



Mosses and liverworts in the glacier forelands and mature tundra of Svalbard (High Arctic): diversity, ecology, and community composition

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Abstract: The harsh polar environment results in the dominance of mosses and liverworts in tundra communities. To date, very little research has been devoted to the diversity and ecology of these groups in the High Arctic. The aim of this research was to investigate the diversity and community composition of mosses and liverworts in various stages of the ecogenesis of Svalbard ecosystems, and to identify environmental factors affecting species distribution. In 2017, 270 plots were established in a grid in eight glacier forelands and the mature tundra surrounding them. Within these plots, the percentage cover of mosses and liverworts was investigated. In 201 plots, soil samples were taken and environmental data (aspect, bare ground cover, biological soil crust cover, distance from the glacier forehead, rock cover, slope, time elapsed since the glacier's retreat, Topographic Wetness Index, and total insolation) were



obtained. In total, 105 species were recorded. Species number and composition depended on effects of both habitat type (foreland and mature tundra) and the geographical locations of glaciers, while species cover was also associated with the interaction between those factors. The following factors affected species distribution: cover of bare ground and vascular plants, distance from the glacier forehead, soil conductivity, contents of total organic carbon and total nitrogen in soil, K^+ content, silt and sand contents, soil pH, time elapsed since the glacier's retreat, and total insolation. In the glacier forelands, mosses and liverworts are less exposed to competition from other species. Therefore, in the future, if global warming progresses at its current rate, forelands may serve as important species refugia.

Key words: Arctic, Spitsbergen, bryophytes, cryptogams, plant-soil interactions, species diversity.

Introduction

The harsh environment of the Arctic results in the dominance of cryptogamic species in tundra communities. Cryptogams are essential components contributing significantly to the diversity of plant communities. They play many important roles in Arctic ecosystems, e.g. participation in the carbon cycle (Rydin and Jeglum 2006), nitrogen fixation (Solheim *et al.* 1996), hydrology regulation (Beringer *et al.* 2001), peat accumulation, development of microtopography (Turetsky *et al.* 2012), and permafrost preservation (Yoshikawa *et al.* 2003). Among the numerous representatives of cryptogams are mosses and liverworts, which are extremely abundant in many high-latitude ecosystems. However, they were recognised only few decades ago as essential components of tundra communities (Turetsky *et al.* 2012).

Apart from mature tundra communities, mosses and liverworts are widespread in recently deglaciated areas of glacier forelands, where habitat conditions limit competition from vascular plants (Wietrzyk *et al.* 2018). Due to their high degree of phenotypic plasticity, tolerance to desiccation, broad response of net assimilation rates to temperature, and capacity for CO_2 assimilation at low temperatures and with exposure to irradiance, they can grow and survive in unfavourable habitats (Turetsky *et al.* 2012), e.g. in areas newly exposed after being covered by ice, where they contribute to initial soil development. Compared to other cryptogams, e.g. lichens, they are characterised by higher growth rates and greater ability to trap wind-blown material. Therefore, they contribute to the accumulation of organic matter in soil, thereby creating conditions favourable for the growth of vascular plants (Smith and Russell 1982). Furthermore, their rhizoids penetrate rocks, accelerating physical and chemical weathering (Hughes 1982; Longton 1988). Because of these features, mosses and liverworts are considered pioneer species.

As indicated by Descamps *et al.* (2017), the Arctic region is a global 'hot-spot' which is changing and warming quicker than other regions of the Earth.

These changes also affect Arctic terrestrial ecosystems and are evidenced by increases in temperature, reductions in the extent of glaciers, melting of permafrost, and increases in the productivity of vegetation (Sturm *et al.* 2001; Ims and Ehrich 2013; Hansen *et al.* 2014). On one hand, mosses and liverworts possess immense colonisation ability; on the other, on-going climate changes causing the expansion and increased growth of vascular plants (Forbes *et al.* 2010) may limit the availability of habitats for them. Walker *et al.* (2006) showed, in standardised warming experiments across the tundra biome, that an increase in temperature reduced cryptogam cover. However, van Wijk *et al.* (2003) suggested that this pattern was less clear for mosses than for lichens. Other studies conducted in the Arctic indicate that moss abundance has either increased over the last decades or remained relatively stable (Hudson and Henry 2009; Prach *et al.* 2010; Amesbury *et al.* 2017). Due to these heterogeneous trends, it appears necessary to capture the variability existing in the process of primary succession, enabling observation of species diversity and the dynamics of the progression from initial to mature tundra communities.

In the Svalbard archipelago, data on mosses and liverworts inhabiting glacier forelands and their surrounding mature communities are limited (Frisvoll and Elvebakk 1996). In south-western Spitsbergen, Kuc (1996) investigated species occurring in the foreland of Werenskiöldbreen. *Sanionia uncinata* (Hedw.) Loeske and species of the family Polytrichaceae, as well as the genera *Bryum* and *Drepanocladus*, were reported in the Kongsfjorden area (Moreau *et al.* 2005, 2008, 2009). Recently, Belkina and Vilnet (2015) analysed some aspects of the development of moss population on Svalbard glaciers, and some species new to records of the Svalbard archipelago were published (e.g. Ellis *et al.* 2016a, 2016b, 2017). However, no detailed research has been conducted with a focus on mosses and liverworts while taking into account species diversity, composition of mature and initial communities, and environmental factors potentially influencing the colonisation of recently deglaciated areas.

Substrate properties are known to be important in the process of primary colonisation by bryophytes. The physical properties of the soil (e.g. moisture, texture) appear to be particularly essential (Gornall *et al.* 2007), as they do more to limit the growth of bryophytes than chemical properties (e.g. nutrient availability) (Skre and Oechel 1981). Absorption of cations contributes to the adaptation of species to substrates; mosses may be dependent on acidity and carbonate and cation contents in the soil (Koedam and Büscher 1983). Nutrients are taken up by bryophytes over their entire surface as well as through the rhizoids (Chapin *et al.* 1987; Büscher *et al.* 1990; Glime 2017). The content of exchangeable cations in the substrate influences the soil pH and affects the availability of cations for bryophytes (Büscher *et al.* 1990; Ketterings *et al.* 2007). For example, acidophilous bryophytes can grow in soil rich in exchangeable aluminium and hydrogen but poor in exchangeable calcium, whereas neutrophils prefer substrates richer in calcium (Büscher *et al.* 1990). As observed

by Rydgren *et al.* (2014) many previous studies on factors which may affect species succession failed to account for various environmental data, resulting in problematic conclusions. Therefore, we decided to analyse multiple biotic and abiotic variables that might potentially influence species distribution, including micro-habitat properties, the presence of vascular plants and biological soil crusts, and physical and chemical soil properties.

The main aim of this research was to investigate the diversity of mosses and liverworts in the foreland of eight glaciers and in the mature tundra in the immediate vicinity. Moreover, we investigated and tested the effect of both habitat type (glacier foreland vs mature tundra) and geographical location of glacier forelands on the number and cover of species and community composition. Finally, we determined environmental factors affecting species distribution. We formulated the following hypotheses: A) habitat type (glacier foreland vs mature tundra) is a more important determinant of species number, species cover and community composition than the geographical location of a particular glacier foreland; B) distribution of mosses and liverworts are mainly dependent on physical soil properties, whereas chemical soil properties and terrain factors play a secondary role.

Material and methods

Study area. — The fieldwork was conducted in the summer of 2017 in the Svalbard archipelago in the forelands of eight glaciers (referred to hereafter as foreland) and in the mature tundra surrounding them (referred to hereafter as tundra). Study areas were located in Spitsbergen in the forelands of the following glaciers: Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, Vestre Lovénbreen, Rieperbreen, Svenbreen, and Ferdinandbreen (Fig. 1). Supplementary Table 1 presents major characteristics of the studied areas in terms of geology, climate, and vegetation.

Data sampling. — In each foreland and surrounding tundra, a series of plots, each 1 m², was established in a square grid (Fig. 1). In total, 270 plots were investigated. In each plot, data on percentage cover of species of mosses and liverworts were compiled. Samples of mosses and liverworts were collected for subsequent laboratory identification in order to meet taxonomical identification requirements. In 201 plots, randomly selected from 270 plots, surface soil samples were taken from under the vegetation to a depth of 10 cm (each sample weighing ca. 300 g). Moreover, for each plot, percentage cover of the following variables was obtained: rock, bare ground, biological soil crusts (BSCs), and vascular plants.

Moss and liverwort identification. — Traditional taxonomical methods and standard light microscopy were used for species identification. The following

