Patterns and drivers of cryptogam and vascular plant diversity in glacier forelands

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HIGHLIGHTS

- Several same factors affect diversity and cover of cryptogams and vascular plants.
- Vascular plant cover has positive effect on diversity and cover of cryptogams.
- Cryptogam diversity significantly differs between locations and habitat type.
- Cryptogam cover in foreland varies between studied locations.
- Study location and habitat type affect diversity and cover of vascular plants.

GRAPHICAL ABSTRACT
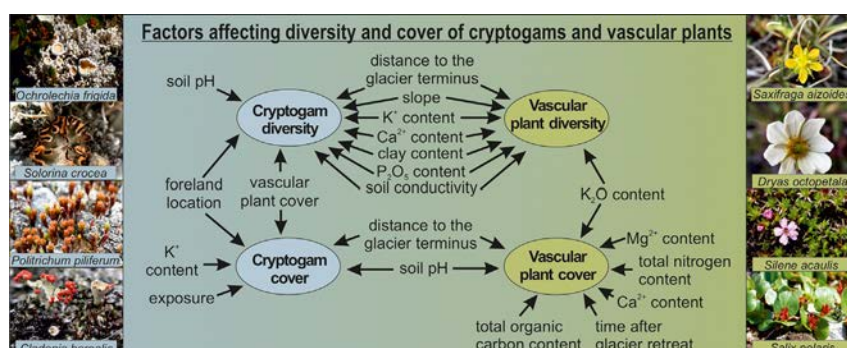
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ABSTRACT

Vascular and nonvascular plants are affected by environmental factors determining their distribution and shaping their diversity and cover. Despite the cryptogam commonness in Arctic communities, previous studies have often focused on limited number of factors and their impact on only selected species of vascular plants or cryptogams. Our study aimed to investigate in detail the differences in species diversity and cover of cryptogams and vascular plants in the glacier forelands and mature tundra on Svalbard. Furthermore, we determined the biotic and abiotic factors that affected diversity, cover and distribution of cryptogam and vascular plant species. In 2017, we established 201 plots in eight locations (each including habitat type of foreland and mature tundra) and surveyed species abundance, sampled soils and environmental data. Results revealed that diversity and cover of analysed groups differed significantly between locations and habitat types, except for cryptogam cover in mature tundra in terms of location. Distance to the glacier terminus, slope, soil conductivity, nutrient content, and clay content impacted both plant groups' diversity. In contrast, distance to the glacier terminus, nutrient content and soil pH affected their cover. In addition, for cryptogam diversity and cover, foreland location and vascular plant cover were also important, while for vascular plant cover time elapsed after glacier retreat was significant. Distribution of both groups' species in forelands was associated with time elapsed after glacier retreat, soil pH, and nutrient contents. Soil texture and distance to the glacier terminus additionally influenced cryptogam distribution. The positive impact of vascular plants on cryptogam diversity and cover indicates complex relationships between these groups, even in forelands' relatively simple communities. As the cryptogam

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diversity in the polar areas is high but still largely unknown, future studies on species ecology and climate change impact on vegetation should consider both vascular plants and cryptogams and interactions between these groups.

1. Introduction

Arctic plant communities are among the most sensitive and the most affected by climate change (Huntington and Fox, 2005; Post et al., 2009). Cryptogams especially are undergoing substantial changes in their abundance, biomass and composition due to alteration of their environments (Bates and Farmer, 1992; Callaghan et al., 2004; Cornelissen et al., 2007). Cryptogams are spore-bearing organisms such as lichens and bryophytes (Belnap and Lange, 2013). They differ from vascular plants in their growth forms, lack of specialized structures to regulate water loss, ability to survive in a dormant state during desiccation, as well as nutrition strategy including limited ability to take up soil nutrients (Pointing et al., 2015; Roos et al., 2019). In comparison to vascular plants, their small size and the difficulty with taxonomic identification contribute to their underrepresentation in ecological studies and, consequently, our understanding of their diversity (Cornelissen et al., 2007).

