 2013; Cowan et al., 2014; Núñez-Montero and Barrientos, 2018; Meier et al., 2019).

The deglaciated areas of Antarctica enable the study of the physical/chemical and biological conditions of both the permafrost and active layer. One of the largest deglaciated areas is located in the northern part of James Ross Island and is part of the Ulu Peninsula. Deglaciation of the lower-lying parts of the Ulu Peninsula began approximately 12.9 ka ago and continued throughout the Holocene, making the deglaciated area of the Ulu Peninsula the largest and also one of the oldest in the Antarctic Peninsula region (Nývlt et al., 2014; Hrbáček et al., 2017; Jennings et al., 2021). The regions of James Ross Island are underlaid by continuous permafrost approximately 6–67 m thick in the lowlands near the sea (Fukuda et al., 1992; Borzotta and Trombotto, 2004). The active layer above the continuos permafrost is 0.5–1.2 m thick (Hrbáček et al., 2023).

Even in Antarctic soils, which are extreme habitats, a rich and diverse prokaryotic community has previously been described. The microbiological research in this area has mainly focused on investigating diversity and taxonomy (Kosina et al., 2016; Sedláček et al., 2017, 2019, 2020; Grillová et al., 2018; Pantůček et al., 2018), cyanobacterial research (Strunecký et al., 2010, 2012; Komárek et al., 2012), and relationships between microbes from different environments (Kollár et al., 2023). To date, only one study has investigated the pedogenic and microbial relationships in the soils of the Ulu Peninsula (Meier et al., 2019) and focused on the Santa Martha Cove and Brandy Bay soil profiles on Cretaceous sedimentary rocks, with depths of 90 and 60 cm, respectively.

To our knowledge, our study is one of the first on James Ross Island on the Ulu Peninsula in Antarctica, which deal with the microbial research of deeper part of the permafrost. Furthermore, this is one of the first studies on this topic in Antarctica, in which we examine soil samples from the Mendel 1 core, which had an overall depth of 350 cm and was extracted from the northernmost coastal region of the Ulu Peninsula on James Ross Island, Antarctica. The objective of the study was to combine information from metagenomic data obtained through 16S rRNA gene sequencing and geochemical analyses to study the effect of geochemical properties on microbial composition and diversity and *vice versa.* Although geochemical properties are a key aspect of the study, we recognize that other environmental factors, such as historical thawing events and conditions present during permafrost aggradation, may also play an important role in shaping microbial communities.

2. Materials and methods

2.1. Samples collected from the Mendel 1 core

Eighteen soil and rock samples were collected from the Mendel 1 core (named after the neighbouring Johann Gregor Mendel Czech Antarctic Station) located on the Ulu Peninsula, James Ross Island, Antarctica (63°48′1,44″S, 57°53′1,68″W), during the austral summers in 2016 and 2021 (Fig. 1A). James Ross Island is the largest island in the north-eastern Antarctic Peninsula region (area over 2400 km^2), which is separated from the mainland by the Prince Gustav Channel, which is 12–20 km wide (Davies et al., 2013). Using a core drill with a diameter of 7.5 cm (Fig. 1B), the Mendel 1 core with a total depth of 350 cm was drilled into a Holocene marine terrace and penetrated into the underlying Cretaceous marine sedimentary rocks (deeper than ~ 260 cm) (Mlčoch et al., 2020). Six samples were taken from the current active layer with a total depth of 80 cm and twelve samples from the underlying permafrost with different lithologies (Fig. 1B; Table S1).

2.2. Geochemical properties of the Mendel 1 core samples

Soil texture was analyzed using analytical sieves (0.25; 0.5; 1 and 2 mm) and a Bettersize S3 laser granulometer (Bettersize Instruments, China) by means of optical and laser diffraction for the fraction < 0.25 mm. The results were classified into categories of clay (<0.04 mm); silt (0.04–0.063 mm) and sand (0.063–2.0 mm).

For the subsequent analysis, air-dried material of the <2.0 mm fraction was used. Soil pH and Electrical Conductivity (EC) were measured using 5 g of material in a 1:5 ratio solution with deionised water using an HI9813-6N meter (Hanna Instruments, USA). The elemental composition of soil samples from one sedimentary profile of Mendel 1 core was determined by a hand-held Niton XL5 Plus X-ray fluorescence (XRF) analyzer (Thermo Fisher Scientific, USA), allowing fast and non-destructive scanning of sedimentary profiles with high resolution. Due to the sometimes lower accuracy of XRF compared to other geochemical laboratory methods (e.g. ICP-OES), instrument settings were optimized and attention was paid to sample preparation as stated below (McLaren et al., 2012; Rothwell and Croudace, 2015; Ravansari et al., 2020). Individual dried samples were measured in plastic bags using four positions of filter wheel – High (50 kV), Main (40 kV), Low (12 kV) and Light (6 kV) in Mining mode, for 80 s with each position. According to manufacturers' information, portable XRF analysis of samples in the manufacturer's recommended Mining mode through a plastic or paper bag provides valuable and reliable data (Thermo Fisher Scientific, USA).

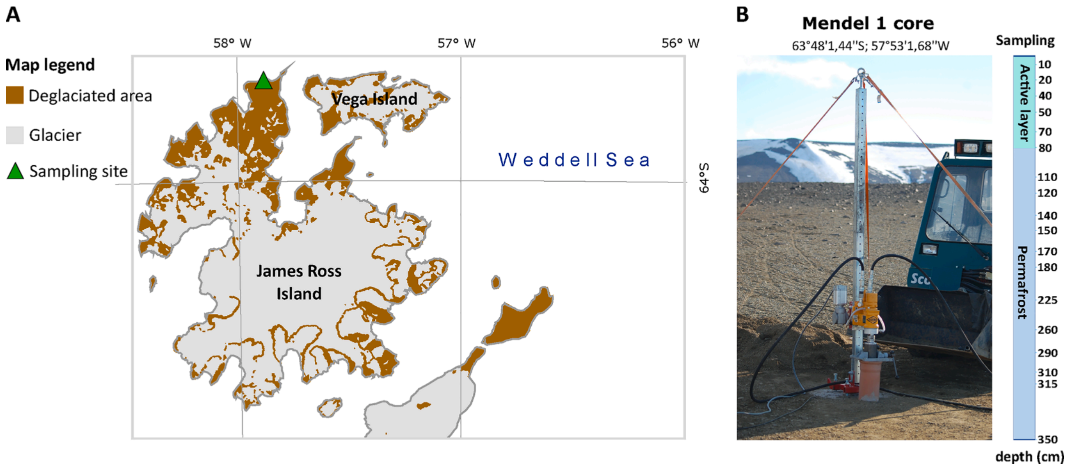


Fig. 1. Soil samples (n = 18) collected from various depths of active layer and permafrost. **A.** Location of the Mendel 1 core, Ulu Peninsula, James Ross Island, Antarctica. **B.** Core drill with a diameter of 7.5 cm.

Before starting the measurement, the instrument was calibrated and a standard (USGS SdAR-M2 Control Sample; Thermo Fisher Scientific) was measured. This standard was also used for the normalization of measured values, according to Eq. 2 (normalization using CRMs) from Parsons et al., (2013). The measurement time was empirically derived from several test samples to correspond to the highest measurement quality. At the same time, it was empirically tested that plastic bags do not distort the measurement results, as they mainly contain light elements (atomic number < 13) that cannot be detected by the device. In this study we used chemical elements – Ag, Al, Cd, Cr, Cu, Fe, Mn, Nb, Ni, Pb, Pd, Sn, Th, Ti, U, V, W, Y, Zn, Zr, Ba, Ca, Sr, K, Rb, P, S, and Si. All the mentioned elements had, at least in the part of the profile, values higher than the detection limit of the instrument and a standard deviation many times lower than the measured values. Organic (TOC) and inorganic (TIC) carbon and sulphur (TS) content were determined with an ELTRA 1000 CS elemental analyzer (Eltra, Germany). Elements with values below the detection limit of both instruments were not included in statistical analysis. Within one profile, the trends of individual elements (rather than their absolute values) and above all the elemental ratios, that better characterize the natural environment (e.g., Kylander et al., 2011; Davies et al., 2015), are more important.

2.2.1. Elemental ratios background

In this study, we use Rb/Sr as a suitable proxy for weathering processes due to the different bond strengths of Rb and Sr in the crystal lattices of minerals during physical and chemical weathering (a higher Rb/Sr ratio indicates a predominance of physical weathering; Dasch, 1969; Xu et al., 2010; Hošek et al., 2014). Fe/Mn ratio was used because of its relation to changes in redox conditions (Boyle, 2001; Naeher et al., 2013; Davies et al., 2015) and also the ability of bacteria to participate in reductive dissolution of iron (Warren and Haack, 2001). We used the Sr/Ba and S/TOC ratios as proxies for salinity. Compared to Ba, Sr is more abundant in the marine environment, and higher values of their ratio are thus correlated with higher salinity (Wei and Algeo, 2020). The S/TOC ratio can also be used, although it has less informative value when distinguishing between marine and brackish environments, and at the same time it is more robust at TOC values higher than 1 %. However, since combining information from multiple sources is always better, we decided to keep this ratio as well (Jaraula et al., 2014; Wei and Algeo, 2020 and references therein). Accuracy and precision of XRF for these elements (based on the Control Sample measurement) varies from <3 % to ~20 % (for Fe and Mn). All the ratios used in this study were used for the comparisons within the profile of Mendel 1 core.

2.3. Soil thermal regime and thaw depth

Soil temperatures were measured with A-class Pt100/8 resistance temperature detectors (EMS Brno, Czech Republic) placed directly in the ground at a depth of 200 cm over the period from 2011 to 2022 at a meteorological station – automatic weather station Johann Gregor Mendel (AWS-JGM) – located 100 m from the Mendel 1 core. We used annual averages calculated from 30-min records. The active layer thickness was measured using mechanical probing in the period 2014–2023. The specific depth was determined from the grid point x80; y60 in the Circumpolar Active Layer Monitoring-South site (CALM-S JGM); which is located approx. 20 m from the Mendel 1 core. The active layer thickness measurement is performed annually around 15th February, when the seasonal maximum occurs (Hrbáček et al., 2023).

