Microbial Ecology

Microbial Assemblages in Soil Microbial Succession After Glacial Retreat in Svalbard (High Arctic)

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Abstract

Microbial community composition (cyanobacteria and eukaryotic microalgae abundance and diversity, bacterial abundance, and soil respiration) was studied in subglacial and periglacial habitats on five glaciers near Ny-Ålesund, Svalbard (79°N). Soil microbial communities from nonvegetated sites (subglacial, recently deglaciated, and cryoconite sediments) and sites with plant cover (deglaciated some hundreds of years ago) were analyzed. Physicochemical analyses (pH, texture, water content, organic matter, total C and N content) were also performed on the samples. In total, 57 taxa of 23 genera of cyanobacteria and algae were identified. Algae from the class Chlorophyceae (25 species) and cyanobacteria (23 species) were richest in biodiversity. The numbers of identified species in single habitat types were 23 in subglacial, 39 in barren, 22 in cryoconite, and 24 in vegetated soils. The highest cyanobacterial and algal biovolume and cell numbers, respectively, were present in cryoconite ($13 \times 10^4\ \mu m^3\ mg^{-1}$ soil and 508 cells per mg of soil), followed by barren (5.7×10^4 and 188), vegetated (2.6×10^4 and 120), and subglacial (0.1×10^4 and 5) soils. Cyanobacteria prevailed in all soil samples. Algae (mainly green algae) were present only as accessory organisms. The density of bacteria showed a slightly different trend to that of the cyanobacterial and algal assemblages. The highest number of bacteria was present in vegetated (mean: $13{,}722 \times 10^8$ cells per mg of soil dry wt.), followed by cryoconite (3802×10^8), barren (654×10^8), and subglacial (78×10^8) soils. Response of cyanobacteria and algae to physical parameters showed that soil texture and water content are important for biomass development. In addition, it is shown that nitrogen and water content are the main factors affecting bacterial abundance and overall soil respiration. Redundancy analysis (RDA) with forward selection was used to create a model explaining variability in cyanobacterial, algal, and bacterial abundance. Cryoconites accounted for most of the variation in cyanobacteria and algae biovolume, followed by barren soils. Oscillatoriales, desmids, and green coccoid algae preferred cryoconites, whereas Nostocales and Chroococcales occurred mostly in barren soils. From the data obtained, it is evident that of the studied habitats cryoconite sediments are the most suitable ones for the development of microbial assemblages. Although subglacial sediments do not provide as good conditions as cryoconites, they support the survival of microbial communities. Both mentioned habitats are potential sources for the microbial recolonization of freshly deglaciated soil after the glacier retreat.

Introduction

Soil habitats are widespread in the polar regions of both hemispheres. Despite being subject to extremes of environmental stress, principally freezing [13, 54] and desiccation [55], they provide living space for numerous organisms.

Cyanobacteria and eukaryotic microalgae, being oxyphototrophic organisms, are important parts of microbial communities inhabiting terrestrial ecosystems both in the Arctic and Antarctic. They play an indispensable role in soil formation and stabilization against wind and water erosion, increasing soil organic matter and nitrogen content and preparing substrata for the ensuing successional stages of organisms [4, 28]. Except for cyanobacteria and microalgae, bacteria play an important role transforming "algal litter" into soil organic matter and releasing nutrients for subsequent colonizers.

As there is a belief of annual cell circulation among soil, ice, and atmosphere [9, 14, 33, 52], with wind and

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water being the agents of transport, the spores of cyanobacteria, algae, and other microorganisms are assumed to survive on glacier surfaces [35, 44], or entombed in the ice or frozen subglacial sediment [22, 40, 45]. The frozen habitats might then play the role of a pool of propagules for microbial colonization after glacier retreat, which is supported by the fact that microbial assemblages in ice and soil habitats are relatively similar [58, 59]. However, the proportion of the ice survivors on the colonization processes to wind-borne spores is still unclear. Also, the role of physicochemical factors of the soil in recolonization might be of great importance.

Much attention has been paid to the reinvasion and establishment of plant and animal life after retreat of glaciers and to the effects of climate warming (e.g. [11, 12, 47]). Although higher plant invasion and subsequent plant community development is dependent on primary succession of cyanobacteria, algae, and associated microorganisms, researchers have placed little emphasis on the primary colonizers.

For these reasons, the present study focused on the community structure and abundance of cyanobacteria and algae, and abundance and activity of bacteria in different types of periglacial and subglacial soils. Research also provided data on the potential ability of algae and cyanobacteria to take part in the recolonization processes of barren soils, and on the effects of physical and biological factors in soil on the microbial distribution patterns and community structure.

Materials and Methods

Study Area. In August 2002, fieldwork was undertaken in the vicinity of five glaciers near Ny-Ålesund in northwest Spitsbergen, Svalbard (79°N)—Vestre Brøggerbreen (VB) and Austre Brøggerbreen (AB), Vestre Lovénbreen (VL), Midre Lovénbreen (ML), and Austre Lovénbreen (AL)—and at three sites near Ny-Ålesund where vegetation was already developed (NA) (Fig. 1). Soils were sampled from four different glacial habitat types—subglacial sediments, cryoconite holes, barren and vegetated soil.

Subglacial sediments were sampled at glacier margins where crevasses enabled a direct approach to the bedrock. The maximum depth reached was approximately 10 m. Sediment from cryoconite holes, which are created when windblown material melts into ice surfaces because of its relatively low albedo [36], was sampled in the lower part of all studied glaciers. Two types of soil from which glacier had retreated (referred to as periglacial soils) were sampled: first, newly deglaciated barren soil with no vegetation, assumed to be an early successional stage of microbial colonization in close proximity of glacier fronts (up to 300 m), and second, vegetated soil where plant cover (dominance of vascular plants and mosses) exceeded 60%. A special type of barren soil was the hummocks at the front of glaciers (Fig. 1). Due to a low number of samples, those were included into barren soil samples.

Sampling. At each site, three replicate samples (soil surface layer 10 cm^2 in area and 1–3 cm deep) were collected into sterile 100-mL polypropylene bags by a sterile spatula and frozen immediately after being returned to the laboratory.

