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ORIGINAL RESEARCH PAPER

From barren substrate to mature tundra – lichen colonization in the forelands of Svalbard glaciers

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Abstract

This paper contributes to studies on the lichen biota of Arctic regions. The research was carried out in the forelands of eight glaciers and in the mature tundra surrounding them. Study areas were located in two parts of Svalbard: in the Kongsfjord (forelands of Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen) and in the Isfjord (forelands of Rieperbreen, Svenbreen, and Ferdinandbreen). In each foreland and in the mature tundra surrounding it, a series of 1-m^2 plots was established, within which a percentage cover for each species was determined. In total, 133 lichens and one lichenicolous fungus were recorded. Nineteen species were recorded for the first time in Svalbard: *Agonimia allobata*, *Atla wheldonii*, *Bacidia herbarum*, *Catolechia wahlenbergii*, *Epigloea soleiformis*, *Lecanora behringii*, *Lepraria subalbicans*, *Leptogium arcticum*, *Pertusaria pseudocorallina*, *Placidiopsis custnani*, *Protothelenella corrosa*, *Pyrenidium actinellum*, *Spilonema revertens*, *Stereocaulon saxatile*, *Thelocarpon sphaerosporum*, *Toninia coelestina*, *Verrucaria elaeina*, *Verrucaria murina*, and *Verrucaria xyloxena*. The lichen richness was the lowest in the Ferdinandbreen foreland (24 species) and the highest in the Rieperbreen foreland (82 species). Significant differences in species composition were found among the forelands studied, except for Austre and Vestre Brøggerbreen whose lichen composition was similar. The differences in lichen composition between mature tundra in the vicinity of the following forelands were identified: Vestre Brøggerbreen and Svenbreen, Austre Brøggerbreen and Svenbreen, and Austre Brøggerbreen and Ferdinandbreen. The most dominant group of lichens in both forelands and mature tundra were chlorolichens, not cyanolichens.

Keywords

cryptogamic species; primary succession; Kongsfjord; Isfjord; Spitsbergen; Arctic

Introduction

The harsh environment rendered by the geographical location of the Arctic contributes to the specific habitat conditions encountered by living organisms that inhabit this region. Tundra plant communities are dominated by cryptogamic species that are perfectly adapted to an environment that is inadequate for the majority of vascular plants [1,2]. Although cryptogams are the main components of the Arctic tundra, including both climax communities and recently deglaciated forelands [2–4], the majority of studies in Svalbard have neglected their importance. One of the most significant cryptogamic groups are lichens. In the Arctic, lichens are an important component of biodiversity in plant communities [5]. There are approximately 1,750 species of lichen in the Arctic, with 742 known to inhabit Svalbard [6–8]. Lichens are complex symbiotic organisms consisting of associations between fungi and photobionts that host hyperdiverse microbial communities [9]. Due to the fact that photobionts may facilitate the ability of lichens to colonize extreme environments such as glacier forelands [10], they play a dominant role in primary succession as pioneers in this process [11]. Epigeic lichens in glacier forelands, together with bryophytes, bacteria, and cyanobacteria, create so-called BSCs (biological soil crusts). The presence of cyanobacteria having the ability to bind atmospheric nitrogen as symbiotic components of lichens increases the colonization potential of species [12,13], contributing to the biogeochemical nitrogen cycle that is critical in barren and nutrient-poor soils present in freshly deglaciated areas [14,15]. Climate change is driving the growth of ice-free areas in glacier forelands, galvanizing the need for further research on the primary succession of lichens [16,17]. Retreating glaciers uncover new habitats that can easily be colonized by lichens as pioneering species [18,19]. However, studies conducted in both the Arctic and subarctic regions indicate that lichen diversity appears to decrease as a result of global warming [20]. Nevertheless, glacier forelands offer habitat conditions wherein lichens are less vulnerable, in that they are exposed to less competition from vascular plants compared to tundra communities with more developed vascular plant cover [18]. Consequently, glacier forelands may serve as important lichen refugia in the future.

The main aim of the present study was to investigate terricolous lichen diversity and the composition of terricolous lichen communities in the foreland of eight glaciers and in the mature tundra that surrounds them, as well as the differences in terricolous lichen composition between selected locations. The following hypotheses were set: (***i***) considering the plant communities surrounding the glacier forelands whose development was not disturbed by the glacier as climax communities, the species richness of mature tundra differs from the species richness of glacier forelands; (***ii***) with regard to similar habitat conditions in the glacier foreland, the lichen composition and species richness of the glacier forelands under investigation are similar; and (***iii***) the species number and percentage cover of nitrogen-binding cyanolichens is higher in the glacier forelands than in mature tundra, while the species number and percentage cover of chlorolichens show the opposite pattern.

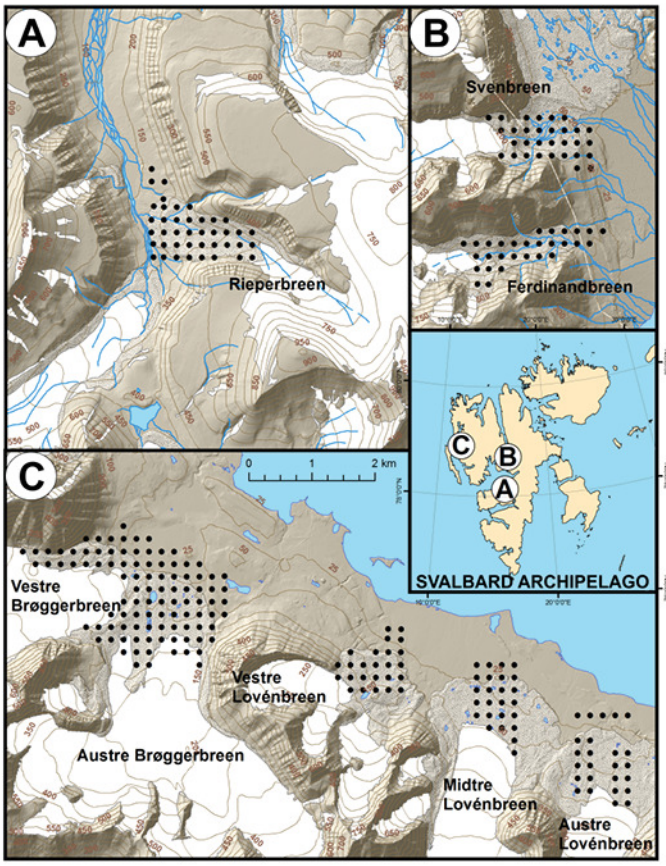

Fig. 1 Location of sampling plots within study areas. Isfjord: A – Rieperbreen, B – Ferdinandbreen and Svenbreen; Kongsfjord: C – Austre and Vestre Brøggerbreen, Austre, Midtre, and Vestre Lovénbreen (© Norwegian Polar Institute 2018; http://www.npolar.no).

Material and methods

Study area

The research was carried out in the summer of 2017 in the forelands of eight glaciers (whose deglaciation process began at the end of the Little Ice Age) and in the mature tundra which surrounds them. Study areas were located in two parts of Spitsbergen, (***i***) the biggest island of the Svalbard archipelago (the biggest island of the Svalbard archipelago): in Kongsfjord, located in the northwestern part of Spitsbergen where the forelands of Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen are located, and (***ii***) in Isfjord, situated in the central part of Spitsbergen where the forelands of Rieperbreen, Svenbreen, and Ferdinandbreen are located (Fig. 1).

Data sampling

In each foreland and surrounding mature tundra, a series of 1-m^2 plots was established in a square grid. Fig. 1 presents the location of sampling plots (black dots). Altogether, 276 plots were investigated: 175 in Kongsfjord and 101 in Isfjord. At each plot, the cover of each terricolous lichen species was estimated on a percentage scale (the present study did not include epilithic lichens). With respect to Austre Brøggerbreen, Vestre Brøggerbreen, Rieperbreen, Svenbreen, and Ferdinandbreen, the forelands were completely covered by square grids, while in the forelands of Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen, only part of the area was covered by grids (Fig. 1). Regarding taxonomically problematic specimens, samples of lichen thalli were collected for laboratory identification.

