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# Biological soil crusts on patterned grounds and their influence on plant succession

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**Abstract:** The taxonomical diversity of cyanobacterial-microalgal crusts (CMC) forming on various types of patterned grounds (PG) and their dependence on some environmental variables were studied. The research was carried out in southwestern Spitsbergen, Svalbard. In total, 82 taxa of cyanobacteria and 79 taxa of algae, 6 species of liverworts, 20 of mosses, 10 of angiosperms and 2 of lichens were identified. The species and quantitative composition of CMC on different PG types were different, and the differentiating factor was moisture. Distinctive for PG types of high sorting activity was the occurrence of string like grey-beige cyanobacteria crusts. A general pattern of changes in the structure of crusts have appeared, starting from the dominance of filamentous cyanobacteria with co-dominance of coccoid species, forming gelatinous sheats. Next, a decrease in their share, up to stop a forming crust in the phases with visible development of the plant cover were observed, although groups of filamentous green algae and diatoms still occurred. In addition, a relationship between taxonomic diversity of CMC and the diversity of subsequent plant cover was studied. A difference in dominance of some species of liverworts and mosses between the labyrinth and circle types of patterned grounds was noted and both of these types were taxonomically different in relation to CMC.

**Keywords:** Arctic, Svalbard, cyanobacteria, soil crusts morphology, polar bryophytes, vegetation development, environmental factors.

## Introduction

Microorganisms colonizing bare rocks and soil are pioneer organisms. The structure of their assemblages and the order of settlement have a key impact on the development of the ecosystem and the biocenoses occurring in them (Borchhardt *et al.* 2017). Arctic terrestrial habitats need autotrophic microorganisms to weather rocks and thus release nutrients. This is a necessary stage for subsequent colonization processes by heterotrophic microorganisms and other autotrophs, including bryophytes, lichens and vascular plants (Mataloni *et al.* 2000).

So far, there are few research on early colonization processes related to the occurrence of cyanobacteria and algae in polar ecosystems. However, later stages of succession, based on moss and vascular vegetation, are analyzed quite thoroughly (Brinkmann *et al.* 2007; Nakatsubo *et al.* 2010; Walker *et al.* 2011; Prach and Rachlewicz 2012; Wietrzyk *et al.* 2016; Wietrzyk-Pełka *et al.* 2020 and literature cited wherein). Cyanobacteria, due to their high resistance to environmental factors, are the dominant microorganisms in these ecosystems (Cannone *et al.* 2004; Matuła *et al.* 2007; Komárek *et al.* 2012; Richter *et al.* 2015, 2018; Pietryka *et al.* 2016, 2018; Borchhardt *et al.* 2017; Vincent *et al.* 2000). Elster *et al.* (1999) and Komárek and Elster (2008) observed that cyanobacteria created specific morphological forms called mats or crusts. Cyanobacterial crusts stabilize soil particles by "gluing" them together with mucus, which causes the formation of biological soil crusts (BSC), which also contain microalgae, fungi, lichens and mosses. They reduce the intensity of wind and water erosion and retain water. By fixing atmospheric nitrogen, they improve the nutrient status in the upper soil (Dickson 2000). The presence of crusts improves the thermal conditions of the ground (Gold 1998). Therefore, Williams *et al.* (2017) emphasize that ecosystem services provided by cryptogamic crusts in Polar Regions are of high importance. Therefore, the species composition of cyanobacterial and microalgal assemblages forming BSCs and their variability depending on the specificity of habitats require detailed research (Pushkareva and Elster 2013).

Patterned grounds (PG) are a special type of habitat for plants in polar regions. They are formed during constantly repeated processes of freezing and thawing of the soil. Freezing processes sort and move soil fragments towards soil-rich areas and stones towards stone-rich areas. Stones are transported along the axis of elongated stone domains, which are compressed and confined as the frozen soil domains expand. This results in the formation of characteristic structures: circles, polygons, labyrinths and elongated strips, with regularly spaced areas that differ in soil structure, *i.e*., coarse grained peripheries and fine grained centres (Kessler and Werner 2003). According to the cited authors, the pattern of emerging PG depends on factors such as concentration of stones, the hillslope gradient and the degree of lateral confinement. Frost activity is not homogenous and declines at peripheries while in centres of this forms is still highly active (Anderson and Bliss 1998). Thawing processes make this habitat available for colonization by autotrophic organisms. Lawley *et al.* (2004) noted that repeated soil disturbances caused by frost may tear the emerging moss-lichen communities into fragments and damage the roots of vascular plants. Similarly, Haugland and Beatty (2005) pointed out that frost disturbance in patterned grounds seems to delay successional trends of vegetation communities when compared with terrain without frost sorting. The cited authors note that the dominant forms in such conditions are only clusters of cyanobacteria and microalgae capable to withstanding low levels of frost.

Previous BSCs analyzes conducted in polar pioneer habitats have shown that they were differencest in taxonomic composition of communities and in the number of individual taxa of cyanobacteria and microalgae, which was reflected in their macroscopic differences, *e.g.,* different color, consistency, and morphology (Pietrasiak *et al.* 2013; Pushkareva and Elster 2013; Richter *et al.* 2014, 2015, 2018; Pietryka *et al.* 2016, 2018; Weber *et al.* 2016). A still poorly known aspect of the ecology of BSCs is the impact of environmental gradients on their occurrence and species composition. Taş *et al.* (2018) showed that within one PG district there were zones with different humidity conditions, *i.e.*, dry on the edges and moist in the central part. It can therefore be expected that BSCs forming within PG will differ ecologically and taxonomically. Richter's field observations in the Svalbard region showed repeated macroscopic differentiation of cryptogamic crusts depending on the zone and the form of PG.

Successional relationships in PG habitats based on the interaction of bryophytes and vascular plants with taxonomically different CMC have not been thoroughly analyzed so far, although the species composition of plant communities developing in these habitats has been studied several times (Rzętkowska 1988; Anderson and Bliss 1998; Cannone *et al.* 2004; Haugland and Beatty 2005). There is also a few research on the interactions of CMC with other groups of plants depending on habitat conditions. Read *et al.* (2016) observed a tendency for BSCs to transform from cyanobacterial assemblages to moss-dominated communities along a gradient of increased humidity.

The main goals of this study were (*i*) to determine what types of PG were colonized by cyanobacteria, algae and plants in the Hornsund fjord area, (*ii*) to identify the taxonomic diversity of BSCs forming on the distinguished types of PG, (*iii*) to examine the relationship between the taxonomic composition of cyanobacterial-microalgal crusts (CMC) and environmental variables such as: sorting activity, humidity, and rubble size (rubble layout), and (*iv*) determining whether the taxonomic diversity of CMC affects the species composition of subsequent successional stages. The last aim of this research is related to the question whether, knowing the composition of the CMC, it is possible to predict in terms of species the further course of settlement in PG? In other words, can the CMCs taxonomical composition be an indicator of a specific future species sequence?

Here, it was initially assumed that the species and quantitative composition of CMC differs on different forms of PG, and that CMC within active frost sorting zones is taxonomically distinguished from zones where frost processes are no longer active. Further, it was assumed that the species composition of the plant cover developing on taxonomically different CMCs is different.

## Materials and methods

### Study area

Study was conducted on the northwest side of Hornsund fjord located in southern part of Spitsbergen (Svalbard Archipelago). Studied PG are located in the area of raised marine terrace, Fuglebergsletta, and within an unglaciated Fuglebekken catchment (Fig. 1). The bedrock of the study area consists mainly of old metamorphic schists (with mica, garnet, and calcite) and paragneiss (Szymański *et al.* 2015). The climate on the Spitsbergen island is a polar and marine type. The period with air temperature over 0°C is very short, no longer than four months (June-September). The annual mean air temperature for the period 1979−2010 was −4.2°C, but for the period 2012−2023 increased by 0.7°C. The long-term annual mean of precipitation for the period 1979−2023 was 20−450 mm (Szymański *et al.* 2015; Hanselman *et al.* 2024).

Seven types of PG were selected for this study, differing in shape, sorting activity of soil material, size of rock debris and degree/stage of succession (Table 1, Figs. 2 and 3). The PG typology is original and based mainly on the first author's own field observations and types described in the literature (Kessler and Werner 2003).

