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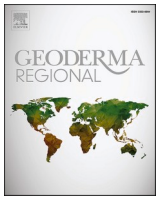

Morphology and distribution of biological soil crusts and their potential role in soil-forming processes under dry high-altitude periglacial conditions (Eastern Pamir, Tajikistan)

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ABSTRACT

Under demanding climatic conditions that limit the development of vascular vegetation, biological soil crusts (BSCs) drive the processes of soil formation and nutrient sequestration. Though BSCs were studied in glacier forelands worldwide, the high-altitude areas with a combination of glaciation/deglaciation and arid or hyperarid climate remain almost unstudied in this respect. Therefore, we provided the first data on BSCs from a glacier foreland in the E Pamir. These characteristics can be crucial for assessing BSC's role in soil-forming processes in dry, high-altitude periglacial environments. During our research, we assessed (1) BSCs' morphology and distribution; (2) microbial biomass and nutrient retention patterns in morphologically differentiated BSC types, (3) C, N and P accumulation in BSCs biomass in comparison to sub-crust soils; (4) sub-crust soils enrichment in C, N and P in comparison to bare soils and soils under vascular plants; (5) potential origin and transformation degree of organic matter accumulated by BSCs. Our study showed that the distribution and development of BSCs were noticeably restricted, probably due to low temperatures, aridity and intense periglacial processes, resulting in continuous soil surface remodeling. Thus, poorly developed BSCs were the dominating biologically active soil cover type and, thus, most likely the main biological soil-forming factor in the foreland. BSCs accumulated C, N and P in their biomass and enriched their sub-crust soils in these nutrients. The average enrichment observed for soils under advanced crusts was similar to those obtained for soils under vascular plants. In all types of the studied samples, including bare soils, n-alkanes of vascular plant origin dominated, indicating mixing and uniform distribution of organic matter. Over the course of aridification projected for the Pamir Mountains, the BSCs could potentially become the most important player in the accumulation of soil nutrients in this area. However, due to the dominance of the simplest BSC type, soil formation in the Uisu Glacier foreland will be relatively slow.

1. Introduction

Biological soil crusts (BSCs) are morphologically distinct complex terrestrial microecosystems formed within and on the exposed topsoil by taxonomically and ecologically diverse communities of prokaryotes and eukaryotes (Belnap and Lange, 2003; Weber et al., 2016). BSCs have a long evolutionary history, with predecessors in early terrestrial habitats originating possibly 1.5–3 billion years ago (Graham et al., 2018). BSCs have a worldwide distribution (Belnap and Lange, 2003), and estimates of the total terrestrial area covered by BSCs reach 12% (Maier et al., 2018). BSCs occur in specific habitats in all major climatic zones (e.g., Agnelli et al., 2021; Baumann et al., 2019; Bastida et al., 2014; Colesie et al., 2014; Guan et al., 2018; Jung et al., 2018; Kotas et al., 2018; Rosentreter and Belnap, 2001; Wietrzyk-Pełka et al., 2021; Zaady et al.,

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2010). However, since the BSC-building organisms are often desiccation adapted and generally extremotolerant or even extremophilic, these associations are especially abundant in arid and hyperarid regions, where they can cover up to 70% of soil area (Rodriguez-Caballero et al., 2013 and references therein).

BSCs play many vital functions in their environments, including stabilization of the soil surface and protection from erosion (Rossi et al., 2018), modification of water permeability and water-holding capacity of soils (Li et al., 2021), or even modification of soil albedo and soil temperatures. The consequences of BSCs' activity range from the local impact on the soil biogeochemical processes, through local weather modification, to the broader effects on global climate change (e.g., Xiao and Bowker, 2020). Most importantly, BSCs have a significant impact on nutrient cycling and soil formation. Due to the high share of photoautotrophs, nitrogen-fixing prokaryotes and cyanolichens (lichenized fungi with cyanobacterial symbionts), and producers of exopolysaccharides (compounds excreted by microorganisms that bind soil particles, biomass, and necromass together, e.g., Rossi et al., 2018), BSCs fix and accumulate substantial amounts of nutrients, most notably carbon (C), nitrogen (N), and phosphorus (P) in their biomass and necromass (e.g., Baumann et al., 2019; Borchhardt et al., 2019; Couradeau et al., 2017; Jung et al., 2018; Kotas et al., 2018; Mager, 2010; Xu et al., 2021). BSCs' contribution to the global C fixation is estimated to reach 7% of that of terrestrial plants and almost 50% of the total terrestrial N fixation (Elbert et al., 2012). The BSC-building microorganisms also produce a wide suite of *endo*- and extracellular metabolites, which interact with organic matter and mineral components of the soil underneath (Borin et al., 2009; Agnelli et al., 2021). Especially lichenized fungi can have a particularly significant role in mineral weathering, as they produce various organic acids (Chen et al., 2000) and oxidative enzymes (Beckett et al., 2013), and some lichen taxa also have the ability to translocate water and presumably nutrients from the underlying soil/rock thanks to their filamentous rhizoids (Green et al., 2018). In addition, nutrient (C, N, P) leaching from BSC biomass to the subcrust soil is frequently reported (e.g., Young et al., 2022), and these nutrients and metabolites are proposed to exert, in turn, an overall stimulating effect on sub-crust soil microbial communities (Liu et al., 2017). The impact of BSCs on the nutrient cycling of the underlying soil/rock depends, among others, on their complexity. There is accumulating evidence that the most complex BSCs (usually moss-lichen or moss crusts) can potentially have the greatest soil-forming potential (Agnelli et al., 2021; Chamizo et al., 2012; Jung et al., 2018; Maier et al., 2018), possibly due to significant biomass of the BSC-forming organisms and their synergistic effects on the biogeochemistry of the underlying soil/rock. Due to all these features, BSCs essentially drive the processes of soil formation, especially in ecosystems lacking the well-developed cover of vascular vegetation, e.g., in recently disturbed, deglaciated areas (Wietrzyk-Pełka et al., 2020).

Glacier forelands enable insights into the biotic and abiotic factors responsible for soil formation due to the occurrence of more or less clear chronosequences (e.g., Zumsteg et al., 2012), which usually facilitate research by providing means for "space-for-time substitution" (although not always, see Wojcik et al., 2021). The soil formation rates in these ecosystems are mediated by pioneering organisms, especially by often dominant BSCs. The impact of BSCs on nutrient accumulation and cycling depends on their composition, cover and interactions with pioneering higher vegetation (e.g., Wietrzyk-Pełka et al., 2021). Globally observed acceleration of glacier retreat due to climate warming (e.g., Hugonnet et al., 2021) exposes more and more land surface to biotic colonization, with potentially significant consequences for soil formation and overall nutrient budgets, which therefore emphasizes the need for studying the role of BSCs in these ecosystems. BSCs were studied in glacier forelands in several locations of the world, e.g., in the High Arctic (Wietrzyk-Pełka et al., 2021 - Svalbard), Antarctic (Colesie et al., 2014), North America (Breen and Lévesque, 2008), South America (Schmidt et al., 2008), and European Alps (Karsten and Holzinger, 2014), encompassing studies from almost all major climatic zones. These studies have shown that the BSCs may cover a significant area in glacier forelands, even over 80% (Wietrzyk-Pełka et al., 2021). Development of BSCs often follows the glacier chronosequences, and the crust's morphological and taxonomic complexity increases with the soil's stability and growing distance from the glacier terminus, from the simple cyanobacterial crusts to complex moss- and lichen-dominated crusts (e.g., Schulz et al., 2013). Well-developed and the most advanced types of crusts in forelands located in a more humid climate and at lower altitudes are usually dominated by species-rich communities of lichens (including cyanolichens) and mosses (e.g., Williams et al., 2017). Contrastingly, in extreme ecosystems of continental Antarctica, BSCs cover and diversity are significantly reduced (e.g., Colesie et al., 2014). BSCs in glacier forelands were found to accumulate substantial amounts of nutrients (e.g., Breen and Lévesque, 2008). One of the specific features of these ecosystems is the presence of old sediments, buried under the ice, exposed after the glacier retreat, and often reworked due to glaciofluvial activity (Duncan et al., 2018; Wojcik et al., 2021). This old organic matter can be reused by colonizing organisms (e.g., Agnelli et al., 2021), explaining the paradox that heterotrophic microorganisms often precede autotrophs during succession in these ecosystems (Bardgett et al., 2007). Nevertheless, the origin and transformation degree of organic matter accumulated in BSC biomass is rarely studied (e.g., Koyama et al., 2018).

Currently, BSCs are commonly investigated in glacier forelands located in high-altitude areas but with relatively humid climates (e.g., the Peruvian Andes, Schmidt et al., 2008) or in forelands located in arid-hyperarid lowlands (e.g., continental Antarctica, Colesie et al., 2014). The areas with a combination of high altitude and arid or hyperarid climate remain almost unstudied. There are only a few studies dealing specifically with cyanobacteria and cyanobacterial crusts from Himalaya (Čapková et al., 2016; Janatková et al., 2013). This is surprising, given that organisms occurring in such extreme conditions are likely to be highly adapted and, therefore, highly susceptible to the slightest disturbances, being ideal candidates for indicators of change (Bowker et al., 2008). BSC-forming organisms equilibrate tissue water content to that of the environment (poikilohydry). Thus, they are potentially prone to climate change-driven alterations in precipitation regime, humidity and temperature (Escolar et al., 2012). We can expect that any such disturbance will affect the composition and cover of BSCs, resulting in disruptions of nutrient cycling and soil formation in certain areas.

One of such areas are the mountains of Central Asia, including the Karakoram-Hindukush range and the Pamir range. The Pamir Mountains are located in the southeastern part of Central Asia (mainly in Tajikistan, with outskirts reaching Kyrgyzstan, China and Afghanistan) and, together with other ranges surrounding the Tibetan Plateau, belong to the world's largest reservoir of glaciers, snow and permafrost outside the poles. As such, the Pamir Mountains are an essential source of water for the Central Asian lowlands (Aizen, 2011; Barandun et al., 2020; Kayumov, 2010; Mölg et al., 2018; Rojan, 2007). Permanent glaciers, mostly of the continental type, cover 10–13% of the Tajik Pamir, with the surface currently estimated at between 8000 and 12,000 km^2 (Aizen, 2011; Kayumov, 2010; Mölg et al., 2018; Rojan, 2007). There is a well-documented trend of growing air temperatures combined with a general decrease in precipitation in the mountains of Central Asia (Finaev et al., 2016; Kayumov, 2010; Normatov and Normatov, 2020), which will most likely affect the condition of glaciers, and as a result also the distribution and cover of foreland-inhabiting BSCs and pioneering higher vegetation. However, to the best of our knowledge, there is no comprehensive study from the Pamirs focused on BSCs.

Therefore, we provide the first description of the occurrence, morphological diversity, and cover of biological soil crusts from the dry high-altitude glacial foreland in the Eastern Pamir. Additionally, by performing detailed chemical analyses, we provide the first quantitative and qualitative data on their biomass, C, N, P content, and n-alkane content. Given the extreme environmental conditions that are highly

unfavorable for higher vegetation in the investigated area, we expected that (I) the BSCs of different developmental stages are overall the dominant part of the biologically active soil cover and that (II) the microbial biomass and total nutrient retention patterns in BSCs are positively related to their developmental stage. Moreover, since we were primarily interested in investigating the differences in microbial biomass and nutrient accumulation by BSCs in comparison with bare, uncolonized soils (BS), we hypothesized that (III) microbial biomass in BS is negligible, and consequently (IV) there is noticeable C, N, P accumulation in BSCs and sub-crust soils relative to BS. Subsequently, to assess the potential importance of BSCs for nutrient accumulation/mobilization processes in the Uisu Glacier foreland soils, we compared the C, N, and P enrichment in soils under the BSCs with the same parameters in soils under vascular plants. Finally, to assess the potential origin and transformation degree of organic matter accumulated by BSCs, we analyzed the contents of n-alkanes in BSC biomass and sub-crust soils and compared them to n-alkane contents in the soil underneath vascular plants. Taken together, the results of these investigations allowed us to assess the potential impact of BSCs on nutrient accumulation processes in soils of extremely dry high-altitude glacial foreland in the (hyper)arid region of the Eastern Pamir.