2.4. DNA isolation from core samples, preparation of 16S rRNA gene library and sequencing

DNA isolation from Antarctic soil and rock samples was performed using a Pure-Link™ Microbiome DNA Purification Kit (Thermo Fisher Scientific, USA) according to the manufacturer's protocol. Isolated DNA was used as a template in PCR reactions targeting the hypervariable V4 region (EMP 515–806) of the bacterial 16S rRNA gene according to the 16S Metagenomic Sequencing Library Preparation protocol (Illumina, USA) (Table S2). Sequencing was performed using MiSeq Reagent Kits v2 in a MiSeq 2000 sequencer according to the manufacturer's instructions (Illumina, USA).

2.5. Bioinformatics and statistical analysis

The sequencing reads were first evaluated using FastQC v0.11.9 (available at: https://www.bioinformatics.babraham.ac.uk/projects/fastqc/) and then analyzed with the QIIME2 v2019.10.0 pipeline (Bolyen et al., 2019) using the following plugins. Sequencing pools were demultiplexed and trimmed with Cutadapt (Marcel, 2011) and denoised and chimeras removed with DADA2 (Callahan et al., 2016). The representative amplicon sequence variants (ASV) were assigned to taxonomy using the precomputed feature classifier silva-132-99-515-806-nb-classifier.qza (Bokulich et al., 2018) prepared from the Silva v132 16S rRNA database clustered at 99 % identity (Quast et al., 2013). After filtering, the number of sequences in the samples ranged from 2257 to 384,920, with a median of 44,608 reads per sample. Finally, the ASV were aligned with MAFFT (Katoh and Standley, 2013), and the rooted phylogenetic tree was created using FastTree (Price et al., 2010) to generate alpha and beta diversity indexes and rarefaction curves, which were computed with core-metrics-phylogenetic, alpha-rarefaction and emperor plugins (Bolyen et al., 2019). Taxonomic names of bacterial phyla obtained from the Silva version 123 reference database (Quast et al., 2013) were corrected according to the publication by Oren and Garrity (2021).

Statistical analysis of bacterial compositions was performed at the phylum and genus level. The Shannon diversity index (Ortiz-Burgos, 2015) was chosen to estimate the bacterial diversity and uniformity of the microbial community. Non-parametric Mann–Whitney U for multiple testing was used to test the differences between different soil samples. Results were considered significant at $p < 0.05$. A Principal Component Analysis (PCA) plot and Principal Coordinates Analysis (PCoA) plot of the Bray-Curtis distance matrix were used to show the differences in geochemical parameters or bacteria composition between different parts of the core.

3. Results

3.1. Geochemical properties of soil/sediment samples from the Mendel 1 core

Three main sample clusters were identified based on all the measured geochemical parameters and grain size characteristics, according to the PCA plot (Fig. 2A). The first cluster included mainly active layer (A) samples, the second cluster grouped samples from the upper permafrost zone (P1), and the third cluster grouped samples from the deeper permafrost zone (P2). Fig. 2A also shows that higher values of elements such as Ba, Cu, Zn and others were more common in permafrost layers compared to the active layer.

The main factors influencing the formation of these clusters were the differences in the grain size characteristics (Fig. 2B). The sand fraction dominated throughout the Mendel 1 core, with the highest measured sand content (98.3 %) at a core depth of 10 cm. The fraction of clay and silt increased with depth. The first important increase in silt could be found in the lower part of the A zone, and a further significant increase was detected in the lower P2 zone (silt, P1xP2: $p = 0.03$; clay, AxP2: $p = 0.01$).

Geochemical elements mentioned in the Materials and Methods section were measured in all active layer and permafrost samples, and the ratios of selected elements were calculated for each depth (Fig. 2C, Table S1). Rb/Sr ratio was the highest in active layer and decreased sharply below the active layer/permafrost boundary. The Fe/Mn ratio fluctuates down to the depth 180 cm. The Sr/Ba and S/TOC ratios have

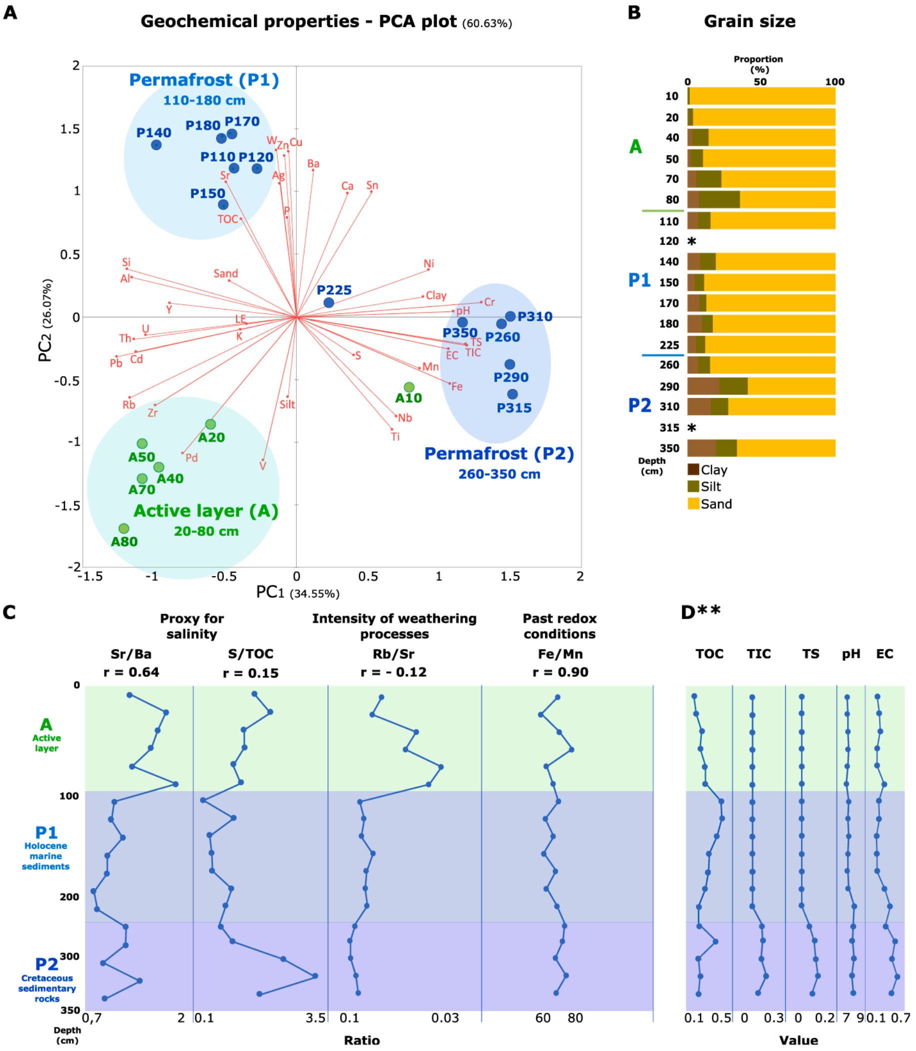


Fig. 2. Geochemical properties and grain-size characteristics of Mendel 1 core. **A.** PCA plot based on all measured geochemical parameters and grain size characteristics. The red arrows indicate the direction and intensity of the original variables in the space of the principal components. **B.** Grain-size analysis of the soil. *Measurements from the 120 and 315 cm layers are missing. **C.** Geochemical ratios. **D.** Distribution of total organic and inorganic carbon, total sulphur, pH and electrical conductivity. **TOC – total organic carbon, TIC – total inorganic carbon, TS – total sulphur, EC – electrical conductivity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

higher values in the A and P2 zones. TOC values were increased in the P1 zone, and TIC, TS, pH and EC mainly in the P2 zone (Fig. 2D).

Strongest relationships (correlations) were described between sand and silt ($r = -0.89$), clay and Rb/Sr ($r = -0.69$), pH and EC ($r = 0.63$), Rb/Sr and pH ($r = -0.75$), and Sr/Ba and Ba ($r = -0.96$). All these correlations are at the level of significance $p < 0.01$.

3.2. *Soil temperature and active layer thickness*

The minimum mean annual soil temperature (−6.5 °C) at a depth of 200 cm at AWS-JGM was recorded in 2011, then gradually increased, with the highest value measured in 2022 (−4.7 °C) (Table 1). Similarly, the lowest annual minimum temperature increased from −9.6 °C (2011) to −6.4 °C (2022). The increase in the maximum annual temperature was less pronounced, from −4.0 °C (2013 and 2014) to −3.6 °C (2022). All of the trends were found statistically significant at levels $p < 0.01$ up to $p < 0.5$ (Table 1).

The active layer thickness also exhibited an increasing trend from 77 cm (2014) to 100 cm (2023). However, the lowest value (75 cm) was recorded in 2019. Notably, the values of active layer thickness obtained in 2016 and 2021 were relatively similar, reaching 84 and 79 cm, respectively.

Table 1
Annual temperatures and their trends for the period 2011 to 2023 measured at a depth of 200 cm at a location 20 m from the Mendel 1 core (AWS-JGM).

Year	Temperature (°C)			Active layer (cm)
	Average	Maximum	Minimum	
2011	−6.5	−3.9	−9.6	–
2012	−6.0	−3.9	−8.5	–
2013	−6.0	−4.0	−9.0	–
2014	−5.6	−4.0	−7.8	77
2015	−6.0	−3.8	−9.7	87
2016	−5.2	−3.9	−7.9	84
2017	−5.2	−3.5	−7.5	85
2018	−5.4	−3.7	−7.8	85
2019	−5.8	−3.8	−8.7	75
2020	−5.7	−3.7	−8.9	93
2021	−5.4	−3.7	−8.6	79
2022	−4.7	−3.6	−6.4	81
2023	–	–	–	100
Average	−5.5	−3.8	−8.0	84.6
Median	−5.6	−3.8	−8.5	84.5
Trend	0.13/yr	0.021/yr	0.199/yr	1.208 (cm/yr)
Significance*	$p < 0.01$	$p < 0.05$	$p < 0.1$	$p < 0.01$

* Trend and statistic calculated using Mann Kendall trend test.