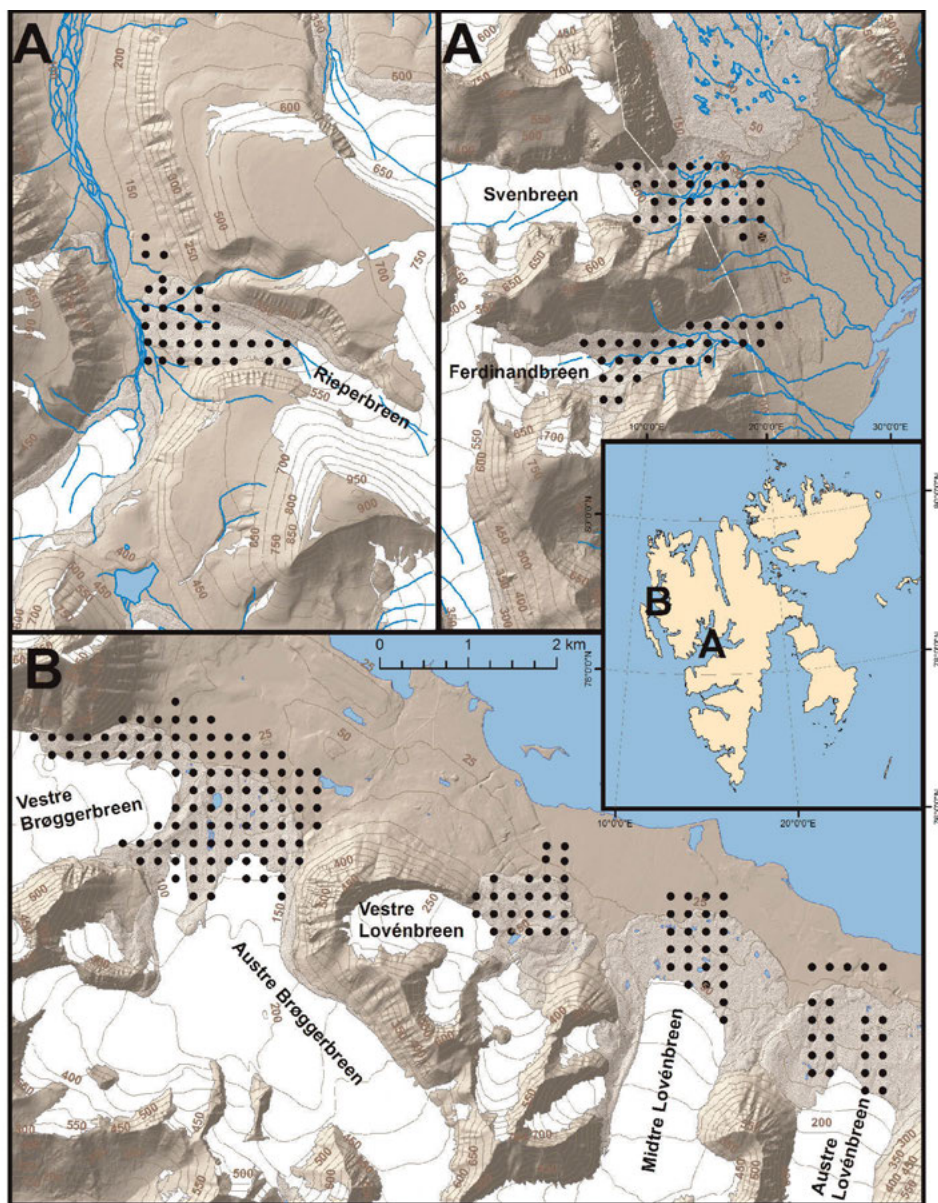


Fig. 1. Location of study areas and sampling plots (black dots). (A): Rieperbreen, Ferdinandbreen and Svenbreen; (B): Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen (© Norwegian Polar Institute 2019; <http://www.npolar.no>).

publications were used for species determination: Damsholt (2002, 2013), Frey *et al.* (2006), Frisvoll and Elvebakk (1996), Nyholm (1987, 1990, 1993, 1998), and Smith (2004). Species nomenclature follows Hill *et al.* (2006) for mosses and Söderström *et al.* (2016) for liverworts. Species samples were deposited in the Herbarium of the Institute of Botany at Jagiellonian University in Kraków.

Spatial analyses. — Spatial data were obtained from open-access databases (Fick and Hijmans 2017; Porter *et al.* 2018) and analysed with SAGA GIS 7.0.0 software (Conrad *et al.* 2015), which enabled us to obtain the following variables for each plot: time elapsed since the glacier's retreat (on the basis of glacier extent in the past), distance to the current glacier forehead, total insolation, slope, aspect, Topographic Wetness Index. To obtain these parameters, Digital Terrain Model, with a resolution of 2 m, was used (Porter *et al.* 2018), with the following tools: Potential Incoming Solar Radiation (Conrad *et al.* 2015) to obtain information about the amount of light reaching the plot and Basic Terrain Analysis (Conrad *et al.* 2015) to obtain basic parameters based on the Digital Terrain Model, such as slope, aspect, and Topographic Wetness Index (TWI). Total insolation included direct and diffuse insolation. Direct insolation was a combination of the solar zenith angle, solar flux at the top of the atmosphere, atmospheric transmittance, solar illumination angle on the slope, and sky obstruction; diffuse insolation comprised solar geometry, elevation, and the scattering and absorbing characteristics of the atmosphere (Luković *et al.* 2015). TWI, hydrologically-based topographic index which determines the tendency of an area to accumulate water, was defined as $TWI = \ln (SCA/\tan \phi)$, where SCA was the Specific Catchment Area, ϕ was the slope angle, and uniform soil properties were assumed (Mattivi *et al.* 2019).

Soil samples analyses. — Soil samples were oven-dried at 30°C for 24 h, subsequently gently crushed and sieved using a 2 mm sieve to remove the coarse material (fraction > 2 mm). All laboratory analyses (except particle-size distribution) were conducted on fine earth material (fraction < 2 mm). Contents of total carbon and total nitrogen (TN) were analysed in triplicate via gas chromatography using a CHN elemental analyser (Vario Micro Cube) and then averaged. Content of total carbon in non-calcareous samples was treated as total organic carbon (TOC). Content of carbonates was measured using the volumetric calcimeter method (Loeppert and Suarez, 1996). Content of TOC in calcareous samples was calculated by subtraction of carbon content in carbonates from total carbon content. Concentration of exchangeable cations such as Ca^{2+} , Mg^{2+} , K^{+} , Na^{+} was determined via flame atomic absorption spectrometry (FAAS) after extraction with 1M ammonium acetate at pH=7. Content of plant-available phosphorus (P_2O_5), magnesium (MgO), and potassium (K_2O) was determined using the colorimetric method. Soil pH was measured in distilled water in a 1:2.5 soil/water ratio using a glass electrode (Thomas 1996). Electrical conductivity of soil water extracts (1:2.5 soil/water ratio) was measured using a HM Digital COM-80 Electrical Conductivity Tester after 24 h when the solution was in equilibrium with the soil and therefore stable. Particle-size distribution was conducted on fine soil material below 1 mm using laser diffraction via the use of a Malvern Mastersizer 3000 instrument after a 3-minute ultrasound dispersion of the sample.

Statistical analyses. — Visualisation of species number in all study areas, based on 270 plots, was presented on a map generated with the kernel distance

matrix function (search radius = 200 m; function = triangular Kernel; 10 m pixel with decay ratio = 0) in QGIS 3.4.3 software (QGIS Development Team 2019). As a result, raster heatmaps of species numbers were created. The colour range scale was adjusted using percentiles of raster values.

Using STATISTICA 13 software (StatSoft, Tulsa, OK, USA), two-way analysis of variance (habitat type $\times$ location), followed by Tukey's (HSD) test, was performed to reveal significant differences in species number and species cover between habitat types (foreland and tundra) as well as between geographical locations (Rieperbreen, Ferdinandbreen, Svenbreen, Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen and Vestre Lovénbreen). Prior to the analysis, the normality of the distribution was verified using the Kolmogorov-Smirnov test; Levene's test was performed to assess the equality of variances. Data that did not meet the assumptions were Box-Cox transformed to obtain a normal distribution of the transformed data and a constant variance.

Two-way PERMANOVA (habitat type $\times$ location; 999 permutations) was used to investigate significant differences in species composition between habitat types (foreland and tundra), and between locations (Rieperbreen, Ferdinandbreen, Svenbreen, Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen and Vestre Lovénbreen). Subsequently, indicator species analysis measured with Pearson's phi coefficient was applied to identify species related to certain foreland and to particular tundra. The analyses were carried out using PAST 3.10 (Hammer *et al.* 2001) and CRAN R-3.4.2 (R Core Team, 2013).

Canonical correspondence analysis (CCA), applied in order to determine which environmental variables were related to cover of mosses and liverworts as well as to plots, was performed using CANOCO 4.5 (ter Braak and Šmilauer 2002) on 201 plots for which 26 environmental variables were obtained. Previously, square-root transformation of species data had been performed to reduce the dominant contribution of abundant species. An automatic procedure for forward selection of the explanatory variable from the set of all available variables was applied; rare species were downweighted. A Monte Carlo permutation test was used to assess the statistical significance of relationships between species and environmental factors. Plots without species cover were excluded from the above-mentioned analyses.

Results

Number and cover of species and community composition in forelands and tundra at different locations. — In total, 105 species were identified: 85 species of mosses and 20 species of liverworts (Supplementary Table 2). The highest number of species in plots located in tundra was recorded in the surroundings of Austre Brøggerbreen (28 species), the lowest in the vicinity of

Table 1

The results of two-way ANOVA for the effects of habitat type (foreland vs tundra) and geographical location (glacier foreland) on number and cover of species; and two-way PERMANOVA for the effects of habitat type (foreland vs tundra) and geographical location (glacier foreland) on species composition. Significant effects ($p < 0.05$) are shown in bold.

Variable	Location		Habitat type		Location x Habitat type	
	F	p	F	p	F	p
Species number	5.25	<0.001	29.44	<0.001	1.92	0.067
Species cover	9.66	<0.001	116.6	<0.001	3.52	0.001
Species composition	3.67	<0.001	13.78	<0.001	13.27	1.00

Midtre Lovénbreen (8 species). In terms of forelands, the highest number of species was recorded in that of Rieperbreen (41 species), the lowest in that of Svenbreen (18 species).

Figure 2 presents species number across the studied areas. Both habitat type and geographical location had significant effects on species number (Table 1; Fig. 3). Rieperbreen tundra showed the greatest species diversity, Svenbreen foreland the least (Fig. 3). The species number at the Rieperbreen location was significantly higher compared to other locations, with the exception of Austre Lovénbreen and Ferdinandbreen. The Svenbreen location was characterised by a significantly lower species number compared to Austre Lovénbreen and Rieperbreen; the other locations did not differ significantly in terms of species number (Table 1; Fig. 3).

Two-way ANOVA revealed that habitat type and location had a significant effect on species cover; however, significant interaction between location and habitat type was also recorded (Table 1; Fig. 3). The plots located in tundra were characterised by slightly greater species cover than foreland plots regardless of location; however, the differences between the tundra plots were not always significant (habitat type $\times$ location interaction) (Fig. 3). The greatest significant differences in species cover were observed between plots located in the tundra of Vestre Lovénbreen, Rieperbreen, Svenbreen, Ferdinandbreen and those located in the forelands of Austre and Vestre Brøggerbreen, Midtre Lovénbreen, and Ferdinandbreen (Fig. 3).