### Field Sampling

Within all of the distinguished PG types three research plots of 20 cm$^2$ were determined for collection of cyanobacteria and algae. In every plot, for to six samples were collected. In the case of three PG showing a zonal arrangement of soil

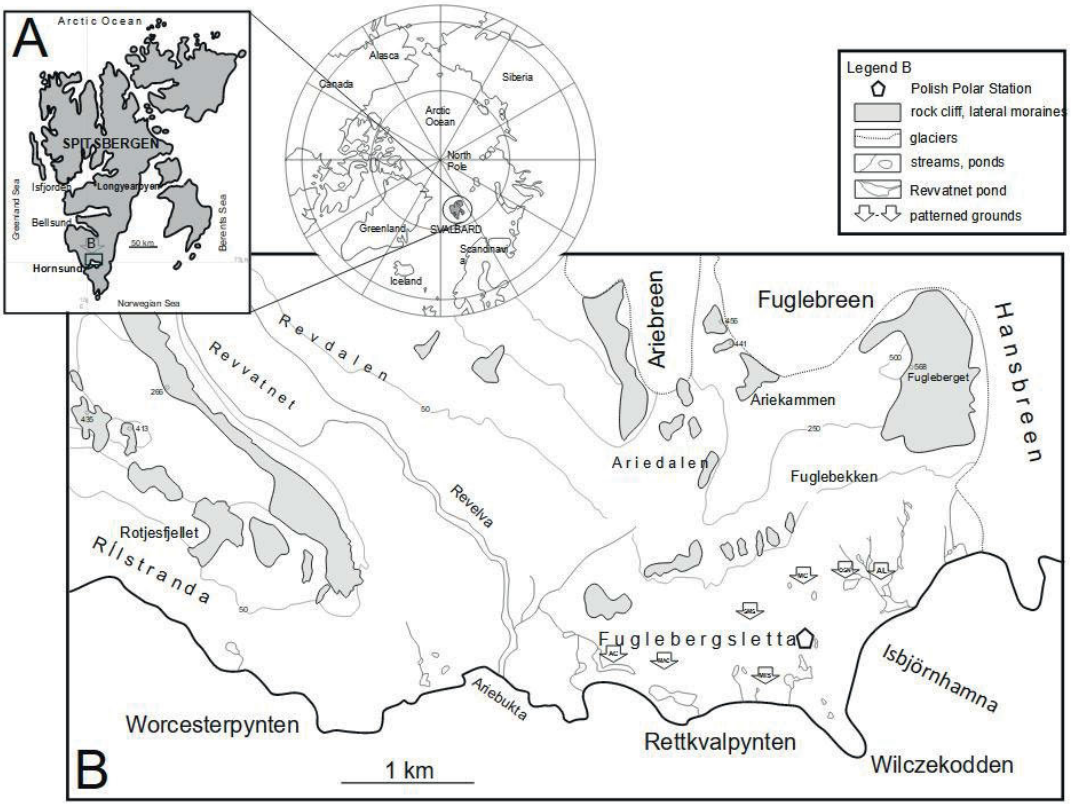

**Fig. 1.** Location of the research area, **A** – Svalbard, **B** – Hornsund fjord, arrows show selected patterned ground area.

**Table 1.** Characteristics of types of patterned grounds (PG) distinguished.

| Symbol of PG type | Number of zones | Rubble layout | Frost-sorting activity | Degree of soil fragmentation | Presence of cyanobacterial and algal crusts and their location; % of cover | Presence of plants and lichens and their location |
|---|---|---|---|---|---|---|
| Active circle sorter patterned grounds | | | | | | |
| AC | 2 | regular circles, each with wide and high wreath of stones | active | fine grained substratum in centre, on margins medium sized rock rubble up to 5 cm in the diameter | in both zones: in central "boiling" part (gelatinous -80%) and on margins (60%) | mosses on margins (40%) |
| Moderately active circles sorted patterned grounds | | | | | | |
| MAC | 2 | regular circles, each with wide and high wreath of stones | moderately active | fine grained substratum in centre, on margins big stones up to 15 cm in the diameter | mostly in central part - gelatinous crust (80–90%) and black crustaceous crust (10%); scattered on margins | in both zones: in central part scattered liverworts and angiosperms (10%); on margins mosses (70%) and scattered angiosperms (5%) |

*Table 1 continued*

| Symbol of PG type | Number of zones | Rubble layout | Frost-sorting activity | Degree of soil fragmentation | Presence of cyanobacterial and algal crusts and their location; % of cover | Presence of plants and lichens and their location |
|---|---|---|---|---|---|---|
| Mature regular circles nonsorted patterned grounds | | | | | | |
| MC | 3 | regular circles, each covered with stones | inactive | large stones (15 cm and more in the diameter) also in the centre | lack of zonation of plant cover: cyanobacteria and algae crust on the whole surface of circle- 30% | mosses (80%) and angiosperms (5%) on the whole surface of circle |
| Active labyrinths sorter patterned grounds | | | | | | |
| AL | 3 | linear and irregular forms resembling labyrints with visible stripes of stones along | active | medium-sized (up to 5 cm in the diameter) rock rubble in strips, fine grained substratum inside | in central "boiling" part black crustaceous crust (10%); along it - narrow (10 cm) stripes of grey-beige gelatinous crust (60%) and scattered black crust; the most outer stripes - scattered gelatinous crust (30%) | in stripes along "boiling" centrum mosses (40%) and angiosperms (10%); on outer margins more mosses (70%), also lichens (5%) and angiosperms (10%) |
| Moisture irregular stripes nonsorted patterned grounds | | | | | | |
| MIS | 1 | linear, irregular stripes with flowing water limited by strips of stones along | inactive | in stony strips stones of different sizes, medium-sized to large; fine grained substratum inside | only on outer margins; both grey-beige gelatinous and black crusts (50%) | mosses (40–50%) and angiosperms (10%) on the outer margins |
| Strongly matured stripes nonsorted patterend grounds | | | | | | |
| SMS | 1 | linear, irregular stripes built of stones or fine grained substratum | inactive | stones of different sizes cover almost the whole area | dry crustaceous crust (40%) on the whole surface of stripes | mosses (30%) and angiosperms (15%) on the whole surface of stripes |
| Overgrown stripes nonsorted patterned grounds | | | | | | |
| OSN | 1 | slightly visible linear, irregular stripes with stones or fine grained substratum | inactive | stones of different sizes cover almost the whole area | cyanobacteria and algae (10%) among stems of mosses | overgrown with moss tundra (90%) |

material (Active Circle Sorter patterned grounds (AC), Moderately Active Circles sorted patterned grounds (MAC), Active Labyrinths sorter patterned grounds (AL), samples were collected separately from the surface of each zone in order to determine possible differences in BSCs. The research plot for lichens, mosses and vascular plants covered

