Soil organic matter interactions along the elevation gradient of the James Ross Island (Antarctica)

Vítězslav Vlček[1], David Juřička[2], Martin Valtera[3], Helena Dvořáčková[1], Vojtěch Štulc[1], Michaela Bednaříková[4], Jana Šimečková[1], Peter Váczi[4], Miroslav Pohanka[6], Pavel Kapler[5], Miloš Barták[4], Vojtěch Enev[7].

[1] Mendel University in Brno, Faculty of AgriSciences, Department of Agrochemistry, Soil Science, Microbiology and Plant Nutrition, Zemědělská 1, 613 00 Brno, Czech Republic.
[2] Mendel University in Brno, Faculty of Forestry and wood technology, Department of Geology and Pedology, Zemědělská 3, 613 00 Brno, Czech Republic.
[3] Mendel University in Brno, Faculty of Forestry and wood technology, Department of Forest Botany, Dendrology and Geobiocoenology, Zemědělská 3, 613 00 Brno, Czech Republic.
[4] Masaryk University, Faculty of Science, Department of Experimental Biology, Kamenice 5, 62500 Brno, Czech Republic.
[5] Masaryk University, Faculty of Science, Department of Geography, Kotlářská 2, 611 37 Brno, Czech Republic.
[6] University of Defence, Faculty of Military Health Sciences, Třebešská 1575, CZ-500 01 Hradec Králové, Czech Republic.
[7] Brno University of Technology, Faculty of Chemistry, Institute of Physical and Applied Chemistry, Purkynova 118, 612 00 Brno, Czech Republic.

Correspondence to: Vítězslav Vlček (vitezslav.vlcek@mendelu.cz)

Abstract. Around half of the Earth's soil organic carbon (SOC) is presently stored in the Northern permafrost region. In polar permafrost regions, low temperatures particularly inhibit both the production and biodegradation of organic matter. In such conditions, abiotic factors such as mesoclimate, pedogenic substrate or altitude are thought to be more important for soil development than biological factors. In Antarctica, biological factors are generally underestimated in soil development due to the rare occurrence of higher plants and the short time since deglaciation. In this study, we aim to assess the relationship between SOC and other soil properties related to the pedogenic factors or properties. Nine plots were investigated along the altitudinal gradient from 10 to 320m at the deglaciated area of James Ross Island (Ulu Peninsula) with a parallel tea-bag decomposition experiment. SOC contents showed a positive correlation with the contents of easily extractable glomalin-related soil proteins (EE-GRSP; Spearman r = 0.733, P=0.031) and the soil buffer capacity (expressed as a ΔpH; Spearman r = 0.817, P=0.011). The soil available P was negatively correlated with altitude (Spearman r = -0.711, P=0.032) and the exchangeable Mg was negatively correlated to the content of rock fragments (Spearman r = -0.683, P=0.050)No correlation was found between the available mineral nutrients (P, K, Ca, Mg) and SOC nor GRSP. This may be a consequence of the inhibition of biologically mediated nutrient cycling in the soil. Therefore, the main factor influencing nutrient availability in these soils seems to be not the biotic, but rather the abiotic environment influencing the mesoclimate (altitude) or the level of weathering (rock content). Incubation in tea bags for 45 days resulted in the consumption and/or translocation of more labile polyphenolic and water-extractable organic matter, along with changes in C content (increase of up to +0.53% or decrease of up to -1.31% C) and a decrease in the C:N ratio (from 12.5 to 7.1-10.2), probably due to microbial respiration and an increase in the abundance of nitrogen binding microorganisms. Our findings suggest that one of the main variables influencing SOC/GRSP

content is not altitude or coarse fraction content (whose correlation with SOC/GRSP were not found) but probably other factors that are difficult to quantify, such as the availability of liquid water.

1 Introduction

The oceans and underground fossil resources are the two largest carbon 'pools' within the global carbon cycle, while topsoil, with an estimated 2,000 + petagrams (Pg-C) of sequestered carbon, is considered the third greatest carbon sink. Most of this carbon (2200Pg-C) is in the form of soil organic matter (SOM), with a limited amount in the form of carbonates (Batjes, 1996). In addition, a further 600 Pg-C is stored in the form of vegetation, while ca. 780 Pg-C is stored in the atmosphere (Rackley, 2017). The oceans, fossil sources, and the atmosphere contain vast stores of carbon, and soil, particularly soil organic matter (SOM), plays a crucial role in the carbon cycle.

Soil carbon dynamics are mainly influenced by climatic factors and soil properties, which determine both the stability and decomposition rate of SOM (Aerts, 1997). Overall, the annual level of soil carbon flux, i.e. the amount of carbon emitted from the soil to the atmosphere due to microorganisms and root respiration, is estimated to be between 70–100 Pg-C (Bond-Lamberty & Thomson, 2010). An important factor in this global carbon cycle flux is SOM mineralisation, which contributes ca. 58 Pg-C annually to the total (Zech et al. 1997; Houghton, 2007). On a local scale, other factors will also play a role in the cycling of carbon, such as the nature of the organic matter, local topography and composition of local vegetation and the microbial community (Makkonen et al., 2012, Bonanomi et al., 2013). Most of these factors, however, are directly or indirectly related to (micro)-climatic conditions (Röder et al., 2016; Wilcke et al., 2008).

Currently, extensive research is being undertaken on the impact of climate change on terrestrial ecosystems, with permafrost areas seen as amongst the most vulnerable (Masson-Delmotte et al. 2006; Durán et al. 2021; Swati et al. 2021). The cold conditions prevalent at high latitudes are assumed to stunt the biological decomposition of organic matter, leading to the formation of soils rich in organic matter. This is especially true in northern hemisphere permafrost regions, where it is estimated that around half of the Earth's soil organic carbon (SOC) is presently stored (Tarnocai et al., 2009). Under Antarctic conditions, however, soil formation processes are thought to be affected more by climate, soil substrate and topography (e.g. altitude) than biological factors, due both to a general absence of higher vegetation and the relatively short period for pedogenesis (soil formation) since deglaciation. Consequently, soils in the Antarctic region tend to have a very low SOM content (Vlček et al. 2018; Pospíšilová et al. 2017; Zvěřina et al. 2012) with rare occurrence of organic horizons (Campbell and Claridge, 1987).

Glomalin, or more commonly 'glomalin-related soil protein' (GRSP; a crude extract containing many substances, including humic acids), is a hypothetical glycoprotein produced abundantly on the hyphae and spores of arbuscular mycorrhizal fungi (AMF; Glomeromycota) in the soil and roots and, as such, is an important component in SOM (Schüßler et al., 2001). Though there is some debate over its origin (e.g. see Gillespie et al. 2011; Holátko et al. 2021), GRSP is thought to be a sequential homologue of the chaperone protein group, involved in the folding of primary proteins, widespread across all domains of life, after their translation on ribosomes (Alaei et al., 2021). Arbuscular mycorrhiza is the most widespread form of mutualism

between photobionts and fungi, represented in 70–90 % of vascular plant species (Basu et al., 2018; Błaszkowski, 2012; Fitter et al., 2008; Smith & Read, 2008). Fossil records indicate that arbuscular mycorrhiza has played an important role in terrestrial ecosystems for as long as 250–400 million years (Harper, et al. 2013; Redecker et al., 2000; Remy et al., 1994), with examples present in the earliest stages of the plant world's colonisation of terrestrial ecosystems (Blackwell, 2000; Pirozynski & Malloch, 1975; Simon et al., 1993).

The main factors determining the presence and growth of AMF appear to be soil properties and vegetation composition (Melo et al 2019). Despite the extreme conditions found in Antarctica, non-lichenised fungi are found in the soil (Bridge & Newsham, 2009; Arenz et al., 2014) alongside lichen, which can produce allelochemicals that affect AMF (Martins et al., 2010; Tigre et al., 2012) by influencing mycorrhizal associations and acting as mutualism stimulators (Santiágo et al., 2018). Furthermore, some organic compounds produced by lichens, such as usnic and perlatolic acid, are also important carbon sources for the soil microbial community (Stark and Hyvärinen 2003). Thus, it can be assumed that lichens and fungi are ecosystem drivers, especially in polar regions eith few other organic compound producers. Alongside the fungi and lichens, mosses, the simplest terrestrial plants, also act as photobionts, thereby playing an important role in SOC dynamics and nutrient cycling, as well as maintaining soil structure, stability and water retention (Lovato et al. 1995; Smith & Read 1997). Numerous previous studies have confirmed symbiotic relationships between AMF and mosses (e.g. Rayner 1927; Kelley 1950; Russell & Bulman 2005). In recent years, the Antarctic (Trinity) Peninsula has been undergoing unprecedented deglaciation due to significant local warming, which has been reported as to be the most rapid on the planet over the last 50 years (Turner et al., 2005). From this perspective, the Antarctic Peninsula region represents a unique research location for early monitoring of the future development of soils in polar regions.