2. Materials and methods

2.1. Location of study plots

The Uisu Glacier is one of the glaciers in the northeastern part of the Pamir Mountains (Fig. 1.). At 4400 m a.s.l. at the glacier, the terminus starts the Koksoy River Valley (ca. 16 km long), which adjoins the upper Markansu River Valley at the main road from Khorog to Osh, approximately 60 km north of Lake Karakul. The annual precipitation in this area reaches ca. 80 mm (data from the meteorological station in Karaat village on the eastern shore of Lake Karakul) (Mischke et al., 2017), the mean annual air temperature reaches −7.3 °C and the mean annual soil temperature − 0.87 °C (data from one-year-long measurements in the Uisu Glacier foreland) (Kabała et al., 2021). The UV index measured during our study in the Uisu Glacier foreland was between 10 and 11 (on a cloudless day at noon, measured with Smart Meter Tenmars TM-213 UVA UVB).

As the Last Glacial maximum in this area is estimated at 15–19 ka BP, all landforms in the foreland have developed since the Late Pleistocene (Kabała et al., 2021; Komatsu, 2016). The current position of the Uisu's terminus results from the continuous retreat process after the Little Ice Age. According to Gądek et al. (2022), the position of the glacial terminus has not changed since at least 1946; hence the immediate foreland zone is relatively stable.

According to Kabała et al. (2021), four major landforms can be distinguished in the Uisu Glacier foreland. The lowermost landform was a seasonally flooded braided plain, with highly variable relief shaped by proglacial waters (hereafter referred to as fluvial channels, see Fig. 1.) (Kabała et al., 2021). Sampling plots on this landform were located between the active channels, on the better-drained recent terraces covered with sparse vegetation. Above the seasonally flooded braided plain, glaciofluvial terraces were located (hereafter referred to as river terraces, see Fig. 1.), namely terrace T1 (1.0–1.5 m above the plain), terrace T2 (2–3 m above the plain) and terrace T3 (~6 m above the plain). Traces of ancient riverbeds and sorted polygons were clearly discernible on the terraces. The polygons were extensively developed on T2 and T3, signifying intense cryoturbation and negligible surface erosion. Vegetation on the river terraces had the highest coverage and species diversity in the Uisu Glacier foreland (Gądek et al., 2022; Kabała et al., 2021). On the terraces T1 and T3, clusters of long-tailed marmot burrows were present (Chibowski et al., 2023). However, none of our sampling plots on these landforms was placed in the vicinity of a recognizable burrow. In the study area's north- and southeastern parts, between 7 and 16 km from the glacier terminus, the third landform was located, namely the moraines (see Fig. 1.). This landform was exposed to noticeably stronger winds, and hence easily recognizable aeolian phenomena were visible on the soil surface, including patches of thin aeolian deposits (sand) covering the ground. Vegetation growing on the moraines was characterized by medium coverage and medium species diversity (Kabała et al., 2021). The fourth landform in the Uisu Glacier

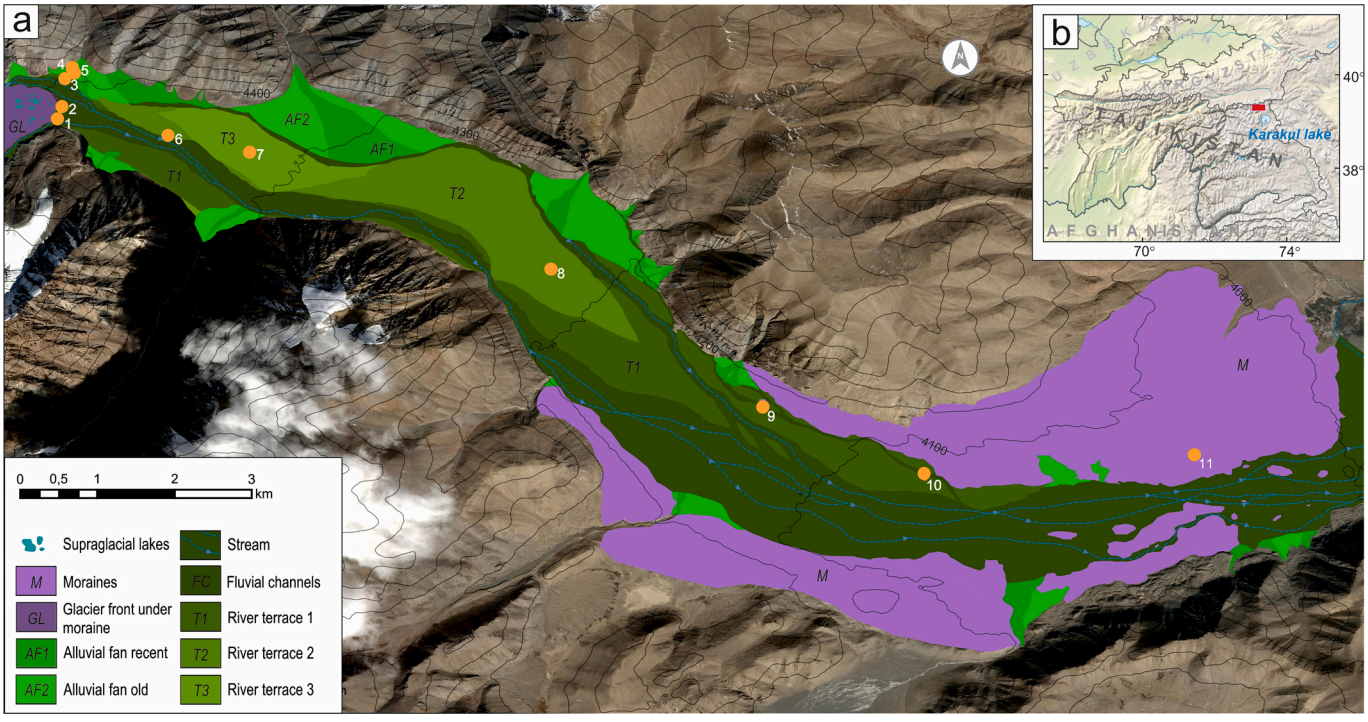

Fig. 1. Map of the study area: (A) localization of the study plots in the Uisu Glacier foreland (schematic geomorphological map modified from Kabała et al., 2021), (B) Geographical setting of the area. Orange points with white numbers – study plots.

foreland was a series of alluvial fans (see Fig. 1.) formed chiefly by proglacial waters at the outlets of seasonal tributary rivers and streams. The oldest sections of the fans were covered with sorted polygons, signifying intense cryoturbation and negligible surface erosion (Gądek et al., 2022, Kabała et al., 2021).

Regardless of the age and type of landforms, soils of the Uisu Glacier foreland were poorly developed, loose and had high skeleton and carbonate content. Moreover, they contained extremely low soil organic carbon, typically at the level of 0.1–0.2% in the topsoil layers. Such results are among the smallest recorded in the glacier forelands worldwide. Similarly, soils in the foreland were characterized by low nitrogen and phosphorus content (Kabała et al., 2021).

During two field campaigns – in July 2018 and July 2019 – eleven study plots were established in locations representative of the major landforms distinguished in the foreland (Table 1).

Nine out of eleven plots, namely 1–2, 4–7, and 9–11, were located next to soil profiles described by Kabała et al. (2021) (see supplementary materials for Kabała et al., 2021, soil profiles FC1, T12, T21, T22, T23, T32, AF21, M11, M13). According to the IUSS Working Group WRB soil classification (2015), profiles in study plots 1–2, 5–6, 8, and 10 represented Calcaric Hyperskeletic LEPTOSOLS with supplementary Fluvic and Protic characteristics; in the study plot 7 – Calcaric Skeletic Fluvic CAMBISOL with supplementary Ochric characteristics; and in the study plot 11 – Calcaric Endoskeletic REGOSOL with supplementary Ochric and Areninovic characteristics (Kabała et al., 2021). The study plots formed a distance gradient starting at 50 m and ending at 12.3 km from the glacier terminus (Table 1.).

2.2. Analysis of the biologically active soil cover

We use the term „biologically active soil cover" for soil covered either by BSCs or by vegetation. However, we acknowledge that stone-covered soils/skeletal soils might be inhabited by hypolithic microbial communities, which might, to some extent, contribute to organic matter and nutrient cycling in such soils (e.g., Mergelov et al., 2020). However, incorporating hypolithic communities was beyond the scope of this study.

In each study plot, we identified the main types of soil cover based on their gross morphology visible with the naked eye and under a magnifying glass (x20). Lichens were only tentatively identified to morphotypes (Brodo et al., 2001; Rosentreter et al., 2016; Smith et al., 2009), while no attempt was made to identify mosses. Species of vascular plants were identified according to Ikonnikov (1963). Species names were updated in accordance with The Plant List of The Royal Botanic Gardens, Kew (http://www.theplantlist.org/). To visually assess the percentage coverage of identified soil cover types, a 0.5 × 0.5 m metal grid with a mesh of 2.5 cm was used. The first grid was always placed in a representative location; other grids (between 3 and 9) were thrown randomly within a 20 m range from the first location. From each study plot, we collected samples of a loose soil layer with no indication of living organisms visible (bare soil), samples of biological soil crusts (biomass), samples of soils located immediately under the crusts (sub-crust soil), and samples of soils located immediately under vascular plants (namely a soil sample was taken from under each type of crust identified in each study plot, and from under the most common species of vascular plants in each study plot). To decrease potential within-site heterogeneity, obtain a proper amount of material and not destroy limited sites of crusts, subsamples of crust biomass and sub-crust soil were gathered within a 20 m range from the first location of a crust and combined into mixed samples. In total, ten samples of the loose soil layer, 13 samples of biological soil crusts, 13 samples of sub-crust soils, and 32 samples of the soil underneath vascular plants were collected from the Uisu Glacier foreland.

2.3. Analyses of microbial biomass

We applied two commonly used markers of living microbial biomass to determine its amount in bare, uncolonized soil, BSCs, and sub-crust soils - Phospholipid Fatty Acids (PLFAs) and ergosterol.

The PLFAs are constituents of the cell lipid membranes that might be isolated directly from the environment, e.g., soil and water, without the cultivation of microorganisms on solid media (Frostegård et al., 1993; Płociniczak et al., 2013). Since PLFAs are structural constituents of the cells (Zelles, 1999), they are supposed to reflect the quantitative aspect of the microbial community (i.e., the biomass) and enable direct (also cross-Kingdom) comparison of the biomass of microbial groups (Frostegård et al., 1993), as opposed to primarily qualitative DNA-based methods. Moreover, due to rapid PLFAs degradation after cell death (Zhang et al., 2019), they are usually regarded as a marker of living biomass, while DNA-based analyses can also incorporate cellular and relic DNA (Nielsen et al., 2007). The phospholipid fatty acid methyl esters were isolated from 10 g of fresh soil as described by Frostegård et al. (1993), with some modifications introduced by Pennanen et al. (1999). In short, soils were extracted with chloroform:methanol:citrate buffer mixture (1:2:0.8, *v*/v), and the lipids were separated into neutral lipids, glycolipids, and phospholipids on a silicic acid column. The phospholipids were subjected to a mild alkaline methanolysis and the fatty acid methyl esters were separated with a gas chromatograph (Agilent 7820A) coupled with a flame ionization detector (FID) using Ultra-2 capillary column (Agilent, length 25 m, inner diameter 0.22 mm, film thickness 0.33 μm) and hydrogen as the carrier gas. PLFAs compounds were identified using the MIDI Microbial Identification System software (Sherlock TSBA 6.1 method and TSBA 6.1 library; MIDI Inc., Newark, DE, USA). Peak areas were quantified by adding methyl nonadecanoate fatty acid (19:0) as an internal standard, and then the results were calculated and presented in nmol PLFAs g-1 d.w. of soil. Total biomass (TotPLFA) was calculated as the sum of all extracted PLFAs (as in Cycoń et al., 2013), the sum of 16:1ω9, 16:1ω7t, cy17:0 18:1ω7, cy19:0 PLFAs was used to determine the biomass of Gram negative (GN) bacteria and the sum of i15:0, a15:0, i16:0, i17:0, a17:0 PLFAs - to assess the biomass of Gram positive (GP) bacteria. The biomass of non-specific bacteria was calculated as the sum of straight PLFAs (12:0, 14:0, 15:0,

Table 1
Location of study plots 1–11 with a number of grids performed.