3.3. *Metagenomic composition throughout the Mendel 1 core*

Based on the 16S rRNA metagenomic analysis, the highest bacterial diversity was found in the transient active layer, represented by the deepest sample from the active layer (80 cm), then slowly decreased with depth and significantly decreased in the P2 zone ($p = 0.001$) (Fig. 3). At depths of approximately 80 cm, 120 cm and 310 cm, we detected three main shifts in bacterial composition (Fig. 3). The first shift was mainly due to the active layer/permafrost interface, where *Actinomycetota* ($p = 0.01$), *Acidobacteriota* ($p = 0.01$), *Chloroflexota* ($p = 0.01$), and *Verrucomicrobiota* ($p = 0.02$) were the dominant phyla in the active layer, while *Pseudomonadota* ($p = 0.01$) was the dominant phylum in the permafrost. At the 16S rRNA sequencing genus level, only unassigned *Micrococcaceae* were significantly more abundant in the active layer ($p = 0.001$) (Fig. 3). The second shift was characterized by a significant increase in the total number of bacterial genera with mineral weathering capacity ($p = 0.04$). The group of these mineral weathering bacteria was significantly more prevalent in the permafrost layer compared to the active layer. Bacteria with mineral weathering capacity (*Rhizobium*, *Sphingomonas*, *Achromobacter*, *Janthinobacterium*, *Acinetobacter*, *Acidithiobacillus*, *Pseudomonas*, *Shewanella*, *Bacillus*, *Mycobacterium*, *Staphylococcus*, and *Streptomyces*) were selected according to Uroz et al. (2009) and detected in our set of samples and analyzed for their abundance throughout the Mendel 1 core. The third, deepest shift in P2 layers was characterized by a significant increase in *Bacteroidota* ($p = 0.01$) and *Bacillota* ($p = 0.03$).

3.4. *The relationship between bacterial diversity and soil/sediment geochemistry*

A PCoA plot based on dissimilarity values between bacterial communities at different depths in Mendel 1 core revealed clustering of bacteria associated with the active layer and the permafrost layer – Holocene marine sediments and Cretaceous sedimentary rocks (Fig. 4A). From the PCoA plot it is evident that the different geochemical composition of the Mendel 1 core layers was also reflected in the different composition of the microbiota. The highest sample from the Holocene marine sediment (P110) was clustered close to the active layer – to the last sample from the active layer (A80). Similarly, the highest samples of Cretaceous sediments (P260 and P290) were clustered near the deepest sample of Holocene marine sediments (P225). Different PCoA displays are visible in Fig. 4B-D.

High bacterial diversity, as measured by the Shannon index, correlated with increased sand fraction ($r = 0.61$), the intensity of weathering processes (Rb/Sr; $r = 0.68$) and Sr/Ba ($r = 0.54$) (Fig. 5). The Shannon index further showed a strong negative correlation with TIC ($r = -0.71$), pH ($r = -0.62$), and EC ($r = -0.62$) values. Abundance of different bacterial phyla or genera was positively correlated with sand fraction in particular. The strongest positive correlation between the bacterial phyla abundance and TOC levels was described for "*Cyanobacteria*" ($r = 0.60$) and *Pseudomonadota* ($r = 0.34$). Phylum *Pseudomonadota* positively correlated with Rb/Sr ($r = 0.71$) and Sr/Ba ($r = 0.31$) ratios. Phylum *Acidobacteriota* positively correlated mainly with salinity ratios Sr/Ba ($r = 0.30$) and S/TOC ($r = 0.23$).

4. Discussion

In our study, the highest bacterial diversity was found in the transient active layer, which is the interface between the active layer and the permafrost, where cell accumulation associated with water percolation likely contributes to this diversity. The same can be expected for nutrients that do not 'pass through' the permafrost table barrier. The number of species gradually decreased from the depth of 80 cm similar to other studies in permafrost conducted in maritime Antarctica (Krauze et al., 2021) or Qingai-Tibet Plateau (Wu et al., 2021).

The overall microbiota of the Mendel 1 core was dominated by the phyla *Pseudomonadota* and *Actinomycetota*, which is consistent with observations in other continental and maritime Antarctic soils (Yergeau et al., 2007; Cary et al., 2010; Ganzert et al., 2011; Bajerski and Wagner, 2013; Meier et al., 2019). Higher abundances of *Acidobacteriota* were observed in the active layer compared to permafrost. *Acidobacteria* are one of the dominant microbial communities in Antarctic habitats (Meier et al., 2019; Micenková et al., 2024) and studies also report their significantly higher abundance in the active layer compared to permafrost in e.g., wetlands of the Canadian High Arctic (Wilhelm et al., 2011). Probably due to their broad adaptation to stressors, such as the ability to regulate DNA and protein synthesis, they are highly abundant in the active layer environment (Ward et al., 2009; Li et al., 2022). As the active layer thaws, *Acidobacteriota* and other groups of bacteria can accelerate the decomposition of frozen soil, releasing more carbon dioxide (CO_2) and methane (CH_4) into the atmosphere, which can exacerbate climate change (Graham et al., 2012; Wei et al., 2024; Zhu et al., 2024). According to current knowledge, the phylum *Acidobacteriota* consists of acidophilic bacteria with the ability to produce acids and assist in the soil biogeochemical cycles (Lee et al., 2008). In addition to physical factors, *Acidobacteriota* may also play a significant role in soil

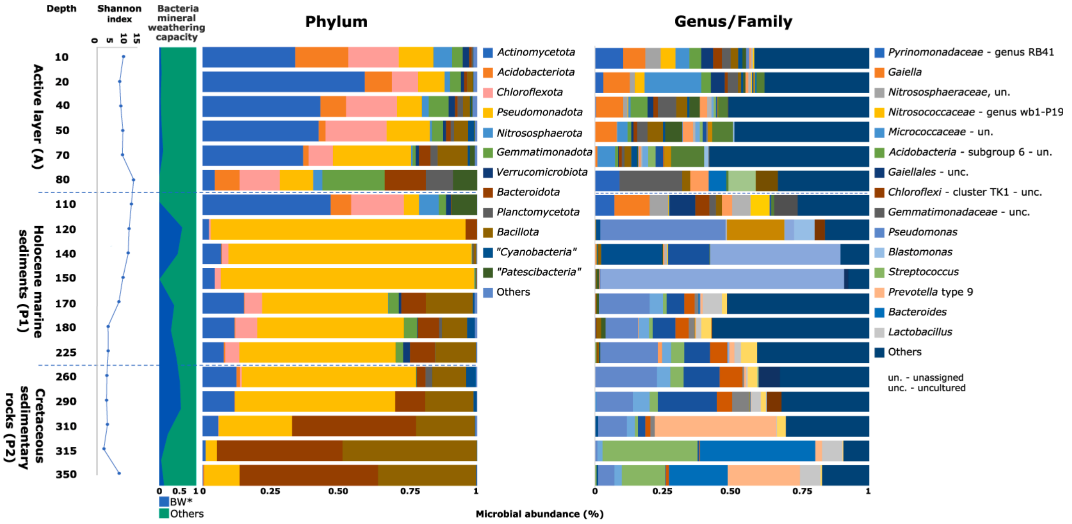


Fig. 3. Metagenomic analysis of the active layer and permafrost of Mendel 1 core, at phylum and genus level. *Bacteria with mineral weathering capacity (BW) – a group of bacteria selected based on the publication Uroz et al., 2009.

