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The hidden network of biocrust successional stages in the High Arctic: Revealing abiotic and biotic factors shaping microbial and metazoan communities

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HIGHLIGHTS

- Ecological dynamics in High Arctic biocrusts: microbial and metazoan succession
- Nitrogen and Phosphorus are two limiting factors that drive the biocrust succession.
- Cyanobacteria and Nematoda are key taxa in cyanobacteria-dominated biocrust.
- Tardigrades and Rotifers are the main metazoan groups in late successional biocrusts.

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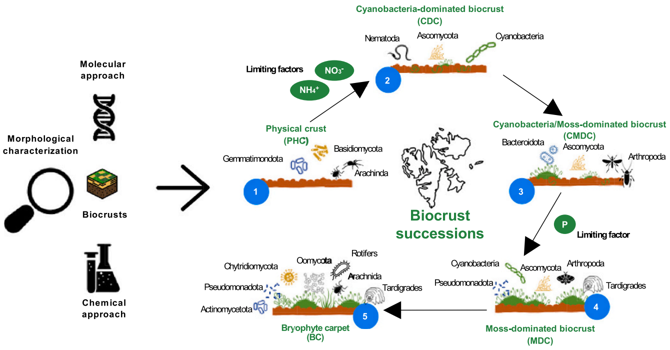
GRAPHICAL ABSTRACT



ABSTRACT

Despite the important role that biocrust communities play in maintaining ecosystem structure and functioning in deglaciated barren soil, few studies have been conducted on the dynamics of biotic communities and the impact of physicochemical characteristics in shaping the different successional stages.

In this study an integrated approach encompassing physicochemical parameters and molecular taxonomy was used for identifying the indicator taxa and the presence of intra- and inter-kingdom interactions in five different crust/biocrust successional stages: i) physical crust, ii) cyanobacteria-dominated biocrust, iii) cyanobacteria/moss-dominated biocrust, iv) moss-dominated biocrust and v) bryophyte carpet.

Abbreviations: EPSs, extracellular polymeric substances; PHC, physical crust; CDC, cyanobacteria-dominated biocrust; CMDC, cyanobacteria/moss-dominated biocrust; MDC, moss-dominated biocrust; BC, bryophyte carpet; EC, electrical conductivity; TOC, total organic carbon; TN, total nitrogen; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; SOM, soil organic matter; ITS2, internal transcribed spacer region 2; COX1, cytochrome *c* oxidase I region; PCA, principal component analysis; NMDS, non-metrical multidimensional scaling; OTUs, operational taxonomic units.

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Co-occurrence
Soil chemistry

The phylum Gemmatimonadota was the bacterial indicator taxon in the early stage, promoting both inter- and intra-kingdom interactions, while Cyanobacteria and Nematoda phyla played a pivotal role in formation and dynamics of cyanobacteria-dominated biocrusts. A multitrophic community, characterized by a shift from oligotrophic to copiotrophic bacteria and the presence of saproxylic arthropod and herbivore insects was found in the cyanobacteria/moss-dominated biocrust, while a more complex biota, characterized by an increased fungal abundance (classes Sordariomycetes, Leotiomycetes, and Dothideomycetes, phylum Ascomycota), associated with highly trophic consumer invertebrates (phyla Arthropoda, Rotifera, Tardigrada), was observed in moss-dominated biocrusts. The class Bdelloidea and the family Hypsibiidae (phyla Rotifera and Tardigrada, respectively) were metazoan indicator taxon in bryophyte carpet, suggesting their potential role in shaping structure and function of this late successional stage.

Nitrogen and phosphorus were the main physicochemical limiting factors driving the shift among different crust/biocrust successional stages. Identification and characterization of indicator taxa, biological intra- and inter-kingdom interactions and abiotic factors driving the shift among different crust/biocrust successional stages provide a detailed picture on crust/biocrust dynamics, revealing a strong interconnection among micro- and macrobiota systems. These findings enhance our understanding of biocrust ecosystems in High Arctic, providing valuable insights for their conservation and management in response to environmental shifts due to climate change.

1. Introduction

Global warming caused by human activities is the primary driver of the retreat of ice caps and glaciers, which is the most sensitive and readily visible indicator of climate change (Marzeion et al., 2014; Zemp et al., 2019). The rising temperatures release increasing portions of deglaciated barren soils, progressively colonized by biological soil crusts (biocrusts) (Williams et al., 2017). Biocrusts are complex associations between soil particles and a network of pioneer microscopic (archaea, cyanobacteria, bacteria, yeasts, filamentous fungi and algae) and macroscopic (lichens, bryophytes and microarthropods) organisms (Weber et al., 2022). They exhibit highly differentiated metabolic aptitudes, i.e., poikilohydry, autotrophy, heterotrophy or saprotrophy. All biocrust components are embedded within a matrix of extracellular polymeric substances (EPSs) occupying from the top to a few centimeters of soil (Rossi et al., 2018; Weber et al., 2022). Biocrustś primary producers, namely cyanobacteria, algae, lichens and bryophytes, modify the barren soil through the establishment of a complex soil food web, allowing the growth of nutritionally more demanding microorganisms (i.e., bacteria, yeasts, fungi, protozoa and metazoa) (Darby and Neher, 2016). Biocrusts cover large terrestrial areas, enhancing soil biological diversity and providing a number of ecological benefits, including primary production, carbon storage, nitrogen fixation, soil aggregation, and long-term promotion of vascular plant growth (Faist et al., 2021; Lan et al., 2012).

Biocrusts are currently classified into a few well-differentiated successional stages according to the dominance of the biological components and to their relative proportions. In polar regions cyanobacteria often represent the pioneer organisms colonizing the early successional stages, forming cyanobacteria-dominated biocrusts (Williams et al., 2017). Later, mosses and lichens colonize the soil surface leading to moss- or lichen-dominated biocrusts (Maier et al., 2018). The final successional stage is the formation of bryophyte-dominated biocrusts, which are often widespread in polar areas, sometimes characterized by a low presence of vascular plants (Weber et al., 2022).

The Svalbard archipelago includes high-latitude islands where biocrusts represents the dominant soil coverage (Colesie et al., 2014). The exposition of archipelago to the global warming and its relatively easy accessibility for field research, make it a privileged site for studying the impact of ongoing climate change on polar ecosystems, including the formation of different biocrust successional stages as the result of biological colonization of deglaciated barren soil (Klimešová et al., 2012; Piskozub, 2017).

The use of microbial descriptors contributes to classify different soil ecological habitats (Agnelli et al., 2021) in association with physicochemical parameters. Accordingly, most studies on biocrust communities found in polar regions (i.e. Arctic and Antarctic environments) have been so far focused almost exclusively on the description of bacterial, fungal and, sometimes, microalgal diversity (Barrera et al., 2022; Glaser et al., 2022; Pushkareva et al., 2021, 2022; Rippin et al., 2018) while protozoa and metazoa have been largely neglected, although those organisms can be considered essential components of many ecosystems through their contribution to the balance of microbial populations (due to the presence of predator specific taxa) and to the regulation of nutrient cycles and spore dispersions (Darby and Neher, 2016). Besides, no previous studies have explored so far the structure of bacterial, fungal, metazoan and protozoan communities (including their possible interactions) along different biocrust successional stages. Moreover, information about the soil indicator microbial taxa affecting the biocrust successional stage composition and functioning, in association to the abiotic factors, is also lacking. An accurate assessment of biocrust indicator taxa and the limiting factors driving the soil colonization appears urgently needed to give a more detailed picture of the biological colonization dynamics of High Arctic deglaciated barren soils.

In the present investigation, the microbiota of five different crust/biocrust successional stages (physical crust, cyanobacteria-dominated biocrust, cyanobacteria/moss-dominated biocrust, moss-dominated biocrust and bryophyte carpet) has been characterized in order to describe the barren soil colonization of the Svalbard archipelago, which can be used as a model of High Arctic ecosystem.

In this study, the concept of indicator taxa was used to identify specific bacterial, fungal, protozoan and metazoan taxa that are strongly associated with specific community types, habitat conditions, or environmental changes (Carignan and Villard, 2002; De Cáceres et al., 2010; McGeoch and Chown, 1998; Niemi and McDonald, 2004). Accordingly, the indicator taxa analysis is currently used for studying the structure of resident biological communities (i.e., presence–absence, abundances, etc.) to compare different ecosystems (Dufrêne and Legendre, 1997). Hence, the Indicator Value (IV) is used to quantify the association strength of a given taxa (e.g. phylum, order, family, genus) for a particular habitat or environmental condition: it is calculated taking into consideration both the abundance and the frequency of occurrence of a given taxon in relation to the overall community of a specific ecosystem (Dufrêne and Legendre, 1997). In addition, network analysis of co-occurrence, measured by correlations between abundances of microbial taxa, was conducted to unravel the complex microbial intra- and inter-kingdom interactions among the main bacterial, fungal, protozoan, and metazoan taxa.