Physicochemical Characteristics of Soil. Subsamples were used for pH measurements (soil/water 1:5 w/v), water content (drying at 80°C for 5 h), organic matter content (dry combustion at 450°C for 5 h), and texture (wet sieving, fine fraction <0.5 mm and coarse fraction >0.5 mm).

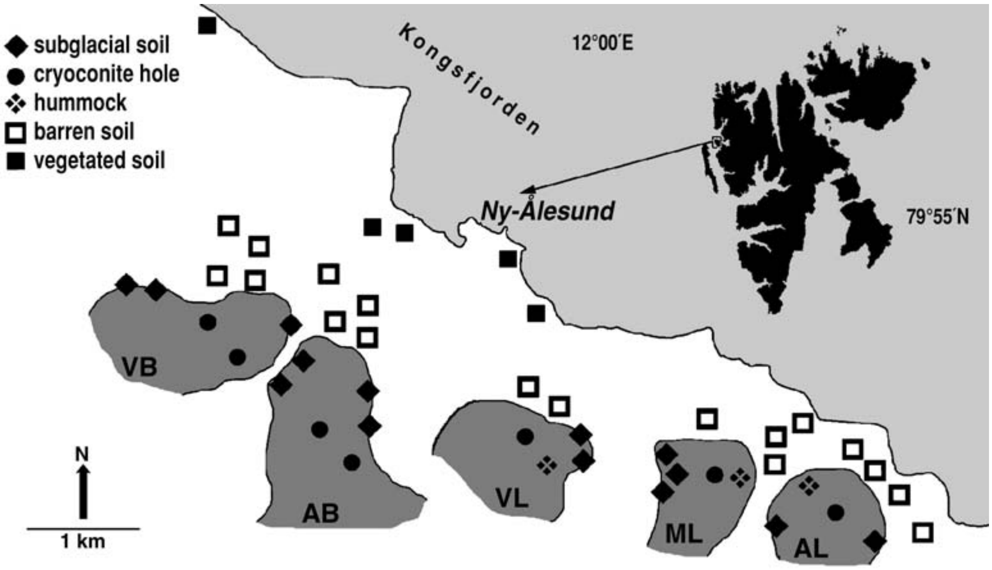

Figure 1. Map of the sampling sites on the Brøggerhalvøya, northwest Spitsbergen (VB: Vestre Brøggerbreen; AB: Austre Brøggerbreen; VL: Vestre Lovénbreen; ML: Midre Lovénbreen; AL: Austre Lovénbreen; NA: Ny-Ålesund). For analyses, glacial hummocks were included into barren soil samples.

Total C and N contents were determined from nonfractionated subsamples using an elemental analyzer (NC 2100, ThermoQuest, Milan, Italy). Carbonates were removed using 7% HCl prior to the analyses.

Algal and Cyanobacterial Abundance and Diversity. Biovolume [37] and the number of algal and cyanobacterial cells as well as the taxonomical composition of communities were determined using light and epifluorescence microscopy (Olympus BX 60). Green and blue excitation (MWB filter cube blue excitation 450–480, emission 515+ for eukaryotic algae, MWG filter cube green excitation 510–550, emission 590+ for cyanobacteria) was used. Seven different groups of cyanobacteria and algae were recognized under epifluorescence microscopy according to their morphological features, and were calculated as separate groups (Chroococcales, Oscillatoriales, Nostocales, green coccoid and green filamentous algae, diatoms, and desmids). Green coccoid and filamentous algae included species from the classes Chlorophyceae and Tribophyceae, because they were impossible to distinguish under the epifluorescence microscope.

The dilution plate method was used for isolation and culturing of algae and cyanobacteria. Aliquots of each sample (100 μl) were placed on sterile plates with BG-11 and Z medium solidified with 1.5% agar to obtain pure cultures. The cultures were allowed to grow at 15°C and 80 μmol m^{-2} s^{-1} for 2 weeks and examined using light microscopy. These cultures were used for further detailed identification of species.

Bacterial Abundance and Respiration. The number of bacterial cells was counted in soil suspension (water/soil 100:1 v/w) using the epifluorescent DAPI staining method [5]. Soil respiration (basal and potential) was measured as CO_2 production using gas chromatography (HP 6850 Agilent, USA) equipped with TC detector, HP Plot molecular sieve 5A and HP Plot Q molecular sieve. Soil suspension (soil/water 2:1 w/v) either unamended (basal respiration) or amended (potential respiration) with glucose (2 mg per g dry soil) was incubated in hermetically sealed vials at 20°C for 3 days and CO_2 production was measured at the end of the incubation. Results were expressed on organic matter basis.

Statistical Analyses. Statistical comparison between studied habitats in all measured parameters was conducted using one-way ANOVA followed by Tukey's honest significant difference (HSD) test in Statistica 6.0.

A linear constrained ordination, redundancy analysis (RDA) with forward selection was used to create a model explaining variability in cyanobacterial and algal community structure using total biovolume data, bacterial density, and respiration. The Monte Carlo permutation test (499 permutations) was applied to compute the significance of hypothetical relations. Algal and cyanobacterial community structure and total biovolume data, and bacterial density and respiration were used as predicted values in three different models. Physicochemical parameters of soil (texture, pH, water content, organic matter content, total carbon, and total nitrogen), algal biovolume, and characteristics of bacterial communities (bacterial abundance, potential and basal respiration, and potential to basal respiration ratio) were used as predictors. All calculations were run using the

