www.czasopisma.pan.pl PAN POLSKA AKADEMIA NAUK www.journals.pan.pl

POLISH POLAR RESEARCH
vol. 41 no. 2, pp. 151-186, 2020 DOI: 10.24425/ppr.2020.133011

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

Paulina WIETRZYK-PEŁKA[1], Beata CYKOWSKA-MARZENCKA[2],
Fumino MARUO[3], Wojciech SZYMAŃSKI[4] and Michał Hubert WĘGRZYN[1]

[1]Professor Z. Czeppe Department of Polar Research and Documentation, Institute of Botany, Faculty of Biology, Jagiellonian University, Gronostajowa 3, 30-387 Kraków, Poland

[2]Department of Mycology, W. Szafer Institute of Botany Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland

[3]Department of Biological Sciences, Faculty of Science and Engineering, Chuo University, 1-13-27, Kasuga, Bunkyo-ku, 112-8551, Tokyo, Japan

[4]Department of Pedology and Soil Geography, Institute of Geography and Spatial Management, Faculty of Geography and Geology, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland

corresponding author < paulina.wietrzyk@gmail.com>

ORCID ID:
PWP: 0000-0002-1324-2012
BCM: 0000-0002-5468-4909
MHW: 0000-0001-7638-4803
WS: 0000-0002-5894-5176

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 cryptogram 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 m^2, 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

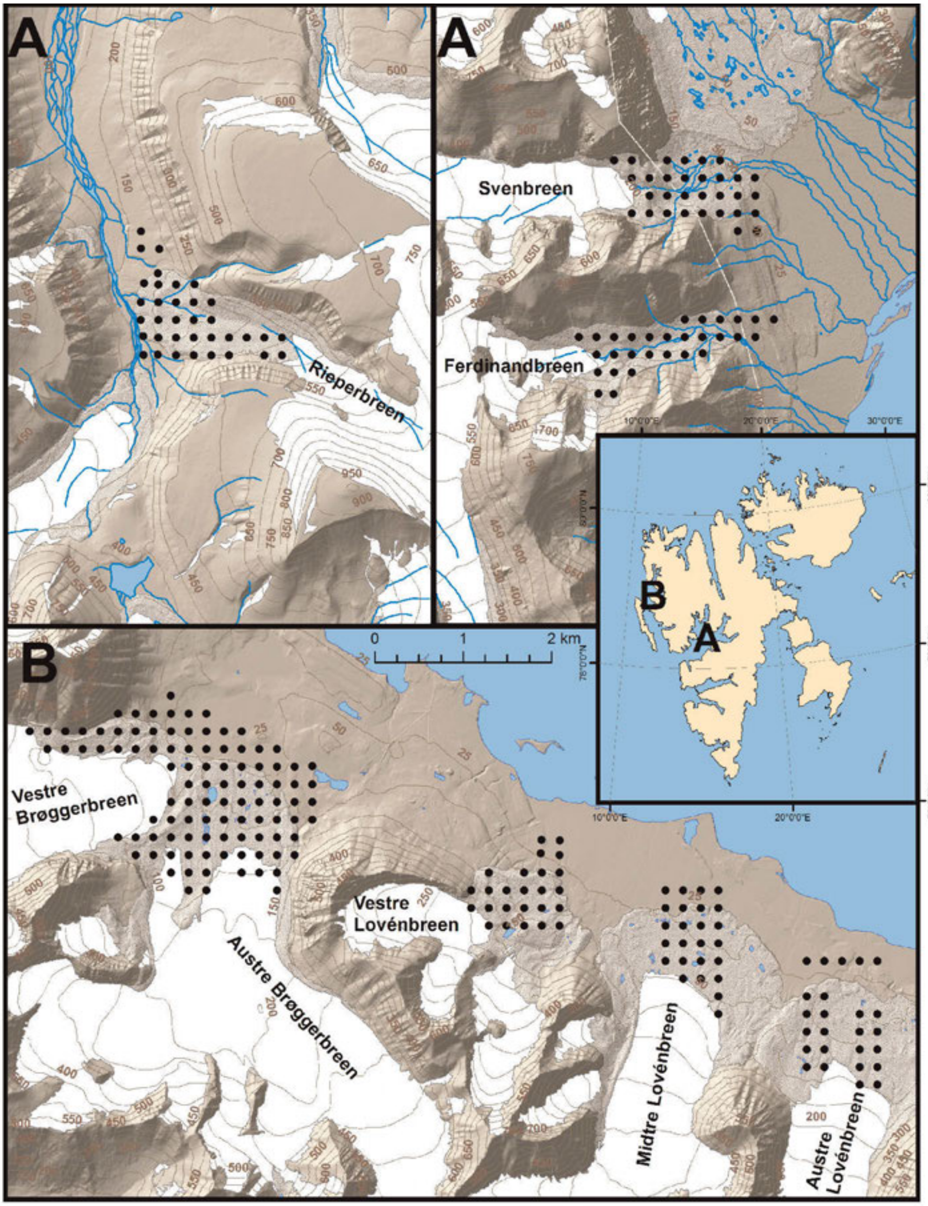

Fig. 1. Location of study areas and sampling plots (black dots). (A): Rieperbreen, Ferdinandbreen and Svenbreen; (B): Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen (© Norwegian Polar Institute 2019; http://www.npolar.no).

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 $TWI = \ln(SCA/\tan\varphi)$, 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 × 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 × 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 × 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*