Two-way PERMANOVA showed that habitat type and location had a significant effect on community composition; however, interaction between these factors was not significant (Table 1). Indicator species analysis identified species associated with a particular habitat type and location (Tables 2, 3). As shown by indicator species analysis, dissimilarity in species composition of forelands was connected with the presence of following distinctive species: *Encalypta procera*

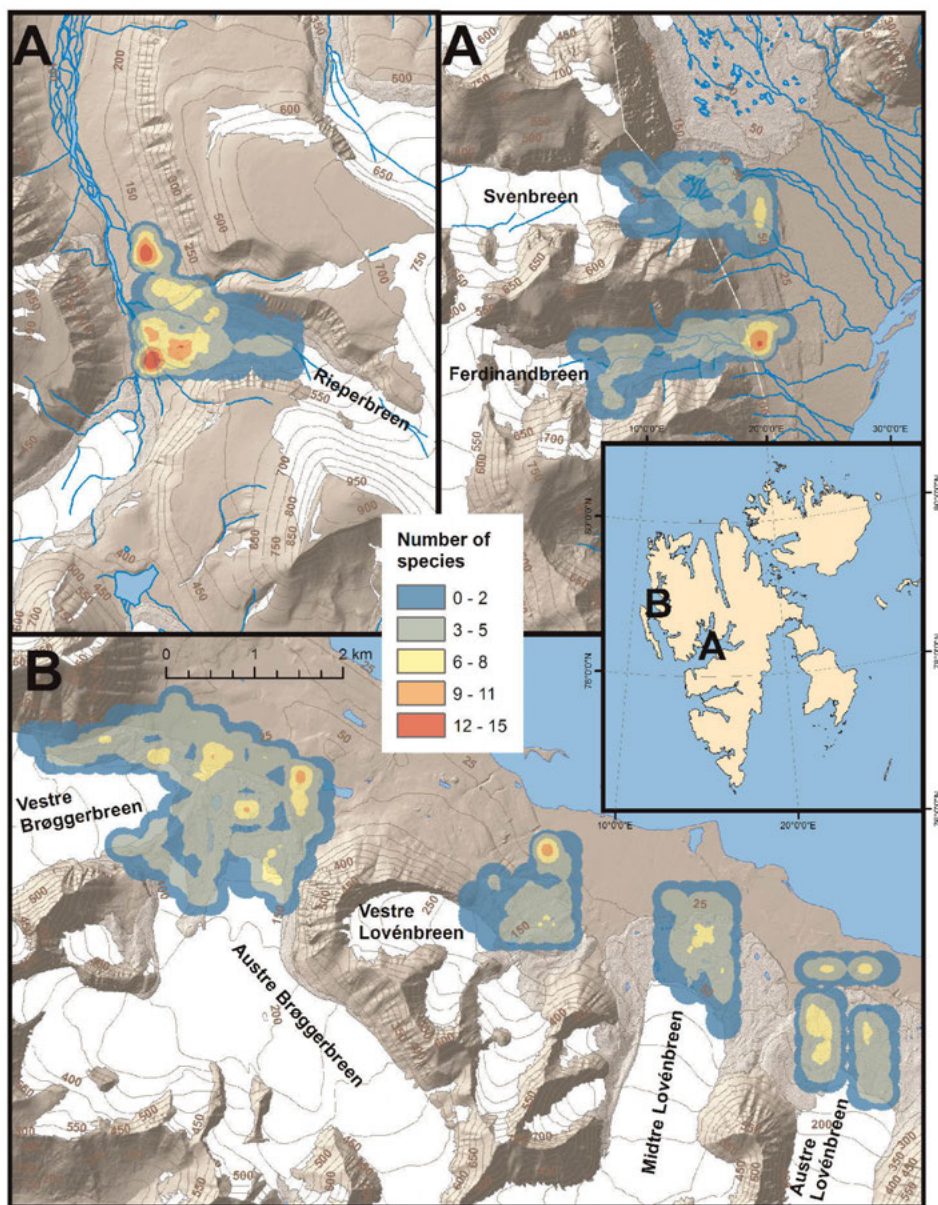


Fig. 2. Species richness in the study areas. (A): Rieperbreen, Ferdinandbreen and Svenbreen; (B): Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen (© Norwegian Polar Institute 2019; <http://www.npolar.no>).

Bruch and *Oncophorus virens* (Hedwig) Bridel for Austre Lovénbreen; *Didymodon acutus* (Bridel) K. Saito for Midtre Lovénbreen; *Neoorthocaulis hyperboreus* (R.M. Schust.) L. Söderstr., De Roo *et* Hedd. for Vestre Lovénbreen; *Distichium hagenii* Ryan *ex* H. Philib. for Austre Brøggerbreen; *Hymenoloma crispulum* (Hedw.) Ochyra, *Schistidium papillosum* Culm. for

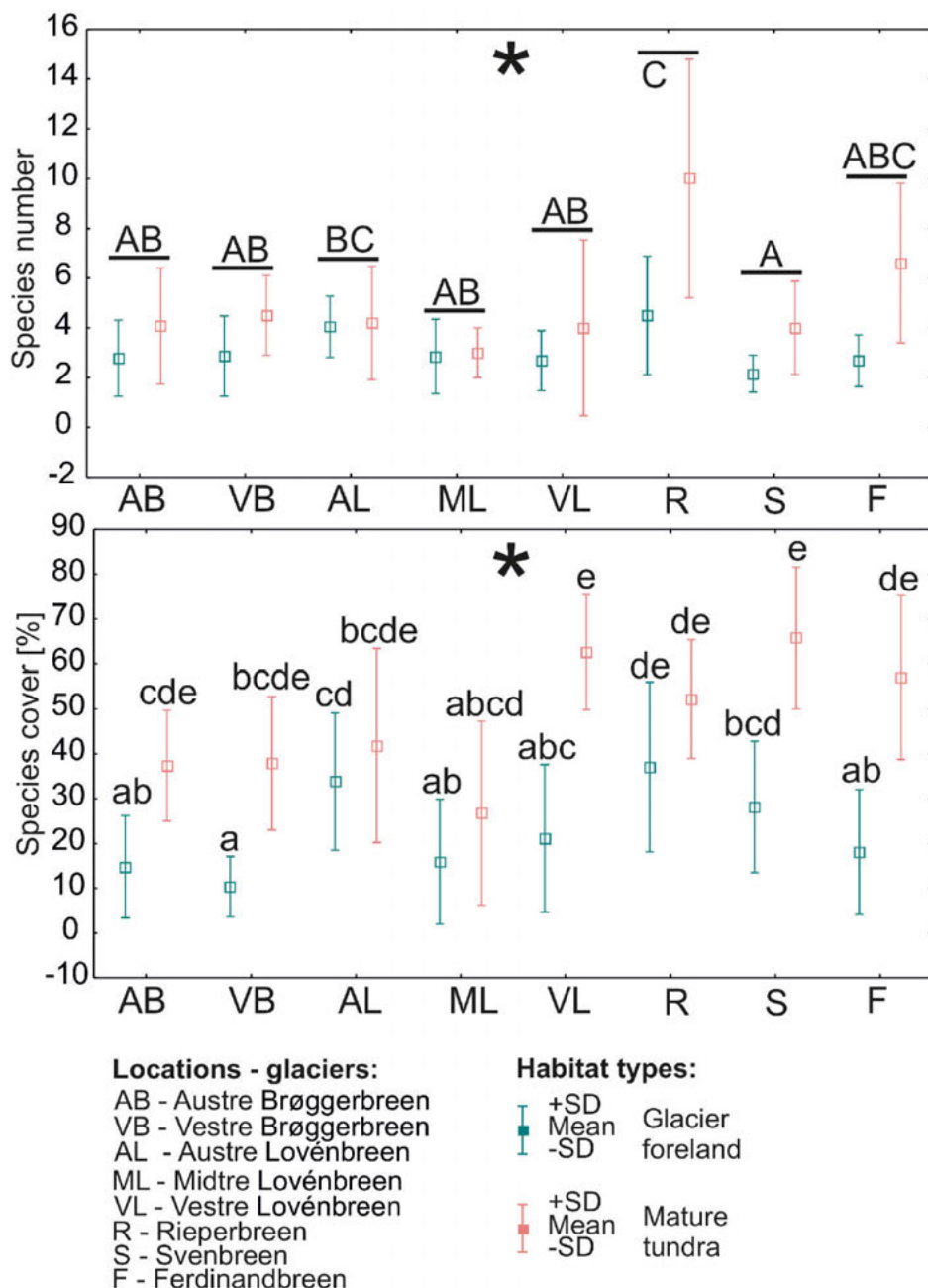


Fig. 3. Mean $\pm$ SD of number and cover of species including habitat type (foreland vs tundra) and location (glacier foreland). The results of ANOVA and Tukey's tests are presented graphically ($p < 0.05$). The different letters above the bars indicate statistically significant differences: the capital letters show the significant main effect of the location; the lowercase letters indicate the statistically significant interaction between habitat type and location; the asterisks (*) indicate the significant main effect of habitat type (see Table 1 for details on the main effects and interactions).

Vestre Brøggerbreen; *Distichium inclinatum* (Hedw.) Bruch & Schimp., *Ditrichum cylindricum* (Hedw.) Grout for Svenbreen; *Encalypta alpina* Sm. for Ferdinandbreen; *Anthelia juratzkana* (Limpr.) Trevis., *Pogonatum urnigerum* (Hedw.) P. Beauv., *Pohlia wahlenbergii* (F. Weber et D. Mohr) A.L. Andrews, *Polytrichum hyperboreum* R. Br., *P. piliferum* Hedw., *P. strictum* Menzies ex Brid., *Trilophozia quinquedentata* (Huds.) Bakalin, Vadim A. for Rieperbreen (Table 2). For tundra plots these were: *Psilopilum laevigatum* (Wahlenb.) Lindb. for Austre Lovénbreen; *Polytrichum hyperboreum* for Austre Brøggerbreen; *Orthothecium strictum* Lorentz for Vestre Brøggerbreen; *Aneura pinguis* (L.) Dumort., *Blepharostoma trichophyllum* (L.) Dumort., *Ditrichum cylindricum* for Ferdinandbreen; and *Dicranum laevidens* R.S. William, *Gymnomitrium corallioides* Nees, *Lophozia wenzelii* (Nees) Stephani, *Polytrichum strictum*, *Ptilidium ciliare* (L.) Hampe for Rieperbreen (Table 3).

Table 2.

Results of indicator species analysis with Pearson's phi coefficient values for forelands of the following glaciers: AL – Austre Lovénbreen, ML – Midtre Lovénbreen, VL – Vestre Lovénbreen, AB – Austre Brøggerbreen, VB – Vestre Brøggerbreen, S – Svenbreen, F – Ferdinandbreen, R – Rieperbreen. The species characteristic to particular foreland are in bold.