Lichen identification

Traditional taxonomical methods and standard light microscopy were used for species identification. The following guides were used: Andreev et al. [21,22], Brodo et al. [23], Smith et al. [24], and Thomson [25,26]. Chemical analysis of lichen substances were conducted according to the technique developed by Orange et al. [27]. The taxonomical nomenclature followed the Index Fungorum [28]. The distribution of taxa in Svalbard was confirmed according to Elvebakk and Hertel [29], Øvstedal et al. [8], Redchenko et al. [30], Kristinsson et al. [31], Zhurbenko and Brackel [32], and the Svalbard Lichen Database [33]. Lichen samples were deposited in the Herbarium of the Institute of Botany at Jagiellonian University in Kraków (KRA).

Statistical analyses

The Mann–Whitney *U* test was applied to investigate the differences in species richness between Kongsfjord and Isfjord as well as the differences in species richness between plots located in glacier forelands and mature tundra. The differences in percentage cover and species number of cyanolichens and chlorolichens between all of the glacier foreland plots and all of the mature tundra plots were also investigated using this test. The Wilcoxon test was applied to study the differences in species number and percentage cover between lichens with different symbiotic components for glacier foreland and mature tundra separately. Differences in species richness among the forelands studied were tested using the Kruskal–Wallis test.

Nonmetric multidimensional scaling (NMDS) followed by a multivariate statistical test (one-way PERMANOVA; 999 permutations) with a sequential Bonferroni procedure were applied to determine similarities in lichen composition among the glacier forelands studied as well as among mature tundra that surrounds particular glaciers. The same analysis was used to test differences in lichen composition between Kongsfjord and Isfjord for plots located in glacier forelands and plots designated in mature tundra separately. Indicator species analysis measured with Pearson's phi coefficient was performed to investigate the lichens related to each glacier foreland and the surrounding mature tundra. This analysis allowed us to distinguish indicator species representing lichens characteristic of each foreland or each mature tundra. Data from plots without species cover were excluded from the above-mentioned analyses. The changes in species richness along the forelands were presented on a heat map (based on kernel density estimation) which was created using Quantum GIS software [34]. The statistical analyses were carried out using STATISTICA 12 (Statsoft, Tulsa, OK, USA), PAST 3.10 [35], and CRAN R-3.4.2 [36].

Results

Species richness and composition of lichen communities

Overall, a total of 133 lichen taxa and one lichenicolous fungus were found in the study areas. Tab. 1 presents the recorded lichen species occurring in each foreland and surrounding mature tundra.

Tab. 1 A list of the lichen taxa recorded in the studied glacier forelands and mature tundra in their vicinity. A star (*) indicates lichenicolous fungi. Abbreviations used: AL – Austre Lovénbreen; ML – Midtre Lovénbreen; VL – Vestre Lovénbreen; AB – Austre Brøggerbreen; VB – Vestre Brøggerbreen; R – Rieperbreen; S –Svenbreen; F – Ferdinandbreen. Species new to Svalbard are in bold.

		Glacier foreland of								Mature tundra of							
	Species name	AL	ML	VL	AB	VB	S	F	R	AL	ML	VL	AB	VB	S	F	R
1	***Agonimia allobata* (Stizenb.) P. James**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
2	*Agonimia gelatinosa* (Ach.) M. Brand & Diederich	×	×	×	×	×	-	-	-	×	×	×	×	×	-	×	-
3	*Amandinea punctata* (Hoffm.) Coppins & Scheid.	-	×	-	×	-	-	-	×	-	×	-	-	-	-	-	-
4	*Arctomia delicatula* Th. Fr.	-	-	-	-	×	-	-	×	×	×	×	×	×	-	-	×
5	*Arthonia lapidicola* (Taylor) Branth & Rostr.	-	-	-	-	-	×	-	×	-	-	-	-	-	×	-	×
6	*Arthrorhaphis citrinella* (Ach.) Poelt	×	-	×	×	-	×	-	×	×	×	×	×	×	-	×	-
7	*Athallia pyracea* (Ach.) Arup, Frödén & Søchting	×	×	×	×	-	×	×	×	×	×	-	×	×	×	×	×
8	*Atla alpina* Savić & Tibell	-	-	-	-	-	×	-	×	-	-	-	-	-	-	×	-
9	***Atla wheldonii* (Travis) Savić & Tibell**	×	×	×	×	×	×	×	-	×	×	×	×	×	-	×	-
10	*Bacidia bagliettoana* (A. Massal. & De Not.) Jatta	×	×	×	×	×	×	-	-	×	×	×	×	-	-	-	-
11	***Bacidia herbarum* (Stizenb.) Arnold**	-	-	×	-	-	-	-	-	×	×	-	-	-	-	-	-
12	*Baeomyces rufus* (Huds.) Rebent.	×	-	-	-	-	-	-	×	-	-	-	×	-	-	-	-
13	*Biatora carneoalbida* (Müll. Arg.) Coppins	×	-	-	-	-	-	-	-	×	-	×	-	-	×	×	×
14	*Biatora cuprea* (Sommerf.) Fr.	-	×	×	-	-	-	-	×	×	-	-	×	×	-	×	×
15	*Biatora ementiens* (Nyl.) Printzen	×	×	×	×	×	-	-	×	×	×	×	×	×	×	×	×
16	*Biatora subduplex* (Nyl.) Printzen	×	×	×	-	-	-	-	×	×	×	×	×	×	-	-	×
17	*Bilimbia lobulata* (Sommerf.) Hafellner & Coppins	×	×	×	×	-	×	-	-	×	-	-	×	×	×	×	-
18	*Bilimbia sabuletorum* (Schreb.) Arnold	×	×	-	-	-	×	-	-	×	-	-	-	×	-	×	-
19	*Blastenia ammiospila* (Ach.) Arup, Søchting & Frödén	×	-	-	-	-	-	-	×	×	-	-	×	×	-	-	×
20	*Bryobilimbia hypnorum* (Lib.) Fryday, Printzen & S. Ekman	-	-	-	×	-	-	-	-	×	-	-	×	×	-	×	×
21	*Bryonora castanea* (Hepp) Poelt	-	-	-	-	-	-	-	-	-	-	×	-	×	-	-	×
22	*Bryoplaca tetraspora* (Nyl.) Søchting, Frödén & Arup	-	×	×	×	-	-	-	×	×	×	×	×	×	-	-	×
23	*Buellia disciformis* (Fr.) Mudd	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
24	*Buellia elegans* Poelt	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
25	*Buellia geophila* (Flörke ex Sommerf.) Lynge	-	-	-	-	-	-	-	×	×	×	-	×	×	-	-	-
26	*Buellia insignis* (Nägeli ex Hepp) Th. Fr.	-	-	-	-	-	-	-	×	-	-	×	×	-	-	-	×
27	*Buellia papillata* (Sommerf.) Tuck.	-	-	-	-	-	-	×	×	×	-	-	-	-	-	×	×

