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Soil cover shapes organic matter pools and microbial communities in soils of maritime Antarctica

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ABSTRACT

Bryophytes and biological soil crusts (biocrusts) are the two major biological soil cover types of maritime Antarctica and play a crucial role for key ecosystem functions in the barely vegetated and little developed soils. Besides their profound impacts on nutrient cycling, they also provide habitats and activity hotspots for unique soil microbial communities. Yet, the effects of biological soil cover on the physical and chemical soil environment and belowground microbial communities have not been comprehensively studied in this fragile ecosystem.

We here address the research question how biocrusts and mosses shape the quantity and structure of the soil organic matter pool, and the activity and composition of subjacent microbial communities. Towards this end, we sampled soils under two common, but physiologically distinct moss species, *Polytrichastrum alpinum* and *Sanionia unicinata*, and adjacent biological soil crusts at two sites on Deception Island, South Shetland Islands.

We found that biocrusts and mosses differentially influenced central soil properties and subjacent soil microbial communities. All major SOM compound groups (carbohydrates, aromatics and phenols, lipids, N-containing polymers) as well as microbial biomass were more abundant in soil under biocrusts. However, microbial mass-specific growth rates were higher in soil under mosses. Our results showed moss-species-specific effects in addition to effects of soil cover type, as *P. alpinum* affected the activity and structure of soil microbial communities and the composition of soil organic matter stronger than *S. unicinata*.

Our study highlights the interconnectedness between soil cover and soil biogeochemistry, which is crucial for deepening our understanding of belowground functioning in Antarctic soils. This linkage is of particular importance in the context of ongoing rapid climate change on the Antarctic Peninsula, as future shifts in the distribution and abundance of soil cover may substantially impact multiple soil processes in this vulnerable ecosystem.

1. Introduction

In Antarctica, harsh environmental conditions such as sub-zero temperatures, poorly developed soils, strong winds, and radiative forces (Robinson et al., 2003) impose severe pressure on the sparse vegetation (Jung et al., 2018). Ice-free surfaces in continental and maritime Antarctica are mostly dominated by non-vascular cryptogamic vegetation (i.e., mosses, lichens, hornworts, liverworts, green algae, cyanobacteria) (Olech, 2002; Singh et al., 2018; Zúñiga-González et al., 2016), and biological soil crusts (biocrusts) (Weber et al., 2022). Mosses represent an essential part of the polar flora, as they can persist under requirements that are too hostile for vascular plants. They can endure frequently occurring forms of stress such as freezing or desiccation with the help of specific growth habits or via entering a state of suspended metabolic activity (Oliver and Bewley, 1996; Proctor et al., 2007). Other important primary producers in polar regions are biological soil crusts (Rippin et al., 2018), often recognized as ecosystem engineers with important pioneering functions (Elbert et al., 2012; Jung et al., 2018).

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Biocrusts are symbiotic communities comprised by an assortment of photoautotrophic and heterotrophic organisms from all three domains of life (Weber et al., 2022). While bacteria, archaea, and fungi contribute to the heterotrophic component of biocrusts (Belnap et al., 2001; Bowker et al., 2018), the photoautotrophic component is composed of cyanobacteria and non-vascular cryptogams (Pushkareva et al., 2016). Mosses can hence either occur as autonomous vegetation cover (Bramley-Alves et al., 2014; Weber et al., 2022), or as photoautotrophic constituent within the consortium of biocrust organisms (Belnap, 2006, Seppelt et al., 2016). The key photoautotrophic microbial groups of polar biocrusts are cyanobacteria and green algae, which are also the dominant photobionts of lichens (Pushkareva et al., 2016). In the ice-free habitats of Antarctica, biocrusts dominated by soil algae and cyanobacteria are typically considered the first colonizers during early soil development, whereas moss-dominated biocrust consortia are more associated with later successional stages (Belnap et al., 2016; Rybalka et al., 2023). Nevertheless, it is mostly the combination of microclimatic and edaphic factors that determine the identity, composition, and spatially patchy distribution of the prevailing moss and biocrust communities (Hughes et al., 2006; Melick and Seppelt, 1997; Weber et al., 2022).

Biological soil crusts and cryptogamic vegetation are known to influence soil processes directly and indirectly, for example they can protect the soil surface against wind and water erosion (Belnap et al., 2001), add to soil surface stabilization via aggregation (Weber et al., 2022), shape the soil microclimate (Xiao et al., 2019, 2016), or modify soil pH (Belnap et al., 2001). Moreover, they are important determinants of soil carbon and nutrient contents (Benavent-González et al., 2018; Cheng et al., 2021; Elbert et al., 2012). This effect might be especially pronounced in Antarctic soils, where biological soil crusts and mosses represent the dominant form of primary producers in the absence of vascular plants (Turetsky, 2003) and are hence the main contributors to organic matter buildup. They create small islands of fertility (Benavent-González et al., 2018) within oligotrophic soils like in Antarctica, leading to the establishment of favorable habitats (Rippin et al., 2018) for a variety of (micro-) organisms (Gerson, 1982; Lindo and Gonzalez, 2010; Xiao and Veste, 2017). Such resulting activity hotspots (Turetsky, 2003; Weber et al., 2022) are often accompanied by an increased food web complexity and characterized by enhanced microbial organic matter turnover and nutrient cycling (Benavent-González et al., 2018; Liu et al., 2014). Hence, the unique microbial communities of Antarctic soils are directly and indirectly shaped by their overlying biological cover (Belnap et al., 2001).

In Antarctic soils, mosses and biocrusts likely play a critical role as carbon and nutrient source for the energy and nutrient limited subjacent microbial communities. For example, pulses of labile organic compounds that could prime microbial communities in a similar manner to root exudation in vascular plants, have been shown to leach from moss biomass into the surrounding soils as consequence of drying-rewetting or freeze–thaw cycles (Slate et al., 2019; Wilson and Coxson, 1999). Extracellular polymeric substances (EPS) derived from biocrust microorganisms (Rossi et al., 2018) can also provide essential inputs of polysaccharides, proteins, lipids and nucleic acids (Flemming, 2016). An especially important role for biogeochemical cycling in Antarctic soils is attributed to cyanobacteria (Makhalanyane et al., 2015). Besides being a major constituent of biocrusts, cyanobacteria can also occur in association with certain bryophyte groups, e.g., feather mosses (Stewart et al., 2011, Warshan et al., 2017). The phylum provides substantial C- inputs into the soil, which is essential for early soil development and soil stability (Belnap and Lange, 2001). Cyanobacterial occurrence also considerably mediates how mosses and biocrusts affect soil N- availabilities (Elbert et al., 2012). Via their ability of N_2-fixation, cyanobacteria can increase N- inputs, which is especially beneficial in N-scarce and pristine environments (Alvarenga and Rousk, 2022; Elbert et al., 2012). Yet, the fate of fixed nitrogen might vary substantially between the two soil cover types, as mosses mainly retain nutrients within their biomass for rather long timeframes (Koranda and Michelsen, 2021; Rousk et al., 2017, 2014), while biocrusts release it to the soil environment within days or weeks (Belnap, 2001; Elbert et al., 2012; Rousk et al., 2016).

However, biocrusts and mosses also potentially exert negative effects on subjacent soil microbial communities. For example, moss litter is often associated with slow decomposition rates as many bryophytes are known to contain a range of bioactive compounds such as antioxidants, antibiotics, other substances with anti-microbial properties, lignin-similar compounds, or specific cell wall polysaccharides (Turetsky, 2003, Xie and Lou, 2009, Cianciullo et al., 2022). Since also biocrusts are known to synthesize various secondary metabolites, including antimicrobial agents (Rippin et al., 2018), antagonistic interactions between biocrusts and associated microbial communities might occur in a similar manner (Van Goethem et al., 2021).

The impacts of mosses and biocrusts on soil biogeochemical processes are widely acknowledged (Elbert et al., 2012; Turetsky, 2003) and investigated in a variety of ecosystems, with a substantial proportion of studies being focused on e.g., non-polar deserts, mediterranean drylands, or the Arctic (i.a., Angel and Conrad, 2013; Gornall et al., 2007; Heindel et al., 2019; Maestre et al., 2013; Maier et al., 2018; Mugnai et al., 2020; Muñoz-Martín et al., 2019; Rousk et al., 2013; Turetsky et al., 2012). Yet, despite their great ecological relevance in Antarctica, moss- and biocrust- impacts remain comparatively understudied in the remote ecosystem. Due to their dominance in the prevailing flora and their substantial role for organic matter inputs, their effects on microbial communities and soil functions might be more pronounced in the little developed soils of Antarctica than in other ecosystems with more developed soils and more complex vegetation communities. Albeit significant advances have been made in characterizing the identity, diversity and functioning of biocrust- (i.a., Jung et al., 2018; Pushkareva et al., 2024, 2022; Rippin et al., 2018; Steven et al., 2013) and moss-associated microbial communities in polar regions (i.a., Holland-Moritz et al., 2021, 2018; Kauserud et al., 2008; Park et al., 2013; Tveit et al., 2020), it remains comparatively less well investigated how biocrusts and mosses might impact their underlain soil microbial communities (Koranda and Michelsen, 2021, Navarro-Noya et al., 2014). As global climate warming will likely lead to a retreat in the ice-covered area of Antarctica (Lee et al., 2017), new habitats for colonization by existing species will be exposed (Convey et al., 2009), and shifts in abundance- and distribution patterns of mosses and biocrusts might occur (Benavent-González et al., 2018). A better understanding of how different biological soil cover types affect the functioning and development of Antarctic soils is therefore urgently needed.

The overarching research question of the present study was to elucidate how mosses and biocrusts, the two most common biological ground cover types in the ice-free areas of Antarctica influence the structure and activity of the subjacent soil microbial communities, as well as the chemical composition of the soil organic matter (SOM) pool. Additionally, we explored possible species-specific effects of the two most common moss species in maritime Antarctica (Zúñiga-González et al., 2016), *Polytrichastrum alpinum* (Hedw.) G. L. Smith and *Sanionia unicinata* (Hedw.) Loeske, on the subjacent belowground functions and microbial communities. Despite acknowledged species-specific connections of vascular plants with belowground functioning, the role of bryophyte identity is clearly understudied (Jonsson et al., 2015).

2. Materials and methods

2.1. Climatic and edaphic background of Deception Island

Deception Island (62°57′S; 60°38′W), located in the Bransfield Strait, South Shetland Islands, has a polar oceanic climate, that is characterized by relatively high precipitation rates and frequent summer rainfalls. The annual temperature range is moderate, at a mean annual temperature (MAT) of −3° C at sea level (Ramos et al., 2017). Deception Island is

among the regions with severe atmospheric warming in Antarctica (+3 °C MAT since 1950) (Marshall et al., 2002; Meredith and King, 2005). As an active stratovolcano, its surface is not only covered by glaciers, but the island also harbors volcanoclastic soils with development of ice-rich permafrost even at beach level. The active layer can reach depths of up to ~ 30 cm (Goyanes et al., 2014). Ice-free areas are mainly located on coastal strips and rocky ridges and allow the establishment of bryophyte and biocrust communities (Benavent-González et al., 2018).

2.2. Sites, soil sampling approach and sample storage

Soil samples were collected in January 2018 at two sites with contrasting nutrient availability. "Fumarole Bay" (S62° 57.940' W60° 42.875') is a rather sheltered and nutrient rich area in the southwest, while "Telephone Bay" further north (S62° 55.231' W60° 40.108') of the island is a site on an exposed crest with a poorer nutrient status.

At both sites, we sampled soils under vital moss cover and under patches of biological soil crusts (see Supplementary Materials and Methods). The biocrusts consisted of lichen, algae, fungal and bacterial biomass, together with senescent biomass of the occurring moss species. The mosses which we considered in our study were *Polytrichastrum alpinum* and *Sanionia unicinata*, two often dominating and very common, yet taxonomically and physiologically distinct species in maritime Antarctica (Pizarro et al., 2019; Zúñiga-González et al., 2016). Due to their adaptations to different habitats, the two species did not occur together. *Polytrichastrum alpinum* grew in vital, dense, and high-grown moss turfs, and was sampled at Fumarole Bay. *Sanionia uncinata* formed a rather sparse cover of slow growing, prostrate moss carpets, and was sampled in Telephone Bay.

We collected samples from four randomly selected blocks within an area of approximately 0.2 ha at each site, obtaining in total 16 samples (2 sites à 4 replicate blocks with each moss- and biocrust cover). The selected patches covered by the dominant moss species of the respective site plus biocrusts were in adjacent vicinity to another to minimize possible effects of small-scale differences in topography, soil characteristics or disturbance history. We collected the top 2 cm of mineral soil underneath both soil cover types to ensure their direct influence on the subjacent soil layer. We used sterilized equipment for soil sampling and for removing the respective soil cover as precisely as possible. Samples were kept cool at field temperatures until further use, samples for measuring microbial growth and respiration rates were processed on the same day. Soils used for DNA extraction were immediately preserved in RNAlater™ Stabilization Solution (ThermoFisher Scientific).

2.3. Investigated moss species

As an acrocarpous species, *Polytrichastrum alpinum* is characterized by an erect, unbranched growth habit forming open moss turfs and cushions, preferring well drained soils (Zúñiga-González et al., 2016; British Bryological Society, 2022a). The species is known to be endohydric, i.e., has rudimentary conductive tissues, and cuticular waxes to prevent water loss from leaves (Grimingham and Smith, 1971). Furthermore, it is characterized by rhizoids that increase stability in the substrate (Odu, 1978) and facilitate water-and nutrient-uptake from the soil (Ayres et al., 2006).

Sanionia unicinata is a pleurocarpous species exhibiting a prostrate and branched growth form, spreading into dense moss carpets (Zúñiga-González et al., 2016; British Bryological Society, 2022b). The species is ectohydric, i.e., water uptake is mediated via the whole plant surface (Grimingham and Smith, 1971). It is considered a colonizer as it can establish on hard substrates, regenerates quickly after disturbances, and grows fast (Davis, 1981; Robinson et al., 2003). Associations with epiphytic N_2-fixing cyanobacteria (Benavent-González et al., 2018), as commonly observed with the order of feather mosses (Rousk et al., 2013) might also benefit its pioneering lifestyle (Pizarro et al., 2019; Uchida et al., 2002).