Similarly, most studies on environmental variables affecting species occurrence have focused on vascular plants rather than cryptogams (Wietrzyk et al., 2016; Nakatsubo et al., 2010; Prach and Rachlewicz, 2012). This underrepresentation is particularly true for the Arctic tundra vegetation, despite cryptogams being a major component of Arctic plant communities (Longton, 1997; Breen and Lévesque, 2008; Belnap and Lange, 2013). Cryptogams participate in various ecological processes, such as nitrogen and carbon cycling, organic matter accumulation, soil moisture retention, and bio-stabilization against soil erosion (Belnap and Lange, 2013; Shively et al., 2001; Garcia-Pichel and Wojciechowski, 2009; Pushkareva et al., 2017; Rippin et al., 2018). Since Arctic cryptogams are subject to substantial changes, with potential impact on ecosystem functioning, it is important to identify factors that determine species occurrence and reveal how modification of these factors can affect vascular plant and cryptogam communities in the future.

The Arctic's cold climate promotes ecosystems characterised by low vascular plant cover that provide a niche for cryptogams (Cornelissen et al., 2001; Jung et al., 2018). On the other hand, positive relationships between selected vascular and cryptogam species have also been observed, such as vascular plants' facilitating role for bryophyte growth (Longton, 1997; Pharo et al., 1999). Nevertheless, cryptogams are usually patchily distributed between vascular plants. In spaces where vascular plants are less abundant, cryptogams can dominate the community. This dominance is the case in glacier forelands, which are primary successional and initial habitats. Competition from vascular plants is still an important factor limiting cryptogam distribution (Cornelissen et al., 2001; Gornall et al., 2011; Belnap and Lange, 2013). However, in glacier forelands, vegetation succession is tightly linked to the underlying substrate characteristics (i.e., age, exposure, moisture, terrain, and microsite conditions) (Matthews and Whittaker, 1987; Jones and del Moral, 2005; Moreau et al., 2008, 2009; Wojtuń et al., 2008; Burga et al., 2010; Wietrzyk et al., 2016; Eichel, 2019). Both the physical and chemical properties of soils are important for several species of cryptogams and vascular plants (Skre and Oechel, 1981; Longton, 1988; Gornall et al., 2007; Burga et al., 2010; Rydgren et al., 2014; Wietrzyk et al., 2018; Eichel, 2019). Distance to the glacier terminus (the end of the glacier) can also have a strong influence on the development of vascular plants and cryptogams (Haugland and Beatty, 2005; Jones and del Moral, 2005; Rodriguez et al., 2018; Wietrzyk et al., 2016, 2018). However, previous studies have been limited to a single or a few species of vascular plants or cryptogams together with a small number of selected environmental factors, which may lead to incorrect conclusions of diversity patterns (Rydgren et al., 2014).

Therefore, our understanding of drivers and the co-colonising of glacier forelands by cryptogam and vascular plant species is limited.

This study aimed to investigate the differences in species diversity (measured by species richness, Shannon index and dominance index), distribution and cover of cryptogams and vascular plants in the forelands and mature tundra of eight glaciers on Svalbard. Furthermore, we determined multiple biotic and abiotic factors affecting diversity, distribution and cover of cryptogams and vascular plants. Finally, we compared if the same set of factors impacted the diversity and cover of cryptogams and vascular plants. Based on the theory of primary succession (Walker and del Moral, 2003), we expect cryptogams to be dominant in foreland habitats because they are well adapted to nutrient-poor soils, while vascular plants require more nutrients from their environment, reducing their presence and minimizing the amount of competition for cryptogams in forelands. We tested the following hypotheses: (1) diversity and cover of vascular plants is higher in mature habitats, while cryptogams dominate and show higher diversity in initial habitats of forelands because of differences in their nutrient requirements; and (2) apart from distance to the glacier terminus, nutrient availability affects the diversity and cover of vascular plants, while diversity and cover of cryptogams are primarily limited by competition from vascular plants.

Climate change is a potential threat to cryptogam survival (Callaghan et al., 2004). However, increasing temperatures combined with other environmental changes have led to the expansion of ice-free areas across the Arctic and alpine regions, providing new land areas for colonisation by vascular and non-vascular plant species. Therefore, to study the processes taking part in glacier forelands, including species interactions and environmental impact on organisms, is truly of global significance.

2. Materials and methods

2.1. Study area

We conducted our study in glacier foreland and mature tundra of the following eight locations in the Svalbard archipelago: Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, Vestre Lovénbreen, Rieperbreen, Svenbreen, and Ferdinandbreen glaciers (Fig. 1).