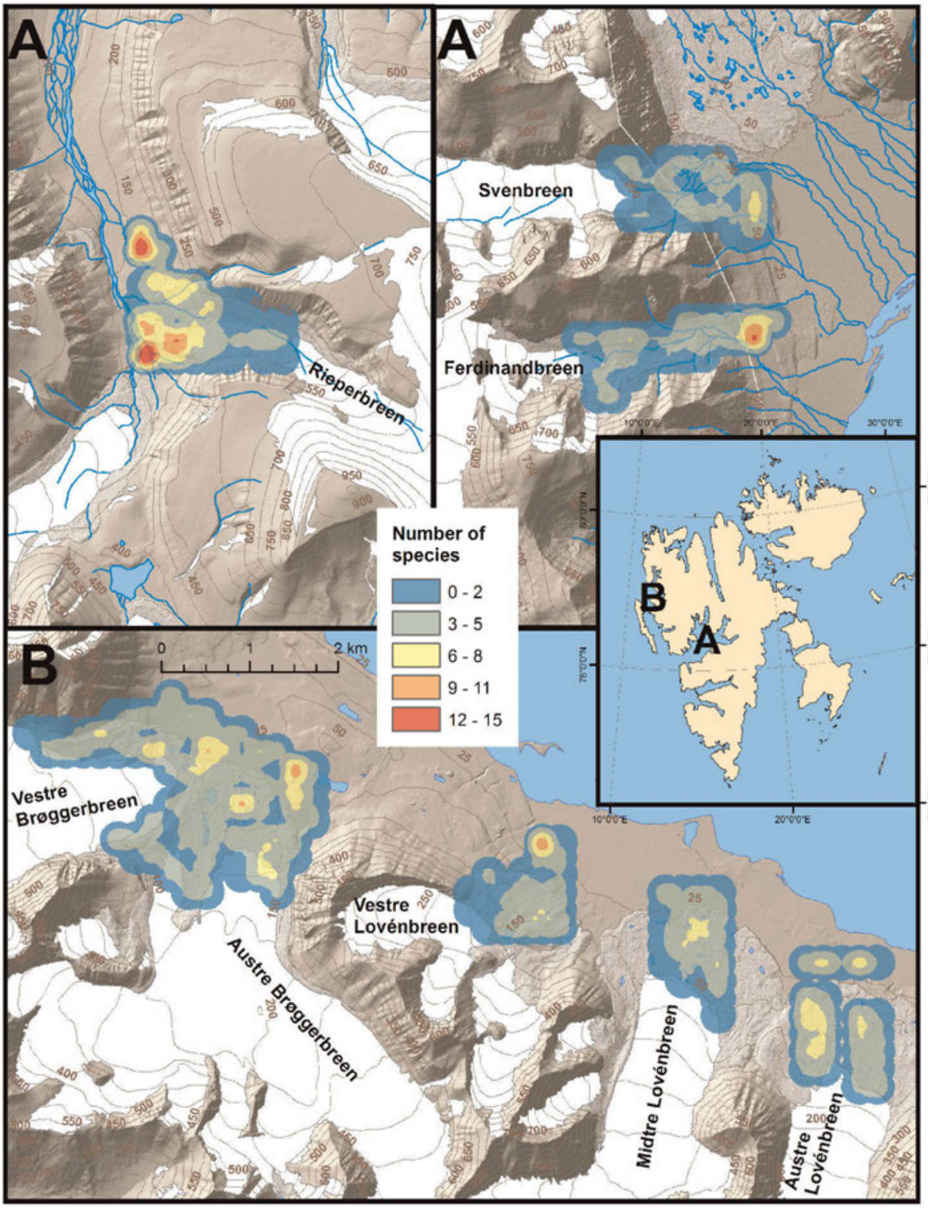

Fig. 2. Species richness in the study areas. (A): Rieperbreen, Ferdinandbreen and Svenbreen; (B): Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen (© Norwegian Polar Institute 2019; http://www.npolar.no).

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

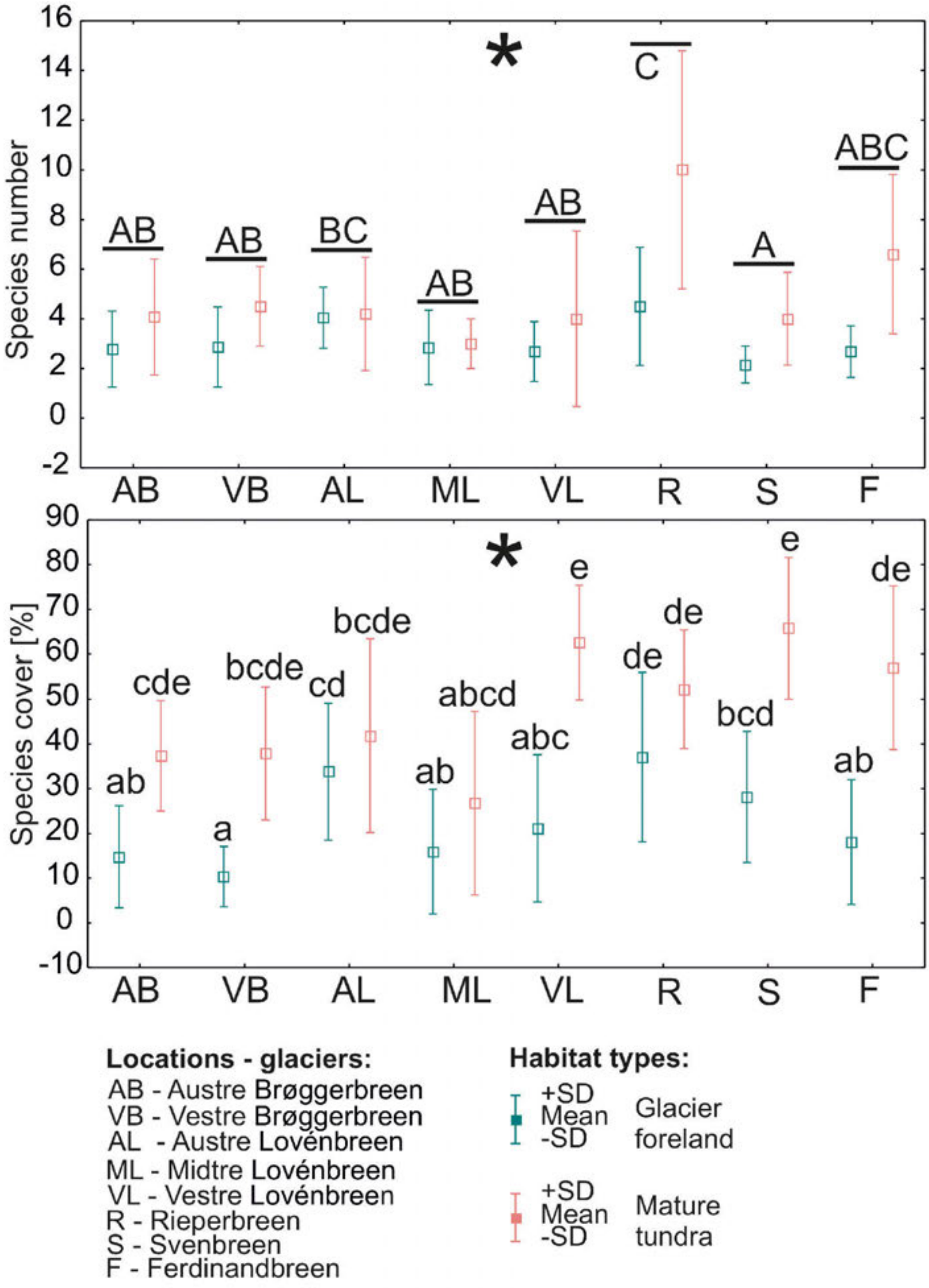

Fig. 3. Mean±SD of number and cover of species including habitat type (foreland vs tundra) and location (glacier foreland). The results of ANOVA and Tukey's tests are presented graphically ($p < 0.05$). The different letters above the bars indicate statistically significant differences: the capital letters 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 cilindricum* (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, *Gymnomitrion 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	***Encalypta procera***	**0.665**	*Racomitrium lanuginosum*	0.39	***Oncophorus virens***	**0.316**
	Bryum pseudotriquetrum var. *pseudotriquetrum*	0.566				
	Ditrichum flexicaule	0.677				
	Distichium capillaceum	0.614				
ML	*Bryum pseudotriquetrum* var. *pseudotriquetrum*	0.566	***Didymodon acutus***	**0.359**		
	Distichium capillaceum	0.614				
VL	*Ditrichum flexicaule*	0.677			***Neoorthocaulis hyperboreus***	**0.324**
	Distichium capillaceum	0.614				