2.4. Physicochemical soil parameters and nutrient pools

The soil samples were analyzed for pH, gravimetric water content and soil texture. Soil total Carbon (Soil C) and Nitrogen (Soil N) pools and isotopic composition were measured via elemental analyzer (EA 1110, CE Instruments, Italy) coupled to a continuous-flow isotope ratio mass spectrometer (IRMS, DeltaPlus, Finnigan MAT). As the investigated soils did not contain any carbonates, the presented soil total C concentrations denote soil organic carbon concentrations. Soil total Phosphorus (Soil P) was measured photometrically in 0.5 M H_2SO_4 extracts based on malachite-green method (D'Angelo et al., 2001) following a modified ignition method by (Kuo, 1996) to convert organic P to inorganic P. Total dissolved organic Carbon (TDC) and Nitrogen (TDN) pools were quantified in 1 M KCl extracts via TOC/TN- Analyzer (Shimadzu, TOC-VCPH/CPNTNM-1 analyzer). Total dissolved Phosphorus (TDP) was measured in 0.5 M $NaHCO_3$ extracts (Olsen et al., 1954) that have been subjected to alkaline persulfate digestion (Rowland and Haygarth, 1997) using the photometric malachite-green assay (D'Angelo et al., 2001). For a detailed description of these methods, see Supplementary Materials and Methods.

2.5. Microbial biomass and stoichiometry

Soil microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) pools were determined via the chloroform-fumigation extraction method (48 h incubation period followed by 1 M KCl extraction for MBC and MBN and 0.5 M $NaHCO_3$ extraction for MBP; Vance et al., 1987; Brookes et al., 1982), and calculated as the difference between fumigated samples and non-fumigated controls and applying an extraction conversion factor 0.45 for C and N and 0.4 for P. Due to the lack of chloroform in the field, fumigations and extractions were performed ten days after sampling. Extracts were analyzed on a Shimadzu TOC-VCPH/CPNTNM-1 analyzer.

2.6. Soil organic matter chemical composition

We investigated the chemical composition of soil organic matter (SOM) using Pyrolysis-Gas Chromatography/Mass Spectrometry (CDS Pyroprobe 6200, CDS Analytical coupled to Pegasus BT, LECO) with a polar column (Supelcowax™ 10 Fused Silica Capillary Column, 30 m x 0.25 mm x 0.25 μm film thickness, Sigma Aldrich), with a high-throughput semi-automated approach that is described in more detail in the Supplementary Materials and Methods. In short, a reference-sample was chosen from the set of samples and manually analyzed it for its chromatographic fingerprint. We identified chemical compounds using NIST Libraries of Mass Spectrometry (U.S. Department of Commerce National Institute of Standards and Technology) and compiled a library of identified compounds (see Supplementary Compound Library File). This library was used for the analysis of the remaining samples via automated similarity matching processes implemented in ChromaTOF software (version 5.0, LECO), that were followed by manual adjustment- and correction-steps. As result, we obtained a presence-absence list of compounds plus their corresponding peak areas for all samples and blanks. Subsequently, we performed quality measures which included the removal of chromatographic "background noise" by discarding peaks with a low signal to noise ratio (SN $\geq$ 2000) and performing a blank correction step. We further normalized peak areas to respective soil carbon contents and pyrolyzed sample amounts, since those factors are known to influence peak area and baseline height. Subsequently, we calculated individual compound abundances (μg C mg^{-1} soil DW) using the assumption that the sum of all compound areas within a sample equals its carbon content. As final filtering step, compounds with a lower relative abundance of $<$ 0.1 % per sample were excluded, resulting in 513 individual substances considered for further analyses.

We assigned all identified substances from the established compound library to six SOM compound groups: "aromatics & phenols",

"carbohydrates", "N-containing compounds", "lignin-derived compounds" and "lipids" (see Supplementary Compound Library File). This procedure was supported by extensive literature research or by taking their respective molecular structure into account if no literature reference was available. Substances without biomarker characteristics for the aforementioned groups, plus substances matching the unique mass spectra of a compound without a name reference within our library (e.g., "Peak_1") were merged into the group "compounds of general & unknown origin". The 513 considered substances were allocated into 25 "aromatics & phenols", 25 "carbohydrates", 16 "N-containing compounds", 2 "lignin-derived compounds", 6 "lipids" and 439 "general & unknown" compounds.

Due to pronounced differences in C concentrations between individual samples, we used relative abundances of compounds (after filtering out compounds with marginal abundance as described above) for the multivariate representation of the SOM fingerprint. Calculated compound abundances were used to analyze differential contributions of SOM compound groups between treatments. For a more detailed description, see Supplementary Materials and Methods.

2.7. Soil microbial communities – DNA Extraction, amplicon sequencing, and digital droplet (dd)PCR

We extracted microbial DNA from 400 mg FW soil using the FastDNA™ SPIN Kit for Soil (MP Biomedicals, Santa Ana, USA) following the manufacturers' instructions with minor modifications for cleaning the samples from the RNAlater™ Stabilization Solution. To rule out contamination, we included extraction blanks in subsequent quantification and sequencing steps. DNA concentrations were quantified via Quant-iT™ PicoGreen® dsDNA Assay Kit (Thermo Fisher Scientific, Waltham, USA). For a more detailed description, see Supplementary Materials and Methods.

Amplicon sequencing and raw data processing was performed at the Joint Microbiome Facility of the Medical University of Vienna and the University of Vienna (JMF project ID JMF-1903–5) using DNA extracts that have been normalized to a concentration of 1.25 ng μl^{-1}. A two-step barcoding approach was used to generate amplicon libraries of archaeal, bacterial, and fungal communities using Illumina MiSeq (V3 Kit) in the 2 x 300 bp configuration (Pjevac et al., 2021). The V4 hypervariable region of the 16S rRNA gene was amplified using primer pairs 515F (GTGYCAGCMGCCGCGGTAA, Parada et al., 2016) and 806R (GGACTACNVGGGTWTCTAAT, Apprill et al., 2015). The fungal ITS1 region was amplified using primer pairs ITS1F (CTTGGTCATTTAGAGGAAGTAA, Smith and Peay, 2014) and ITS2 (GCTGCGTTCTTCATCGATGC, White et al., 1990). Details on the amplification conditions are presented in the Supplementary Materials and Methods. Amplicon pools were extracted from the raw sequencing data using the FASTQ workflow in BaseSpace (Illumina) with default parameters. Demultiplexing was performed with the python package demultiplex (Laros JFJ, github.com/jfjlaros/demultiplex) allowing one mismatch for barcodes and two mismatches for linkers and primers (Pjevac et al., 2021). Amplicon sequence variants (ASVs) were inferred using the DADA2 R package applying the recommended workflow (Callahan et al., 2016a,b). FASTQ reads 1 and 2 were trimmed at 150 nt with allowed expected errors of 2 (16S rRNA gene) and 230 nt with allowed expected errors of 4 and 6 (ITS1 region), respectively. For 16S rRNA gene data, ASV sequences were subsequently classified using SINA version 1.6.1 (Pruesse et al., 2012) and the SILVA database SSU Ref NR 99 release 138.1 (Quast et al., 2013) using default parameters. Fungal ASVs were subsequently classified using DADA2 and the UNITE all eukaryotes general FASTA release version 8.2 (Abarenkov et al., 2020) using default parameters. Datasets were deposited in the NCBI Sequence Read Archive under BioProject accession number PRJNA1031541.

Subsequently, we improved the quality of the datasets via removing the sequences obtained in DNA extraction blanks plus all non-archaeal, −bacterial or −fungal sequences. Further, we further filtered out rare ASVs with a relative abundance < 0.1 % (bacteria and archaea) or < 0.25 % (fungi) respectively, and finally obtained 1068 bacterial and archaeal, and 190 fungal ASVs.

Digital droplet PCR (ddPCR) was performed to quantify 16S rRNA genes and ITS1 regions with the same primers used for sequencing. Each ddPCR reaction had a volume of 22 μL and consisted of 1x QX200 ddPCR EvaGreen Supermix (BioRad), 0.1 μmol/L of each primer and either 0.1 ng or 0.5 ng of template for the quantification of 16S rRNA genes or ITS1 regions, respectively. Droplets were generated on a QX200TM Droplet Generator (BioRad) and immediately subjected to PCR amplification. Details on the amplification conditions are presented in the Supplementary Materials and Methods. PCR products in droplets were kept at 4 °C for at least one hour to increase their separation before their fluorescence intensity was measured on a QX200 Droplet Reader (BioRad). Gene copy numbers were calculated using the QuantaSoft (BioRad) software where thresholds between positive and negative droplet populations were set consistently for each sample using the histogram as a guide. Final ddPCR results were expressed as gene copy number per gram of soil dry weight (DW).

Abundances of individual taxa (gene copy number corrected reads g^{-1} DW) were calculated by multiplying the 16S rRNA or ITS gene copy numbers measured in ddPCR assays with the respective relative abundances derived from the unfiltered amplicon sequencing datasets. For a standardization in a comparable way to the relative abundance data filtering, we discarded ASVs accounting for < 0.1 % (bacteria and archaea) and < 0.25 % (fungi) of the total gene copy corrected reads per sample. As only five ASVs were identified to belong to the domain of archaea, representing only 0.025 % of all gene copy number corrected reads from the entire dataset, we decided to use the simplified term 'bacterial community composition' throughout the manuscript.

The assessed α-diversity parameters included richness (number of observed ASVs), and diversity (Inverse Simpson Index). Due to pronounced differences in the number of obtained reads per sample, and to avoid discarding the majority of obtained sequences, we decided against rarefaction but used the respective unfiltered count (reads) datasets. We used relative abundances of bacterial and fungal taxa (after exclusion of rare ASVs as described above) for β-diversity analyses since individual samples differed substantially in their microbial biomass. While we performed a normalization of the library size using the geometric mean of pairwise ratios (gmpr) to account for zero-inflated count data (Chen et al., 2018) for the bacterial dataset, the data structure of the fungal dataset did not allow the application of this standardization method. ddPCR-derived abundance data of individual phylogenetic groups were used to explore quantitative differences between the treatments. For a detailed description of these methods, see Supplementary Materials and Methods.

2.8. Soil microbial extracellular enzymatic activity, growth, and respiration

We measured the potential extracellular activities of the four hydrolytic enzymes betaglucosidase, exochitinase (N-acetyl-β-glucosaminidase), protease (leucine-aminopeptidase) and acid phosphatase, following microplate fluorometric assays as described in (Canarini et al., 2021). Microbial growth- and respiration-rates were determined under ambient temperatures in the field directly after sampling. Respiration rates were measured on 400 mg fresh soil subsamples and calculated as the difference in CO_2 concentration after the incubation period of 26 h. Gas samples were analyzed on a Trace GC Ultra (ThermoFischer, Waltham, USA). Community level gross growth rates were determined on the same samples following a stable isotope method that is based on the incorporation of ^{18}O from labelled water into microbial DNA as described earlier (Spohn et al., 2016; Walker et al., 2018). ^{18}O-incubated soils were amended with 1 ml RNAlater™ Stabilization Solution (ThermoFisher Scientific), stored cool in the field and at −80 °C in the laboratory in Vienna until DNA extraction. We calculated microbial

mass-specific respiration- and growth-rates by relating the gross rates to the microbial biomass carbon concentrations obtained by chloroform fumigation extraction. For a more detailed description, see Supplementary Materials and Methods.

2.9. Statistical analyses and data visualization

All analyses were performed in R studio Version 4.1.2 (R Core Team, 2017, version 4.1.2). Significances of relationships were tested against a $p < 0.05$ threshold. Severe outliers from the variability of the entire dataset were identified via Grubb's test (extreme studentized deviant method) (function grubbs.test() within package *outliers* (Komsta, 2011)) and excluded them from further analyses.

For all obtained univariate variables, we applied linear-mixed-effects models (lmes) to test the fixed effects of 'sampling site' and 'soil cover type' and their interaction, while also accounting for the random effect by the replicate sampling block within each site (model <- lmer(variable ~ soil cover * site + (1|samplingblock:site). Samples collected under moss- and biocrust-cover within the same replicate sampling block were treated as dependent samples. We used the packages: *lme4* (Bates et al., 2015), *lmerTest* (Kuznetsova et al., 2017), *emmeans* (Lenth et al., 2022), and *car* (Fox, 2019). Model results were inspected with the anova() function. We used post hoc tests (adjust='tukey') to investigate pairwise differences between soil cover types (emmeans(model, pairwise ~ soil cover|site, adjust='tukey') and sites respectively emmeans (model, pairwise ~ site|soil cover, adjust='tukey')).

We checked for homogeneity of variances and normality of residuals by inspecting frequency histograms, boxplots of residuals, QQ-plots and via Shapiro and Levene tests for the model residuals. If model assumptions were not met, we applied log or sqrt transformations. In case of no agreement after transformation, we performed pairwise non-parametric two-sided Wilcox tests (function wilcox.test()) for the two factors 'soil cover' and 'site' and used respective subsetted datasets for the investigation of differences between (a) different soil cover types within the same site and (b) the difference between the sites for the same type of soil cover.

The *phyloseq* package (McMurdie and Holmes, 2013) was employed for handling the multivariate datasets on SOM chemical composition and amplicon sequencing. For multivariate visualizations, we performed Principal Coordinates Analyses (PCoAs) using the function 'ordinate ()'. To explore differences between the soil cover types and the two sites, we first calculated Bray-Curtis dissimilarity matrices with the function phyloseq::distance(phyloseq.object, method = "bray"). Subsequently, we performed permutational analysis of variance (permanova) with the 'adonis()' function (999 permutations) implemented in *vegan* (version 2.5–7, Oksanen et al., 2020) and checked for homogenous dispersal of the groups using the betadisper() function (999 permutations). Pairwise multilevel comparisons were performed using the paiwise.adonis() function (999 permutations, p.adjust.m='bonferroni)'.

Plots were generated using *ggplot2* (Wickham, 2016), and partly edited using Inkscape version 0.92.4 (Inkscape, 2020).