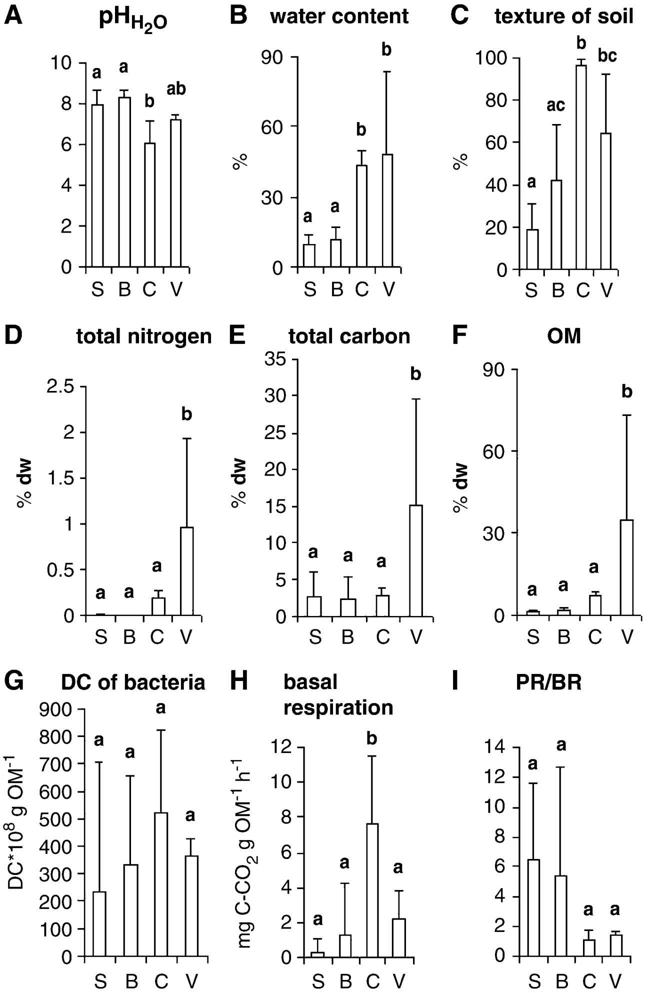

Figure 2. Physical, chemical, and bacterial parameters of four types of soil (S: subglacial; B: barren; C: cryoconite; V: vegetated) at Svalbard glaciers. *Box and whiskers* indicate mean ± SD. *Different letters above boxes* indicate significant difference on the probability level $p < 0.01$. (A) pH of soil extract, (B) percentage of water content, (C) texture of soil, percentage of fine fraction (>0.5 mm), (D) total nitrogen content (percent dry weight), (E) total carbon content (percent dry weight), (F) organic matter content (percent dry weight), (G) direct bacterial counts $\times 10^8$ g OM^{-1}, (H) basal respiration mg C-CO_2 g OM^{-1} h^{-1}, (I) potential to basal respiration ratio.

Table 1. Species richness and representation of cyanobacteria and algae in periglacial and subglacial soils at five glaciers near Ny-Ålesund

Habitat species	*S*	*B*	*C*	*V*
Cyanobacteria (23)				
Chlorogloea sp.			+	
cf. *Komvophoron*		+		
Leptolyngbya boryana ANAGN. & KOM.		+		+
Leptolyngbya cf. *delicatula*		+		
Leptolyngbya foveolarum (RABENH. ex GOM.) ANAGN. & KOM.		+		+
Leptolyngbya cf. *montana*				+
Leptolyngbya cf. *notata*		+		+
Leptolyngbya cf. *tenerima*		+		+
Leptolyngbya tenuis (GOM.) ANAGN. & KOM.		+		
Leptolyngbya sp. long cells	+	+	+	+
Leptolyngbya sp. short cells	+	+	+	+
Leptolyngbya sp.	+	+		
Leptolyngbya sp. brown				+
Leptolyngbya sp. longer cells, constricted		+		
Microcoleus vaginatus (VAUCH.) GOM., JOURN.		+		+
Nodularia sp.				+
Nostoc sp.		+	+	+
Oscillatoriales	+			+
Phormidium fonticolum KÜTZ.		+		+
Phormidium sp.	+	+	+	+
cf. *Phormidium*		+		
cf. *Pseudanabaena*		+	+	
Pseudophormidium sp.				+
Trichormus sp.		+		
Total of cyanobacteria	5	18	6	15
Chlorophyceae (25)				
Bracteacoccus sp.		+		
Chlorella homeosphaera SKUJA	+	+	+	+
Chlorella minutissima FOTT & NOVÁKOVÁ	+	+	+	
Chlorella cf. *minutissima*	+	+		
Chlorella vulgaris BEIJ.		+		+
Chlorella sp.	+	+	+	+
cf. *Chlorococcum*			+	+
Coleochlamys cuccumis (REISIGL) ETTL & GAERTNER		+	+	
Coleochlamys cf. *cuccumis*	+			
Klebsormidium flaccidum (KÜTZ.) SILVA, MATTOX & BLACKWELL	+		+	
Klebsormidium cf. *flaccidum*		+		
Klebsormidium cf. *montanum*	+			
Klebsormidium cf. *scopulinum*	+			
Klebsormidium sp.		+	+	
Muriella terestris J.B. PETERSEN	+	+		+
Muriella sp.	+			
cf. *Muriella*	+	+		
Pseudococcomyxa simplex KORS.	+	+	+	+
cf. *Pseudococcomyxa*			+	
Scotiellopsis sp.		+		
Stichococcus bacilaris NÄG.	+	+	+	+
Stichococcus cf. *chlorelloides*			+	
Stichococcus minutus GRINTZ. & PÉTERFI	+	+		+
cf. *Trochisciopsis*			+	
Unidentified green coccoid 1	+			
Unidentified green coccoid 2			+	
Total of Chlorophyceae	15	15	13	8

Table 1. Continued

Habitat species	*S*	*B*	*C*	*V*
Zygnematophyceae (1)				
Cylindrocystis sp.		+	+	
Total of Zygnematophyceae	0	+	+	0
Unidentified yellow-green coccoid	+			
Total of Tribophyceae	1	2	1	0
Bacillariophyceae (5)				
Achnanthes cf. *minutissima*	+			
Achnanthes sp.	+			
Hannaea arcus (EHRENB.) PATR.		+		
Nitzschia sp.		+		
Unidentified pennate diatom		+	+	+
Total of Bacillariophyceae	2	3	1	1
Total	23	39	22	24

S: subglacial; B: barren; C: cryoconite; V: vegetated.

multivariate data analysis software CANOCO for Windows. The programs CANODRAW 4.0. and CANOPOST [51] were used for graphical presentation of ordination results. The results were summarized using biplot diagrams. In the biplot diagram, the relative length and position of arrows show the extent and direction of response of microbial parameters to the environmental factors.

Results

Characteristics of Localities. The physical and chemical characteristics of soil samples from all the habitats were very variable. pH values ranged from 4.7 (cryoconite sediment, Midre Lovénbreen) to 8.7 (subglacial soil, Vestre Brøggerbreen) (Fig. 2A). The lowest pH was recorded in cryoconite holes, fed by meltwater from upper parts of the glacier, whereas the highest values were obtained in samples from subglacial and deglaciated barren soil close to glacial fronts, which are particularly influenced by the bedrock (made up of limestone, marble, phyllite, and psammite) [23]. Water content was higher in vegetated soil and cryoconite sediments than in subglacial and barren soil (Fig. 2B). The highest water content was found in a sample from a peat bog near Ny-Ålesund, and the lowest in a sample from subglacial soil at Vestre Brøggerbreen.