The main objectives of this study were (i) to determine the relationship between GRSP, SOC, SOM and environmental conditions (e.g. altitude, content of coarse soil fraction, availability of liquid water), and (ii) to assess the influence of environmental conditions on GRSP production and SOC content. We hypothesise that the highest GRSP and SOC content will be found in soils located at the lowest elevations, along with the lowest coarse fraction content (H1). We further hypothesise that GRSP content will be negatively correlated with the content of exchangeable phosphorous (P) (H2) and that SOC will be positively correlated with GRSP content (H3). In addition, we will (iii) monitor the initial stages of decomposition of a 'standardised organic matter sample' (tea bag) using thermogravimetric analysis (TGA). We hypothesise a more rapid OM decomposition rate associated with increased soil SOC and GRSP content, and that this will be indicative of environments with increased microbial activity (H4). Our results will contribute to improving our understanding of the processes underlying carbon deposition in (sub-)polar Antarctic areas under ongoing climate change.

2. Material and methods

2.1 Study area

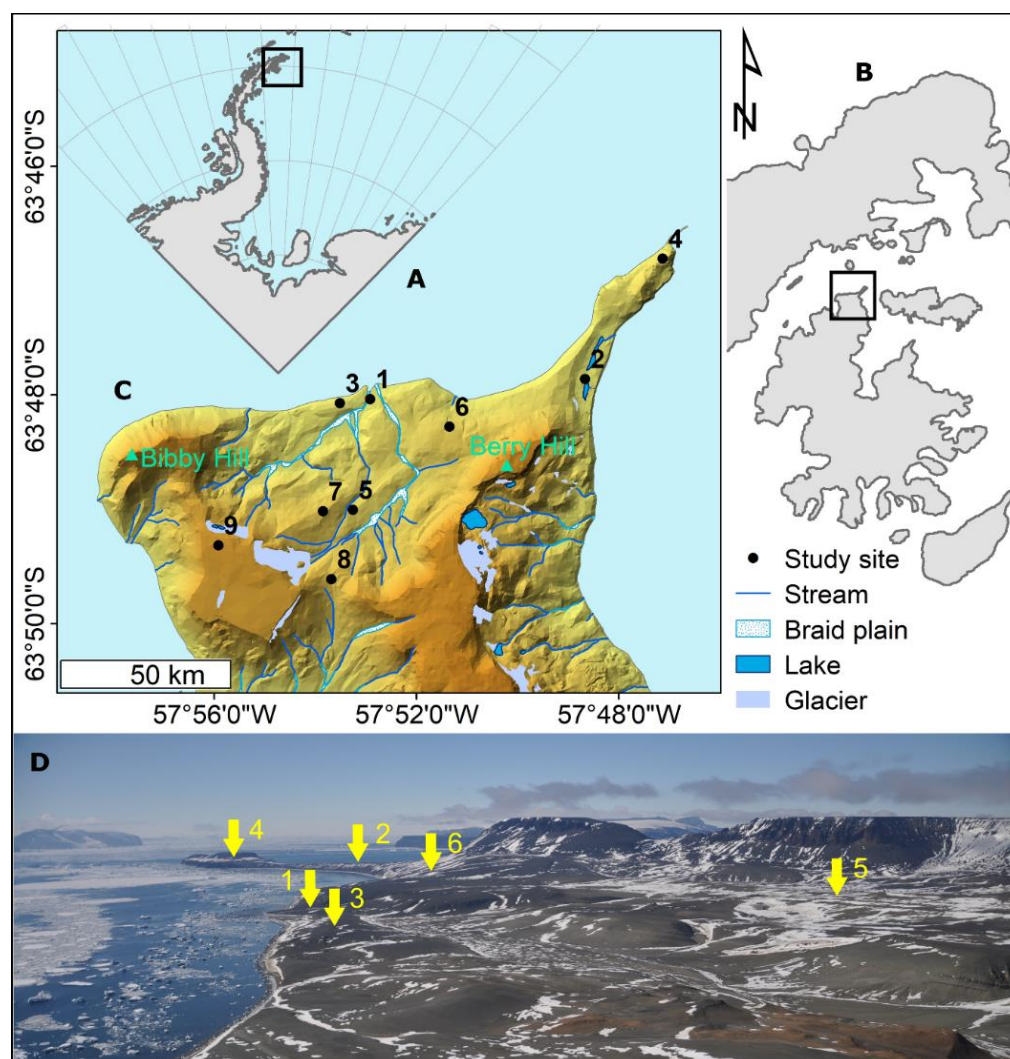
In this study, we focus on soil formation processes near the Johann Gregor Mendel Czech Antarctic Research Station in James
100   Ross Island, one of the largest islands off the north-eastern tip of the Antarctic Peninsula. The island has an area of approx. 2
600km², of which 80% is covered with permanent glaciers. We selected nine study sites on a 300-km² deglaciated area on the
Ulu Peninsula in the northern part of the island, an area covered with valleys and dome glaciers (Fig. 1). The climate is cold,
with a 10-year mean annual temperature of -7.3°C along the coastal area near the Research Station, and -8°C at Bibby Hill
(375-m ~~na~~a.s.l. ~~m.~~) further inland (Matějka et al., 2021), with temperature inversions typically occurring during winter.
105   According to Láska & Prošek (2013), elevation has little influence on temperature amplitude. Annual snow precipitation

reaches 200-mm water equivalent (Strelin & Sone, 1998). Considering that the snow was subsequently redistributed by the wind, the occurrence of liquid water is more a matter of micro-relief.

Figure 1: Situational plan of (A) the northernmost tip of the Antarctic Peninsula, with (B) James Ross Island (inset in A), (C) a digital terrain model (DTM) of the north coast of James Ross Island (Ulu Peninsula), and (D) a panoramic image of (C) with study sites 1–6 indicated (yellow arrows; view from Bibby Hill). Map created in ArcGIS Desktop v.10.8.1, DTM and map layers generated using the Czech Geological Survey ČGS 2009 dataset, situational plan created in Inkscape 1.2.2. Photograph: archive of first author.

2.2 Site description

The nine study sites were selected to cover a topographic gradient from lowest to highest elevation (Table 1). Site 1, known as the 'Long-Term Research Plot' (see Barták et al. 2015), was located close to the Johann Gregor Mendel Czech Antarctic Station. The site consists of two 'plots', one open to the elements (Plot 1a) and the second in an open-topped enclosure (OTE; Plot 1b; Table 1). The land surface is covered by the marsh bryum moss *Bryum pseudotriquetrum* Hedw., which forms thick carpets interspersed with patches of lichen, such as *Rhizoplaca melanophthalma* (DC.) Leuckert & Poelt and the elegant sunburst lichen *Rusavskia elegans* (Link) S.Y. Kondr & Kärnefelt (2003). The area is rich in microbial mats formed of *Nostoc* sp. colonies and cyanobacterial species (e.g. *Microcoleus* sp.), found in seepages. Site 2 was situated between the Large and Small Lachman Lakes and consisted of two plots divided by soil moisture conditions (dryer Plot 2a and waterlogged Plot 2b). The vegetation here is dominated by the lichens *R. elegans*, *Dermatocarpon polyphyllizum* (Korber) Hasse, *Hypnum revolutum* (Mitt.) Lindb., *Bryum argenteum* Hedw. and *Schistidium halinae* Ochyra. The site has a liquid water supply during the short summer period, though this quickly freezes as temperatures drop. Site 3, situated near the research station, was also split into two, with one part close to a seal cadaver (Plot 3a) and the second further away in an unaffected area (Plot 3b), both sites being without vegetation cover. Site 4 was located on the side of the hill forming the Lachman Peninsula. Owing to its proximity of the shoreline, and the annual availability of water from snow melt, the site was classed as semi-moist to moist. Sites supplied with snow melt water have a layer of vegetation comprised of mosses such as *H. revolutum*, *B. argenteum* and *S. halinae*. Site 5 was located on a slope above a rivulet dubbed "the Dirty Stream", and had a surface covered with the mosses *H. revolutum* and *B. argenteum*. Owing to the annual availability of water from snow melting from the western face of the Johnson Messa foothills, the site was classed as medium-moist. Site 6 was located at the foot of the northern slope of Berry Hill and received water from thawing snow fields on the hill. Mosses including *H. revolutum*, *B. argenteum* and *S. halinae* (Barták et al. 2015) were concentrated in the troughs of small periodic streams. Site 7 was located at the foot of the western slope of an un-named hill between "the Bohemian Stream" and "the Dirty Stream" and is classed as dry and without vegetation. Site 8 was located in the "Crame Col pass", a flat plain between the Bibby Point massive and the Lachman Crags. Again, the site is classed as dry and without vegetation. Site 9 was located on the top of Berry Hill, with one sub-plot inside (Plot 9b) an OTE and one outside (Plot 9a). The land surface is comprised of early-developmental stage organomineral substrate and is covered with patches of lichen (*Usnea sphacelata*, *Umbilicaria decussata*).

Table 1: Altitude, bedrock (according to Mlčoch et al., 2020), exposure and vegetation cover at each study site. M = moss, L = lichen.