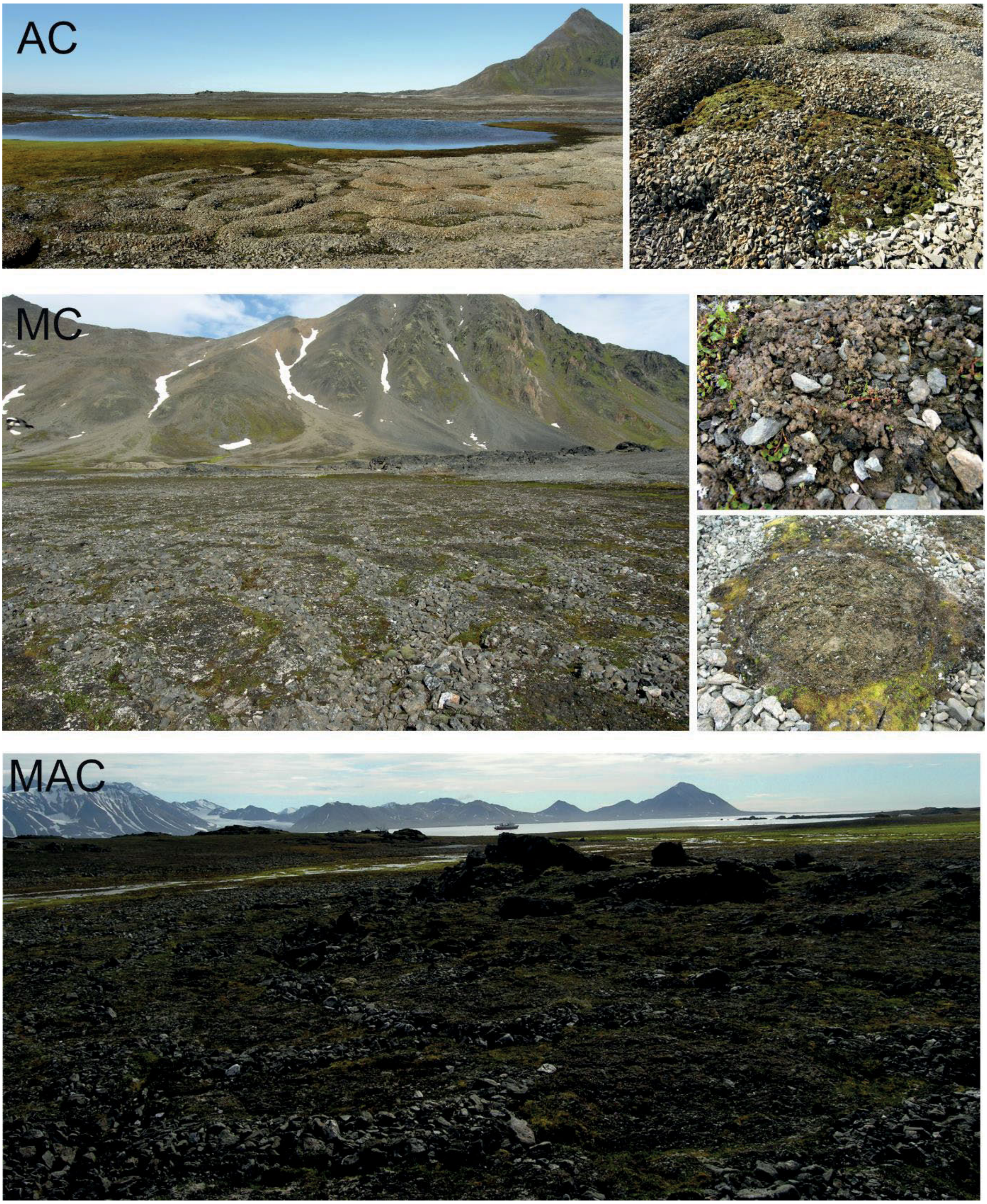

**Fig. 2.** The appearance of patterned ground of the circles type. Symbols: AC – Active Circle sorter patterned grounds, MC – Mature Regular Circles nonsorted patterned grounds and MAC – Moderately Active Circles sorted patterned grounds.

an area of 50 cm$^2$. Samples of all observed species were collected for further microscopic identification in the laboratory. At the sampling site, the estimated percentage share of individual taxonomic groups within the research plot was recorded. In relation to the BSC, the color and consistency/ structure of the crusts were also noted.

Selected habitat parameters were assessed visually using own author's scales. In relation to sorting activity, a 4 – point scale was adopted, where: 1 meant the most active polygons (boiling), 2 – moderately active, 3 – matured and 4 overground (polygons with completed sorting processes). Relative humidity was assessed according to a 3-point scale, in

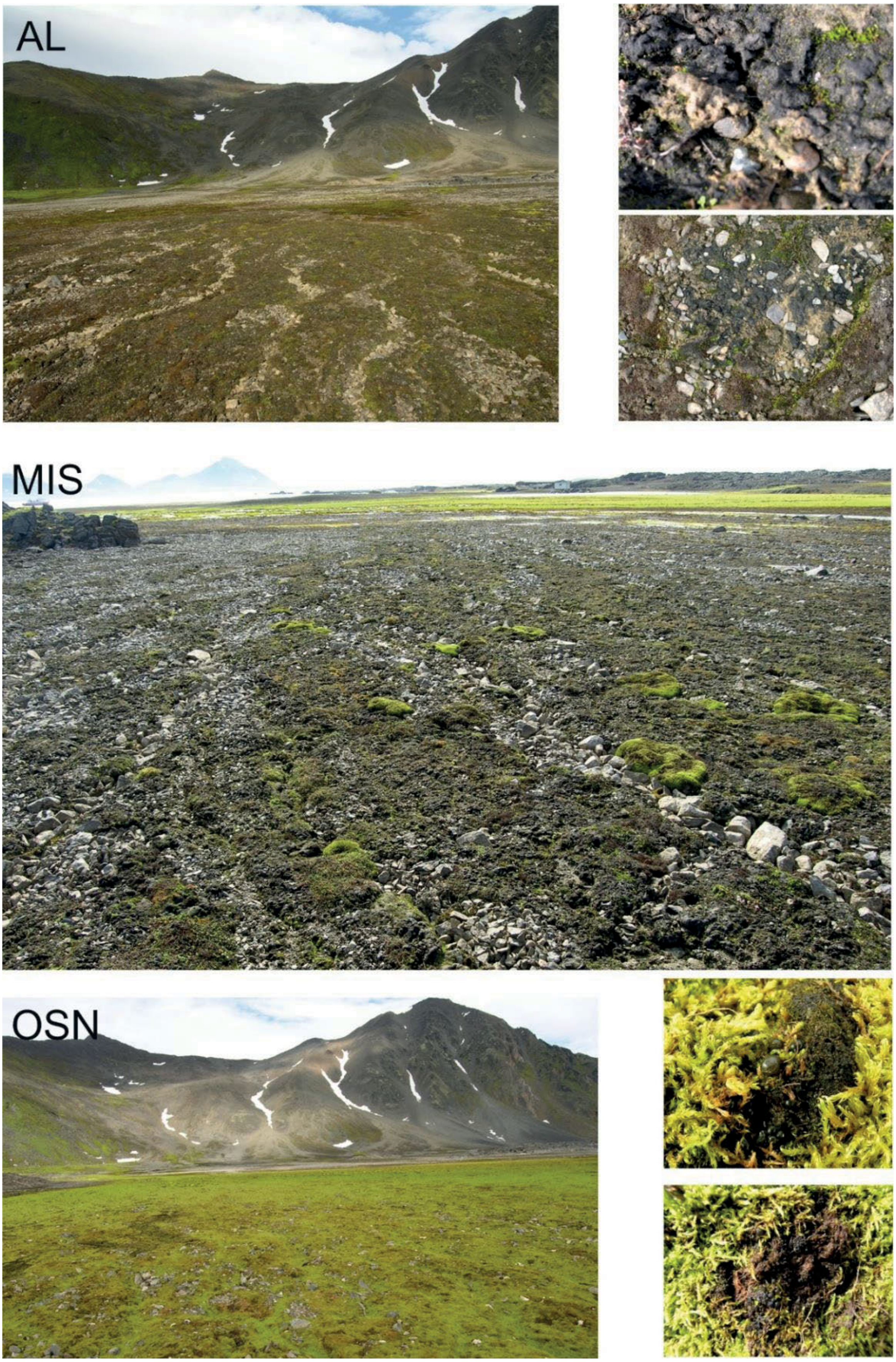

**Fig. 3.** The appearance of patterned ground of the irregular stripe type. Symbols: AL – Active Labyrinths sorter patterned grounds, MIS – Moisture Irregular Stripes nonsorted patterned grounds and OSN – Overgrown Stripes Nonsorted patterned grounds.

which 1 concerned moderately wet habitats, 2 – wet, 3 – permanent supply of water. The scale for assessing the size of rock debris included 4 degrees, starting from 0, *i.e*., the lack of rock debris in the soil structure, 1 – the dominance of stones with the smallest diameter (ø < 5cm), 2 – medium-sized stones (ø = 5–15cm), 3 – stones with the largest diameter (ø > 15cm). To assess the amount of plant cover, the following grades were adopted: 1 – few individuals occupying no more than 5% of the research plot area, 2 – 5–40% cover, 3 – cover above 40%.

### Microscopic analysis

Cyanobacteria and algae species were identified with used of Nikon Eclipse TE2000-S digital microscope equipped with a Nikon DS-Fi1 camera. The taxa were identified according to taxonomic literature (Komàrek and Anagnostidis 1999, 2005; Coesel and Meesters 2007; Bąk *et al.* 2012; Komàrek 2013; Raabová *et al.* 2017; Škaloud *et al.* 2018). The quantitative of cyanobacteria and algae taxa was determined under the microscope using modified Starmach's scale (1955), where 1 means the individual occurrence of a given species; 2 – from 1 to 20 units (specimens) on standard viewing surface; 3 – from 20 to 30 units on standard viewing surface; and 4 – dominant or forming crusts (over 30 units in every field). The share of mosses and liverworts was assessed only in relation to the collected samples, which was not possible in the field. The following scale was adopted: 1 – from 1 to 5 individual specimens (stems), with share less than 0.1% of the total sample; 2 – more specimens than 5, sharing 0.1−10% of the sample; 3 – any number of specimens which share of 10.1–50% of the sample; 4 – any number of specimens which share of 50.1–100% of the sample. The identification of bryophytes was based on taxonomic keys: (Smith 2004; Hill *et al.* 2023), and their nomenclature was standardized according to Hodgetts *et al.* (2020).