Similar geological and climatic features characterise the locations of Austre Lovénbreen, Midtre Lovénbreen, Vestre Lovénbreen. The bedrock is composed of phyllite, quartzite, and schist (from Proterozoic), dolomite and limestone (from Carboniferous and Permian), as well as sandstone, shale, and conglomerate (from Carboniferous and Paleocene) (Saalmann and Thiedig, 2000). Austre Brøggerbreen and Vestre Brøggerbreen locations are also characterised by Permian chert, shale, sandstone, limestone and Triassic shale, siltstone, and sandstone (Saalmann and Thiedig, 2000). The soils of all these locations belong to Haplic Cryosols according to WRB classification (Hengl et al., 2017). There is some variation in the mean annual air temperature (MAAT) and mean annual precipitation (MAP) for the different locations. The MAAT of Austre Lovénbreen, Midtre Lovénbreen, Vestre Lovénbreen is −6 °C, while mean annual precipitation reaches 420 mm (Fick and Hijmans, 2017). The MAAT of Austre Brøggerbreen and Vestre Brøggerbreen is one degree colder, and MAP is 10 mm higher than Austre, Midtre and Vestre Lovénbreen (Fick and Hijmans, 2017). Northern Arctic tundra vegetation (prostrate dwarf-shrub/herb tundra of subzone B) occurs in all locations (CAVM, 2003; Jónsdóttir, 2005).

The bedrock of the Rieperbreen location is characterised by sandstone, siltstone, mudstone and shale from the Cretaceous, Paleocene and Eocene periods (Dallmann et al., 2001). Contrastingly, Svenbreen and Ferdinandbreen locations consist mainly of granitic gneiss, migmatite, amphibolite, quartzite, mica schist, and marble (from the Proterozoic); sandstone, siltstone, shale, and conglomerate (from the late Devonian); clastic and carbonate rocks (from the Carboniferous); and carbonate rocks (from the Permian) (Dallmann, 1999; Dallmann et al., 2004, 2009). The soils are Haplic Cryosols and Turbic Cryosols (Hengl et al., 2017). These locations have a MAAT of −8 °C (Fick and Hijmans, 2017). Svenbreen and Ferdinandbreen locations have a MAP of 300 mm, while Rieperbreen is 100 mm higher (Fick and Hijmans, 2017). Vegetation represents middle Arctic tundra (prostrate/hemiprostrate dwarf-shrub tundra of subzone C) (CAVM, 2003; Jónsdóttir, 2005).

2.2. Fieldwork

In the summer of 2017, we established 201 plots (plot number per location and habitat type are presented in the Supplementary file 1) in eight locations, including initial habitats in glacier foreland (blue dots in Fig. 1) and mature habitats (orange dots in Fig. 1). In each plot, we collected data on the percent cover of cryptogam and vascular plant species using a 1 m² frame divided into 100 10 cm² squares. The presence of species in one square corresponded to 1% cover; therefore, each species' cover in the plot was determined in the range 1–100%. Vascular plant and cryptogam species unable to be identified in the field were collected and identified using traditional taxonomy methods. For full details of the species identification methodology, see Wietrzyk-Pełka et al. (2018, 2020a). After specimen collection, within each plot, soil samples were collected for subsequent laboratory analyses. For each plot, after plant and biological soil crust removal, we collected four soil cores (diameter of ca. 10 cm) to a depth of ca. 10 cm and then mixed them into one soil sample.

2.3. Spatial analyses

For each plot, we calculated the time elapsed since the glacier's retreat (based on historical glacier extent from satellite images), distance to the current glacier terminus, slope, exposure, and topographic wetness index (TWI). Time elapsed since the glacier's retreat and distance to the current glacier terminus were obtained by digitalisation of glacier terminus in the past on available satellite data. We used available Landsat (2020) and Modified Copernicus Sentinel (2020) data as a source. Slope, exposure, and TWI were calculated in SAGA GIS 7.0.0 software (Conrad et al., 2015) using ArcticDEM (2 m grid) as a terrain data source (Porter et al., 2018). We computed TWI to determine the tendency of an area to accumulate water according to the formula 1:

$$TWI = ln \frac{SCA}{\tan \varphi} \tag{1}$$

where *SCA* is the Specific Catchment Area and φ is the slope angle, and the assumption of uniform soil properties is set (Mattivi et al., 2019).