3. Results

3.1. Physicochemical soil parameters and stoichiometry

Soil cover specific effects were visible in soil stoichiometry with higher C:N and lower N:P ratios under mosses than under biocrusts (Table 1). This observation was likely linked to the reduced soil N contents that were found under mosses.

Several soil parameters exhibited site specific differences (Table 1). In Telephone Bay, soil texture was characterized by higher silt content and pH was higher than in Fumarole Bay, where soils were more sandy. Fumarole Bay was further characterized by an almost twice as high soil P pool, and a tendency for higher soil C and N contents. Soil $\delta^{15}N$ values were higher, hinting towards greater ecosystem N losses and hence a comparatively more open N cycle at this site.

In general, both sites showed indications for poorly developed soils. These included relatively low clay contents of around 3 % accompanied by a high proportion of coarse fragments, such as small stones and sand particles, and the absence of distinct soil horizons. Further, soil C:N and P:N ratios were high (Table 1).

3.2. Microbial biomass and stoichiometry

Microbial biomass was higher in soils under biocrusts than under mosses (Table 2). Altogether, the patterns of microbial biomass-C, −N, and −P were very similar to each other. We noted the on average highest values under biocrusts in Fumarole Bay, lowest values under mosses in Fumarole Bay, and intermediate values in Telephone Bay. The fact that differences in soil microbial biomass between soil cover types were more pronounced in Fumarole Bay than in Telephone Bay caused an interactive effect with sampling site. Bacterial and fungal gene copy numbers per gram dry soil used as additional biomass proxy confirmed a consistent pattern to the biomass estimates obtained by chloroform fumigation extraction method (Table 2).

The type of soil cover also affected microbial stoichiometry, as microbial biomass C:P and N:P ratios were significantly lower under mosses than under biocrusts (Table 2). Microbial C:N ratios were however unaffected, presumably due to homeostatic behavior.

Table 1
Soil pools and stoichiometry. Presented are means ± standard errors (n = 4). Exceptions with (n = 3) are depicted with (°). Soil texture (sand, silt, and clay content [%]) was analyzed in one composite soil sample per sampling site (*). P-values of linear mixed effects (lme) model ANOVA results or Wilcox tests are stated with respective (F-) and (w-) test statistics in parenthesis. In case of Wilcox tests, no test results for the interactive effect between site and soil cover are available (N.A.).

	Fumarole Bay		Telephone Bay		Soil Cover effect	Site effect	Site x Soil cover effect
	Moss	*Crust*	*Moss*	*Crust*			
pH	5.36 ± 0.18	5.49 ± 0.29	6.14 ± 0.09 (°)	5.95 ± 0.08	p = 0.991 (2e^{-4})	p = 0.051 (5.87)	p = 0.232 (1.82)
Sand [%]	78.75 (*)		60.66 (*)				
Silt [%]	18.16 (*)		36.29 (*)				
Clay [%]	3.09 (*)		3.05 (*)				
Soil C [mg g^{-1} DW]	13.39 ± 2.35	17.87 ± 3.37	10.88 ± 1.34 (°)	10.10 ± 0.29	p = 0.365 (0.96)	p = 0.090 (4.03)	p = 0.229 (1.80)
Soil N [mg g^{-1} DW]	0.69 ± 0.26	1.32 ± 0.28	0.36 ± 0.05 (°)	0.60 ± 0.09	**p = 0.025 (9.92)**	p = 0.071 (7.54)	p = 0.376 (0.94)
Soil P [mg g^{-1} DW]	0.39 ± 0.01	0.39 ± 0.04	0.21 ± 0.02 (°)	0.21 ± 0.01	p = 0.774 (0.09)	**p = 9.96 e^{-5} (77.2)**	p = 0.804 (0.07)
Soil C/N (molar)	17.77 ± 1.70 (°)	14.09 ± 0.93	30.28 ± 0.54 (°)	17.77 ± 2.22	**p = 6.4 e^{-4} (23.83)**	**p = 6.4 e^{-4} (23.85)**	**p = 0.024 (7.09)**
Soil N/P (molar)	1.73 ± 0.65	3.36 ± 0.66	1.68 ± 0.11 (°)	2.82 ± 0.36	**p = 0.003 (27.43)**	p = 0.645 (0.23)	p = 0.473 (0.60)
DOC [µg/g DW]	9.66 ± 3.89	25.79 ± 2.29 (°)	22.59 ± 1.68	20.06 ± 2.93	**p = 0.031 (9.13)**	p = 0.288 (1.39)	**p = 0.009 (18.30)**
TDN [µg/g DW]	2.06 ± 0.36	4.17 ± 1.03	1.43 ± 0.54	1.70 ± 0.77	p = 0.316 (1.09)	p = 0.055 (4.52)	p = 0.416 (0.71)
TDP [µg/g DW]	13.43 ± 2.92	9.06 ± 0.63	3.04 ± 0.08	3.29 ± 0.24	p = 0.174 (2.38)	**p = 0.003 (24.03)**	p = 0.134 (3.00)
Soil $\delta^{13}C$ [‰ VDB]	−25.86 ± 0.10	−26.14 ± 0.04	−25.76 ± 0.05 (°)	−24.97 ± 0.39	p = 0.613 (w = 23)	**p = 0.014 (w = 7)**	N.A.
Soil $\delta^{15}N$ [‰ VDB]	8.46 ± 0.53	5.65 ± 1.31	1.20 ± 0.13 (°)	0.68 ± 0.29	p = 0.152 (w = 15)	p = 3.1 e-4 (w = 56)	N.A.

Table 2
Microbial pools and stoichiometry. Presented are means ± standard errors (n = 4). Exceptions with (n = 3) are depicted with (°). P-values of linear mixed effects (lme) model ANOVA results are stated with respective (F-) test statistics in parenthesis.

	Fumarole Bay		Telephone Bay		Soil Cover effect	Site effect	Site x Soil cover effect
	Moss	*Crust*	*Moss*	*Crust*			
MBC [µg/g DW soil]	181.0 ± 35.0	1374.8 ± 248.8 (°)	975.1 ± 277.6	1232.2 ± 165.5	**p = 0.003 (23.56)**	p = 0.220 (1.85)	**p = 0.021 (9.90)**
MBN [µg/g DW soil]	20.6 ± 6.3	173.4 ± 28.7 (°)	99.5 ± 26.9	140.8 ± 21.2	**p = 4.90 e^{-4} (52.68)**	p = 0.416 (0.76)	**p = 0.007 (17.28)**
MBP [µg/g DW soil]	4.6 ± 0.9	12.3 ± 1.7 (°)	5.5 ± 0.6	6.9 ± 1.9	**p = 0.005 (23.16)**	p = 0.404 (0.81)	**p = 0.020 (11.37)**
microbial C/N (molar)	11.4 ± 2.9	8.5 ± 0.9	9.7 ± 0.4	9.6 ± 2.4	p = 0.450 (0.61)	p = 0.885 (0.02)	p = 0.498 (0.49)
microbial C/P (molar)	50.2 ± 21.3	112.6 ± 7.9	170.9 ± 29.3	207.0 ± 45.0	**p = 0.020 (7.19)**	**p = 9.0 e^{-4} (19.14)**	p = 0.077 (3.75)
microbial N/P (molar)	4.7 ± 1.4	13.5 ± 0.8	17.5 ± 2.7	23.0 ± 4.3	**p = 0.019 (7.30)**	**p = 0.001 (17.65)**	p = 0.562 (0.36)
Bacterial & archaeal gene copies [g^{-1} DW soil]	2.34 e^{+8} ± 7.93 e^{+7}	1.26 e^{+9} ± 2.91 e^{+8}	4.03 e^{+8} ± 5.52 e^{+7}	4.06 e^{+8} ± 1.43 e^{+8}	**p = 0.013 (8.52)**	p = 0.438 (0.64)	**p = 0.006 (11.04)**
fungal gene copies [g^{-1} DW soil]	1.67 e+^{6} ± 6.65 e+^{5}	4.28 e+^{7} ± 1.27 e+^{7}	4.46 e^{+6} ± 1.52 e^{+6}	1.42 e^{+7} ± 5.63 e^{+6}	p = 0.001 (18.46)	p = 0.990 (2 e^{-4})	p = 0.044 (5.05)

3.3. Soil organic matter (SOM) composition

The pyrolysis – GC/MS biomarker fingerprinting approach revealed a significant difference in the structural SOM composition between soils covered by mosses and biological soil crusts (Fig. 1). The comparison of soil organic matter pools between Fumarole Bay and Telephone Bay indicated exceedingly similar fingerprints under the biocrusts, while a higher, yet not significant degree of variability in the chemical composition was observed under the two moss species.

Soils under biological soil crusts showed significantly higher absolute abundances of carbohydrates, lipids, and N-containing compounds and tended to have more aromatics and phenols than soils under mosses (see Supplementary Figure S1). In contrast, the type of soil cover did not affect the absolute abundance of general and unknown compounds (moss: 8.38 ± 0.57; crust: 7.35 ± 1.15 mg C g^{-1} DW M ± SE; lme: F = 0.67, p = 0.430; data not shown).

Carbohydrates and aromatics and phenols had the highest relative contribution to the SOM pools after general and unknown compounds, which represented the largest fraction in all soils (moss: 71.7 ± 5.6; crust: 53.0 ± 3.3 %; M ± SE). Carbohydrates and aromatics and phenols were similarly abundant under moss cover in relative terms (carbohydrates: 11.0 ± 3.2; aromatics & phenols: 12.7 ± 1.5 %; M ± SE), but under biocrusts, carbohydrates contributed on average 6 % more to the respective SOM pool than aromatics and phenols (carbohydrates: 22.5 ± 2.3; aromatics & phenols: 16.5 ± 0.9 %; M ± SE).

3.4. Soil bacterial community composition

Principal Coordinates Analysis displayed that the soil bacterial community composition differed predominantly by sampling site (Figure 2a). With respect to the effects of soil cover type, bacterial communities were clearly distinct in Fumarole Bay, while they showed a

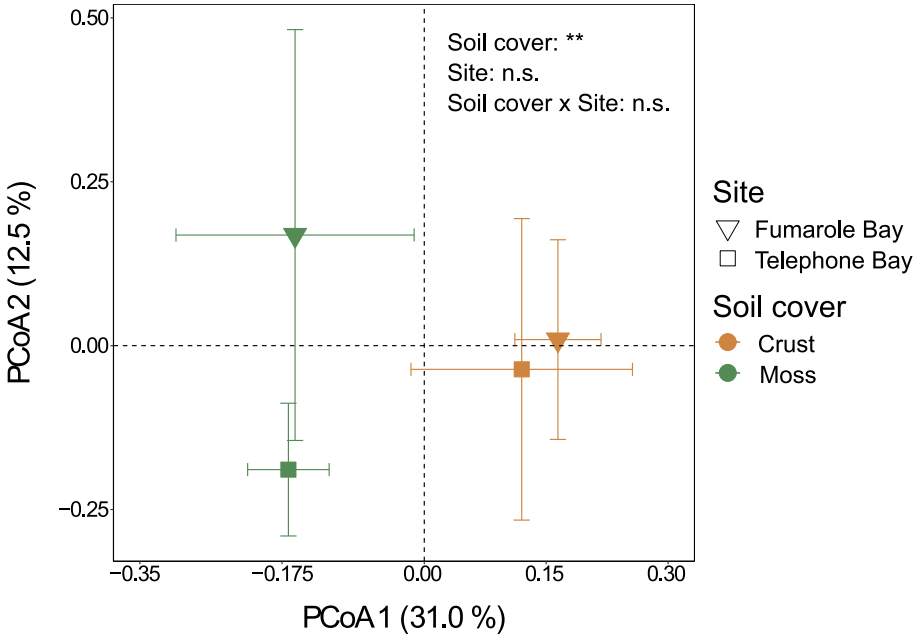

Fig. 1. Soil organic matter composition determined via Pyrolysis − GC/MS biomarker fingerprinting. Principal Coordinates Analysis (PCoA) depicting dissimilarity in relative abundances of 513 considered compounds. Represented are means ± standard deviations of respective treatment groups (n = 4), except for Telephone Bay $_{Moss}$ (n = 3). Results of Permutational analysis of variance stated top right. PERMANOVA: Soil cover effect: p = 0.005 (F = 2.89), Site effect: p = 0.210 (F = 1.20), Soil cover x Site effect: p = 0.154 (F = 1.31). Soils under mosses are shown in green, soils under biocrusts are shown in brown. Samples collected in Fumarole Bay are depicted in triangles, samples collected in Telephone Bay are shown in squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

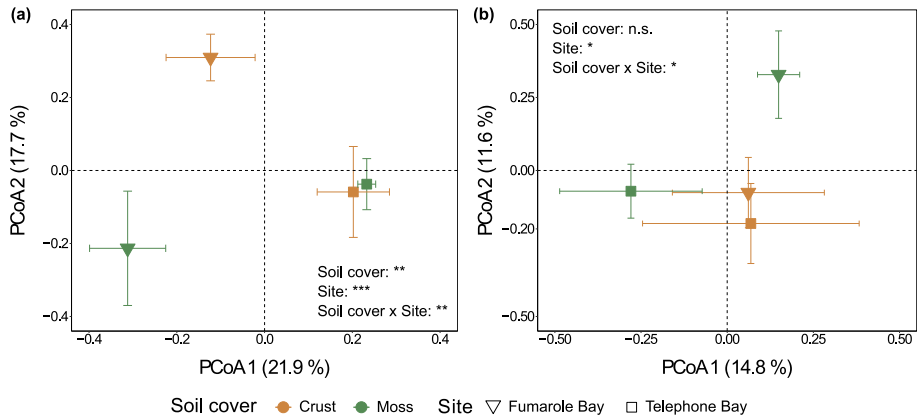

Fig. 2. Soil microbial community composition visualized via Principal Coordinates Analysis (PCoA). Shown are means ± standard deviations of the respective treatment groups (n = 4) and respective Permutational analysis of variance results. **(a)** Bacterial community composition determined via 16S rRNA amplicon sequencing. Depicted are differences in the relative abundance of 1068 considered taxa after excluding ASVs with < 0.1 % relative abundance. PERMANOVA: Soil cover effect: p = 0.007 (F = 2.12), Site effect: p = 0.001 (F = 3.75), Soil cover x Site effect: p = 0.03 (F = 2.28) **(b)** fungal community composition determined via ITS 1 region amplicon sequencing showing differences in the relative abundance of 190 considered taxa after excluding ASVs with < 0.25 % relative abundance. PERMANOVA: Soil cover effect: p = 0.054 (F = 1.35), Site effect: p = 0.011 (F = 1.67), Soil cover x Site effect: p = 0.013 (F = 1.65). Soils under mosses are shown in green, soils under biocrusts are shown in brown. Samples collected in Fumarole Bay are depicted in triangles, samples collected in Telephone Bay are shown in squares. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

high level of similarity in Telephone Bay. This observation was also reflected in bacterial alpha diversity measures. In Fumarole Bay, we observed the on average highest bacterial richness (number of observed ASVs) and alpha diversity (inverse Simpson Index) under biocrusts (Supplementary Table S3), whereas the respective lowest values were noted under moss cover, a finding that corresponds to the observed microbial biomass pattern. Roughly 250 ASVs less were found under *Polytrichastrum alpinum* than under the respective biocrust at this site.