### Statistical analysis

Based on field observations and literature, it was assumed that the most important factors shaping the observed diversity are, from the most important: activity of sorting ground, moisture, and rubble layout. Constrained ordination analysis was used to determine the relationship between species occurrence and these habitat parameters. The taxonomic composition of crusts for these analyses was characterized on the basis of dominant species, due to their importance in the formation of crusts. The elimination of taxa occurring in small numbers did not affect the arrangement on the axis, but improved the readability of the obtained diagram. In order to create a model for data structuring and to determine the ordination technique, the DCA was conducted (Hill and Gauch 1980), which suggested the use of an ordination technique directly on the linear PCA (gradient analysis) data and RDA (redundancy analysis) data, which, consequently, enabled the study of relationships between the occurrence of species and the parameters of habitats. A step-by-step selection of variables and Monte Carlo permutation test with a stepwise variable selection (499 permutations) were conducted in order to confirm the statistical relevance of every environmental variable. For a qualitative comparison of the PG studied, a hierarchical cumulative classification from the Multi Variate Statistical Package (MVSP) package was used using the Sörensen similarity coefficient. This analysis took into account the structural differentiation (zonation) of some types of PGs resulting from the soil sorting activity within them. The Shannon-Weaver species diversity index was used to assess biodiversity (species richness). The statistical analyses were conducted with the CANOCO 4.5 software (ter Braak and Šmilauer 2002). Statistical analyses were performed using STATISTICA v. 13.3 packages (www.statsoft.com) (StatSoft Inc. 2017).

## Results

### Taxonomical diversity of patterned grounds studied

In total, 82 taxa of cyanobacteria and 79 taxa of algae, 6 species of liverworts, 20 of mosses, 10 of vascular plants and 2 of lichens were identified. The Shannon-Weaver diversity index calculated for different PG types was from 2 784 to 3 923 (Table 2). The lowest values were recorded for both zones of the AC type, while the highest for zones 2 and 3 of the AL type. Both these types of PG were different in shape. The values of the evenness index indicated the highest evenness of species representation in the community in AL2 and MAC2. However, the most diverse species shares were found in the case of AC1 and OSN. In relation to the latter types of PG, the values of the equivalence index were almost identical, although they were different in terms of structure, activity and the presence of permanent plant cover.

The studied PG types and their individual zones were clearly different in terms of the overall species richness of cyanobacteria, algae, plants and lichens (Table 2). The AC type was the poorest in species (both zones), and the AL type was the richest (zones 2 and 3). The MIS type can also be considered relatively rich. With regard to circle-shaped PGs, the results were shown increasing species richness and Shannon-Wiener index values depending on the decreasing soil sorting activity what was expected in the light of the existing literature (Cannone *et al.* 2004; Haugland and Beatty 2005). Labyrinth-shaped PGs did not show such a clear tendency.

### Structure of cyanobacterial-microalgal crust assemblages on various types of PG and analysis of their taxonomical similarity

Each of the studied PG types was distinguished by its characteristic structure of cyanobacterial-microalgal crusts (CMC) (Table 3) and taxonomic composition with its own dominant species (Table 4). Three morphological types of CMC were distinguished (Table 3). The most common of them was the gelatinous bright beige cyanobacteria crust,

**Table 2.** The values of Shannon-Wiener diversity index, evenness and total number of species for the selected types of studied patterned grounds.

| Patterned ground | Index Shannon - Wiener | Evenness | Total number of species |
|---|---|---|---|
| AC 1 | 2.784 | 0.945 | 19 |
| AC 2 | 2.844 | 0.966 | 19 |
| MAC 1 | 3.007 | 0.959 | 23 |
| MAC 2 | 3.312 | 0.974 | 30 |
| MC | 3.312 | 0.964 | 31 |
| AL 1 | 3.326 | 0.968 | 31 |
| AL 2 | 3.923 | 0.974 | 56 |
| AL 3 | 3.500 | 0.969 | 37 |
| MIS | 3.386 | 0.960 | 34 |
| SMS | 3.102 | 0.964 | 25 |
| OSN | 3.043 | 0.946 | 25 |

**Table 3.** Characteristics of the biological soil crusts morphology in the patterned ground studied. D – dominant, p – present; 1, 2, 3 – zones distinguished within some patterned ground; symbols of the patterned ground studied as in Table 1.

| Morphology of crust | AC1-2 | MAC1-2 | MC | AL1-3 | MIS | SMS | OSN |
|---|---|---|---|---|---|---|---|
| String like grey-beige cyanobacteria crust | D-1,<br>p-2 | | | D-2 | | | |
| Gelatinous bright beige cyanobacteria crust | D-1<br>p-2 | D-1<br>p-2 | D | D-2<br>p-3 | D | D | |
| Crustaceous black crust | | p-1 | | D-1; p-2 | p | | |
| Groups of filamentous cyanobacteria and algae between stems of plants | | | | D-3 | | | p |
| Groups of filamentous cyanobacteria (*Nostoc commune*) created spherical colonies with firm periderm | | | | | | | D |
| Groups of coccoid algae between stems of plants | | | | | | | p |
| Groups of diatoms between stems of plants | | p-2 | | | p | p | |

which was recorded in 6 types of PG while string like grey-beige form of cyanobacteria crust was recorded only in those PG types in which high sorting activity was observed.

In PG types with active soil sorting zones, there was a certain morphological difference of crusts in their individual zones. In the AC type, characterized by high activity and ongoing formation processes, in zone 1 almost exclusively string like grey-beige cyanobacteria crust developed, accompanied by clusters of cocal cyanobacteria. This form of crust also occurred in the second zone, but in a large company of gelatinous bright beige cyanobacteria crust. In the same zone, the share of cocal cyanobacteria decreased. In the MAC type, which represents a less active circular form of PG, in zone 1 with frost processes still taking place, the gelatinous bright beige cyanobacteria crust dominated but with an additional large share of crustaceous black crust. Zone 2 of MAC type (non-sorting active) was characterized by the presence of concentrations of algae and cyanobacteria that no longer formed distinct crusts. In type of AL, zone 1 (“boiling”) was dominated by crustaceous black crust, while in zone 2, with moderate sorting activity, two additional morphological forms appeared, among which string like grey-beige cyanobacteria crust and groups of coccoid cyanobacteria dominated. Distinctive for zone 3 in AL type, inactive, was the gelatinous

**Table 4.** Taxa of cyanobacteria and algae dominating (D) or present in larger amounts (p) in the cyanobacterial-microalgae crusts developing on various types of patterned ground (PG). s – found in very limited quantities, less than 5% in a sample; symbols of PG types as in the Table 1.