Tab. 1 Continued

	Species name	Glacier foreland of								Mature tundra of							
		AL	ML	VL	AB	VB	S	F	R	AL	ML	VL	AB	VB	S	F	R
28	*Caloplaca caesiorufella* (Nyl.) Zahlbr.	-	-	-	-	-	-	-	×	-	-	-	×	-	-	-	×
29	*Caloplaca cerina* (Hedw.) Th. Fr.	×	×	×	×	-	×	×	×	×	×	×	×	×	×	×	-
30	*Catapyrenium cinereum* (Pers.) Körb.	-	-	-	-	-	-	-	×	-	-	-	-	-	×	-	×
31	***Catolechia wahlenbergii* (Ach.) Körb.**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
32	*Cetraria aculeata* (Schreb.) Fr.	-	×	-	×	-	-	-	-	-	×	×	×	-	-	-	-
33	*Cetraria ericetorum* Opiz	-	-	-	×	-	-	-	-	-	-	×	×	-	-	-	-
34	*Cetraria islandica* (L.) Ach.	-	-	-	×	-	-	-	-	-	-	-	×	×	-	-	-
35	*Cetrariella delisei* (Bory ex Schaer.) Kärnefelt & A. Thell	×	×	×	×	×	×	-	×	×	×	×	×	×	×	×	×
36	*Cladonia borealis* S. Stenroos	-	-	-	-	-	×	-	×	-	-	×	×	-	-	-	×
37	*Cladonia chlorophaea* (Flörke ex Sommerf.) Spreng.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
38	*Cladonia coccifera* (L.) Willd.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
39	*Cladonia cornuta* (L.) Hoffm.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
40	*Cladonia ecmocyna* Leight.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	×
41	*Cladonia macroceras* (Delise) Ahti	-	-	-	-	-	-	-	×	-	-	×	×	-	-	×	×
42	*Cladonia mitis* Sandst.	-	-	-	-	-	-	-	×	-	-	×	-	-	-	-	-
43	*Cladonia pocillum* (Ach.) O. J. Rich.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
44	*Cladonia pyxidata* (L.) Hoffm.	×	×	-	×	×	×	-	×	-	-	×	×	×	×	×	×
45	*Cladonia squamosa* (Scop.) Hoffm.	-	-	-	-	×	-	-	-	-	-	-	-	-	-	-	-
46	*Cladonia uncialis* (L.) Weber ex F. H. Wigg.	-	-	-	-	-	-	-	-	-	-	×	-	-	-	-	×
47	*Collema tenax* (Sw.) Ach.	×	-	-	×	×	-	-	×	×	-	×	×	×	×	×	×
48	***Epigloea soleiformis* Döbbeler**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
49	*Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell	-	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-
50	*Flavocetraria nivalis* (L.) Kärnefelt & A. Thell	-	-	-	×	-	×	-	×	×	-	×	×	×	-	×	-
51	*Frigidopyrenia bryospila* (Nyl.) Grube	×	×	×	×	×	×	×	×	×	×	×	×	×	×	-	-
52	*Frutidella caesioatra* (Schaer.) Kalb	-	-	-	-	×	-	-	×	-	-	-	-	-	×	-	×
53	*Fulgensia bracteata* (Hoffm.) Räsänen	×	×	-	-	×	×	×	-	×	-	-	-	-	×	×	-
54	*Huneckia pollinii* (A. Massal.) S. Y. Kondr., Kärnefelt, Elix, A. Thell, Jung Kim, A. S. Kondr. & Hur	×	×	×	×	-	-	-	-	×	×	×	×	×	-	-	-

Tab. 1 Continued

	Species name	Glacier foreland of								Mature tundra of							
		AL	ML	VL	AB	VB	S	F	R	AL	ML	VL	AB	VB	S	F	R
55	*Japewia tornoensis* (Nyl.) Tønsberg	-	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-
56	*Lathagrium cristatum* (L.) Otálora, P. M. Jørg. & Wedin	×	-	×	×	×	×	-	-	-	-	-	×	-	-	-	-
57	***Lecanora behringii* Nyl.**	-	-	-	-	-	-	-	×	-	-	×	-	-	-	-	-
58	*Lecanora epibryon* (Ach.) Ach.	×	×	×	×	-	×	×	-	×	×	×	×	-	×	×	-
59	*Lecidea berengeriana* (A. Massal.) Nyl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×	-
60	*Lecidea ramulosa* Th. Fr.	×	×	×	×	×	×	×	-	×	×	×	×	×	×	×	×
61	*Lecidella wulfenii* (Ach.) Körb.	-	-	×	-	-	-	-	×	×	×	×	×	×	-	×	×
62	*Lecidoma demissum* (Rutstr.) Gotth. Schneid. & Hertel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×
63	*Leciophysma finmarkicum* Th. Fr.	×	×	×	×	×	-	-	-	×	×	×	×	×	-	×	-
64	*Leciophysma furfurascens* (Nyl.) Gyeln.	-	-	-	×	×	-	-	-	-	×	×	×	-	-	-	-
65	***Lepraria subalbicans* (I. M. Lamb) Lendemer & B. P. Hodk.**	-	-	-	-	×	-	-	×	-	-	-	-	-	-	-	-
66	***Leptogium arcticum* P. M. Jørg.**	-	×	×	-	-	-	-	-	-	-	-	-	×	-	-	-
67	*Lopadium coralloideum* (Nyl.) Lynge	-	-	-	-	-	-	-	×	-	-	-	×	-	-	×	×
68	*Megaspora verrucosa* (Ach.) Hafellner & V. Wirth	-	×	-	×	-	-	-	-	×	-	×	×	×	×	-	-
69	*Micarea crassipes* (Th. Fr.) Coppins	-	×	-	-	-	-	-	-	-	-	-	-	-	-	-	-
70	*Micarea incrassata* Hedl.	-	-	-	-	-	-	-	×	-	×	×	×	×	-	-	-
71	*Mycobilimbia microcarpa* (Th. Fr.) Brunnb.	×	×	×	×	×	×	×	-	×	×	×	×	×	×	×	-
72	*Myriolecis zosterae* (Ach.) Śliwa, Zhao Xin & Lumbsch	×	×	×	×	×	×	×	×	×	×	×	×	-	×	×	×
73	*Nephroma expallidum* (Nyl.) Nyl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×
74	*Ochrolechia androgyna* (Hoffm.) Arnold	×	×	×	-	×	×	×	×	×	×	-	×	×	×	-	×
75	*Ochrolechia frigida* (Sw.) Lynge	×	×	×	×	×	×	-	×	×	×	×	×	×	×	×	×
76	*Parvoplaca tiroliensis* (Zahlbr.) Arup, Søchting & Frödén	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
77	*Peltigera aphthosa* (L.) Willd.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
78	*Peltigera didactyla* (With.) J. R. Laundon	×	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
79	*Peltigera leucophlebia* (Nyl.) Gyeln.	-	-	-	-	-	-	-	×	-	-	×	-	-	-	-	×
80	*Peltigera polydactylon* (Neck.) Hoffm.	×	-	-	-	-	-	-	×	-	-	-	-	-	-	-	×
81	*Peltigera venosa* (L.) Hoffm.	-	-	-	-	×	-	-	-	-	-	-	-	-	-	-	×

Tab. 1 Continued

	Species name	Glacier foreland of								Mature tundra of							
		AL	ML	VL	AB	VB	S	F	R	AL	ML	VL	AB	VB	S	F	R
82	***Pertusaria pseudocorallina* (Sw.) Arnold**	-	-	-	-	-	-	-	×	-	-	×	-	-	-	-	×
83	*Phaeorrhiza nimbosa* (Fr.) H. Mayrhofer & Poelt	-	-	×	×	-	-	-	×	×	×	×	×	×	-	-	×
84	*Phaeorrhiza sareptana* (Tomin) H. Mayrhofer & Poelt	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	×
85	***Placidiopsis custnani* (A. Massal.) Körb.**	-	-	-	-	-	×	-	-	-	-	-	-	-	×	-	-
86	*Placidiopsis pseudocinerea* Breuss	-	-	-	-	-	-	-	-	×	-	-	-	×	-	-	-
87	*Polyblastia bryophila* Lönnr.	×	×	×	×	×	-	-	×	×	×	×	×	-	-	-	-
88	*Polyblastia gothica* Th. Fr.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
89	*Polyblastia schaereriana* (A. Massal.) Müll. Arg.	-	-	-	-	-	×	×	×	-	-	-	-	-	-	-	-
90	*Polyblastia sendtneri* Kremp.	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
91	*Porina mammillosa* (Th. Fr.) Zahlbr.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
92	*Protomicarea limosa* (Ach.) Hafellner	-	-	-	-	-	-	-	-	-	-	-	×	-	-	-	×
93	*Protopannaria pezizoides* (Weber) P. M. Jørg. & S. Ekman	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	×
94	***Protothelenella corrosa* (Körb.) H. Mayrhofer & Poelt**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
95	*Protothelenella sphinctrinoidella* (Nyl.) H. Mayrhofer & Poelt	-	-	-	-	-	-	-	×	-	-	-	×	-	-	-	×
96	*Protothelenella sphinctrinoides* (Nyl.) H. Mayrhofer & Poelt	-	-	-	-	-	-	×	×	-	-	-	-	-	-	-	-
97	*Psoroma hypnorum* (Vahl) Gray	-	-	-	-	×	-	-	-	×	-	×	×	-	-	-	×
98	*Psoroma tenue* Henssen	-	-	-	×	×	-	-	×	-	-	×	×	×	-	-	×
99	***Pyrenidium actinellum* Nyl.**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
100	*Rhymbocarpus neglectus* (Vain.) Diederich & Etayo	×	×	×	×	×	×	-	-	×	×	×	-	×	-	-	-
101	*Rinodina roscida* (Sommerf.) Arnold	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
102	*Rinodina turfacea* (Wahlenb.) Körb.	×	×	×	×	-	×	×	-	×	×	×	×	×	×	×	×
103	*Rostania ceranisca* (Nyl.) Otálora, P. M. Jørg. & Wedin	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
104	*Schadonia fecunda* (Th. Fr.) Vězda & Poelt	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
105	*Scytinium gelatinosum* (With.) Otálora, P. M. Jørg. & Wedin	×	×	×	×	×	×	-	-	×	-	×	×	×	-	-	-
106	*Scytinium tenuissimum* (Hoffm.) Otálora, P. M. Jørg. & Wedin	-	-	-	×	-	-	-	-	-	-	-	-	-	-	-	-