Glacier foreland	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
AL	<i>Encalypta procera</i>	0.665	<i>Racomitrium lanuginosum</i>	0.39	<i>Oncophorus virens</i>	0.316
	<i>Bryum pseudotriquetrum</i> var. <i>pseudotriquetrum</i>	0.566				
	<i>Ditrichum flexicaule</i>	0.677				
	<i>Distichium capillaceum</i>	0.614				
ML	<i>Bryum pseudotriquetrum</i> var. <i>pseudotriquetrum</i>	0.566	<i>Didymodon acutus</i>	0.359		
	<i>Distichium capillaceum</i>	0.614				
VL	<i>Ditrichum flexicaule</i>	0.677			<i>Neoorthocaulis hyperboreus</i>	0.324
	<i>Distichium capillaceum</i>	0.614				

Glacier foreland	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
AB	<i>Distichium hagenii</i>	0.498				
	<i>Bryum arcticum</i>	0.483				
VB	<i>Bryum arcticum</i>	0.483	<i>Hymenoloma crispulum</i>	0.404		
			<i>Schistidium papillosum</i>	0.346		
S	<i>Distichium inclinatum</i>	0.766				
	<i>Ditrichum cylindricum</i>	0.550				
F	<i>Psilopilum laevigatum</i>	0.422			<i>Encalypta alpina</i>	0.367
	<i>Distichium capillaceum</i>	0.614			<i>Pohlia drummondii</i>	0.373
					<i>Pohlia nutans</i>	0.358
					<i>Pogonatum dentatum</i>	0.333
R	<i>Polytrichum hyperboreum</i>	0.679	<i>Pohlia wahlenbergii</i>	0.500	<i>Anthelia juratzkana</i>	0.340
	<i>Polytrichum piliferum</i>	0.519	<i>Pogonatum urnigerum</i>	0.392	<i>Pohlia drummondii</i>	0.373
	<i>Trilophozia quinquedentata</i>	0.480	<i>Racomitrium lanuginosum</i>	0.39	<i>Pohlia nutans</i>	0.358
	<i>Polytrichum strictum</i>	0.439			<i>Pogonatum dentatum</i>	0.333
	<i>Psilopilum laevigatum</i>	0.422				

Environmental factors influencing species distribution. — CCA analysis resulted in division of the dataset into two groups. The first comprised plots located in tundra with high carbon and nitrogen contents in the soil, high values of vascular plants and biological soil crusts covers, and low values of rock cover, as well as locations farther from the glacier forehead; this group was also characterised by older substrate. The second group represented plots located in forelands, showing the opposite pattern in terms of environmental variables (Fig. 4; Table 4).

The forward selection procedure of the environmental variables revealed that, of 26 studied variables (Supplementary Table 3), 12 significantly affected species

Table 3.

Results of indicator species analysis with Pearson's phi coefficient values for mature tundra in the vicinity of following glaciers: AL – Austre Lovénbreen, ML – Midtre Lovénbreen, VL – Vestre Lovénbreen, AB – Austre Brøggerbreen, VB – Vestre Brøggerbreen, S – Svenbreen, F – Ferdinandbreen, R – Rieperbreen.
The species characteristic to particular tundra are in bold.

Mature tundra	$p \leq 0.001$	phi	$0.001 \leq p < 0.01$	phi	$0.01 \leq p < 0.05$	phi
AL					<i>Psilopilum laevigatum</i>	0.632
ML			<i>Distichium capillaceum</i>	0.677		
VL						
AB			<i>Polytrichum hyperboreum</i>	0.655		
VB			<i>Orthothecium strictum</i>	0.612		
S			<i>Distichium capillaceum</i>	0.677		
F			<i>Ditrichum cylindricum</i>	0.706	<i>Blepharostoma trichophyllum</i>	0.686
					<i>Aneura pinguis</i>	0.592
					<i>Pohlia nutans</i>	0.632
R	<i>Pohlia cruda</i>	0.874	<i>Dicranum laevidens</i>	0.762	<i>Gymnomitrium corallioides</i>	0.640
			<i>Ptilidium ciliare</i>	0.732	<i>Lophozia wenzelii</i>	0.632
					<i>Polytrichum strictum</i>	0.632
					<i>Pohlia nutans</i>	0.632

occurrence, including both chemical and physical habitat features (Table 4), such as: bare ground cover, soil conductivity, distance to the glacier forehead, K^+ content, TN content, TOC content, soil pH, silt content, sand content, time elapsed since glacier's retreat, total insolation, and vascular plant cover (Table 4). Occurrence of *Barbilophozia hatcheri* (A. Evans) Loeske, *Cryptocolea imbricate* R.M. Schust., *Hymenoloma crispulum* (Hedw.) Ochyra, *Hypnum bambergeri* Schimp., and *Polytrichum juniperinum* Hedw. was associated with longer time

Table 4

Results of forward selection and Monte Carlo permutation tests from CCA (Fig. 4 and 5). Environmental variables are listed by the order of their inclusion in the model (lambda A). Significant variables are in bold ($p < 0.05$).

Variable	Lambda 1	Lambda A	F	p
Soil pH	0.48	0.48	8.60	0.001
Time elapsed since glacier's retreat	0.34	0.32	5.89	0.001
Bare ground cover	0.19	0.16	2.97	0.001
Total insolation	0.13	0.11	2.01	0.006
Substrate conductivity	0.10	0.10	1.89	0.017
Total organic carbon in soil	0.16	0.10	1.89	0.011
Vascular plant cover	0.22	0.09	1.58	0.015
Distance to the glacier foreland	0.29	0.08	1.52	0.024
K ⁺	0.20	0.08	1.49	0.043
MgO	0.19	0.08	1.46	0.058
Sand	0.07	0.08	1.51	0.034
Silt	0.06	0.08	1.63	0.022
Total nitrogen in soil	0.15	0.08	1.58	0.025
Aspect	0.08	0.07	1.28	0.102
Ca ²⁺	0.19	0.07	1.19	0.211
CaCO ₃	0.07	0.06	1.15	0.248
Mg ²⁺	0.15	0.06	1.15	0.252
Slope	0.14	0.06	1.16	0.223
Topographic Wetness Index	0.08	0.06	1.21	0.179
K ₂ O	0.14	0.05	0.96	0.536
Na ⁺	0.21	0.05	0.87	0.629
P ₂ O ₅	0.10	0.05	0.97	0.451
Rock cover	0.20	0.05	1.10	0.298
Biological soil crust cover	0.16	0.03	0.58	0.962
C/N	0.12	0.03	0.67	0.898
Clay	0.14	0.03	0.78	0.842

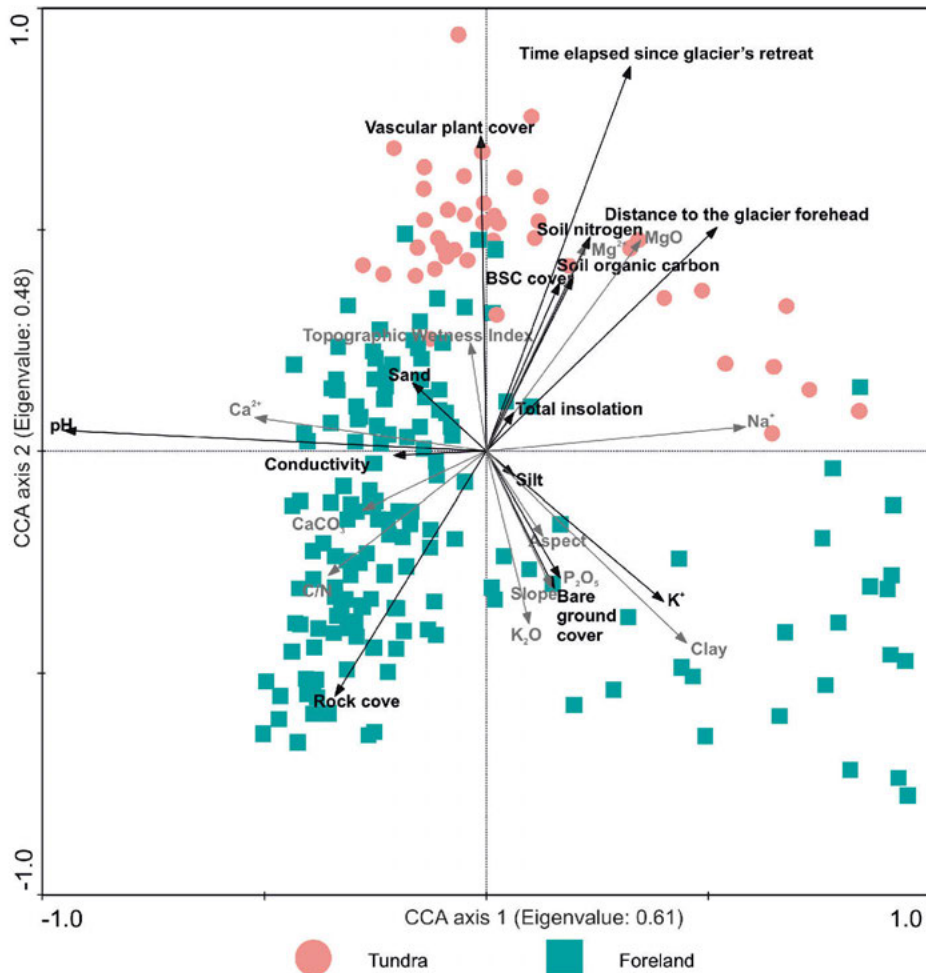


Fig. 4. CCA biplot with plots and environmental variables. Variables identified as significant in forward selection procedure are in black, while insignificant in grey (Table 4).

after glacier retreat, further distance to the glacier forehead, higher content of TOC and TN (Fig. 5). Opposite trend was presented by *Bryum arcticum* (R. Br.) Bruch *et* Schimp., *Bryum bimum* (Schreb.) Turner, *Bryum pallescens* Schleicher Schwägr., *Ditrichum flexicaule* (Schwägr.) Hampe, *Distichium hagenii* Ryan *ex* H. Philib., *Dicranella varia* (Hedw.) Schimp., *Encalypta procera*, and *Meesia uliginosa* Hedw. (Fig. 5). *Aneura pinguis*, *Blepharostoma trichophyllum*, *Catoscopium nigrum* (Hedw.) Brid., *Oncophorus virens*, *Orthothecium intricatum* (Hartm.) Schimp., *Orthothecium strictum*, and *Sanionia uncinata* preferred places with high vascular plants cover. Their opposition was *Bryum calophyllum* R. Br. which favoured areas with higher bare ground cover. *Jungermannia polaris* Lindb. was associated with higher soil conductivity. Several species were associated with lower substrate pH, i.e. *Dicranum*



scoparium Hedw., *Lophozia wenzelii*, *Racomitrium lanuginosum* (Hedw.) Brid., and *Polytrichum strictum*, while *Jungermannia polaris*, *Distichium capillaceum* (Hedw.) Bruch *et* Schimp., and *Encalypta alpina* preferred higher pH (Fig. 5). These species together with *Distichium inclinatum* and *Ditrichum cylindricum* were connected with higher sand content, lower silt and K^+ contents (Fig. 5). Opposite pattern was shown by *Cephaloziella varians* var. *arctica* (Bryhn *et* Douin) Damsholt, *Isopaches bicrenatus* (Schmidel) H. Buch, *Psilopilum laevigatum*, *Pohlia drummondii* (Müll. Hal.) A.L. Andrews, and *Pohlia wahlenbergii*. The length of the total insolation vector was short indicating its relatively lesser importance in explaining variability in species occurrence (Fig. 5). The Monte Carlo permutation test showed that both the first axis and all canonical axes taken together were statistically significant ($F = 8.25$, $p = 0.001$ and $F = 1.90$, $p = 0.001$, respectively).