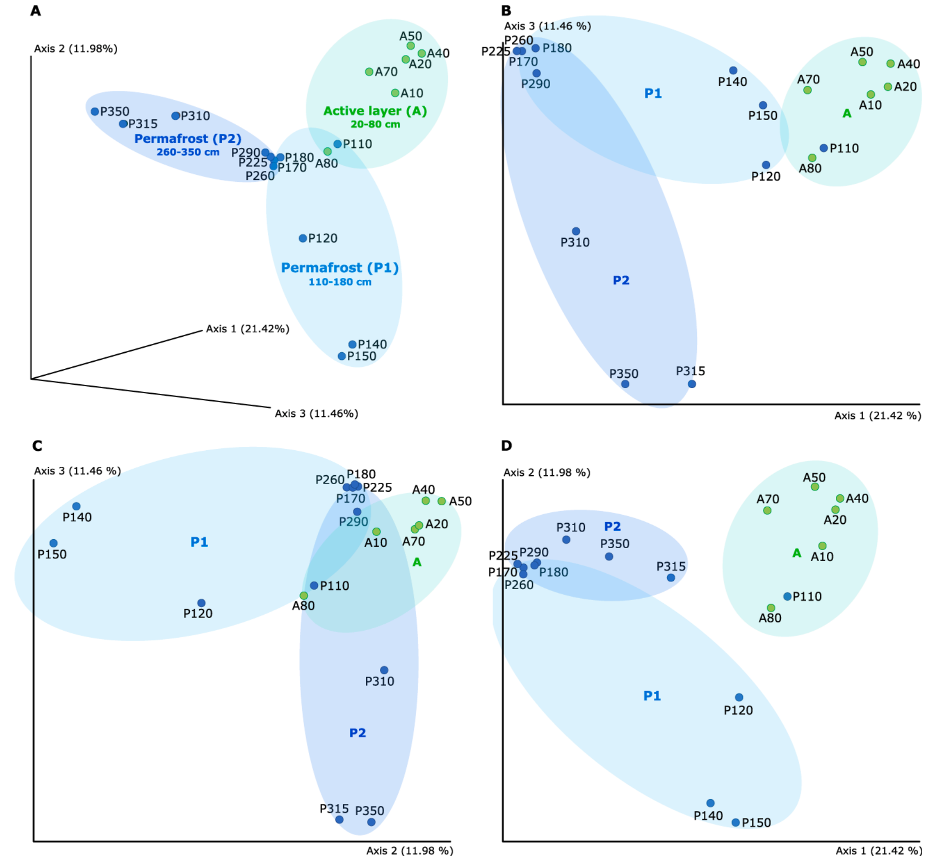


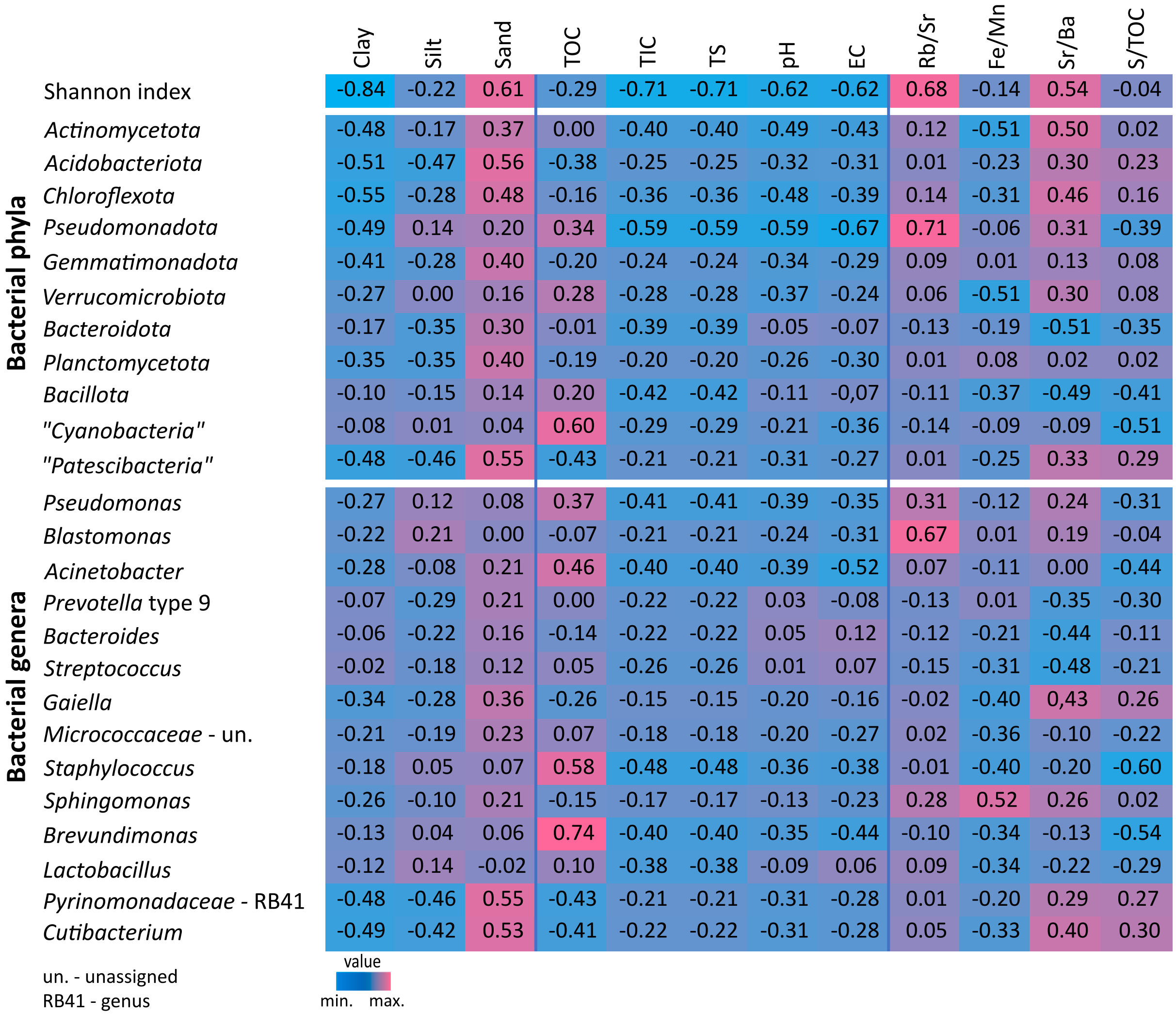
Fig. 4. **A.** Principal coordinates analysis (PCoA) plot for bacterial amplicon sequence variants (ASV) based on Bray-Curtis dissimilarity values between bacterial communities at different depths of the Mendel 1 core. Samples are colored by the depth – green for Active layer (A) samples and blue for Permafrost (P). Elipses are drawn around samples collected from A and P layers – Holocene marine sediment (P1) and Cretaceous sedimentary rocks (P2). **B.** PCoA display: Axis 1 vs Axis 3. **C.** PCoA display: Axis 2 vs Axis 3. **D.** PCoA display: Axis 1 vs Axis 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

changes. They are abundant in acidic, organic-rich tundra soils and are resistant to freeze–thaw cycles (Männistö et al., 2009). In our study, *Acidobacteriota* abundance showed a negative correlation with pH level, with the lowest pH throughout the Mendel 1 core being found in the layers where their abundance was higher.

The abundance of *Pseudomonadota* increased primarily at depths of 120–150 cm within Holocene marine sediments. Bacterium *Pseudomonas* is typically associated with permafrost soils (Hazra et al., 2004; Singh et al., 2017). This genus, known for its efficient ice-nucleating proteins (which can initiate nucleation at −3.8 °C), is particularly well-suited to the temperature conditions at these depths. In our study, the average soil temperature at 2 m depth for permafrost near the Czech Antarctic Station Johann Gregor Mendel between 2011 and 2022 was −5.5 °C, suggesting that these conditions provide favorable environments for the genus *Pseudomonas* and their diverse family of ice nucleator proteins, which play a key role in freezing at temperatures ranging from approximately −2 to −7 °C and in controlling the structure of interfacial water (Roeters et al, 2021; Lukas et al., 2022). Bacterial genera including e.g., *Bacillus*, *Pseudomonas*, *Acinetobacter*, and *Streptomyces* are associated with microbial weathering (Uroz et al., 2009). The relative abundance of these bacteria was higher in the permafrost – in the Holocene marine sediments and upper layers of the Cretaceous sedimentary rocks (depths 110–290 cm). In conclusion, the most widespread mineral weathering bacterium *Pseudomonas*, with its efficient ice nucleating proteins and various alkaline proteases, is perfectly adapted to life in permafrost.

The Fe/Mn ratio can reflect past redox conditions when sediments were in contact with water (Boyle, 2001; Davies et al., 2015). A higher Fe/Mn ratio indicates anoxic conditions, as Mn is more soluble in reducing environments (Boyle, 2001; Naeher et al., 2013). However, this ratio's negative correlation with current bacterial diversity may not represent present redox conditions, as it could differ from the environment when the Fe/Mn signal originated. Redox changes can also affect trace elements (e.g., Cu, Pb, Zn), influencing bacterial communities, though no strong correlation was found in our study. In the active layer, where redox changes due to melting and aeration occur, bacterial activity may accelerate the dissolution of Fe and Mn oxyhydroxides (Warren & Haack, 2001), which may reduce the Fe and Mn values faster than abiotic processes. In our study, a positive correlation between the *Sphingomonas* and Fe/Mn ratio has been described, these bacteria can reduce Fe(III) and belong to the group of manganese oxidizing bacteria (Peng et al., 2016; Cai et al., 2023).

The Sr/Ba and S/TOC ratios serve as proxies for salinity (Wei and Algeo, 2020), and their higher values in Active layer (A) and Cretaceous sedimentary rocks (P2) compared to Holocene marine sediments (P1) of Mendel 1 core may indicate variations in lithology and the chemical composition of those sediments. However, both ratios reflect the nature of the environment in which the sedimentation occurred (marine/brackish/freshwater) as reviewed by Wei and Algeo (2020). The difference between zones P2 and P1 may thus reflect different conditions during their formation. Based on the Sr/Ba ratio, it was a marine environment all the time, but the S/TOC ratio for the middle part of the profile would instead indicate a brackish to freshwater environment. However, in the case of S/TOC, we do not meet the condition of a higher TOC content (>1 %), so its indicative value is also weaker when distinguishing between brackish and marine environments. The Sr/Ba ratio