Site	Altitude (m)	WGS84	Bedrock	Exposure	Vegetation cover
1a, 1b	10	63.80126S 57.88058W	Fluvial sediment	Flat	M, L
2a, 2b	15	63.79875S 57.80982W	Lacustrine sediment	Flat	M, L
3a, 3b	20	63.80178S 57.89056W	Conglomerate with mudstone and sandstone dominated intervals	Flat	None
4	70	63.78135S 57.78379W	Bedded vesicular agglomerate with scoria intercalation	NW	M, L
5	100	63.81735S 57.88680W	Volcanoclastic sandstone, mudstone, subordinate conglomerate	N	M
6	102	63.80543S 57.85468W	Solifluction slope sediment	N	M, L
7	130	63.81751S 57.89668W	Volcanoclastic sandstone, mudstone, subordinate conglomerate	W	None
8	179	63.82741S 57.89416W	Sandstone, siltstone, concretionary horizons, mudstone, accretionary lapilli	NW	None
9a, 9b	320	63.82225S 57.93125W	Basalt, sub-aerial lava (delta caprock)	Flat	L

2.3 Soil properties

Composite soil samples (N=13), consisting of 3 individual samples arranged in a triangular pattern with a 5 m spacing, were collected from a depth of 0–5 cm at each site around the point where experiments on the decomposition of standardized organic matter were to be conducted. oil samples (N=13) were collected from a depth of 0–5 cm at each site at the point where the decomposition of standardised organic matter experiments was to be undertaken (see Section 2.4). Soil samples were dried immediately after collection in an oven at 60-°C. The fraction smaller than 2mm and the soil skeleton were subsequently separated. Only the fine-earth fraction was used for further analyses.

The soil reaction (pH) was determined in either distilled water or 1 M KCl at a ratio of 1:2.5 and measured on 914 Metrohm pH Meter/Conductometer. Available nutrients (P, K, Ca, Mg) were extracted using Mehlich III reagent (Mehlich A., 1984)

and then assessed using an Agilant 55B AA atomic emission spectroscope (Agilent, CA, USA). All analyses were performed in triplicate. For a full description of the TGA and derivative thermogravimetric (DTG) analysis of soil (other elements – SOC, N), see section 2.4.1 In this context, ΔpH refers to changes or differences in pH values (pH in water minus pH in KCl). The term ΔpH was used to indicate the difference in hydrogen ion concentration. However, a fixed ΔpH can have varying effects depending on the initial pH of the water. Therefore, it is recommended to calculate the corresponding change in hydrogen ion concentration ($\Delta[H+]$) in addition to ΔpH to fully understand the chemical implications of pH differences (Fassbender, et.al. 2021).

2.3.1 Glomalin (GRSP) determination

Easily-extractable glomalin-related soil protein (EE-GRSP) was extracted from soil according to the procedure of Wright & Upadhyaya (1996). Briefly, 1g of soil sample was added to 8mL of 20mM trisodium citrate solution (pH 7.0). The mixture was homogenised for 30min on a GFL 3015 orbital shaker (Gesellschaft für Labortechnik mbH, Germany). The sample was then autoclaved for 60min at 121°C and, after cooling, it was immediately centrifuged for 30min at 3 900rpm on an MPW 223e centrifuge (MPW Med. Instruments, Poland). The supernatant was then frozen at -22°C for later analysis using the method of Bradford (1976). Measurements were made in triplicate for each sample. Total glomalin (GRSP) was processed in the same manner, but instead of a 20mM trisodium citrate solution, a 50mM solution (pH 8.0) was used. All analyses were performed in triplicate.

2.4 Standardised organic matter (tea-bag) decomposition experiment

Two four-sided tetrahedral nylon bags containing 2g (dry weight) of green tea (89% Lipton Unilever green tea (Keuskamp et al., 2013); EAN: 8714100770542) were placed into pits 5 cm below the surface at each site during the 2019 summer season and then recovered with soil. The bags had a mesh size of 0.25 mm, allowing microorganisms to enter the bags (Keuskamp et al., 2013). After 45 days of exposure to the active permafrost layer, the tea bags were removed and then dried at 60-°C, reweighed, and transported back to the Czech Republic for further analysis. Note that, though tea bags were buried at all 13 sites, only half of the samples (7 of 13) were ultimately analysed as i) some samples were destroyed by periodic freeze/thaw cycles at wetter locations, despite the test taking place in the Austral summer, and ii) some samples were taken or moved by the South Polar skua (*Stercorarius maccormicki* H. Saunders).

2.4.1 Thermogravimetric analysis (TGA)

Analysis of the relative element content in organic matter from the soil and tea samples was carried out through TGA analysis. First, 0.8–1.1-mg of the tea and 8–11-mg of soil werewas weighed into tin capsules, which were then packaged and combusted at 980 °C using oxygen (O_2) injection as the combustion medium and helium as the carrier of the products formed. Relative content of nitrogen (N), carbon (C), and hydrogen (H) were evaluated based on gas chromatography determined using an EA

3000 CHNOS elemental analyser (Euro Vector, Pavia, Italy), using sulphanilamide as a standard reference for analyser calibration. The content of O_2 was calculated from the residual combustible mass, and the data obtained were then being adjusted for the moisture and ash content of the samples. All analyses were performed in triplicate. Sulphur (S) content proved to be below the detection limit (0.5 wt.%) for all samples analysed.

Thermogravimetry (TG) analysis -was used to assess changes in the mass of the sample over time as temperature changes. For the soil samples, 5–15 mg of the sample was weighed onto a platinum sample pan and placed into a TA Q50 thermogravimetric analyser (TA Instruments, New Castle, DE, USA). The residual mass of the sample was then continuously recorded ($\pm$0.1 mass accuracy) as the sample was heated from ambient temperature to 950-°C at 10-°C÷min^{-1} in an oxidative atmosphere (air) or inert N2 atmosphere (both 50-mL÷min^{-1} flow rate), inducing a process of thermal degradation under pyrolysis. All measured thermograms were evaluated using the TA Universal Analysis 2000 software, in which the derivation of the TG curves was also performed. DTG analysis of the tea samples was undertaken in the same manner as the soil samples, but using TA Q5000 thermogravimetric analyser (TA Instruments, New Castle, DE, USA). Prior to measurement, all samples were homogenised by grinding in an agate mortar. For both soil and tea, the moisture content was determined from the relative weight loss corresponding to the minimum DTG curve, the residual mass at 950-°C representing the ash content (inorganic moieties). The SOM content was calculated according to the relationship SOM $(\mathrm{mg} \cdot \mathrm{g}^{-1}) = 1 - (\mathrm{wt.}_{ash} + \mathrm{wt.}_{moisture}) \cdot 1000$, and the data were obtained by thermogravimetric analysis using the oxidative atmosphere.

2.4.2 UV-Vis spectrophotometry

UV-Vis spectrophotometry was used to measure polyphenolic and water-extractable compounds from organic matter in tea samples, according to the modified Folin-Ciocalteho method of Gao et al. (2019), using a Hitachi U3600H dual beam UV-Vis spectrometer (Hitachi, Tokyo, Japan) with a wavelength range of 650–850-nm and gallic acid as a calibration solution. The content of all water-extractable polyphenolic compounds was measured in triplicate for each sample.

2.5 Statistical analysis

The difference between potential and actual soil reaction (pH) was expressed as $\Delta\mathrm{pH} = \mathrm{pH}_{KCl} - \mathrm{pH}_{water}$. The absolute difference between potential and actual H$^+$ concentration was calculated by de-logarithming the pH values as $\Delta[\mathrm{H}^+] = 10^\wedge(-\mathrm{pH}_{KCl}) - 10^\wedge(-\mathrm{pH}_{water})$. Pairwise regression analysis was used to assess the significant difference between soil properties and selected environmental covariates in R v.4.2.2 (R Core Team 2022). All regression models were considered statistically significant at $p < 0.05$.

3. Results

3.1 Soil nutrient content

Analysis of nutrient content at each site revealed very low levels of exchangeable phosphorus (P), ranging from 0.0051–0.037 mg.g^{-1}, highly variable calcium (Ca) levels, ranging from 2.75–11.64 mg.g^{-1}, and magnesium (Mg) and potassium (K) levels ranging from 0.65–2.30 mg.g^{-1} and 3.57–2.20 mg.g^{-1}, respectively (Table 2). The values of pH$_{water}$ and pH$_{KCl}$ ranged from 6.48–8.17 (from slightly acidic to alkaline) and 5.53–6.67 (from acidic to neutral), respectively (Table 2). The storage acidity (ΔpH) ranged from -0.74 – -1.79, the difference in hydrogen ion concentration ($\Delta[H^+]$) from $10^{(-5.57)}$ – $10^{(-6,71)}$ and the coarse fraction (>2.00mm) content from 3.8–64.4% mass (Table 2).

Table 2: Analysis of available nutrients (P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium; mg.kg^{-1}; according to Mehlich 1984) content at each study site, along with percentage of coarse fraction. Site moisture conditions: w (wet)= liquid water throughout the vegetation period, sd (semi-dry)= variable dry periods, d = dry site. pH values: pH$_{water}$ = in distilled deionised water, pH$_{KCl}$ = in potassium chloride solution, ΔpH = difference between pH$_{water}$ and pH$_{KCl}$, $\Delta[H^+]$ = converted to hydrogen ion concentration.