Glacier foreland	**$p \leq 0.001$**	**phi**	**$0.001 \leq p < 0.01$**	**phi**	**$0.01 \leq p < 0.05$**	**phi**
AB	***Distichium hagenii***	**0.498**				
	Bryum arcticum	0.483				
VB	*Bryum arcticum*	0.483	***Hymenoloma crispulum***	**0.404**		
			Schistidium papillosum	**0.346**		
S	***Distichium inclinatum***	0.766				
	Ditrichum cyilindricum	0.550				
F	*Psilopilum laevigatum*	0.422			***Encalypta alpina***	**0.367**
	Distichium capillaceum	0.614			*Pohlia drummondii*	0.373
					Pohlia nutans	0.358
					Pogonatum dentatum	0.333
R	***Polytrichum hyperboreum***	**0.679**	***Pohlia wahlenbergii***	**0.500**	***Anthelia juratzkana***	**0.340**
	Polytrichum piliferum	**0.519**	***Pogonatum urnigerum***	0.392	*Pohlia drummondii*	0.373
	Trilophozia quinquedentata	**0.480**	*Racomitrium lanuginosum*	0.39	*Pohlia nutans*	0.358
	Polytrichum strictum	**0.439**			*Pogonatum dentatum*	0.333
	Psilopilum laevigatum	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					***Psilopilum laevigatum***	**0.632**
ML			*Distichium capillaceum*	0.677		
VL						
AB			***Polytrichum hyperboreum***	**0.655**		
VB			***Orthothecium strictum***	**0.612**		
S			*Distichium capillaceum*	0.677		
F			***Ditrichum cylindricum***	**0.706**	***Blepharostoma trichophyllum***	**0.686**
					Aneura pinguis	**0.592**
					Pohlia nutans	0.632
R	*Pohlia cruda*	0.874	***Dicranum laevidens***	**0.762**	***Gymnomitrion corallioides***	**0.640**
			Ptilidium ciliare	**0.732**	***Lophozia wenzelii***	**0.632**
					Polytrichum strictum	**0.632**
					Pohlia nutans	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_2O	0.14	0.05	0.96	0.536
Na^+	0.21	0.05	0.87	0.629
P_2O_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

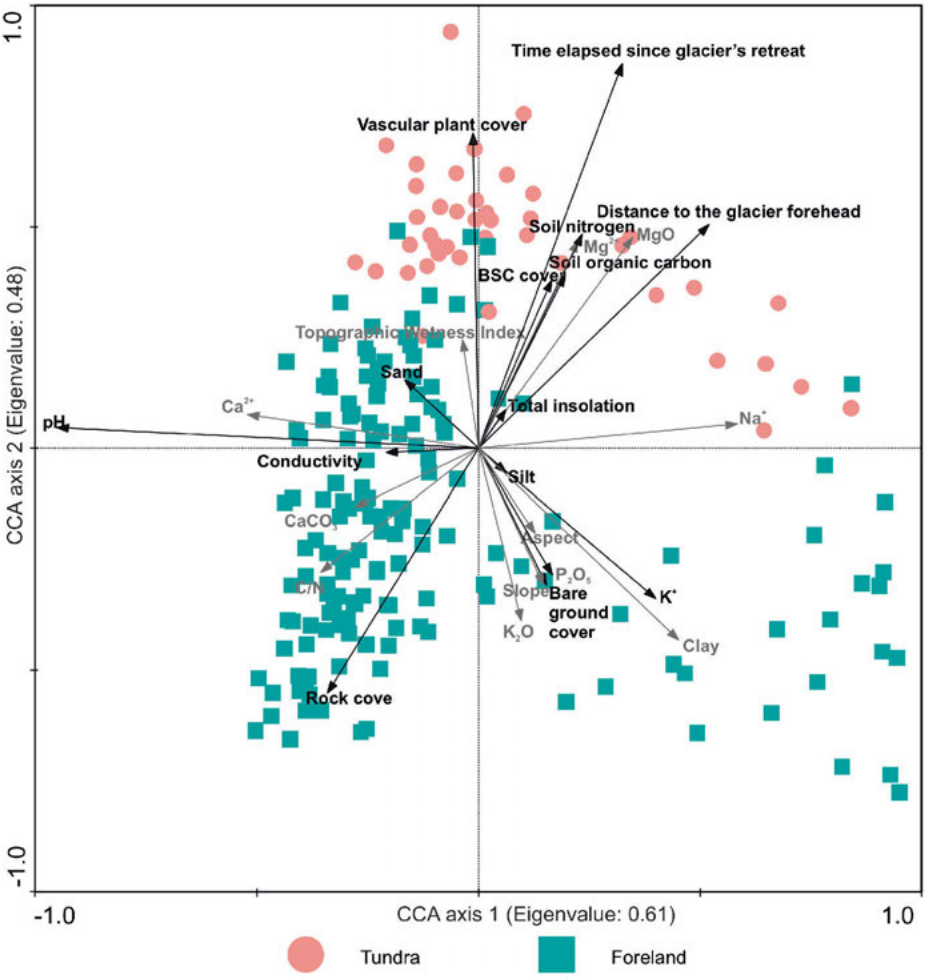

Fig. 4. CCA biplot with plots and environmental variables. Variables identified as significant in forward selection procedure are in black, while insignificant in grey (Table 4).