Study plot	Latitude	Longitude	Elevation [m a.s.l.]	Distance from the galcier terminus [m]	Landforms according to Kabała et al., 2021	Number of grids
1	39.325300	73.196733	4307	50	fluvial channels (FC)	no grids
2	39.326700	73.197067	4469	65	river terrace 2 (T2)	6
3	39.330150	73.197683	4416	245	river terrace 1 (T1)	5
4	39.330883	73.198583	4451	355	old alluvial fan (AF2) higher	no grids
5	39.330883	73.198583	4434	355	old alluvial fan (AF2) lower	7
6	39.323617	73.209650	4352	1190	river terrace 2 (T2)	5
7	39.321733	73.219017	4345	2015	river terrace 3 (T3)	5
8	39.308200	73.253967	4215	5315	river terrace 2 (T2)	6
9	39.291933	73.278517	4188	8000	fluvial channels (FC)	5
10	39.283917	73.297067	4131	9850	river terrace 1 (T1)	10
11	39.285033	73.328950	4080	12,230	moraines (M)	10

16:0, 17:0, 18:0 and 20:0). Unsaturated PLFA 18:2ω6 (linoleic acid) was used to represent predominantly the Eukaryotic biomass, including fungi (Zelles, 1999). However, it was also reported from some cyanobacteria (Kenyon, 1972; Kenyon et al., 1972; Potts et al., 1987). The content of all identified PLFAs in the studied samples in nmol/g d.w. is provided in Table S1 in Supplementary Materials 1.

Ergosterol is a principal cell membrane sterol of most fungi (Weete et al., 2010). It is commonly used as an indicator of living fungal biomass (e.g., Ruzicka et al., 2000). However, there are some concerns about its higher-than-expected stability in natural conditions (Mille-Lindblom et al., 2004). In the field, samples of crusts and soils for ergosterol analyses (2 g of fresh material) were put into Falcon tubes and covered in MeOH (HPLC grade, Sigma Aldrich, Germany) to prevent degradation. In the laboratory, MeOH was evaporated under the N_2 atmosphere and the samples underwent a preparatory procedure as described in Bååth (2001) and De Ridder-Duine et al. (2006), starting with extraction with 4 ml 10% KOH in MeOH (HPLC grade, Sigma Aldrich, Germany). After extraction, samples were vortexed for 30 s, sonicated for a further 15 min, and finally subjected to saponification in a water bath (80 °C) for 90 min. After that, 1 ml of distilled water and 2 ml of pentane (HPLC grade, Sigma Aldrich, Germany) was added to each sample, and separation was carried out by vortexing for 1 min. The upper organic phase was recovered, and separation was repeated two more times. Collected phases were pooled, and pentane was evaporated. After that, 1 ml of methanol was added, and each sample was sonicated for 1 min. Redissolved samples were quantitatively transferred to HPLC vials using a syringe with a PTFE syringe filter (Sigma Aldrich, Germany); additionally, evaporation dishes of each sample were rinsed with 1 ml of methanol, and that mixture was added to respective sample-containing HPLC vials after PTFE purification. Ergosterol content was determined on HPLC UV–Vis (Agilent Technologies 1260 Infinity) with Phenomenex reverse-phase column (C18, 250 × 4.6 mm × 5 μm), with the external standard of ergosterol (Sigma Aldrich, Germany). Conditions of analysis: isocratic elution with methanol (HPLC-grade, Sigma Aldrich, Germany) as mobile phase, flow speed 1 ml/min, injection volume 10 μl, λ = 282 nm. The retention time for ergosterol was between 10.5 and 11.0 min; the correlation coefficient for the calibration curve was above R^2 = 0.999.

2.4. Analyses of C, N, P contents and potential accumulation in the studied soils and BSCs

In order to assess the potential accumulation of C, N and P in BSCs, sub-crust soils, soils under vascular plants and bare soils, contents of these elements were measured in oven-dried (at 50 °C), grounded and sieved (1 mm mesh grade) samples of crusts and soils. Total nitrogen (TN) and total organic carbon (TOC, after carbonates removal with HCl) were measured with a CHNS elemental analyzer FLASH 2000. For total (nitric acid-digestible) phosphorus (TP) determination, soil samples were subjected to microwave-assisted digestion in concentrated nitric acid (ISO 16729, 2013) using Berghof Speedwave, in temperatures reaching 230 °C and subsequently analyzed with continuous flow analyzer SAN++ Skalar. Olsen's method was used to determine available phosphorus (Pav), which is recommended for calcareous soils (Bashour and Sayegh, 2007).

To assess the potential accumulation of C, N and P in different types of BSCs, we calculated ratios of TOC, TN, TP and Pav contents in crust biomass to their contents in sub-crust soil (e.g., $TOC_{BSC}/TOC_{sub\text{-}crust\ soil}$). To assess nutrient enrichment (C, N and P) in sub-crust soils in comparison to soils under vascular plants, we calculated ratios of TOC, TN, TP and Pav contents in sub-crust and sub-plant soils to their contents in bare soils taken from the same location (e.g., $TOC_{sub\text{-}crust\ soil}/TOC_{bare\ soil}$ and $TOC_{sub\text{-}plant\ soil}/TOC_{bare\ soil}$).

2.5. Analyses of the origin and transformation degree of organic matter in the studied soils and BSCs

For the assessment of the origin and transformation degree of organic matter, simple aliphatic compounds of n-alkanes were used. Based on n-alkanes composition in a sample, specific ratios are calculated to assess which organisms produced the studied organic matter and how advanced is its decomposition stage. Among them, Carbon Preference Index (CPI) and Average Chain Length (ALC) are widely used (Cabrerizo et al., 2016). According to Ofiti et al. (2021), fresh plant-derived organic matter is characterized by CPI values around 10, while highly degraded organic matter has CPI values close to 1. Plant-derived organic matter usually contains longer n-alkanes (above C24) than microbial-derived organic matter and thus is characterized by a higher ACL index (Ofiti et al., 2021).

Analyses of n-alkanes followed a protocol described in Jambrina-Enríquez et al. (2016), starting with the extraction of lipids in an accelerated solvent extractor ASE 350 (Dionex) with a dichloromethane (DCM) and methanol (MeOH) mixture (9:1) at 100 °C and 1500 psi for 5 min in 3 cycles. The obtained extracts were evaporated under a nitrogen stream to the volume of 2 ml, which was transferred directly onto Pasteur pipettes conditioned at 500 °C and filled with high-purity silica gel (60 Å pore, Sigma Aldrich) activated for eighth at 120 °C. During fractionation, the n-hexane fraction was obtained as the first and was analyzed using the Agilent 7890B gas chromatograph with a capillary column HP-5 ms Ultra Inert (30 m × 0.25 mm × 0.25 μm) and coupled with the 5977A MSD mass spectrometer. The carrying gas was He with a constant flow of 2 ml/min and the following temperature program was used: 70 °C (1 min) to 120 °C at 20 °C/min, then to 300 °C (held 30 min) at three °C/min. The compounds were identified by comparison of their retention times with those of the reference compounds from Sigma Aldrich C8-C40 Alkanes Calibration Standard 40,147-U and verified with mass spectra from the NIST Mass Spectral Library. Quantification was based on calibration curves prepared for the above-mentioned standard (r^2 for the curve was 0.97). As an internal standard, androstane was used with a mean recovery rate of 92%. The content of all identified n-alkanes in the studied samples in ug/g d.w. is provided in Table S2 in Supplementary Materials 1. Finally, for the assessment and interpretation of n-alkanes data, we identified mid-chain (MCA, C16-C21), long-chain (LCA, C22-C26) and very long-chain (VLC, C27-C33) n-alkanes after Carrizo et al. (2019), calculated Carbon Preference Index (CPI) according to Marzi et al. (1993), and Average Chain Length (ACL) according to Bush and McInerney (2013).

2.6. Statistical analyses

Basic descriptive statistics for the studied soil and crust parameters were performed with Statistica for Windows v. 13. Data from samples of soil under vascular plants were averaged for every location where the vascular plants were present. Thus, we obtained nine average values of each studied parameter for soils under plants. Data on the identified plant species with individual values of each parameter at each location are provided in Table S3 in Supplementary Materials 1. Due to the unequal representation of identified sample categories, we decided to perform multivariate statistics, namely Principal Component Analyses (PCA) and Linear Discrimination Analyses (LDA) with CANOCO for Windows, Version 4.5 (ter Braak and Smilauer, 1998), to assess general variability of soil and crust parameters, and to identify statistically significant differences between the studied sample categories.

A complete database with results used in the statistical analyses is provided in Table S4 in Supplementary Materials 1.

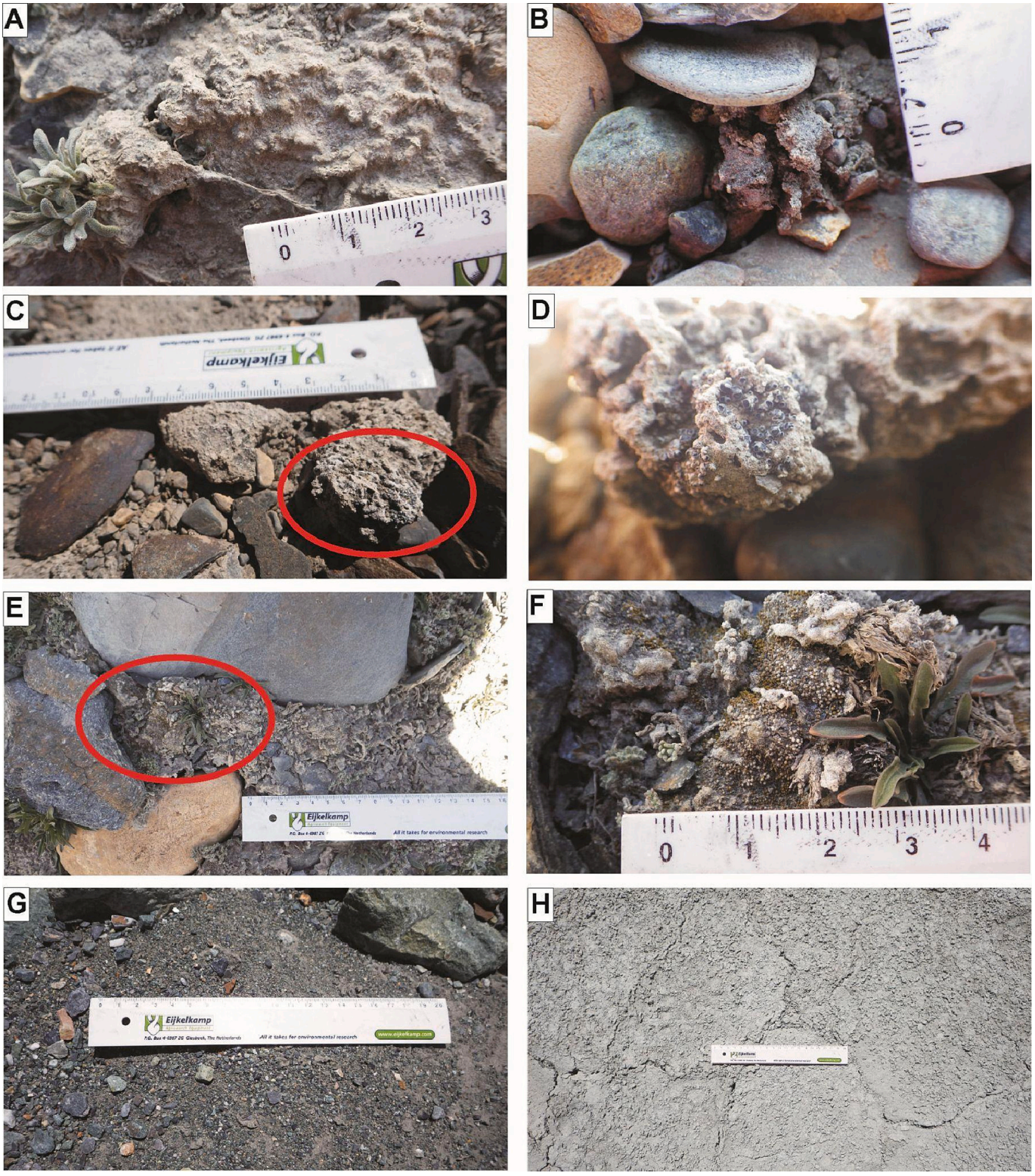

Fig. 2. Types of soil cover identified in the study plots. A – the fungal-algal crust (FAC), B – a dark type of the fungal-algal crust (dark FAC), C – the fungal-algal-lichen crust (FALC), a red circle shows a part of the crust that is enlarged on picture D, D – a close-up showing numerous black apothecia, E – the fungal-algal-lichen-moss crust (FALMC), a red circle shows a part of the crust that is enlarged on picture F, F – a close-up of the FALMC presented on picture E. G – bare soil (BS), H – the physical crust. Photos by Iwona Jasser.