Tab. 1 Continued

	Species name	Glacier foreland of								Mature tundra of							
		AL	ML	VL	AB	VB	S	F	R	AL	ML	VL	AB	VB	S	F	R
107	*Solorina bispora* Nyl.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	×	-
108	*Solorina crocea* (L.) Ach.	-	-	-	-	×	-	-	-	×	-	-	×	×	-	-	-
109	*Sphaerophorus globosus* (Huds.) Vain.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×
110	*Spilonema revertens* Nyl.	-	-	-	-	-	-	-	-	×	-	×	×	×	-	-	-
111	***Sporodictyon terrestre* (Th. Fr.) Savić & Tibell**	-	×	-	-	×	×	×	×	×	-	-	-	-	×	×	-
112	*Steinia geophana* (Nyl.) Stein	×	×	×	-	-	-	×	×	-	×	-	-	-	×	×	×
113	*Stereocaulon alpinum* Laurer	×	×	×	×	-	×	-	×	-	×	×	×	-	-	-	×
114	*Stereocaulon arcticum* Lynge	-	-	-	-	-	-	-	×	-	×	×	-	-	-	-	-
115	*Stereocaulon botryosum* Ach.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
116	*Stereocaulon capitellatum* H. Magn.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
117	*Stereocaulon condensatum* Hoffm.	-	×	×	-	-	-	-	-	-	-	-	-	-	-	-	-
118	*Stereocaulon glareosum* (Savicz) H. Magn.	-	-	-	-	-	-	×	×	-	-	-	-	-	-	-	×
129	*Stereocaulon paschale* (L.) Hoffm.	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	×
120	*Stereocaulon rivulorum* H. Magn.	×	×	×	×	×	×	-	×	-	-	-	×	-	×	×	×
121	***Stereocaulon saxatile* H. Magn.**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
122	*Strigula sychnogonoides* (Nitschke) R. C. Harris	×	-	-	-	-	×	×	×	-	-	-	×	-	-	-	-
123	*Thamnolia vermicularis* (Sw.) Schaer.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×	-
124	*Thelidium minimum* (A. Massal. ex Körb.) Arnold	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
125	*Thelocarpon epibolum* Nyl.	-	-	×	-	×	-	-	-	-	-	-	-	-	-	-	-
126	*Thelocarpon impressellum* Nyl.	-	×	-	-	-	-	-	-	-	-	-	-	-	-	-	-
127	***Thelocarpon sphaerosporum* H. Magn.**	-	-	-	-	-	×	-	-	-	-	-	-	-	-	-	-
128	*Toninia aromatica* (Turner) A. Massal.	×	×	×	×	-	×	×	×	×	×	×	-	×	×	×	-
129	***Toninia coelestina* (Anzi) Vězda**	-	-	-	-	-	×	-	-	-	-	-	-	-	×	×	-
130	*Toninia verrucarioides* (Nyl.) Timdal	-	-	-	-	-	-	-	-	-	-	-	×	-	-	-	-
131	***Verrucaria elaeina* Borrer**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	×	-
132	***Verrucaria murina* Leight.**	-	-	-	-	-	-	-	×	-	-	-	-	-	-	-	-
133	***Verrucaria xyloxena* Norman**	-	-	-	×	-	-	-	-	-	-	-	-	-	-	-	-
Sum of recorded species		43	44	41	45	36	39	24	82	52	40	53	61	46	32	42	54

Eighteen lichen species were recorded for the first time in Svalbard: *Agonimia allobata*, *Atla wheldonii*, *Bacidia herbarum*, *Catolechia wahlenbergii*, *Epigloea soleiformis*, *Lecanora behringii*, *Lepraria subalbicans*, *Leptogium arcticum*, *Pertusaria pseudocorallina*, *Placidiopsis custnani*, *Protothelenella corrosa*, *Spilonema revertens*, *Stereocaulon saxatile*, *Thelocarpon sphaerosporum*, *Toninia coelestina*, *Verrucaria elaeina*, *Verrucaria murina*, and *Verrucaria xyloxena*. Furthermore, one species of lichenicolous fungi, *Pyrenidium actinellum*, was observed for the first time in Svalbard.

Regarding species number in the glacier forelands, the greatest species diversity was observed in the Rieperbreen foreland – 82 species, while the lowest was observed in the Ferdinandbreen foreland – 24 species. Comparing the mature tundra plots, the greatest diversity was exhibited by the plant community in the vicinity of Austre Brøggerbreen – 61 species, while the lowest was in the surroundings of Svenbreen – 32 species (Tab. 1). When comparing the overall species richness between plots located in glacier forelands and plots designated in mature tundra, the species richness of mature tundra plots was significantly higher ($Z = 6.799$, $p < 0.05$; Fig. 2).

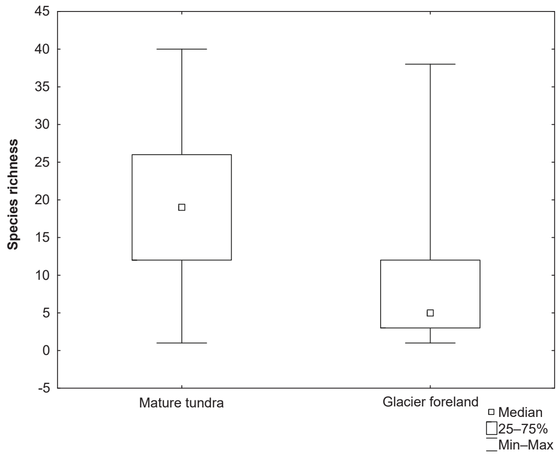

Fig. 2 The difference ($p < 0.05$) in species richness between plots located in mature tundra and glacier forelands.

The same pattern was observed in all study areas: species richness gradually increased from the glacier forehead to the mature tundra surrounding the glacier foreland. Plots localized near the glacier forehead or in the vicinity of glacier-fed rivers showed the lowest species number, while plots located in mature tundra and in the terminal part of forelands showed the highest, reaching as many as 40 species (Fig. 3).

Comparing the overall species number between Kongsfjord and Isfjord, the analysis performed showed no differences ($Z = -1.648$, $p > 0.05$). Similarly, the analysis showed no differences when analyzing the number of species between the mature tundra of Kongsfjord and Isfjord ($Z = -0.586$, $p > 0.05$). Nevertheless, the differences were significant when analyzing the number of species occurring in glacier forelands among the above-mentioned locations ($Z = -2.164$, $p < 0.05$). The species number in Kongsfjord forelands was significantly lower than in Isfjord forelands: mean species number per plot was 7 and 10, respectively. In the analysis of species richness between particular forelands, differences were observed only between certain studied forelands (Fig. 4). The differences were significant for: Austre Lovénbreen and Austre Brøggerbreen ($Z = 3.174$, $p < 0.05$); Austre Lovénbreen and Vestre Brøggerbreen ($Z = 3.433$, $p < 0.05$); Midtre Lovénbreen and Vestre Brøggerbreen ($Z = 3.177$, $p < 0.05$); Austre Brøggerbreen and Rieperbreen ($Z = 5.022$, $p < 0.001$); Vestre Brøggerbreen and Rieperbreen ($Z = 5.069$, $p < 0.0001$); and Rieperbreen and Ferdinandbreen ($Z = 4.545$, $p < 0.0001$). There were no significant differences in species richness among plots located in mature tundra surrounding any particular glacier.