In this framework, the scientific questions that this study aims to answer are: i) what is the structure of the bacterial, fungal, protozoan and metazoan communities along the different crust/biocrust successional stages of the Svalbard archipelago? ii) what are the abiotic parameters putatively driving these communities? iii) what are indicator taxa of the different crust/biocrust successional stages? iv) could the identification of intra- and inter-kingdom interactions be used to hypothesize the existence of successional processes? Answering these questions would provide a fundamental contribution for understanding the colonization dynamics and interactions among the bacterial, fungal, protozoan, and metazoan kingdoms in biocrusts colonizing High Arctic deglaciated barren soils. Their composition and areal coverage associated to the soil chemical composition could contribute to understand their role in biogeochemical nutrient cycles and possible climate change scenarios.

2. Materials and methods

2.1. Sampling area

Biocrust samples were collected during a survey campaign carried out along the Kongsfjorden area (west coast of the Spitsbergen Island, Svalbard Archipelago, High Arctic) in August 2014. Samples were recorded and collected at nine different sites: i) around the Ny-Ålesund area, on the Brøgger peninsula (Brøggerhalvøya) and on the shore of the bay of Kongsfjorden (7 sampling sites), which is composed of large U-shaped valleys occupied by the large terrestrial glaciers (Austre Brøggerbreen, Vestre Lovénbreen, Midtre Lovénbreen), and ii) in the Ossian Sarsfjellet area, (2 sampling sites), which is located on the opposite west coast of the fjord, surrounded by several small lakes and streams, including the Lake Sarsvatnet, near which the samples were collected (Fig. S1). All the above sampling sites have been selected in order to include in the study all the successional stages occurring in bay of Kongsfjorden, which could be considered an in-situ model for exploring the different biocrust colonization degree. The biocrust coverage ranged between 18 and 90 % of the total surface of the different sites (Williams et al., 2017).

Soils (up to about 5–10 cm depth) covered by biological soil crusts were collected after gently removing the surface coverage. Samples showing different degrees of development were collected, sometimes appearing as small and irregular spots, and other times more diffusely colonizing the substrate. Five different crust/biocrust successional stages (representative of the biological variability recorded and used as an in-situ model of the ecological variability of the biocrusts found in the area) were selected for analysis: physical crusts (PHC – found at only one site), cyanobacteria-dominated biocrusts (CDC, one site), cyanobacteria/moss-dominated biocrusts (CMDC – four sites), moss-dominated biocrusts (MDC – two sites) and bryophyte carpet (BC – one site) (Table S1; Fig. S1). A total of 5 biological replicates were collected for each sampling site. Topsoils were collected aseptically, preserved in sterile plastic containers or bags, stored and transported under freezing conditions to the laboratory, where they were kept at −20 °C until analysis.

2.2. Soil physicochemical properties

Soil physicochemical (abiotic) properties were determined using standard operating procedures. Soil pH and electrical conductivity (EC) was determined using a pH/Conductivity Meters (Hanna Instruments – HI 2210). Total organic carbon (TOC) and total nitrogen (TN) were determined using a Flash EA 1112 elemental analyzer (Thermo Scientific, Germany). Dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were quantified using a Shimadzu analyzer (Model TOC-L-5050A, Japan). Soil organic matter (SOM) was determined mathematically by multiplying TOC with the Van Bemelmans's factor (1.724) (Broadbent, 1965). Available P (PO_4^{3-}) was determined according to Murphy and Riley's (1962) and FAO (2021). Nitrate (NO_3^-) and ammonium (NH_4^+) was using a Hanna instruments NO_3^--ion selective electrode (HI7609829-12) and the colorimetric Berthelot method (Rhine et al., 1998), respectively.

2.3. DNA extraction, libraries preparation and sequencing

Total DNA was extracted from 0.25 g of crust/biocrust sample using Power Soil Pro DNA Isolation Kit (Qiagen, Germany). DNA concentrations were determined using QuBit 2.0 Fluorometer Assay (Life Technologies Corporation, USA). The (i) bacterial 16S rRNA gene (region V3-V4), (ii) fungal internal transcribed spacer region 2 (ITS2) and (iii) protozoa metazoans cytochrome *c* oxidase I region (COX1) were amplified using specific primers (Leray et al., 2013; Takahashi et al., 2014; Tedersoo et al., 2015) (Table S2).

The PCR products were sequenced using an Illumina MiSeq platform (BMR Genomics, Italy).

Raw sequences of each dataset (16S rRNA, ITS2 and COX1) were independently pre-processed, quality filtered, trimmed, de-noised, merged, modelled and analyzed using QIIME2 (Bolyen et al., 2019) and DADA2 (Callahan et al., 2016). Then, DADA2 was also used to check and discard chimeras with the 'consensus' method (Callahan et al., 2016). Amplicon sequence variants (ASV) were clustered into Operations Taxonomy Units (OTUs) using VSEARCH within qiime2, with a 97 % similarity threshold (Rognes et al., 2016). Taxonomy was assigned to OTUs using Silva 138 99 % OTUs full-length sequences (silva-138-99-nb-classifier.qza), UNITE+INSD 8.2 (https://unite.ut.ee/repository.php), NCBI and BOLD (v4) (Ratnasingham and Herbet, 2006) databases for bacteria, fungi, protozoan and metazoans, respectively.

2.4. Statistical analyses

Statistical analyses were carried out with R software (R version 4.2.0) (R Core Team, 2021). OTU- and taxonomy tables were cleaned and rarefied; relative abundance, alpha-diversity (coefficients Observed and Shannon) were performed by package phyloseq (McMurdie and Holmes, 2013). Pairwise comparisons of biodiversity indices among the different samples were performed by ANOVA post-hoc testing with Hochberg correction ($p < 0.05$). Community dissimilarities among the crust/biocrust successional stages were assessed by non-metrical multidimensional scaling (NMDS) based on Bray-Curtis distances using the package vegan. The "envfit" function was used to highlight the correlation between chemical parameters and the composition of crust/biocrust microbial communities. Co-occurrences among bacteria, fungi, protozoa, and metazoans were inferred considering the OTUs classified both at the phylum and family level (relative abundance > 1 %) by Pearson's coefficient and considering only interaction with $p < 0.05$. Indicator Species Analysis (including Indicator Value - IV - calculation) was performed by R package "indicspecies" (De Cáceres et al., 2010).

3. Results

3.1. Physicochemical properties in the different crust/biocrust successional stages

The pH of the different crust/biocrust successional stages significantly ($p < 0.05$) decreased from PHC to BC samples, while the EC followed an opposite trend from PHC to MDC (Table 1).

The NO_3^- content in PHC was significantly ($p < 0.05$) lower compared to the more evolved biocrust successional stages. Ammonium contents followed the same trend of NO_3^-, which significantly increased ($p < 0.05$) from PHC to BC. The amount of PO_4^{3-} was variable along the crust/biocrust successional stages, however the significant ($p < 0.05$) lowest values were observed in MDC, while the highest was found in BC. On the other hand, DOC, DON, TN, TOC, and SOM displayed a significant ($p < 0.05$) increasing trend from PHC to the more evolved biocrust successional stages, characterized by an increasing level of biological colonization (Table 1).

The differentiation of the crust/biocrust successional stages based on their physicochemical properties was visualized by PCA ordination (82.2 % of the total variance explained by the first two dimensions). A

Table 1

Physico-chemical (abiotic) parameter reporting the different content of pH, electrical conductivity (EC), NO_3^-, NH_4^+, PO_4^{3-}, dissolved organic carbon (DOC), dissolved organic nitrogen (DON), total N (TN), total organic C (TOC), and soil organic matter (SOM) in the different crust/biocrust successional stages: PHC = physical crust; CDC = cyanobacteria-dominated biocrust; CMDC = cyanobacteria/moss-dominated biocrust; MDC = moss-dominated biocrust; BC = bryophyte carpet. Different superscript letters indicate significant ($p < 0.05$) differences.