Soil texture was analyzed as two fractions: the fine fraction (less than 0.5 mm) and the coarse fraction (greater than 0.5 mm). Cryoconite sediments contained the highest proportion of the fine fraction (98.4%, Vestre Brøggerbreen), followed by vegetated and barren soils. The coarsest texture was recorded in subglacial sediment at Vestre Lovénbreen, containing only 1.4% of fraction less than 0.5 mm (Fig. 2C). Pebbles and small stones were often present in periglacial and subglacial soils.

Total nitrogen, carbon, and organic matter content assessments showed that the most developed vegetated soils contained the highest amount of nutrients, with a wide range of measured values (nitrogen 0.15–2.28%, carbon 3.64–31%, OM 4.76–80.44%). Low total nitrogen content and organic matter was found in barren and subglacial soil, in most cases below detection limits (Figs. 2D–F).

Bacterial counts (number of cells per gram of organic matter) and soil respiration activity was lower, but extremely variable in subglacial and barren soils as

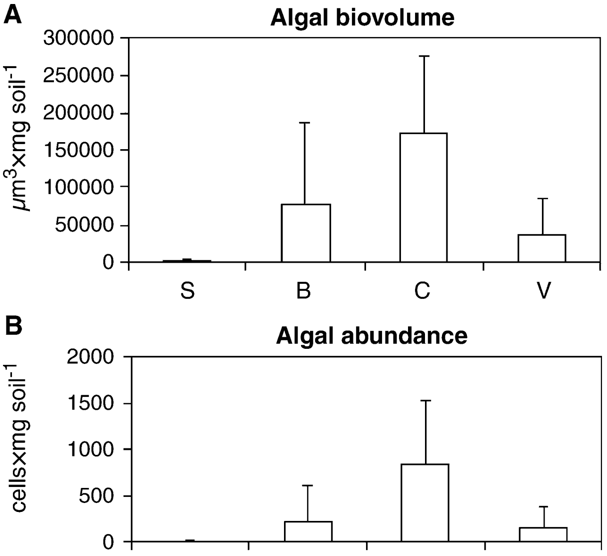

Figure 3. (A) Algal biovolume (μm^3 mg^{-1} soil). (B) Algal abundance (cells × mg^{-1} soil) of periglacial and subglacial soils (S: subglacial; B: barren; C: cryoconite; V: vegetated) at Ny-Ålesund glaciers. Box and whiskers indicate mean ± SD.

Table 2. Abundance (Abund.) of cyanobacterial, algal and bacterial cells per mg of soil (cells mg^{-1} soil), and cyanobacterial and algal biovolume per mg of soil ($\mu m^3 \cdot mg^{-1}$ soil) in periglacial and subglacial soils at five glaciers near Ny-Ålesund

Localities	*Type of habitat*	*Cyano and algae abund*	*Cyano and algae biovolume*	*Cyano abund*	*Green algae abund*	*Bacteria* $\times 10^8$ *abund*	*Chrooc abund*	*Oscill abund*	*Nost abund*	*Green coc abund*	*Green fil abund*	*Diatom abund*	*Desmid abund*
Austre Brøggerbreen	B	14.7	1390.9	14.5	0.2	183.6	1.8	12.6	0	0.2	0	0	0
Austre Brøggerbreen	B	71.6	75,167.6	71.6	0	263.6	19.2	52.4	0	0	0	0	0
Austre Brøggerbreen	B	591.0	249,340.9	532.8	58.3	1405.3	11.9	165.7	355.1	58.3	0	0	0
Austre Brøggerbreen	B	537.9	291,620.8	536.5	1.4	1397.4	10.1	96.7	429.7	0	0	1.2	0.2
Austre Lovénbreen	B	30.2	3021.2	30.2	0	1308.0	0	30.2	0	0	0	0	0
Austre Lovénbreen	B	294.4	168,544.9	294.4	0	31.9	3.8	28.2	262.4	0	0	0	0
Austre Lovénbreen	B	5.5	728.7	1.8	3.7	22.9	1.8	0	0	3.7	0	0	0
Austre Lovénbreen	B	71.7	11,219.9	40.6	31.1	1461.3	4.3	36.3	0	28.7	0	2.4	0
Austre Lovénbreen	B	1511.9	137,712.3	240.8	1271.1	705.4	2.5	26.5	211.8	1271.1	0	0	0
Midre Lovénbreen	B	12.2	2951.3	11.4	0.8	2802.3	0	11.4	0	0.8	0	0	0
Midre Lovénbreen	B	0.1	8.4	0	0.1	196.2	0	0	0	0.1	0	0	0
Midre Lovénbreen	B	2.0	171.0	2.0	0	87.8	0.7	1.3	0	0	0	0	0
Midre Lovénbreen	B	27.3	3289.5	26.4	0.9	1098.0	8.6	17.8	0	0.6	0	0.3	0
Midre Lovénbreen	B	232.7	46,008.8	227.8	4.8	1208.8	10.3	192.9	24.7	1.5	0	3.4	0
Vestre Brøggerbreen	B	129.5	18,383.4	125.2	4.3	234.5	8.9	116.3	0	1.9	1.7	0.7	0
Vestre Brøggerbreen	B	1.4	304.1	1.4	0	35.3	1.4	0	0	0	0	0	0
Vestre Brøggerbreen	B	249.1	141,342.6	241.2	8.0	199.3	3.3	12.9	225.0	8.0	0	0	0
Vestre Brøggerbreen	B	144.0	42,007.0	131.0	13.0	433.9	2.3	110.8	17.9	11.6	0.9	0.5	0
Vestre Lovénbreen	B	6.7	678.8	6.0	0.7	471.7	1.7	4.3	0	0.7	0	0	0
Vestre Lovénbreen	B	3.5	950.4	3.5	0	164.8	1.5	2.0	0	0	0	0	0
Vestre Lovénbreen	B	7.4	694.5	7.4	0	14.6	1.1	6.3	0	0	0	0	0
Mean		187.8	56,930.3	121.3	66.6	653.6	4.5	44.0	72.7	66.1	0.1	0.4	0
SD		349.0	88,467.4	197.8	277.8	724.7	5.1	57.6	135.1	276.4	0.4	0.9	0
Austre Brøggerbreen	C	517.8	103,889.4	509.7	8.1	1717.1	6.8	470.6	32.3	6.3	0	1.8	0
Austre Brøggerbreen	C	986.5	223,539.3	792.7	193.8	538.0	87.7	573.6	131.4	192.1	0	1.7	0
Austre Lovénbreen	C	26.7	82,250.5	14.2	12.5	3022.1	1.3	12.9	0	3.2	2.2	0.3	6.7
Midre Lovénbreen	C	467.0	93,588.0	381.2	85.9	7525.3	1.4	378.8	1.0	84.5	0	0	1.4
Vestre Brøggerbreen	C	314.4	174,130.5	286.4	28.1	4342.8	7.2	62.1	217.0	27.1	0	0	1.0
Vestre Brøggerbreen	C	74.5	34,831.9	59.9	14.6	7192.7	5.3	54.6	0	7.4	0.5	5.3	1.4
Vestre Lovénbreen	C	1169.2	196,103.7	1164.7	4.5	2276.4	29.4	1019.3	116.0	4.5	0	0	0
Mean		508.0	129,761.9	458.4	49.6	3802.1	19.9	367.4	71.1	46.5	0.4	1.3	1.5
SD		433.0	68,812.5	480.5	75.7	2695.3	31.4	364.0	85.1	70.5	0.8	2.0	2.4
Austre Brøggerbreen	S	0.5	75.1	0	0.5	103.2	0	0	0	0.5	0	0	0
Austre Brøggerbreen	S	4.1	704.2	3.9	0.2	57.3	0	3.9	0	0.2	0	0	0
Austre Brøggerbreen	S	16.0	1801.5	15.9	0.1	29.9	0	15.9	0	0.1	0	0	0
Austre Brøggerbreen	S	1.9	169.4	1.9	0	6.4	0.6	1.3	0	0	0	0	0
Austre Lovénbreen	S	0.7	102.6	0.6	0.1	4.8	0.6	0	0	0.1	0	0	0
Austre Lovénbreen	S	0.6	107.1	0.6	0	9.0	0.6	0	0	0	0	0	0
Midre Lovénbreen	S	0.4	25.5	0.4	0	147.1	0.4	0	0	0	0	0	0
Midre Lovénbreen	S	5.2	524.2	5.0	0.1	37.0	1.2	3.8	0	0.1	0	0	0
Midre Lovénbreen	S	9.6	942.4	9.6	0	55.1	0.6	9.1	0	0	0	0	0