Discussion

The rapid recession of glaciers since the end of the Little Ice Age enables the study of moss and liverwort development in recently deglaciated forelands, resulting from primary succession and eventually leading to the establishment of stable mature communities (Moreau *et al.* 2008). Burga *et al.* (2010) showed that colonisation by mosses in areas gradually exposed by melting glaciers is accomplished within a few years. The earliest appearance of bryophytes in the primary succession process has been observed in other forelands (Moreau *et al.* 2009; Wietrzyk *et al.* 2018). Mosses have even been reported from the margins of glaciers and ice sheets in the form of supraglacial globular moss cushions (Porter *et al.* 2008; Belkina and Vilnet 2015), indicating their extreme pioneering abilities. Our results showed a clear division between plots located in forelands and tundra based on species composition and various environmental factors, demonstrating that even in the marginal parts of forelands, communities of mosses and liverworts are still not fully developed and have not yet reached the climax stage (Fig. 4). This was also confirmed by significant differences in species composition between forelands and tundra (Tables 1–3). In general, the cover of species in tundra was greater than in forelands (Fig. 3). Moreover, in terms of selected locations, the number of species in tundra was greater than in forelands, e.g. Rieperbreen and Ferdinandbreen (Fig. 3). This may have resulted from a much longer period of plant community development connected with a lack of disturbance by glaciers in the past as well as milder microclimatic conditions (Wietrzyk *et al.* 2016). The habitat type and the geographical location of a glacier significantly affected species number, while variation in species cover also resulted from the interaction between these two factors (Table 1). This is in line with Mizuno (2005), who suggested that each foreland represents a different degree of substrate exposure to species colonisation. Apart from the

species base provided by surrounding tundra communities, species distribution across forelands and their development in the higher ground cover and biomass-producing moss-turf communities depend on local environmental factors (Favero-Longo *et al.* 2012). Anderson *et al.* (2007) and Burga *et al.* (2010) suggested that plant succession is connected with a complex set of factors, i.e. terrain features, snow retention, moisture, soil development, water availability, soil texture, and substrate age. As suggested by Rydgren *et al.* (2014), great deal of research considering age as the main factor influencing species distribution does not account for additional environmental data, without which any conclusions regarding variation in foreland vegetation may be problematic. In our research, we examined the influence of 25 variables other than substrate age on species distribution (Supplementary Table 3). Environmental variables significantly affecting species presence included both chemical and physical features of habitat (Table 4; Fig. 5). Therefore, our second hypothesis, which assumed that the distribution of mosses and liverworts was mainly dependent on physical soil properties such as texture and moisture whereas chemical soil properties and climatic factors played a secondary role, was not fully confirmed.

Depending on substrate age and distance from the forehead of the relevant glacier, varying degrees of frost action influence species succession (Haugland and Beatty 2005). Wietrzyk *et al.* (2016, 2018) showed that in the foreland of Irenebreen (north-western Spitsbergen) and Gåsbreen (southern Spitsbergen), distance from the glacier's foreland had a stronger impact on vegetation succession than time elapsed since deglaciation. On the other hand, Moreau *et al.* (2008, 2009) suggested that time elapsed since deglaciation is the most important factor affecting vegetation development. The dependence of bryophytes on substrate age was also reported by Haugland and Beatty (2005). In the case of the presence of mosses and liverworts, both of these factors played important roles, while time elapsed since glacier retreat had a stronger effect on species distribution (Table 4; Fig. 5).

Development of initial soil in glacier forelands and changes in its parameters influence the primary succession process (Moreau *et al.* 2008; Wietrzyk *et al.* 2018). An important factor affecting bryophyte colonisation is soil texture. As early as 1970, Kuc suggested that pioneer bryophytes, usually dwarf acrocarpous mosses forming short-lived colonies of great fertility, commonly inhabit fine-textured soils. Longton (1988) indicated that bryophytes prefer finer and moister material in hollow compared to other cryptogams. The importance of the texture of the surface soil layer to species colonisation had been reported previously from the forelands of Midtre Lovénbreen and Gåsbreen (Moreau *et al.* 2009; Wietrzyk *et al.* 2016). Our results showed that several species were associated with more coarse-grained (higher sand content) soil, while others preferred higher silt content (Fig. 5).

Microscale habitat conditions, e.g. micro-depressions (Tishkov 1986) and frost activity causing microscale disturbance (Haugland and Beatty 2005), are important in primary succession, as they shape forelands and influence nutrient availability,

which in habitats liberated from ice, is the primary factor limiting plant growth (Porter *et al.* 2008). Moreover, the conductivity level of the substrate can serve as an indirect indicator of the amount of water-soluble nutrients available for plant uptake: the higher the level, the more nutrient-rich the substrate. The importance for mosses and liverworts of nutrient contents in substrates was confirmed by our results. The presence of particular species was connected with higher or lower contents of TOC, TN, and K^+ (Table 4; Fig. 5). Taking TOC content as a measure of soil development, we can conclude that some species were strictly linked to habitats where the soil was better developed, while others preferred areas with less-developed soil, thus showing their connection with earlier stages of primary succession. This enabled us to distinguish a group of early colonisers inhabiting barren areas with low TOC and TN contents, and more bare ground cover, such as *Bryum* spp., *Ditrichum flexicaule*, *Distichium hagenii*, *Dicranella varia*, *Encalypta procera*, and *Meesia uliginosa*. As suggested by Watson (1960), the presence of bare substrate is of great importance for taxa with a direct rhizoidal connection with the substrate. On the other hand, the group of late colonisers, such as *Barbilophozia hatcheri*, *Cryptocolea imbricata*, *Hymenoloma crispulum*, *Hypnum bambergeri*, and *Polytrichum juniperinum* (Fig. 5), preferred more mature areas with higher contents of TOC and TN and significant cover of vegetation. In the process of inhabiting barren foreland areas, symbiosis with cyanobacteria appears to play a special role, enabling colonisation of sites with low TN content (Davey *et al.* 2017). Studies from the Arctic describe species from the genera *Bryum*, *Sanionia*, *Calligeron*, *Dupontia*, and *Grimmia* as the most abundant hosts for cyanobacteria (Solheim and Zielke, 2002). Moreover, as suggested by Pharo *et al.* (1999), vascular plants also showed potential as surrogates for the species richness of some bryophyte species. Moreau *et al.* (2009) indicated that increased occurrence of *Drepanocladus* sp. (current name *Sanionia* sp.) and *Polytrichum* sp. is associated with mature tundra formations. Our results confirmed this pattern for *Polytrichum juniperinum* and for *Sanionia uncinata* (Fig. 5; Supplementary Table 2). As noted by Gornall *et al.* (2011), vascular plants may benefit mosses by generating a favourable microclimate; however, more frequently they suppress the growth of mosses.

According to CCA analysis, substrate pH exerted the strongest influence on distribution of species (Table 4; Fig. 5). Some bryophytes grow only within a specific narrow pH range (Saxena 2004). For instance, *Polytrichastrum* spp. preferred areas with lower pHs (Fig. 5) resulting from better developed soil and higher vegetation cover; these areas were usually located closer to the tundra. This is in agreement with results obtained by Moreau *et al.* (2005) considered species from genus *Polytrichastrum* as hydrophiles in the foreland of Midtre Lovénbreen, that is in line with species' ecological amplitude as described by Dierssen (2001). Burga *et al.* (2010) suggested that local water supply is one of the main drivers of vegetation succession. However, our results showed that the TWI had no significant influence on species distribution. This may be connected

with bryophytes' great tolerance of dehydration and desiccation, along with their aggregation into globular or lenticular cushions, which increases evaporative resistance and reduces water losses (Longton 1988; Porter *et al.* 2008), thus enabling them to survive in both moist and periodically dry habitats. Furthermore, bryophytes possess no stomata, as vascular plants do, and lose water from tissues readily (Proctor 2000). As they lack roots for extracting water from soil, they depend on the availability of water from humid air, the soil surface, or precipitation (Street *et al.* 2012). Therefore, it may be assumed that the recorded species were more dependent on air humidity and precipitation than on the tendency of the area to accumulate water, as represented by TWI.

Our results indicated that total insolation affects bryophyte occurrence (Table 4); however, the short vector of this factor prevented us from distinguishing specific species connected to this parameter (Fig. 5). Oechel and Sveinbjörnsson (1978) suggested that the occurrence of bryophytes in various light conditions resulted from the requirement for greater humidity associated with sites protected from wind and direct sun, and not as a reaction to light intensity *per se*. Moreover, many species of bryophytes seem to be wholly tolerant of insolation, and even develop a 'sun-red' pigmentation as a result of full insolation (Oechel and Sveinbjörnsson 1978). On the other hand, they also possess the ability to maintain photosynthesis and respiration under conditions of low light (Longton 1988; Porter *et al.* 2008), enabling them to survive in a variety of light conditions.

Conclusions

In the present paper, we studied eight glacier forelands and the mature tundra areas in front of them in order to investigate the diversity and community composition of mosses and liverworts. We found that habitat type and location had a significant influence on species number. Species cover differed in terms of habitat type and location, as well as interaction between these two variables. The effects of habitat type and location were also significant for community composition, showing that each studied area is a separate ecosystem inhabited by a specific group of mosses and liverworts. Generally, the spatial-temporal species dynamics in studied areas were very complex due to highly variable local environmental conditions. Both biotic and abiotic variables significantly affected species distribution, i.e. cover of bare ground and vascular plants, distance from the relevant glacier forehead, soil conductivity, contents of TOC, TN, and K⁺, silt and sand contents, soil pH, time elapsed since glacier's retreat, and total insolation. Glacier forelands offer specific habitat conditions preferred by some pioneer species of mosses and liverworts. In these places, they are less exposed to competition from other species. Consequently, forelands may serve as important species refugia, especially, if global warming progresses, in the future.