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* Schleich. *ex* 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 nigritum* (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*

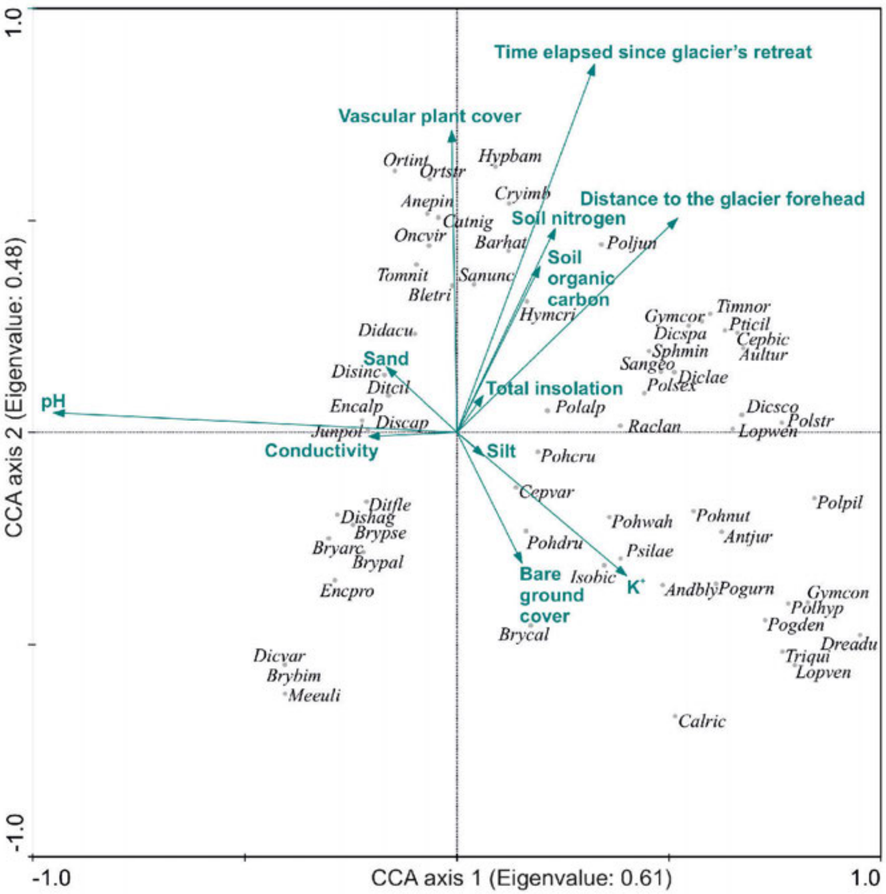

Fig. 5. CCA biplot with species and significant environmental variables identified in forward selection procedure (Table 4). Species fit range is between 3 and 100% (i.e. 105 species were reduced to 62). Abbreviations of species names: *Andbly – Andreaea blytii*; *Anepin – Aneura pinguis*; *Antjur – Anthelia juratzkana*; *Aultur – Aulacomnium turgidum*; *Barhat – Barbilophozia hatcheri*; *Bletri – Blepharostoma trichophyllum*; *Bryarc – Bryum arcticum*; *Brybim – Bryum bimum*; *Brycal – Bryum calophyllum*; *Brypal – Bryum pallescens*; *Brypse – Bryum pseudotriquetrum*; *Calric – Calliergon richardsonii*; *Catnig – Catoscopium nigritum*; *Cepbic – Cephalozia bicuspidata*; *Cepvar – Cephaloziella varians var. arctica*; *Cryimb – Cryptocolea imbricata*; *Diclae – Dicranum laevidens*; *Dicsco – Dicranum scoparium*; *Dicspa – Dicranum spadiceum*; *Dicvar – Dicranella varia*; *Didacu – Didymodon acutus*; *Discap – Distichium capillaceum*; *Dishag – Distichium hagenii*; *Disinc – Distichium inclinatum*; *Ditcil – Ditrichum cilindricum*; *Ditfle – Ditrichum flexicaule*; *Dreadu – Drepanocladus aduncus*; *Encalp – Encalypta alpina*; *Encpro – Encalypta procera*; *Gymcon – Gymnomitrion concinnatum*; *Gymcor – Gymnomitrion corallioides*; *Hymcri – Hymenoloma crispulum*; *Hypbam – Hypnum bambergeri*; *Isobic – Isopaches bicrenatus*; *Junpol – Jungermannia polaris*; *Lopven – Lophozia ventricosa*; *Lopwen – Lophozia wenzelii*; *Meeuli – Meesia uliginosa*; *Oncvir – Oncophorus virens*; *Ortint – Orthothecium intricatum*; *Ortstr – Orthothecium strictum*; *Pogden – Pogonatum dentatum*; *Pogurn – Pogonatum urnigerum*; *Pohcru – Pohlia cruda*; *Pohdru – Pohlia drummondii*; *Pohnut – Pohlia nutans*; *Pohwah – Pohlia wahlenbergii*; *Polalp – Polytrichastrum alpinum*; *Polhyp – Polytrichum hyperboreum*; *Poljun – Polytrichum juniperinum*; *Polpil – Polytrichum piliferum*; *Polsex – Polytrichastrum sexangulare*; *Polstr – Polytrichum strictum*; *Psilae – Psilopilum laevigatum*; *Pticil – Ptilidium ciliare*; *Raclan – Racomitrium lanuginosum*; *Sangeo – Sanionia georgicouncinata*; *Sanunc – Sanionia uncinata*; *Sphmin – Sphenolobus minutus*; *Timnor – Timmia norvegica*; *Tomnit – Tomentypnum nitens*; *Triqui – Trilophozia quinquedentata*.

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 cilindricum* 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 Brož (*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-Pełka 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.

References

Amesbury M.J., Roland T.P., Royles J., Hodgson D.A., Convey P., Griffiths H. and Charman D.J. 2017. Widespread biological response to rapid warming on the Antarctic Peninsula. *Current Biology* 27: 1616–1622.

Anderson K.J. 2007. Temporal patterns in rates of community change during succession. *The American Naturalist* 169: 780–793.

Belkina O.A. and Vilnet A.A. 2015. Some aspects of the moss population development on the Svalbard glaciers. *Czech Polar Reports* 5: 160–175.

Beringer J., Lynch A.H., Chapin III F.S., Mack M. and Bonan G.B. 2001. The representation of arctic soils in the land surface model: the importance of mosses. *Journal of Climate* 14: 3324–3335.

Burga C.A., Krüsi B., Egli M., Wernli M., Elsener S., Ziefle M., Fisher T. and Mavris C. 2010. Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): Straight forward or chaotic? *Flora-Morphology, Distribution, Functional Ecology of Plants* 205: 561–576.

Büscher P., Koedam N. and Van Speybroeck D. 1990. Cation-exchange properties and adaptation to soil acidity in bryophytes. *New Phytologist* 115: 177–186.

Chapin F.S. III, Oechel W.C., Cleve K. Van and Lawrence W. 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. *Oecologia* 74: 310–315.

Conrad O., Bechtel B., Bock M., Dietrich H., Fischer E., Gerlitz L., Wehberg J., Wichmann V. and Böhner J. 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4, *Geoscientific Model Development* 8: 1991–2007.

Damsholt K. 2002. *Illustrated Flora of Nordic Liverworts and Hornworts*. Nordic Bryological Society, Lund.

Damsholt K. 2013. *The liverworts of Greenland*. Oikos Editorial Office, Lund.