Site	Moisture	P	K	Ca	Mg	pH$_{water}$	pH$_{KCl}$	ΔpH	$\Delta[H^+]$	Coarse Texture fraction class > 2 mm (% mass)
1a	sd	17.1±0.3	757±7	4537±74	956±13	7.22±0.02	5.78±0.05	-1.4	$10^{(-5.80)}$	23.3
1b	sd	13.9±0.3	446±12	3710±91	754±16	6.98±0.00	5.87±0.01	-1.1	$10^{(-5.91)}$	13.6
2a	w	37.1±0.6	1417±23	4952±99	2340±40	6.48±0.01	5.74±0.06	-0.7	$10^{(-5.83)}$	6.2
2b	sd/w	35.9±0.4	1400±22	4735±96	2314±40	6.54±0.03	5.76±0.04	-0.8	$10^{(-5.84)}$	3.8
3a	d	20.2±0.4	703±13	3976±83	867±39	8.13±0.01	6.34±0.01	-1.8	$10^{(-6.35)}$	16.5
3b	d	18.1±0.3	1258±24	3528±70	861±15	8.00±0.04	6.45±0.01	-1.6	$10^{(-6.46)}$	23.6
4	sd/w	8.8±0.2	2201±33	3418±68	1855±15	6.56±0.07	5.53±0.00	-1,0	$10^{(-5.57)}$	49.5
5	w	14.9±0.3	354±16	11640±133	670±32	7.69±0.02	6.67±0.02	-1,0	$10^{(-6.71)}$	22.2
6	w	14.9±0.3	882±14	4739±95	1652±11	7.29±0.00	5.57±0.03	-1.7	$10^{(-5.58)}$	25.1
7	d	10.1±0.2	394±20	3841±77	861±28	8.17±0.01	6.67±0.03	-1.5	$10^{(-6.68)}$	63.4
8	d	5.1±0.2	357±6	9687±184	649±15	8.03±0.02	6.67±0.04	-1.4	$10^{(-6.69)}$	12.8
9a	d/sd	12.1±0.2	1000±23	2745±68	1007±19	7.82±0.04	6.07±0.01	-1.8	$10^{(-6.08)}$	57.9

| 9b | */**d/sd | 10.9±0.3 | 1185±19 | 3479±69 | 1255±22 | 7.30±0.03 | 5.85±0.03 | -1.5 | $10^{(-5.87)}$ | 53.2 |

3.2 Relationship between soil organic related fractions and environmental conditions

225 GRSP and EE-GRSP content were generally low, ranging from 0.096–0.968 mg.g^{-1} and 0.072–0.752 mg.g^{-1}, respectively (Table 3). SOM content ranged from 2.79–15.04 wt.%, while SOC content ranged between 0.09–9.89 wt.%., though, with few exceptions, most values were ≤ 1.5 wt.% (Table 3).

We recorded a very strong positive correlation between SOC and SOM (+0.93) and between GRSP and EE-GRSP (+0.91), and a strong correlation between EE-GRSP and SOC (+0.73). On the other hand, we recorded strong negative correlations 230 between coarse fraction content and EE-GRSP (-0.67) and GRSP (-0.80), respectively, and between altitude and exchangeable P content (-0.71) (Figure 2).

3.3 Thermogravimetric and derivative thermogravimetric analysis of soil samples

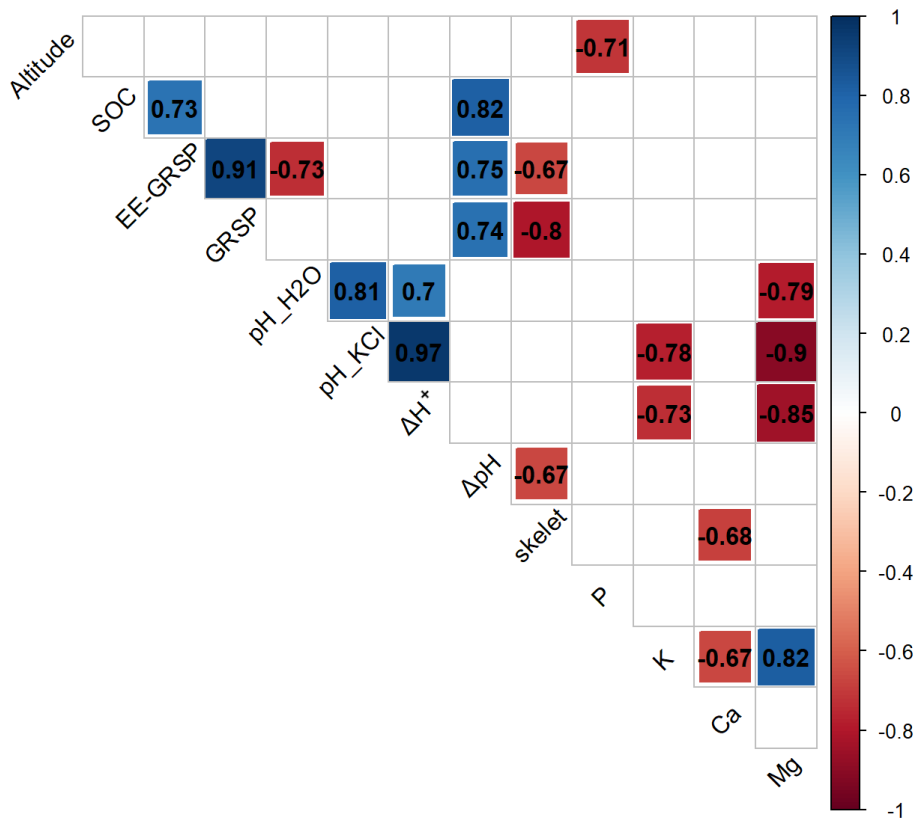
Highest levels of soil loss (1.48–7.35 wt.%) were recorded in the lowest temperature range 200–430 °C, indicating that the majority of SOM fractions were relatively labile (Table 3). The mass loss in this temperature range was strongly correlated 235 with both SOM (0.87) and SOC (0.73) content (Figure 2). Relatively high mass loss (0.77–2.76 wt.%) was also recorded at 430–590 °C, a range typically associated with loss of mineral fractions (i.e. clays) and organic matter associated with the clay fraction. The lower levels of mass loss recorded at 590–750 °C (0.36–1.73 wt.%) are typically representative of the least labile carbonates. Unexpectedly, the highest mass loss at Site 6 was recorded at 430–590 °C (1.84 wt.%), where N and SOM content are 0.1 wt.% and 1.4 wt.%, respectively (Table 3).

240

Figure 2: Correlation diagram for selected environmental variables (altitude) and physical (skelet = coarse fraction content), chemical (SOC = soil organic carbon, EE-GRSP = easily extractable glomalin-related soil protein, GRSP = glomalin-related soil protein) and physicochemical (pH, exchangeable ion: K = potassium, Ca = calcium, Mg =

magnesium, P = phosphorus contents) properties in Antarctic topsoil. Only significant correlations at P<0.05 are shown.

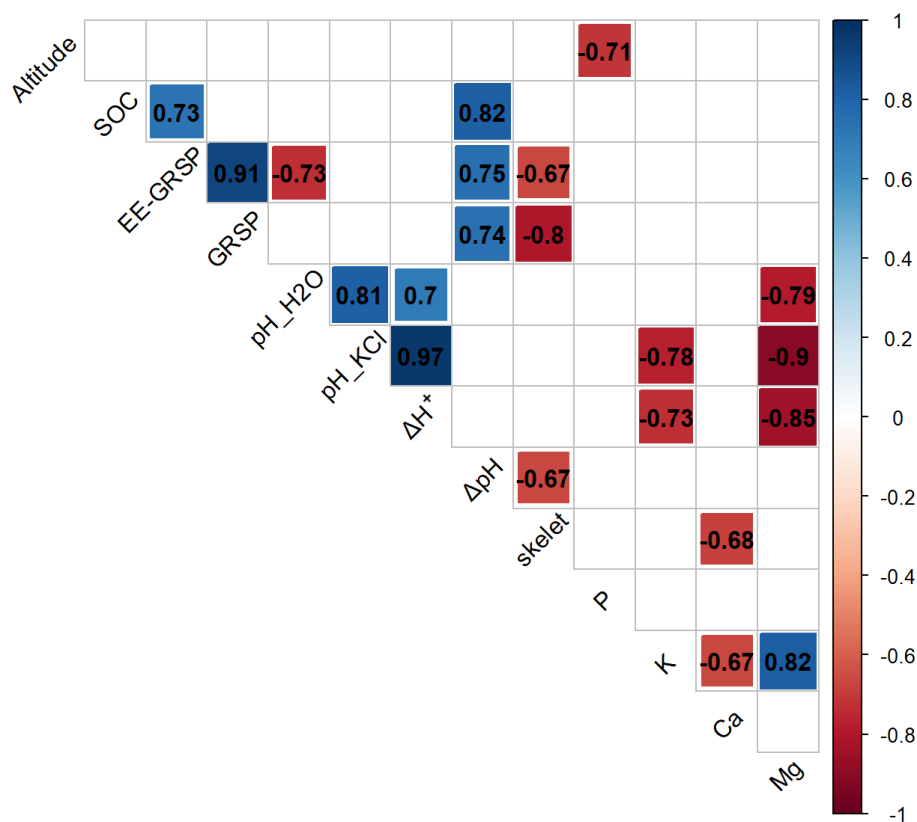



Table 3: Soil properties analysed thermogravimetry. Soil organic related fraction content, showing glomalin fractions (EE-GRSP = easily extractable glomalin-related soil protein, GRSP = glomalin-related soil protein), soil organic matter (SOM), soil organic carbon (SOC) and total nitrogen (N; mean±SE) and mass loss (wt. %) during thermogravimetry over three temperature ranges, T1 = 200–430°C, T2 = 430–590°C, T3 = 590–750°C.