Crust/biocrust successional stages	pH	EC	NO_3^-	NH_4^+	PO_4^{3-}	DOC	DON	Total N	Total C	SOM
PHC ($n = 5$)	7.79 ± 0.06^{a}	61.5 ± 2.50^{d}	3.50 ± 1.50^{c}	0.42 ± 0.01^{d}	0.17 ± 0.02^{c}	13.93 ± 0.35^{d}	0.86 ± 0.03^{d}	0.52 ± 0.04^{d}	6.19 ± 0.56^{d}	10.67 ± 0.96^{d}
CDC ($n = 5$)	7.36 ± 0.07^{b}	337.25 ± 13.18^{ab}	5.62 ± 0.44^{ab}	1.95 ± 0.19^{c}	0.19 ± 0.03^{c}	55.98 ± 1.19^{c}	4.97 ± 0.11^{c}	2.23 ± 0.07^{c}	33.32 ± 2.21^{c}	57.45 ± 3.81^{c}
CMDC ($n = 20$)	7.58 ± 0.37^{ab}	203.06 ± 124.09^{bc}	5.34 ± 0.30^{b}	3.22 ± 2.28^{bc}	0.33 ± 0.14^{b}	93.60 ± 77.40^{c}	10.47 ± 9.30^{c}	2.37 ± 1.83^{c}	33.47 ± 27.78^{bc}	59.50 ± 48.50^{bc}
MDC ($n = 10$)	7.35 ± 0.11^{b}	294.26 ± 64.12^{a}	5.76 ± 0.22^{a}	3.74 ± 0.23^{a}	0.08 ± 0.05^{d}	116.78 ± 7.05^{b}	12.73 ± 2.94^{b}	4.06 ± 0.54^{b}	47.09 ± 10.04^{b}	81.18 ± 17.31^{b}
BC ($n = 5$)	6.17 ± 0.02^{c}	149.00 ± 5.52^{c}	5.49 ± 0.32^{ab}	3.52 ± 0.20^{ab}	0.60 ± 0.08^{a}	463.20 ± 21.80^{a}	44.60 ± 2.18^{a}	12.11 ± 0.57^{a}	244.12 ± 12.74^{a}	420.86 ± 21.96^{a}

clear separation between PHC and BC was found along the first dimension of the ordination. The samples corresponding to the intermediate biocrust successional level (CDC, CMDC and MDC) were also separated and well clustered, except for the samples collected from the site CMDC6, whose peculiarity was affected by significantly ($p < 0.05$) higher levels of NO_3^- and NH_4^+ and EC (Fig. S2).

3.2. Biodiversity indexes and communities' structure of the different crust/biocrust successional stages

Table 2 illustrates the trend of biodiversity indexes observed in the different crust/biocrust successional stages. Although some fluctuations were observed, PHC exhibited significantly ($p < 0.05$) higher values of bacterial diversity (i.e. richness and Chao-1 indexes), together with significantly ($p < 0.05$) lower values of fungal, protozoan and metazoan diversity.

Taxonomy assignment of sequences reveals the presence of 8 dominant (relative abundance > 1 %) bacterial phyla (Fig. 1A). PHC showed a significantly ($p < 0.05$) higher abundance of Acidobacteriota, Gemmatimonadota and Myxococcota. On the other hand, Cyanobacteria exhibited a significantly ($p < 0.05$) lower abundance in PHC (Fig. 1A) but became dominant in CDC and CMDC. In addition, a significant ($p < 0.05$) higher content of reads associated to the Bacillota phylum was found in CDC. CMDC showed a significantly ($p < 0.05$) lower abundance of Actinomycetota and Acidobacteriota, as well as a significantly ($p < 0.05$) higher abundance of Bacteroidota. Pseudomonadota were dominant in PHC, MDC and BC (Fig. 1A).

Although some site-specific overlaps were observed, the NMDS ordination revealed that the bacterial communities of the crust/biocrust successional stages were well differentiated (Fig. 1B; Table S3), confirming their differential distribution driven by their chemical features. Most of chemical parameters (except PO_4^{3-}) significantly ($p < 0.05$) correlated with the structure of bacterial communities colonizing the different successional stages (Fig. 1B; Table S3).

Regarding the fungal components, Basidiomycota and Chytridiomycota were the dominant phyla in PHC (Fig. 2A). On the other hand, Ascomycota dominated the other successional stages, while Zoopagomycota was the second most abundant group in MDC (Fig. 2A).

The NMDS ordination of the structure of fungal communities in dependence of the crust/biocrust successional stages was found (Fig. 2B; Table S3). PHC showed a different clustering pattern, while CDC and CMDC (and partially MDC) exhibited a common clustering trend. A similar overlapping was also found for MDC and BC, confirming the biological similarity of contiguous successional stages. All chemical parameters (including PO_4^{3-}) affected the structure of fungal communities colonizing the different crust/biocrust successional stages (Fig. 2B; Table S3).

Metazoan communities, which were dominated by Arthropoda, exhibited a similar trend correlated to the crust/biocrust successional stages (Fig. S3). The abundance of Nematoda was significantly ($p < 0.05$) higher in CDC. On the contrary, the abundance of Rotifera and Tardigrada, which was significantly ($p < 0.05$) lower in PHC, increased along the crust/biocrust successional stages (Fig. 3A). Because of the structure of protozoan community did not exhibit significant ($p > 0.05$) variations along the different successional stages (Fig. S3), the NMDS ordination was approached only for the metazoan communities, which exhibited a trend depending on the crust/biocrust successional stages similar to that observed for bacteria and fungi, in close correlation with all chemical parameters (Fig. 3B; Table S3).

3.3. Identification of the indicator taxa of the different crust/biocrust successional stages

The indicator taxa of the different crust/biocrust successional stages

Table 2

Alpha-diversity among different crust/biocrust successional stages: PHC = physical crust; CDC = cyanobacteria-dominated biocrust; CMDC = cyanobacteria/moss-dominated biocrust; MDC = moss-dominated biocrust; BC = bryophyte carpet. Different superscript letters indicate significant ($p < 0.05$) differences.

	Bacteria			Fungi			Protozoa and Metazoa		
Crust/biocrust successional stages	Richness	Shannon_H	Chao-1	Richness	Shannon_H	Chao-1	Richness	Shannon_H	Chao-1
PHC ($n = 5$)	878.8 ± 118.9^{a}	5.8 ± 0.1^{a}	1034.0 ± 199.3^{a}	67.0 ± 6.1^{c}	3.2 ± 0.1^{b}	67.1 ± 6.0^{d}	17.0 ± 1.7^{c}	1.7 ± 0.4^{a}	17.0 ± 1.7^{c}
CDC ($n = 5$)	429.00 ± 155.7^{c}	4.9 ± 0.4^{b}	448.8 ± 174.8^{c}	198.0 ± 42.5^{b}	3.5 ± 0.5^{ab}	227.4 ± 50.4^{bc}	171.8 ± 23.1^{a}	4.0 ± 0.7^{a}	209.8 ± 39.8^{a}
CMDC ($n = 20$)	612.8 ± 121.1^{bc}	5.2 ± 0.2^{b}	705.8 ± 166.5^{bc}	172.3 ± 50.6^{b}	3.1 ± 0.4^{b}	197.9 ± 66.8^{c}	110.2 ± 48.4^{b}	3.2 ± 1.0^{a}	127.3 ± 56.7^{b}
MDC ($n = 10$)	695.8 ± 127.2^{ab}	5.7 ± 0.1^{a}	761.3 ± 181.6^{ab}	318.6 ± 63.3^{a}	3.9 ± 0.2^{a}	362.6 ± 86.4^{a}	150.7 ± 84.2^{ab}	3.0 ± 1.5^{a}	196.8 ± 106.2^{ab}
BC ($n = 5$)	670.6 ± 248.2^{ac}	5.6 ± 0.4^{a}	743.3 ± 320.6^{ac}	306.7 ± 92.6^{a}	4.0 ± 0.7^{a}	339.8 ± 105.5^{ab}	94.6 ± 22.4^{b}	2.7 ± 0.3^{a}	113.8 ± 34.1^{b}