Davey M.L., Skogen M.J., Heegaard E., Halvorsen R., Kauserud H. and Ohlson M. 2017. Host and tissue variations overshadow the response of boreal moss-associated fungal communities to increased nitrogen load. *Molecular Ecology* 26: 571–588.

Descamps S., Aars J., Fuglei E., Kovacs K.M., Lydersen C., Pavlova O., Pedersen A.Ø., Ravolainen V. and Strøm H. 2017. Climate change impacts on wildlife in a High Arctic archipelago – Svalbard, Norway. *Global Change Biology* 23: 490–502.

Dierssen K. 2001. *Distribution, ecological amplitude and phytosociological characterization of European bryophytes*. Bryophytorum Bibliotheca 56. J. Cramer in der Gebr.-Borntraeger-Verl.-Buchh, Berlin-Stuttgart.

Ellis L.T., Aleffi M., Alegro A., Segota V., Asthana A.K., Gupta R., Singh V.J., Bakalin V.A., Bednarek-Ochyra H., Cykowska-Marzencka B., Benitez A., Borovichev E.A., Vilnet A.A., Konstantinova N.A., Buck W.R., Cacciatoro C., Sérgio C., Csiky J., Deme J., Kovács D., Damsholt K., Enroth J., Erzberger P., Fedosov V.E., Fuertes E., Gradstein S.R., Gremmen N.J.M., Hallingbäck T., Jukonienė I., Kiebacher T., Larraín J., Lebouvier M., Lüth M., Mamontov Y.U.S., Potemkin A.D., Nemeth C.S., Nieuwkoop J.A.W., Nobis M., Węgrzyn M., Wietrzyk P., Osorio F., Parnikoza I., Virchenko V.M,. Peralta D.F., Carmo D.M., Plášek V., Skoupá Z., Poponessi S., Venanzoni R., Puche F, Purger D., Reeb C., Rios R., Rodriguez-Quiel E., Arrocha C., Sabovljević M.S., Nikolić N., Sabovljević A.D., Dos Santos E.L., Segarra-Moragues J.G., Ştefănuţ S. and Stončius D. 2016a. New national and regional bryophyte records, 48. *Journal of Bryology* 38: 235–259.

Ellis L.T., Agcagil E., Kirmaci M., Aleffi M., Bakalin V.A., Bednarek-Ochyra H., Cykowska-Marzencka B., Stryjak-Bogacka M., Bojaca G.F.P., Fantacelle L.B., Araújo C.A.T., Maciel-Silva A.S., Bruno Silva J., Calleja J.A., Cano M.J., Castillo Diaz J., Gabriel R., Dias Dos Santos N., Enroth J., Erzberger P., Garilleti R., Hájek M, Hedenäs L., Heras P., Infante M., Kiebacher T., Koczur A., Krawczyk R., Kučera J., Lebouvier M., Lüth M., Mazimpaka V., Vigalondo B., Lara F., Nagy J., Németh C.S., Kovács A., Nobis M., Węgrzyn M., Wietrzyk P., Norhazrina N., Vanderpoorten A., Nowak A., Poponessi S., Gigante D., Venanzoni R., Plášek V., Rangel Germano S., Schäfer-Verwimp A., Sérgio C., Claro D., Garcia C.A., Shirzadian S., Akhoondi Darzikolaei S., Stebel A., Suleiman M., Yong K.-T., Virchenko V.M., Vončina G., Yoon Y.-J., Choi H.-G. and Kim J.H. 2016b. New national and regional bryophyte records, 49. *Journal of Bryology* 38: 327–347.

Ellis L.T., Afonina O.M., Andriamiarisoa R.L., Bednarek-Ochyra H., Cykowska-Marzencka B., Stryjak-Bogacka M., Bell N.E., Boiko M., Callaghan D.A., Campisi P., Dia M.G., Marino M.L., Provenzano F., Eckstein J., Enroth J., Erzberger P., Ezer T., Gargano M.L., Ginzburg E., Górski P., Gradstein S.R., Reeb C., Hannoire C., Infante M., Jukonienė I., Kushnevskaya E.V., Lebouvier M., Nagy J., Opmanis A., Plášek V., Skoupá Z., Sabovljević M.S., Sabovljević A.D., Shevock J.R., Singh D.K., Majumdar S., Skudnik M., Uselienė A., Venturella G., Węgrzyn M., Wietrzyk P., Yoon Y.-J., Kim J.H. and Yücel E. 2017. New national and regional bryophyte records, 53. *Journal of Bryology* 39: 368–387.

Favero-Longo S.E., Worland M.R., Convey P., Smith R.I.L., Piervittori R., Guglielmin M. and Cannone N. 2012. Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, maritime Antarctic. *Antarctic Science* 24: 323–336.

Fick S.E. and Hijmans R.J. 2017. WorldClim 2: new 1 — km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*37: 4302–4315.

Forbes B.C., Fauria M.M. and Zetterberg P. 2010. Russian Arctic warming and ‘greening’ are closely tracked by tundra shrub willows. *Global Change Biology* 16: 1542–1554.

Frey W., Frahm J.-P., Fischer E. and Lobin W. 2006. *The Liverworts, Mosses and Ferns of Europe*. Harley Books, Essex.

Frisvoll A.A and Elvebakk A. 1996. Bryophytes. *In*: A. Elvebakk and P. Prestrund (Eds) *A catalogue of Svalbard plants, fungi, algae and cyanobacteria.* Part 2. Norsk Polarinstitut Skrifer. Norsk Polarinstitutt, Oslo 198: 57–172.

GLIME J.M. 2017. Nutrient Relations: Uptake and Location. Chapter 8–4. *In*: J.M Glime (Ed.) *Bryophyte Ecology*. Michigan Technological University, International Association of Bryologists, Michigan: 1–36.

GORNALL J.L., JÓNSDÓTTIR I.S., WOODIN S.J. and VAN DER WAL R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia* 153: 931–941.

GORNALL J.L., WOODIN S.J., JÓNSDÓTTIR I.S. and VAN DER WAL R. 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. *Oecologia* 166: 769–782.

HAMMER Ø., HARPER D.A.T. and RYAN P.D. 2001. PAST-palaeontological statistics, ver. 1.89. *Palaeontologia Electronica* 4: 1–9.

HANSEN B.B., ISAKSEN K., BENESTAD R.E., KOHLER J., PEDERSEN Å.Ø., LOE L.E., COULSON S.J., LARSEN J.O. and VARPE Ø. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letter* 9: 114021.

HAUGLAND J.E. and BEATTY S.W. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* 32: 145–153.

HILL M.O., BELL N., BRUGGEMAN-NANNENGA M.A., BRUGUÉS M., CANO M.J., ENROTH J., FLATBERG K.I., FRAHM J.-P., GALLEGO M.T., GARILLETI R., GUERRA J., HEDENÄS L., HOLYOAK D.T., HYVÖNEN J., IGNATOV M.S., LARA F., MAZIMPAKA V., MUÑOZ J. and SÖDERSTRÖM L. 2006. An annotated checklist of the mosses of Europe and Macaronesia. *Journal of Bryology* 28: 198–267.