3. Results

3.1. Distribution and coverage of the identified soil cover types

During our studies in the Uisu Glacier foreland, we identified four distinct types of biologically active soil cover. (1) Fungal-algal crust (FAC) – a folded and compact structure with a thickness of 0.7–0.8 cm and no indication of living organisms visible on the outside (Fig. 2.A). When broken, numerous filaments became visible, and the green color was discernible in the near-surface layer. FAC was usually rather pale in color; however, in some places, it became noticeably darker (Fig. 2.B.) while retaining its original characteristics. (2) Fungal-algal-lichen crust (FALC) – a heavily folded and compact structure with a walnut-like surface and maximum thickness of ~2 cm (Fig. 2.C.). Folds were bright and partially covered by grayish-whitish lichen thalli, while hollows between them were often darkly colored due to the presence of dark apothecia (Fig. 2.D.). When broken, numerous filaments became visible. (3) Fungal-algal-lichen-moss crust (FALMC) – a heavily folded structure between 2 and 3 cm in thickness, with well-developed moss and lichen thalli, with visible dark apothecia (Fig. 2.E., Supplementary Materials 2). Tops of the folds were noticeably paler than other parts of the FALMC structure (Fig. 2.F.). Sometimes vascular plants were present. When broken, numerous filaments became visible. Only one lichen morphotype, cf. *Rinodina* sp. was found to form FALCs and FALMCs (see Supplementary Materials 2 for additional information). The only other lichen morphotype present sporadically and in small amounts on these crusts was brightly yellow cf. *Caloplaca* sp. s.l. (Supplementary Materials 2). No other distinct lichen morphotypes were found of BSCs, even though other lichen species were present on bigger stones and rocks in the neighborhood (Supplementary Materials 2). No cyanolichens were detected on BSCs in the investigated plots. In several places, usually located near the glacier terminus, crusts with mosses but with no visible lichen thalli or apothecia were observed. For further characteristics, FALC and FALMC crusts will be treated jointly as advanced crusts (ADV). (4) Vascular plants – 19 cryophytic species, comprising small shrubs (e.g., *Ajania tibetica* (Hook.f. & Thomson) Tzvelev, *Braya pamirica* (H. Karst.) O.Fedtsch., *Krascheninnikovia ceratoides* (L.) Gueldenst.) and cushion plants (e.g., *Acantholimon hedinii* Ostenf., *Astragalus nivalis* Kar.

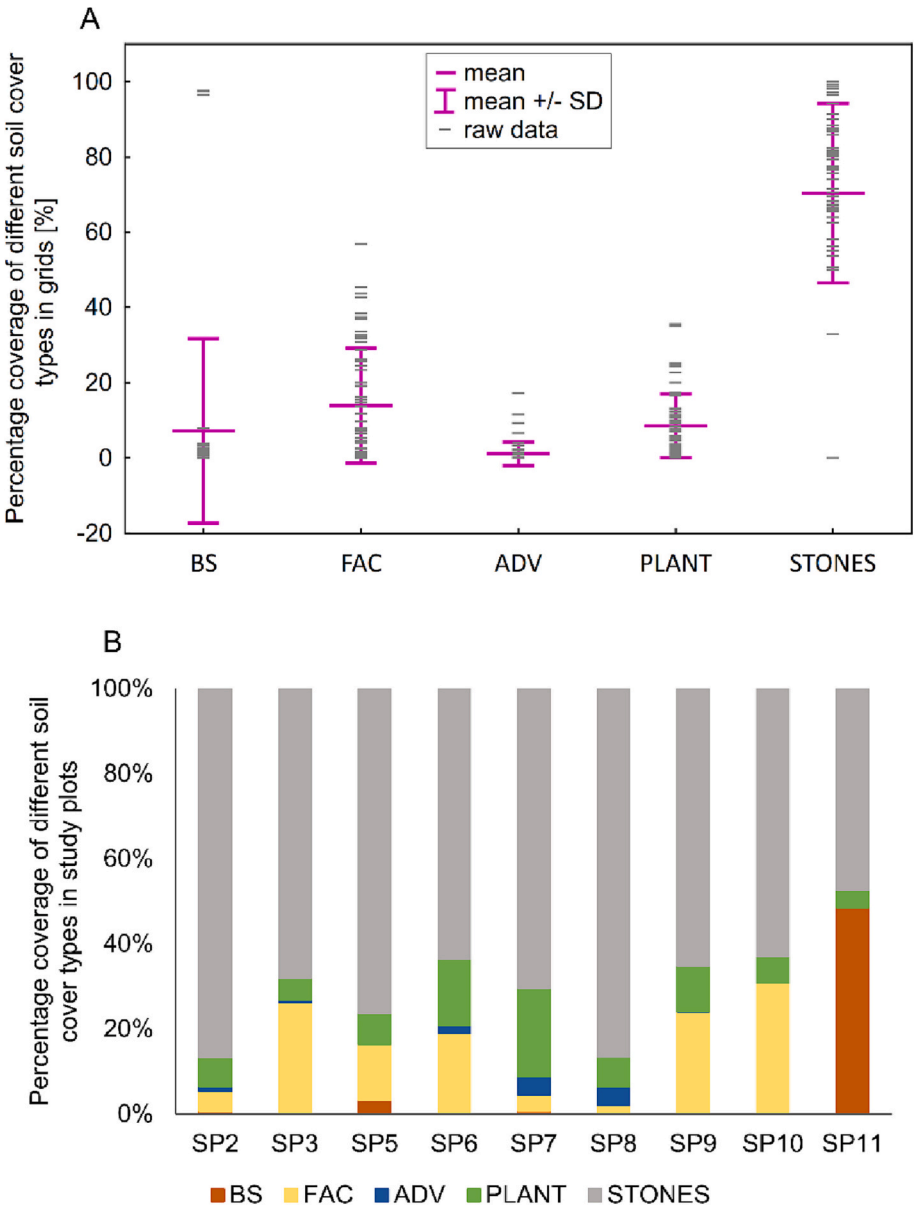

Fig. 3. A - Percentage coverage of different soil cover types in grids [%]. Raw data shown in the graph are mean coverage values for each soil cover type calculated per grid. B - Mean percentage coverage of different soil cover types in study plots where grids were calculated. SP - study plot, numbers according to Table 1.

& Kir., *Oxytropis* sp.), perennial forbs (e.g., *Cerastium lithospermifolium* Fisch., *Pleurospermum lindleyanum* (Klotzsch) B. Fedtsch., *Psychrogeton olgae* Novopokr. ex Nevski) and perennial graminoids (*Poa tianschanica* (Regel) Hack. ex O.Fedtsch.). Individuals were distributed randomly or often formed multispecies assemblages. A list of all identified species and data on their occurrence are provided in Supplementary Materials 1 (Table S3). Additional information on the plant communities and cover in the area is provided in Kabała et al., 2021. Interestingly, we observed in the field that many samples of all BSC types were colonizing dead bryophyte and vascular plant remains, including woody tissues (Supplementary Materials 2).

Considering the distribution of the identified biologically active soil cover types in our study plots, FAC occurred in all but two study plots (SP1 50 m from the glacier terminus and SP11 on moraines) and covered on average 14.0% of the studied area. In study plots SP3 and SP9–10 it covered roughly between 20% and 50% of the area, differing from grid to grid, resulting in averages above 20% (Fig. 3.A and B). Advanced soil crusts (FALC and FALMC) covered on average 1.1% of the studied area, yet in SP5 and SP9 their coverage was very low (0.1%), and they were absent from SP10 and SP11. FALC type was present with the coverage below 1% close to the glacier terminus (SP2, SP3 and SP5), peaked to 2.2% in SP8 (middle of the foreland), and decreased back to below 1% in SP9 (8000 m from the glacier terminus). The most advanced FALMC type was observed only between 1190 and 5315 m from the glacier terminus in the study plots SP6-SP8 (river terraces in the middle of the foreland), with an average coverage between 1.8% and 4.3%. Maximum coverage with advanced crusts was recorded in a single grid from SP7 and a single grid from SP8, where it reached above 10% (Fig. 3.). Vascular plants covered on average 8.6% of the studied area (Fig. 3.A). Plant coverage of over 20% was recorded in several grids from SP6, SP7 and SP10. In the grids from SP10, both the maximum plant coverage (35.6%) and a complete absence of vascular plants were recorded. Generally, study plots in the middle of the foreland were the most differentiated, as they comprised all (SP8) or all but one type of biologically active soil cover (SP6 and SP7 without FALC morphotype). Though no clear gradient-related pattern in the BSCs distribution was recorded, we observed that the advanced BSC types were more common near vascular plants and/or on slopes of small dry channels formed along the foreland, mostly on slopes facing S-SW.

Areas devoid of biologically active soil cover types were dominated by coarse pebbles, stones, and/or bare soil (BS). Coarse pebbles and stones were a part of the soil skeleton fraction, with grain diameter > 20 mm (IUSS WRB, 2015). They covered between 33.0% and 99.0% of the area in the grids (Fig. 3.), except for several grids from SP11 (moraines), where bare soils were dominant. Coarse pebbles and stones were not included in biogeochemical analyses. Bare soil was distinguished as a loose surface layer of soil composed mostly of gravel and sand, with no indication of living organisms visible under the magnifying glass (Fig. 2. G.). In places under the direct influence of proglacial waters, located near the glacier terminus, bare soil was covered with a physical crust (Fig. 2.H.), which, similarly to BS, had no indication of living organisms visible under the magnifying glass. In study plots where grids were performed, BS occurred on average in 7.1% of the researched area (Fig. 3.A). However, there were some study plots in which BS was absent from all or several grids (SP3, SP6, SP9, SP10, and some grids from SP11) (Fig. 3.B). Stones were the dominant cover type in these plots, with high participation of FAC (between 19% and 33%) and, in the case of SP6 (middle of the valley), vascular plants (over 15%). Study plot 11 (moraines) was quite specific, as on half of the grids performed there, BS (loose aeolian sand deposit) occurred on over 95% of the area, while in the other half of the grids stones dominated. No crusts were present there, only scattered plants, covering on average 4% of the area (Fig. 3.A and B).

3.2. Multivariate analysis of microbial biomass, nutrient content and organic matter transformation in the studied soils and BSCs

The PCA performed on all but soil under plants samples (Fig. 4.A.) showed that bare soils, FAC biomass and FAC sub-crust soils were characterized by similar PLFA content and composition, main nutrients content, and n-alkanes content and composition. Samples of ADV biomass, and to a lesser extent, of ADV sub-crust soils were characterized by a higher content of total ergosterol and total PLFA, with high participation of Eukaryotic PLFA and low participation of PLFA typical for Gram-positive and Gram-negative bacteria. ADV biomass was characterized by a higher content of all the analyzed main nutrients, and soils under ADV by a higher content of n-alkanes, with higher participation of compounds with odd and very long chains. These observations were confirmed by LDA analysis (Fig. 4.B.), showing two variables that significantly differentiated the analyzed sample types. Eukaryotic PLFA explained 21.0% of the observed variance (p-value = 0.0002). Its highest values were recorded in samples of ADV biomass and, to a lesser extent, in samples of ADV sub-crust soils. VLCA explained 8.1% of the observed variance (p-value = 0.0002); its highest values were recorded in samples of ADV sub-crust soils.