		Clay	Silt	Sand	TOC	TIC	TS	pH	EC	Rb/Sr	Fe/Mn	Sr/Ba	S/TOC
	Shannon index	-0.84	-0.22	0.61	-0.29	-0.71	-0.71	-0.62	-0.62	0.68	-0.14	0.54	-0.04
Bacterial phyla	*Actinomycetota*	-0.48	-0.17	0.37	0.00	-0.40	-0.40	-0.49	-0.43	0.12	-0.51	0.50	0.02
	Acidobacteriota	-0.51	-0.47	0.56	-0.38	-0.25	-0.25	-0.32	-0.31	0.01	-0.23	0.30	0.23
	Chloroflexota	-0.55	-0.28	0.48	-0.16	-0.36	-0.36	-0.48	-0.39	0.14	-0.31	0.46	0.16
	Pseudomonadota	-0.49	0.14	0.20	0.34	-0.59	-0.59	-0.59	-0.67	0.71	-0.06	0.31	-0.39
	Gemmatimonadota	-0.41	-0.28	0.40	-0.20	-0.24	-0.24	-0.34	-0.29	0.09	0.01	0.13	0.08
	Verrucomicrobiota	-0.27	0.00	0.16	0.28	-0.28	-0.28	-0.37	-0.24	0.06	-0.51	0.30	0.08
	Bacteroidota	-0.17	-0.35	0.30	-0.01	-0.39	-0.39	-0.05	-0.07	-0.13	-0.19	-0.51	-0.35
	Planctomycetota	-0.35	-0.35	0.40	-0.19	-0.20	-0.20	-0.26	-0.30	0.01	0.08	0.02	0.02
	Bacillota	-0.10	-0.15	0.14	0.20	-0.42	-0.42	-0.11	-0,07	-0.11	-0.37	-0.49	-0.41
	"Cyanobacteria"	-0.08	0.01	0.04	0.60	-0.29	-0.29	-0.21	-0.36	-0.14	-0.09	-0.09	-0.51
	"Patescibacteria"	-0.48	-0.46	0.55	-0.43	-0.21	-0.21	-0.31	-0.27	0.01	-0.25	0.33	0.29
Bacterial genera	*Pseudomonas*	-0.27	0.12	0.08	0.37	-0.41	-0.41	-0.39	-0.35	0.31	-0.12	0.24	-0.31
	Blastomonas	-0.22	0.21	0.00	-0.07	-0.21	-0.21	-0.24	-0.31	0.67	0.01	0.19	-0.04
	Acinetobacter	-0.28	-0.08	0.21	0.46	-0.40	-0.40	-0.39	-0.52	0.07	-0.11	0.00	-0.44
	Prevotella type 9	-0.07	-0.29	0.21	0.00	-0.22	-0.22	0.03	-0.08	-0.13	0.01	-0.35	-0.30
	Bacteroides	-0.06	-0.22	0.16	-0.14	-0.22	-0.22	0.05	0.12	-0.12	-0.21	-0.44	-0.11
	Streptococcus	-0.02	-0.18	0.12	0.05	-0.26	-0.26	0.01	0.07	-0.15	-0.31	-0.48	-0.21
	Gaiella	-0.34	-0.28	0.36	-0.26	-0.15	-0.15	-0.20	-0.16	-0.02	-0.40	0,43	0.26
	Micrococcaceae - un.	-0.21	-0.19	0.23	0.07	-0.18	-0.18	-0.20	-0.27	0.02	-0.36	-0.10	-0.22
	Staphylococcus	-0.18	0.05	0.07	0.58	-0.48	-0.48	-0.36	-0.38	-0.01	-0.40	-0.20	-0.60
	Sphingomonas	-0.26	-0.10	0.21	-0.15	-0.17	-0.17	-0.13	-0.23	0.28	0.52	0.26	0.02
	Brevundimonas	-0.13	0.04	0.06	0.74	-0.40	-0.40	-0.35	-0.44	-0.10	-0.34	-0.13	-0.54
	Lactobacillus	-0.12	0.14	-0.02	0.10	-0.38	-0.38	-0.09	0.06	0.09	-0.34	-0.22	-0.29
	Pyrinomonadaceae - RB41	-0.48	-0.46	0.55	-0.43	-0.21	-0.21	-0.31	-0.28	0.01	-0.20	0.29	0.27
	Cutibacterium	-0.49	-0.42	0.53	-0.41	-0.22	-0.22	-0.31	-0.28	0.05	-0.33	0.40	0.30

un. - unassigned
RB41 - genus

Fig. 5. Correlations between bacterial diversity values, abundance of all detected bacterial phyla or the most dominant genera, and geochemical property values and core grain fraction Mendel 1, James Ross Island, Antarctica.

is most influenced by barium, which increases in zone P1. As evidenced by Wei and Algeo (2020), Ba reaches its highest values in the brackish environment. In the P1 zone, significant deposition of TOC could support a shallow marine environment supplied by melting glaciers during the Holocene (Haumann et al., 2016). Lower values of Sr/Ba and S/TOC ratios in zone P1 may not be related to different lithology but to decreased salinity. The higher salinity in the active layer may be related to the blowing of seawater droplets and, thus, the recent addition of salt to the upper layers. The relative abundance of e.g., *Actinomycetota* and *Acidobacteriota* phyla increased in the active layer with typically higher salinity, and these phyla contain a variety of halotolerant species that can survive in these conditions (Chen et al., 2021; Xie and Pathom-Aree, 2021). Alternatively, the lower content of marine salts (Sr/Ba and S/TOC ratios) in the Holocene marine sediments (P1) might be explained by the secondary removal of the chemicals by the percolating freshwater from the thawing of accumulated snow before these layers became part of the permafrost, i.e. early after their uplifting from marine to subaerial position. Such removal affected only unconsolidated Holocene marine sediments, but not the underlying lithified Cretaceous sedimentary rocks. The observed variations in Sr/Ba and S/TOC ratios reflect different depositional environments and salinity conditions over time, with potential influences from salinity fluctuations, freshwater percolation, and microbial adaptation to these conditions.

In Antarctica, glacial activity, the influence of water in its various states (liquid, ice and steam), salt-induced weathering, insolation and wind are mainly responsible for physical weathering, rock disintegration and soil formation (Campbell and Claridge, 1987; Ugolini and Bockheim, 2008), while chemical weathering is very slow due to extremely low temperatures and limited precipitation, or the availability of liquid water (Nezat et al., 2001). The more intense hydrological and biological cycles that result in weak chemical weathering are due to relatively mild temperatures in coastal Antarctica compared to continental Antarctica (Simas et al., 2007; Haus et al., 2016). The values of the Rb/Sr ratio increased sharply at the transient active layer (Shur et al., 2005) in which the highest bacterial diversity was detected. Probably also due to the liquid water, bacteria sink into this layer, which lies above the permafrost table. The predominance of physical weathering is also evidenced by our profile's Rb/Sr record. In the case of chemical weathering, Rb would be strongly bound in the crystal lattice of the mineral (Dasch, 1969; Xu et al., 2010; Hošek et al., 2014), but here, it is leached from the upper layers of the zone A and accumulated at the transition of zones A and P1. It is, therefore, a question whether the higher diversity of bacteria is related to coarser material (predominance of sand in zone A) or rather to the accumulation of weathering products and nutrients originated primarily from the active layer.

The Cretaceous sedimentary rocks exhibited a characteristic decreased diversity of the bacterial community; if any bacteria were present, the predominant genera were those with the ability to weather minerals. By understanding how mineral-weathering bacteria in soil/rock systems are affected by changes in weathering efficiency depending on depth, pattern, and community structure, we can better understand the different roles that bacteria play in mineral weathering, element cycling, and soil formation in different soil/rock environments (Huang et al., 2014).

Analysis of temperature data showed a gradual increase in mean annual permafrost temperature from 2011 to 2023 at a depth of 200 cm. An increasing trend was detected on James Ross Island in previously published data of mean annual active layer temperature at the depths of 5, 50, and 75 cm during the period of 2011 to 2021 (Kaplan Pastíriková et al., 2023). A long-term warming trend accompanied by gradual thawing of the upper permafrost layers and increasing active layer thickness could have several important implications. It may facilitate greater mixing of bacterial species in the deeper soil/rock layers. There is the possibility that species that previously thrived predominantly in the active layer will extend their range to a depth > 100 cm in subsequent years. Similar results when permafrost thawing significantly increased bacterial richness in the active layer were previously reported for soils in the Tibetan Plateau, in the high Arctic, and on the northernmost coast of Alaska (Chen et al., 2017; Schostag et al., 2019; Wu et al., 2018; Ji et al., 2020).

5. Conclusions

In summary, the diversity and abundance of microbial taxa were influenced by the spatial characteristics of geochemical abiotic parameters in all zones of the Mendel 1 core. While weathering processes (Rb/Sr ratio) were more intense in the active layer, the group of bacterial genera capable of mineral weathering (*Pseudomonas*, *Acinetobacter*, *Sphingomonas* and others) increased in the upper zone of the permafrost. The active layer/permafrost interface and the boundary between the Holocene marine sediments and the Cretaceous sedimentary rocks are of critical importance for bacterial composition and diversity. The highest identified diversity in the deepest part of the active layer (transient active layer) suggests that the bacteria here have been gradually cryopreserved, possibly sinking from the upper layers. Given the observed increase in soil temperature at depth and the increase in the thickness of the active layer, it is very likely that in the coming years the thickness of the active layer will be higher, and the original active layer microbiome will be affected by the bacteria currently located in the upper layers of the permafrost.

CRediT authorship contribution statement

Lenka Micenková: Investigation, Writing – review & editing, Writing – original draft, Formal analysis, Visualization. **Martin Kadlec:** Methodology, Data curation, Writing – review & editing. **Ivana Mašlaňová:** Investigation, Writing – review & editing, Methodology, Data curation. **Ivo Sedláček:** Investigation, Writing – review & editing, Supervision, Methodology, Sampling, DNA isolation, Data curation, Project administration. **Pavel Švec:** Writing – review & editing, Supervision, Methodology, Sampling, DNA isolation, Data curation, Conceptualization. **Vojtěch Kovařovic:** Software. **Roman Pantůček:** Writing – review & editing, Supervision, Funding acquisition. **Michaela Kňažková:** Methodology, Data curation. **Daniel Nývlt:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Filip Hrbáček:** Investigation, Writing – review & editing, Supervision, Methodology, Funding acquisition.

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.

Acknowledgements

This work was supported by the CzechPolar2 Research Infrastructure (LM2015078) and the Czech Antarctic Research Programme and the RECETOX Research Infrastructure (LM2018121), both financed by the Ministry of Education, Youth and Sports of the Czech Republic, and the National Institute of Virology and Bacteriology (Programme EXCELES, ID Project LX22NPO5103) - Funded by the European Union - Next Generation EU. The work of MK and FH was supported by Czech Science Foundation project (GM22-28659M).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2024.108694.

References

Alekseev, I., Zverev, A., Abakumov, E., 2020. Microbial communities in permafrost soils of Larsemann Hills, Eastern Antarctica: environmental controls and effect of human impact. Microorganisms 8 (8), 1202. https://doi.org/10.3390/microorganisms8081202.

Altshuler, I., Goordial, J., Whyte, L.G., 2017. Microbial Life in Permafrost. In: Margesin, R. (Ed.), Psychrophiles: from Biodiversity to Biotechnology. Springer, Cham. https://doi.org/10.1007/978-3-319-57057-0_8.

Bajerski, F., Wagner, D., 2013. Bacterial Succession in Antarctic Soils of Two Glacier Forefields on Larsemann Hills. East Antarctica. FEMS Microbiol. Ecol. 85, 128–142. https://doi.org/10.1111/1574-6941.12105.