Vestre Brøggerbreen	S	2.1	208.0	2.1	0	141.7	0	2.1	0	0	0	0	0
Vestre Brøggerbreen	S	16.0	1554.6	15.3	0.7	332.8	0.5	14.8	0	0.7	0	0	0
Vestre Brøggerbreen	S	7.4	1741.6	6.3	1.2	143.0	1.9	4.4	0	1.2	0	0	0
Vestre Lovénbreen	S	6.0	7865.9	4.0	2.0	11.9	4.0	0	0	1.8	0	0.2	0
Vestre Lovénbreen	S	1.9	164.7	1.7	0.1	15.8	0.4	1.3	0	0.1	0	0	0
Mean		5.2	1141.9	4.8	0.4	78.2	0.8	4.0	0	0.4	0	0	0
SD		5.4	2040	6.5	0.6	90.7	1.1	5.4	0	0.5	0	0.1	0
Ny-Ålesund	V	3.1	1725.1	3.1	0	26,185.4	0.5	0.4	2.2	0	0	0	0
Ny-Ålesund	V	416.4	89,975.0	401.0	15.4	238.6	17.7	309.2	74.1	15.4	0	0	0
Ny-Ålesund	V	16.1	2761.7	15.0	1.1	2478.5	5.1	9.9	0	1.1	0	0	0
Ny-Ålesund	V	1.0	811.5	0.8	0.3	38,205.4	0.8	0	0	0.3	0	0	0
Vestre Lovénbreen	V	162.5	33,940	161.5	1.0	1500.9	2.5	156.7	2.3	0.8	0	0.2	0
Mean		119.8	25,842.7	116.3	3.6	13,721.7	5.3	95.3	15.7	3.5	0	0	0
SD		179.1	38,469.1	176.6	6.8	17,409.4	7.2	136.8	32.6	6.7	0	0.1	0

S: subglacial; C: cryoconite; B: barren; V: vegetated.

For each habitat type, mean and standard deviation (SD) were calculated. Cyano: cyanobacteria; Chrooc: Chroococcales; Oscill: Oscillatoriales; Nost: *Nostoc*; Green coc: green coccoid algae; Green fil: green filamentous algae.

compared with cryoconite sediments and vegetated soils. Potential/basal respiration ratio followed the opposite trend. It was higher in subglacial and barren soil than in vegetated soil and cryoconite sediments (Figs. 2G–I).

Species Composition of Cyanobacteria and Algae. A total of 57 taxa in 23 genera were identified from the soil samples, of which *Leptolyngbya*, *Chlorella*, and *Klebsormidium* were the most represented genera. Algae from the class Chlorophyceae (25 species) and cyanobacteria (23 species) were the most common. Diatoms (five species), Tribophyceae (three species) and desmids (one species) were the less represented groups (Table 1). Rich assemblages of cyanobacteria and algae were found in all investigated subglacial and periglacial habitats. Different groups were variously present in all the habitats examined, but surprisingly the sum of all species in single habitat types was similar (23 species in periglacial, 22 in cryoconite, and 24 in vegetated soils), with the exception of barren soil, where 39 species were found (Table 1). Only 36 algal species were isolated from all samples and transferred into pure cultures. The most unique strains come from the subglacial systems, e.g. *Achnanthes* cf. *minutissima*, *Klebsormidium flaccidum*, and *Leptolyngbya* sp. In these systems, algal species composition has not been studied yet. The strains are currently held at the Culture Collection of Algae at the Laboratory of Algology (CCALA) algal collection in Tøeboò. Strains were often isolated from samples in which the species had not been observed in epifluorescent microscopy; on the other hand, relatively abundant species were sometimes impossible to isolate and culture.