Site	EE-GRSP (mg.g^{-1})	GRSP (mg.g^{-1})	SOC (mg.g^{-1})	N (mg.g^{-1})	SOM (mg.g^{-1})	T1 (wt.%)	T2 (wt.%)	T3 (wt.%)
1a	0.160±0.002	0.216±0.007	2.5 ±0.56	0.2 ±0.02	33.4	1.77	1.16	0.61
1b	0.088±0.005	0.560±0.008	4.7 ±0.09	0.4 ±0.01	38.0	2.05	1.08	0.55
2a	0.752±0.013	0.968±0.006	98.9 ±3.31	6.3 ±0.28	143.8	7.35	2.76	1.73
2b	0.640±0.002	0.904±0.005	45.1 ±1.15	3.6 ±0.05	150.4	6.70	1.70	1.21
3a	0.112±0.009	0.176±0.001	2.4 ±0.05	0.2 ±0.01	32.2	1.60	1.07	0.51
3b	0.080±0.001	0.192±0.007	0.9 ±0.02	0.1 ±0.00	27.9	1.48	0.99	0.41

4	0.552±0.004	0.672±0.006	31.2 ±1.49	0.2 ±0.01	65.5	3.31	1.08	0.79
5	0.128±0.003	0.192±0.002	5.9 ±0.13	0.6 ±0.00	41.7	2.32	1.16	0.65
6	0.104±0.007	0.136±0.009	1.4 ±0.07	0.1 ±0.01	35.5	1.75	1.84	1.29
7	0.072±0.006	0.096±0.004	11.5 ±1.11	0.3 ±0.01	46.6	2.03	1.34	0.90
8	0.216±0.001	0.760±0.015	14.6 ±0.74	0.2 ±0.02	40.7	1.66	1.05	0.69
9a	0.088±0.006	0.120±0.002	1.1 ±0.08	0.1 ±0.01	31.1	1.70	0.77	0.36
9b	0.176±0.004	0.200±0.003	3.9 ±0.14	0.3 ±0.00	38.7	1.89	1.00	0.51

3.4 Thermogravimetric and derivative thermogravimetric analysis of standardised organic matter (tea) before and after decomposition.

For all samples, DTGs of tea before decomposition showed a gradual decrease in mass as temperatures increased (Figs. 3, 4),
255 with the most rapid loss coinciding with three peaks at 204, 300 and 350-°C, indicating loss of volatile compounds, hemicellulose and cellulose, respectively (Fig. 3). Peak mass loss during pyrolysis occurred at 300-°C, with a lesser peak occurring at 350-°C, though there was considerable overlap in the two peaks.

~~Figure 3: Derivative thermogravimetric curve of a pre-decomposition tea sample during pyrolysis in an N₂ atmosphere.~~
260

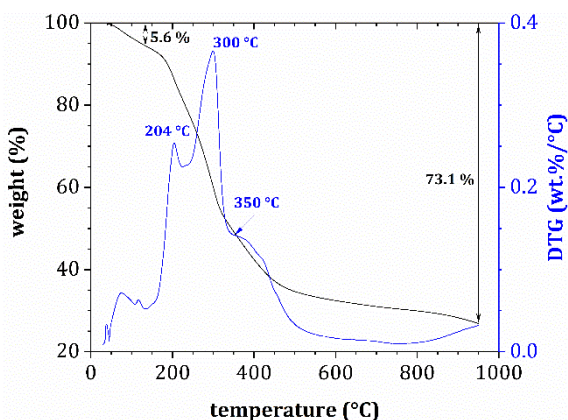



Figure 3: Derivative thermogravimetric curve of a tea sample (before decomposition) during pyrolysis in an N₂ atmosphere.

265 DTG plots for post-decomposition samples (Fig. 4) showed two main mass loss peaks at 320–351-°C and 396–416-°C. In all cases, the first peak found in pre-decomposition samples around 204 °C was either missing or much less pronounced. On the other hand, a less pronounced peak appeared sporadically in post-decomposition samples over the range 617–648-°C, which could be assigned to the highly stable substances such as lignin residues or humic substances in SOM. As such, post-

decomposition OM showed higher thermal stability than the original samples, with the second and third mass loss peaks shifted

270   slightly toward higher temperatures.

Figure 4: Post-decomposition tea samples derivative thermogravimetric curves (45 days exposure) during pyrolysis in

275   **an N_2 atmosphere. Left = site 3a (seal cadaver); Right = site 6.**

While N content increased at all sites post-decomposition (up to +2.6 wt.%), C content remained relatively stable, with only a slight increase or decrease (-1.01 – +1.3 %). As a result, the C:N ratio decreased from 12.5 to 7.1–10.2 post-decomposition, with the highest values recorded in the OTE at Site 9b. Overall, the C:N ratio tended to be lowest at lower altitude sites and

280   sites supplied with water (see Tables 1, 4). In all cases, abundance of polyphenolic and water-extractable compounds decreased post-decomposition, while ash content decreased slightly at OTE sites (Sites 1b, 9b) but increased elsewhere, with the greatest increase (+3.14 %) at site 2. At all sites, the amount of OM decreased by 2–6 % post-decomposition (Table 4).

Table 4: thermogravimetric analysis of tea samples pre- and post-decomposition. Values for nitrogen (N) and carbon

285   **(C) = mean±SE, OM = organic matter.**

Site	N (wt.%)	C (wt.%)	C:N ratio	Ash (wt.%)	OM (wt.%)	Polyphenols (mg·g^{-1})	Water-extractable compounds (mg·g^{-1})
			Before decomposition				
	3.69±0.06	46.18±0.66	12.5	4.02	90.70	78.78±8.54	8.88±1.04
			After decomposition				
1b	6.53±0.45	46.44±0.28	7.1	3.93	87.52	2.62±0.21	0.41±0.11
2a	6.04±0.19	46.71±0.75	7.7	7.16	84.84	2.65±0.18	1.12±0.30

3a	5.42±0.28	45.31±0.21	8.4	4.24	87.62	17.51±6.49	1.24±0.19
3b	4.93±0.09	44.94±0.20	9.1	4.96	85.93	8.46±0.81	0.99±0.10
6	6.30±0.27	47.35±0.71	7.5	5.33	87.58	3.55±0.26	0.59±0.11
7	4.62±0.19	44.87±0.24	9.7	4.29	86.84	16.92±0.29	2.02±0.30
9b	4.42±0.09	45.17±0.52	10.2	3.58	88.62	103.04±25.01	5.39±0.46

4. Discussion

4.1 Interaction between environmental conditions and available nutrients in fine-earth (Hypotheses H1 and H2).

~~We hypothesise that the highest GRSP and SOC content will be found in soils located at the lowest elevations, along with the lowest coarse fraction content (H1). We further hypothesise that GRSP content will be negatively correlated with content of~~
290 ~~exchangeable phosphorous (P) (H2)~~

The lack of any correlation between available nutrients and OM in our results suggest that the main factor determining nutrient distribution in Antarctic deglaciated soils is not presence of organic matter but rather environmental factors that accelerate mineral weathering processes. This is most likely due to the inhibition of biologically mediated nutrient cycling in the soil due to the extreme aridity and cold prevalent in Antarctica (McCraw, 1960; Campbell & Claridge, 1987). The important role of
295 environmental factors, such as water availability and topography, is backed up by the positive correlation between available P and altitude (Fig. 2; thereby disproving Hypothesis H2). Unlike N, P lacks a biological fixation mechanism (Alewell et al., 2020). While sources of P are diverse, the primary source, particularly within Antarctic conditions, is through weathering of apatite (Filippelli & Souch, 1999), i.e. the inorganic 'pool' in which unweathered, mostly biologically-unavailable material, typically dominates (Cross & Schlesinger, 2001). A second major source, particularly in coastal areas, could be seabird
300 droppings; however, P values recorded in previous studies (e.g. Zhu et al., 2014) suggest that levels in seabird droppings are around three orders of magnitude lower than those recorded in this study. As such, the correlation between available P and altitude is more likely to be indicative of a decrease in weathering intensity along the altitudinal gradient, with the intensity of weathering affected by the presence of running liquid water.

We forecast that ongoing warming from global climate change observed since the second half of 20th century will lead to an
305 expansion in soil biodiversity and vegetation cover along the Antarctic weathering gradient due to an increase in mineral weathering intensity as levels of liquid water increase (Turner et al., 2005). This will further strengthen the relationship between fungal and photoautotrophic organisms, i.e. AMF, whereby the fungi give plants access to mineral-weathered P and the plants provide products of photosynthesis (i.e. C) to fungi. According to Blackwell (2000) and Simon (1993), this relationship has been in place since the earliest stages of terrestrial ecosystem colonisation.