Bokulich, N.A., Kaehler, B.D., Rideout, J.R., Dillon, M., Bolyen, E., Knight, R., Huttley, G. A., Gregory Caporaso, J., 2018. Optimizing taxonomic classification of marker-gene amplicon sequences with QIIME 2`s q2-feature-classifier plugin. Microbiome. 6 (1), 90. https://doi.org/10.1186/s40168-018-0470-z.

Bolyen, E., Rideout, J.R., Dillon, M.R., Bokulich, N.A., Abnet, C.C., Al-Ghalith, G.A., Alexander, H., Alm, E.J., Arumugam, M., Asnicar, F., 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.

Borzotta, E., Trombotto, D., 2004. Correlation between frozen ground thickness measured in Antarctica and permafrost thickness estimated on the basis of the heat flow obtained from magnetotelluric soundings. Cold Reg. Sci. Technol. 40, 81–96. https://doi.org/10.1016/j.coldregions.2004.06.002.

Boyle, J.F., 2001. Inorganic geochemical methods in palaeolimnology. In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Volume 2: Physical and Geochemical Methods. Kluwer Academic Publishers, Dordrecht, pp. 83–142. https://doi.org/10.1007/0-306-47670-3_5.

Burkert, A., Douglas, T.A., Waldrop, M.P., Mackelprang, R., 2019. Changes in the Active, Dead, and Dormant Microbial Community Structure across a Pleistocene Permafrost Chronosequence. Appl. Environ. Microbiol. 85 (7), e02646–18. https://doi.org/10.1128/AEM.02646-18.

Cai, Y., Yang, K., Qiu, C., Bi, Y., Tian, B., Bi, X., 2023. A Review of Manganese-Oxidizing Bacteria (MnOB): Applications, Future Concerns, and Challenges. Int. J. Environ. Res. Public Health 20 (2), 1272. https://doi.org/10.3390/ijerph20021272.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods 13 (7), 581–583. https://doi.org/10.1038/nmeth.3869.

Campbell, I.B., Claridge, G.G.C., 1987. Chapter 5 Physical Weathering and Rock Disintegration. Developments in Soil Science, Elsevier, Amsterdam, New York. 16, 97–122, doi: 10.1016/S0166-2481(08)70153-3.

Cary, S.C., McDonald, I.R., Barrett, J.E., Cowan, D.A., 2010. On the Rocks: The Microbiology of Antarctic Dry Valley Soils. Nat. Rev. Microbiol. 8, 129–138. https://doi.org/10.1038/nrmicro2281.

Chen, Y.-L., Deng, Y., Ding, J.-Z., Hu, H.-W., Xu, T.-L., Li, F., Yang, G.-B., Yang, Y.-H., 2017. Distinct microbial communities in the active and permafrost layers on the Tibetan Plateau. Microb. Ecol. 26, 6608–6620. https://doi.org/10.1111/mec.14396.

Chen, Y., Zhang, Z., Luo, H., Li, Z., 2021. Salt tolerance of halotolerant bacteria from coastal soils and sediments near saltern field of Hainan Island. China. Arch. Microbiol. 203 (10), 5921–5930. https://doi.org/10.1007/s00203-021-02461-w.

Cowan, D.A., Makhalanyane, T.P., Dennis, P.G., Hopkins, D.W., 2014. Microbial ecology and biogeochemistry of continental Antarctic soils. Front. Microbiol. 5, 154. https://doi.org/10.3389/fmicb.2014.00154.

Dasch, E.J., 1969. Strontium isotopes in weathering profiles, deep-sea sediments, and sedimentary rocks. Geochim. Cosmochim. Acta. 33, 1521–1552. https://doi.org/10.1016/0016-7037(69)90153-7.

Davies, B.J., Glasser, N.F., Carrivick, J.L., Hambrey, M.J., Smellie, J.L., Nývlt, D., 2013. Landscape evolution and ice-sheet behaviour in a semi-arid polar environment: James Ross Island, NE Antarctic Peninsula. In: Hambrey, M.J., Barker, P.F., Barrett, P.J., Bowman, V., Davies, B., Smellie, J.L., Tranter, M. (Eds.), Antarctic Palaeoenvironments and Earth-Surface Processes. Geological Society, London, Special Publications. 381, 353–395.

Davies, S.J., Lamb, H.F., Roberts, S.J., 2015. Micro-XRF Core Scanning in Palaeolimnology: Recent Developments. In: Croudace, I.W., Rothwell, R.G. (Eds.), Micro-XRF Studies of Sediment Cores. Application of non-destructive tool for the environmental sciences. Springer, Dordrecht, pp. 189–226. https://doi.org/10.1007/978-94-017-9849-5_7.

Díaz-Puente, F.J., Schmid, T., Pelayo, M., Rodríguez-Rastrero, M., Herraiz, M.J.S., O'Neill, T., López-Martínez, J., 2021. Abiotic factors influencing soil microbial activity in the northern Antarctic Peninsula region. Sci. Total Environ. 750, 141602. https://doi.org/10.1016/j.scitotenv.2020.141602.

Dziurzynski, M., Gorecki, A., Pawlowska, J., Istel, L., Decewicz, P., Golec, P., Styczynski, M., Poszytek, K., Rokowska, A., Gorniak, D., Dziewit, L., 2023. Revealing the diversity of bacteria and fungi in the active layer of permafrost at Spitsbergen island (Arctic) - Combining classical microbiology and metabarcoding for ecological and bioprospecting exploration. Sci. Total. Environ. 856, 159072. https://doi.org/10.1016/j.scitotenv.2022.159072.

Fukuda, M., Shimokawa, K., Takahashi, N., Sone, T., 1992. Permafrost in Seymour Island and James Ross Island, Antarctic Peninsula region. Geogr. Rev. Jpn. Ser. A65, 124–131.

Ganzert, L., Lipski, A., Hubberten, H.-W., Wagner, D., 2011. The Impact of Different Soil Parameters on the Community Structure of Dominant Bacteria from Nine Different Soils Located on Livingston Island, South Shetland Archipelago, Antarctica, FEMS Microbiol. Ecol. 76, 476–491. https://doi.org/10.1111/j.1574-6941.2011.01068.x.

Garrido-Benavent, I., Pérez-Ortega, S., Durán, J., Ascaso, C., Pointing, S.B., Rodríguez-Cielos, R., Navarro, F., de Los Ríos, A., 2020. Differential Colonization and Succession of Microbial Communities in Rock and Soil Substrates on a Maritime Antarctic Glacier Forefield. Front. Microbiol. 11, 126. https://doi.org/10.3389/fmicb.2020.00126.

Graham, D.E., Wallenstein, M.D., Vishnivetskaya, T.A., Waldrop, M.P., Phelps, T.J., Pfiffner, S.M., Onstott, T.C., Whyte, L.G., Rivkina, E.M., Gilichinsky, D.A., Elias, D. A., Mackelprang, R., VerBerkmoes, N.C., Hettich, R.L., Wagner, D., Wullschleger, S. D., Jansson, J.K., 2012. Microbes in thawing permafrost: the unknown variable in the climate change equation. ISME J. 6 (4), 709–712. https://doi.org/10.1038/ismej.2011.163.

Grillová, L., Sedláček, I., Páchníková, G., Staňková, E., Švec, P., Holochová, P., Micenková, L., Bosák, J., Slaninová, I., Šmajs, D., 2018. Characterization of four Escherichia albertii isolates collected from animals living in Antarctica and Patagonia. J. Vet. Med. Sci. 80, 138–146. https://doi.org/10.1292/jvms.17-0492.

Haumann, F., Gruber, N., Münnich, M., Frenger, I., Kern, S., 2016. Sea-ice transport driving Southern Ocean salinity and its recent trends. Nature 537, 89–92. https://doi.org/10.1038/nature19101.

Haus, N., Wilhelma, K., Bockheim, J., Fournelle, J.B., Miller, M., 2016. A case for chemical weathering in soils of Hurd Peninsula, Livingston Island, South Shetland Islands, Antarctica. Geoderma 263, 185–194. https://doi.org/10.1016/j.geoderma.2015.09.019.

Hazra, A., Saha, M., De, U.K., Mukherjee, J., Goswami, K., 2004. Study of ice nucleating characteristics of *Pseudomonas aeruginosa*. J. Aerosol. Sci. 35, 1405–1414. https://doi.org/10.1016/j.jaerosci.2004.06.075.

Horrocks, C.A., Newsham, K.K., Cox, F., Garnett, M.H., Robinson, C.H., Dungait, J.A.J., 2020. Predicting climate change impacts on maritime Antarctic soils: a space-for-time substitution study. Soil Biol. Biochem. 141, 107682. https://doi.org/10.1016/j.soilbio.2019.107682.

Hošek, J., Pokorný, P., Kubovčík, V., Horáček, I., Žáčková, P., Kadlec, J., Rojik, F., Lisá, L., Bučkuliaková, S., 2014. Late glacial climatic and environmental changes in eastern-central Europe: Correlation of multiple biotic and abiotic proxies from the Lake Švarcenberg, Czech Republic. Palaeogeogr. Palaeoclimatol. Palaeoecol. 396, 155–172. https://doi.org/10.1016/j.palaeo.2013.12.024.

Hrbáček, F., Kňažková, M., Nývlt, D., Láska, K., Mueller, C.W., Ondruch, J., 2017. Active layer monitoring at CALM-S site near J.G.Mendel Station, James Ross Island, eastern Antarctic Peninsula. Sci. Total Environ. 601–602, 987–997. https://doi.org/10.1016/j.scitotenv.2017.05.266.

Hrbáček, F., Oliva, M., Hansen, C., Balks, M., O'Neill, T.A., de Pablo, M.A., Ponti, S., Ramos, M., Vieira, G., Abramov, A., Kaplan Pastíriková, L., Guglielmin, M., Goyanes, G., Francelino, M.R., Schaefer, C., Lacelle, D., 2023. Active layer and permafrost thermal regimes in the ice-free areas of Antarctica. Earth-Sci. Rev. 242, 104458. https://doi.org/10.1016/j.earscirev.2023.104458.