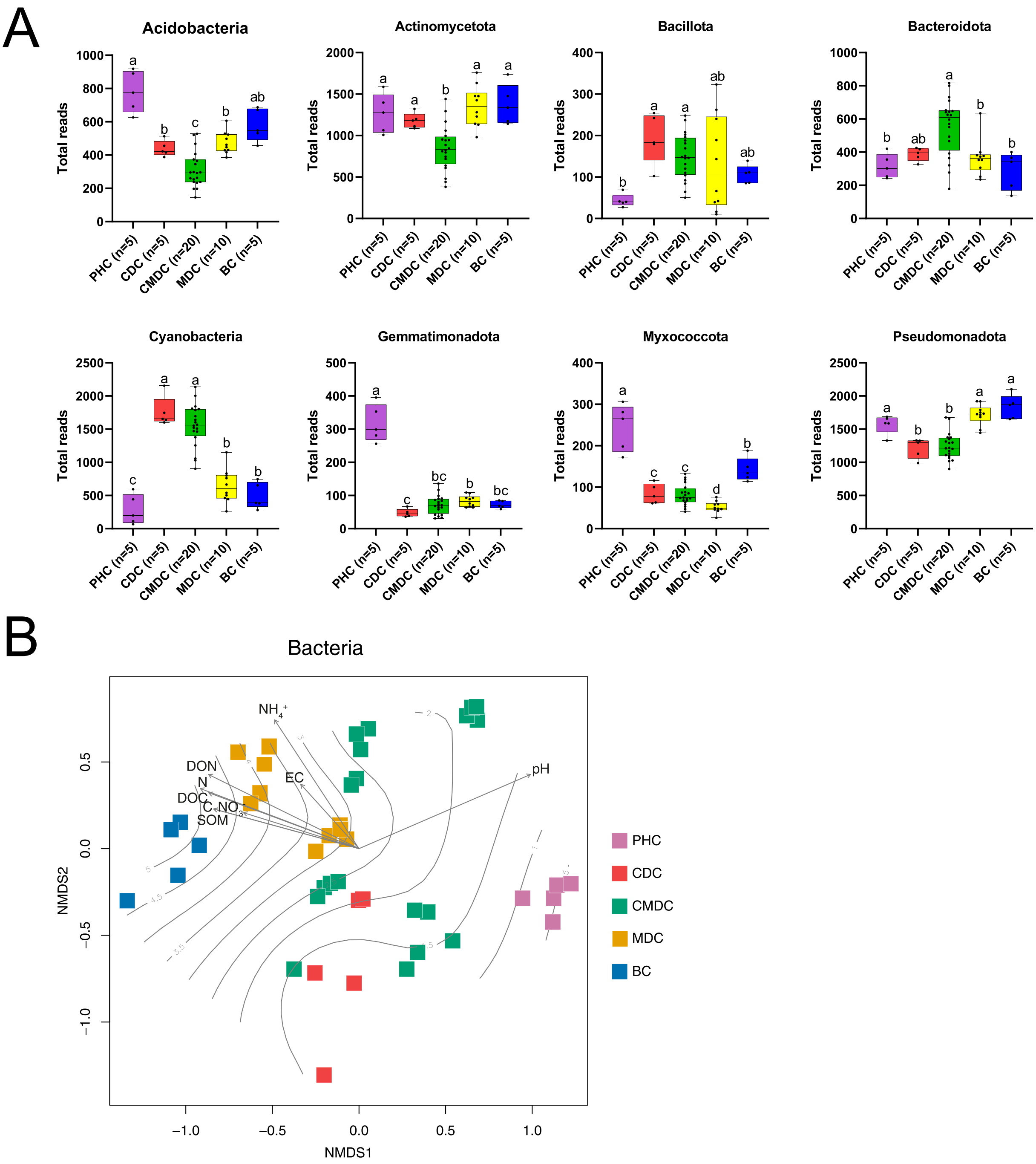

Fig. 1. A = Abundance of the dominant bacterial phyla (relative abundance > 1 %) in the different biocrust successional stages: PHC = physical crust; CDC = cyanobacteria-dominated biocrust; CMDC = cyanobacteria/moss-dominated biocrust; MDC = moss-dominated biocrust; BC = bryophyte carpet. Different small letters indicate significant differences ($p < 0.05$). B = Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the differences (Bray-Curtis distance) in the structure of bacterial communities. Black lines represent the temporal variations. The envfit function was used to show the chemical and physical parameters affecting bacterial communities. Only the significant ($p < 0.05$) vectors were fitted to the NMDS ordination.

were identified for bacteria, fungi, protozoa and metazoa, taking into consideration of both their highest IV and the highest frequency of occurrence of a given taxon, i.e. the number of OTUs in the crust/biocrust successional stages (Tables S4–S8).

Accordingly, the following indicator taxa were identified in PHC (Table S4): i) the phyla Gemmatimonadota (family Gemmatimonadaceae), Pseudomonadota (families Gammaproteobacteria and Alphaproteobacteria) and Acidobacteriota for bacteria; ii) the genera *Solicoccozyma* (Basidiomycota), *Betamyces* (Chytridiomycota) and the phyla Ascomycota (*Tetracladium* as prevalent taxon) and Rozzellomycota for fungi; iii) the phyla Arthropoda (families Oppiidae, Selenopidae and Endomychidae), Heterokontophyta and Amoebozoa for metazoan and protozoa, respectively.

The indicator taxa identified in CDC were as follows (Table S5): i) the phyla Acidobacteriota (family Bryobacteraceae), Cyanobacteria (families Oscillatoriaceae and Gloeobacteraceae) and Actinomycetota for bacteria; ii) the phylum Ascomycota (classes Leotiomycetes and Eurotiomycetes) and Rozellomycota; iii) the phyla Arthropoda (class Arachnida), Cnidaria (class Hydrozoa), Rotifera (class Bdelloidea) and Nematoda (order Plectida, family Plectidae) for metazoa; iv) the phylum

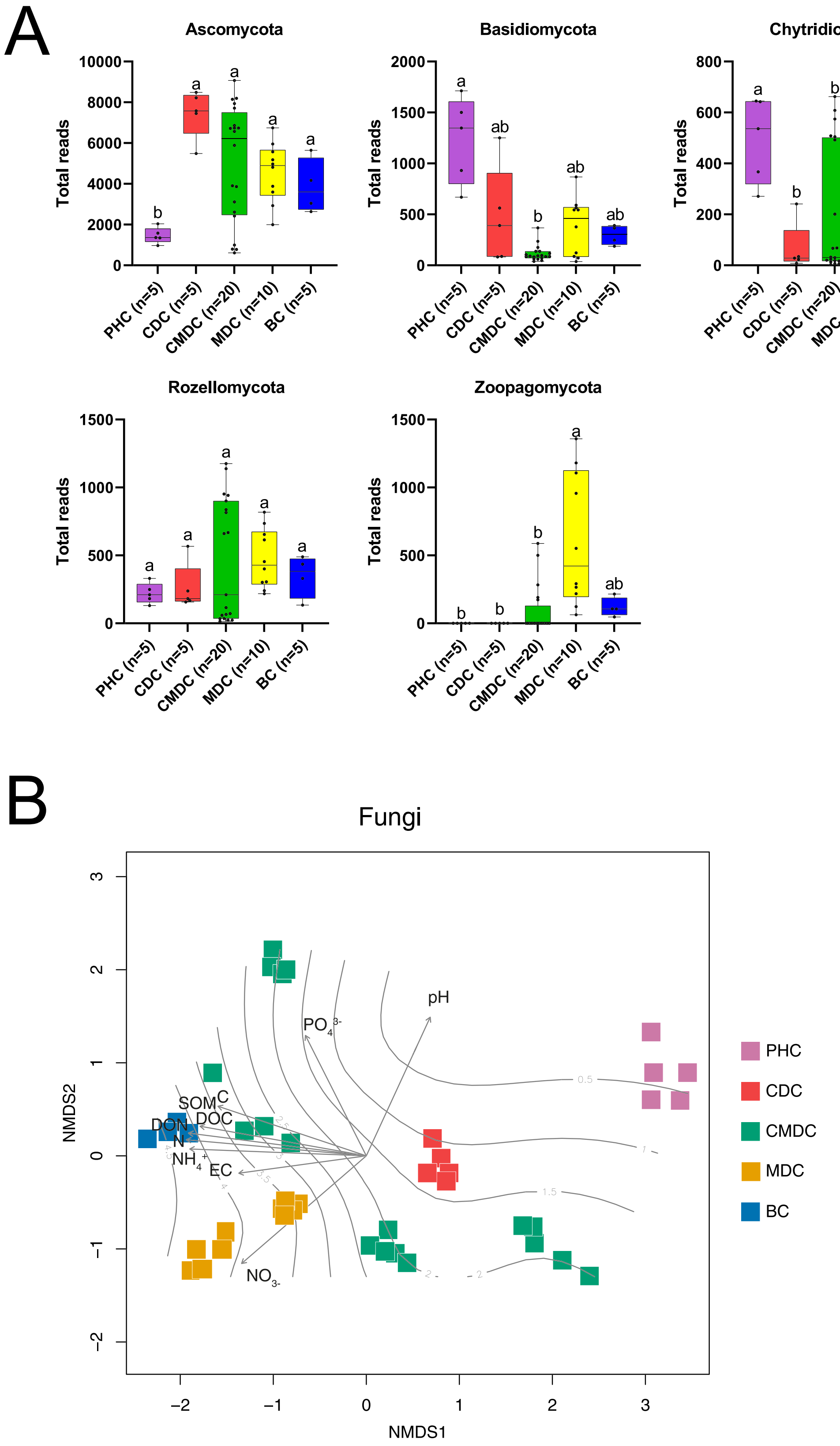

Fig. 2. A = Abundance of the dominant fungal phyla (relative abundance > 1 %) in the different biocrust successional stages: PHC = physical crust; CDC = cyanobacteria-dominated biocrust; CMDC = cyanobacteria/moss-dominated biocrust; MDC = moss-dominated biocrust; BC = bryophyte carpet. Different small letters indicate significant differences ($p < 0.05$). B = Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the differences (Bray-Curtis distance) in the structure of fungal communities. Black lines represent the temporal variation. The envfit function was used to show the chemical and physical parameters affecting fungal communities. Only the significant ($p < 0.05$) vectors were fitted to the NMDS ordination.