4.2 Relationship between soil organic carbon and easily extractable glomalin-related soil protein (Hypothesis H3)

We further hypothesise that SOC will be positively correlated with GRSP content (H3). Under the Antarctic conditions, the main sources of SOC are mosses (carbon = 40–50%; Green et al., 2008; Vingiani et al., 2004), lichens (genus Usnea; carbon = 25%; Shukla et al., 2019) and microorganisms associated with AMF (GRSP), with AMF hyphae containing around 50% carbon (Zhu & Miller, 2003) and glomalin (associated with AMF) containing levels range from 28 to 45% (Huang et al., 2011). In our case, however, we believe the main source of SOC was from glomalin (GRSP), as suggested by i) the strong correlation (r = 0.73) between EE-GRSP and SOC (thus confirming hypothesis H3), and ii) the relatively low SOC in SOM (Table 3), which imply a lower presentation of SOC (54% on average) in SOM (it means conversion factor (0.361.600 with r=0.907). for the linear curve correlation between SOC and SOM (Table 3). In comparison, van Bemmelen (1889) reported a typical content of carbon 58% with conversion factor of 0.581.724, while the UN FAO (2019) reports a common content between conversion factor of 0.43 to 0.58 (i.e. 43 5 and 58% SOC in SOM). This would suggest that the absence of any relationship between the glomalin fraction (GRSP) and mass loss over the first temperature interval during TGA (where OM fraction mass loss is expected) could have been caused by the lower C content in both glomalin fractions, i.e. lower than the commonly reported 58% C in OM (van Bemmelen, 1889).

The glomalin fraction content reported in this study (up to 0.97 mg.g^{-1} GRSP; Table 2) was considerably higher than that reported in a previous study from James Ross Island, i.e. 0.01–0.15mg.g^{-1} (Pohanka & Vlček, 2018). This was most likely due to the study site of Pohanka & Vlček (2018) being situated close to the Whisky Glacier (Davis Dome), where the environmental conditions were unsuitable for vegetation. Surprisingly, the glomalin (GRSP) values in this study were actually higher than those recorded for agricultural soils, i.e. 0.30–0.70 mg.g^{-1} (Wright & Anderson, 2000; Wuest et al., 2005). The high glomalin values (GRSP) recorded in our study were the result of slow mineralisation of OM and its subsequent long-time accumulation. Glomalin (GRSP) clearly plays an important role in Antarctic soil genesis, not least due to its influence on buffering capacity. Correlations between Δ pH and SOC (0.82), Δ pH and GRSP (0.74) and Δ pH and EE-GRSP (0.75) all tend to indicate that fungi and their metabolites are contributing to the soil's buffering capacity; though the absence of any correlation between $\Delta[H^+]$ and SOC, EE-GRSP and GRSP does introduce some uncertainty.

As mentioned by Vlček et al. (2018), a SOC content of $\geq$ 2% is not unusual in Antarctica; however, it should be noted that Vlček et al. (2018) measured SOC was using the modified Walkley-Black method (1934), which can underestimate SOC values. Walkley (1947), for example, state that Walkley-Black recovery factors can range from 60 to 86%, while Grewal et al. (1991) reported recovery factors of 75 to 85%. In the present study, TGA/DTG values were comparable with those of Siewet (2004), who reported values ranging from 0.7 to 3.2% for 28 sites without vegetation on King George Island in the South Shetlands.

4.3 Changes in the decomposition of standardised organic matter indicated by thermogravimetric analysis (Hypothesis H4)

We hypothesise a more rapid OM decomposition rate associated with increased soil SOC and GRSP content, and that this will be indicative of environments with increased microbial activity (H4). As expected, OM decomposition was intrinsically linked with microbial activity (Fig. 4; Hypothesis H4). There was an apparent decrease in the abundance of polyphenolic and water-extractable compounds in the post-decomposition tea sample, indicating that the most thermally-labile OM fractions (corresponding to a TGA peak at 204°C in the original sample) had all been 'lost' during decomposition. Furthermore, the partially overlapping between the TGA and DTG curves in the incubated samples may indicate the formation of a complex organic compounds from labile fractions (which are characterised by a slightly bounded thermal stability).

Unexpectedly, we observed little change in total C post-decomposition but a noticeable decrease in the C:N ratio, suggesting that the tea sample had been colonised by N-fixing microorganisms (Utalie et al., 2021; Tóth et al., 2017; Kouchi et al., 2004). This could also help explain the relatively low C loss across sites, with any losses during mineralisation being compensated for by OM produced from microbial biomass (Paul; 2014; Keuskamp et al., 2013). This phenomenon is typical for the initial phase of mineralisation, where balance in the system has yet to be established (Golchin et al., 2018).

5. Conclusion

The study indicates that nutrient distribution in Antarctic deglaciated soils is primarily influenced by environmental factors, such as topography, rather than the presence of OM. The altitude determines water availability as the main factor accelerating the weathering of rock minerals. This was supported by lack of any connections between available nutrients and OM, most likely a result of inhibition of biologically mediated nutrient cycling in the soil due to the extreme climate. ~~The primary factor affecting nutrient accessibility in Antarctic soils proved not to be OM content but rather abiotic environmental factors that accelerate the weathering of minerals~~Global warming is expected to enhance soil biodiversity and vegetation cover along the Antarctic weathering gradient by increasing mineral weathering intensity and water availability. ~~, e.g. availability of liquid water.~~~~Most studies to date have assumed that climate, soil substrate and altitude are more important for Antarctic soil development than biological factors. In this study, we found that the main source of SOC in the deglaciated soils in James Ross Island, Antarctica, was the GRSP produced by microorganisms, an assumption supported by the low SOC:SOM conversion factor.~~ The study confirms a positive correlation between SOC and GRSP content, identifying glomalin produced by microorganisms as a primary source of SOC in Antarctic soils. The higher GRSP content observed in this study suggests slow mineralisation and long-term accumulation of organic matter, highlighting glomalin's role in the Antarctic soil development. ~~During d~~Decomposition ~~of a standardised OM sample~~test ~~(tea bag),~~shows a decrease in the most labile OM fractions (polyphenols and water-extractable compounds) and a shift in the carbon-to-nitrogen ratio, suggesting colonisation by nitrogen-fixing microorganisms, which helps balance carbon loss during the initial phases of mineralisation. ~~the most labile~~

OM elements (polyphenols and water-extractable compounds) were lost relatively rapidly, after which the OM was colonised by N-fixing microorganisms, resulting in a decrease in the C:N ratio.

The primary factor affecting nutrient accessibility in Antarctic soils proved not to be OM content but rather abiotic
375 environmental factors that accelerate the weathering of minerals, e.g. availability of liquid water. Nevertheless, OM had a significant buffering function where GRSP was important in the development of polar soils. This was supported by the lack of any relationship between available nutrients and OM, most likely a result of inhibition of biologically mediated nutrient cycling in the soil due to the region's extreme aridity and cold climate.

Acknowledgement
380

The authors would like to thank to all the members of at Masaryk University based Czech Antarctic Research Programme for providing data and for fieldwork support.

References
385

Aerts, R.: Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. Oikos, 79(3), 439-449, https://doi.org/10.2307/3546886, 1997.

Alaei, L., Ashengroph, M. and A Moosavi-Movahedi, A.: The concept of protein folding/unfolding and its impacts on human health. Adv. Protein Chem. Struct. Biol., 227–278, DOI: 10.1016/bs.apcsb.2021.01.007, 2021.

390 Alewell, C., Ringeval, B., Ballabio, C., Robinson D. A., Panagos P. and Borrelli P.: Global phosphorus shortage will be aggravated by soil erosion. Nat Commun 11, 4546, https://doi.org/10.1038/s41467-020-18326-7, 2020.

Arenz, B. E., Blanchette R. A. and Farrell R. L. Fungal diversity in Antarctic soils, in: Antarctic Terrestrial Microbiology, edited by Cowan D. A., Springer-Verlag, Berlin Heiderberg, 35–53, DOI: 10.1007/978-3-642-45213-0_3, 2014.

Barták, M., Váczi, P., Stachoň, Z. and Kubešová, S.: Vegetation mapping of moss-dominated areas of northern part of James
395 Ross Island (Antarctica) and a suggestion of protective measures. Czech Polar Rep., 5, 75-87, https://doi.org/10.5817/CPR2015-1-8, 2015.

Basu, S., Rabara, R.C., Negi, S., AMF: The future prospect for sustainable agriculture. Physiol. Mol. Plant Pathol., 102, 36–45, https://doi.org/10.1016/j.pmpp.2017.11.007, 2018.

Batjes N. H.: Total carbon and nitrogen in the soils of the world. Eur J Soil Sci, 47(2), 151–163, https://doi.org/10.1111/j.1365-
400 2389.1996.tb01386.x, 1996.

Blackwell, M.: Evolution. Terrestrial life - fungal from the start? Science 289, 1884–1885, doi: 10.1126/science.289.5486.1884, 2000.

Błaszkowski, J.: Glomeromycota. W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, 303 pp., ISBN 978-83-89648-82-2. 2012.

405 Bonanomi, G., Incerti, G., Giannino, F., Mingo, A., Lanzotti, V. and Mazzoleni, S.: Litter quality assessed by solid state ^{13}C NMR spectroscopy predicts decay rate better than C/N and Lignin/N ratios. Soil Biol. Biochem., 56, 40–48. https://doi.org/10.1016/j.soilbio.2012.03.003, 2013.

Bond-Lamberty B. and Thompson A.: A global database of soil respiration data. Biogeosciences, 7(6), 1915–1926, https://doi.org/10.5194/bg-7-1915-2010, 2010.

410 Bradford M. M.: A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem., 72(1–2), 248–254, https://doi.org/10.1016/0003-2697(76)90527-3, 1976.