HUDSON J.M.G. and HENRY G.H.R. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* 90: 2657–2663.

HUGHES J.G. 1982. Penetration by rhizoids of the moss *Tortula muralis* Hedw. into well cemented oolitic limestone. *International Biodeterioration* 18: 43–46.

IMS R.A. and EHRICH D. 2013. Arctic terrestrial Ecosystem. *In*: H.Meltofte (Ed.) *Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity*, Conservation of Arctic Flora and Fauna, Akureyri: 384–440.

KOEDAM N. and BÜSCHER P. 1983. Studies on the possible role of cation exchange capacity in the soil preference of mosses. *Plant and Soil* 70: 77–93.

KETTERINGS Q., REID S. and RAO R. 2007. *Cation exchange capacity (CEC). Fact sheet, 22*. College of Agriculture and Life Sciences, Cornell University, New York.

KUC M. 1970. Additions to the Arctic Moss Flora. V. The role of mosses in plant succession and the development of peat on Fitzwilliam Owen Island (Western Canadian Arctic). *Revue Bryologique et Lichénologique* 37: 931–939.

KUC M. 1996. The vegetation zones of the Hornsund area (SW Spitsbergen). *In:* W.E. Krawczyk (Ed.) *23rd Polar Symposium*, University of Silesia, Sosnowiec: 67–82.

LONGTON R.E. 1988. *Biology of polar bryophytes and lichens*. Cambridge University Press, Cambridge.

LOEPPERT R.H. and SUAREZ D.L. 1996. Carbonate and gypsum. *In*: D.L. Sparks, A.L. Page, P.A. Helmke, R.H. Loeppert, P.N. Soltanpour, M.A. Tabatabai, C.T. Johnston, M.E. Sumner (Eds) *Methods of Soil Analysis. Part 3. Chemical Methods*. Soil Science Society of America Book Series vol. 5. American Society of Agronomy-Soil Science Society of America, Wisconsin: 437–474.

LUKOVIĆ J.B., BAJAT B.J., KILIBARDA M.S. and DEJAN, J. 2015. High resolution grid of potential incoming solar radiation for Serbia. *Thermal Science* 19: 427–435.

MATTIVI P., FRANCI F., LAMBERTINI A., and BITELLI G. 2019. TWI computation: a comparison of different open source GISs. *Open Geospatial Data, Software and Standards* 4: 1–12.

MIZUNO K. 2005. Glacial fluctuation and vegetation succession on Tyndall Glacier, Mt Kenya. *Mountain Research and Development* 25: 68–76.

MOREAU M., LAFFLY D., JOLY D. and BROSSARD T. 2005. Analysis of plant colonization on an arctic moraine since the end of the Little Ice Age using remotely sensed data and a Bayesian approach. *Remote Sensing of Environment* 99: 244–253.

Moreau M., Mercier D., Laffly D. and Roussel E. 2008. Impacts of recent paraglacial dynamics on plant colonization: a case study on Midtre Lovénbreen foreland, Spitsbergen (79°N). *Geomorphology* 95: 48–60.

Moreau M., Laffly D. and Brossard T. 2009. Recent spatial development of Svalbard strand flat vegetation over a period of 31 years. *Polar Research* 28: 364–375.

Nyholm E. 1987, 1990, 1993, 1998. *Illustrated Flora of Nordic Mosses*. Fasc. 1–4. Oikos Editorial Office, Lund.

Oechel W.C. and Sveinbjörnsson B. 1978. Primary production processes in arctic bryophytes at Barrow, Alaska. *In*: L.L Tieszen (Eds) *Vegetation and production ecology of an Alaskan Arctic tundra. Ecological Studies (Analysis and Synthesis)*. Springer, New York 29: 269–298.

Qgis Development Team 2019. QGIS Geographic Information System. Available via Open Source Geospatial Foundation Project http://qgis.osgeo.org.

Pharo E.J., Beattie A.J. and Binns D. 1999. Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology* 13: 282–292.

Porter P.R., Evans A.J., Hodson A.J., Lowe A.T. and Crabtree M.D. 2008. Sediment–moss interactions on a temperate glacier: Falljökull, Iceland. *Annals of Glaciology* 48: 25–31.

Porter C., Morin P., Howat I., Noh M.-J., Bates B., Peterman K., Keesey S., Schlenk M., Gardiner J., Tomko K., Willis M., Kelleher C., Cloutier M., Husby E., Foga S., Nakamura H., Platson M., Wethington M., Williamson C., Bauer G., Enos J., Arnold G., Kramer W., Becker P., Doshi A., D'souza C., Cummens P., Laurier F. and Bojesen M. 2018. ArcticDEM. Available via Harvard Dataverse. https://www.pgc.umn.edu/data/arcticdem/.

Prach K., Košnar J., Klimešová J. and Hais M. 2010. High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biology* 33: 635–639.

Proctor M.C.F. 2000. The bryophyte paradox: tolerance of desiccation, evasion of drought. *Plant Ecology* 151: 41–49.

R Core Team 2013. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Rydgren K., Halvorsen R., Töpper J.P. and Njøs J.M. 2014. Glacier foreland succession and the fading effect of terrain age. *Journal of Vegetation Science* 25: 1367–1380.

Rydin H. and Jeglum J. 2006. *The Biology of Peatlands*. Oxford University Press, Oxford.

Saxena D. 2004. Uses of bryophytes. *Resonance* 9: 56–65.

Skre O. and Oechel W.C. 1981. Moss functioning in different Taiga ecosystems in interior Alaska. 1. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. *Oecologia* 48: 50–59.

Smith A.J.E. 2004. *The Moss Flora of Britain and Ireland*. Cambridge University Press, Cambridge.

Smith V.R. and Russell S. 1982. Acetylene reduction by bryophyte-cyanobacteria associations on a Subantarctic island. *Polar Biology* 1: 153–157.

Solheim B., Endal A. and Vigstad H. 1996. Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. *Polar Biology* 16: 35–40.

Solheim B. and Zielke M. 2002. Associations Between Cyanobacteria and Mosses. *In*: A.N. Rai, B. Bergman and U. Rasmussen (Eds) *Cyanobacteria in Symbiosis*. Springer, Dordrecht.