The PCA performed on all the available samples (Fig. 4.C.) confirmed poor differentiation of samples of bare soils, FAC biomass and FAC sub-crust soils, and higher content of all the analyzed main nutrients in ADV biomass. Soils under plants and under ADV were characterized by a higher content of n-alkanes, with higher participation of compounds with odd and very long chains. These observations were confirmed by LDA (Fig. 4.D.), showing two variables that significantly differentiated the analyzed sample types. TOC explained 13.7% of the observed variance (p-value = 0.0001); its highest values were recorded in ADV biomass. VLCA explained 11.5% of the observed variance (p-value = 0.0002); its highest values were recorded in soils under ADV and soils under plants. Samples of bare soils, FAC biomass and/or FAC sub-crust soils located in Fig. 4.C and D close to the samples of soils under ADV and/or soils under plants were collected on sites with the highest plant cover.

3.3. Microbial biomass in the studied soils and BSCs

The mean content of total PLFA was the lowest in bare soils (7.87 nmol/g d.w., SD = 7.35). In soils under FAC it was twice as much (13.67 nmol/g d.w., SD = 5.40). In FAC biomass, total PLFA content doubled once more and reached 25.52 nmol/g d.w. (SD = 11.52) (Fig. 5.A.). ADV biomass and sub-crust soils were characterized by a noticeably higher total PLFA content – 195.73 nmol/g d.w. (SD = 61.88) and 80.74 nmol/g d.w. (SD = 65.79) respectively. Total ergosterol content showed a similar trend – it was below the detection limit in bare soil samples, reaching 19.42 μg/g d.w. (SD = 3.86) in soils under FAC and doubled in FAC biomass to 30.49 μg/g d.w. (5.44) (Fig. 5.A.). In ADV biomass and their sub-crust soils, ergosterol content was noticeably higher – 121.75 μg/g d.w. (SD = 69.52) and 79.03 μg/g d.w. (SD = 36.24) respectively. Considering PLFA composition in the studied samples, bare soils, FAC biomass, and their sub-crust soils showed similar profiles, with PLFA typical for Gram-negative bacteria constituting on average over 30% and the content of Eukaryotic PLFA below 4% (Fig. 5.B.).

Samples of ADV biomass and sub-crust soils under ADV were characterized by different profiles of PLFA, namely, by noticeably higher input of Eukaryotic PLFA (over 25% and over 10% respectively) and lower input of PLFA typical for Gram-negative bacteria (26.53% and 18.77% respectively). The input of PLFA typical for Gram-positive bacteria was comparable in all the samples (between 6.54% and 8.88%), with a slightly lower value for ADV biomass (3.82%). The input of PLFA typical for non-specified bacteria was similar for bare soils, FAC biomass and sub-crust soils (between 10.05 and 12.39), and slightly higher for ADV biomass and sub-crust soils (19.44% and 15.18%, respectively).

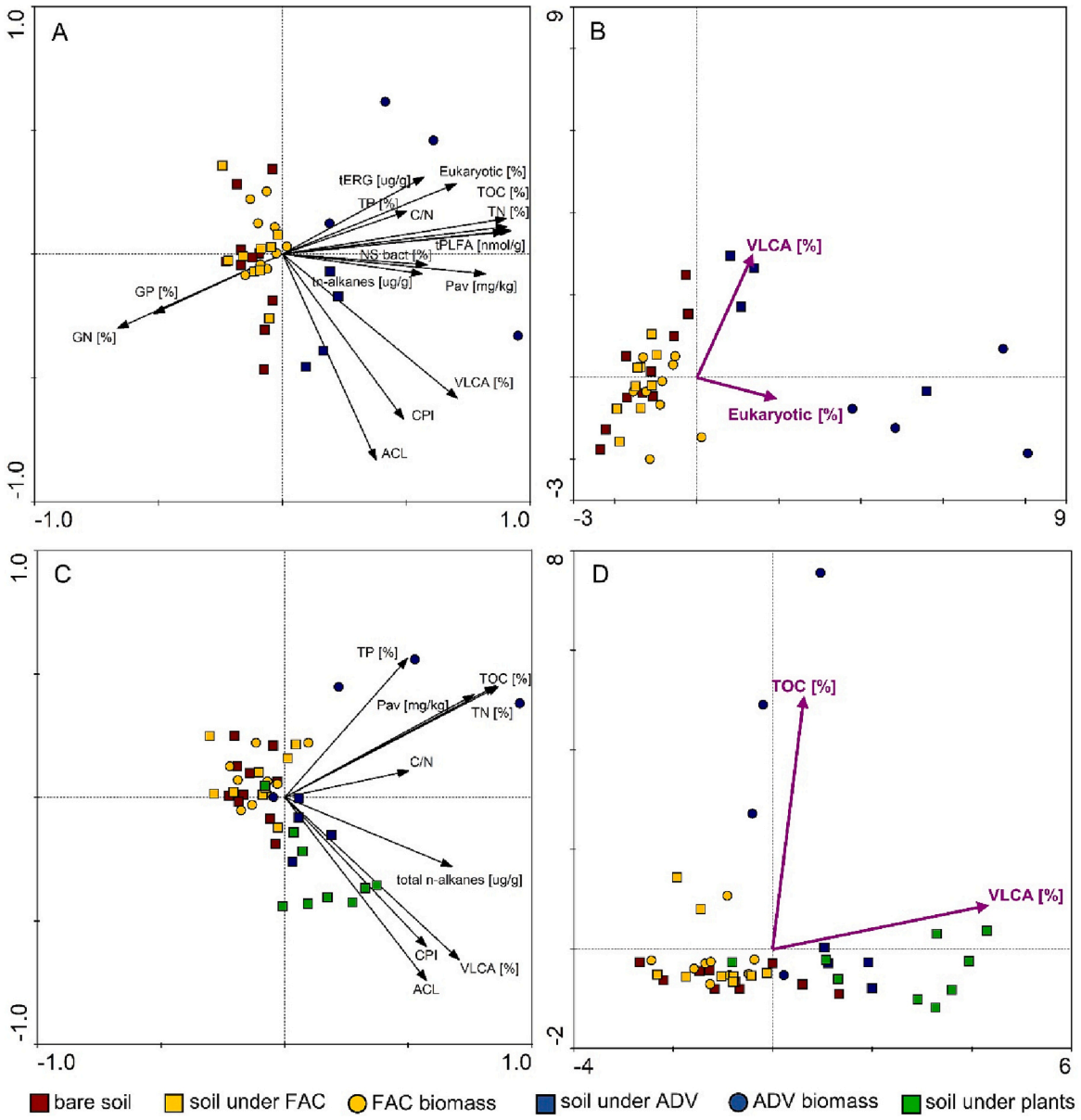

Fig. 4. A – PCA performed for all variables (including PLFA and ergosterol), with the exclusion of samples of soils under plants (eigenvalues: $\lambda_1 = 0.485$; $\lambda_2 = 0.126$; $\lambda_3 = 0.097$; $\lambda_4 = 0.082$). B – LDA performed for all variables (including PLFA and ergosterol), with the exclusion of samples of soils under plants (canonical eigenvalues: $\lambda_1 = 0.851$; $\lambda_2 = 0.315$, *p* value for canonical eigenvalues 0.0004). C – PCA performed on all samples, with the exclusion of data on PLFA and ergosterol (eigenvalues: $\lambda_1 = 0.463$; $\lambda_2 = 0.258$; $\lambda_3 = 0.097$; $\lambda_4 = 0.079$). D – LDA performed on all samples, excluding data on PLFA and ergosterol (canonical eigenvalues: $\lambda_1 = 0.688$; $\lambda_2 = 0.571$, p value for canonical eigenvalues 0.0001). TN – total nitrogen content, TP – total phosphorus content, TOC – total organic carbon content, tPLFA - total Phospholipid Fatty Acids content, GP – PLFA representing biomass of Gram-positive bacteria, GN – PLFA representing biomass of Gram-negative bacteria, NS bact – PLFA representing biomass of non-specified bacteria, Eukaryotic – PLFA representing Eukaryotic biomass, tERG - total ergosterol content, tn-alkanes - total n-alkanes content, CPI – carbon preference index, ACL – average chain length, VLCA – very long-chain n-alkanes.

3.4. Potential accumulation and enrichment in N, C and P in the studied soils and BSCs

Mean TN content in bare soils (0.04%, SD = 0.02) and in soils under FAC (0.07%, SD = 0.05), under ADV (0.08%, SD = 0.02), and under plants (0.08%, SD = 0.04) was low and did not exceed 0.1% (Fig. 5.C.). Concerning crust biomass, mean TN content in FAC biomass reached comparable values as in bare and sub-crust soils (0.06%, SD = 0.04), while in ADV biomass mean TN content was approximately ten times higher and reached 0.35% (SD = 0.26). Mean TP content was uniform in crust biomass (both FAC and ADV) and sub-crust soils (0.03–0.05% with SDs between 0.00 and 0.01). However, we observed the differences in the relative content of Pav. While it constituted around 1% of TP in samples of bare and sub-crust soils and in FAC biomass, in ADV biomass its share increased on average to 3.1% (SD = 2.8) (Fig. 5.C.). Mean TOC content was the lowest in bare soils (0.27%, SD = 0.13), approximately twice as high in FAC biomass (0.48%, SD = 0,35) and in soils under FAC (0.51, SD = 0.47), under ADV (0.63%, SD = 0.02), and under plants (0.67%, SD = 0.39) (Fig. 5.D.). In ADV biomass mean TOC content was ten times higher than in bare soils (3.16%, SD = 2.28). Mean C/N ratio values were slightly lower for bare soils and soils under FAC (around 7.0) than in other samples (around 8.0) (Fig. 5.D.).

To assess the potential accumulation of nutrients in BSCs, we calculated ratios of TN, TOC, TP and Pav content in crust biomass to their content in sub-crust soils. For FAC, mean values of crust to sub-crust soil ratios for TN and TOC were 1.25 (SD = 1.10) and 1.56 (SD