Cyanobacterial, Algal, and Bacterial Assemblages in Different Habitats and Localities. Total cyanobacterial and algal biovolume at the sampling sites varied from 8.4 to 291,621 μm^3 mg^{-1} of soil. On average, the highest algal biovolume was present in cryoconite sediments (129,762 μm^3 mg^{-1} of soil), followed by barren (56,930) and vegetated soils (25,843). The lowest biovolume was found in subglacial soil (1142) (Fig. 3A and Table 2). The numbers of cyanobacterial and algal cells per milligram of soil are shown in Fig. 3B. Trends in algal abundance followed biovolume values in all the habitats studied. The highest algae cell numbers were counted in cryoconite sediments (mean 508 cells per mg of soil) followed by barren (mean 188) and vegetated (mean 120) soils. In the subglacial sediments, almost no cells (mean 5) were recorded (Table 2). From Table 2, it is also obvious that in barren soils the numbers of cells per milligram of soil fluctuated widely (mean 188, SD 349), i.e. close to the glacial front of Austre Lovénbreen 1512 cell per mg of soil were found and, by contrast, in a similar position near Midre Lovénbreen <1 cell per mg.

Cyanobacteria comprised the major proportion of the algal assemblages (often >90% of the community) of the soils investigated. Green algae were relatively minor components of these communities. The cyanobacteria/algae ratio was as follows: subglacial soil 12, vegetated soils 32, and cryoconite sediments 8. In barren soil, higher percentage of algae was found (2).

From Tables 1 and 2, it can be concluded that filamentous cyanobacteria of the order Oscillatoriales, particularly species of the genera *Leptolyngbya* and *Phormidium*, and of the order Nostocales (*Nostoc*) predominated in most communities, and made up the largest part of soil biovolume in the localities examined.

Redundancy Analysis Models. The RDA plot describes total cyanobacterial and algal biovolume and distribution among cyanobacteria and algal groups in relation to sampling localities and habitat types (Fig. 4). Cryoconites explained most of the variation in the cyanobacterial and algal biovolume (26.5% of data variability, p = 0.02), followed by barren soil (9% of data variability, p = 0.05). The localities did not have a significant influence on the algal biovolume. Different algal groups occurred in distinct habitats: desmids, Oscillatoriales, and green coccoid algae preferred cryoconite sediments, whereas cyanobacteria from the orders Nostocales and Chroococcales occurred most frequently in deglaciated barren soils. The response of total cyanobacterial and algal biovolume and its component groups to physical (water content, texture), chemical (pH, nitrogen, carbon, organic matter content), and biological (abundance of bacteria, basal respiration, basal respiration related to organic matter, potential/basal respiration ratio) parameters is shown in Fig. 5. The model explained 51.2% of the total variability. The best predictor of variability in cyanobacterial and algal biovolume was soil texture, explaining 32% of the data variability (p = 0.002); the second important predictor for cyanobacterial and algal biovolume was water content (8.6% of data variability, p = 0.012). Algae preferred finer soil structure and higher water content for growth. Other parameters (nitrogen, carbon, organic matter, pH, abundance of bacteria, and bacterial respiration) did not have significant effects on cyanobacterial and algal biovolume. In addition, a nonsignificant trend in the plot showed that cyanobacteria of the order Nostocales were present more often at sites with higher pH and lower amounts of nitrogen and organic matter. In contrast, green algae grew better in samples with lower pH and higher water content.

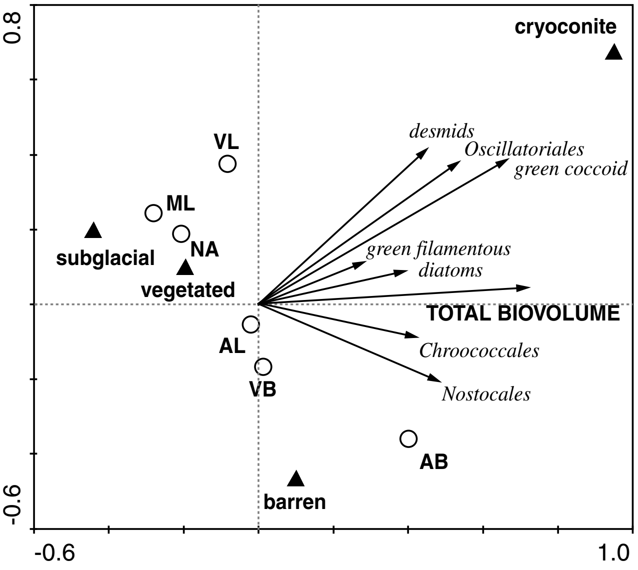

Figure 4. Results of redundancy analysis describing total algal biovolume and its individual groups (Chroococcales, Oscillatoriales, Nostocales, green coccoid and green filamentous algae, diatoms, desmids) in relation to the sampling localities (VB: Vestre Brøggerbreen; AB: Austre Brøggerbreen; VL: Vestre Lovénbreen; ML: Midre Lovénbreen; AL: Austre Lovénbreen; NA: Ny-Ålesund). The localities are presented by *empty circles*, types of habitat by *full triangles* (qualitative explanatory variables). Cyanobacterial and algal biovolume (response variables) is presented by *arrows*.

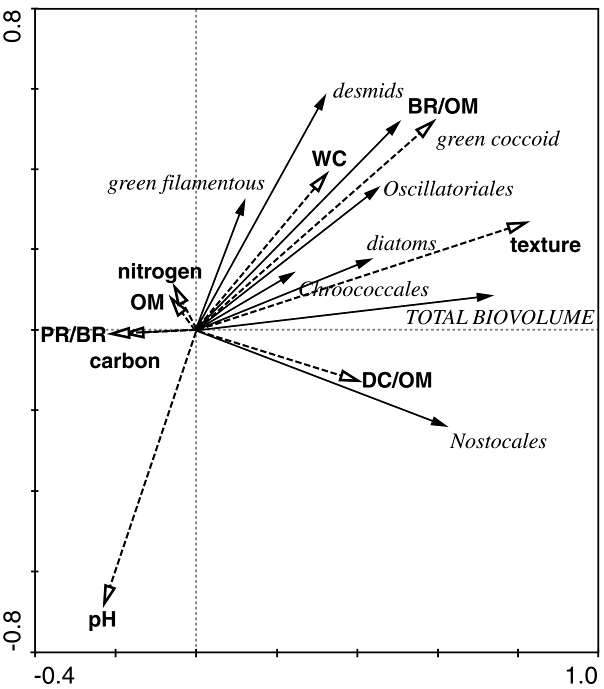

Figure 5. Results of redundancy analysis describing total algal biovolume and its individual groups (Chroococcales, Oscillatoriales, Nostocales, green coccoid and green filamentous algae, diatoms, desmids) in relation to physical [water content (WC), texture], chemical [pH, nitrogen, carbon, organic matter (OM)], and biological [bacterial abundance per organic matter (DC/OM), basal respiration per organic matter (BR/OM), ratio of potential and basal respiration] soil parameters. *Dashed arrows* indicate explanatory variables, *full arrows* the response variables.