Acknowledgement. — We are grateful to Wojciech Moskal (Norwegian Polar Institute, Institute of Oceanology of the Polish Academy of Sciences), Marek Broż (Clione ship) and Dominika Dąbrowska for their help during fieldwork and transport of research material. We would like to thank Robert Zubel (Maria Curie Skłodowska University in Lublin) for assistance in the preliminary species determination. We wish to thank Mateusz Stolarczyk (Jagiellonian University, Institute of Geography and Spatial Management) for his support during laboratory analyses. We are also grateful to anonymous reviewers for their suggestions and remarks on manuscript. 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.

Funding. — The field research leading to these results has received funding from the European Union's Horizon 2020 project INTERACT (grant agreement No. 730938). The laboratory analyses were financed by National Science Centre in Poland within Preludium project (No. 2017/27/N/ST10/00862). The work of Paulina Wietrzyk-Pelka was supported by Etiuda project of the National Science Centre in Poland (No. 2019/32/T/ST10/00182), while work of Beata Cykowska-Marzencka was supported by the statutory fund of the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków.

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Received 28 November 2019

Accepted 25 March 2020

Supplementary Table 1.

Geological (Dallmann 1999; Dallmann et al. 2001, 2004, 2009; Saalmann and Thiedig 1998), climatic (Fick and Hijmans 2017) and vegetation (CAVM 2003; Elvebakk 2005; Jónsdóttir 2005) characteristics of studied areas.

Location	Geology	Mean annual temperature	Mean annual precipitation	Warmest month	Coldest month	Vegetation
Austre, Midtre and Vestre Lovénbreen	Phyllite, quartzite, and schist from Proterozoic; dolomite and limestone (Carboniferous and Permian); sandstone, shale, and conglomerate (Carboniferous and Paleocene).	-6°C	420 mm	July: 6-7°C	January: -15°C to -18°C	Northern Arctic tundra; prostrate dwarf-shrub/herb tundra; Subzone B
Austre and Vestre Brøggerbreen	Phyllite, quartzite, and schist (Proterozoic); dolomite and limestone (Carboniferous, Permian); sandstone, shale, and conglomerate (Carboniferous and Paleocene); chert, shale, sandstone, and limestone (Permian), shale, siltstone, and sandstone (Triassic).	-7°C	430 mm			
Svenbreen and Ferdinandbreen	Granitic gneiss, migmatite, amphibolite, quartzite, mica schist, and marble (Proterozoic); sandstone, siltstone, shale, and conglomerate (Devonian); elastic and carbonate rocks (Carboniferous); carbonate rocks (Permian).	-8°C	300 mm		January: -19°C	Middle Arctic tundra; prostrate/hemiprostrate dwarf-shrub tundra; Subzone C
Rieperbreen	sandstone, siltstone, mudstone, and shale (Cretaceous, Paleocene, Eocene).		400 mm			

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Supplementary Table 2.
 List of identified species in forelands and tundra at different locations (AL - Austre Lovénbreen, ML - Midtre Lovénbreen, VL - Vestre Lovénbreen, AB - Austre Brøggerbreen, VB - Vestre Brøggerbreen, S – Svenbreen, F – Ferdinandbreen, R – Rieperbreen).

Habitat type			Mature tundra								Glacier forelands							
No.	Species name	Group	AB	VB	AL	ML	VL	R	S	F	AB	VB	AL	ML	VL	R	S	F
1	<i>Amblystegium serpens</i>	moss								X			X	X			X	
2	<i>Andreaea blyttii</i>	moss														X		X
3	<i>Aneura pinguis</i>	liverwort			X					X								
4	<i>Anthelia juratzkana</i>	liverwort						X								X		
5	<i>Aulacomnium turgidum</i>	moss						X										
6	<i>Barbilophozia hatcheri</i>	liverwort					X								X			
7	<i>Blepharostoma trichophyllum</i>	liverwort	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
8	<i>Blindia acuta</i>	moss													X			X
9	<i>Brachythecium turgidum</i>	moss												X				
10	<i>Bryobrittonia longipes</i>	moss									X							
11	<i>Bryoerythrophyllum recurvirostrum</i>	moss										X						
12	<i>Bryum algovicum</i>	moss									X	X						
13	<i>Bryum arcticum</i>	moss	X							X	X	X		X	X			
14	<i>Bryum argenteum</i>	moss			X					X	X	X						
15	<i>Bryum bimum</i> (=B. pseudotriquetrum var. bimum)	moss									X							
16	<i>Bryum calophyllum</i>	moss												X		X		

Habitat type			Mature tundra								Glacier forelands							
No.	Species name	Group	AB	VB	AL	ML	VL	R	S	F	AB	VB	AL	ML	VL	R	S	F
17	<i>Bryum gemmiparum</i>	moss													X			
18	<i>Bryum pallescens</i>	moss	X	X					X	X	X	X	X	X	X	X	X	X
19	<i>Bryum pseudotriquetrum</i> var. <i>pseudotriquetrum</i>	moss					X				X	X	X	X	X	X		
20	<i>Bucklandiella sudetica</i> (= <i>Racomitrium sudeticum</i>)	moss										X						
21	<i>Calliergon richardsonii</i>	moss														X		
22	<i>Campyliadelphus chrysophyllus</i>	moss														X	X	
23	<i>Campyllum arcticum</i> (= <i>Drepanocladus arcticus</i>)	moss		X														
24	<i>Campyllum stellatum</i>	moss	X	X	X	X					X	X					X	X
25	<i>Campylopus schimperi</i>	moss	X								X							
26	<i>Catoscopium nigrum</i>	moss	X	X														
27	<i>Cephalozia bicuspidata</i>	liverwort						X										
28	<i>Cephalozia varians</i> var. <i>arctica</i>	liverwort				X		X			X	X	X	X	X	X		X
29	<i>Ceratodon purpureus</i>	moss												X	X			
30	<i>Cryptocolea imbricata</i>	liverwort		X														
31	<i>Dicranella varia</i>	moss									X							
32	<i>Dicranum acutifolium</i>	moss	X															
33	<i>Dicranum elongatum</i>	moss						X		X							X	
34	<i>Dicranum laevidens</i>	moss			X			X			X		X			X		
35	<i>Dicranum scoparium</i>	moss	X	X														
36	<i>Dicranum spadicetum</i>	moss	X				X	X								X		
37	<i>Didymodon acutus</i>	moss			X	X	X							X	X			
38	<i>Didymodon asperifolius</i>	moss											X					
39	<i>Didymodon fallax</i>	moss									X							
40	<i>Didymodon tophaceus</i>	moss									X			X				

Habitat type			Mature tundra								Glacier forelands							
No.	Species name	Group	AB	VB	AL	ML	VL	R	S	F	AB	VB	AL	ML	VL	R	S	F
41	<i>Distichum capillaceum</i>	moss			X	X			X	X	X	X	X	X	X	X	X	X
42	<i>Distichum hageni</i>	moss	X	X							X	X					X	X
43	<i>Distichum inclinatum</i>	moss	X						X	X	X	X		X		X	X	X
44	<i>Dirichium cylindricum</i> (= <i>Trichodon cylindricus</i>)	moss		X	X				X	X	X	X			X	X	X	X
45	<i>Dirichium flexicale</i>	moss	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X
46	<i>Drepanocladus aduncus</i>	moss														X		
47	<i>Encalyptia alpina</i>	moss				X			X		X		X	X		X	X	X
48	<i>Encalyptia procera</i>	moss			X					X	X	X	X					X
49	<i>Encalyptia rhabdocarpa</i>	moss										X						
50	<i>Gymnomitrium concinnatum</i>	liverwort																
51	<i>Gymnomitrium corallitoides</i>	liverwort	X	X			X	X								X		
52	<i>Hygrohypnum alpestre</i>	moss			X							X						
53	<i>Hygrohypnum polare</i>	moss										X						
54	<i>Hymenoloma crispulum</i> (= <i>Dicranoweissia crispula</i>)	moss			X			X		X	X	X				X	X	
55	<i>Hymenosyllum recurvirostrum</i>	moss	X									X						
56	<i>Hypnum bambergeri</i>	moss								X								
57	<i>Hypnum revolutum</i>	moss		X														
58	<i>Isopachtes bicrenatus</i>	liverwort									X					X		
59	<i>Isoperlygiopsis pulchella</i>	moss		X				X			X	X						
60	<i>Jungermannia polaris</i>	liverwort						X		X	X	X	X	X		X		X
61	<i>Lophozia ventricosa</i>	liverwort														X		
62	<i>Lophozia wenzelii</i>	liverwort						X						X		X		
63	<i>Marsipella arctica</i>	liverwort												X				
64	<i>Meesia uliginosa</i>	moss										X						
65	<i>Neorhacaulis hyperboreus</i>	liverwort													X			

Habitat type			Mature tundra								Glacier forelands							
No.	Species name	Group	AB	VB	AL	ML	VL	R	S	F	AB	VB	AL	ML	VL	R	S	F
66	<i>Niphoarichum ericoides</i> (= <i>Racomitrium ericoides</i>)	moss									X						X	
67	<i>Oncophorus virens</i>	moss	X				X						X					
68	<i>Oreas maritima</i>	moss	X															
69	<i>Orthohecium intricatum</i>	moss		X														
70	<i>Orthohecium strictum</i>	moss		X														
71	<i>Pogonatum denatum</i>	moss														X		X
72	<i>Pogonatum urnigerum</i>	moss							X							X		
73	<i>Pohlia cruda</i>	moss	X					X		X	X	X	X	X		X		X
74	<i>Pohlia drummondii</i>	moss	X	X				X			X	X	X			X	X	X
75	<i>Pohlia nutans</i>	moss						X		X				X		X		X
76	<i>Pohlia prolifera</i>	moss											X					
77	<i>Pohlia wahlenbergii</i>	moss	X	X				X		X	X	X	X	X	X	X	X	X
78	<i>Polytrichastrum alpinum</i>	moss			X	X	X	X			X		X			X		
79	<i>Polytrichastrum sexangulare</i>	moss	X	X		X	X				X					X		X
80	<i>Polytrichum hyperboreum</i>	moss	X													X		
81	<i>Polytrichum juniperinum</i>	moss						X		X								
82	<i>Polytrichum piliferum</i>	moss						X								X		
83	<i>Polytrichum strictum</i>	moss														X		
84	<i>Psilopilum laevigatum</i>	moss			X											X		X
85	<i>Pterigynandrum filiforme</i>	moss													X			
86	<i>Ptilidium ciliare</i>	liverwort	X					X			X					X		
87	<i>Racomitrium lanuginosum</i>	moss	X				X	X					X			X		
88	<i>Sanionia georgicounclata</i>	moss	X	X												X		
89	<i>Sanionia uncinata</i>	moss	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
90	<i>Sauteria alpina</i>	liverwort		X														
91	<i>Schistidium frigidum</i>	moss										X						