| Species | AC 1–2 | MAC1-2 | MC | AL 1–3 | MIS | SMS | OSN |
|---|---|---|---|---|---|---|---|
| Cyanobacteria | | | | | | | |
| Gelatinous species | | | | | | | |
| *Aphanocapsa muscicola* (Meneghini) Wille | | D-1 | | D-1 | | D | |
| *Aphanothece caldariorum* Richter | D-1; p-2 | | p | | D | | |
| *Aphanothece saxicola* Nägeli | s1; s-2 | | s | | D | | |
| *Chroococcus* cfr. *varius* A. Braun | p-1 | | | | D | | |
| *Chroococcus coherens* (Brébisson) Nägeli | D-1 | | | s-1 | | | |
| *Chroococcus helveticus* Nägeli | s-1; s-2 | | | | D | D | |
| *Chroococcus minutus* (Kützing) Nägeli | | | | D-1; s-2 | | | |
| *Cyanosarcina* sp. 1 | | D | | | | | |
| *Gloeocapsa biformis* Ercegović | s-1 | | | p-2 | | s | |
| *Gloeocapsa kuetzingiana* Nägeli ex Kützing | | D-1; p-2 | | p-1; p-2; | | | |
| *Gloeocapsa punctata* Nägeli | D-1; p-2 | | D | D-2 | | s | |
| *Gloeocapsa tornensis* Skuja | | | | D-2 | | | |
| *Gloeothece* cfr. *palea* (Kützing) Nägeli | | | | D-2 | | | |
| *Pleurocapsa* sp. | | | | p-1; D-2 | | | |
| *Pseudocapsa dubia* Ercegović | | | D | | | | |
| Pseudofilamentous species | | | | | | | |
| *Pleurocapsa* cfr. *aurantiaca* Geitler | | | | | | D | |
| filamentous species | | | | | | | |
| *Komvophoron* sp. | | | | D-1 | | | |
| *Leptolyngbya sieminskae* D. Richter and Matuła | | | | p-1 | D | | |
| *Leptolyngbya* sp. 2 | | | | s-1; D-2 | | | s |
| *Microcoleus lacustris* Farlow ex Gomont | | | | | D | | |
| *Schizothrix calcicola* Gomont | D-1; D-2 | | | | | | |
| *Schizothrix lacustris* A. Braun ex Gomont | | | | D-2; D-3 | | | |
| *Schizothrix* sp. | | D-1 | D | | | | |
| *Schizothrix tenuis* Woronichin | | | | D-1; D-2; D-3 | D | | |
| *Symplocastrum friesii* (Gomont) ex Kirchner | D-1; D-2 | D-1; D-2 | D | D-1; D-2; D-3 | D | s | |
| Heterocytous species | | | | | | | |
| *Nostoc* cfr. *minutum* Desmaziéres ex Bornet et Flahault | D-1 | | | | | | s |
| *Nostoc commune* Vaucher ex Bornet and Flahault (2 forms) | | | | D-1; D-2 | | s | D |
| *Nostoc punctiforme* Hariot | D-1; D-2 | D-1; s-2 | D | D-1; D-2 | D | | |

*Table 4 continued*

| Species | AC 1–2 | MAC1-2 | MC | AL 1–3 | MIS | SMS | OSN |
|---|---|---|---|---|---|---|---|
| Bacillariophyceae | | | | | | | |
| *Caloneis* cfr. *silicula* (Ehrenberg) Cleve | | | | s-2 | D | | |
| *Cymbopleura* cfr. *naviculiformis* (Auerswald ex Heiberg) Krammer | | D-1 | | | | | |
| *Diatoma vulgaris* Bory | | D-1; p-2 | s | s-2 | | s | |
| *Navicula* sp. 1 | | | | | | | D |
| *Nitzschia commutata* Grunow | | | | | | | D |
| *Odontidium hymeale* (Roth) Kützing | | | | s-2 | D | | |
| *Pinnularia subcapitata* W. Gregory | s-1; p-2 | s-2 | D | p-2; s-3 | D | | p |
| unidentificate penate diatom | | | D | | | | |
| Chlorophyta | | | | | | | |
| filamentous species | | | | | | | |
| *Microspora* sp. | | | D | | | | D |
| coccoid species | | | | | | | |
| *Trochiscia* cfr. *granulata* (Reinsch) Hansgirg | | | D | | | | s |
| unidentificate coccoid green algae | | | p | | | | D |

bright beige cyanobacteria crust with a large proportion of filamentous algae occurring between the plant stems.

The taxonomic analysis of species dominating in crusts in individual types of PG (Table 4) showed that only two species of cyanobacteria: *Nostoc punctiforme* and *Symplocastrum friesii,* appeared as dominants. At the same, 22 species of cyanobacteria and algae identified in the study dominated in only one type of PG. Of the latter, the largest number of 7 was recorded in the AL type.

Studied PGs were grouped, according to the Sörensen similarity coefficient, based on the similarity of CMC species (Fig. 4). The dendrogram showed a clear distinctiveness of the OSN type. This type of PG was distinguished from the others by the lack of crusts. The remaining PG types have formed two groups, with a small distance between them. The first one grouped all zones distinguished both within AL and MAC, with AL3 showing almost equal similarity to zones MAC1−2 and AL1−2. The fact that both active and inactive zones of these two PGs' types were in the same similarity group indicates that the assumed taxonomic dissimilarity of CMC depending on the zone of sorting activity was not important.

Also in the second group, both zones of AC type, showed the greatest taxonomic similarity. The remaining grouped PG types (SMS, MIS, MC) differed in their CMC taxonomic composition. Within this group, there was a gradation of similarity depending on the degree of development of the plant cover, from inactive, heavily vegetated SMS through MIS, MC, AC2 to active, plantless AC1.

### Influence of habitat factors on the species structure of BSC

RDA redundancy analysis showed that the highest correlations among environmental variables and sample locations were for moisture, according to the axis 1 gradient. This variable (moisture) was significant and accounted for 15% of the variability. The remaining factors were not significant (Tables 5 and 6, Fig. 5).

In the hierarchical classification accumulating MVSP diagram (Fig. 4), species were grouped along the first axis in relation to the factor: moisture. The dendrogram shows that CMC were dominated by different species (marked in green), independently of the PG's humidity. Thus, these results are consistent with the initial assumption that the species and quantitative composition of CMC on different PG types differs. In the most hydrated habitats, crusts were formed mainly by the filamentous cyanobacteria *Schizothrix tenuis*, a freshwater, submersed species, characteristic for beds of streams (Komárek and Anagnostidis 2005), accompanied by cocal cyanobacteria such as: *Chroococcus helveticus*, *Aphanothece saxicola* and *Chroococcus* cfr. *varius*, often recorded in polar habitats (Cavacini 2001; Komárek and Elster 2008; Davydov 2021a). They were also abundant in crusts some other species. These were: *Microcoleus lacustris* described by Komárek and Anagnostidis (2005) to be freshwater, benthic species; *Leptolyngbya sieminskae* reported by Richter and Matuła (2013) from the surface wet soil and stones in shallow water or in streams flowing through the mosses; diatoms *Caloneis* cfr.

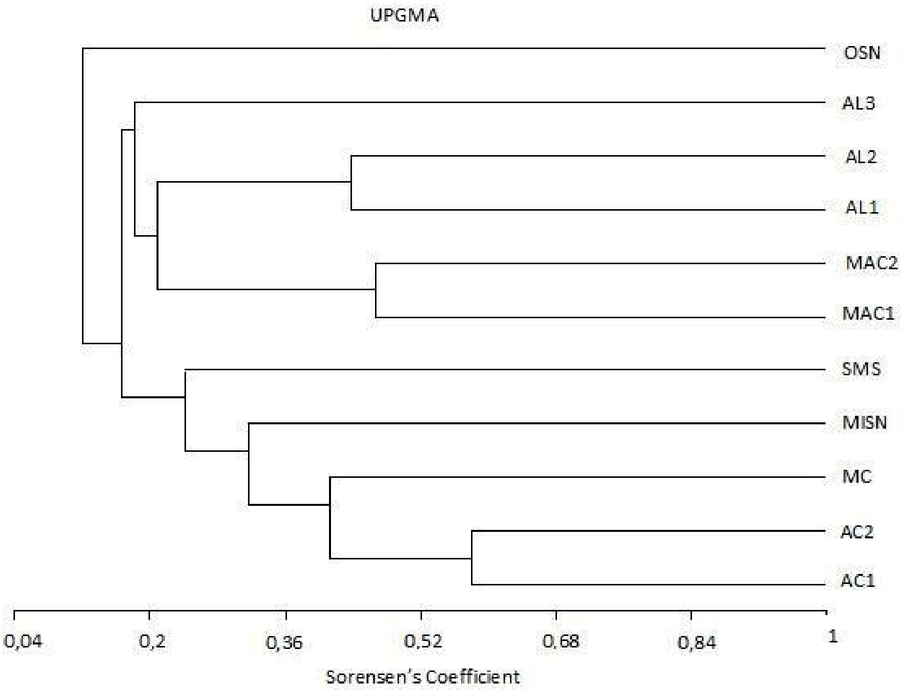

**Fig. 4.** Hierarchical classification accumulating Multi Variate Statistical Package similarities of the studied patterned ground types in terms of taxonomic composition and quantity of cyanobacteria and algae.