Söderström L., Hagborg A., Von Konrat M., Bartholomew-Began S., Bell D., Briscoe L., Brown E., Cargill D.C., Costa D.P., Crandall-Stotler B.J., Cooper E.D., Dauphin G., Engel J.J., Feldberg K., Glenny D., Gradstein S.R., He X., Heinrichs J., Hentschel J., Ilkiu-Borges A.L., Katagiri T., Konstantinova N.A., Larraín J., Long D.G., Nebel M., Pócs T., Puche F., Reiner-Drehwald E., Renner M.A.M., Sass-Gyarmati A., Schäfer-Verwimp A., Moragues J.G.S., Stotler R.E., Sukkharak P., Thiers B.M., Uribe J., Váňa J., Villarreal J.C., Wigginton M., Zhang L. and Zhu R.-L. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1–821.

STREET L.E., STOY P.C., SOMMERKORN M., FLETCHER B.J., SLOAN V.L., HILL T.C. and WILLIAMS M. 2012. Seasonal bryophyte productivity in the sub-Arctic: a comparison with vascular plants. *Functional Ecology* 26: 365–378.

STURM M., RACINE C. and TAPE K. 2001. Climate change - Increasing shrub abundance in the Arctic. *Nature* 411: 546–547.

TER BRAAK C.J.F. and ŠMILAUER P. 2002. *CANOCO 4.5 reference manual and CanoDraw for Windows user's guide: software for canonical community ordination*. Ithaca: Microcomputer Power, New York.

THOMAS G.W. 1996. Soil pH and soil acidity. *In*: D.L. Sparks, A.L. Page, P.A. Helmke, R.H. Loeppert, P.N. Soltanpour, M.A. Tabatabai, C.T. Johnston and M.E. Sumner ME (Eds) *Methods of Soil Analysis. Part 3. Chemical Methods.* Soil Science Society of America Book Series vol. 5. American Society of Agronomy-Soil Science Society of America, Wisconsin: 475–490.

TISHKOV A.A. 1986. Primary succession in arctic tundra on the west coast of Spitsbergen (Svalbard). *Polar Geography and Geology* 10: 148–156.

TURETSKY M.R., BOND-LAMBERTY B., EUSKIRCHEN E., TALBOT J., FROLKING S., MCGUIRE A.D. and TUITTILA E.S. 2012. The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist* 196: 49–67.

VAN WIJK M.T., CLEMMENSEN K.E., SHAVER G.R., WILLIAMS M., CALLAGHAN T.V., CHAPIN III F.S., CORNELISSEN J.H.C., GOUGH L., HOBBIE S.E., S. JONASSON S., LEE J.A., MICHELSEN A., PRESS M.C., RICHARDSON S.J. and RUETH H. 2003. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology* 10: 105–123.

WALKER M.D., WAHREN C.H., HOLLISTER R.D., HENRY G.H.R., AHLQUIST L.E., ALATALO J.M., BRET-HARTE M.S., CALEF M.P., CALLAGHAN T.V., CARROLL A.B., EPSTEIN H.E., JÓNSDÓTTIR I.S., KLEIN J.A., MAGNÚSSON B., MOLAU U., OBERBAUER S.F., REWA S.P., ROBINSON C.H., SHAVER G. R., SUDING K.N., THOMPSON C.C., TOLVANEN A., TOTLAND Ø., TURNER P.L., TWEEDIE C.E., WEBBER P.J. and WOOKEY P.A. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103: 1342–1346.

WATSON E.V. 1960. A quantitative study of the bryophytes of chalk grassland. *Journal of Ecology* 48: 397–414.

WIETRZYK P., WĘGRZYN M. and LISOWSKA M. 2016. Vegetation diversity and selected abiotic factors influencing the primary succession process on the foreland of Gåsbreen, Svalbard. *Polish Polar Research* 37: 493–509.

WIETRZYK P., ROLA K., OSYCZKA P., NICIA P., SZYMAŃSKI W. and WĘGRZYN M. 2018. The relationships between soil chemical properties and vegetation succession in the aspect of changes of distance from the glacier forehead and time elapsed after glacier retreat in the Irenebreen foreland (NW Svalbard). *Plant and Soil* 428: 195–211.

YOSHIKAWA K., BOLTON W.R., ROMANOVSKY V.E., FUKUDA M. and HINZMAN L.D. 2003. Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *JGR Atmospheres* 107(D1): FFR4-1–FFR4-14.

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); clastic 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			

References:

CAVM TEAM 2003. *Circumpolar Arctic vegetation map 1:7.500.000*, CAFF, Akureyri.

DALLMANN W.K. 1999. *Lithostratigraphic lexicon of Svalbard. Upper Palaeozoic to Quaternary bedrock. Review and recommendations for nomenclature use.* Committee on the Stratigraphy of Svalbard, Norwegian Polar Institute, Tromsø.

DALLMANN W.K., KJÆRNET T. and NØTTVEDT A. 2001. *Geological map of Svalbard 1:100 000. Sheet C9Q Adventdalen.* Temakart 31/32. Norwegian Polar Institute, Tromsø

DALLMANN W.K., OHTA Y., BIRJUKOV A.S., KARNOUŠENKO E.P., SIROTKIN A.N., and PIEPJOHN K. 2004. *Geological map of Svalbard, 1:100 000. Sheet C7G Dicksonfjorden.* Norsk Polarinstitutt Temakart 35. Norwegian Polar Institute, Tromsø.

DALLMANN W.K., PIEPJOHN K., BLOMEIER D. and ELVEVOLD S. 2009. *Geological map of Svalbard, 1:100 000. Sheet C8G Billefjorden.* Norsk Polarinstitutt Temakart 43. Norwegian Polar Institute, Tromsø.

JÓNSDÓTTIR I.S. 2005. Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. *Biology and Environment-Proceedings of the Royal Irish Academy* 105(3):155–165.

SAALMANN K., and THIEDIG F. 1998. Structural Evolution of the Tertiary West Spitsbergen Fold-and-Thrust Belt on Broggerhalvoya, NW-Spitsbergen. *Polarforschung* 68:111–119.