Habitat type			Mature tundra								Glacier forelands							
No.	Species name	Group	AB	VB	AL	ML	VL	R	S	F	AB	VB	AL	ML	VL	R	S	F
92	<i>Schistidium papillosum</i>	moss										X						
93	<i>Schistidium rivulare</i>	moss										X						
94	<i>Schljakovianthus quadrilobus</i>	liverwort													X			
95	<i>Scorpidium revolvens</i>	moss	X															
96	<i>Scorpidium scorpioides</i>	moss	X															
97	<i>Sphenolobus minutus</i>	liverwort					X	X					X			X		
98	<i>Syntrichia ruralis</i>	moss								X				X				
99	<i>Timmia bavarica</i>	moss												X	X			
100	<i>Timmia norvegica</i>	moss					X	X										
101	<i>Timmia sibirica</i>	moss													X			
102	<i>Tomenypnum nitens</i>	moss	X	X					X	X	X							X
103	<i>Tortella fragilis</i>	moss										X						
104	<i>Tortella tortuosa</i>	moss										X					X	
105	<i>Trilophozia quinqueidentata</i>	liverwort														X		
SUM			28	22	15	8	14	26	10	20	34	33	20	24	21	41	18	23

Supplementary Table 3.
Descriptive statistics (mean, SD, min and max) for studied variables at different locations including the division into two habitat types.

Variable	Austre Brøggerbreen		Vestre Brøggerbreen		Austre Lovénbreen		Midtre Lovénbreen		Vestre Lovénbreen		Rieperbreen		Svenbreen		Ferdinandbreen		
	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	
Aspect (rad)	Mean	3,94	4,39	2,24	2,39	3,52	4,97	4,04	5,67	3,75	5,24	4,32	3,82	3,09	2,69	3,32	0,64
	SD	1,74	1,88	1,87	2,18	2,16	1,29	2,00	0,33	2,41	1,01	0,82	0,50	2,38	1,96	1,99	0,37
	Min	0,14	0,21	0,22	0,23	0,04	2,90	0,41	5,38	0,03	3,48	2,69	2,95	0,03	0,84	0,60	0,28
	Max	6,12	5,62	5,80	5,28	6,16	6,27	6,02	6,18	6,22	6,04	6,11	4,20	5,96	5,90	5,96	1,17
Bare ground cover (%)	Mean	9,50	2,14	7,50	2,00	1,65	0,00	2,50	0,00	5,58	0,00	27,71	0,00	15,60	0,80	19,40	0,00
	SD	13,16	5,67	8,53	2,74	3,86	0,00	6,44	0,00	13,85	0,00	32,51	0,00	18,87	1,79	21,61	0,00
	Min	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Max	45,00	15,00	24,00	5,00	13,00	0,00	27,00	0,00	60,00	0,00	88,00	0,00	65,00	4,00	65,00	0,00
Biological soil crust cover (%)	Mean	26,69	57,57	18,33	50,40	48,30	67,20	41,60	64,80	33,79	56,60	37,29	56,40	23,50	55,40	9,60	67,80
	SD	17,81	31,57	12,25	13,45	21,02	21,25	23,36	32,37	21,99	25,01	28,75	11,24	21,77	25,02	17,13	13,20
	Min	0,00	5,00	0,00	32,00	10,00	31,00	3,00	10,00	0,00	13,00	0,00	39,00	0,00	25,00	0,00	59,00
	Max	64,00	93,00	39,00	60,00	90,00	85,00	80,00	94,00	70,00	75,00	85,00	70,00	70,00	82,00	60,00	90,00
Ca ²⁺ (cmol/kg)	Mean	9,64	6,47	11,53	9,80	11,30	9,96	7,32	4,16	8,27	5,17	4,24	3,87	8,32	15,48	6,70	16,46
	SD	3,19	3,90	4,98	2,10	4,08	4,62	1,87	0,32	4,67	1,78	1,08	2,57	3,70	5,59	2,53	2,91
	Min	2,72	2,25	2,93	7,73	4,32	5,94	3,64	3,68	2,37	3,64	2,84	2,11	3,87	8,20	1,49	14,44
	Max	14,68	11,49	17,69	12,06	16,53	16,87	10,46	4,45	15,99	7,99	7,57	8,19	18,34	23,89	11,10	21,49
CaCO ₃ (mg/g)	Mean	9,65	4,13	29,47	9,61	3,48	1,62	1,24	0,34	19,42	0,33	0,00	0,00	4,68	13,44	2,81	3,52
	SD	11,67	7,87	26,18	12,41	1,32	1,51	0,72	0,44	23,03	0,43	0,00	0,00	5,22	23,99	2,87	7,87
	Min	0,00	0,00	0,00	0,00	1,55	0,00	0,09	0,00	0,04	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Max	53,80	21,33	65,34	31,06	6,93	2,98	3,39	1,03	69,45	0,83	0,00	0,00	18,23	56,24	11,02	17,60
Clay (%)	Mean	4,71	4,90	9,59	7,21	7,19	2,04	6,11	3,88	5,00	1,43	12,89	9,33	7,00	5,30	8,69	4,41
	SD	1,67	4,01	3,19	3,35	3,81	0,78	2,82	1,38	2,95	0,56	3,10	1,85	3,02	2,71	2,69	1,59
	Min	2,21	1,93	5,18	2,90	1,16	0,81	1,79	2,99	1,23	0,78	7,01	7,33	2,83	3,26	3,46	2,97
	Max	8,50	12,79	13,59	11,48	12,78	2,75	10,76	6,30	10,52	1,94	19,57	11,92	14,97	9,46	12,85	6,99

Variable	Austre Brøggerbreen		Vestre Brøggerbreen		Austre Lovénbreen		Midtre Lovénbreen		Vestre Lovénbreen		Rieperbreen		Svenbreen		Ferdinandbreen		
	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	
C/N	Mean	56,01	18,66	113,38	26,48	33,28	17,84	24,21	11,36	81,12	13,15	12,62	12,65	40,47	35,80	54,01	17,79
	SD	45,09	14,47	85,54	11,88	14,77	7,92	12,38	2,15	84,19	3,80	2,74	2,50	9,86	41,42	10,03	11,56
	Min	5,78	8,74	5,89	13,06	15,45	11,04	9,97	9,48	7,48	9,69	8,15	10,18	25,48	12,77	24,49	11,64
	Max	194,47	49,52	234,98	38,72	69,43	28,31	48,82	15,05	238,48	19,38	18,11	16,68	60,53	109,03	67,54	38,39
Soil conductivity	Mean	59,19	44,00	76,58	43,40	88,70	92,80	81,80	48,80	56,21	42,60	64,95	63,62	48,80	100,20	43,90	103,20
	SD	17,16	19,79	21,77	9,40	29,63	43,75	29,71	17,77	19,95	15,68	54,46	61,07	15,32	34,69	16,23	35,51
	Min	30,00	19,00	28,00	29,00	52,00	61,00	36,00	22,00	24,00	25,00	15,00	11,00	22,00	55,00	15,00	65,00
	Max	101,00	81,00	105,00	55,00	155,00	169,00	176,00	66,00	81,00	68,00	225,00	161,00	71,00	149,00	79,00	153,00
Distance to the glacier terminus (m)	Mean	789,64	1441,19	450,26	949,34	825,27	1683,82	691,80	1263,58	623,84	1207,33	1232,40	1821,45	595,24	1279,82	917,78	2038,42
	SD	387,41	334,86	181,43	161,62	306,13	31,41	274,87	100,67	292,00	100,92	495,36	250,87	334,06	72,19	480,37	174,23
	Min	181,32	978,02	170,25	765,30	265,98	1657,91	301,38	1093,51	99,28	1087,12	113,55	1497,39	82,16	1173,72	211,56	1857,72
	Max	1485,31	1882,76	760,58	1173,96	1359,20	1735,67	1164,44	1355,27	1064,61	1348,68	1787,53	2116,05	1104,72	1374,79	1700,97	2293,72
K ⁺ (cmol/kg)	Mean	0,08	0,08	0,10	0,09	0,18	0,07	0,15	0,08	0,09	0,10	0,23	0,20	0,11	0,09	0,15	0,12
	SD	0,03	0,05	0,03	0,03	0,08	0,02	0,07	0,02	0,03	0,03	0,04	0,09	0,03	0,02	0,05	0,01
	Min	0,04	0,05	0,05	0,05	0,05	0,04	0,05	0,06	0,04	0,07	0,14	0,10	0,08	0,06	0,09	0,11
	Max	0,13	0,19	0,16	0,11	0,30	0,09	0,33	0,12	0,13	0,13	0,32	0,31	0,16	0,11	0,28	0,13
K ₂ O (mg/g)	Mean	6,37	3,29	3,46	2,59	10,60	4,53	9,67	5,34	5,07	4,71	10,41	7,72	5,83	3,50	6,37	6,33
	SD	2,65	1,44	1,80	0,97	4,47	4,87	4,92	2,66	2,53	0,65	2,07	3,29	2,54	1,41	1,95	1,89
	Min	2,01	1,77	1,32	1,38	4,44	1,68	2,96	2,93	1,01	3,99	5,45	3,56	3,41	1,93	3,14	4,21
	Max	13,30	6,16	7,07	3,38	18,27	13,18	19,39	9,87	10,13	5,47	16,22	12,13	14,49	5,60	10,57	8,62
Mg ²⁺ (cmol/kg)	Mean	0,67	1,75	1,16	3,10	0,63	1,46	0,52	0,70	0,64	1,62	1,55	1,31	1,01	1,87	1,16	3,08
	SD	0,27	0,93	0,78	1,59	0,17	0,87	0,16	0,34	0,17	0,67	0,72	0,90	0,42	0,90	0,38	1,08
	Min	0,37	0,82	0,58	0,54	0,28	0,65	0,26	0,39	0,40	0,74	0,88	0,76	0,58	0,73	0,28	1,56
	Max	1,44	3,32	3,46	4,84	0,90	2,76	0,93	1,09	1,00	2,59	3,37	2,88	2,22	2,62	1,99	4,25