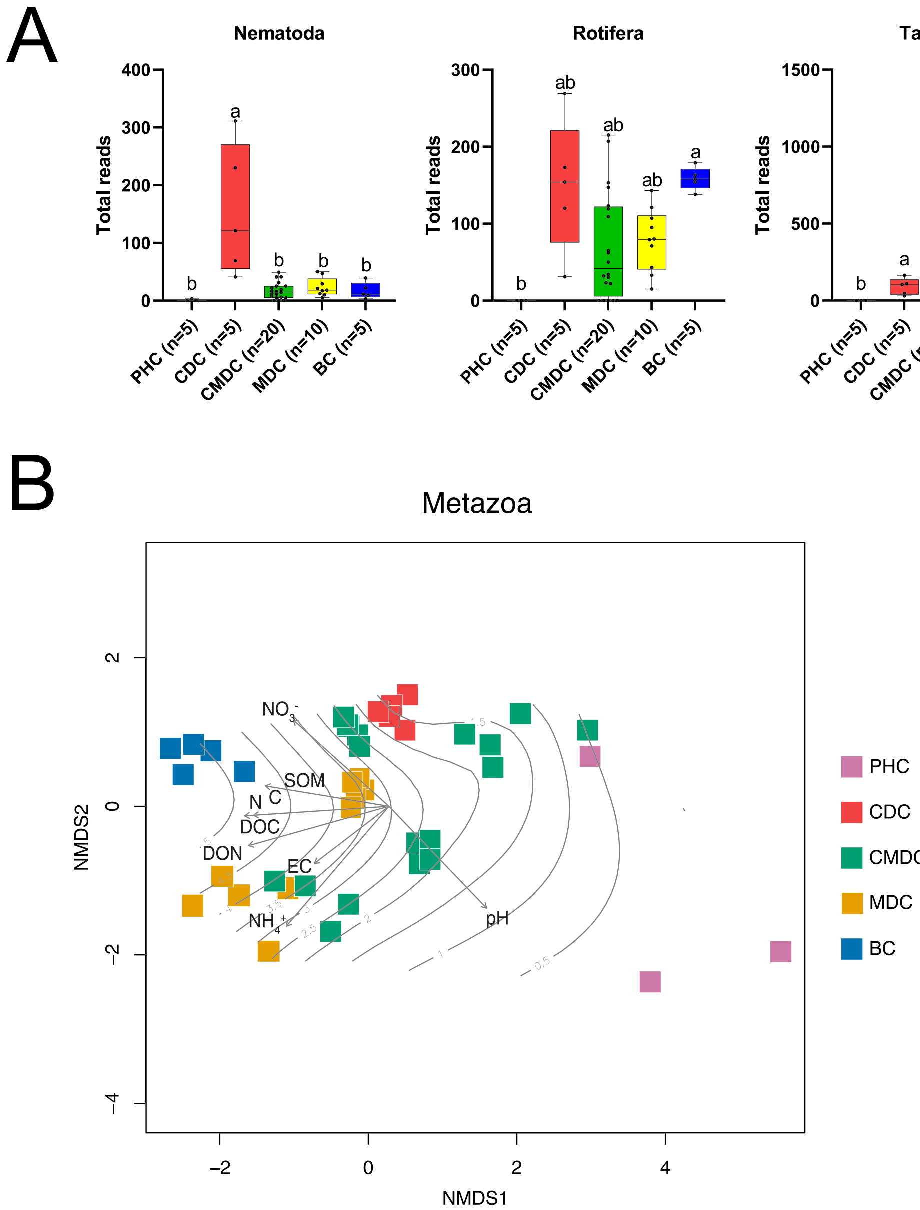

Fig. 3. A = Abundance of the dominant metazoan phyla (relative abundance > 1 %) in the different biocrust successional stages: PHC = physical crust; CDC = cyanobacteria-dominated biocrust; CMDC = cyanobacteria/moss-dominated biocrust; MDC = moss-dominated biocrust; BC = bryophyte carpet. Different small letters indicate significant differences ($p < 0.05$). B = Two-dimensional non-metric multidimensional scaling (NMDS) ordination of the differences (Bray-Curtis distance) in the structure of metazoan communities. Black lines represent the temporal variation. The envfit function was used to show the chemical and physical parameters affecting metazoan communities. Only the significant ($p < 0.05$) vectors were fitted to the NMDS ordination.

Heterokontophyta (class Oomycota, especially the genus *Phytophthora*).

The following indicator taxa were identified in CMDC (Table S6): i) the phyla Pseudomonadota, Cyanobacteria and Bacteroidota for bacteria; ii) the phylum Ascomycota (class Euromycetes and Dothideomycetes) for fungi; iii) Arthoproda (class Insecta) and Heterokontophyta (class Oomycota) for metazoan and protozoa, respectively.

The indicator taxa identified in MDC were as follows (Table S7): i) the phyla Pseudomonadota (orders Hyphomicrobiales and Burkholderiales), Actinobacteriota, Chloroflexota, Cyanobacteria (family Nostocaceae) and Acidobacteriota (family Bryobacteraceae); ii) the phyla Ascomycota (class Sordariomycetes and Dothideomycetes), Rozzellomycota and Chytridiomycota for fungi; iii) the phyla Rotifera (class Bdelloidea), Arthropoda (specifically the class Arachnida) and Tardigrada (classes Heterotardigrada and Eutardigrada) for metazoa.

Finally, the following indicator taxa were identified in BC (Table S8): i) the phyla Acidobacteriota (class Vicinamibacteria and Bryobacterales), Pseudomonadota (class Alphaproteobacteria and Gammaprotebacteria), Bacteroidota (family Chitinophagaceae) and Myxococcota (family Haliangiaceae) for bacteria; ii) the phylum Ascomycota (specifically classes Leotimycetes; Dothideomycetes, Sordariomycetes and Euromycetes) for fungi; iii) the phyla Heterokontophyta (specifically the class Oomycote, genus *Phytophthora*), Rotifera (class Bdelloidea, genera *Macrotrachela* and *Adineta*), Arthropoda (class Arachnida) and Tardigrada (genera *Pseudechiniscus* and *Acutuncus*) for protozoa and metazoa, respectively.

Considering the frequency of occurrence of indicator taxa, evidence of generalist habitus was found in the bacterial genus *Bryobacter* (phylum Acidobacteriota) and in the protozoan genus *Phytophtora* (phylum Heterokontophyta), which were found in all crust/biocrust successional stages, except on PHC and CMDC, respectively (Tables S4–S8). On the contrary, some fungal taxa exhibited a more specialist habitus: the genus *Tetracladium* (class Leotiomycetes) exhibited adaptation to incipient development stages (PHC and CDC), while the psychrophilic yeast genus *Glaciozyma* (class Microbotryomycetes) exhibited a preference for more evolved successional stages characterized by the presence of cyanobacteria and bryophytes (CDC and BC) (Tables S4–S8). Concerning the metazoan taxa, the genus *Adineta* (phylum Rotifera) was found in more evolved successional stages (CDC, MDC and BC) as well as the genus *Pseudechiniscus* (class Heterotardigrada) was associated to MDC and BC, while the presence of the metazoan genus *Acutuncus* (class Eutardigrada) was observed in CDC and BC (Tables S4–S8).

3.4. *Co-occurrences among dominant biological taxa of the different crust/biocrust successional stages*

Significant ($p < 0.05$) co-occurrences observed among dominant (abundance > 1 %) taxa are reported in Fig. 4. Considering the phylum