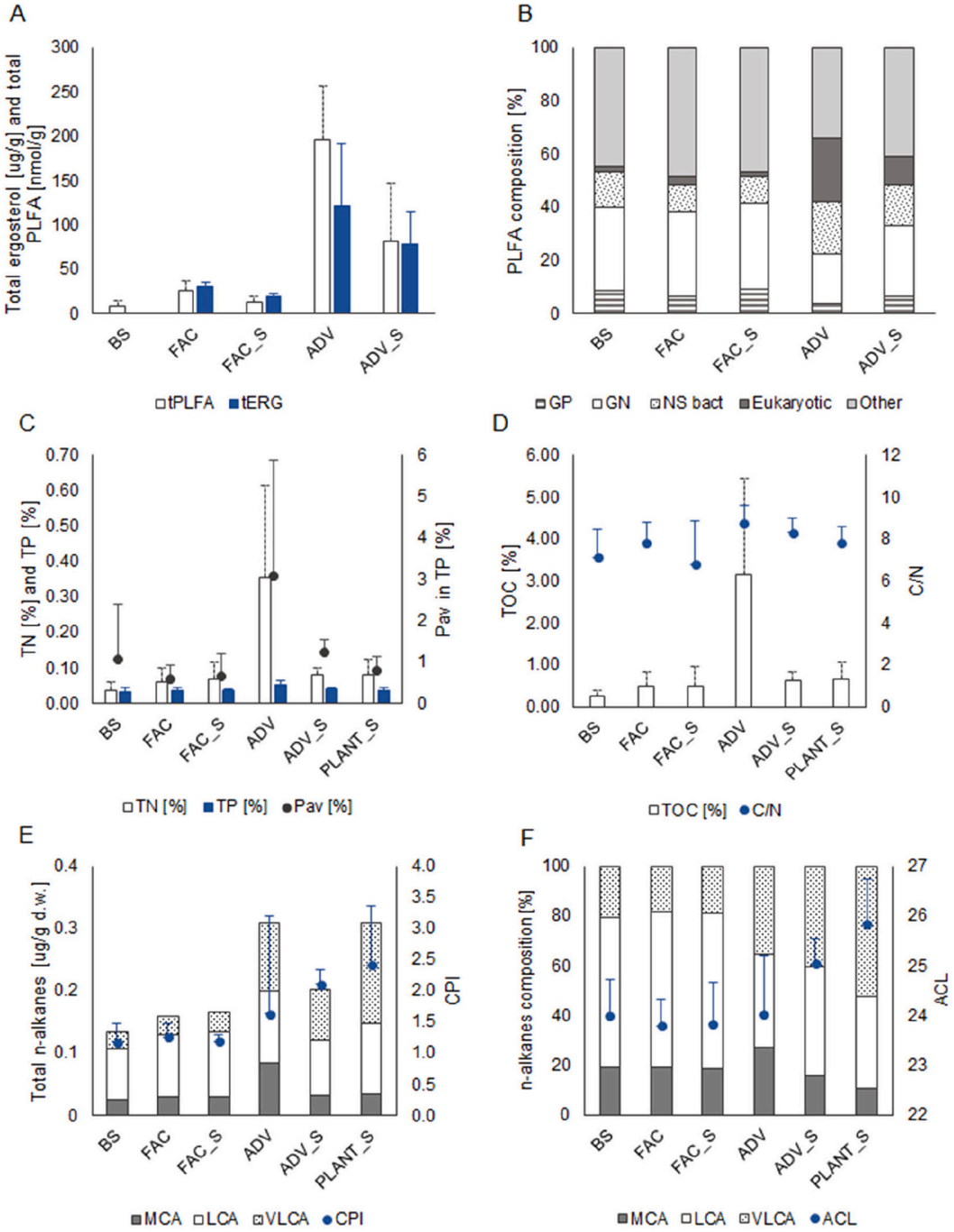

Fig. 5. Characteristics of organic matter in the studied samples. BS – bare soil, FAC – fungal-algal crust, FAC_S – soils under FAC, ADV - fungal-algal-lichen and fungal-algal-lichen-moss crusts, ADV_S – soils under ADV, PLANT_S – soils under plants. tPLFA -total Phospholipid Fatty Acid content, tERG – total ergosterol content. GP – PLFA representing biomass of Gram-positive bacteria, GN – PLFA representing biomass of Gram-negative bacteria, NS bact – PLFA representing biomass of non-specified bacteria, Eukaryotic – PLFA representing Eukaryotic biomass, Other - PLFA outside the categories mentioned above. TN – total nitrogen content, TP – total phosphorus content, TOC – total organic carbon content, Pav in TP – available phosphorus as a percent of total phosphorus content. n-alkanes - total n-alkanes content, CPI – carbon preference index, ACL – average chain length, MCA – mid-chain n-alkanes (C16-C21), LCA – long-chain n-alkanes (C22-C26), VLCA - very long-chain n-alkanes (C27-C33).

= 1.29), respectively. As such, they were roughly six times lower than TN and TOC ratios for ADV (Table 2.). For TP, mean values of crust to sub-crust soil ratios were around 1 for both FAC (1.05, SD = 0.24) and ADV (1.31, SD = 0.35). For Pav, mean values of crust to sub-crust soil ratios were 2.24 (SD = 2.87) for FAC and 3.40 (SD = 3.36) for ADV. The ranges of crust to sub-crust soil ratios for all the studied nutrients were rather wide (Table 2.), with high SD values. For half of the FAC biomass samples and one ADV biomass sample, the contents of TN, TOC, TP and Pav were lower or equal to those in the respective subsoil.

To assess nutrient enrichment in sub-crust soils, we calculated ratios of TN, TOC, TP and Pav content in sub-crust soils to bare soils from the same location. We also made the same calculation for soils under vascular plants. Mean values of sub-crust soil to bare soil ratios for TN and TOC for ADV were comparable to the ratio calculated for sub-plant soils (in all cases around 2.5), and higher than values calculated for FAC sub-crust soils (for both variables 1.5). The mean values of sub-crust soil

Table 2
Potential accumulation of total nitrogen (TN), total organic carbon (TOC), total phosphorus (TP) and available phosphorus (Pav) in BSC biomass expressed as a ratio of nutrient content in crust biomass to sub-crust soil and nutrient enrichment in sub-crust/sub-plant soils expressed as a ratio of nutrient content in sub-crust/sub-plant soil to bare soil taken from the same location. TN – total nitrogen, TOC – total organic carbon, TP – total phosphorus.

Ratio of main nutrients content		Statistics	TN	TOC	TP	Pav
Potential accumulation	in FAC biomass to FAC sub-crust soil ($N = 10$)	mean ± SD	1.25 ± 1.10	1.56 ± 1.29	1.05 ± 0.24	2.24 ± 2.87
		median (range)	0.98 (0.16–3.79)	1.39 (0.11–4.56)	1.01 (0.62–1.45)	0.98 (0.14–9.36)
	in ADV biomass to ADV sub-crust soil ($N = 4$)	mean ± SD	5.72 ± 5.77	6.41 ± 6.69	1.31 ± 0.35	3.40 ± 3.36
		median (range)	4.34 (0.59–13.81)	4.63 (0.56–15.81)	1.41 (0.81–1.60)	2.15 (0.95–8.36)
Nutrient enrichment	in FAC sub-crust soil to bare soil (N = 10)	mean ± SD	1.59 ± 1.31	1.84 ± 2.16	1.03 ± 0.24	1.32 ± 1.25
		median (range)	1.30 (0.60–4.89)	1.13 (0.52–7.69)	0.99 (0.68–1.35)	1.16 (0.03–3.91)
	in ADV sub-crust soil to bare soil (N = 4)	mean ± SD	2.41 ± 0.92	2.62 ± 1.02	1.33 ± 0.35	3.50 ± 2.08
		median (range)	2.69 (1.08–3.18)	2.84 (1.20–3.61)	1.46 (0.81–1.59)	3.90 (0.92–5.30)
	in PLANT subsoil to bare soil ($N = 11$)	mean ± SD	2.32 ± 1.58	2.96 ± 1.99	1.07 ± 0.22	2.16 ± 2.63
		median (range)	2.17 (0.75–5.43)	2.83 (0.85–5.74)	1.10 (0.75–1.36)	1.25 (0.09–8.48)

to bare soil ratios calculated for TP were around one in all sub-crust/sub-plant samples. However, mean values of sub-crust soil to bare soil ratios calculated for Pav were around one only in FAC sub-crust soils. In the case of soils under ADV and plants, mean ratios for Pav were between two and three (Table 2.). The ranges of sub-crust/sub-plant soil to bare soil ratios for crusts and plants were relatively wide, with high SD values (especially for soils under FAC), except for TP (Table 2.). For half of the FAC sub-crust soil samples, TN, TOC, TP and Pav contents were lower than in the respective bare soil.

3.5. Origin and transformation of organic matter in the studied soils and BSCs

The mean content of total n-alkanes was comparable in bare soils, FAC biomass and FAC sub-crust soils and reached 0.14 μg/g d.w. (SD = 0.05), 0.16 μg/g d.w. (SD = 0.11) and 0.17 μg/g d.w. (SD = 0.10) respectively. A slightly higher value was recorded for soils under ADV (0.21 μg/g d.w., SD = 0.14), and noticeably higher values were observed for ADV biomass and soils under plants – 0.31 μg/g d.w. (SD = 0.13) and 0.32 μg/g d.w. (SD = 0.11) respectively (Fig. 5.E.). The absolute content of MCA was alike in all types of samples (approximately 0.03 μg/g d.w.), except for ADV biomass, in which it reached 0.08 μg/g d.w. Similarly, the absolute content of LCA was comparable in all types of samples and ranged between 0.8 and 0.12 μg/g d.w. The biggest differences were observed in the absolute content of VLCA, which in bare soils, FAC biomass and FAC sub-crust soils was around 0.03 μg/g d.w., almost three times higher VLCA content was recorded in soils under ADV (0.08 μg/g d.w.). The highest content was measured in ADV biomass and soils under plants - 0.11 μg/g d.w. and 0.16 μg/g d.w., respectively. CPI index was lower for bare soils, FAC biomass and FAC sub-crust soils (between 1.17 and 1.26) and higher for ADV biomass, soils under ADV and soils under plants (between 1.63 and 2.41) (Fig. 5.E.). Similar trends were recorded for percentage participation of mid-, long- and very long-chain n-alkanes, and for ACL (Fig. 5.F.). Bare soils, FAC biomass and FAC sub-crust soils were characterized by the domination of long-chain n-alkanes constituting around 60% of the total n-alkanes content. Mid-chain and very long-chain n-alkanes constituted approximately 20% each in these types of samples. Samples of ADV biomass were characterized by the highest relative content of mid-chain n-alkanes (~27%), with long and very long chain n-alkanes constituting approximately 35% each. In soils under ADV and under plants, the relative content of mid-chain n-alkanes was the lowest (approximately 16% and 11%, respectively), and the relative content of very long-chain n-alkanes was the highest (approximately 40% and 53%, respectively). The content of long-chain n-alkanes in soils under ADV and under plants was around 40%. Accordingly, bare soils, FAC biomass and FAC sub-crust soils were characterized by lower ACL index (between 23.79 and 23.99), while ADV biomass, ADV sub-crust soils and soils under plants - by higher ACL index (between 24.01 and 25.85).

4. Discussion

4.1. BSC cover and distribution in the Uisu Glacier foreland

We expected a well-developed cover of BSCs in the Uisu Glacier foreland since crusts are often described as dominants covering between 30% and 90% of ground surfaces in deglaciated areas and in hot and cold deserts (Büdel et al., 2014; Garibotti et al., 2018; Janatková et al., 2013; Jung et al., 2018; Rippin et al., 2018; Rosentreter and Belnap, 2001; Wietrzyk-Pełka et al., 2021). However, according to our field observations, BSC cover in the foreland of the Uisu Glacier was significantly lower than in the majority of the available literature, with simple crusts covering on average 14% of the studied area and advanced crusts covering on average 1.1% of the studied area. As most of the available data on BSC come from regions with Mean Annual Precipitation (MAP) values higher than for the north-eastern part of the Pamir Mountains (ca. 80 mm), we believe that both air and soil moisture may explain the observed differences in BSC cover. However, BSC cover in the Uisu Glacier foreland is lower even in comparison to studies performed under similar climatic conditions in the arid Himalaya (up to 40% BSC cover with MAP below 100 mm) (Janatková et al., 2013). Lower BSC cover values were reported only from continental Antarctica, where Colesie et al. (2014) found extremely scarce crusts covering 3.3% of the soil surface in the McMurdo Dry Valleys and only 0.8% in a location in the Darwin Mountains. While mean annual precipitation in these areas is comparable to values typical for the Uisu Glacier foreland (~100 mm), the temperature regime is far more extreme, with a mean annual air temperature of -20 °C and only brief periods of temperatures above zero during summer (Hund, 2014), being probably a reason behind such low BSC cover. BSC cover in the Uisu Glacier foreland was rather uniformly dominated by the least advanced type of BSC (over 80% of all recorded BSC cover in most study locations). Crusts of this type were two times thicker in comparison to data provided by Jung et al. (2018), who reported a simple crust (no lichens nor bryophytes present) with a thickness of approximately 4 mm as the thickest of this type known in the literature. Increased crust thickness observed in the Uisu Glacier foreland could result from the increased production of extracellular polysaccharides by the crust-inhabiting microorganisms as a response to high UV levels and other stressors (Rossi and De Philippis, 2015) or/and slower microbial biomass/necromass turnover in these conditions, leading to higher accumulation of biomass/necromass (Aichner et al., 2021).