Out of the total number of 1068 bacterial ASVs, only eight were shared among all samples, and 131 were shared among the four treatment groups. 111 ASVs occurred uniquely under *Sanionia unicinata*, 155 under *Polytrichastrum alpinum*, 86 under biocrusts in Telephone Bay, and 129 under biocrusts in Fumarole Bay, corresponding to 10 %, 8 %, 12 %, and 15 % of all taxa in the dataset, respectively. (Supplementary Figure S2a). Only five ASVs belonged to the domain of archaea, with all sequences found in soils under *Polytrichastrum alpinum*.

Calculating amplicon sequencing data to gene copy number corrected reads per gram dry soil allowed us to estimate absolute abundances of individual bacterial groups. Bacterial phylum abundance data and respective linear mixed effects model results are shown in Supplementary Table S2. The phyla Bacteroidota, Actinobacteriota, Proteobacteria, Verrucomicrobiota and Acidobacteriota were the five most abundant ones in all four treatment groups. Desulfobacterota were additionally very abundant under *Polytrichastrum alpinum*. In concordance with the observed microbial biomass pattern, many bacterial phyla occurred in highest abundances under biocrusts in Fumarole Bay. Cyanobacteria were most abundant under biological soil crusts, partly present under *Sanionia unicinata*, but not present at all under *Polytrichastrum alpinum*.

3.5. Soil fungal community composition

The soil fungal community composition showed striking interactive effects between soil cover type and sampling site, with the communities under *Polytrichastrum alpinum* being clearly distinct from all other communities (Figure 2b). Hence, the difference between fungal communities under moss versus biocrust cover was very pronounced in Fumarole Bay, but only minor in Telephone Bay. Further, it resulted in the fungal communities under the two moss species being also more different to each other than those below biocrusts.

Neither sampling site, nor the soil cover type influenced the number of observed fungal taxa or α-diversity (Supplementary Table S4). Of the 190 fungal ASVs, over 80 % were specific to either one of the four investigated treatment groups (Supplementary Figure S2b). Soils under *Polytrichastrum alpinum* had the largest share, harboring 76 unique fungal taxa. Only two ASVs were shared among all treatment groups.

The three most abundant fungal phyla in the dataset were Ascomycota, Basidiomycota and Mortierellomycota (Supplementary Table S2). Nonetheless, taxa that are unknown on the phylum level accounted for one third (32.6 %) of all obtained gene copy number corrected reads in the dataset and were found in greater abundances under biocrusts than under mosses (Supplementary Table S3). The phyla Glomeromycota, Rozellomycota, and Zoopagomyccota were solely detected in soils under *Polytrichastrum alpinum*.

3.6. Soil microbial respiration, growth, and enzymatic activity

For investigating the effects of differential soil cover on soil microbial activity, we normalized the presented respiration- and growth-rates, and the potential enzymatic activities with respect to their microbial biomass, as treatment groups varied substantially in this factor.

Microbial biomass-specific respiration rates (Fig. 3a) and biomass-specific enzyme activities involved in N and P cycling (Fig. 4b, c, d) were higher under mosses than under biocrusts. For biomass-specific growth rates (Fig. 3b), we found interactive effects between soil cover type and sampling site. High growth rates under biocrusts in Telephone Bay were in strong contrast to low rates under biocrusts in Fumarole Bay (emmeans pairwise test: p = 0.087, t = -2.01), while those under the two investigated moss species were similar (emmeans pairwise test: p = 0.420, t = -0.86). Hence, an effect of soil cover was only visible in Fumarole Bay (emmeans pairwise test: p = 0.073, t = -2.26) but not in Telephone Bay (emmeans pairwise test: p = 0.373, t = 0.98).

We detected site-specific effects for the microbial biomass-specific activities of C- and N- cycling enzymes. In soils of Fumarole Bay, the biomass-corrected β-glucosidase-, exochitinase-, and leucine aminopeptidase – rates exceeded those observed in Telephone Bay (Fig. 4 a, b, c).

4. Discussion

Our study is among the first to comparatively assess the influence of the two dominant forms of biological soil cover on subjacent soils in

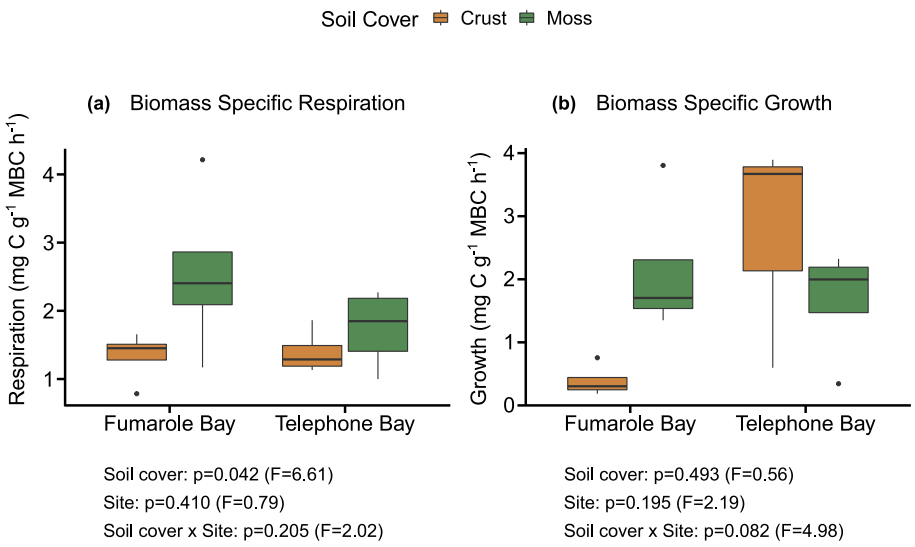

Fig. 3. **(a)** Microbial biomass specific respiration rates (mg C g^{-1} MBC h^{-1}) and **(b)** microbial biomass specific growth rates (mg C g^{-1} MBC h^{-1}). Respective ANOVA results from the linear mixed effect models (lme) are stated below each panel. Soils under mosses are shown in green, soils under biocrusts are shown in brown (n = 4, except for Biomass Specific Growth:Telephone Bay $_{Crust}$ n = 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

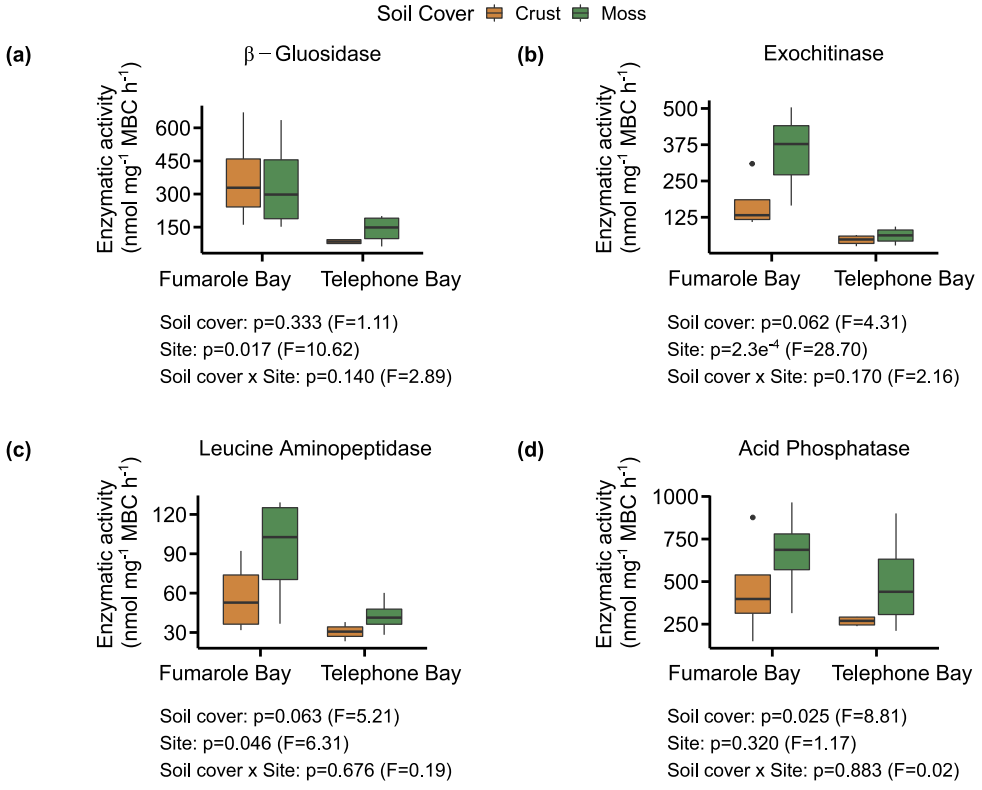

Fig. 4. Potential extracellular enzymatic activities of four key enzymes involved in C-, N-, and P- cycling normalized to microbial biomass carbon (nmol substrate mg^{-1} MBC h^{-1}) **(a)** β-Glucosidase **(b)** Exochitinase **(c)** Leucine Aminopeptidase **(d)** Acid Phosphatase. ANOVA results of linear mixed effect models (LME) are stated below each panel. Soils under moss soil cover are shown in green, soils under biocrusts are shown in brown (n = 4, except for Exochitinase: Fumarole Bay $_{Moss}$ n = 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

maritime Antarctica. We here provide evidence that numerous biological, chemical, and physical soil characteristics differ substantially under moss and biocrust cover, including nutrient concentrations and stoichiometry, SOM composition, microbial biomass, and community composition, as well as biomass-specific respiration rates and potential enzyme activities. Our data suggests that different types of biological soil cover have the potential to modify their immediate soil environment in different ways with possible repercussions for the functioning of subjacent soil microbial communities, biogeochemical cycling, and soil development. The soil characteristics in turn can also affect the soil cover. Further, we argue that the identity of the two investigated moss species exerted contributory impacts in addition. Species-specific traits

might have been responsible for the frequently observed interactive effects between soil cover type and sampling site, e.g., in the case of the composition of soil microbial communities. Even some site-specific effects might have been accompanied or partly caused by confounding effects of moss identity. Particularly in the context of bacterial and fungal community composition, microbial biomass specific growth, and enzymatic rates, we suggest that *Polytrichastrum alpinum* exerted stronger direct and indirect effects on subjacent soils than *Sanionia unicinata*, due to its specific traits (i.e., larger plant biomass per unit of soil surface, and the occurrence of rhizoids). We hence advert that mosses should not be considered as a uniform group regarding their impacts on belowground functioning.

Compared to other cold ecosystems such as for example the Arctic tundra, soil C- and N-contents were low to moderate for topsoils (Table 1), which is a commonly recognized feature of Antarctica's little developed ice-free soils (Bockheim and Haus, 2014; Bokhorst et al., 2007). Due to their young age and the prevailing harsh conditions, these soils have received comparatively little inputs of organic matter and are hence poorly stratified and characterized by a high proportion of coarse skeletal fractions (Bölter, 2011). This underpins the great importance of biological soil covers as main contributors of soil organic matter buildup and hence for soil development in this ecosystem (Benavent-González et al., 2018). Whereas soil C- and P- contents did not differ under the two types of soil cover, soils under biocrusts were characterized by a higher soil N content. The observation was also reflected in lower soil C:N and higher soil N:P ratios under biocrusts than under mosses (Table 1). In contrast to soil C:N ratios of about 18–30 under the mosses that reflected inputs of the plant tissue, C:N ratios of around 14–17 under biocrusts indicated a greater contribution of microbial biomass (Mooshammer et al., 2014). We suggest that the relatively larger pool of soil N under biocrusts is most likely connected to the occurrence of diazotrophic cyanobacteria (Weber et al., 2022) or other potentially N_2-fixing bacteria in the crust consortium, and to the overall higher abundance of soil microbial biomass (−N). Another, yet minor effect that might have also contributed to the observed differences in N availability between the soil covers could be the comparatively more efficient N-sequestration and retention in mosses (Ayres et al., 2006). In this oligotrophic environment where the growth period is very short, the quick and efficient sequestration of available nutrients might be a beneficial strategy for bryophytes (Rousk et al., 2016). Even though mosses were traditionally assumed to only have limited access to soil nutrients due to the lack of roots and a vascular system, evidence emerged that certain endohydric mosses are capable of N-uptake from the soil (Ayres et al., 2006). Finally, the higher soil N contents under biocrusts might also reflect slower microbial N-cycling rates or less N losses (Benavent-González et al., 2018). Altogether, our results indicate that soil microbial communities under moss cover may have less N available than under biocrusts, but instead experience higher substrate inputs in form of moss litter or leachates, with a presumably high C:N ratio.