Bridge P. D. and Newsham K. K.: Soil fungal community composition at Mars Oasis, a southern maritime Antarctic site, assessed by PCR amplification and cloning. Fungal Ecol., 2, 2, 66–74, https://doi.org/10.1016/j.funeco.2008.10.008, 2009.

Campbell I. B. and Claridge G. G. C. Antarctica: Soils, Weathering Processes and Environment. Developments in Soil Science

415 16, Elsevier Science, 367 pp., ISBN 9780444427847, 1987.

Cross A. F. and Schlesinger W. H.: Biological and geochemical controls on phosphorus fractions in semiarid soils. Biogeochemistry, 52, 155–172, https://doi.org/10.1023/A:1006437504494, 2001.

Czech Geological Survey: James Ross Island - Northern Part. Topographic map 1:25 000. CGS, Praha, ISBN 978-80-7075-734-5, 2009.

420 Durán J., Rodríguez A., Heiðmarsson S., Lehmann J.R.K., del Moral Á., Garrido-Benavent I., De los Ríos A.: Cryptogamic cover determines soil attributes and functioning in polar terrestrial ecosystems. Sci. Total Environ., 762, https://doi.org/10.1016/j.scitotenv.2020.143169, 2021.

FAO: Measuring and modelling soil carbon stock and stock changes in livestock production systems. Guidelines for assessment (Version 1), Livestock Environmental Assessment and Performance (LEAP) Partnership, Rome, FAO, 170 pp.,

425 ISBN 978-92-5-131408-1, 2019.

Fassbender, A. J., Orr, J. C., Dickson, A. G.: Technical note: Interpreting pH changes. Biogeosciences, 18, 1407–1415, https://doi.org/10.5194/bg-18-1407-2021, 2021.

Filippelli, G. M. and Souch C.: Effects of climate and landscape development on the terrestrial phosphorus cycle. Geology 27, 2, 171–174, DOI:10.1130/0091-7613 (1999)027<0171:EOCALD>2.3.CO;2, 1999.

430 Fitter, A. H., Heinemeyer, A. and Staddon, P. L. The impact of elevated CO_2 and global climate change on arbuscular mycorrhizas: a mycocentric approach. New Phytol., 147, 179–187, https://doi.org/10.1046/j.1469-8137.2000.00680.x, 2008.

Gao, M. R., Xu, Q. D., He, Q., Sun, Q. and Zeng W.-C.: A theoretical and experimental study: the influence of different standards on the determination of total phenol content in the Folin–Ciocalteu assay. J. Food Meas. Charact., 13, 1349–1356, https://doi.org/10.1007/s11694-019-00050-6, 2019.

435 Gillespie, A. W., Farrell R.E., Walley F. L., Ross A. R., Leinweber P., Eckhardt K. U., Regier T. Z. and Blyth R. I.: Glomalin-related soil protein contains non-mycorrhizal-related heat-stable proteins, lipids and humic materials. Soil. Biol. Biochem., 43, 766–777, https://doi.org/10.1016/j.soilbio.2010.12.010, 2011.

Golchin, A., Baldock, J. A. and Oades, J. M.: A model linking organic matter decomposition, chemistry, and aggregate dynamics, in: Soil processes and the carbon cycle, edited by: Lal, R., Kimble J. M., Follet F. and Stewart B. A., CRC Press,

440   245–266, https://doi.org/10.1201/9780203739273 , 2018.

Green, T. G. A., Nash, T. H. and Lange, O. L.: Physiological ecology of carbon dioxide Exchange. in: Lichen Biology, edited by: Nash III T.H., Cambridge University Press, 152–181, DOI: https://doi.org/10.1017/CBO9780511790478.010, 2008.

Grewal, K. S., Buchan, G. D. and Sherlock, R. R.: Comparison of three methods of organic carbon determination in some New Zealand soils. Eur. J Soil Sci., 42, 251–257, https://doi.org/10.1111/j.1365-2389.1991.tb00406.x, 1991.

445   Harper, C. J., Taylor, T. N., Krings, M. and Taylor, E. L.: Mycorrhizal symbiosis in the Paleozoic seed fern Glossopteris from Antarctica. Rev. Palaeobot. Palynology, 192, 22–31. DOI: 10.1016/j.revpalbo.2013.01.002, 2013.

Holátko, J., Brtnický, M., Kučerík J., Kotianová, M., Elbl J., Kintl, A., Kynický, J., Benada, O., Datta, R. and Jansa, J.: Glomalin – Truths, myths, and the future of this elusive soil glycoprotein. Soil Biol. Biochem., 153, 108116, https://doi.org/10.1016/j.soilbio.2020.108116, 2021.

450   Houghton, R. A.: Balancing the global carbon budget. Annu. Rev. Earth Planet. Sci., 35, 313–347. https://doi.org/10.1146/annurev.earth.35.031306.140057, 2007.

Huang, Y., Wang, D. W., Cai, J. L. and Zheng, W. S.: Review of glomalin-related soil protein and its environmental function in the rhizosphere. Chin. J. Plant Ecol., 35(2), 232–236, DOI: 10.3724/SP.J.1258.2011.00232, 2011.

Kelley, A. P.: Mycotrophy in plants. Chronica Botanica, Waltham, MA, 223 pp., ISBN-13: 978-1121005679, 1950.

455   Kondratyuk, S. Y. and Kärnefelt, I.: Revision of three natural groups of xanthorioid lichens (Teloschistaceae, Ascomycota). Ukrainskiy Botanichnyi Zhurnal, 60 (4), 427–437, 2003.

Konvalinková, T., Püschel, D., Řezáčová, V., Gryndlerová, H. and Jansa, J.: Carbon flow from plant to arbuscular mycorrhizal fungi reduced under phosphorous fertilization. Plant Soil 419, 319–333, DOI 10.1007/s11104-017-3350-6, 2017.

Kouchi, H., Shimomura, K., Hata, S., Hirota, A., Wu, G. J., Kumagai, H., Tajima, S., Suganuma, N., Suzuki, A., Aoki, T.,

460   Hayashi, M., Yokoyama, T., Ohyama, T., Asamizu, E., Kuwata, Ch., Shibata, D. and Tabata, S.: Large-scale analysis of gene expression profiles during early stages of root nodule formation in a model legume, Lotus japonicus. DNA Res, 11(4), 263–274, doi: 10.1093/dnares/11.4.263, 2004.

Láska, K. and Prošek, P. Klima a klimatický výzkum ostrova James Ross, in: Prošek, P. (Ed.) Antarktida, Academia, 348 pp., ISBN 978-80-200-2140-3, 2013.

465   Lovato, P. E., Schuepp, H., Trouvelot, A. and Gianinazzi, S.: Application of arbuscular mycorrhizal fungi (AMF) in orchid and ornamental plants, in: Mycorrhiza, edited by: Varma, A. and Hock, B., Springer, Berlin Heidelberg New York, 443–468, DOI:10.1007/978-3-662-03779-9_19, 1995.

Makkonen, M., Berg, M. P., Handa, I. T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P. M. and Aerts, R.: Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecol. Lett., 15(9),

470   1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x, 2012.

Martins, M. C. B., de Lima, M. J. G., Silva, F. P., Azevedo-Ximenes, E., da Silva, N. H. and Pereira, E. C.: Cladia aggregata (lichen) from Brazilian Northeast: chemical characterization and antimicrobial activity. Braz Arch Biol Technol, 53, 1, 115–122, DOI:10.1590/S1516-89132010000100015, 2010.

475 Masson-Delmotte, V., Kageyama, M., Braconnot, P., Charbit, S., Krinner, G., Ritz, C., Guilyardi, E., Jouzel, J., Abe-Ouchi, A., Crucifix, M., Gladstone, R. M., Hewitt, C. D., Kitoh, A., LeGrande, A. N., Marti, O., Merkel, U., Motoi, T., Ohgaito, R., Otto-Bliesner, B., Peltier, W. R., Ross, I., Valdes, P. J., Vettoretti, G., Weber, S. L., Wolk, F. and Yu, Y.: Past and future polar amplification of climate change: climate model intercomparisons and ice-core constraints. Clim Dyn 26, 513–529, https://doi.org/10.1007/s00382-005-0081-9, 2006.

Matějka, M., Láska, K., Jeklová, K. and Hošek, J. High-Resolution Numerical Modelling of Near-Surface Atmospheric Fields 480 in the Complex Terrain of James Ross Island, Antarctic Peninsula. Atmosphere, 12(3), 360; https://doi.org/10.3390/atmos12030360, 2021.

McCraw, J. D.: Soils of the Ross Dependency, Antarctica. A preliminary note. N. Z. Soc. Soil Sci. Proc. 4: 30–35, 1960.

Mehlich, A.: Mehlich 3 soil test extractant: A modification of the Mehlich 2 extractant. Commun. Soil Sci. Plant Anal., 15(12), 1409–1416, https://doi.org/10.1080/00103628409367568, 1984.

485 Melo, C.D., Walker, C., Krüger, C., Borges, P. A. V., Luna, S., Mendoca, D., Fonseca, H. M. A. C. and Machado A. C.: Environmental factors driving arbuscular mycorrhizal fungal communities associated with endemic woody plant Picconiaazorica on native forest of Azores. Ann Microbiol 69, 1309–1327, https://doi.org/10.1007/s13213-019-01535-x, 2019.