Variable	Austre Brøggerbreen		Vestre Brøggerbreen		Austre Lovénbreen		Midtre Lovénbreen		Vestre Lovénbreen		Rieperbreen		Svenbreen		Ferdinandbreen	
	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra
MgO (mg/g)	Mean	10,38	28,24	15,91	41,08	10,23	28,16	8,46	13,82	10,30	33,10	30,09	17,12	30,51	19,25	49,62
	SD	4,05	15,13	8,60	19,55	2,34	15,67	3,29	8,36	2,42	15,21	13,40	6,24	14,05	5,74	14,74
	Min	5,10	9,05	8,95	8,82	4,78	13,68	4,03	5,93	6,59	13,69	16,70	10,30	12,64	5,75	27,20
	Max	20,26	54,92	37,73	55,12	13,11	49,76	17,21	23,23	15,98	54,74	61,52	34,22	43,44	29,26	63,91
Na ⁺ (cmol/kg)	Mean	0,03	0,04	0,03	0,05	0,03	0,04	0,04	0,04	0,02	0,05	0,07	0,04	0,04	0,05	0,05
	SD	0,01	0,02	0,01	0,02	0,01	0,02	0,01	0,01	0,01	0,03	0,03	0,01	0,02	0,03	0,01
	Min	0,01	0,01	0,02	0,04	0,02	0,02	0,02	0,02	0,02	0,02	0,05	0,02	0,03	0,02	0,04
	Max	0,06	0,06	0,05	0,08	0,05	0,07	0,06	0,05	0,04	0,08	0,18	0,07	0,06	0,12	0,06
P ₂ O ₅ (mg/g)	Mean	1,25	0,73	3,25	1,26	3,37	1,09	1,32	1,30	1,45	0,70	4,74	1,63	1,43	1,02	1,74
	SD	0,65	0,90	5,28	0,79	3,38	0,53	0,86	0,41	0,58	0,26	2,93	0,38	0,40	0,42	0,46
	Min	0,03	0,02	0,88	0,67	0,17	0,32	0,54	0,93	0,30	0,30	1,43	1,10	0,91	0,39	1,18
	Max	2,21	1,89	19,84	2,61	13,30	1,51	4,61	1,94	2,50	0,89	13,48	2,10	2,46	1,88	2,45
Soil pH	Mean	8,45	7,28	8,36	8,21	8,34	7,75	8,40	7,58	8,50	7,43	5,45	8,16	7,78	7,44	7,41
	SD	0,20	1,13	0,38	0,47	0,12	0,46	0,23	0,86	0,15	0,93	0,90	0,26	0,35	1,16	0,26
	Min	7,92	5,69	7,41	7,39	8,11	6,97	7,55	6,33	8,17	6,35	3,99	7,59	7,46	3,91	7,11
	Max	8,75	8,36	8,65	8,59	8,49	8,18	8,58	8,47	8,78	8,27	7,37	8,48	8,19	8,25	7,83
Rock cover (%)	Mean	63,19	20,71	70,83	36,20	50,05	3,40	52,35	26,60	59,89	1,40	34,10	61,35	14,80	71,50	7,00
	SD	18,94	29,04	18,63	23,08	20,84	3,21	26,65	38,17	19,76	1,95	14,66	18,70	18,40	21,99	5,70
	Min	27,00	0,00	33,00	3,00	10,00	0,00	1,00	0,00	30,00	0,00	4,00	30,00	0,00	35,00	0,00
	Max	100,00	80,00	97,00	68,00	90,00	7,00	92,00	90,00	96,00	4,00	70,00	95,00	45,00	100,00	15,00
Sand (%)	Mean	42,05	46,78	37,29	31,34	41,90	59,59	42,81	54,32	44,30	59,29	31,75	46,67	36,92	38,85	37,49
	SD	13,68	19,77	15,71	20,43	17,95	12,78	15,27	8,07	12,81	13,69	10,83	18,55	12,77	12,11	3,03
	Min	21,86	15,17	19,97	14,49	23,25	40,42	29,18	49,10	27,87	46,48	11,19	9,20	18,36	20,11	34,40
	Max	75,04	63,00	69,61	66,59	76,99	75,48	76,91	68,52	65,98	74,24	58,40	76,82	53,91	66,91	41,30

Variable	Austre Brøggerbreen		Vestre Brøggerbreen		Austre Lovénbreen		Midtre Lovénbreen		Vestre Lovénbreen		Rieperbreen		Svenbreen		Ferdinandbreen	
	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra
Silt (%)	Mean	53,23	48,31	53,12	61,45	50,91	38,37	51,08	41,80	50,71	39,28	55,35	63,72	46,33	57,78	58,10
	SD	12,53	15,96	13,47	17,99	14,81	12,15	12,86	8,09	10,54	13,13	9,32	8,57	16,10	11,87	2,34
	Min	22,75	34,53	25,21	30,51	21,85	23,71	20,83	28,12	32,79	24,98	34,59	56,36	20,36	39,46	55,38
	Max	72,19	72,03	67,29	77,04	69,02	56,90	61,99	47,91	65,02	51,58	76,89	76,89	79,71	72,18	61,48
Slope (rad)	Mean	0,12	0,07	0,19	0,07	0,14	0,03	0,10	0,03	0,26	0,05	0,23	0,09	0,25	0,07	0,11
	SD	0,09	0,07	0,13	0,05	0,09	0,01	0,09	0,01	0,19	0,01	0,10	0,04	0,21	0,03	0,10
	Min	0,00	0,01	0,00	0,01	0,03	0,02	0,00	0,02	0,04	0,04	0,05	0,05	0,03	0,04	0,03
	Max	0,39	0,20	0,39	0,13	0,35	0,05	0,31	0,05	0,70	0,07	0,38	0,15	0,75	0,11	0,28
Time elapsed after glacier retreat (years)	Mean	53,42	120,00	50,67	120,00	48,35	120,00	64,50	120,00	76,53	120,00	64,86	120,00	84,75	120,00	120,00
	SD	24,28	0,00	21,20	0,00	18,66	0,00	27,82	0,00	25,07	0,00	35,20	0,00	25,02	0,00	0,00
	Min	25,00	120,00	24,00	120,00	21,00	120,00	32,00	120,00	23,00	120,00	7,00	120,00	24,00	120,00	120,00
	Max	117,00	120,00	89,00	120,00	102,00	120,00	117,00	120,00	107,00	120,00	117,00	120,00	117,00	120,00	120,00
Topographic Wetness Index	Mean	6,05	6,47	6,07	6,09	5,13	6,87	5,70	7,11	4,73	6,08	5,06	6,72	5,30	6,87	6,78
	SD	2,90	1,63	3,79	1,15	1,99	0,96	1,91	1,08	1,58	1,05	1,34	1,45	1,47	0,88	1,66
	Min	2,45	3,67	2,99	4,60	3,26	6,04	3,17	5,96	2,27	4,75	2,99	5,00	2,84	6,11	4,97
	Max	14,88	9,23	14,12	7,59	10,87	8,44	9,58	8,43	8,24	7,14	8,96	8,67	7,71	8,33	9,23
Total Insolation	Mean	796,83	782,17	753,26	766,97	777,28	816,83	792,09	811,61	732,77	806,08	757,83	798,08	665,72	791,60	766,64
	SD	41,02	37,28	93,62	63,25	53,59	14,11	34,67	3,43	63,87	18,07	93,02	17,15	110,92	25,82	45,82
	Min	711,87	735,74	530,43	698,75	670,70	803,92	719,42	806,94	564,30	782,94	543,26	776,46	475,06	756,63	688,61
	Max	886,72	815,75	866,77	833,55	857,00	839,95	851,17	815,53	818,92	833,45	875,66	822,13	807,48	823,59	800,69
Total nitrogen in soil (%)	Mean	0,03	0,12	0,05	0,15	0,03	0,17	0,03	0,06	0,03	0,16	0,08	0,22	0,05	0,26	0,34
	SD	0,01	0,09	0,01	0,08	0,01	0,17	0,02	0,05	0,01	0,14	0,01	0,15	0,01	0,19	0,18
	Min	0,02	0,04	0,03	0,04	0,01	0,03	0,01	0,03	0,03	0,04	0,06	0,08	0,03	0,05	0,12
	Max	0,07	0,31	0,08	0,24	0,06	0,45	0,08	0,14	0,04	0,36	0,11	0,41	0,07	0,46	0,62

Variable	Austre Brøggerbreen		Vestre Brøggerbreen		Austre Lovénbreen		Midtre Lovénbreen		Vestre Lovénbreen		Rieperbreen		Svenbreen		Ferdinandbreen	
	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra	foreland	tundra
Total organic carbon in soil (%)	Mean	0,51	1,55	1,40	2,03	2,04	0,32	0,68	0,54	2,40	1,08	2,60	1,29	3,75	3,89	4,45
	SD	0,36	1,15	1,28	0,75	2,04	0,19	0,53	0,41	2,74	0,35	1,62	0,62	2,19	2,33	1,71
	Min	0,05	0,31	0,22	1,15	0,58	0,14	0,14	0,11	0,37	0,54	0,91	0,45	0,80	0,68	2,63
	Max	1,44	3,36	4,86	3,08	5,46	0,98	1,46	1,44	6,97	1,84	4,54	2,50	6,32	9,89	7,22
Vascular plant cover (%)	Mean	22,23	49,71	7,75	38,20	65,60	39,30	77,20	27,79	68,60	15,43	45,00	30,90	51,20	15,50	39,80
	SD	19,26	17,12	9,47	18,14	11,28	20,37	20,36	19,95	22,30	12,70	11,98	13,25	20,77	14,56	12,68
	Min	0,00	19,00	0,00	9,00	54,00	5,00	54,00	0,00	45,00	0,00	28,00	8,00	34,00	0,00	26,00
	Max	62,00	70,00	26,00	58,00	83,00	83,00	95,00	77,00	90,00	54,00	56,00	53,00	85,00	56,00	59,00