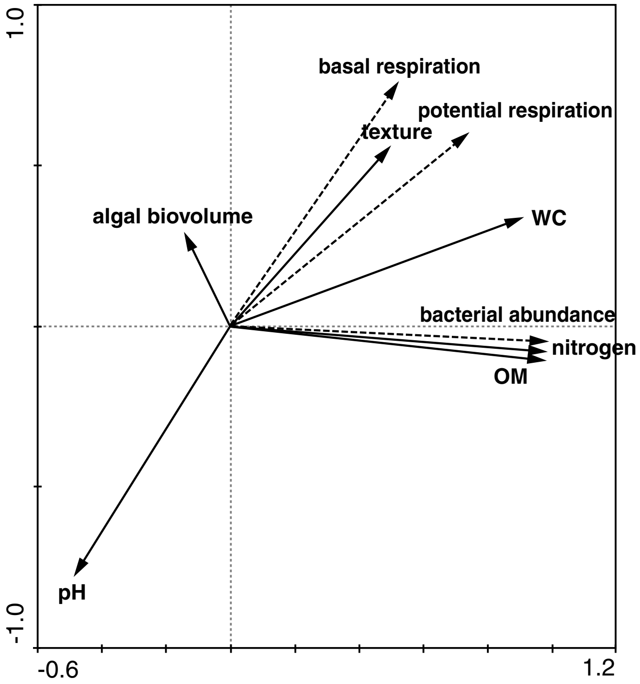

Figure 6. Results of redundancy analysis describing soil bacterial abundance and respiration (basal and potential respiration) in relation to physical [water content (WC), texture], chemical [pH, nitrogen, organic matter (OM)], and biological (algal biovolume) soil parameters. *Full arrows* indicate explanatory variables, *dashed arrows* the response variables.

The response of bacterial abundance and soil respiration to physical (water content, texture), chemical (pH, nitrogen, organic matter), and biological (algal biovolume) parameters is shown in Fig. 6. The model explained 97.2% of the total variability. RDA analysis revealed nitrogen and water content to be the main factors affecting bacterial abundance and microbial activity. The best predictor of variability in bacterial abundance and soil respiration was soil nitrogen content, explaining 90.8% of data variability ($p = 0.002$). The second important predictor was water content (4.6% of data variability, $p = 0.012$). Other parameters (soil texture, organic matter, pH, and algal biovolume) did not have significant effect on bacterial abundance and soil respiration.

Discussion

In the vicinity of Ny-Ålesund, the glacial and periglacial soil habitats are colonized by a wide range of bacteria, cyanobacteria, and eukaryotic microalgae. As described [14, 18, 19, 38, 57–59], cyanobacteria and eukaryotic microalgae are primary colonizers during reinvasion after deglaciation, and heterotrophic bacteria and microfungi totally depend on them for fixed carbon. It was also suggested [9, 15, 33, 52] that there are several physical (wind and subsequent water transport) and biological (birds and mammals including humans) agents, which may transport organic particles including microbial spores. As there is obvious similarity in microbial communities in glacial and periglacial habitats, it has been assumed that either their cells or spores survive on glacial surfaces [35, 36, 44] or can survive embedded in subglacial soils [22, 40] and/or in the glacial ice itself [25, 41, 45]. After thawing, they participate in the recolonization processes in newly exposed soils. Such heterogeneous populations may act as a propagule bank for microbial succession processes [57, 58]. However, the ratio of such ice survivors or microorganisms living on ice surfaces to windborne spores brought into deglaciated forelands from more or less distant sites is unclear. In Antarctica, cyanobacteria are known to survive in the ice covering lakes, forming aggregates in which phototrophic and heterotrophic activity was recorded [39]. These microorganisms are assumed to originate from nearby microbial mats [24]. Generally, it seems clear that the early colonization processes depend mainly on the local microbial bank [59]. This study reports on data elucidating this ecological problem.

Direct cyanobacteria and algae cell counts showed opposite results to those found by Getsen [21] and Elster and co-workers [17] that green algae dominated in modern Arctic tundra environments. Our study showed that cyanobacteria dominated in all four of the soil habitat types examined. This contradiction is unlikely to be caused by seasonal succession, as the studies covered the major part of the season.

Major differences in community structure and in the abundance of microbial populations and of soil physicochemical parameters occurred between cryoconite sediments on glacial surfaces, subglacial, and recently deglaciated soils as well as soils with vegetation cover.

A rather low number of strains was isolated from the soil samples, and relatively abundant species were sometimes impossible to isolate and culture. This may have been caused by using inappropriate media or culture conditions. However, the most suitable media and conditions were chosen from those tested previously (unpublished data).