**Table 5.** Results of the RDA analysis based on the cyanobacteria and algae taxa dominating in the structure of crusts.

| Axes | 1 | 2 | 3 | 4 | Total variance |
|---|---|---|---|---|---|
| eigenvalues | 0.170 | 0.115 | 0.062 | 0.227 | 1.000 |
| species-environment correlations | 0.977 | 0.945 | 0.909 | 0.000 | |
| cumulative percentage variance | | | | | |
| of species data | 17.0 | 28.5 | 34.7 | 57.5 | |
| of species-environment relation | 48.8 | 82.0 | 100.0 | 0.0 | |
| sum of all eigenvalues | | | | | 1.000 |
| sum of all canonical eigenvalues | | | | | 0.347 |

**Table 6.** Results of stepwise selection of variables during redundancy analysis – conditional effects.

| Variable | Var. N | Lambda A | P | F |
|---|---|---|---|---|
| moisture | 1 | 0.15 | 0.044 | 1.60 |
| activity | 2 | 0.11 | 0.262 | 1.18 |
| rubble layout | 4 | 0.09 | 0.510 | 0.94 |

*silicula*, noted also in Antarctic and Northeast Greenland, in soil algae assemblages (Kerckvoorde *et al.* 2000; Mataloni *et al.* 2000) and *Odontidium hymeale*, typically occurring on montane stream liverworts in cool, oligotrophic subalpine streams (Cantonati 2001; Bishop and Spaulding 2015). The above-mentioned species dominated only in the MIS type of PG, a habitat characterized by the highest humidity, washed by water flowing from the mountains (Table 4).

In conditions of moderate humidity, the formation of crusts was dominated by cyanobacteria *S. fresii*, a species widely distributed in the Arctic (Pietryka *et al.* 2018; Davydov 2021a). It was accompanied by cocal cyanobacteria forming aggregates of *Chroococcus minutus*, *Gloeothece* cfr. *palea*, *Gloeocapsa tornensis*, *G. biformis*, *G. kutzingiana*, typical components of BSC in the Arctic regions (Broady 2005; Cockell and Stokes 2006; Komárek and Elster 2008; Richter *et al.* 2015; Pietryka *et al.* 2018) or groups of filamentous cyanobacteria, such as: *Leptolyngbya* sp., *Komvophoron* sp., pseudofilamentous *Pleurocapsa* sp. and *Schizothrix lacustris*. The latter was previously reported from Svalbard as occurring in very humid sites and described as planktic form in streams, pond and lake or sub- and aerophitic form in moss tundra (Richter *et al.*

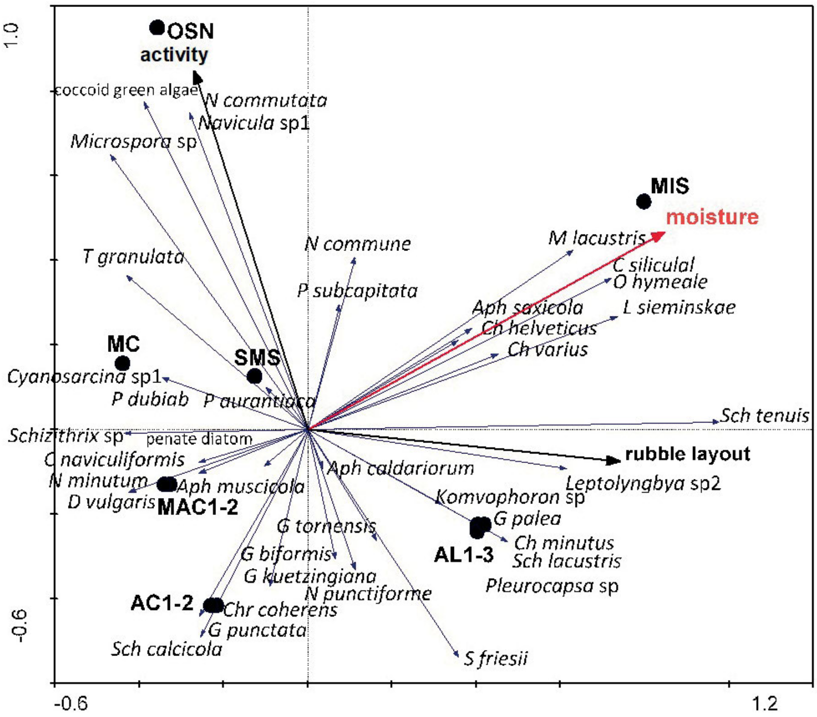

**Fig. 5.** Results of redundancy analysis for relationships between some environmental factors and cyanobacterial-microalgae crust taxa (only dominants). Symbols: AC – Active Circles sorted patterned grounds, MAC – Moderately Active Circles sorted patterned grounds, MC – Mature regular Circles nonsorted patterned grounds, AL – Active Labyrinths sorted patterned grounds, MIS – Moisture Irregular Stripes nonsorted patterned grounds, SMS – Strongly Matured Stripes nonsorted patterned grounds, OSN – Overgrown Stripes Nonsorted patterned grounds.

2015; Richter 2018; Pietryka *et al.* 2018). Our research showed that the above-mentioned species dominated only in the AL type of PG (Table 4).

In conditions of lower humidity, other *Schizothrix* dominated quantitatively in the CMC structure. A clearly separate group was formed by *Sch. calcicola*, which dominated only in the AC type (Table 4). This species has wide ecological spectrum and was recorded from the Arctic in flow water cyanobacteria mats tundra habitats (Matuła *et al.* 2007; Richter *et al.* 2009, 2015). It was accompanied in large numbers by *Chroococcus coherens* – another exclusive dominant in AC type, as well as *Gloeocapsa punctata* and *N. punctiforme*, which were not typical for any of the PG types. Species of the genus *Nostoc* were often noted on soils with visible cryptogamic crusts (Broady 2005; Pócs 2009).

The dominant share of unidentified taxa of the genus *Schizothrix* distinguished two clusters on the same side of the axis on the redundancy analysis (Fig. 5). One of them was characterized by a large quantitative share of species exclusively dominant in the MAC type: cyanobacteria *Aphanocapsa mucicola*, diatoms *Diatoma vulgaris, Cymbopleura cfr. naviculiformis* and unidentificate penate diatom. They were accompanied by heterocytic *Nostoc* cfr. *minutum*. However, this species dominated only in the AC type (Table 4). The second cluster was characterized by high abundance of *Pseudocapsa dubia* – dominant in the MC type. This species was described as widespread on moist, shaded calcareous surface on cliffs and slopes (Pentecoust and Witton 2012). Another co-dominant species in creating crust on MC was *Cyanosarcina* sp., typical for crusts growing on dry and stony ground (Pósc 2009). An isolated position in the vicinity of these two clusters was occupied by *Pleurocapsa cfr aurantiaca*, exclusively dominant species in the SMS type (Table 4). This species is very specific, and so far recorded mainly on rocks, in the southern Europe, *i.e.*, Bosnia and Herzegovina (Kamberović *et al.* 2019) and Brazil (Gama *et al.* 2014).

Two other clusters (Fig. 5) did not have a crust character. One was composed of the cocal cyanobacteria *Nostoc commune* with a large share of the diatom *Pinnularia subcapitata*, and in the other dominated filamentous green algae of the genus *Microspora*, accompanied by numerous coccoid green algae and diatoms, including *Navicula* sp., *Nitzschia commutata*.

## Relationships between taxonomical structure of BSC and accompanying plants and lichens

The plant cover developed mainly in habitats with weakly active frost sorting processes (*e.g.,* AC-2, MAC1-2, AL2) or already inactive (*e.g.,* MC, SMS, OSN, AL3) (Table 7) and occupied from 30 to 100 % area of research plots (Table 1). The taxonomic analysis of the collected samples showed that the studied PG types were different in species composition of plant cover, especially in relation to the dominant species or those with a greater abundance (Table 7). About 37% abundance of this group were recorded in only one PG type, with the largest number of 6 in the AL type. Among the remaining species, there were several that did not show any attachment to a specific type of PG and occurred in several of them. These include some species common in post-glacial habitats throughout Svalbard such as liverworts: *Blepharostoma trichophyllum, Gymnomitrion coralloides, Sphenolobus minutus* and moss *Pohlia wahlenbergii,* as well as species which were described as a permanent component of the moss tundra *Scorpidium revolvens*, *Sanionia uncinata* and *Straminergon strami-*

**Table 7.** Taxa of liverworts, mosses, angiosperms and lichens occurring in the biological soil crusts developing on various types of patterned ground studied with estimation of their quantity. D – more than 40% in a sample, p – present in larger amounts, between 10–40% in a sample, s – found in very limited quantities, less than 5% in a sample; symbols of patterned ground types as in the Table 1.