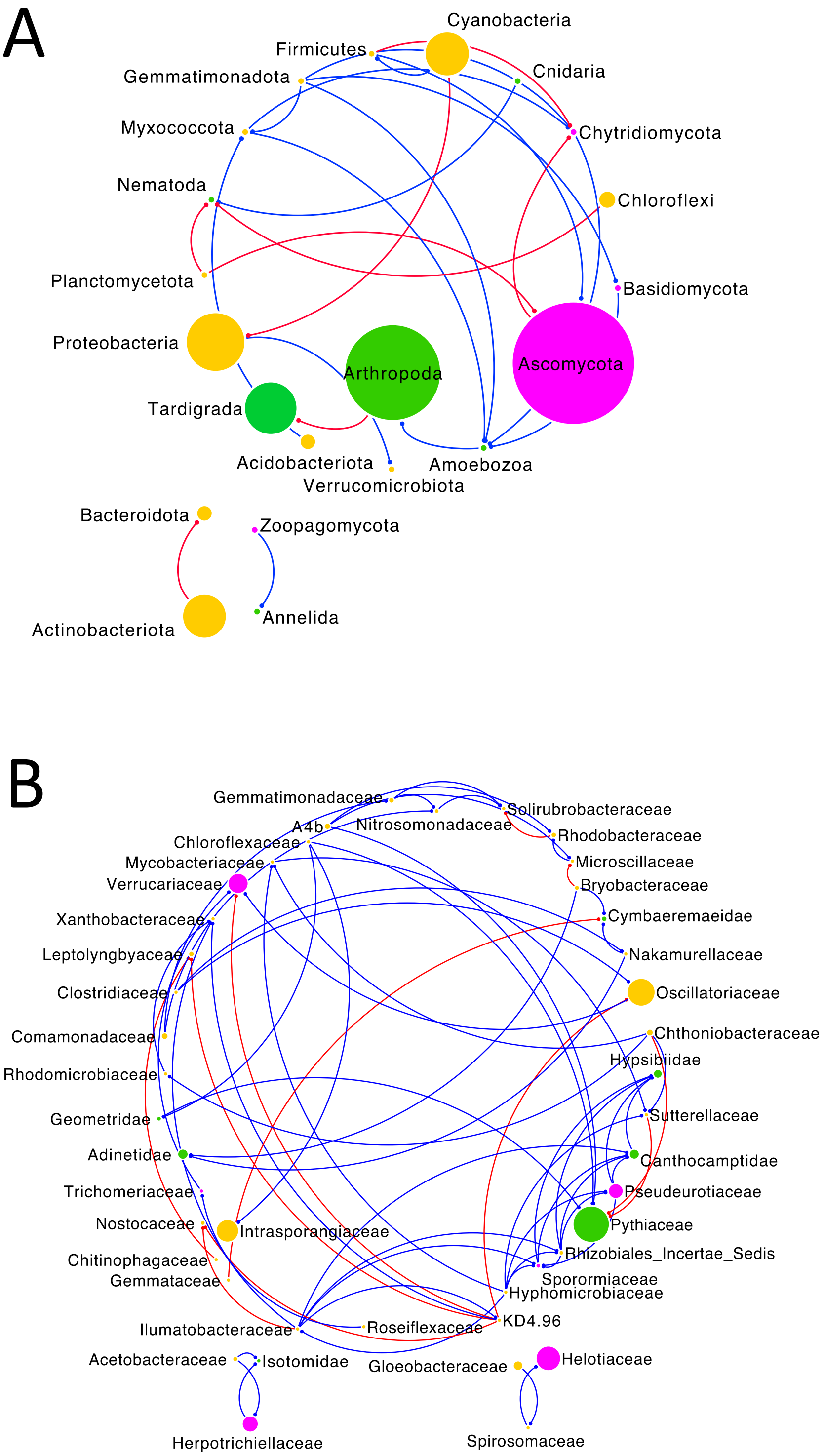

Fig. 4. Ecological networks of significant ($p < 0.05$) co-occurrences based on Pearson correlation analysis between the dominant (relative abundance > 1 %) bacterial, fungal, protozoan and metazoan phyla (A) and families (B). Yellow circles = bacteria; purple circles = fungi; green circles = protozoa and metazoa. Blue lines = positive correlations; red line = negative correlations. The size of each node is proportional to the taxon relative abundance.

level, three significant ($p < 0.05$) intra-kingdom (bacteria vs bacteria, fungi vs fungi and metazoa vs metazoa) and six inter-kingdoms (bacteria vs fungi, bacteria vs metazoa, bacteria vs protozoa, fungi vs protozoa, fungi vs metazoa and protozoa vs metazoa) co-occurrences were found (Fig. 4A; Table S9). Going down from the taxonomic level of phyla to that of family, a high number of significant ($p < 0.05$) intra-kingdom co-occurrences was found among bacteria (twenty-five positive and seven negative co-occurrences), while the fungal and the metazoan families exhibited two and one positive intra-kingdom co-occurrences, respectively. Concerning inter-kingdom co-occurrences, nine positive and one negative interactions were detected between bacteria and fungi, ten (nine positive and one negative) between bacteria and metazoans, four (two positive and two negative) between bacteria and protozoa, and five positive interactions between fungi and metazoans (Fig. 4B; Table S10).

4. Discussion

As reported above, biocrusts are considered the primary drivers of soil formation in polar ecosystems (Mugnai et al., 2020; Agnelli et al., 2021). After the glacier retreat, exposed barren soils are firstly colonized by pioneer microbial species, followed by vegetation establishment. Therefore, understanding the structural dynamics of biological communities along the crust/biocrust successional stages is a key question for unravelling the ecology of High Arctic ecosystems.

4.1. Physical crust (PHC)

In the present study an increase of TOC has been observed along crust/biocrust successional stages, probably due to the metabolic activities associated with resident microbial and metazoan communities, in agreement with a previous study (Agnelli et al., 2021). The N content in PHC was significantly lower than in the other successional stages, confirming the pivotal role of both NO_3^- and NH_4^+ in biomass production, which underlies the succession from early (PHC) to more evolved biocrusts, consistent with previous studies (Agnelli et al., 2021; Kidron et al., 2015). The low concentration of both NO_3^- and NH_4^+ in PHC was related with the resident microbial communities: PHC exhibited significant ($p < 0.05$) higher values of bacterial diversity (witnessed by the richness and Chao-1 indexes) together with a significant ($p < 0.05$) lower abundance of N-fixing bacteria (including Cyanobacteria), supporting the hypothesis of N-related limitations and confirming the crucial pioneering role of Cyanobacteria in both soil microbial colonization and ecological succession (Pushkareva et al., 2015).

The bacterial indicator taxa identified in PHC were Acidobacteriota, Gemmatimonadota, Myxococcota and Pseudomonadota. Among them, the families Sphingomonadaceae and Nitrosomonadaceae include species specifically involved in both carbohydrate degradation and NH_4^+ and NO_2^- oxidation (Loganathachetti et al., 2022). The phyla Gemmatiomonadota (especially species of the family Gemmatimonadaceae) and Acidobacteriota can play an essential role in the primary evolution stages of PHC due to their ability to produce organic compounds (e.g. EPS) in nutrient-deficient soils (Costa et al., 2020; Khan and Khan, 2020). Additionally, Gemmatimonadota exhibited some inter-kingdom positive co-occurrences with the fungal phyla Basidiomycota and Chytridiomycota and with the protozoan phylum Amoebozoa, supporting the hypothesis of the presence of an inter-kingdom network in PHC. Therefore, the phylum Gemmatimonadota can be regarded as one of the leading key bacterial taxa in PHC, in agreement with a recent study (Mujakić et al., 2022).

PHC exhibited a significantly ($p < 0.05$) lower value of both fungal and metazoan diversity, confirming their role as secondary colonizers and consumers in the early crust/biocrust successional stages (Maier et al., 2018). Fungal indicator taxa found in PHC included both the yeasts genus *Solicoccozyma* (phylum Basidiomycota) and zoosporic fungi belonging to the phylum Chytridiomycota. Although the ecology of Basidiomycota as dominant phylum when restricted to yeast life forms has been well characterized in cold ecosystems, (Ludley and Robinson, 2008; Buzzini et al., 2017; Sannino et al., 2017), less is known about the role of Chytridiomycota, where the saprophytic genus *Betamyces* (identified as indicator taxon for PHC) is known to contribute to soil organic matter decomposition (Gonçalves et al., 2023).

The indicator taxa of the metazoan and protozoan community of PHC were the classes Arthropoda, Heterokontophyta and Amoebozoa, respectively. The phylum Heterokontophyta exhibited significant inter-kingdom correlations with a few bacterial and fungal phyla (i.e. Gemmatimonadota, Myxococcota, Basidiomycota and Chytridiomycota, respectively), suggesting the presence in PHC of carriage of bacterial food (proto-farming) and defense against competitors (Disalvo et al., 2015). On the other hand, some mobile mites (phylum Arthropoda, family Oppiidae) are characterized by the ability to primarily colonize air-filled pore spaces. Due to their predatory ability against microbial cells, they may constitute one more important link occurring in the PHC trophic network (Gwiazdowicz and Coulson, 2011). In addition, a few predatory macro-invertebrates of the phylum Arthropoda (i.e. the genera *Selenopidae* and *Endomychidae*), occupy the higher trophic levels and act as detritivores, decomposers and predators (Roy et al., 2018).