Differences in lichen composition among study areas were presented as the results of NMDS plots for glacier forelands and mature tundra separately (Fig. 5, Fig. 6), followed by one-way PERMANOVA (Tab. 2) and species indicator analyses (Tab. 3, Tab. 4).

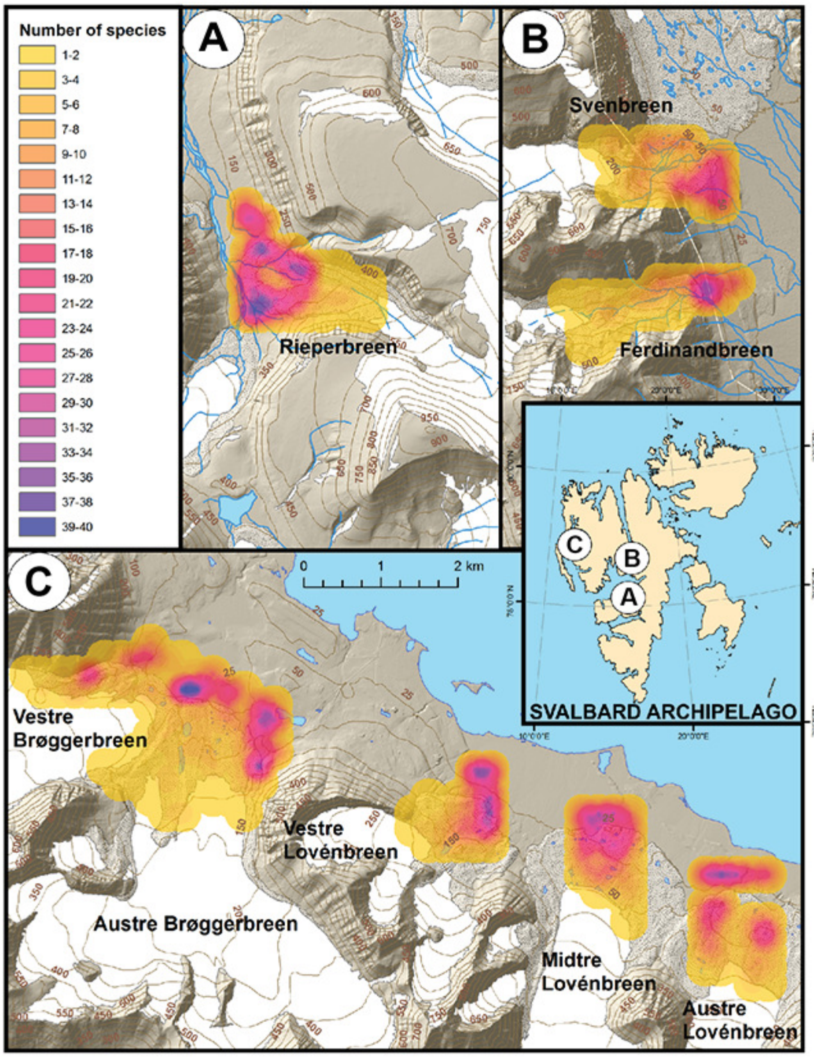

Fig. 3 Species richness of study areas. Isfjord: (**A**) Rieperbreen, (**B**) Ferdinandbreen and Svenbreen; Kongsfjord: (**C**) Austre and Vestre Brøggerbreen, Austre, Midtre, and Vestre Lovénbreen.

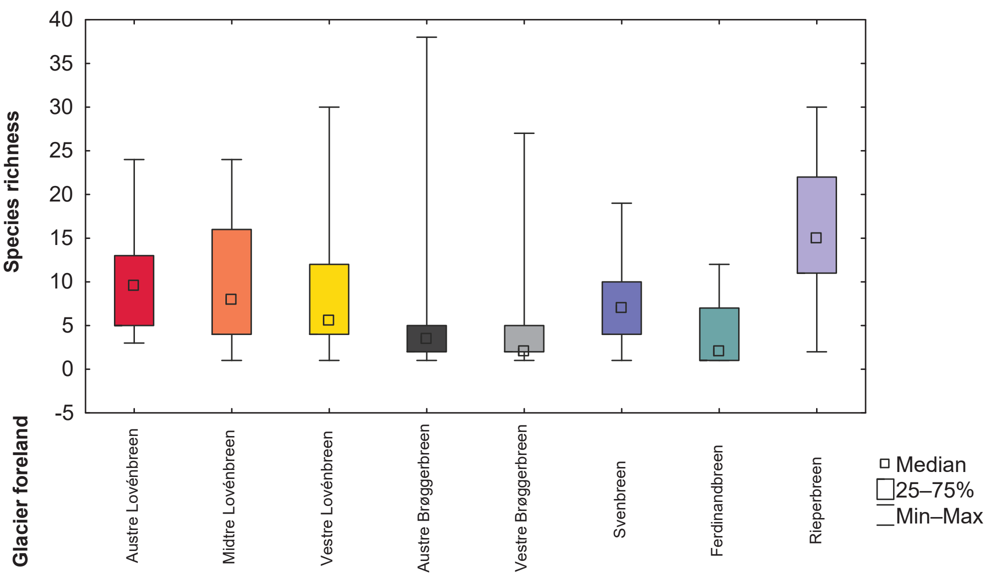

Fig. 4 The differences in species richness among forelands studied (Kruskal–Wallis analysis: chi-square = 40.4, p = 0.00001).

With respect to both the forelands studied and the mature tundra in their vicinity, significant differences in lichen composition were observed between Kongsfjord and Isfjord (Tab. 2).

Analyses comparing the species composition in glacier forelands indicated significant differences among nearly all forelands studied (Fig. 5, Tab. 2). The only exception were the forelands of Austre Brøggerbreen and Vestre Brøggerbreen, between which no difference was recorded (Fig. 5, Tab. 2, Tab. 3). Rieperbreen foreland differed the most within all forelands and showed the highest species individuality (Fig. 5, Tab. 3). Regarding the forelands of Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen, several species were recorded as common to all of these forelands (Tab. 3). A similar trend was observed for the forelands of Ferdinandbreen and Svenbreen (Tab. 3). When

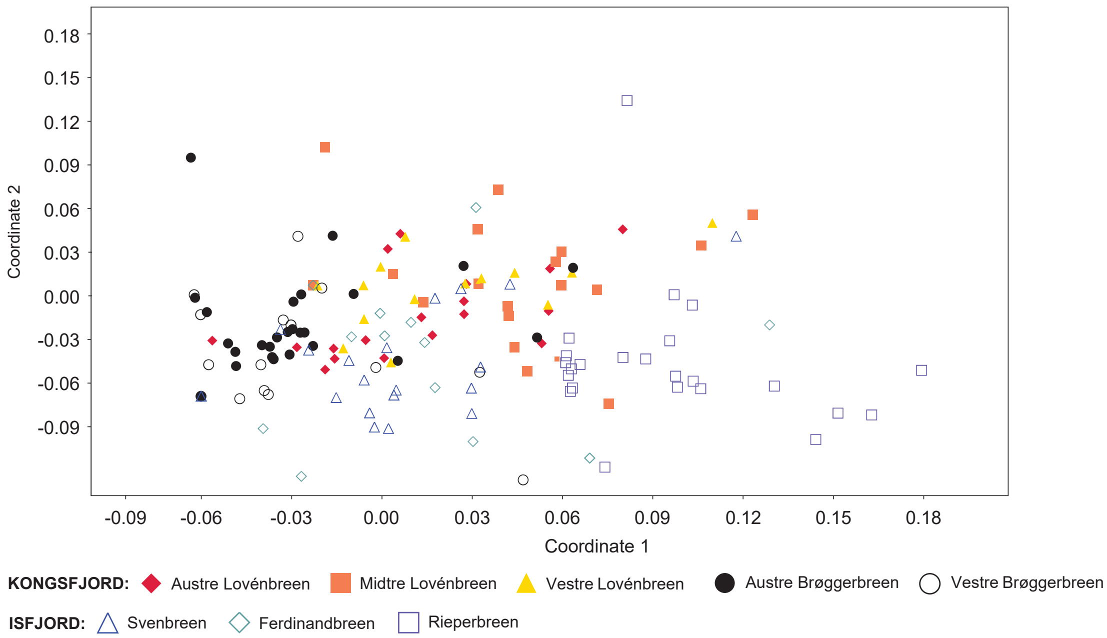

Fig. 5 NMDS analysis of plots located in the glacier forelands (with the Morisita index as a dissimilarity measure). The first axis (Coordinate 1) explains 35% of the variability and the second (Coordinate 2) explains 20%.