Mlčoch, B., Nývlt, D. and Mixa, P.: Geological map of James Ross Island Northern Part 1:25,000. Czech Geol. Survey, Prague. ISBN: 978-80-7075-996-7, 2020.

490 Paul, E. (Ed.): Soil microbiology, ecology and biochemistry. Academic press, 604 pp., ISBN: 9780124159556, 2014.

Pirozynski, K. A. and Malloch, D. W.: The origin of land plants: a matter of mycotropism. Biosystems, 6, 153–164, doi: 10.1016/0303-2647(75)90023-4, 1975.

Pohanka, M. and Vlček, V.: Assay of glomalin using a quartz crystal microbalance biosensor. Electroanalysis, 30, 3, 453–458, https://doi.org/10.1002/elan.201700772, 2018.

495 Pospíšilová, L., Vlček, V., Hybler, V., Uhlík, P.: Carbon content and macroelement in cryosols, Humic substances research, 13, 13–17, 2017.

Rackley, S. A.: Carbon capture and storage, Butterworth-Heinemann, 698 pp., ISBN: 9780128120415, 2017.

Rayner, M. C.: Mycorrhiza. New Phytologist Reprint No. 15, Weldon &Wesley, London, 1927.

Redecker, D., Kodner, R. and Graham, L. E.: Glomalean fungi from the Ordovician. Science, 289, 1920–1921, DOI: 500 10.1126/science.289.5486.1920, 2000.

Remy, W., Taylor, T.N., Hass, H., Kerp, H.: Four hundred-million-year-old vesicular arbuscular mycorrhizae. Proc. Natl. Acad. Sci. U. S. A., 91, 25, 11841–11843, doi: 10.1073/pnas.91.25.11841, 1994.

Röder, J., Detsch, F., Otte, I., Appelhans, T., Nauss, T., Peters, M. K. and Brandl, R.: Heterogeneous patterns of abundance of epigeic arthropod taxa along a major elevation gradient. Biotropica, 217–228, https://doi.org/10.1111/btp.12403https://doi.org/10.1111/btp.12403, 2016.

Russell, J. and Bulman, S.: The liverwort Marchantia foliacea forms a specialized symbiosis with arbuscular mycorrhizal fungi in the genus Glomus. New Phytol, 165, 567–579, DOI: 10.1111/j.1469-8137.2004.01251.x, 2005.

Santiago, R., Silva, N. H., Silva, F.P., Martins, M. C. B., de Vasconcelos, T. L., Yano-Melo, A. M., Pereira, E. C. Interactions of the lichen Cladonia salzmannii Nyl. with soil, microbiota, mycorrhizae and Genipa Americana. J. Soil Sci. Plant Nutr., 18, 3, 833–850, http://dx.doi.org/10.4067/S0718-95162018005002402, 2018.

Shukla, V., Bajpai, R., Pandey, U., Upreti, D. K.: Do Lichens have the Ability to Remove Arsenic from Water? Int. J. Plant and Environ., 5, 1, 47–49, DOI: 10.18811/ijpen.v5i01.8, 2019.

Schüßler, A., Schwarzott, D. and Walker, Ch.: A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycol. Res., 105, 1413–1421, https://doi.org/10.1017/S0953756201005196, 2001.

Siewert, Ch.: Rapid screening of soil properties using thermogravimetry. Soil Sci. Soc. Am. J., 68, 5, 1656–1661, DOI:10.2136/sssaj2004.1656, 2004.

Simon, L., Bousquet, J., Levesque, R.C. and Lalonde, M.: Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. Nature 363, 67–69, https://doi.org/10.1038/363067a0, 1993.

Smith, S. E. and Read, D. J.: Mycorrhizal Symbiosis. Academic Press, San Diego, USA, 800pp, https://doi.org/10.1016/B978-0-12-370526-6.X5001-6, 2008.

Stark, S., Hyvärinen, M.: Are phenolics leaching from the lichen Cladina stellaris sources of energy rather than allelophatic agents for soil microorganisms? Soil Biol. Biochem., 35, 10, 1381–1385, https://doi.org/10.1016/S0038-0717(03)00217-7, 2003.

Strelin, J. A. and Sone, T.: Rock glaciers on James Ross Island, Antarctica, in: Permafrost, 7th. International Conference Proceedings, Yellowknife (Canada), edited by: Lewkowicz, A. G. and Allard, M., Collection Nordicana University Laval, Quebec, 1027–1032, 1998.

Swati, J., Bajpai, A., Narain Johri, B. Extremophilic fungi at the interface of climate change, in: Fungi Bio-Prospects in Sustainable Agriculture, Environment and Nano-technology, edited by: Kumar, V. S., Shah, M. P., Parmar, S. and Kumar A., Academic Press, 1–22, ISBN 9780128219256, https://doi.org/10.1016/B978-0-12-821925-6.00001-0https://doi.org/10.1016/B978-0-12-821925-6.00001-0, 2021.

Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G. and Zimov S.: Soil organic carbon pools in the northern circumpolar permafrost region. Glob. Biogeochem. Cycle, 23, DOI:10.1029/2008GB003327, 2009.

Tóth, Z., Táncsics, A., Kriszt, B., Kröel-Dulay, G., Ónodi, G. and Hornung, E.: Extreme effects of drought on composition of the soil bacterial community and decomposition of plant tissue. Eur. J. Soil Sci., 68, 4, 504–513, https://doi.org/10.1111/ejss.12429, 2017.

Turner, J., Colwell, S. R., Marshall, G. J., Lachlan-Cope, T. A., Carleton, A. M., Jones, P. D., Lagun, V., Reid, P. A. and Iagovkina, S.: Antarctic climate change during the last 50 years. Int. J. Climatol., 25, 279–294, doi: 10.1002/joc.1130, 2005.

van Bemmelen, J. M.: Über die Bestimmungen des Wassers, den Humus, des Schwefels, der in den colloidalen Silikaten gebunden Kieselsäuren, des mangans, u.s.w. im Ackerboden. *Landwirtschaftliche Versuch Station* 37, 279–290, 1889.

540 Vingiani, S., Adamo P. and Giordano, S.: Sulphur, nitrogen and carbon content of Sphagnum capillifolium and Pseudevernia furfuracea exposed in bags in the Naples urban area. Environ. Pollut., 129, 1, 145–158, https://doi.org/10.1016/j.envpol.2003.09.016, 2004.

Vlček, V., Pospíšilová, L., Uhlík, P.: Mineralogy and chemical composition of Cryosols and Andosols in Antarctica. Soil Water Res., 13, 2, 61–73, doi: 10.17221/231/2016-SWR, 2018.

545 Walkley, A. and Black, I. A.: An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Science 37, 1, 29–38, http://dx.doi.org/10.1097/00010694-193401000-00003, 1934.

Walkley, A.: A Critical Examination of a Rapid Method for Determining Organic Carbon in Soils: Effect of Variations in Digestion Conditions and of Inorganic Soil Constituents. Soil Sci., 63, 251–264, http://dx.doi.org/10.1097/00010694-
550 194704000-00001, 1947.

Wilcke, W., Oelmann, Y., Schmitt, A., Valarezo, C., Zech, W. and Homeier, J.: Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. Journal of Plant Nutrition and Soil Science, 171, 220–230. https://doi.org/10.1002/jpln.200625210, 2008.

Wright, S.F. and Anderson, R. L.: Aggregate stability and glomalin in alternative crop rotations for the central Great Plains.
555 Biol. Fertil. Soils, 31, 3/4, 249–253, http://dx.doi.org/10.1007/s003740050653, 2000.

Wright, S.F. and Upadhyaya, A.: Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Sci., 161, 575–586, http://dx.doi.org/10.1097/00010694-199609000-00003, 1996.

Wuest, S. B., Caesar-TonThat, T. C., Wright, S. F., Williams, J. D.: Organic matter addition, N, and residue burning effects on infiltration, biological, and physical properties of an intensively tilled silt–loam soil. Soil and Tillage Research, 84, 154–
560 167, https://doi.org/10.1016/j.still.2004.11.008, 2005.

Yergeau, E., Bokhorst, S., Kang, S., Zhou J., Greer Ch. W., Aerts, R. and Kowalchuk G. A.: Shifts in soil microorganisms in response to warming are consistent across a range of Antarctic environments. ISME J 6, 692–702, DOI: 10.1038/ismej.2011.124, 2012.

Zech, W., et al.: Factors controlling humification and mineralization of soil organic matter in the tropics. Geoderma, 79, 117–
565 161, https://doi.org/10.1016/S0016-7061(97)00040-2, 1997.

Zhu, Y-G. and Miller, R.M.: Carbon cycling by arbuscular mycorrhizal fungi in soil-plant systems. Trends Plant Sci., 8, 9, 407–409, DOI: 10.1016/s1360-1385(03)00184-5, 2003.

Zhu, R., Wang, Q., Wang, C., Hou, L. and Ma, D.: Penguins significantly increased phosphine formation and phosphorus contribution in maritime Antarctic soils. Sci. Rep., 4, 7055, DOI: 10.1038/srep07055, 2014.

570   Zvěřina, O., Coufalík, P., Vaculovič, T., Kuta, J., Zeman, J. and Komárek, J.: Macro-and microelements in soil profile of the moss-covered area in James Ross Island, Antarctica. Czech Polar Rep., 2, 1, 1–7, https://doi.org/10.5817/CPR2012-1-1, 2012.