Soil microbial biomass was lower under moss- than under biocrust-cover, yet with comparatively more pronounced differences in Fumarole Bay than in Telephone Bay (Table 2). We acknowledge, that minor contributions of biomass deriving from the overlaying biocrust consortia to the extracted subjacent soil microbial biomass pool might be possible, but we mainly ascribe the observation to an interplay of various factors. First, differences in litter quality and quantity, as suggested by the observed difference in soil stoichiometry and SOM fingerprints between soils under mosses versus biocrusts, are known to strongly control soil microbial communities (Cleveland et al., 2014). Second, as also indicated in our study by lower soil N- contents under biocrusts and higher activities of N-scavenging enzymes under mosses, microbial communities might be more prone to experience shortcomings of growth-limiting nutrients under moss cover than under biocrusts. Certain moss groups, such as the endohydric Polytrichaceae might be able to limit the growth of the soil microbial biomass pool by a comparatively more efficient sequestration of soil N. Third, microbial communities under mosses might experience increased top-down pressure by a more developed soil faunal community (Davis, 1981; Kinchin, 1990,1989), leading to a smaller microbial biomass pool with a higher turnover rate. Last, the two investigated moss species can generate chemically diverse and bioactive metabolites (Duan et al., 2021). Cytotoxic and growth-inhibiting substances, such as benzophenones, flavonoids, cinnamoyl and coumarin glucosides (Bhattarai et al., 2009; Duan et al., 2021; Seo et al., 2008) might have accumulated in the subjacent soil matrix. The fact that the differences between biocrust versus moss cover were stronger pronounced in Fumarole Bay, might relate to specific characteristics of the moss *Polytrichastrum alpinum,* such as e.g., its greater biomass, litter mass and the occurrence of rhizoids.

Soil cover was the main factor determining SOM composition. We detected qualitative differences in terms of the occurring substances (Fig. 1), but also quantitative differences in four major compound classes (Supplementary Figure S1), suggesting distinct organic matter inputs by mosses and biocrusts that translate to the subjacent SOM compound pool. However, the SOM fingerprint also suggested that the chemical composition of SOM was more different to one another under the two moss species, than it was under the respective crusts. Hence, also moss-species-specific traits that shape the quality of litter, such as rhizoids or cuticular waxes, may be central drivers of the SOM pool composition.

The fact that neither bryophytes (Turetsky, 2003) nor biocrusts (Erdtman, 1972) can synthesize lignin, might explain why only two lignin-derived compounds were identified in two soil samples, and in exceptionally low abundance (<1 % of the samples' soil C content respectively). Possible sources of lignin derivates in soils of our study may include OM inputs by grasses, marine algae (Martone et al., 2009), bird guano or human activity (Held and Blanchette, 2017). Nevertheless, carbohydrates, aromatic and phenolic substances, N-containing compounds, and lipids occurred in notably bigger quantities and were more abundant in soils under biocrusts than under mosses. For protection and better coherence and integrity of the biocrust, cyanobacteria and other microbes synthesize extracellular polymeric substances (EPS) (Belnap et al., 2001; Belnap and Lange, 2001; Philippot et al., 2024), consisting of substantial proportions of carbohydrates, proteins, lipids, and other polymers like extracellular DNA (Flemming, 2016; Jung et al., 2018). Soil algae excrete mucilage in an analogous manner (Broady, 1979; Metting, 1981) and can accumulate a variety of fatty acids, lipids, oils, sterols, and hydrocarbons within their cells (Borowitzka, 1995; Rybalka et al., 2023). Phenolic compounds are important biochemical characteristics of lichens (Shukla et al., 2010) and possibly accumulate in the soil upon the decay of biocrusts (Benavent-González et al., 2018). Finally, soils under biocrusts were not only characterized by a higher absolute abundance of all major SOM compound classes, but also had a higher relative contribution of carbohydrates to their SOM pool. Preceding desiccation, many biocrust organisms accumulate high concentrations of soluble carbohydrates that help them keeping the structure and functioning of membranes and macromolecules in the cytoplasm intact (Elster, 2004; Pushkareva et al., 2016). Together with the known positive effects of biocrusts on soil aggregation (Weber et al., 2022), such higher contribution of carbohydrates might indicate a higher potential for OM storage or faster soil development, than under moss cover.

We provided quantitative and qualitative insights into the soil microbial communities found under biocrusts and mosses in maritime Antarctica. The most abundant bacterial phyla (Acidobacteria, Actinobacteria, Protebacteria, Bacteroidota, Verrucomicrobiota and Cyanobacteria) and fungal phyla (Ascomycota, Basidiomycota and Mortierellomycota) in our dataset were also denoted dominant in Antarctica by other studies (Boyd et al., 2013; da Silva et al., 2022; Doytchinov and Dimov, 2022). Antarctic soils are thought to harbor a relatively low bacterial diversity (Ji et al., 2022) and in concordance, also a low archaeal abundance and diversity is repeatedly recorded (Ayton et al., 2010; Cowan et al., 2014; Dragone et al., 2022; Richter

et al., 2014). The contribution of archaea to our dataset was also marginal. Only five out of the more than 1000 considered ASVs obtained from 16S rRNA amplicon sequencing belonged to this domain. Our dataset comprised 216 fungal ASVs, fitting to the range of 100 – 350 taxa reported for Deception Island (Baeza et al., 2017; Held and Blanchette, 2017; Rosa et al., 2020). The high proportion of fungal taxa unknown at phylum level in our dataset reflects the circumstance that only about 1,000 taxa of fungi are currently described for Antarctica and that fungal diversity is less well documented in Antarctic soils than in other geographical regions (Bridge and Spooner, 2012; da Silva et al., 2020). We presume that several of these fungal taxa might live in symbiosis with green algae or cyanobacteria, forming lichen. Indeed, a diverse algal community had been documented for the soils of Deception Island (Câmara et al., 2021), but despite their importance for this ecosystem, generally even less data seems available on Antarctic edaphic algae (Pushkareva et al., 2016; Rybalka et al., 2023).

The soil bacterial community composition was mainly determined by sampling site (Figure 2a). This presumably relates to the sites' history, or local climatic or edaphic conditions (Opelt et al., 2007), such as e.g., the observed difference in soil pH. However, also the identity of the moss species might play an additional direct or indirect role in shaping subjacent microbial communities (Bach et al., 2009). For example, we detected substantial numbers of bacterial and archaeal taxa that were unique under *Polytrichastrum alpinum* and *Sanionia unicianata* respectively (Supplementary Figure S2a), and even several phyla (Fibrobacterota, Nitrospirota, Candidatus Sumerlaeota, Candidatus Thermoplasmatota, Nanoarchaeota FCPU426, RCP2-54) were exclusive for either one species. The cyanobacterial family Nostocaceae depicts another example of a moss-species specific microbial group. Cyanobacteria inhabit almost all terrestrial habitats (Makhalanyane et al., 2015), but particularly their association with mosses is widely recognized and studied (Rousk et al., 2013; Warshan et al., 2017). As such, Nostocaceae certainly belong to the most studied groups. So far, members of this family have solely been recorded epiphytically on feather mosses (Benavent-González et al., 2018; DeLuca et al., 2002), but not with other moss groups. This fact might explain their absence under *Polytrichastrum alpinum*, while cyanobacterial DNA was likely introduced to the subjacent soil matrix via litter from *Sanionia unicinata*. The effects of soil cover on bacterial communities were also mainly associated with the phylum cyanobacteria. As key group of the biocrust consortium (Belnap et al., 2001), their DNA occurred also in higher abundance in soils under biocrusts than under the mosses (Supplementary Table S1). Once more, an important role was taken by the filamentous Nostocaceae, which are known to dominate Antarctic biocrusts (Büdel and Colesie, 2014). The soil fungal community composition was dominated by the distinct fingerprint found under *Polytrichastrum alpinum* (Figure 2b), as also indicated by the largest number of unique taxa (Supplementary Figure S2b). One of the three phyla exclusively occurring under this species were Glomeromycota (Supplementary Table S2), which can form arbuscular mycorrhizal associations with bryophytes (Brundrett and Tedersoo, 2018).

Moss-associated bacterial (Navarro-Noya et al., 2014; Tveit et al., 2020) and fungal (Davey et al., 2012; Kauserud et al., 2008) communities can be strongly host-specific. However, this effect might not only be connected to direct species-specific interactions between microbial taxa and the moss but could also be due to specific microclimate- and nutrient-conditions that are formed by the plant (Jonsson et al., 2015). For our study, we suggest that differences in key characteristics between the two moss species i.e., the higher water retention capacity (Benavent-González et al., 2018) and the occurrence of rhizoids in *Polytrichastrum alpinum,* might be decisive for shaping the identity and abundance of bacterial, archaeal, and fungal groups underneath them. Although species-specific relationships between vegetation and soil microbial communities have been so far mainly demonstrated for vascular plants (Grayston and Prescott, 2005; Saetre and Bååth, 2000; Viitamäki et al., 2022), they might also play a role in mosses (Bach et al., 2009).

Potential soil enzymatic activity differed substantially between soil cover types. We mainly found stimulative effects by moss cover, similar to the results of previous studies (Benavent-González et al., 2018, Cheng et al., 2021). Considering the higher potential activity of exochitinase, leucine aminopeptidase, and acid phosphatase (Fig. 4b, c, d), microbes under mosses seemed to invest comparatively more resources per unit of biomass into N- and P-acquisition than microbes under crusts. We suggest that this observation relates to the differential SOM properties (Fig. 1), or to the microbial communities being adapted to experiencing high organic matter pulses from the mosses, e.g., in response to freeze–thaw or drying-rewetting cycles (Slate et al., 2019). In the case of enzymes that decompose N-containing polymers, enhanced activity under moss cover might also hint towards N-mining, to balance possible N-uptake by the plants (Ayres et al., 2006; 2021; Rousk et al., 2014). We additionally also detected site-specific effects with higher β-glucosidase, exochitinase, and leucine aminopeptidase activities per unit of microbial biomass in Fumarole Bay (Fig. 4a, b, c). While this matches the slightly higher soil C- and N-contents at this site (Table 1), we also suspect that the characteristics of the two investigated moss species exerted a confounding effect. Via its rhizoids and larger biomass per unit of soil surface, *Polytrichastrum alpinum* might have provided more organic matter inputs into the soils of Fumarole Bay, both, as vital moss, and as dead biomass within the biocrust consortium.

Biomass-specific respiration was also significantly higher under mosses than under biocrusts (Fig. 3a), which we mostly also ascribe to their distinct SOM properties (Fig. 1). Experiments with soils from maritime Antarctica confirmed that SOM decomposition rates were strongly influenced by the local composition of functional plant types, mainly through the variability in the chemical composition of their structural components (Bokhorst et al., 2007). However, decomposition rates also largely depend on soil temperature and moisture levels (Aerts, 2006; Davidson and Janssens, 2006; Park et al., 2018; Smith, 2003). Effects might be especially pronounced in Antarctica, where microbial activity is often constrained by low temperatures, and/or low water- and carbon- availability (George et al., 2021, Hopkins et al., 2006). Besides their effect on SOM properties, mosses can increase soil moisture (Blok et al., 2011) and insulate soils (Koranda and Michelsen, 2021). We thus assume for our study that mosses might have altered soil conditions in direct or indirect ways that led to a smaller microbial biomass pool (Table 2), but at the same time caused the establishment of more active communities with higher respiration rates and enzyme activities on a mass-specific level (Fig. 3a, Fig. 4).

To our best knowledge, microbial mass-specific growth rates have not yet been investigated under the influence of both, mosses (Purcell et al., 2023) and biocrusts in maritime Antarctica at *in-situ* temperatures. Microbial growth is generally limited by the availability of C (Soong et al., 2020). We hence infer from the comparable mass-specific growth rates below *Polytrichastrum alpinum*, *Sanionia unicinata*, and the biocrusts in Telephone Bay, that the microbial communities of these oligotrophic soils benefited from organic matter inputs into the so called "moss and crust fertility islands" (Benavent-González et al., 2018). However, the exceptionally low mass specific growth rates under biocrusts in Fumarole Bay imply that the soil microbial communities have been limited by something else besides C- availability. The assumption gets support by equally effective SOM decomposition under biocrusts at both sites, as indicated by similar mass-specific respiration rates.

In summary, our study demonstrates distinct effects of mosses and biocrusts on belowground functions and microbial communities. Thus, considering the interconnectedness between soil cover types and the activity of subjacent microbial communities is necessary to deepen our understanding of soil biogeochemistry under the harsh conditions in Antarctica, and likely will become even more important under the aspect of ongoing rapid climate change. Substantial shifts in distribution- and abundance patterns of mosses and biological soil crusts might occur along the Western Antarctic Peninsula (Benavent-González et al., 2018). Both mosses, *Polytrichastrum alpinum* and *Sanionia unicinata*, will

likely respond to warming with increased growth and coverage (Hebel et al., 2021; Shortlidge et al., 2017), so their abundance in maritime Antarctica might overtake those of biocrusts in the future. However, establishing predictions from observations on how soil cover will respond to warming is difficult, as interactive effects with other climate change parameters such as changes in precipitation patterns will be decisive. Nevertheless, by highlighting how important the links between soil cover identity and belowground soil functions are in this vulnerable ecosystem, the results of our study will provide a baseline for future research in this area.

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CRediT authorship contribution statement

Victoria Martin: Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Hannes Schmidt:** Writing – review & editing, Formal analysis, Data curation. **Alberto Canarini:** Writing – review & editing, Formal analysis, Data curation. **Marianne Koranda:** Writing – review & editing, Methodology. **Bela Hausmann:** Methodology, Formal analysis. **Carsten W. Müller:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Andreas Richter:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Conceptualization.

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.

Data availability

Data will be made available on request.

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Author contributions

VM is the lead author responsible for laboratory work setup and writing of the manuscript with feedback from all co-authors. AR is responsible for the main scientific conceptualization of this work, provided scientific guidance for the progress of the project, input during manuscript writing and financial support for sample analyses. CWM is together with AR responsible for the fieldwork setup and additionally provided conceptual guidance during project development, manuscript writing, logistical planning, and execution of the field work campaign in 2018. AC was involved in conceptualizing the workflow of SOM fingerprinting via Pyr-GC/MS and provided help with enzyme assays and during manuscript writing. HS helped with sample preparation for amplicon sequencing and ddPCR assays, the analysis of microbial community composition data, and writing of the manuscript. MK provided scientific input during statistical analyses and manuscript writing. BH processed raw amplicon sequencing data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2024.116894.

References

Abarenkov, K., Zirk, A., Piirmann, T., Pöhönen, R., Ivanov, F., Nilsson, R.H., Kõljalg, U., 2020. UNITE general FASTA release for eukaryotes. 2. UNITE Commun. https://doi.org/10.15156/BIO/786371.