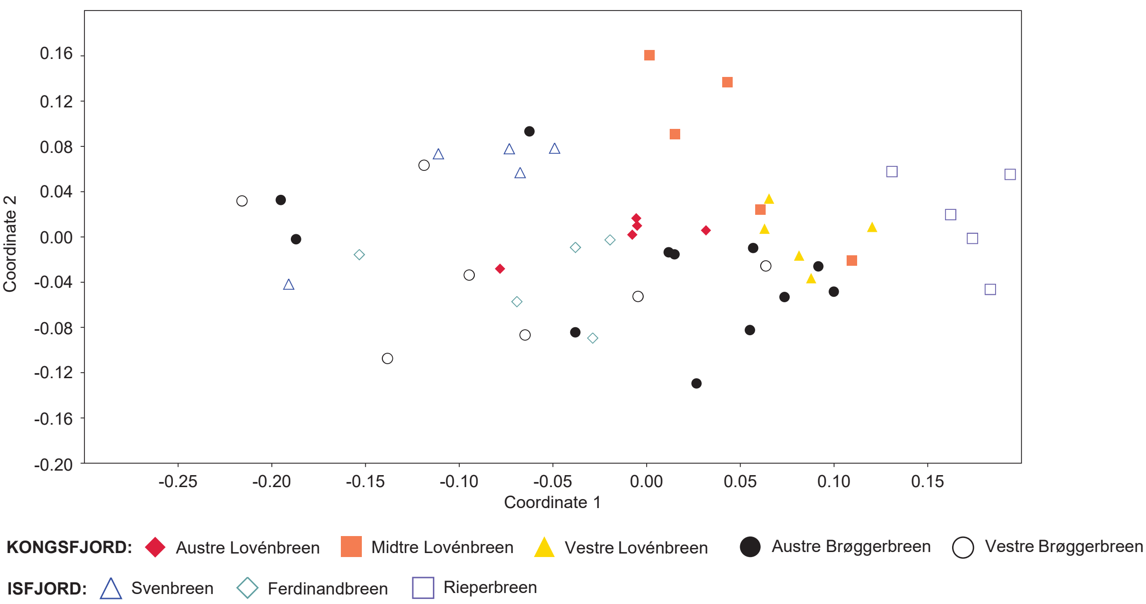

Fig. 6 NMDS analysis of plots located in the mature tundra (with the Bray–Curtis index as a dissimilarity measure). The first axis (Coordinate 1) explains 52% of the variability and the second (Coordinate 2) explains 12%.

Tab. 2 Results of one-way PERMANOVA with sequential Bonferroni significance.

Differences in lichen composition between:	One-way PERMANOVA				Sequential Bonferroni significance; *p*
	Total sum of squares	Within-group sum of squares	*F*	*p*	
Kongsfjord and Isfjord mature tundra	11.52	10.66	3.757	0.001	0.001
Kongsfjord and Isfjord glacier forelands	42.54	37.99	18.79	0.001	0.001
Mature tundra in front of each glacier foreland	11.85	7.428	3.486	0.001	Austre Brøggerbreen and Svenbreen, Ferdinandbreen: 0.001; Vestre Brøggerbreen and Svenbreen: 0.001
All studied glacier forelands	48.65	29.24	12.44	0.001	Austre Brøggerbreen and Vestre Brøggerbreen: 0.455; other forelands: <0.01

Tab. 3 Results of indicator species analysis with Pearson's phi coefficient values for foreland plots. The species characterized for each particular foreland are in bold.

	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
Austre Lovénbreen	*A. gelatinosa*	0.507	*C. delisei*	0.491	*B. ammiospila*	0.341
	A. wheldonii	0.636	*O. frigida*	0.629	*F. bryospila*	0.444
	L. ramulosa	0.664	*P. didactyla*	0.403	*L. epibryon*	0.418
	M. microcarpa	0.59	*P. gothica*	0.613	*P. sendtneri*	0.756
	R. ceranisca	0.854	*R. turfacea*	0.447		
	S. geophana	**0.586**				
	S. alpinum	0.697				
	T. aromatica	0.615				
Midtre Lovénbreen	*A. gelatinosa*	0.507	*C. delisei*	0.491	*B. bagliettoana*	0.404
	A. wheldonii	0.636	*H. pollinii*	0.491	*F. bracteata*	0.427
	B. ementiens	0.628	*O. frigida*	0.629	*F. bryospila*	0.444
	C. pocillum	0.7	*P. gothica*	0.613	*L. epibryon*	0.418
	L. ramulosa	0.664	*R. turfacea*	0.447	*P. sendtneri*	0.756
	M. microcarpa	0.59	*S. rivulorum*	0.544		
	O. androgyna	0.698				
	S. alpinum	0.697				
Vestre Lovénbreen	*A. gelatinosa*	0.507	*C. delisei*	0.491	*B. bagliettoana*	0.404
	A. wheldonii	0.636	*H. pollinii*	0.491	*B. subduplex*	0.34
	M. microcarpa	0.59	*L. cristatum*	0.429	*F. bryospila*	0.444
	S. alpinum	0.697	*R. turfacea*	0.447	*L. epibryon*	0.418
	T. aromatica	0.615	*S. rivulorum*	0.544	*P. sendtneri*	0.756
Austre Broggerbreen	*A. wheldonii*	0.636	*L. cristatum*	0.429	*P. sendtneri*	0.756
	R. ceranisca	0.854				
Vestre Broggerbreen	*A. wheldonii*	0.636	*L. cristatum*	0.429	*P. sendtneri*	0.756
	R. ceranisca	0.854	*S. rivulorum*	0.544		
Svenbreen	*L. ramulosa*	0.664	*P. gothica*	0.613	***F. bracteata***	**0.427**
	M. microcarpa	0.59	*R. turfacea*	0.447	*L. epibryon*	0.418
	O. androgyna	0.698	*S. rivulorum*	0.544	*P. sendtneri*	0.756
	R. ceranisca	0.854			*S. terrestre*	0.4
	T. aromatica	0.615				
Ferdinandbreen	*O. androgyna*	0.698	*P. gothica*	0.613	*L. epibryon*	0.418

Tab. 1 Continued

	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
	T. aromatica	0.615	***R. turfacea***	**0.447**	*P. sendtneri*	0.756
Rieperbreen	***B. rufus***	**0.506**	*B. papillata*	0.454	*A. punctata*	0.328
	B. ementiens	0.628	*O. frigida*	0.629	*B. ammiospila*	0.341
	B. insignis	**0.566**	*P. didactyla*	0.403	*B. subduplex*	0.34
	C. borealis	**0.716**	***P. sphinctrinoidella***	**0.346**	***L. coralloideum***	**0.346**
	C. caesiorufella	**0.447**	***S. saxatile***	**0.346**	*S. terrestre*	0.4
	C. chlorophaea	**0.529**	***S. sychnogonoides***	**0.447**		
	C. pocillum	0.7				
	C. pyxidata	**0.675**				
	F. caesioatra	**0.645**				
	M. incrassata	**0.529**				
	P. nimbosa	**0.479**				
	P. pezizoides	**0.959**				
	P. tenue	**0.763**				
	S. bispora	**0.529**				
	S. glareosum	**0.474**				
	S. paschale	**0.632**				

Tab. 4 Results of indicator species analysis with Pearson's phi coefficient values for mature tundra plots. The species characterized for each particular mature tundra location are in bold.