4.2. Cyanobacterial dominated biocrusts (CDC)

The successional shift from PHC to CDC was characterized by the reduction of bacterial diversity (associated with the increased abundance of the phyla Cyanobacteria and Bacillota) and by a parallel increase of fungal and metazoan diversity. As previously suggest by fluorescence measurements (Palombi and Raimondi, 2021), cyanobacteria are primary producers playing the role of “ecosystem engineers” (Pushkareva et al., 2022). They dominate barren soils usually within a few years after release, prior to the vegetation establishment, exerting a strong impact on both vegetation dynamics and bacterial diversity (Kim et al., 2022). The cyanobacterial genus *Phormidium* (family Oscillatoriaceae) and the bacterivorous nematode genus *Plectus* (order Plectida, family Plectidae) were identified as indicator taxa in CDC. Motile Cyanobacteria (i.e. members of the genus *Phormidium* and *Leptolyngbya*) are considered pioneer organisms due to their ability to glide across the soil and to create a complex EPS matrix (Chamizo et al., 2018; Mugnai et al., 2018). They contribute to soil aggregation and fertilization, increasing the carbon and nitrogen contents, and promoting the soil stabilization. The main cyanobacterial group able to N_2 fixation are heterocystous forms. However, according to Bergman et al., 2017, some non-heterocystous cyanobacteria also exhibit the ability to fix N_2. Among them *Phormium*, the predominant genus in CDC, could potentially contribute to atmospheric N_2 fixation, playing a crucial role in the shift from PHC to CDC (Table S11). This holds particular importance, given nitrogen's role as a limiting factor in biocrust formation. On the other hands, Nematoda are recognized to play an important role in soil food web dynamics (Convey and Wynn-Williams, 2002; Devetter et al., 2021). Their abundance in CDC was apparently correlated to the reduction of bacterial diversity: a significant negative co-occurrence between Nematoda and the bacterial phyla Chloroflexota and Planctomycetota (probably due to a putative antibacterial predatory activity) has been found, in agreement with previous studies (Almela et al., 2019; Darby and Neher, 2016). Nematoda, whose activity in biocrusts is strictly connected with Cyanobacteria, can be classified as secondary consumers and indicator taxa in this biocrust successional stage. Therefore, both Nematoda and Cyanobacteria could be used as key indicator taxa of community shift in the earliest successional stages (as in our case from PHC to CDC). Interestingly, members of the class Arachnida (phylum Arthropoda), detected as indicator taxa in CDC, were recently found in biocrusts of hot ecosystem (Sosa-Quintero et al., 2022).

The successional shift from PHC to CDC was also characterized by a significant ($p < 0.05$) increase of fungal abundance, mainly due to the members of the phylum Ascomycota. Among them, the classes

Eurotiomycetes, Leotyomycetes and Lecaromycetes were identified as indicator fungal taxa of this successional stage, which play an important role in affecting the fungal community structure and networks. These results were also supported by other studies in which the genera *Polyblastia* and *Verrucaria* (class Eurotiomycetes) identified as indicator genera of CDC, were found to play the role of keystone taxa in High Arctic Polar desert (Choe et al., 2021). On the other hand, the saprotrophic psychrophilic yeast genera *Glaciozyma* and *Rhodotorula* (phylum Basidiomycota), which were identified as fungal indicator taxa of this successional stage, were already found in cold environments worldwide (Buzzini et al., 2017; Sannino et al., 2023).

4.3. Cyanobacteria/moss dominated biocrusts (CMDC)

Moss establishment in CMDC and MDC was promoted by nitrogen-fixing cyanobacteria belonging to the families Nodosilineaceae and Nostocaceae (phylum Cyanobacteria) (Rossi et al., 2017). These non-motile heterocystous cyanobacteria are rich in sunscreen pigments (e.g., scytonemin, mycosporine-like amino acids, and carotenoids), providing the dark color of biocrusts, and thus may also facilitate many other organism colonization because these pigments decrease the soil albedo and increase the crust surface temperature (Couradeau et al., 2016). Therefore, the significantly ($p < 0.05$) lower abundances of the bacterial phyla Actinomycetota and Acidobacteriota found in CMDC suggests the shift from oligotrophic to eutrophic condition (from CDC to CMDC), where a significantly ($p < 0.05$) higher abundance of copiotrophic members of both the phylum Bacterioidota and heterotrophic members of the phylum Pseudomonadota (especially the genera *Hyphomonas* and *Sphingomonas*) (Fierer et al., 2007; Selman et al., 2020) was found. The lichen-forming fungi belonging to the family Verrucariaceae (whose genus *Atla* firstly colonize and dominate in the glacier foreland soils) and the P uptake-associated fungi of the order Pleosporales (Long and Yao, 2020; Zhang et al., 2016a) were identified as the fungal indicator taxa in CMDC. While the microarthropod saproxylic beetle belonging to the genus *Limoniscus* and herbivores insects belonged to the family Cecidomyiidae, which are supposed to play an important role in the food web dynamics (Schauer et al., 2018), were identified as the metazoan indicator taxa in CMDC.

The high variability found among different CMDC sampling sites in terms of community diversity and structure, and soil chemical properties was probably due, as well as by peculiar local microclimatic differences between the different sampling samples, to the variable ratio between dominant biological components (i.e. cyanobacteria/moss), indicating a possible interchange between these two biological groups. In particular, samples collected in the site CMDC6 were dominated by a dried white carpet of green algae belonging to the species *Ulva lactuca* (bleached by sun), whose presence was recently reported in the Svalbard archipelago (Malavenda et al., 2018), which may be the main reason justifying the different chemical and biological parameters herein found.

4.4. Moss dominated biocrusts (MDC)

The succession shift from CMDC to MDC was characterized by important change in both chemical and biological parameters. The significant decrease of available P found in MDC corroborates the hypothesis that this element might be a chemical proxy stimulating the shift from one successional stage to a more evolved one, in agreement with a previous study (Schmidt et al., 2012). A possible explanation of the significantly ($p < 0.05$) lower content of available P could be associated to the positive correlations observed between the bacterial families Hyphomycrobiaceae (order Caulobacterales) and Hyphomicrobiales *Incertae Sedis* (order Hyphomicrobiales) vs the fungal family Sporomiaceae (Fig. 5B), which was found to be involved in P mobilizations and bryophyte growth promotion (Anderson et al., 2011; Thomas and Cébron, 2016), thus confirming the existence of a metabolic link between fungal and plant in biocrusts (Collins et al., 2008). In addition, the presence of P uptake-associated fungi belonging to the order Pleosporales (class Dothideomycetes) could postulate their role in P cycles in MDC and BC successional stages as key connector in soil food web dynamics (Long and Yao, 2020; Pombubpa et al., 2020). In fact, a significant correlation ($R^2 = 0.74$; p value < 0.05) between Pleosporales abundance and the P content was found in biocrust successions. Dark septate endophyte orders Pleosporales was found responsible for the nutrient translocation in fungal loops due to their dominant role as

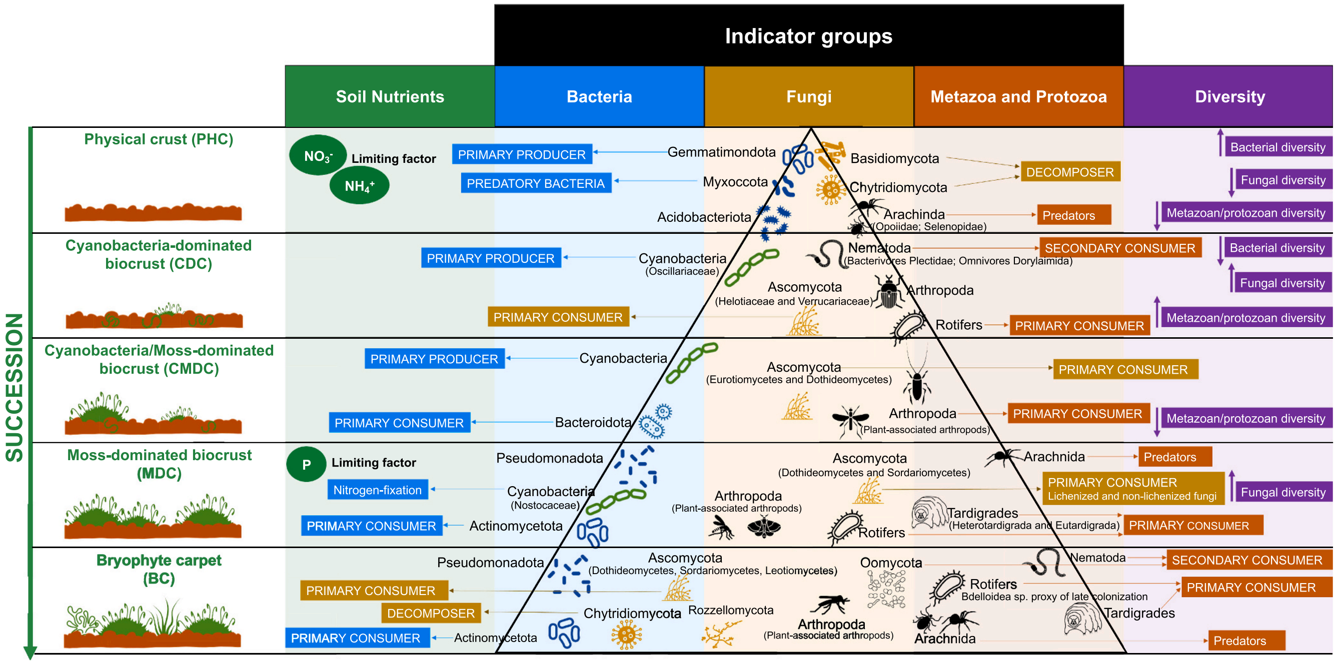

Fig. 5. Synoptic diagram showing the ecology of the different crust/biocrust succession stages of Kongsfjorden area. Along succession, the physicochemical properties (green data), the biodiversity indices (purple data) as well as the indicator taxa of the bacterial (blue data), fungal (yellow data) and metazoan/protozoan (brown data) communities driving the crust/biocrusts succession are shown.

opportunistic plant endophytes in arid environments (Carvajal Janke and Coe, 2021). The correlation of Pleosporales abundance and P level in more evolved successional stages supports the idea of P translocation. This translocation may occur through the mycelia of dark septate endophytes before disseminating into other members of the fungal loop community (Porras-Alfaro et al., 2017).