Aerts, R., 2006. The freezer defrosting: Global warming and litter decomposition rates in cold biomes. J. Ecol. 94, 713–724. https://doi.org/10.1111/j.1365-2745.2006.01142.x.

Alvarenga, D.O., Rousk, K., 2022. Unraveling host–microbe interactions and ecosystem functions in moss–bacteria symbioses. J. Exp. Bot. 73, 4473–4486. https://doi.org/10.1093/jxb/erac091.

Angel, R., Conrad, R., 2013. Elucidating the microbial resuscitation cascade in biological soil crusts following a simulated rain event. Environ. Microbiol. 15, 2799–2815. https://doi.org/10.1111/1462-2920.12140.

Apprill, A., McNally, S., Parsons, R., Weber, L., 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. Aquat. Microb. Ecol. 75, 129–137.

Ayres, E., Van Der Wal, R., Sommerkorn, M., Bardgett, R.D., 2006. Direct uptake of soil nitrogen by mosses. Biol. Lett. 2, 286–288. https://doi.org/10.1098/rsbl.2006.0455.

Ayton, J., Aislabie, J., Barker, G.M., Saul, D., Turner, S., 2010. Crenarchaeota affiliated with group 1.1b are prevalent in coastal mineral soils of the Ross Sea region of Antarctica. Environ. Microbiol. 12, 689–703. https://doi.org/10.1111/j.1462-2920.2009.02111.x.

Bach, L.H., Frostegård, Å., Ohlson, M., 2009. Site identity and moss species as determinants of soil microbial community structure in Norway spruce forests across three vegetation zones. Plant Soil 318, 81–91. https://doi.org/10.1007/s11104-008-9819-6.

Baeza, M., Barahona, S., Alcaíno, J., Cifuentes, V., 2017. Amplicon-metagenomic analysis of fungi from antarctic terrestrial habitats. Front. Microbiol. 8, 2235. https://doi.org/10.3389/fmicb.2017.02235.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Belnap, J., 2001. Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Springer, Heidelberg, Heildelberg, pp. 241–261, 10.1007/978-3-642-56475-8_19.

Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydyrological Process. 20, 3159–3178. https://doi.org/10.1002/hyp.

Belnap, J., Büdel, B., Lange, O.L., 2001. Biological Soil Crusts: Characteristics and Distribution. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function, and Management. Ecological Studies, vol 150. Springer, Berlin, Heidelberg, 10.1007/978-3-642-56475-8_1.

Belnap, J., Lange, O.L., 2001. In: Structure and Functioning of Biological Soil Crusts: a Synthesis BT - Biological Soil Crusts: Structure, Function, and Management. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 471–479, 10.1007/978-3-642-56475-8_33.

Belnap, J., Weber, B., Büdel, B., 2016. Biological Soil Crusts as an Organizing Principle in Drylands BT - Biological Soil Crusts: an Organizing Principle in Drylands. Springer International Publishing, pp. 3–13.

Benavent-González, A., Delgado-Baquerizo, M., Fernández-Brun, L., Singh, B.K., Maestre, F.T., Sancho, L.G., 2018. Identity of plant, lichen and moss species connects with microbial abundance and soil functioning in maritime Antarctica. Plant Soil 429, 35–52. https://doi.org/10.1007/s11104-018-3721-7.

Bhattarai, H.D., Paudel, B., Lee, H.K., Oh, H., Yim, J.H., 2009. In vitro antioxidant capacities of two benzonaphthoxanthenones: ohioensins F and G, isolated from the Antarctic moss Polytrichastrum alpinum. Z. Naturforsch. C. 64, 197–200. https://doi.org/10.1515/znc-2009-3-408.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., van Ruijven, J., Parmentier, F.J.W., Maximov, T.C., Berendse, F., 2011. The cooling capacity of mosses: controls on water and energy fluxes in a siberian tundra site. Ecosystems 14, 1055–1065.

Bockheim, J., Haus, N., 2014. Distribution of organic carbon in the soils of antarctica. In: Hartemink, A., McSweeney, K. (Eds.), Soil Carbon. Springer International Publishing Switzerland, Progress in Soil Science, pp. 373–380, 10.1007/978-3-319-04084-4_37.

Bokhorst, S., Huiskes, A., Convey, P., Aerts, R., 2007. Climate change effects on organic matter decomposition rates in ecosystems from the Maritime Antarctic and Falkland Islands. Glob. Chang. Biol. 13, 2642–2653. https://doi.org/10.1111/j.1365-2486.2007.01468.x.

Bölter, M., 2011. Soil development and soil biology on King George Island, Maritime Antarctic. Polish Polar Res. Pol Polar Res. https://doi.org/10.2478/v10183-011-0002-z.

Borowitzka, M.A., 1995. Microalgae as sources of pharmaceuticals and other biologically active compounds. J. Appl. Phycol. 7, 3–15. https://doi.org/10.1007/BF00003544.

Bowker, M.A., Reed, S.C., Maestre, F.T., Eldridge, D.J., 2018. Biocrusts: the living skin of the earth. Plant Soil 429, 1–7. https://doi.org/10.1007/s11104-018-3735-1.

Boyd, W., Staley, J., Boyd, J., 2013. Ecology of Soil Microorganisms of Antarctica. pp. 125–159. https://doi.org/10.1029/AR008p0125.
Bramley-Alves, J., King, D.H., Robinson, S.A., Miller, R.E., 2014. Dominating the Antarctic Environment: Bryophytes in a Time of Change. In: Hanson, D., Rice, S. (Eds.), Photosynthesis in Bryophytes and Early Land Plants. Advances in Photosynthesis and Respiration, vol 37. Springer Science+Business Media Dordrecht.
Bridge, P.D., Spooner, B.M., 2012. Non-lichenized Antarctic fungi: transient visitors or members of a cryptic ecosystem? Fungal Ecol. 5, 381–394. https://doi.org/10.1016/j.funeco.2012.01.007.
British Bryological Society, 2022a. Polytrichastrum alpinum. [WWW Document]. URL https://www.britishbryologicalsociety.org.uk/learning/species-finder/polytrichastrum-alpinum/ (accessed 18.5.2023).
British Bryological Society, 2022b. Sanionia uncinata [WWW Document]. URL https://www.britishbryologicalsociety.org.uk/learning/species-finder/sanionia-uncinata/ (accessed 18.5.2023).
Broady, P.A., 1979. The terrestrial algae of Signy Island, South Orkney Islands - BAS Scientific Report 98.pdf 1-117 c.
Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of microbial biomass phosphorus in soil. Soil Biol. Biochem. 14, 319–329.
Brundrett, M.C., Tedersoo, L., 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. 220, 1108–1115. https://doi.org/10.1111/nph.14976.
Büdel, B., Colesie, C., 2014. Biological soil crusts - antarctic terrestrial microbiology: physical and biological properties of antarctic soils. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 131–161, 10.1007/978-3-642-45213-0_8.
Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869.
Callahan, B.J., Sankaran, K., Fukuyama, J.A., McMurdie, P.J., Holmes, S.P., 2016b. Bioconductor Workflow for Microbiome Data Analysis: from raw reads to community analyses [version 2; peer review: 3 approved]. F1000Research 5. https://doi.org/10.12688/f1000research.8986.2.
Câmara, P.E.A.S., Carvalho-Silva, M., Pinto, O.H.B., Amorim, E.T., Henriques, D.K., da Silva, T.H., Pellizzari, F., Convey, P., Rosa, L.H., 2021. Diversity and ecology of chlorophyta (viridiplantae) assemblages in protected and non-protected sites in deception island (Antarctica, South Shetland Islands) assessed using an NGS approach. Microb. Ecol. 81 (2), 323–334. https://doi.org/10.1007/s00248-020-01584-9.
Canarini, A., Schmidt, H., Fuchslueger, L., Martin, V., Herbold, C.W., Zezula, D., Gündler, P., Hasibeder, R., Jecmenica, M., Bahn, M., Richter, A., 2021. Ecological memory of recurrent drought modifies soil processes via changes in soil microbial community. Nat. Commun. 12, 1–14. https://doi.org/10.1038/s41467-021-25675-4.
Chen, L., Reeve, J., Zhang, L., Huang, S., Wang, X., Chen, J., 2018. GMPR: A robust normalization method for zero-inflated count data with application to microbiome sequencing data. PeerJ 2018, 1–20. https://doi.org/10.7717/peerj.4600.
Cheng, C., Gao, M., Zhang, Y., Long, M., Wu, Y., Li, X., 2021. Effects of disturbance to moss biocrusts on soil nutrients, enzyme activities, and microbial communities in degraded karst landscapes in southwest China. Soil Biol. Biochem. 152, 108065 https://doi.org/10.1016/j.soilbio.2020.108065.
Cianciullo, P., Maresca, V., Sorbo, S., Basile, A., 2022. Antioxidant and antibacterial properties of extracts and bioactive compounds in bryophytes. Appl. Sci. 12 https://doi.org/10.3390/app12010160.
Cleveland, C.C., Reed, S.C., Keller, A.B., Nemergut, D.R., O'Neill, S.P., Ostertag, R., Vitousek, P.M., 2014. Litter quality versus soil microbial community controls over decomposition: a quantitative analysis. Oecologia 174, 283–294. https://doi.org/10.1007/s00442-013-2758-9.
Convey, P., Bindschadler, R., Di Prisco, G., Fahrbach, E., Gutt, J., Hodgson, D.A., Mayewski, P.A., Summerhayes, C.P., Turner, J., Abram, N., Adams, B., Ainley, D., Anderson, J., Arbetter, T., Arthern, R., Atkinson, A., Barbante, C., Bargagli, R., Bargelloni, L., Barnes, D., Barrett, P., Bentley, M., Bergstrom, D., Bertler, N., Bindschadler, B., Bockheim, J., Bodeker, G., Bopp, L., Boutron, C., Bracegirdle, T., Bromwich, D., Chown, S., Clarke, A., Comiso, J., Convey, Peter, Cook, A., Crame, A., Crosta, X., Curran, M., Prisco, Di, Guido, Fahrbach, Eberhard, Fastook, J., Fleming, A., Forcada, J., Francis, J., Frenot, Y., Gili, J.M., Goodwin, I., Goosse, H., Gugliemin, M., Hellmer, H., Hennion, F., Heywood, K., Hodgson, Dominic A., Holland, D., Hong, S.M., Huiskes, A., Isla, E., Jacobs, S., Jenkins, A., Jones, A., Leaper, R., Lefebvre, W., Lenton, A., Linse, K., Lynch, A., Marshall, G., Massé, G., Masson-Delmotte, V., Mayewski, P., Meredith, M., Metzl, N., Monaghan, A., Mulvaney, R., Murray, A., Naveira-Garabato, A., Newsham, K., O'Farrell, S., Orejas, C., Peck, L., Pörtner, H.O., Rintoul, S., Röthilsburger, R., Robinson, S., Roscoe, H., Rossi, S., Scambos, T., Schiel, S., Shanklin, J., Smale, D., Smetacek, V., Sparrow, M., Speer, K., Stevens, M., Summerhayes, C., Trathan, P., Turner, John, Van Der Veen, K., Van Ommen, T., Vanreusel, A., Vaughan, D., Verde, C., Verleyen, E., Vyverman, W., Wang, Z., Webb, D., Wiencke, C., Willems, A., Woodworth, P., Worby, T., Worland, R., Yamanouchi, T., Zane, L., 2009. Antarctic climate change and the environment. Antarct. Sci. 21, 541–563. https://doi.org/10.1017/S0954102009990642.
Cowan, D.A., Makhalanyane, T.P., Dennis, P.G., Hopkins, D.W., 2014. Microbial ecology and biogeochemistry of continental Antarctic soils. Front. Microbiol.
D'Angelo, E., Crutchfield, J., Vandiviere, M., 2001. Rapid, sensitive, microscale determination of phosphate in water and soil. J. Environ. Qual. 30, 2206–2209. https://doi.org/10.2134/jeq2001.2206.
da Silva, T.H., Silva, D.A.S., de Oliveira, F.S., Schaefer, C.E.G.R., Rosa, C.A., Rosa, L.H., 2020. Diversity, distribution, and ecology of viable fungi in permafrost and active layer of Maritime Antarctica. Extremophiles 24, 565–576. https://doi.org/10.1007/s00792-020-01176-y.
da Silva, T.H., Câmara, P.E.A.S., Pinto, O.H.B., Carvalho-Silva, M., Oliveira, F.S., Convey, P., Rosa, C.A., Rosa, L.H., 2022. Diversity of fungi present in permafrost in the south Shetland Islands, Maritime Antarctic. Microb. Ecol. 83, 58–67. https://doi.org/10.1007/s00248-021-01735-6.
Davey, M.L., Heegaard, E., Halvorsen, R., Ohlson, M., Kauserud, H., 2012. Seasonal trends in the biomass and structure of bryophyte-associated fungal communities explored by 454 pyrosequencing. New Phytol. 195, 844–856. https://doi.org/10.1111/j.1469-8137.2012.04215.x.
Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. https://doi.org/10.1038/nature04514.
Davis, R.C., 1981. Structure and Function of Two Antarctic Terrestrial Moss. Ecol. Soc. Am. 51, 125–143.
DeLuca, T.H., Zackrisson, O., Nilsson, M.C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419, 917–920. https://doi.org/10.1038/nature01051.
Doytchinov, V.V., Dimov, S.G., 2022. Microbial community composition of the antarctic ecosystems: review of the bacteria, fungi, and archaea identified through an NGS-based metagenomics approach. Life. https://doi.org/10.3390/life12060916.
Dragone, N.B., Henley, J.B., Holland-Moritz, H., Diaz, M., Hogg, I.D., Lyons, W.B., Wall, D.H., Adams, B.J., Fierer, N., 2022. Elevational constraints on the composition and genomic attributes of microbial communities in antarctic soils. mSystems 7, 1–14. https://doi.org/10.1128/msystems.01330-21.
Duan, X.H., Zhang, X.W., Qin, M., He, P., Pei, L., Zhao, J.C., Chen, Y.L., 2021. Two new benzophenones from the endohydric moss Polytrichastrum formosum. Nat. Prod. Commun. 16, 2–5. https://doi.org/10.1177/1934578X211002623.
Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O., Pöschl, U., 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nat. Geosci. 5, 459–462. https://doi.org/10.1038/ngeo1486.
Elster, J., Benson, E.E., 2004. Life in the polar terrestrial environment a focus on algae and cyanobacteria. In: Fuller, B., Lane, N., Benson, E.E. (Eds.), Life In The Frozen State. Taylor and Francis, London, pp. 111–149 (pp. 111–150).
Erdtman, H., 1972. Lignins: Occurrence, formation, structure and reactions, K. V. Sarkanen and C. H. Ludwig, Eds., John Wiley & Sons, Inc., New York, 1971. 916 pp. J. Polym. Sci. Part B Polym. Lett. 10, 228–230. https://doi.org/https://doi.org/10.1002/pol.1972.110100315.
Flemming, H.C., 2016. EPS—then and now. Microorganisms 4, 1–18. https://doi.org/10.3390/microorganisms4040041.
Fox, J., 2019. John Fox and Sanford Weisberg. Sage Thousand Oaks, CA, USA.
George, S.F., Fierer, N., Levy, J.S., Adams, B., 2021. Antarctic Water Tracks: Microbial Community Responses to Variation in Soil Moisture, pH, and Salinity. Front. Microbiol. 12, 160–164. https://doi.org/10.3389/fmicb.2021.616730.
Gerson, U., 1982. Bryophytes and Invertebrates. In: Smith, A.J.E. (Ed.), Bryophyte Ecology. Springer, Dordrecht, Dordrecht, pp. 291–332, 10.1007/978-94-009-5891-3_9.
Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J., Van Der Wal, R., 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153, 931–941. https://doi.org/10.1007/s00442-007-0785-0.
Goyanes, G., Vieira, G., Caselli, A., Cardoso, M., Marmy, A., Santos, F., Bernardo, I., Hauck, C., 2014. Local influences of geothermal anomalies on permafrost distribution in an active volcanic island (Deception Island, Antarctica). Geomorphology 225, 57–68. https://doi.org/10.1016/j.geomorph.2014.04.010.
Grayston, S., Prescott, C., 2005. Microbial communities in forest floors under four tree species in coastal British Columbia. Soil Biol. Biochem. 37, 1157–1167. https://doi.org/10.1016/j.soilbio.2004.11.014.
Grimingham, C.H., Smith, R.I.L., 1971. Growth form and water relations of mosses in the maritime antarctic. Br. Antarct. Surv. Bull. 25, 1–21.
Hebel, I., Gonzalez, I., Jaña, R., 2021. Genetic Approach on Sanionia uncinata (Hedw.) Loeske to Evaluate Representativeness of in situ Conservation Areas Among Protected and Neighboring Free Access Areas in Maritime Antarctica and Southern Patagonia. Front. Conserv. Sci. https://doi.org/10.3389/fcosc.2021.647798.
Heindel, R.C., Governali, F.C., Spickard, A.M., Virginia, R.A., 2019. The role of biological soil crusts in nitrogen cycling and soil stabilization in Kangerlussuaq, West Greenland. Ecosystems 22, 243–256. https://doi.org/10.1007/s10021-018-0267-8.
Held, B.W., Blanchette, R.A., 2017. Deception Island, Antarctica, harbors a diverse assemblage of wood decay fungi. Fungal Biol. 121, 145–157. https://doi.org/10.1016/j.funbio.2016.11.009.
Holland-Moritz, H., Stuart, J., Lewis, L.R., Miller, S., Mack, M.C., McDaniel, S.F., Fierer, N., 2018. Novel bacterial lineages associated with boreal moss species. Environ. Microbiol. 20, 2625–2638. https://doi.org/10.1111/1462-2920.14288.
Holland-Moritz, H., Stuart, J.E.M., Lewis, L.R., Miller, S.N., Mack, M.C., Ponciano, J.M., McDaniel, S.F., Fierer, N., 2021. The bacterial communities of Alaskan mosses and their contributions to N2-fixation. Microbiome 9, 1–14. https://doi.org/10.1186/s40168-021-01001-4.
Hopkins, D.W., Sparrow, A.D., Elberling, B., Gregorich, E.G., Novis, P.M., Greenfield, L. G., Tilston, E.L., 2006. Carbon, nitrogen and temperature controls on microbial activity in soils from an Antarctic dry valley. Soil Biol. Biochem. 38, 3130–3140. https://doi.org/10.1016/j.soilbio.2006.01.012.
Hughes, K., Ott, S., Bölter, M., 2006. Colonisation processes. In: Bergstrom, D.M., Convey, P., Huiskes, A. (Eds.), Trends in Antarctic Terrestrial and Limnetic Ecosystems: Antarctica as a Global Indicator. Springer, Dordrecht, Dordrecht, pp. 35–54 https://doi.org/https://doi.org/10.1007/1-4020-5277-4.
Ji, M., Kong, W., Jia, H., Delgado-Baquerizo, M., Zhou, T., Liu, X., Ferrari, B.C., Malard, L., Liang, C., Xue, K., Makhalanyane, T.P., Zhu, Y.G., Wang, Y., Pearce, D.A.,