Huang, J., Sheng, X.F., Xi, J., He, L.Y., Huang, Z., Wang, Q., Zhang, Z.D., 2014. Depth-related changes in community structure of culturable mineral weathering bacteria and in weathering patterns caused by them along two contrasting soil profiles. Appl. Environ. Microbiol. 80, 29–42. https://doi.org/10.1128/AEM.02335-13.

Jaraula, C., Siringan, F.P., Klingel, R., Okamoto, T., Maeda, Y., Yokoyama, Y., 2014. Records and causes of Holocene salinity shifts in Laguna de Bay, Philippines. Quarter. Inter. 349, 34–44. https://doi.org/10.1016/j.quaint.2014.08.048.

Jennings, S.J.A., Davies, B.J., Nývlt, D., Glasser, N.F., Engel, Z., Hrbáček, F., Carrivick, J. L., Mlčoch, B., Hambrey, M.J., 2021. Geomorphology of Ulu Peninsula, James Ross Island, Antarctica. J. Maps. 17, 125–139. https://doi.org/10.1080/17445647.2021.1893232.

Ji, M.K., Kong, W.D., Liang, C., Zhou, T.Q., Jia, H.Z., Dong, X.B., 2020. Permafrost thawing exhibits a greater influence on bacterial richness and community structure than permafrost age in Arctic permafrost soils. Cryosphere 14, 3907–3916. https://doi.org/10.5194/tc-14-3907-2020.

Kaplan Pastíriková, L.K., Hrbáček, F., Uxa, T., Láska, K., 2023. Permafrost table temperature and active layer thickness variability on James Ross Island, Antarctic Peninsula, in 2004-2021. Sci. Total Environ. 15 (869), 161690. https://doi.org/10.1016/j.scitotenv.2023.161690.

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol. Biol. Evol. 30 (4), 772–780. https://doi.org/10.1093/molbev/mst010.

Kollár, J., Kopalová, K., Kavan, J., Vrbická, K., Nývlt, D., Nedbalová, L., Stibal, M., Kohler, T.J., 2023. Recently formed Antarctic lakes host less diverse benthic bacterial and diatom communities than their older counterparts. FEMS Microbiol. Ecol. 99, 9, fiad087. https://doi.org/10.1093/femsec/fiad087.

Komárek, J., Nedbalová, L., Hauer, T., 2012. Phylogenetic position and taxonomy of three heterocytous cyanobacteria dominating the littoral of deglaciated lakes, James Ross Island. Antarctica. Polar Biol. 35, 759–774. https://doi.org/10.1007/s00300-011-1123-x.

Kosina, M., Švec, P., Černohlávková, J., Barták, M., Snopková, K., De Vos, P., Sedláček, I., 2016. Description of *Pseudomonas gregormendelii* sp. nov., a Novel Psychrotrophic Bacterium from James Ross Island. Antarctica. Curr. Microbiol. 73, 84–90. https://doi.org/10.1007/s00284-016-1029-5.

Krauze, P., Wagner, D., Yang, S., Spinola, D., Kühn, P., 2021. Influence of prokaryotic microorganisms on initial soil formation along a glacier forefield on King George Island, maritime Antarctica. Sci. Rep. 11, 13135. https://doi.org/10.1038/s41598-021-92205-z.

Kylander, M.E., Ampel, L., Wohlfarth, B., Veres, D., 2011. High-resolution X-ray fluorescence core scanning analysis of Les Echets (France) sedimentary sequence: new insights from chemical proxies. J. Quat. Sci. 26, 109–117. https://doi.org/10.1002/jqs.1438.

Lee, S., Ka, J., Cho, J., 2008. Members of the phylum Acidobacteria are dominant and metaboli-cally active in rhizosphere soil. FEMS Microbiol. Lett. 285, 263–269. https://doi.org/10.1111/j.1574-6968.2008.01232.x.

Li, X., Cui, Y., Ma, D., Song, D., Liu, L., 2022. Vertical distribution of bacterial community diversity in the Greater Khingan Mountain permafrost region. Ecol. Evol. 12 (7), e9106. https://doi.org/10.1002/ece3.9106.

Liang, R., Lau, M., Vishnivetskaya, T., Lloyd, K.G., Wang, W., Wiggins, J., Miller, J., Pfiffner, S., Rivkina, E.M., Onstott, T.C., 2019. Predominance of Anaerobic, Spore-Forming Bacteria in Metabolically Active Microbial Communities from Ancient Siberian Permafrost. Appl. Environ. Microbiol. 85 (15), e00560–19. https://doi.org/10.1128/AEM.00560-19.

Lukas, M., Schwidetzky, R., Eufemio, R.J., Bonn, M., Meister, K., 2022. Toward Understanding Bacterial Ice Nucleation. J. Phys. Chem. B. 126, 1861–1867. https://doi.org/10.1021/acs.jpcb.1c09342.

Männistö, M.K., Tiirola, M., Häggblom, M.M., 2009. Effect of freeze-thaw cycles on bacterial communities of arctic tundra soil. Microb. Ecol. 58, 621–631. https://doi.org/10.1007/s00248-009-9516-x.

Marcel, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet Journal, [S.l.], 17(1), 10-12. doi: 10.14806/ej.17.1.200.

McLaren, T.I., Guppy, C.N., Tighe, M.K., Forster, N., Grave, P., Lisle, L.M., Bennett, J.W., 2012. Rapid, nondestructive total elemental analysis of vertisol soils using portable X-ray fluorescence. Soil Sci. Soc. Am. J. 76 (4), 1436–1445. https://doi.org/10.2136/sssaj2011.0354.

Meier, L.A., Krauze, P., Prater, I., Horn, F., Schaefer, C.E.G.R., Scholten, T., Wagner, D., Mueller, C.W., Kühn, P., 2019. Pedogenic and microbial interrelation in initial soils under semiarid climate on James Ross Island, Antarctic Peninsula region. Biogeosciences 16, 2481–2499. https://doi.org/10.5194/bg-16-2481-2019.

Micenková, L., Sedláček, I., Hrbáček, F., Švec, P., Nývlt, D., Pantůček, R., Mašlaňová, I., 2024. Effect of soil depth on the structure of bacterial composition in the active layer at five geologically distinct sites on James Ross and Vega Islands in Antarctica. Polar. Biol. 47, 295–303. https://doi.org/10.1007/s00300-024-03230-3.

Mlčoch, B., Nývlt, D., Mixa, P., 2020. Geological map of James Ross Island - Northern Part. 1: 25 000, Czech Geological Survey. Praha.

Naeher, S., Gilli, A., North, R.P., Hamann, Y., Schubert, C.J., 2013. Tracing bottom water oxygenation with sedimentary Mn/Fe ratios in Lake Zurich, Switzerland. Chem. Geol. 352, 125–133. https://doi.org/10.1016/j.chemgeo.2013.06.006.

Nezat, A.C., Lyons, W.B., Welch, K.A., 2001. Chemical weathering in streams of a polar desert (Taylor Valley, Antarctica). GSA Bull. 113, 1401–1408. https://doi.org/10.1130/0016-7606(2001)113<1401:CWISOA>2.0.CO;2.

Núñez-Montero, K., Barrientos, L., 2018. Advances in Antarctic Research for Antimicrobial Discovery: A Comprehensive Narrative Review of Bacteria from Antarctic Environments as Potential Sources of Novel Antibiotic Compounds Against Human Pathogens and Microorganisms of Industrial Importance. Antibiotics (Basel) 7, 90. https://doi.org/10.3390/antibiotics7040090.

Nývlt, D., Braucher, R., Engel, Z., Mlčoch, B., team, A.S.T.E.R., 2014. Timing of the northern Prince Gustav Ice Stream retreat and the deglaciation of northern James Ross Island, Antarctic Peninsula during the last glacial–interglacial transition. Quat. Res. 82, 441–449. https://doi.org/10.1016/j.yqres.2014.05.003.

Obu, J., 2021. How Much of the Earth's Surface is Underlain by Permafrost? J. Geophys. Res. Earth Surf. 126, e2021JF006123. https://doi.org/10.1029/2021JF006123.

Oren, A., Garrity, G.M., 2021. Valid publication of the names of forty-two phyla of prokaryotes. Int. J. Syst. Evol. Microbiol. 71, 005056. https://doi.org/10.1099/ijsem.0.005056.

Ortiz-Burgos, S., 2015. Shannon-Weaver Diversity Index. J. Kennish (Ed.), Encyclopedia of estuaries. Encyclopedia of Earth sciences series. Springer, Dordrech.

Pantůček, R., Sedláček, I., Indráková, A., Vrbovská, V., Mašlaňová, I., Kovařovic, V., Švec, P., Králová, S., Krištofová, L., Kekláková, J., Petráš, P., Doškař, J., 2018. Staphylococcus edaphicus sp. nov., Isolated in Antarctica, Harbors the mecC Gene and Genomic Islands with a Suspected Role in Adaptation to Extreme Environments. Appl. Environ. Microbiol. 84, e01746-17. https://doi.org/10.1128/AEM.01746-17.

Parsons, C., Margui Grabulosa, E., Pili, E., Floor, G.H., Roman-Ross, G., Charlet, L., 2013. Quantification of trace arsenic in soils by field-portable X-ray fluorescence spectrometry: considerations for sample preparation and measurement conditions. J. Hazard. Mater. 262, 1213–1222. https://doi.org/10.1016/j.jhazmat.2012.07.001.

Peng, Q.A., Shaaban, M., Wu, Y.P., Hu, R.G., Wang, B.Y., Wang, J., 2016. The diversity of iron reducing bacteria communities in subtropical paddy soils of China. Appl. Soil Ecol. 101 (4), 20–27. https://doi.org/10.1016/j.apsoil.2016.01.012.

Price, M.N., Dehal, P.S., Arkin, A.P., 2010. FastTree 2–approximately maximum-likelihood trees for large alignments. PLoS One 5 (3), e9490. https://doi.org/10.1371/journal.pone.0009490.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41, D590–D596. https://doi.org/10.1093/nar/gks1219.