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	*Amblystegium serpens*	moss								X			X	X			X	
2	*Andreaea blyttii*	moss														X		X
3	*Aneura pinguis*	liverwort			X					X								
4	*Anthelia juratzkana*	liverwort						X								X		
5	*Aulacomnium turgidum*	moss						X										
6	*Barbilophozia hatcheri*	liverwort					X								X			
7	*Blepharostoma trichophyllum*	liverwort	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X
8	*Blindia acuta*	moss													X			X
9	*Brachythecium turgidum*	moss												X				
10	*Bryobrittonia longipes*	moss									X							
11	*Bryoerythrophyllum recurvirostrum*	moss										X						
12	*Bryum algovicum*	moss									X	X						
13	*Bryum arcticum*	moss	X								X	X		X	X			
14	*Bryum argenteum*	moss			X						X	X						
15	*Bryum bimum (=B. pseudotriquetrum* var. *bimum*)	moss									X							
16	*Bryum calophyllum*	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	*Bryum gemmiparum*	moss													X			
18	*Bryum pallescens*	moss	X	X					X	X	X	X	X	X	X	X	X	X
19	*Bryum pseudotriquetrum* var. *pseudotriquetrum*	moss					X				X	X	X	X	X	X		
20	*Bucklandiella sudetica (=Racomitrium sudeticum)*	moss										X						
21	*Calliergon richardsonii*	moss														X		
22	*Campyliadelphus chrysophyllus*	moss														X	X	
23	*Campylium arcticum (=Drepanocladus arcticus)*	moss		X														
24	*Campylium stellatum*	moss	X	X	X	X					X	X					X	X
25	*Campylopus schimperi*	moss	X								X							
26	*Catoscopium nigritum*	moss	X	X														
27	*Cephalozia bicuspidata*	liverwort						X										
28	*Cephaloziella varians* var. *arctica*	liverwort				X		X			X	X	X	X	X	X		X
29	*Ceratodon purpureus*	moss												X	X			
30	*Cryptocolea imbricata*	liverwort		X														
31	*Dicranella varia*	moss									X							
32	*Dicranum acutifolium*	moss	X															
33	*Dicranum elongatum*	moss						X		X							X	
34	*Dicranum laevidens*	moss			X			X			X		X			X		
35	*Dicranum scoparium*	moss	X															
36	*Dicranum spadiceum*	moss	X	X			X	X								X		
37	*Didymodon acutus*	moss			X	X	X							X	X			
38	*Didymodon asperifolius*	moss											X					
39	*Didymodon fallax*	moss									X							
40	*Didymodon tophaceus*	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	*Distichium capillaceum*	moss			X	X			X	X	X	X	X	X	X	X	X	X
42	*Distichium hagenii*	moss	X	X							X	X					X	X
43	*Distichium inclinatum*	moss	X						X	X	X	X		X		X	X	X
44	*Ditrichum cylindricum (=Trichodon cylindricus)*	moss		X	X				X	X	X	X			X	X	X	X
45	*Ditrichum flexicaule*	moss	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X
46	*Drepanocladus aduncus*	moss														X		
47	*Encalypta alpina*	moss				X			X		X		X	X	X	X	X	X
48	*Encalypta procera*	moss			X					X	X	X	X					X
49	*Encalypta rhabdocarpa*	moss										X						
50	*Gymnomitrion concinnatum*	liverwort														X		
51	*Gymnomitrion corallioides*	liverwort	X	X			X	X										
52	*Hygrohypnum alpestre*	moss			X							X						
53	*Hygrohypnum polare*	moss										X						
54	*Hymenoloma crispulum (=Dicranoweissia crispula)*	moss			X			X		X	X	X				X	X	
55	*Hymenostylium recurvirostrum*	moss	X									X						
56	*Hypnum bambergeri*	moss								X								
57	*Hypnum revolutum*	moss		X														
58	*Isopaches bicrenatus*	liverwort									X					X		
59	*Isopterygiopsis pulchella*	moss		X				X			X	X						
60	*Jungermannia polaris*	liverwort						X		X	X	X	X	X		X		X
61	*Lophozia ventricosa*	liverwort														X		
62	*Lophozia wenzelii*	liverwort						X						X		X		
63	*Marsupella arctica*	liverwort												X				
64	*Meesia uliginosa*	moss										X						
65	*Neoorthocaulis hyperboreus*	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	*Niphotrichum ericoides (=Racomitrium ericoides)*	moss									X						X	
67	*Oncophorus virens*	moss	X				X						X					
68	*Oreas martiana*	moss	X															
69	*Orthothecium intricatum*	moss		X														
70	*Orthothecium strictum*	moss		X														
71	*Pogonatum dentatum*	moss														X		X
72	*Pogonatum urnigerum*	moss							X							X		
73	*Pohlia cruda*	moss	X					X		X	X	X	X	X		X		X
74	*Pohlia drummondii*	moss	X	X				X			X	X	X			X	X	X
75	*Pohlia nutans*	moss						X		X				X		X		X
76	*Pohlia proligera*	moss											X					
77	*Pohlia wahlenbergii*	moss	X	X				X		X	X	X		X	X	X	X	X
78	*Polytrichastrum alpinum*	moss			X	X	X	X			X		X			X		
79	*Polytrichastrum sexangulare*	moss	X	X		X	X									X		X
80	*Polytrichum hyperboreum*	moss	X													X		
81	*Polytrichum juniperinum*	moss						X		X								
82	*Polytrichum piliferum*	moss						X								X		
83	*Polytrichum strictum*	moss														X		
84	*Psilopilum laevigatum*	moss			X											X		X
85	*Pterigynandrum filiforme*	moss													X			
86	*Ptilidium ciliare*	liverwort	X					X			X					X		
87	*Racomitrium lanuginosum*	moss	X				X	X					X			X		
88	*Sanionia georgicouncinata*	moss	X	X												X		
89	*Sanionia uncinata*	moss	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
90	*Sauteria alpina*	liverwort		X														
91	*Schistidium frigidum*	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	*Schistidium papillosum*	moss										X						
93	*Schistidium rivulare*	moss										X						
94	*Schljakovianthus quadrilobus*	liverwort													X			
95	*Scorpidium revolvens*	moss	X															
96	*Scorpidium scorpioides*	moss	X															
97	*Sphenolobus minutus*	liverwort					X	X					X			X		
98	*Syntrichia ruralis*	moss								X				X				
99	*Timmia bavarica*	moss												X	X			
100	*Timmia norvegica*	moss					X	X										
101	*Timmia sibirica*	moss													X			
102	*Tomentypnum nitens*	moss	X	X					X	X	X							X
103	*Tortella fragilis*	moss										X						
104	*Tortella tortuosa*	moss										X					X	
105	*Trilophozia quinquedentata*	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_2O (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	27,21	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	16,58	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	15,11	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	55,89	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	0,07	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	0,03	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	0,04	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	0,13	0,07	0,06	0,12	0,06
P_2O_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	1,37	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	0,48	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	0,76	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	1,93	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	5,16	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	0,83	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	4,29	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	6,46	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	15,40	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	6,73	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	10,00	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	27,00	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	26,95	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	9,98	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	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	36,31	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	52,46	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	9,74	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	28,46	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	67,04	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	0,34	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	0,15	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	0,12	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	0,59	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	70,40	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	24,57	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	27,00	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	110,00	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	4,81	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	1,20	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	2,83	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	7,89	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	666,45	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	96,44	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	447,24	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	817,03	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	0,08	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	0,03	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	0,03	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	0,15	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	0,29	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	0,14	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	0,01	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	0,68	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	25,20	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	18,53	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	1,00	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	68,00	83,00	83,00	95,00	77,00	90,00	54,00	56,00	53,00	85,00	56,00	59,00