Cowan, D., 2022. Polar soils exhibit distinct patterns in microbial diversity and dominant phylotypes. Soil Biol. Biochem. 166, 108550 https://doi.org/10.1016/j.soilbio.2022.108550.
Jonsson, M., Kardol, P., Gundale, M.J., Bansal, S., Nilsson, M.C., Metcalfe, D.B., Wardle, D.A., 2015. Direct and indirect drivers of moss community structure, function, and associated microfauna across a successional gradient. Ecosystems 18, 154–169. https://doi.org/10.1007/s10021-014-9819-8.
Jung, P., Briegel-Williams, L., Simon, A., Thyssen, A., Büdel, B., 2018. Uncovering biological soil crusts: Carbon content and structure of intact Arctic, Antarctic and alpine biological soil crusts. Biogeosciences 15, 1149–1160. https://doi.org/10.5194/bg-15-1149-2018.
Kauserud, H., Mathiesen, C., Ohlson, M., 2008. High diversity of fungi associated with living parts of boreal forest bryophytes. Botany 86, 1326–1333. https://doi.org/10.1139/B08-102.
Kinchin, I.M., 1989. The moss fauna 2: Nematodes. J. Biol. Educ. 23, 37–40. https://doi.org/10.1080/00219266.1989.9655021.
Kinchin, I.M., 1990. The moss fauna 3: Arthropods. J. Biol. Educ. 24, 93–99. https://doi.org/10.1080/00219266.1990.9655117.
Komsta, L., 2011. Package 'outliers'. Med. Univ. Lublin, Lublin.
Koranda, M., Michelsen, A., 2021. Mosses reduce soil nitrogen availability in a subarctic birch forest via effects on soil thermal regime and sequestration of deposited nitrogen. J. Ecol. 109, 1424–1438. https://doi.org/10.1111/1365-2745.13567.
Kuo, S., 1996. Phosphorus. Methods of Soil Analysis, Part 3: Chemical Methods. Soil Science Society of America.
Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.
Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D., Terauds, A., 2017. Climate change drives expansion of Antarctic ice-free habitat. Nature 547, 49–54. https://doi.org/10.1038/nature22996.
Inkscape Project. (2020). Inkscape. Retrieved from https://inkscape.org.
Lenth, R. V, Buerkner, P., Herve, M., Love, J., Miguez, F., Riebl, H., Singmann, H., 2022. Package "Emmeans"(Version R Package 1.7. 2): Estimated Marginal Means, Aka Least-Squares Means [Computer Software].
Lindo, Z., Gonzalez, A., 2010. The bryosphere: An integral and influential component of the Earth's biosphere. Ecosystems 13, 612–627. https://doi.org/10.1007/s10021-010-9336-3.
Liu, Y., Yang, H., Li, X., Xing, Z., 2014. Effects of biological soil crusts on soil enzyme activities in revegetated areas of the Tengger Desert, China. Appl. Soil Ecol. 80, 6–14. https://doi.org/10.1016/j.apsoil.2014.03.015.
Maestre, F.T., Escolar, C., de Guevara, M.L., Quero, J.L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B., Gallardo, A., 2013. Changes in biocrust cover drive carbon cycle responses to climate change in drylands. Glob. Chang. Biol. 19, 3835–3847. https://doi.org/10.1111/gcb.12306.
Maier, S., Tamm, A., Wu, D., Caesar, J., Grube, M., Weber, B., 2018. Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts. ISME J. 12, 1032–1046. https://doi.org/10.1038/s41396-018-0062-8.
Makhalanyane, T.P., Valverde, A., Velázquez, D., Gunnigle, E., Van Goethem, M.W., Quesada, A., Cowan, D.A., 2015. Ecology and biogeochemistry of cyanobacteria in soils, permafrost, aquatic and cryptic polar habitats. Biodivers. Conserv. 24, 819–840. https://doi.org/10.1007/s10531-015-0902-z.
Marshall, G.J., Lagun, V., Lachlan-Cope, T.A., 2002. Changes in Antarctic Peninsula tropospheric temperatures from 1956 to 1999: A synthesis of observations and reanalysis data. Int. J. Climatol. 22, 291–310. https://doi.org/10.1002/joc.758.
Martone, P.T., Estevez, J.M., Lu, F., Ruel, K., Denny, M.W., Somerville, C., Ralph, J., 2009. Discovery of lignin in seaweed reveals convergent evolution of cell-wall architecture. Curr. Biol. 19, 169–175. https://doi.org/10.1016/j.cub.2008.12.031.
McMurdie, P.J., Holmes, S., 2013. phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. PLoS One 8, 1–11. https://doi.org/10.1371/journal.pone.0061217.
Melick, D.R., Seppelt, R.D., 1997. Vegetation Patterns in Relation to Climatic and Endogenous Changes in Wilkes Land. Continental Antarctica. J. Ecol. 85, 43. https://doi.org/10.2307/2960626.
Meredith, M.P., King, J.C., 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys. Res. Lett. 32, 1–5. https://doi.org/10.1029/2005GL024042.
Metting, B., 1981. The systematics and ecology of soil algae. Bot. Rev. 47, 195–312.
Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A., 2014. Stoichiometric imbalances between terrestrial decomposer communities and their resources: Mechanisms and implications of microbial adaptations to their resources. Front. Microbiol. 5 https://doi.org/10.3389/fmicb.2014.00022.
Mugnai, G., Rossi, F., Mascalchi, C., Ventura, S., De Philippis, R., 2020. High Arctic biocrusts: characterization of the exopolysaccharidic matrix. Polar Biol. 43, 1805–1815. https://doi.org/10.1007/s00300-020-02746-8.
Muñoz-Martín, M.Á., Becerra-Absalón, I., Perona, E., Fernández-Valbuena, L., Garcia-Pichel, F., Mateo, P., 2019. Cyanobacterial biocrust diversity in Mediterranean ecosystems along a latitudinal and climatic gradient. New Phytol. 221, 123–141. https://doi.org/10.1111/nph.15355.
Navarro-Noya, Y.E., Jiménez-Aguilar, A., Valenzuela-Encinas, C., Alcántara-Hernández, R.J., Ruíz-Valdiviezo, V.M., Ponce-Mendoza, A., Luna-Guido, M., Marsch, R., Dendooven, L., 2014. Bacterial communities in soil under moss and lichen-moss crusts. Geomicrobiol. J. 31, 152–160. https://doi.org/10.1080/01490451.2013.820236.
Odu, E.A., 1978. The adaptive importance of moss rhizoids for attachment to the substratum. J. Bryol. 10, 163–181. https://doi.org/10.1179/jbr.1978.10.2.163.
Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan.
Olech, M., 2002. Plant Communities on King George Island, in: Beyer, L., Bölter, M. (eds) (Ed.), Geoecology of Antarctic Ice-Free Coastal Landscapes. Springer, Berlin, Heidelberg, pp. 215–231. https://doi.org/https://doi-org.uaccess.univie.ac.at/10.1007/978-3-642-56318-8_12.
Oliver, M.J., Bewley, J.D., 1996. Desiccation-tolerance of plant tissues: A mechanistic overview. Vol. 18. ed. Horticult. Rev.
Olsen, S.R., Cole, C.V., Watanabe, F.S., Dean, L.A., 1954. Estimation of available phosphorus in soil by extraction with sodium bicarbonate. J. Chem. Inf. Model. 53 (53), 1689–1699.
Opelt, K., Chobot, V., Hadacek, F., Schönmann, S., Eberl, L., Berg, G., 2007. Investigations of the structure and function of bacterial communities associated with Sphagnum mosses. Environ. Microbiol. 9, 2795–2809. https://doi.org/10.1111/j.1462-2920.2007.01391.x.
Parada, A.E., Needham, D.M., Fuhrman, J.A., 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. Environ. Microbiol. 18, 1403–1414. https://doi.org/10.1111/1462-2920.13023.
Park, H., Launiainen, S., Konstantinov, P.Y., Iijima, Y., Fedorov, A.N., 2018. Modeling the effect of moss cover on soil temperature and carbon fluxes at a tundra site in Northeastern Siberia. J. Geophys. Res. Biogeosci. 123, 3028–3044. https://doi.org/10.1029/2018JG004491.
Park, M., Lee, H., Hong, S.G., Kim, O.S., 2013. Endophytic bacterial diversity of an Antarctic moss, Sanionia uncinata. Antarct. Sci. 25, 51–54. https://doi.org/10.1017/S0954102012000806.
Philippot, L., Chenu, C., Kappler, A., Rillig, M.C., Fierer, N., 2024. The interplay between microbial communities and soil properties. Nat. Rev. Microbiol. 22, 226–239. https://doi.org/10.1038/s41579-023-00980-5.
Pizarro, M., Contreras, R.A., Köhler, H., Zúñiga, G.E., 2019. Desiccation tolerance in the Antarctic moss Sanionia uncinata. Biol. Res. 52, 46. https://doi.org/10.1186/s40659-019-0251-6.
Pjevac, P., Hausmann, B., Schwarz, J., Kohl, G., Herbold, C.W., Loy, A., Berry, D., 2021. An Economical and Flexible Dual Barcoding, Two-Step PCR Approach for Highly Multiplexed Amplicon Sequencing. Front. Microbiol. 12 https://doi.org/10.3389/fmicb.2021.669776.
Proctor, M.C.F., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Cleavitt, N.L., Mishler, B. D., 2007. Desiccation-tolerance in bryophytes: A review. Bryologist 110, 595–621. https://doi.org/10.1639/0007-2745(2007)110[595:DIBAR]2.0.CO;2.
Pruesse, E., Peplies, J., Glöckner, F.O., 2012. SINA: Accurate high-throughput multiple sequence alignment of ribosomal RNA genes. Bioinformatics 28, 1823–1829. https://doi.org/10.1093/bioinformatics/bts252.
Purcell, A.M., Dijkstra, P., Hungate, B.A., McMillen, K., Schwartz, E., van Gestel, N., 2023. Rapid growth rate responses of terrestrial bacteria to field warming on the Antarctic Peninsula. ISME J. 1–13 https://doi.org/10.1038/s41396-023-01536-4.
Pushkareva, E., Johansen, J.R., Elster, J., 2016. A review of the ecology, ecophysiology and biodiversity of microalgae in Arctic soil crusts. Polar Biol. 39, 2227–2240. https://doi.org/10.1007/s00300-016-1902-5.
Pushkareva, E., Elster, J., Holzinger, A., Niedzwiedz, S., Becker, B., 2022. Biocrusts from Iceland and Svalbard: Does microbial community composition differ substantially? Front. Microbiol. 13, 1–11. https://doi.org/10.3389/fmicb.2022.1048522.
Pushkareva, E., Elster, J., Kudoh, S., Imura, S., Becker, B., 2024. Microbial community composition of terrestrial habitats in East Antarctica with a focus on microphototrophs. Front. Microbiol. 14, 1–10. https://doi.org/10.3389/fmicb.2023.1323148.
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, 590–596. https://doi.org/10.1093/nar/gks1219.
R Core Team, R., 2017. A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria 2017.
Ramos, M., Vieira, G., de Pablo, M.A., Molina, A., Abramov, A., Goyanes, G., 2017. Recent shallowing of the thaw depth at Crater Lake, Deception Island, Antarctica (2006–2014). Catena 149, 519–528. https://doi.org/10.1016/j.catena.2016.07.019.
Richter, I., Herbold, C.W., Lee, C.K., McDonald, I.R., Barrett, J.E., Cary, S.C., 2014. Influence of soil properties on archaeal diversity and distribution in the McMurdo Dry Valleys, Antarctica. FEMS Microbiol. Ecol. 89, 347–359. https://doi.org/10.1111/1574-6941.12322.
Rippin, M., Lange, S., Sausen, N., Becker, B., 2018. Biodiversity of biological soil crusts from the Polar Regions revealed by metabarcoding. FEMS Microbiol. Ecol. 94, 1–15. https://doi.org/10.1093/FEMSEC/FIY036.
Robinson, S.A., Wasley, J., Tobin, A.K., 2003. Living on the edge - Plants and global change in continental and maritime Antarctica. Glob. Chang. Biol. 9, 1681–1717. https://doi.org/10.1046/j.1365-2486.2003.00693.x.
Rosa, L.H., da Silva, T.H., Ogaki, M.B., Pinto, O.H.B., Stech, M., Convey, P., Carvalho-Silva, M., Rosa, C.A., Câmara, P.E.A.S., 2020. DNA metabarcoding uncovers fungal diversity in soils of protected and non-protected areas on Deception Island. Antarctica. Sci. Rep. 10, 1–9. https://doi.org/10.1038/s41598-020-78934-7.
Rossi, F., Mugnai, G., De Philippis, R., 2018. Complex role of the polymeric matrix in biological soil crusts. Plant Soil 429, 19–34. https://doi.org/10.1007/s11104-017-3441-4.
Rousk, K., Jones, D.L., DeLuca, T.H., 2013. Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. Front. Microbiol. 4, 1–10. https://doi.org/10.3389/fmicb.2013.00150.