	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
Austre Lovénbreen	*B. bagliettoana*	0.878	*B. tetraspora*	0.741	*P. tiroliensis*	0.733
	H. pollinii	0.82			*P. nimbosa*	0.705
	L. epibryon	0.961			*M. microcarpa*	0.803
					C. pocillum	0.81
					L. ramulosa	0.958
					C. delisei	0.915
Midtre Lovénbreen	*B. bagliettoana*	0.878	*S. alpinum*	0.812	*L. furfurascens*	0.651
	H. pollinii	0.82	*B. tetraspora*	0.741	*P. tiroliensis*	0.733
	L. epibryon	0.961			*M. microcarpa*	0.803
					C. pocillum	0.81
					L. ramulosa	0.958
					C. delisei	0.915
Vestre Lovénbreen	*B. bagliettoana*	0.878	*S. alpinum*	0.812	*L. furfurascens*	0.651
	H. pollinii	0.82	*B. tetraspora*	0.741	*P. nimbosa*	0.705
					M. microcarpa	0.803
					C. pocillum	0.81
					L. ramulosa	0.958
					C. delisei	0.915
Austre Brøggerbreen					*P. nimbosa*	0.705
					L. ramulosa	0.958
					C. delisei	0.915
Vestre Brøggerbreen					*C. tenax*	0.73
					L. ramulosa	0.958
					C. delisei	0.915

Tab. 4 Continued

	$p \le 0.001$	phi	$0.001 \le p < 0.01$	phi	$0.01 \le p < 0.05$	phi
Svenbreen	*L. epibryon*	0.961	*F. bracteata*	0.779	*P. tiroliensis*	0.733
			S. rivulorum	0.761	*C. tenax*	0.73
					M. microcarpa	0.803
					C. pocillum	0.81
					L. ramulosa	0.958
Ferdinandbreen	***T. coelestina***	**0.806**	*F. bracteata*	0.779	*B. papillata*	0.668
	L. epibryon	0.961	*S. rivulorum*	0.761	*C. pyxidata*	0.666
					P. tiroliensis	0.733
					C. tenax	0.73
					M. microcarpa	0.803
					C. pocillum	0.81
					L. ramulosa	0.958
					C. delisei	0.915
Rieperbreen	***P. pseudocorallina***	**0.956**	***P. pezizoides***	**0.775**	***P. tenue***	**0.635**
	C. borealis	**0.902**	***C. caesiorufella***	**0.757**	***N. expallidum***	**0.632**
	S. paschale	**0.894**	***C. macroceras***	**0.735**	***B. papillata***	**0.668**
	L. coralloideum	**0.769**	*S. alpinum*	0.812	***C. pyxidata***	**0.666**
			B. tetraspora	0.741	*P. nimbosa*	0.705
					C. tenax	0.73
					C. pocillum	0.81
					C. delisei	0.915

analyzing differences in species composition between mature tundra in the vicinity of each foreland, significant differences were observed between Austre Brøggerbreen and Svenbreen; Austre Brøggerbreen and Ferdinandbreen; and Vestre Brøggerbreen and Svenbreen (Fig. 6, Tab. 2, Tab. 3). With respect to the mature tundra of other glacier forelands, no significant differences in lichen composition were found and the same species were dominant in the majority of locations (Tab. 2, Tab. 4).

The occurrence of cyanolichens and chlorolichens

The species number of cyanolichens recorded in glacier forelands as well as in mature tundra was significantly lower compared to chlorolichens (respectively: $Z = 5.044$, $p < 0.0001$ and $Z = 4.299$, $p < 0.0001$; Fig. 7). The number of cyanolichen species were higher in mature tundra than in glacier forelands ($Z = 6.694$, $p < 0.0001$; Fig. 7), however there was no difference in their percentage cover between mature tundra and glacier forelands ($Z = -0.078$, $p > 0.05$; Fig. 8). The taxa with green algae components showed similar patterns in terms of species number ($Z = 6.592$, $p < 0.0001$; Fig. 7) and percentage cover ($Z = 0.196$, $p > 0.05$; Fig. 8).

Discussion

Species richness and composition of lichen communities

Lichens are effective colonizers during primary succession in the glacier forelands [1,4]. The substantial number of recorded species as well as their frequency in each foreland would seem to confirm the pioneering abilities of lichens (Tab. 1) [19]. Regarding species presence, the glacier forelands that offer similarly harsh habitat conditions

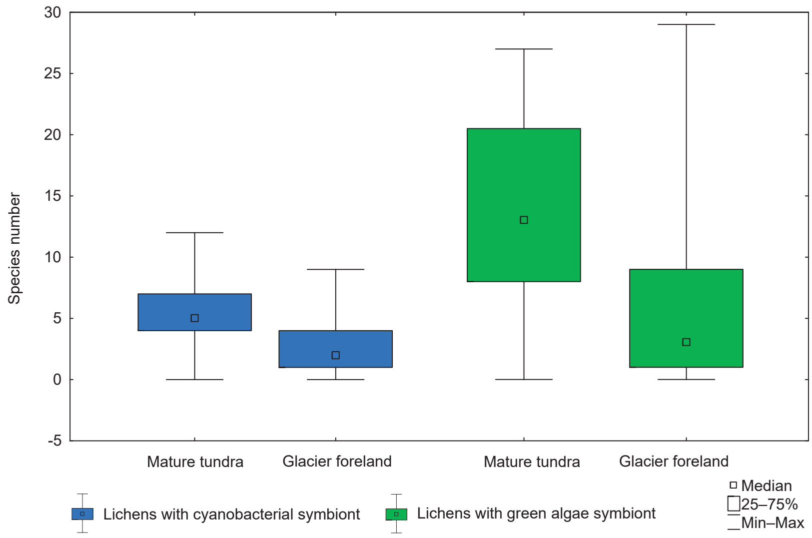

Fig. 7 Number of cyanolichens and chlorolichens in the plots of glacier forelands and mature tundra.

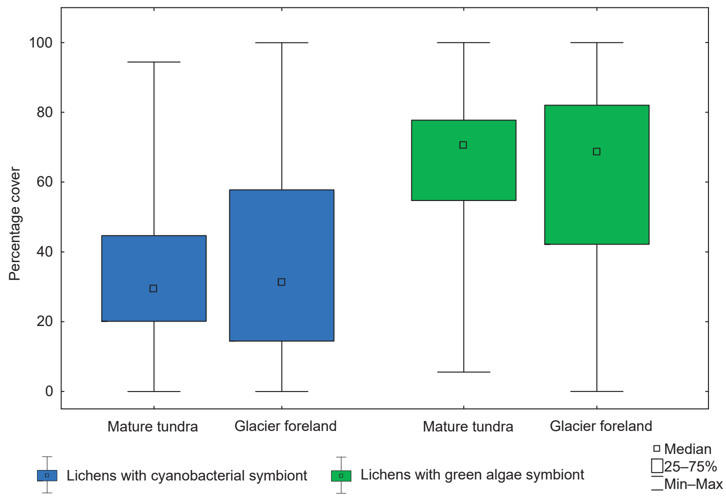

Fig. 8 Percentage cover of cyanolichens and chlorolichens in the plots of glacier forelands and mature tundra.

appear to possess comparable lichen composition; however, the present study did not fully confirm this statement. Significant differences were observed among the glacier forelands studied (Tab. 2).

Considering the lichen composition of communities surrounding the glacier forelands as climax communities, a gradual change in species richness and percentage cover is observed from the glacier foreheads to the ends of the forelands where the near-climax communities are located. A similar pattern was observed in the studies on primary succession on Signy Island by Favero-Longo et al. [37]. Cryptogam species such as lichens and bryophytes which dominate in the colonization process in the forelands modify the edaphic and microclimatic conditions and favor the growth of other taxa that create the next successional community and may replace previous species by competition [1]. The results of the present study showed that the species richness of glacier forelands differs from the species richness of mature tundra. This confirmed our initial hypothesis and indicated that the communities developing at the ends of glacier forelands had not yet reached the climax stage exhibited by mature tundra. Several species were recorded in all mature tundra areas studied; those associated with plant debris and bryophytes presence were: *Athallia pyracea*, *Biatora ementiens*, *Rinodina turfacea*, and *Parvoplaca tiroliensis*. Other species such as *Cetrariella delisei*, *Cladonia pocillum*, *Lecidea ramulosa*, *Ochrolechia frigida*, *Polyblastia gothica*, *Polyblastia sendtneri*, and *Rostania ceranisca* were mainly recorded on soil surface. According the CAVM [38], Jónsdóttir [39], and Elvebakk [40], the mature tundra of Kongsfjord differs from that of Isfjord. Kongsfjord represents northern Arctic tundra [39] and prostrate dwarf-shrub/herb tundra belonging to Subzone B, where the dominant alliance is *Luzulion nivalis* in which species of *Thamnolia* and *Flavocetraria* are common [38,40]. Isfjord represents middle Arctic tundra [39] and prostrate/hemiprostrate dwarf-shrub tundra [38] localized in Subzone C, in which *Peltigera aphthosa*, *Cetrariella deliseii*, *Stereocaulon rivulorum*, *Solorina* sp., and *Thamnolia* sp. commonly occur [38,40]. The statistical analysis showed differences in species composition between Kongsfjord and Isfjord mature tundra; however, further analysis indicated significant differences in mature tundra composition only between Austre Brøggerbreen and Svenbreen, Austre Brøggerbreen and Ferdinandbreen, and Vestre Brøggerbreen and Svenbreen (Tab. 2). This was caused by high participation of *Fulgensia bracteata*, *Stereocaulon rivulorum*, *Lecanora epibryon*, and *Mycobilimbia microcarpa* in the mature tundra in front of the Svenbreen and Ferdinandbreen forelands. These species were either not present at all or were rarely recorded in front of the Austre Brøggerbreen and Vestre Brøggerbreen forelands (Tab. 1, Tab. 4). The dominance of *Fulgensia bracteata* and *Lecanora epibryon* in the vicinity of the Svenbreen and Ferdinandbreen forelands was observed by Redchenko et al. [30]. There were no statistical differences in species composition among mature tundra surrounding other glacier forelands (Tab. 2). The presence of the following indicator species was responsible for this similarity: *Cetrariella delisei*, *Cladonia pocillum*, and *Lecidea ramulosa* (Tab. 4). These species are frequently observed and dominate in climax plant communities on Svalbard [29].