Ravansari, R., Wilson, S.C., Tighe, M., 2020. Portable X-ray fluorescence for environmental assessment of soils: Not just a point and shoot method. Environ. Int. 134, 105250. https://doi.org/10.1016/j.envint.2019.105250.

Roeters, S.J., Golbek, T.W., Bregnhøj, M., Drace, T., Alamdari, S., Roseboom, W., Kramer, G., Šantl-Temkiv, T., Finster, K., Pfaendtner, J., Woutersen, S., Boesen, T., Weidner, T., 2021. Ice-nucleating proteins are activated by low temperatures to control the structure of interfacial water. Nat. Commun. 12 (1), 1183. https://doi.org/10.1038/s41467-021-21349-3.

Rothwell, R.G., Croudace, I.W., 2015. Micro-XRF Studies of Sediment Cores: A Perspective on Capability and Application in the Environmental Sciences. In: Croudace, I.W., Rothwell, R.G. (Eds.), Micro-XRF Studies of Sediment Cores. Application of non-destructive tool for the environmental sciences. Springer, Dordrecht, p. 656.

Schostag, M., Prieme, A., Jacquiod, S., Russel, J., Ekelund, F., Jacobsen, C.S., 2019. Bacterial and protozoan dynamics upon thawing and freezing of an active layer permafrost soil. ISME J. 13, 1345–1359. https://doi.org/10.1038/s41396-019-0351-x.

Sedláček, I., Králová, S., Kýrová, K., Mašlaňová, I., Busse, H.J., Staňková, E., Vrbovská, V., Němec, M., Barták, M., Holochová, P., Švec, P., Pantůček, R., 2017. Red-pink pigmented *Hymenobacter coccineus* sp. nov., *Hymenobacter lapidarius* sp. nov. and *Hymenobacter glacialis* sp. nov., isolated from rocks in Antarctica. Int. J. Syst. Evol. Microbiol. 67, 1975–1983. https://doi.org/10.1099/ijsem.0.001898.

Sedláček, I., Pantůček, R., Holochová, P., Králová, S., Staňková, E., Vrbovská, V., Šedo, O., Švec, P., Busse, H.J., 2019. *Hymenobacter humicola* sp. nov., isolated from soils in Antarctica. Int. J. Syst. Evol. Microbiol. 69, 2755–2761. https://doi.org/10.1099/ijsem.0.003555.

Sedláček, I., Pantůček, R., Zeman, M., Holochová, P., Šedo, O., Staňková, E., Švec, P., Králová, S., Vídeňská, P., Micenková, L., Korpole, S., Lal, R., 2020. *Hymenobacter terrestris* sp. nov. and *Hymenobacter lapidiphilus* sp. nov., isolated from regoliths in Antarctica. Int. J. Syst. Evol. Microbiol. 70, 6364–6372. https://doi.org/10.1099/ijsem.0.004540.

Shur, Y., Hinkel, K.M., Nelson, F.E., 2005. The transient layer: Implications for geocryology and climate-change science. Permafrost Periglac. 16, 5–17. https://doi.org/10.1002/ppp.518.

Simas, F., Schaefer, C., Melo, V., Albuquerque-filho, M., Michel, R., Pereira, V., Gomes, M., Da Costa, L., 2007. Ornithogenic Cryosols from Maritime Antarctica: phosphatization as a soil forming process. Geoderma 138, 191–203. https://doi.org/10.1016/j.geoderma.2006.11.011.

Singh, P., Singh, S.M., Singh, R.N., Naik, S., Roy, U., Srivastava, A., Bölter, M., 2017. Bacterial communities in ancient permafrost profiles of Svalbard. Arctic. J. Basic Microbiol. 57, 1018–1036. https://doi.org/10.1002/jobm.201700061.

Strunecký, O., Elster, J., Komárek, J., 2010. Phylogenetic relationships between geographically separate *Phormidium* cyanobacteria: is there a link between north and south polar regions? Polar. Biol. 33, 1419–1428. https://doi.org/10.1007/s00300-010-0834-8.

Strunecký, O., Elster, J., Komárek, J., 2012. Molecular clock evidence for survival of Antarctic cyanobacteria (Oscillatoriales, *Phormidium autumnale*) from Paleozoic times. FEMS Microbiol. Ecol. 82, 482–490. https://doi.org/10.1111/j.1574-6941.2012.01426.x.

Ugolini, F., Bockheim, J., 2008. Antarctic soils and soil formation in a changing environment: a review. Geoderma 144, 1–8. https://doi.org/10.1016/j.geoderma.2007.10.005.

Uroz, S., Calvaruso, C., Turpault, M.P., Frey-Klett, P., 2009. Mineral weathering by bacteria: ecology, actors and mechanisms. Trends Microbiol. 17, 378–387. https://doi.org/10.1016/j.tim.2009.05.004.

Waldrop, M.P., Chabot, C.L., Liebner, S., Holm, S., Snyder, M.W., Dillon, M., Dudgeon, S.R., Douglas, T.A., Leewis, M.C., Walter Anthony, K.M., McFarland, J.W., Arp, C.D., Bondurant, A.C., Taş, N., Mackelprang, R., 2023. Permafrost microbial communities and functional genes are structured by latitudinal and soil geochemical gradients. ISME J. 17 (8), 1224–1235. https://doi.org/10.1038/s41396-023-01429-6.

Ward, N.L., Challacombe, J.F., Janssen, P.H., Henrissat, B., Coutinho, P.M., Wu, M., Xie, G., Haft, D.H., Sait, M., Badger, J., Barabote, R.D., Bradley, B., Brettin, T.S., Brinkac, L.M., Bruce, D., Creasy, T., Daugherty, S.C., Davidsen, T.M., DeBoy, R.T., Detter, J.C., Dodson, R.J., Durkin, A.S., Ganapathy, A., Gwinn-Giglio, M., Han, C.S., Khouri, H., Kiss, H., Kothari, S.P., Madupu, R., Nelson, K.E., Nelson, W.C., Paulsen, I., Penn, K., Ren, Q., Rosovitz, M.J., Selengut, J.D., Shrivastava, S., Sullivan, S.A., Tapia, R., Thompson, L.S., Watkins, K.L., Yang, Q., Yu, C., Zafar, N., Zhou, L., Kuske, C.R., 2009. Three genomes from the phylum Acidobacteria provide insight into the lifestyles of these microorganisms in soils. Appl. Environ. Microbiol. 75 (7), 2046–2056. https://doi.org/10.1128/AEM.02294-08.

Warren, L.A., Haack, E.A., 2001. Biogeochemical controls on metal behavior in freshwater environments. Earth Sci. Rev. 54, 261–320. https://doi.org/10.1016/S0012-8252(01)00032-0.

Wei, W., Algeo, T.J., 2020. Elemental proxies for paleosalinity analysis of ancient shales and mudrocks. Geochim. Cosmochim. Acta. 287, 341–366. https://doi.org/10.1016/j.gca.2019.06.034.

Wei, L., Wang, Y., Li, N., Zhao, N., Xu, S., 2024. Bacteria-Like Gaiella Accelerate Soil Carbon Loss by Decomposing Organic Matter of Grazing Soils in Alpine Meadows on the Qinghai-Tibet Plateau. Microb. Ecol. 87 (1), 104. https://doi.org/10.1007/s00248-024-02414-y.

Wilhelm, R.C., Niederberger, T.D., Greer, C., Whyte, L.G., 2011. Microbial diversity of active layer and permafrost in an acidic wetland from the Canadian High Arctic. Can. J. Microbiol. 57 (4), 303–315. https://doi.org/10.1139/w11-004.

Wu, M.H., Chen, S.Y., Chen, J.W., Xue, K., Chen, S.L., Wang, X.M., Chen, T., Kang, S.C., Rui, J.P., Thies, J.E., Bardgett, R.D., Wang, Y.F., 2021. Reduced microbial stability in the active layer is associated with carbon loss under alpine permafrost degradation. Proc. Natl. Acad. Sci. USA 118, e2025321118. https://doi.org/10.1073/pnas.2025321118.

Wu, X., Xu, H., Liu, G., Zhao, L., Mu, C., 2018. Effects of permafrost collapse on soil bacterial communities in a wet meadow on the northern Qinghai–Tibetan Plateau. BMC Ecol. 18, 27. https://doi.org/10.1186/s12898-018-0183-y.

Wynn-Williams, D.D., 1990. Ecological aspects of Antarctic microbiology. Adv. Microb. Ecol. 11, 71–146. https://doi.org/10.1007/978-1-4684-7612-5_31990.

Xie, F., Pathom-Aree, W., 2021. Actinobacteria From Desert: Diversity and Biotechnological Applications. Front. Microbiol. 12, 765531. https://doi.org/10.3389/fmicb.2021.765531.

Xu, H., Liu, B., Wu, F., 2010. Spatial and temporal variations of Rb/Sr ratios of the bulk surface sediments in Lake Qinghai. Geochem. Trans. 11 (3), 1–8. https://doi.org/10.1186/1467-4866-11-3.

Xue, Y., Jonassen, I., Øvreås, L., Taş, N., 2019. Bacterial and Archaeal Metagenome-Assembled Genome Sequences from Svalbard Permafrost. Microbiol. Resour. Announc. 8. https://doi.org/10.1128/MRA.00516-19.

Yergeau, E., Newsham, K.K., Pearce, D.A., Kowalchuk, G.A., 2007. Patterns of Bacterial Diversity across a Range of Antarctic Terrestrial Habitats. Environ. Microbiol. 9, 2670–2682. https://doi.org/10.1111/j.1462-2920.2007.01379.x.

Zhu, X., Jia, G., Xu, X., 2024. Accelerated rise in wildfire carbon emissions from Arctic continuous permafrost. Sci. Bull. (Beijing) 69 (15), 2430–2438. https://doi.org/10.1016/j.scib.2024.05.022.