Rousk, K., Jones, D.L., DeLuca, T.H., 2014. Moss-nitrogen input to boreal forest soils: Tracking 15N in a field experiment. Soil Biol. Biochem. 72, 100–104. https://doi.org/10.1016/j.soilbio.2014.01.031.

Rousk, K., Sorensen, P.L., Michelsen, A., 2016. Nitrogen Transfer from Four Nitrogen-Fixer Associations to Plants and Soils. Ecosystems 19, 1491–1504. https://doi.org/10.1007/s10021-016-0018-7.

Rousk, K., Sorensen, P.L., Michelsen, A., 2017. Nitrogen fixation in the High Arctic: a source of 'new' nitrogen? Biogeochemistry 136, 213–222. https://doi.org/10.1007/s10533-017-0393-y.

Rowland, A.P., Haygarth, P.M., 1997. Determination of Total Dissolved Phosphorus in Soil Solutions. J. Environ. Qual. 26, 410.

Rybalka, N., Blanke, M., Tzvetkova, A., Noll, A., Roos, C., Boy, J., Boy, D., Nimptsch, D., Godoy, R., Friedl, T., 2023. Unrecognized diversity and distribution of soil algae from Maritime Antarctica (Fildes Peninsula, King George Island). Frontiers in Microbiology 14 (June), 1–18. https://doi.org/10.3389/fmicb.2023.1118747.

Saetre, P., Bååth, E., 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce–birch stand. Soil Biol. Biochem. 32, 909–917. https://doi.org/10.1016/S0038-0717(99)00215-1.

Seo, C., Choi, Y.-H., Sohn, J.H., Ahn, J.S., Yim, J.H., Lee, H.K., Oh, H., 2008. Ohioensins F and G: protein tyrosine phosphatase 1B inhibitory benzonaphthoxanthenones from the Antarctic moss Polytrichastrum alpinum. Bioorg. Med. Chem. Lett. 18, 772–775. https://doi.org/10.1016/j.bmcl.2007.11.036.

Seppelt, R.D., Downing, A.J., Deane-Coe, K.K., Zhang, Y., Zhang, J., 2016. Bryophytes within Biological Soil Crusts BT - Biological Soil Crusts: an Organizing Principle in Drylands. Springer International Publishing, Cham, pp. 101–120. https://doi.org/10.1007/978-3-319-30214-0_6.

Shortlidge, E.E., Eppley, S.M., Kohler, H., Rosenstiel, T.N., Zúñiga, G.E., Casanova-Katny, A., 2017. Passive warming reduces stress and shifts reproductive effort in the Antarctic moss, Polytrichastrum alpinum. Ann. Bot. 119, 27–38. https://doi.org/10.1093/aob/mcw201.

Shukla, V., Joshi, G.P., Rawat, M.S.M., 2010. Lichens as a potential natural source of bioactive compounds: a review. Phytochem. Rev. 9, 303–314. https://doi.org/10.1007/s11101-010-9189-6.

Singh, J., Singh, R.P., Khare, R., 2018. Influence of climate change on Antarctic flora. Polar Sci. 18, 94–101. https://doi.org/10.1016/j.polar.2018.05.006.

Slate, M.L., Sullivan, B.W., Callaway, R.M., 2019. Desiccation and rehydration of mosses greatly increases resource fluxes that alter soil carbon and nitrogen cycling. J. Ecol. 107, 1767–1778. https://doi.org/10.1111/1365-2745.13162.

Smith, V.R., 2003. Soil respiration and its determinants on a sub-Antarctic island. Soil Biol. Biochem. 35, 77–91. https://doi.org/10.1016/S0038-0717(02)00240-7.

Smith, D.P., Peay, K.G., 2014. Sequence depth, not PCR replication, improves ecological inference from next generation DNA sequencing. PLoS One 9, e90234.

Soong, J.L., Fuchslueger, L., Marañon-Jimenez, S., Torn, M.S., Janssens, I.A., Penuelas, J., Richter, A., 2020. Microbial carbon limitation: The need for integrating microorganisms into our understanding of ecosystem carbon cycling. Glob. Chang. Biol. 26, 1953–1961. https://doi.org/10.1111/gcb.14962.

Spohn, M., Klaus, K., Wanek, W., Richter, A., 2016. Microbial carbon use efficiency and biomass turnover times depending on soil depth - Implications for carbon cycling. Soil Biol. Biochem. 96, 74–81. https://doi.org/10.1016/j.soilbio.2016.01.016.

Steven, B., Lionard, M., Kuske, C.R., Vincent, W.F., 2013. High bacterial diversity of biological soil crusts in water tracks over permafrost in the high arctic polar desert. PLoS One 8, e71489.

Stewart, K.J., Lamb, E.G., Coxson, D.S., Siciliano, S.D., 2011. Bryophyte-cyanobacterial associations as a key factor in N2-fixation across the Canadian Arctic. Plant Soil 344, 335–346. https://doi.org/10.1007/s11104-011-0750-x.

Turetsky, M.R., 2003. The role of bryophytes in carbon and nitrogen cycling American Bryological and Lichenological Society. https://www.jstor.org/stable/3244721. Bryologist 106, 395–409.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D., Tuittila, E.S., 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytol. 196, 49–67. https://doi.org/10.1111/j.1469-8137.2012.04254.x.

Tveit, A.T., Kiss, A., Winkel, M., Horn, F., Hájek, T., Svenning, M.M., Wagner, D., Liebner, S., 2020. Environmental patterns of brown moss- and Sphagnum-associated microbial communities. Sci. Rep. 10, 1–16. https://doi.org/10.1038/s41598-020-79773-2.

Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., 2002. Net photosynthesis, respiration, and production of the moss sanionia uncinata on a glacier foreland in the high arctic, Ny-Ålesund, Svalbard Author (s): Masaki Uchida, Hiroyuki Muraoka, Takayuki Nakatsubo, Yukiko Bekku, Takeshi Ueno, Hiroshi Ka. Arctic. Antarct. Alp. Res. 34, 287–292.

Van Goethem, M.W., Osborn, A.R., Bowen, B.P., Andeer, P.F., Swenson, T.L., Clum, A., Riley, R., He, G., Koriabine, M., Sandor, L., Yan, M., Daum, C.G., Yoshinaga, Y., Makhalanyane, T.P., Garcia-Pichel, F., Visel, A., Pennacchio, L.A., O'Malley, R.C., Northen, T.R., 2021. Long-read metagenomics of soil communities reveals phylum-specific secondary metabolite dynamics. Commun. Biol. 4, 2–11. https://doi.org/10.1038/s42003-021-02809-4.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707. https://doi.org/10.1016/0038-0717(87)90052-6.

Viitamäki, S., Pessi, I.S., Virkkala, A.-M., Niittynen, P., Kemppinen, J., Eronen-Rasimus, E., Luoto, M., Hultman, J., 2022. The activity and functions of soil microbial communities in the Finnish sub-Arctic vary across vegetation types. bioRxiv 2021.06.12.448001. https://doi.org/10.1101/2021.06.12.448001.

Walker, T.W.N., Kaiser, C., Strasser, F., Herbold, C.W., Leblans, N.I.W., Woebken, D., Janssens, I.A., Sigurdsson, B.D., Richter, A., 2018. Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. Nat. Clim. Chang. 8 https://doi.org/10.1038/s41558-018-0259-x.

Warshan, D., Espinoza, J.L., Stuart, R.K., Richter, R.A., Kim, S.-Y., Shapiro, N., Woyke, T., Kyrpides, C., Barry, K., Singan, V., Lindquist, E., Ansong, C., Purvine, S.O., Brewer, M., Weyman, P.D., Dupont, C.L., Rasmussen, U., 2017. Feathermoss and epiphytic Nostoc cooperate differently: expanding the spectrum of plant-cyanobacteria symbiosis. ISME J. 11, 2821–2833. https://doi.org/10.1038/ismej.2017.134.

Weber, B., Belnap, J., Büdel, B., Antoninka, A.J., Barger, N.N., Chaudhary, V.B., Darrouzet-Nardi, A., Eldridge, D.J., Faist, A.M., Ferrenberg, S., Havrilla, C.A., Huber-Sannwald, E., Malam Issa, O., Maestre, F.T., Reed, S.C., Rodriguez-Caballero, E., Tucker, C., Young, K.E., Zhang, Y., Zhao, Y., Zhou, X., Bowker, M.A., 2022. What is a biocrust? A refined, contemporary definition for a broadening research community. Biol. Rev. 97, 1768–1785. https://doi.org/10.1111/brv.12862.

White, Bruns, T., Lee, S., Taylor, J., 1990. White, T. J., T. D. Bruns, S. B. Lee, and J. W. Taylor. Amplification and direct sequencing of fungal ribosomal RNA Genes for phylogenetics. pp. 315–322.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis, Use R! Springer International Publishing.

Wilson, J.A., Coxson, D.S., 1999. Carbon flux in a subalpine spruce-fir forest: Pulse release from Hylocomium splendens feather-moss mats. Can. J. Bot. 77, 564–569. https://doi.org/10.1139/cjb-77-4-564.

Xiao, B., Hu, K., Ren, T., Li, B., 2016. Moss-dominated biological soil crusts significantly influence soil moisture and temperature regimes in semiarid ecosystems. Geoderma 263, 35–46. https://doi.org/10.1016/j.geoderma.2015.09.012.

Xiao, B., Veste, M., 2017. Moss-dominated biocrusts increase soil microbial abundance and community diversity and improve soil fertility in semi-arid climates on the Loess Plateau of China. Appl. Soil Ecol. 117–118, 165–177. https://doi.org/10.1016/j.apsoil.2017.05.005.

Xiao, B., Ma, S., Hu, K., 2019. Moss biocrusts regulate surface soil thermal properties and generate buffering effects on soil temperature dynamics in dryland ecosystem. Geoderma 351, 9–24. https://doi.org/10.1016/j.geoderma.2019.05.017.

Xie, C.F., Lou, H.X., 2009. Secondary metabolites in bryophytes: An ecological aspect. Chem. Biodivers. 6, 303–312. https://doi.org/10.1002/cbdv.200700450.

Zúñiga-González, P., Zúñiga, G.E., Pizarro, M., Casanova-Katny, A., 2016. Soluble carbohydrate content variation in Sanionia uncinata and Polytrichastrum alpinum, two Antarctic mosses with contrasting desiccation capacities. Biol. Res. 49, 1–9. https://doi.org/10.1186/s40659-015-0058-z.