The results only partly confirmed our hypothesis that assumed no differences in lichen composition and species richness among the glacier forelands studied (Fig. 4). The foreland of Rieperbreen seems to be unique in terms of lichen diversity. The high species diversity of this foreland was observed in previous research conducted by Wietrzyk et al. [4]. It may be suggested that the location of Rieperbreen in the Isfjord, which is the warmest and driest area of Svalbard [41–43], may contribute to higher species diversity. Nevertheless, compared to Rieperbreen, the Ferdinandbreen foreland located in an area exposed to similar climatic conditions showed the lowest species richness. A similar trend was observed between the Lovénbreen and Brøggerbreen forelands, located in the Kongsfjord area; however, differences in species richness between certain forelands were noted. This may suggest that apart from the climatic conditions of the fjord, characteristics of the foreland substrate may play an important role in species presence, e.g., substrate acidity, which is strongly correlated with the distribution of lichens and even whole lichen communities [44]. Studies by Wietrzyk et al. [45] in the Irenebreen forelands demonstrated that apart from soil pH, distance from the glacier forehead and total nitrogen content also affects species occurrence and vegetation development. The impact of distance from the glacier forehead on lichen colonization was also reported by Rodriguez et al. [46] in the South Shetlands Islands. Nevertheless, further research is necessary to elucidate the factors influencing lichen occurrence in glacier forelands across broader areas, including the investigation of more than one foreland.

Within all recorded taxa, the following species were present in all studied areas, both in glacier forelands and mature tundra: *Cladonia pocillum*, *Parvoplaca tiroliensis*, *Polyblastia gothica*, *Polyblastia sendtneri*, and *Rostania cerenisca* (Tab. 1). Nevertheless, their percentage cover in the species composition of particular glaciers and mature tundra differs (Tab. 3, Tab. 4). *Polyblastia sendtneri* was an indicator species for each foreland except that of Rieperbreen where it was only occasionally recorded. This species tolerates a wide pH range and occurs on acidic and slightly alkaline, barren substrata [25,47], while *Cladonia pocillum* prefers intermediate substrata pH [47]. This species served as an indicator species of the majority of mature tundra areas studied, except for the mature tundra in front of Austre and Vestre Brøggerbreen, where the taxon was only infrequently present. This may be related to the rather alkaline substrate of mature tundra of the Austre and Vestre Brøggerbreen forelands [48]. Similarly, *Rostania ceranisca* grows on subacid to subneutral substrata [47]. Apart from being an indicator species of Austre and Vestre Brøggerbreen, its occurrence was also connected to the forelands of Austre Lovénbreen and Svenbreen (Tab. 1). According to Olech and Słaby

[49], *Polyblastia gothica* prefers water-logged areas and is most frequently found at the base of long-lasting snow patches. In our study areas, it was a commonly recorded species and no such relationship was observed.

Various analyses showed significant differences in species composition of the forelands studied, except for Austre and Vestre Brøggerbreen (Tab. 2). Four lichens were distinguished as indicator species for these forelands: *Atla wheldonii*, *Lathagrium cristatum*, *Polyblastia sendtneri*, and *Rostania ceranisca*. Within these species, *Atla wheldonii* was an indicator species for all of the forelands located in the Kongsfjord area, growing in acidic and subneutral soil [47,50]. However, *Lathagrium cristatum* occurs only in basic substrata (Tab. 3) [47], which may suggest the basic characteristics of the substrate of Austre and Vestre Brøggerbreen forelands, confirmed by Zhang et al. [48]. With respect to other forelands, their substrates seem to have neutral characteristics with a tendency toward greater acidity, as evidenced by the presence of lichens inhabiting subacidic and acidic habitats such as: *Agonimia gelatinosa* (indicator species for forelands of Austre, Midtre, and Vestre Lovénbreen) [47], *Steinia geophana* (distinctive taxon for Austre Lovénbreen foreland) [24,47], and *Ochrolechia androgyna* (a species that contributed significantly to the lichen composition of the forelands of Midtre Lovénbreen, Ferdinandbreen, and Svenbreen) [47]. Species recorded in the Rieperbreen foreland are also connected with acidic and subacidic soil or with the presence of plant debris (Tab. 3) [24,47]. Nevertheless, the Rieperbreen foreland was the one with the most unique species composition in comparison to the other areas studied (Tab. 3) making it an area that warrants further detailed research.

The occurrence of cyanolichens and chlorolichens

Our results oppose the hypothesis that the number and percentage cover of lichens with cyanobacterial symbionts are higher in the forelands than in mature tundra, while the number and percentage cover of lichens with green algae components show the opposite pattern (Fig. 5, Fig. 6). This indicated that possession of cyanobacterial symbionts is not indispensable to the colonization of glacier forelands. In contrast to chlorolichens, cyanolichens have the ability to conduct net photosynthesis in the presence of elevated water content and stabilize the soil surface [51]. They are therefore able to colonize the wet and unstable surfaces of forelands in contrast to chlorolichens, which do not have the ability to bind nitrogen but are able to conduct photosynthesis at lower water content in drier sites where the process may be activated by high air humidity [51]. Indeed, the ability to bind nitrogen is a very important facet to the colonization and growth of organisms, especially in the early stages of primary succession [52]. Apart from cyanobacterial lichens, the free-living heterocystic cyanobacteria (e.g., *Nostoc* sp., *Scytonema* sp.), which are also BSC components, play an important role in nitrogen fixation and facilitation of the primary succession process [53]. The importance of BSCs in organic matter accumulation and nitrogen fixation was reported in previous studies by Yoshitake et al. [52] and Breen and Lévesque [11,54]. Given that the percent cover of BSCs significantly influences the general vegetation distribution across the foreland [11,54], it may also be assumed to affect the occurrence of lichens.

Conclusions

This study contributes to the understanding of lichen colonization and species composition in the Arctic region, focusing on glacier forelands and the mature tundra that surrounds them. Both in forelands and in mature tundra, the most dominant group was chlorolichens, not cyanolichens. Altogether, 133 species of lichens and one lichenicolous fungus were found in the study areas. Furthermore, 18 species of lichens and one species of lichenicolous fungus were recorded for the first time in the Svalbard. The high number of lichen species that were new to Svalbard indicates the need for further research on the biodiversity of lichens in the Arctic. In particular, the glacier forelands deserve attention if further warming of the climate continues, as species sensitive to competition from vascular plants will move into habitats in the vicinity of glaciers [18]. Thus, long-term monitoring of changes in lichen biota in the glacier forelands will provide valuable information on the impact of global warming on lichen communities in the Arctic. Given that this research did not include epilithic lichen biota, the overall lichen diversity of the study areas is expected to be higher. We suggest that further research is needed to better clarify the factors determining the differences in species occurrence and primary succession patterns among study areas.

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