MDC is the last biocrust successional stage where the assemblage of different organisms reaches a climax, resulting in a stable community with no further biological changes. Indicator taxa identified in MDC included the copiotrophic phyla Actinomycetota, Bacteroidota and Pseudomonadota (especially the classes Alphaproteobacteria and Gammaproteobacteria), consistently with a previous study (Banerjee et al., 2016).

The fungal diversity in MDC reached its maximum value, supporting the hypothesis that a stable biological community has been achieved. Differently from the results observed in hot environments (Lan et al., 2022), Ascomycota remained stable in shift from CMDC to MDC, suggesting their important role in both successional stages. Endophytic taxa belonging to the classes Sordariomycetes and Leotiomycetes (phylum Ascomycota) were identified as indicator taxa of MDC, confirming their presence in the Arctic mosses of the Ny-Ålesund area (Zhang et al., 2016b).

The metazoan community of MDC exhibited no clear taxon-related patterns. This evidence may be affected by the existence of multiple inter-kingdom interactions that may be regarded as a part of a complex food web dynamism. Members of the phyla Arthropoda, Rotifera (genus *Adineta*), Tardigrada (genus *Hypsibius* and *Echiniscus*) and the protozoan phylum Heterokonontophyta were identified as indicator taxa in MDC. Rotifera and Tardigrada are microscopic highly trophic consumers invertebrates commonly found in terrestrial ecosystems, especially in mosses and soils of the Svalbard archipelago (Kaya et al., 2010; Zawierucha et al., 2015).

4.5. Bryophyte carpet (BC)

Despite the attribution of BC to the category of "conventional biocrusts" is a still debated matter (Weber et al., 2022) due to multiple factors that contribute to its formations (i.e. the accumulation of substantial living and dead biomass, including the seabirds manuring) (Vanderpuye et al., 2002), it was the most evolved successional stage found in Kongsfjorden area, probably due to the harsh climatic environment of Svalbard archipelago which prevents any development of high vegetation (Vanderpuye et al., 2002). As for PHC, both PCA and NMDS ordination confirmed BC as a strongly different habitat. The higher biological complexity found in BC than the lesser evolved successional stages is not to be considered surprising, also in relation to the higher contents of DOC, DON, SOM, TN, TOC and available P, which can indicate the achievement of a highly complex biologically driven rate of nutrient cycling. According to Yu et al. (2016), the significant ($p < 0.05$) increase of available P from MDC to BC, associated to the significant ($p < 0.05$) decrease of soil pH, could be due to the release in the surrounding environment of organic acids by Gram-negative bacteria belonging to the order Burkholderiales, which could mobilize bound phosphates and increase P availability (Pérez et al., 2007). Therefore, a nutrient-rich environment could support more complex food web dynamics characterized by a great number of trophic levels, including decomposers, primer producers, primer consumers and secondary consumers.

Although BC exhibited the greatest biological diversity, including the presence of the member of the decomposer phylum Pseudomonadota and the saprophytic phylum Actinomycetota for bacteria, and both phyla Ascomycota and Chytridiomycota for fungi, the three-dimensional structure of mosses could probably be the cause of the observed decrease in metazoan and protozoan diversity, probably as the consequence of competition for resources. The phyla Tardigrada, Arthropoda, Nematoda and Rotifera were identified as metazoan indicator taxa of BC. Consistently with previous studies, the class Bdelloidea (phylum Rotifera) and the families Hypsibiidae and Echiniscidae (phylum Tardigarda) were found to be the dominant metazoan taxa in the Arctic area (especially in moss vegetation) (Kaya et al., 2010; Shaw et al., 2018; Vonnahme et al., 2016). The bryophyte carpet can contribute to the creation of microrefugia with numerous shelters and niches for various macroinvertebrates, such as the indicator taxa belonging to the genera *Sminthurides* and *Isotoma*, maintaining the biodiversity and increasing the resilience (Greiser et al., 2020). Conversely, the BC three-dimensional structure provides suitable living conditions for rotifers (class Bdelloidea) to thrive (Lukashanets et al., 2023). In addition, the identification of the class Oomycota (phylum Heterokontophyta) as an indicator taxon of BC confirmed the presence of dead biomass, in agreement with previous studies (Barde, 2020; Nikolcheva and Bärlocher, 2004).

5. Conclusion

The structure of crust/biocrust communities along the Kongsfjorden area (Svalbard Archipelago) exhibited variations and functionalities depending on the different successional stages (Fig. 5). In particular:

i) the phylum Gemmatimonadota was identified as bacterial indicator taxon in PHC and was found to establish multiple inter- and intra-kingdom interactions;
ii) the families Oscillatoriaceae (phylum Cyanobacteria) and Plectidae (phylum Nematoda) were identified as indicator taxa in CDC: they were respectively involved in biocrust formation (due to the ability of cyanobacteria to create a complex EPS structure) and in the dynamics of the bacterial community (promoted by the bacterivorous nematodes);
iii) CMDC was characterized by a shift from oligotrophic to copiotrophic bacteria (phylum Bacteroidota) and by the onset of saproxylic arthropod (genus *Limoniscus*) and herbivore insects (family Cecidomyiidae);
iv) An increased fungal abundance (i.e. classes Sordariomycetes, Leotiomycetes and Dothideomycetes, phylum Ascomycota) was found in MDC; it was associated with copiotrophic bacteria (phyla Actinomycetota, Bacteroidota and Pseudomonadota) and with highly trophic consumers invertebrates (phyla Arthropoda, Rotifera and Tardigrada);
v) The increased abundance of rotifers (class Bdelloidea) in BC can allow to postulate their ecological preference for moss patches, thus suggesting their ecological role in shaping structure and function of more evolved successional stages. In addition, the high abundance of Tardigrades (family Hypsibiidae), together with their multiple interactions, suggests their pivotal role in controlling the multitrophic interactions in BC.

Abiotic parameters play an important role in driving the biological diversity in crust/biocrust dynamics. Nitrogen resulted the main limiting factor in PHC, affecting the shift from this successional stage to CDC, while the lower availability of phosphorus drove the succession from CMDC to MDC, suggesting its role as a proxy in biocrust shift.

The combination of molecular taxonomy and physicochemical approaches provided novel insights on crust/biocrust successions in High Arctic ecosystems. This study highlights the importance of identifying the indicator taxa (together with their intra- and inter-kingdom interactions) in each crust/biocrust successional stage as a way for giving a more detailed picture of ecosystem dynamics and revealing a strong interconnected micro- and macrobiota. These findings confirm the Svalbard archipelago as an *in-situ* model for studying crust/biocrust community formation and dynamics in the High Arctic ecosystem, addressing key current questions such as the impact of possible climate change scenarios.

CRediT authorship contribution statement

Gianmarco Mugnai: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Irina Pinchuk:** Investigation, Formal analysis, Conceptualization. **Luigimaria Borruso:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Raphael Tiziani:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Ciro Sannino:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Fabiana Canini:** Writing – review & editing, Conceptualization. **Benedetta Turchetti:** Writing – review & editing, Supervision, Conceptualization. **Tanja Mimmo:** Writing – review & editing, Supervision, Resources. **Laura Zucconi:** Writing – review & editing, Supervision, Resources, Conceptualization. **Pietro Buzzini:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The authors declare that there is no conflict of interest.

Data availability

Sequence data generate from this work are available in European Nucleotide Archive (EMBL–EBI) under the accession numbers PRJEB48784 (bacteria), PRJEB48835 (fungi), PRJEB48831 (protozoa and metazoa). Additional data related to this paper may be requested from the corresponding author GM (gianmarco.mugnai@unipg.it).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.171786.

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