| Species | AC 1–2 | MAC 1–2 | MC | AL 1–3 | MIS | SMS | OSN |
|---|---|---|---|---|---|---|---|
| liverworts | | | | | | | |
| *Anthelia juratzkanac* (Limpr.) Trevis. | | | | s-2; s-3 | | | |
| *Blepharostoma trichophyllum* (L.) Dumort. | s-2 | s-2 | s | s-3 | D | | |
| *Cephalozia* cfr. *ambigua* C.Massal. | | | | s-2; s-3 | | | |
| *Gymnomitrion corralioides* Ness | | | | D-3 | p | p | |
| *Sphenolobus minutus* (Schreb. ex D.Cranz) Berggr. | | p-1; p-2 | | D-2 | | | |
| mosses | | | | | | | |
| *Brachythecium turgidum* (Hartm.) Kindb. | | | p | | | | |
| *Calliergon richardsonii* (Mitt.) Kindb. | | | | s-2 | | | |
| *Campylium stellatum* (Hedw.) Lange and C.E.O.Jensen | p-2 | | p | | | | |
| *Ceratodon purpureus* (Hedw.) Brid. | | | | p-3 | | | |
| *Dichodontium pellucidum* (Hedw.) Schimp. | | s-1; p-2 | | | | | |
| *Distichum capillaceum* (Hedw.) Bruch and Schimp. | s-2 | p-2 | p | | | | |
| *Drepanocladus turgescens* (T.Jensen) Broth. | s-2 | | | | | | |
| *Encalypta alpina* Smith in Smith and Sowerby | s-2 | | | | | | |
| *Oncophorus virens* (Hedw.) Brid. | | | | p-2 | s | s | |
| *Pogonatum urnigerum* (Hedw.) P.Beauv. | | | | s-3 | | | |
| *Ptychostomum cryophilum* (Mårtensson) J.R. Spence | | s-1; s-2 | | | | s | |
| *Ptychostomum pseudotriquetrum* (Hedw.) J. R. Spence | p-2 | | | | | | |
| *Racomitrium canescens* (Hedw.) Brid.subsp. *latifolium* (C.E.O. Jensen) Frisvoll | | | | p-3 | | | |
| *Sanionia uncinata* (Hedw.) Loeske | p-2 | p-1; p-2 | | s-2; s-3 | | | |
| *Sarmentyhypnum sarmentosum* (Wahlenb.) Tuom and T. Kop. | | p-2 | | | | | |
| *Scorpidium revolvens* (Sw. ex anon.) Rubers | | D-2 | p | D-3 | s | | D |
| *Splachnum sphaericum* Hedw. | | | | p-2 | | | |
| *Straminergon stramineum* (Dicks. ex Brid.) Hedenäs | | p-2 | | s-3 | | | D |
| sphenophytes | | | | | | | |
| *Equisetum arcticum* Rupr. | | | | p-2; p-3 | | | |

*Table 7 continued*

| Species | AC 1–2 | MAC 1–2 | MC | AL 1–3 | MIS | SMS | OSN |
|---|---|---|---|---|---|---|---|
| angiosperms | | | | | | | |
| *Juncus biglumis* L. | | | | p-2; p-3 | | | |
| *Poa* sp. | | | p | | | p | |
| *Sagina nivalis* (Lindbl.) Fr. | | p-1; p-2 | | p-2 | p | | |
| *Salix polaris* Walenb. | | p-2 | | p-3 | | p | |
| *Saxifraga cespitosa* L. | | | | p-2; p-3 | p | | |
| *Saxifraga nivalis* L. | | | | p-2; p-3 | | | |
| *Saxifraga oppositifolia* L. | | p-1; p-2 | D | D-2 | p | p | |
| lichens | | | | | | | |
| *Cetrariella delisei* (Bory ex Schaer.) Kärnefelt and A. Thell | | p-1 | | p-3 | | p | |
| *Ochrolechia* sp. | | | p | p-3 | | p | |

*neum* (Frahm 1977; Stebel *et al.* 2018; Wietrzyk-Pełka *et al.* 2020) and representatives of angiosperms *Sagina nivalis* and *Saxifraga oppositifolia.* According to Cannone *et al.* (2004) *B. trichophyllum* occurred abundantly in the central parts of active PG circles, which differs from our findings that this liverwort developed en masse in zones with less sorting activity. Wietrzyk-Pełka *et al.* (2020) also noted the occurrence of this species in stabilized habitats with already established plant cover.

Using the Sörensen similarity coefficient, the studied PGs were grouped based on the species similarity of the BSCs developing on them together with the plant cover (Fig. 6). The dendrogram showed the distinctiveness of the OSN, which is due to the lack of cyanobacterial crusts and a strongly developed plant cover creating a moss tundra with dominants such as *S. revolvens* and *S. stramineum*. Two internal AL-type zones (AL1-2) were also clearly separated, even though they were different in terms of the development of vegetation cover: there was no vegetation in zone 1 while in zone 2 some liverworts appeared including the dominant *S. minutus* forming numerous weakly branched creeping stems, as well as a few moss species (including coprophilous *Splachnum sphaericum* and *Oncophorus virens*) and some angiosperm species widespread and common throughout Svalbard, *e.g., Saxifraga nivalis*, *S. cespitosa*, *S. oppositifolia*, *S. nivalis* (Rønning 1996; Wielgolaski 1997).

Among the remaining samples two clusters were distinguished. Visibly separate group constituted both zones of the AC and MC types. These types were different in the activity of sorting processes, but similar in terms of humidity (Fig. 5). In zone 1 of the AC type there were no plants, while in the zone 2 plants were already present: the liverwort *Blepharostoma trichophyllum* with strong stems forming cords, and mosses, among which the greater share was noted for the hygrophilous species noted in moist moss tundra *Ptychostomum pseudotriquetum*, *Campylium stellatum* (Rzętkowska 1988; Stebel *et al.* 2018). The MC type was fully colonized by plants: liverwort *B. trichophyllum* and some moss species: *Brachythecium turgidum*, *C. stellatum*, *Distichum capillaceum*, *Scorpidium revolvens*, which were described as typical for moss tundra (Frahm 1977; Rzętkowska 1988; Stebel *et al.* 2018). There was also a large share of flowering plants *S. oppositifolia.*

The second group included different PG pairs: one created by both MAC zones and the other connecting AL3 and MIS. The SMS type also grouped with all them. MAC type was a habitat of low sorting activity, therefore in zone 1 the following species were present: of liverworts (*Anthelia juratzkanum*, *B. trichophyllum*, *S. minutus*), higrophilous mosses (*Ptychostomum cryophilum*, *Dichodontium pellucidum*) and angiosperms (*S. nivalis*, *S. oppositifolia*). In zone 2 the number of liverwort species and their quantitative share were smaller, but the quantitative share of the moss layer has increased. New species have appeared, among others recorded only in that PG type *Sarmentyhypnum sarmentosum*, observed by other authors in moist moss tundra (Stebel *et al.* 2018). The presence of angiosperm *Salix polaris* was recorded.

In turn, the pair AL3 and MIS were inactive, but both types were different in the degree of hydration. Flowing water was observed in MIS, which limited the occurrence of plants to the outer margins and promoted the development of crusts with a specific taxonomic composition (Table 4). This clear taxonomic difference of CMC did not affect the species composition of the moss layer, which

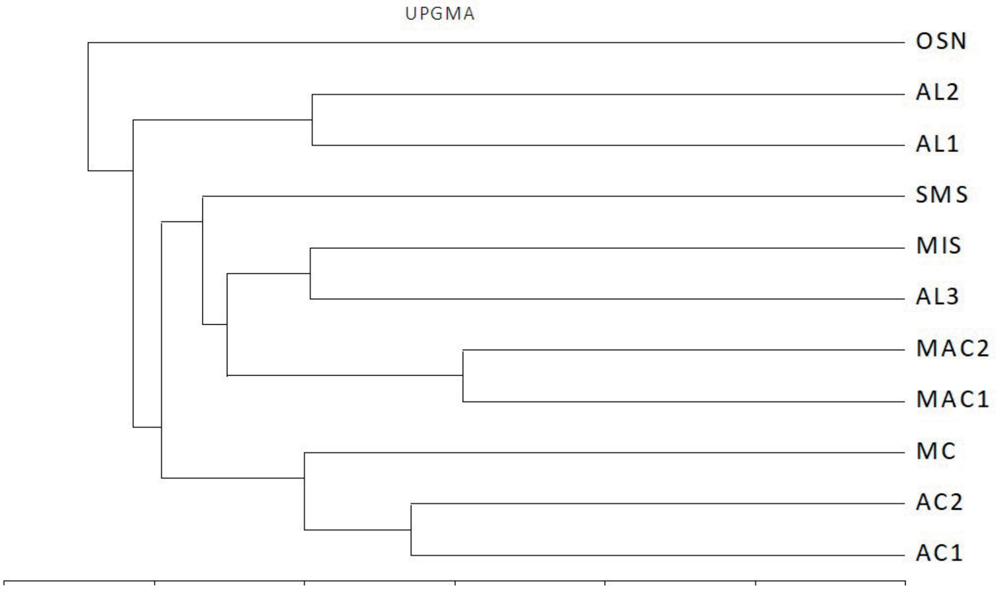

**Fig. 6.** Hierarchical classification accumulating Multi Variate Statistical Package similarities of the studied patterned ground types in terms of taxonomic composition and quantity of cyanobacteria and algae, liverworts, mosses, lichens and vascular plants.