The recorded changes in BSC diversity and distribution showed no apparent connections to the distance from the glacier terminus, which remains in accordance with observations from both Arctic and Antarctic glacier forelands showing no correlation between distance from the glacier terminus and accumulation of soil organic carbon and nitrogen (Beilke and Bockheim, 2013, Wietrzyk-Pełka et al., 2020, 2021). The lack of clear chronosequence in the Uisu Glacier foreland implies that the local environmental conditions might have a more substantial effect

on BSCs development and organic matter accumulation than the age of the terrain. This observation, combined with low coverage of BSCs in general and domination of the least advanced BSC type, indicates that dynamic geomorphological processes frequently rejuvenating soil cover influenced BSCs development in the Uisu Glacier foreland. Such processes, including cryoturbation, fluvial and aeolian processes, and zooturbation were previously described as disruptive factors for this area (Chibowski et al., 2023; Gądek et al., 2022; Kabała et al., 2021). These processes can either completely destroy crust structure or move immobile organisms glued to soil particles of different sizes to deeper positions, restricting their access to light and resulting in the dying off of photoautotrophs (Jung et al., 2018). According to several studies performed in hot and cold deserts, chronic physical disturbance of BSCs results in a loss of crust integrity, decreased coverage and macroscopic biomass, and community compositional changes (usually decline in BSCs richness) (e.g., Barger et al., 2006; Concostrina-Zubiri et al., 2014; Steven et al., 2015). Disturbed sites are easily colonized by cyanobacteria, hence the cover of the least advanced crusts increases, and the cover of lichen and mosses decreases (Barger et al., 2006, Concostrina-Zubiri et al., 2014, Steven et al., 2015). In the case of the Uisu Glacier foreland, more advanced BSC types developed almost exclusively in sheltered places with specific micro-relief and/or near the vascular plants, where otherwise unsteady ground was stabilized and dust accumulation was limited. This observation highlights the importance of habitat micro-structure for BSC development, which is known from the literature (e.g., Borin et al., 2009; Garcia-Pichel et al., 2003; Kotas et al., 2018; Wietrzyk-Pełka et al., 2021). The highest diversity of soil cover types and the highest coverage of advanced crusts were recorded in the older and more stable terraces in the middle part of the Uisu Glacier foreland (SP6–8), where the intensity of either glaciofluvial or aeolian processes was restricted, and climatic conditions were the most favorable. On the contrary, the areas close to the glacier terminus were exposed to seasonal fluvial phenomena and cryoturbation processes combined with the lowest temperatures (Gądek et al., 2022, Kabała et al., 2021); and the moraines located the furthest from the terminus were influenced by intense aeolian processes (sand and silt accumulation) and general dryness, confirmed by the lack of the traces of moisture-dependent cryoturbation processes (Gądek et al., 2022, Kabała et al., 2021). These observations mirror the results from SW Tibet, where Janatková et al. (2013) observed the lowest enzymatic activity of BSCs in both cold and dry ends of the environmental gradient.

4.2. Morphological diversity of BSCs from the Uisu Glacier foreland

Studies from other arid regions usually report members of several lichen genera with diverse morphologies forming morphologically complex advanced crusts (e.g., Belnap and Lange, 2003 and references therein, Zedda et al., 2011). There are also many potentially crust-forming lichen taxa reported from other localities in the Pamirs by Kudratov and Mayrhofer (2002). Therefore, we expected well-developed, morphologically diverse, and lichen-taxon-rich advanced crust communities. Instead, we observed morphologically uniform, poorly developed crusts dominated by one lichen morphospecies. Even though more detailed analyses of our morphospecies involving molecular methods could theoretically reveal the presence of additional morphologically similar species, e.g., from the genus *Rinodina* or *Lecanora*, the paucity of BSC-inhabiting lichen community in our study area is still striking. Equally surprising is the lack of cyanolichens from investigated BSCs in our study area since these lichens are frequently reported from drylands (e.g., Belnap and Lange, 2003 and references therein, Zedda et al., 2011, Maier et al., 2014). Some cyanolichen taxa (genera *Gonohymenia* = *Lichinella*, *Peccania*, *Peltigera, Placynthium,* and *Psorotichia*) are also known from other locations in the Pamirs (Kudratov and Mayrhofer, 2002). Still, none of those were found in our plots. While this alone does not rule out that cyanolichens occur somewhere in the Uisu Glacier foreland, they are certainly not the significant components of BSCs. The reasons for this paucity are probably the same as for the overall low BSC cover observed in our study area – the combination of extreme climatic conditions and soil surface instability. Particularly, the lack of cyanolichens might be connected to the extremely low air humidity, and overall hyperarid conditions in the valley since several experimental studies have shown that they highly depend on the availability of liquid water (Lange et al., 1993; Büdel et al., 2013). However, we cannot rule out also the effects of the geographical isolation of the Uisu Glacier foreland and therefore limited propagule supply, which, combined with strong environmental filters, resulted in simplified crust-forming lichen communities. Similar factors are probably responsible for species- and morphotype-poor soil lichen communities in extreme ecosystems of continental Antarctica (Colesie et al., 2014).

4.3. Microbial biomass in BSCs from the Uisu Glacier foreland

Gram-negative bacteria dominated the PLFA-based microbial biomass in all crust types, sub-crust soils, and bare soils in our study area. This very coarse microbial group comprising the majority of known bacterial phyla includes taxa of various biology and ecology (e.g., Spain et al., 2009). Even though Gram-positive bacteria possess a thicker peptidoglycan cell wall, which is known to facilitate their survival, e.g., under drought stress (Naylor and Coleman-Derr, 2018, and references therein), Gram-negative bacteria are always reported as an overall dominant group in soil microbial communities (e.g., Delgado-Baquerizo et al., 2018), including BSC-forming communities (Baumann et al., 2019; Zaady et al., 2010). Gram-negative bacteria possess hardly permeable lipoprotein-enriched outer membranes, known to protect them from hostile external factors, be they extreme environmental conditions or host immune systems (Cole et al., 2021). Fanin et al. (2019) proposed that Gram-negative bacteria use more labile C sources than Gram-positive bacteria. In shallow and poorly transformed soils of the Uisu Glacier foreland, these more labile forms might be, in general, more common (e.g., microbial extracellular metabolites, decomposition of microbial biomass, root exudates, see, e.g., Miralles et al., 2013), thus influencing abundances of bacteria. Gram-negative and, to a lesser extent, Gram-positive bacteria exhibited generally higher relative abundance in all soils and FACs than in ADV crusts in our study area, possibly indicating strong structuring of bacterial communities by crust-forming lichens and bryophytes in well-developed crusts. Lichen species were previously shown to possess species-specific thallus-inhabiting bacterial communities (Grube et al., 2009) and, as a consequence, to significantly affect the structure and abundance of bacterial communities in BSCs (Castillo-Monroy et al., 2011; Maier et al., 2014; Miralles et al., 2020a, 2020b; Miralles et al., 2021).

The levels of the adopted eukaryotic PLFA marker (18:2ω6 - linoleic acid) were correlated to ergosterol levels (Spearman, r2 = 0.82, $p < 0.001$; bare soil, crust biomass, and sub-crust soils, $N = 35$; also evident from Fig. 4A), suggesting that fungi comprised indeed a large part of eukaryotic microbial biomass in our samples. Joint use of these two fungal biomass markers is crucial for the correct interpretation of PLFA data since linoleic acid is one of the main constituents of the membrane lipid layer in plants (Reszczyńska and Hanaka, 2020) and was also found in some cyanobacteria (Kenyon, 1972; Kenyon et al., 1972; Potts et al., 1987). We feel that if the analyzed samples are likely to contain algae, lichens and bryophyte remains (and most BSC samples surely do), this PLFA marker should always be interpreted with caution. Our results show that the biomass of free-living microorganisms, especially fungi, in non-crusted soils was negligible. Therefore microbial biomass and probably activity, at least in the investigated season, was confined to BSCs. While the simple crusts were colonized by microbial communities dominated by Prokaryotes, including cyanobacteria, they were accompanied by eukaryotic microalgae (as partially indicated by 18:2ω6) and free-living fungi (as indicated by ergosterol and partially by 18:2ω6). Both these groups are known to be important components of crusts (e.g., Samolov et al., 2020; Bates et al., 2010), although microalgae are often

considered of relatively little importance (e.g., Jung et al., 2018). Finally, the most advanced BSCs harbored a high biomass of Prokaryotes and Eukaryotes, with the highest detected levels of ergosterol and PLFA 18:2ω6. These might largely represent lichenized fungi and their microeukaryotic photosymbionts and, to some extent, the bryophytes and free-living cyanobacteria. However, the latter are known to be less abundant in lichen-dominated crusts (Wang et al., 2020). Relatively high levels of ergosterol observed in the ADV sub-crust soil indicated the presence of significant biomass of free-living fungi, possibly promoted by crust-derived organic matter and metabolites, and protected from the harsh environmental conditions by the crust biomass. The parallel use of molecular methods to identify microbial diversity associated with biomass-based metrics could undoubtedly improve our overall understanding of the relationships between different BSC-forming organisms but was behind the scope of the present study.

4.4. Nutrient content and potential accumulation in crust biomass, and nutrient enrichment in sub-crust soils from the Uisu Glacier foreland

The TOC, TN, and TP values in bare soils from the Uisu Glacier foreland fit well into the ranges described by Kabała et al. (2021) for topsoils (0–5 cm) from this location. Kabała et al. (2021) observed that the diversification of nutrient content in topsoils along the foreland was relatively low. In most locations, topsoil TOC content ranged between 0.1% and 0.2%; TN content ranged between 0.01% and 0.02%, and TP content showed uniform values around 0.01%. However, TOC and TN contents in topsoil from locations near the glacier terminus and on the moraines at the far end of the foreland (Fig. 1.) were usually lower than the given ranges (in the case of TOC, even ten times lower). On the other hand, topsoils from locations in the middle part of the foreland, where the most abundant plant cover was observed, had TOC and TN values approximately ten times higher than the given ranges (Kabała et al., 2021). We observed similar trends in the bare soils described in this study. In the case of TP content, bare soils from the Uisu Glacier foreland had uniform values regardless of the location; and Pav values, while diversified in bare soils, were distributed randomly with no apparent connection to the part of the foreland.

Comparison of results for crusts biomass and sub-crust soils from the Uisu Glacier foreland with data obtained for crusts and soils in other regions shows that TOC, TN and TP content in our samples should be recognized as low, even against results from other arid or cold areas (Bastida et al., 2014; Baumann et al., 2019; Borchhardt et al., 2019; Chamizo et al., 2012; Jung et al., 2018; Mager, 2010) (Table 3.).

However, samples of advanced crust biomass collected in the middle part of the Uisu Glacier foreland were a notable exception, with TOC and TN content lower only in comparison to single samples from Andes and Spitsbergen (Wietrzyk-Pełka et al., 2020, Pérez, 1997) (Table 3.). In case of TP content no noticeable increase was observed in any sample type from the Uisu Glacier foreland. Yet, the percentage share of Pav in TP was the highest in the biomass of advanced crusts, suggesting increased P mobilization due to potentially higher microbial activity in this type of BSCs (as in Baumann et al., 2019 and Borchhardt et al., 2019). This assumption is, to some extent, confirmed by PLFA and ergosterol as markers of living microbial biomass, which were negligible in bare soils and increased noticeably with the growing complexity of the crusts.

The accumulation of TN, TOC, TP and Pav in crust biomass as compared to sub-crust soil did not occur in all the samples, as for half of the FAC samples and one ADV sample, the contents of these elements in crust biomass were lower or equal to those in the respective sub-crust soil (Table 2.). Same trend, though less intense, was noticeable even for Pav. There are several potential non-contradictory explanations for this observation. First, it may be caused by some nutrients leaching down the soil profile (under hyperarid conditions, mainly during the freeze-thaw cycle), which is commonly reported from other studies on BSCs (e.g., Ferrenberg et al., 2022; Young et al., 2022). It was found that less-developed crusts formed predominantly by cyanobacteria were less able to retain the nutrients (mostly C and N) than advanced BSC types (Ferrenberg et al., 2022, Young et al., 2022), which to some extent corroborates our results. Moreover, Young et al. (2022) suggested that cyanobacteria-derived metabolites (e.g., C-rich photosynthates) could potentially stimulate N-fixation by associated diazotrophic bacterial communities in the "cyanosphere" developed under these crusts, which can also explain the differences in N content. Finally, generally prolonged residence time of organic matter in soils under dry and cold climate could enable nutrient enrichment in soils under crusts (see Aichner et al., 2021), visible also in our results. Moreover, we should keep in mind that the C:N ratio of crust biomass was very similar to the C:N ratio of sub-crust soils, which according to Janssen (1996), shows that neither accumulation nor dissimilation of organic N and C is preferred, and the C:N ratio retains its value.