Cryoconite Sediments. Cryoconite holes are created when windblown material preferentially melts into ice surfaces due to its relatively low albedo [36]. The sediments within cryoconites contain organic material, cyanobacteria and microalgae, bacteria, microfungi, and microfauna [44]. In the present study, cryoconite sediments appeared to be the most suitable of the habitats investigated for the development of microbial communities. In addition, a low potential/basal respiration ratio indicated a lower limit for microbial activity set by nutrient deficiency, compared with subglacial and barren soils. Säwström and co-workers [44] concluded that photosynthesis in cryoconites was not limited by lack of inorganic nutrients. Filamentous cyanobacteria from the order Oscillatoriales, particularly *Leptolyngbya* and *Phormidium*, dominated in cryoconites around Ny-Ålesund, as they did in other Arctic locations [44] and in Antarctic habitats [35, 36, 56]. The abundance and biomass of desmids and green coccoid algae varied in single study sites. Mueller *et al.* [35] and Säwström *et al.* [44] found snow flagellates, e.g. *Chlamydomonas nivalis* and *Chloromonas nivalis*, which were not recorded in the present study. In the Svalbard samples, *Chlorella* sp., *Coleochlamys cuccumis*, *Pseudococcomyxa simplex*, *Stichococcus bacilaris*, and *K. flaccidum* were often present. Microbial abundance and biomass in cryoconite holes have been previously investigated only by Säwström *et al.* [44]. However, this evaluation was expressed per milliliter of cryoconite water or water with sediments and so comparison with the presented data is difficult.

It was also shown that the high abundance of autotrophs and heterotrophs in cryoconite sediments at Ny-Ålesund was positively influenced by water content and the high proportion of fine sediment fractions. Thus the cryoconite communities resemble rather shallow wetland algal-mat communities [14–16, 53], etc., than true soil ecosystem communities.

Regarding physical and chemical characteristics, cryoconite holes are the most distinct of the four habitats studied in Svalbard. Nutrient levels in cryoconite holes were low and frequently below the limit of detection confirming the oligotrophic status of the water as in cryoconites in the Canadian Arctic, the Antarctic [35, 36], and Svalbard [44]. pH values of the sediment were comparable to those of cryoconite water measured on glaciers in Canada and Antarctica [35, 36]. Organic matter content was similar to that reported from the Canadian Arctic [49] or Alaska [50]. The fine texture of cryoconite sediments, as found in this study and in samples taken from cryoconite holes at other sites [48, 49], is an important factor that enables the early development of microbial assemblages. Cyanobacteria and algae were found attached to the surface of fine particles in thin layers, unlike that in coarse-grained substrata [57]. As suggested by Wynn-Williams [57], cryoconite microbial populations may act as a propagule bank for soil successional development, and cyanobacteria, algae, and bacterial communities of cryoconite sediments might be hot spots of autotrophic and heterotrophic activities from which barren soils are inoculated. However, this is not supported by the observations presented in this study, as communities found in cryconites and barren soils are consistently different.

Subglacial Soil. Cyanobacteria and algae have never been studied within subglacial sediments, and our results are therefore compared with permafrost where physical and chemical parameters are relatively similar. The permafrost microbial community has been characterized as a "community of survivors" by Friedmann [20] based on its continued viability for hundreds to millions of years in the frozen state. A rather broad diversity of viable microorganisms exists in permafrost soils [40], including those which can take part in successional processes after the retreat of glaciers.

Frequencies of viable cyanobacteria and algae in permafrost have been found to be lower than those of bacteria, and to decrease with increasing permafrost age [22]. Results from the Svalbard sites are in agreement with this conclusion; bacterial abundance was many times higher than cyanobacteria and algae. Bacterial counts in subglacial soils obtained in this study are similar to those in permafrost found by Gilichinskii and co-workers [22]. In addition, our results show that the species richness of green algae is higher than that of cyanobacteria. Despite the fact that green algae are more diverse, cyanobacteria make up the dominant part of biovolume in algal communities, which is in contrast with results given by Ponder and co-workers [40].

Barren Soil. Wynn-Williams [57] showed that although bacteria were abundant in these communities and fungi were also present, the dominant colonizers of barren deglaciated soils were cyanobacteria and algae. In the present study, the barren soils were the richest in cyanobacterial and algal diversity. However, many of the species isolated occurred also in other habitats. Barren soils are poor in nitrogen and organic matter content and also usually have higher pH compared with cryoconites. Such conditions are preferred by cyanobacteria of the order Nostocales, which are responsible for nitrogen fixation. Such a "reconstructed" cyanobacterial community starts to enrich the deglaciated barren soil environment in nitrogen and also in the provision of organic matter.

Wynn-Williams [57, 58] described phototrophs producing crusts over barren soil surfaces in the Antarctic in which the dominant morphological forms were filamentous cyanobacteria and aggregates of unicellular eukaryotic algae. Our results from the Arctic support these observations. Filamentous cyanobacteria, together with green coccoid algae, constituted the dominant part of the microbial autotrophic community. It is also apparent that single values of abundance and biovolume varied greatly among sampling localities. Wynn-Williams [57] showed that the distribution of these microorganisms was very heterogeneous and microbial aggregates resemble "rafts" in a loose substratum mosaic. Bacterial assemblages and soil respiration activity depend, physically and metabolically, on the distribution of microphototrophs.

The course of soil development is demonstrated by our results and also those of several other polar studies [3, 10, 26, 38], where organic matter, water content, nitrogen, phosphorus, and the proportion of the fine soil fraction tend to increase with age from the time of deglaciation.

Vegetated Soils. Cyanobacterial and algal assemblages were recorded in vegetated soil composed of many species of which many are considered cosmopolitan. They are also common in soils of both polar regions [1, 7, 8, 17, 29, 34]. There were, however, only three species (*Stichococcus bacillaris*, *Microcoleus vaginatus*, and *Phormidium fonticolum*) found in our investigations, which are listed in the catalog of Svalbard plants, fungi, algae, and cyanobacteria [46]. Our data show that cyanobacteria and algae abundance and biovolume were lower in vegetated soils than in cryoconite sediments and in barren soils. Comparison of cyanobacteria and algae abundance and biovolume with other authors is of limited value; the estimates of algal density in soil populations differ greatly among the various studies since no standards exist for counting methods [32]. The most comparable data available are for different habitats than those examined in Svalbard, e.g. climax soil forests [2, 27, 42] or for secondary successional stages in central Europe [30, 31].

The high bacterial abundance found in vegetated soils in Svalbard correspond with other conclusions (e.g. [6, 43]) that the abundance of these organisms is strongly related to the availability of organic matter, inorganic nutrients, and moisture supply. Our results have shown that nitrogen and water content are the main factors affecting bacterial abundance and soil respiration.

In conclusion, the results of this study show the great significance of physicochemical factors of soil on diversity and abundance of soil microbes, and highlight the important ecological role of cyanobacteria, algae, and associated microorganisms as primary colonizers in the processes of establishment and development of the soil community in glacial soils.

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