was dominated by moss tundra species. In turn, the moist but not wet habitat in the AL3 zone favoured the vegetation of liverworts, among which dense turfs built *Gymnomitrion coralloides* and *Anthelia juratzkanum*, at the same time limiting the growth of CMC. This zone was also hospitable to many flowering plants, for example the SMS type. It is noteworthy the abundant occurrence of moss species typical for moss tundra as well as the presence of moss species colonizing open and unstable sites, *e.g., Ceratodon purpureus*, *Racomitrium canescens* subsp. *latifolium*, *Pogonatum urnigerum* and *Pohlia wahlenbergii* (Dierssen 2001; Stebel *et al.* 2018).

## Discussion

Our research showed that cyanobacteria and algae were present in all zones and types of studied PG. However, the occurrence of bryophytes, lichens and flowering plants in PG with active soil sorting processes was limited to their external zones. Haugland and Beatty (2005) also reported that in PG with active frost processes, vegetation developed only in peripheral zones with reduced intensity of frost action; however, they did not distinguish cryptogamic crust as a separate life-form category.

The most commonly occurring form of CMC in our study was the gelatinous bright beige cyanobacteria crust in which the gelatinous structure retains moisture and stabilizes the substrate by sticking soil particles together. The other crust form, the string like grey-beige form of cyanobacteria crust, was recorded only in those PG types in which high sorting activity was observed. It seems that the thread-like structure of the taxa creates a form of crust that adapts to an unstable substrate, additionally strengthened by gelatinous shells covering the surface. Cannone *et al.* (2004) distinguished only two types of crusts in the Svalbard PG: (*i*) cyanobacterial crust and (*ii*) cyanobacterial jelly formed by *Nostoc* sp. In our study, small spherical colonies of *N. commune* were noted mostly in the OSN type, which was characterized by the lack of CMCs. This species is a characteristic element of polar habitats (Matuła *et al.* 2007; Skácelová *et al.* 2013; Richter *et al.* 2014, 2015; Komárek *et al.* 2015; Davydow 2021b). Pushkareva and Elster (2013) described three types of crusts from other Svalbard habitats, differing in color: black-brown, brown and grey-brown, without information about their morphological structure, and attributed the color of crusts to the number of microorganisms: colourless and light ones are formed when the biomass of cyanobacteria and algae is low.

Both coccoid species and filamentous cyanobacteria played a significant role in the analysed cyanobacteria crusts. It agrees with the previous studies of cyanobacteria on PG in the polar regions which also showed the dominant role of species of the genera *Gloeocapsa*, *Aphanothece* and *Aphanocapsa*, as well as various filamentous species in the formation of soil crusts (Cockell and Stokes 2006; Komárek and Elster 2008). Zhao *et al.* (2009) reported that mucilage sheaths produced by coccoid species contributed to the binding of sand particles and their solidification, and were supported by the development on the soil surface of clusters of threads surrounded by a gelatinous sheath formed by filamentous cyanobacteria.

Here, we documented high taxonomical richness of CMCs developed in various types of patterned grounds and their rather clear taxonomical dissimilarity. Only two species of cyanobacteria: *N. punctiforme* and *S. friesii,* dominated in most of them. These species were very often recorded in Svalbard, and additionally *N. punctiforme* was pointed as easily entering into symbiosis with bryophytes

(Adams and Duggan 2008). In turn, 22 species of cyanobacteria and algae dominated in individual types of PG, creating characteristic soil assemblage.

Extreme taxonomic variability of cryptogamic crusts was found along with the common occurrence of cyanobacteria from the genus *Nostoc*, *Gleocapsa*, *Microcoleus*, *Phormidium*, *Schizotrix* in various habitats of Svalbard (Pushkareva and Elster 2013; Williams *et al.* 2017). Surprisingly, a common in this study species, *S. friesii,* was not found in any of these works. Also Davydov (2021b) classified this species as widely distributed in Svalbard and common in other regions of the Northern Polar region (Ural Mountains) (Davydov 2021a). Pócs *et al.* (2007) emphasized that crypto-biotic crusts from *Schizotrix friesii* developed mainly in regions with great humidity. In our research, *S. friesii* developed in less humid places.

Reports from the Antarctic islands also showed clear taxonomic diversity of CMCs developing in various initial habitats (none of them were PG), including many representatives of mentioned genera (Cavacini 2001; Brinkmann *et al.* 2007) and species, *e.g., Aphanothece saxicola*, *Chroococcus minutus*, *Leptolyngbya* and *Trochiscia granulate* (Broady 2005; Borchhardt *et al.* 2017). As the basic composition of BSCs developing in the polar and subpolar areas of the Urals, Patova *et al.* (2018) identified cosmopolitan cyanobacteria and filamentous green algae with gelatinous sheaths from the genera (*e.g., Phormidium, Leptolyngbya*, *Microcoleus*) previously mentioned, but different species than those in Svalbard. They also found a large variety of diatoms but considered them to be alien newcomers that appeared accidentally with water from melting snow.

We documented a significant impact of the humidity factor on the formation of CMCs composition in various PG types what agrees with the previous studies of Broady (2005) from Antarctica and Richter *et al.* (2015) from Svalbard, in which the importance of water supply in soils for the development of BSCs with a specific species composition was demonstrated. We also showed that two types of PG with active sorting processes, *i.e.*, AL and AC, which had different shapes and developed in different humidity conditions, also had different species composition of the developing plant cover. In the general, assessment circle-shaped PGs seems to be less susceptible to overgrown by plants than wet PGs in the shape of labyrinths, which on the peripheral zones created favourable conditions for the development of moss tundra. Also Read *et al.* (2016) suggested that transformation of cyanobacterial crusts into moss tundra proceeded along a gradient of increased humidity. Both AL and AC types of PG also were different in terms of CMC taxonomic compositions, which suggests that there is a relationship between the taxonomic composition of the CMC and the species composition of the plant cover which develop in subsequent stages of succession. Wietrzyk-Pełka *et al.* (2020) documented that the species composition of moss communities in initial polar habitats depended environmental factors, such as: content of organic carbon and nitrogen in the substrate, soil reaction and texture. Therefore, it seems that further research on the relationships between CMC taxonomcal structure and the bryophytes colonizing them should also include chemical analyses of the substrate.

## Conclusions

Specific dominant species took part in the formation of CMC in particular types of PG: *Schizotrix tenuis* in the MIS and AL types, and *S. calcicola* in the AC type. This supports our preliminary assumption that species and quantitative composition of CMC differ on different PGs. Among the dominant taxa in the structure of crusts, the largest number of distinctive species were found for AL and MIS types, characterized by higher humidity, which is important factor in differentiating the species composition of CMC.

For those types of PG that were characterized by the presence of zones with high sorting activity, the occurrence of string like grey-beige cyanobacteria crust was characteristic and distinctive. However, sorting activity was insignificant as a factor differentiating the taxonomic composition of CMC in individual zones of these PGs.

With progressive succession in all types of PG, a similar pattern of reconstruction of the structure of CMC appeared. In the initial phases, crusts were dominated by filamentous species with co-dominance of coccoid species, forming gelatinous sheets. With the progressive development of the plant cover, a decrease in the species number and share of coccoid species and heterocytic species was recorded. In the phases of advanced development of the plant cover, crusts did not form anymore, but filamentous green algae and diatoms were still present in large numbers between the stems of moss and flowering plants.

The active PGs with different shapes, the labyrinth and circle, were dominated by different species of liverworts and most mosses. There probably is influence of the taxonomic composition of CMC on the species composition of the plant cover developing in later stages.

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