Generally, the main reason for the relatively low nutrient content in crusts and soils from the Uisu Glacier foreland is probably the extremely cold and extremely dry climate typical for the NE part of the Pamir Mountains. Under such a climate, the development of soils is significantly hampered. According to Kabała et al. (2021), the development of soils in the valley has a very low intensity due to climate-caused water deficit, which limits chemical weathering and solute transport in soils. Moreover, low temperatures and aridity, combined with high UV irradiation typical for high-altitude habitats and with continuous disruption of soil cover due to periglacial and aeolian processes, negatively impact the condition of microbial soil communities, preventing the development of more advanced and diversified forms of BSCs, with biomass-rich taxa and higher potential for soil enrichment (e.g., Jung et al., 2018; Marinetti et al., 2021; Rehakova et al., 2011; Rippin et al., 2018). The extreme climate and soil instability also restrict the cover of vascular plants in the foreland (e.g., Janatková et al., 2013; Jung et al., 2018; Marinetti et al., 2021). Considering the limitations mentioned above, soils in the Uisu Glacier foreland are exceedingly poor in organic carbon, with carbon pool among the smallest reported in glacier forelands according to Kabała et al. (2021), low in nitrogen and in phosphorus, as P release from minerals is significantly restricted due to water deficit.

Table 3
Comparison of TOC, TN and TP content in crusts, soils under crusts and soils under vascular plants obtained for the Uisu Glacier foreland with available literature data.

	TOC [%]	TN [%]	TP [%]	References
SIMPLE CRUSTS				
NE Pamir, Tajikistan	0.16%–1.36%	0.03%–0.16%	0.03%–0.05%	this study
Range of literature data	0.34%–6.06%	0.0, %-0.25%	0.01%–0.1%	Baumann et al., 2019, Borchhardt et al., 2019, Mager, 2010
ADVANCED CRUSTS				
NE Pamir, Tajikistan	0.40%–5.79%	0.05%–0.66%	0.04%–0.07%	this study
Range of literature data	0.20%–20%	0.10%–0.90%	0.1%	Bastida et al., 2014, Borchhardt et al., 2019, Chamizo et al., 2012, Pérez, 1997, Wietrzyk-Pełka et al., 2020
SOILS UNDER BSCs/CRYPTOGAM COVER				
NE Pamir, Tajikistan	0.20%–1.52%	0.03%–0.17%	0.03%–0.05%	this study
Range of literature data	0.02%–1.36%	0.05%–0.07%	x	Bastida et al., 2014, Vilmundardóttir et al., 2015
SOILS UNDER VASCULAR PLANTS (ALPINE SPECIES)				
NE Pamir, Tajikistan	0.22%–1.32%	0.03%–0.15%	0.02%–0.04%	this study
Range of literature data	0.02%–1.92%	0.06%–0.17%	0.06%–0.1%	Kabała and Zapart, 2012, Marinetti et al., 2021, Zhang et al., 2021

4.5. Impact of BSCs on soil C, N and P pool as compared to vascular plants

On average, a comparison of TN and TOC content in soils under crusts and under vascular plants with nutrient content in bare soils from the same locations showed enrichment of sub-crust soils by a factor of 1.5 for simple crusts and at least 2.5 for advanced crusts and vascular plants. These values are in accordance with Chamizo et al. (2012), who estimated that BSCs could increase soil C content by 300% and soil N content by 200%. However, we must remember that half of the FAC sub-crust soils contained amounts of TN and TOC similar to or even lower than the bare soils from the same location. These inconsistencies might result from the leaching and prolonged residence time of organic matter described in the previous chapter. Nevertheless, the recorded values indicate significant potential for accumulation of organic carbon and nitrogen under crusts and plants even in extreme hyperarid conditions. Usually, nutrient storage occurs during the non-growing season, when crusts remain dry and inactive, and nutrient cycling occurs during the growing season upon wetting and activation of crusts (Couradeau et al., 2017, Garibotti et al., 2018). In the Uisu Glacier foreland, the efficiency of potential carbon and nitrogen accumulation was related to the development of crust morphological structure, as more advanced crusts with many biomass-rich taxa accumulate nutrients more efficiently than simple crusts (both in crust biomass and in sub-crust soil). The same trend was described by Chamizo et al. (2012), who observed that lichen and moss crusts had twice as much organic carbon in biomass and in topsoils as cyanobacterial crusts. Moreover, Jung et al. (2018) recorded the highest soil C content in soils under crusts dominated by bryophytes. For nitrogen, the content in lichen and moss crusts was 1.5 times as much as in cyanobacterial crusts (Chamizo et al., 2012). In samples from the Uisu Glacier foreland, values of TOC and TN content in soils under advanced crusts were similar to those recorded for these parameters in soils under vascular plants. Interestingly, the ratio of TP in sub-crust soils (and soils under plants) to BSs in the samples from the Uisu Glacier foreland was always around one, and no indications of potential accumulation were observed. However, if Pav is taken into account, the results indicate an accumulation of labile P forms in soils under crusts and vascular plants, which remains in accordance with Baumann et al. (2019) and Borchhardt et al. (2019), who observed that biological soil crusts convert stable P forms into labile ones. This conversion, in turn, supports plant colonization (Borchhardt et al., 2019) and might be another factor (in addition to ground stabilization by plants) leading to the co-occurrence of advanced crusts and vascular plants in the Uisu Glacier foreland. In some cases, we even observed that BSCs were established directly on dead plant biomass (Supplementary Materials 2), possibly providing both shelter and nutrients to the growing crust.

4.6. Origin and transformation of organic matter in BSCs, sub-crust soils and soils under vascular plants

In all the studied samples dominated either long-chain (C22-C26) or very long-chain n-alkanes (C27-C33). The latter were described as typical for vascular plants (Carrizo et al., 2019; Ofiti et al., 2021), hence their high absolute and percentage content in our samples of soil under plants and of ADV biomass and sub-crust soil (this type of BSC was very often located near vascular plants). Long-chain n-alkanes were described by Carrizo et al. (2019) as of bryophyte origin. Thus, we expected them to dominate in ADV biomass and sub-crust soil. However, no such trend was recorded, as LCA absolute content was similar in all types of our samples, and LCA relative content was the highest in bare soils, FAC biomass, and sub-crust soil. Considering the detailed analysis of lipid content in vascular plants from the Uisu Glacier foreland performed by Mętrak et al. (2021), n-alkanes C23-C25 were among the dominants in both above- and underground parts of the studied plants. Therefore, some LCA in our samples can be of vascular plant origin. This observation can be confirmed by Taylor et al. (2019), who recorded an increase in C23 and C25 n-alkanes in peat, accompanied by a decrease in bryophyte remains and an increase in tree remains. LCA can potentially be formed during the bacterial decomposition of vascular plant waxes (Taylor et al., 2019; Zech et al., 2011). The presence of lipids derived directly or indirectly from vascular plants in all of our studied samples (including bare soils) indicates that organic matter in the foreland soils is well mixed and distributed uniformly, probably by aeolian, fluvial and cryoturbation processes. Thus, the differences from the background organic matter composition can be observed only in and under biologically active soil cover types, in which noticeable amounts of fresh organic matter can be produced relatively quickly, primarily due to the presence of mosses and vascular plants. In our case, these differences were domination or high content of VLCA in soils under plants and under ADV, and high content of MCA, especially lichen-related C17 (Cabrerizo et al., 2016), in ADV biomass. The same samples were characterized by higher CPI values of n-alkanes, which were otherwise around 1. Such values indicate significant degradation of organic matter (Ofiti et al., 2021), possibly to some extent amplified by high UV irradiation (e.g., Zhou et al., 2019) and by the admixture of reworked organic matter, typical for ice proximal and perglacial environments (Duncan et al., 2018; Wojcik et al., 2021). These results are again somewhat corroborated by our field observations of BSCs colonizing dead plant remains (Supplementary Material 2).

5. Summary

In the dry high-altitude foreland of the Uisu Glacier (Pamir Mountains, Tajikistan), the dominating type of biologically active soil cover was BSCs, among which poorly developed crusts (FACs) prevailed. Compared to advanced crusts (FALCS and FALMCs), FACs accumulated less total N, total organic C and available P in their biomass. Yet, they were still the main biological soil-forming factor (next to the plants, which had small cover), given that stones and bare soils covered most of the area and that the biomass of microorganisms in non-crusted soils was negligible. Thus, at least in the investigated season, microbial biomass and probably activity were confined to BSCs.

Soil-forming properties of BSCs were confirmed by the enrichment of sub-crust soils in total N, total organic C and available P. This process was noticeable in both poorly developed and advanced crusts yet was more evident in the latter. Moreover, the average enrichment observed for soils under advanced crusts was similar to the results obtained for soils under vascular plants, thus emphasizing the potential importance of BSCs in such extreme environments as the one we investigated.

In all types of the studied samples, including bare soils, organic matter composition was dominated by n-alkanes between C22 and C33, which can be derived directly or indirectly (via microbial decomposition of cuticular waxes) from vascular plants. This observation indicates that organic matter in the soils of the Uisu Glacier foreland is well mixed and distributed uniformly, probably by aeolian, fluvial and cryoturbation processes. As a result, the differences from the background organic matter composition can be observed only in and under biologically active soil cover types, in which noticeable amounts of fresh organic matter can be produced relatively quickly, mostly due to the presence of mosses and vascular plants (namely, ADV crusts and sub-crust soils and soils under plants).

6. Conclusions

In the context of further aridification projected for the area of Pamir and the whole Central Asia (Normatov and Normatov, 2020; Punkari et al., 2014), we may expect restricted access to water and nutrients (due to decreased rate of decomposition and mineralization), resulting in limitation of ecological niches available for vascular plants. Thus, the BSCs could potentially become the most important or even the sole player in the accumulation of soil nutrients in many areas. Poikilohydric lichens and bryophytes are better adapted to extreme environmental

conditions than vascular plants and can withstand prolonged droughts in a dormant state. Nevertheless, ongoing warming, precipitation, and snow cover alterations will negatively impact these BSC-forming organisms (van Zuijlen et al., 2021, Berdugo et al., 2022). Under hyperarid conditions combined with intense periglacial and aeolian processes in the Uisu Glacier foreland, we observed the paucity of lichen taxa, a relatively small cover of lichen-dominated crusts, and the lack of cyanolichens. As a result, the bioweathering of the underlying soil and rock, and the atmospheric nitrogen-fixing ability, which are some of the fundamental roles of BSCs in their environments (Elbert et al., 2012), are in our system restricted mainly to the free-living Prokaryotic part of the microbial BSC-forming community, and this might be the general feature of similar extreme ecosystems. Over the course of aridification, the development of these Prokaryota-dominated BSCs may be further facilitated by increased input of necromass of vascular plants and cryptogams (Nejidat et al., 2016, Berdugo et al., 2021, van Zuijlen et al., 2021). The establishment of BSCs on the dead plant remains observed during our fieldwork in the Uisu Glacier foreland may potentially be a part of such a process. Nevertheless, since the simple crusts are known to have relatively poor multifunctionality (as defined by Pietrasiak et al., 2013 - C and N fixation, and soil aggregate stabilization) and bioweathering capabilities (Agnelli et al., 2021), we can expect that soil formation in the Uisu Glacier foreland will still be a relatively slow process, even in the face of all the potential changes driven by the aridification. However, the questions of the taxonomic identity of BSC-forming organisms, the characterization of different nutrient pools associated with them, their role in bioweathering, nutrient mobilization, leaching, and accumulation, and finally, the relationships between BSCs and plant-derived organic matter all need to be further studied in more detail, and using more advanced methods, to better understand the processes of soil formation in high-altitude periglacial areas in hyperarid regions of the world, and to assess the impact of future climate change on these unique ecosystems.

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

Raw data are presented in the supplementary on-line materials.

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Appendix A. Supplementary data

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