For preparation of the study area map, we used a dataset from the Norwegian Polar Institute (2020) service and ArcGIS Desktop 10.7 software (ESRI, Redlands, California, USA).

2.4. Laboratory analysis

Soil samples were oven-dried at 30 °C for 24 h. Dried soil samples were then passed through a 2 mm sieve to remove the coarse material (fraction >2 mm). We determined total carbon and total nitrogen (TN) content via gas chromatography using a CHN elemental analyser (Vario Micro Cube, Elementar, Hanau, Germany) in triplicate. We measured carbonate content using the volumetric calcimeter method (Loeppert and Suarez, 1996). We calculated total organic carbon content (TOC) in calcareous samples by subtracting the carbon content in carbonates from the total carbon content. We determined the concentration of exchangeable cations, i.e., calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^+), and sodium (Na^+) ions via flame atomic absorption spectrometry (FAAS) after extraction with 1 M ammonium acetate ($C_2H_7NO_2$) (Sumner and Miller, 1996). Plant available phosphorus (P_2O_5) and potassium (K_2O) were extracted according to the protocol given by Egner-Riehm (Egner et al., 1960). The concentration of available phosphorus and potassium was determined using the colorimetric method (Kuo, 1996) and FAAS, respectively. Plant available magnesium (MgO) was extracted according to the protocol given by Schachtschabel (1954) and measured by FAAS. We measured soil pH (Thomas, 1996) and electrical conductivity (COM-80, HM Digital, California, USA) in distilled water (1:2.5 soil/water ratio) after 24 h when the solution was in equilibrium with the soil and therefore stable. Lastly, we determined soil particle-size distribution (fraction <1 mm) using laser diffraction (Mastersizer 3000, Malvern, UK).

2.5. Data analysis

In each plot, we calculated: (1) species richness (number of recorded species), (2) Shannon index, (3) dominance index, and (4) cover (%) using the statistical software PAST 3.25 (Hammer et al., 2001).

The Shannon index included the cover of individuals and the number of species calculated according to the formula 2:

$$\sum_i \frac{n_i}{n} \, ln \, \frac{n_i}{n} \tag{2}$$

where n_i is the cover of species *i*.

The dominance index ranges from 0 (all species equally present) to 1 (one species dominates the community completely) and was calculated according to the formula 3:

$$\sum_i \left(\frac{n_i}{n}\right)^2 \tag{3}$$

where n_i is the cover of species *i*.

To verify differences in species richness, Shannon index, dominance index and cover between habitat type (mature tundra and glacier foreland), as well as geographical location (Rieperbreen, Ferdinandbreen, Svenbreen, Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen) we performed a two-way analysis of variance (habitat type × location) followed by post hoc Tukey's HSD (Honestly Significant Difference) test for unequal sample size ($p < 0.05$) for cryptogams and vascular plants, separately. Prior to the analysis, we verified the normality of the distribution and the equality of variances using the Kolmogorov-Smirnov test ($p > 0.05$) and Levene's test ($p > 0.05$), respectively. The data that did not meet the assumption of variance homogeneity and distribution normality were Box-Cox-transformed. Due to lack of variance homogeneity within habitat type groups of cryptogam cover after Box-Cox data transformation, we tested the differences in the cryptogam cover in mature tundra between locations using Kruskal-Wallis test ($p < 0.05$). The differences in the cryptogam cover in forelands between locations were tested with one-way ANOVA followed by Tukey's HSD test for unequal sample size ($p < 0.05$).

We conducted stepwise multiple linear regression analysis using forward variable selection (with a threshold of $p < 0.05$ to entry) to investigate the variables that affect the diversity and cover of cryptogams and vascular plants in the forelands. Prior to the analysis, we verified the linearity assumptions between variables and the distribution normality of residuals using the Kolmogorov-Smirnov test ($p > 0.05$). We checked the potential collinearity of the predictors by calculating the variance inflation factors (VIFs) using Statgraphics Centurion 18 (StatPoint, Inc.).
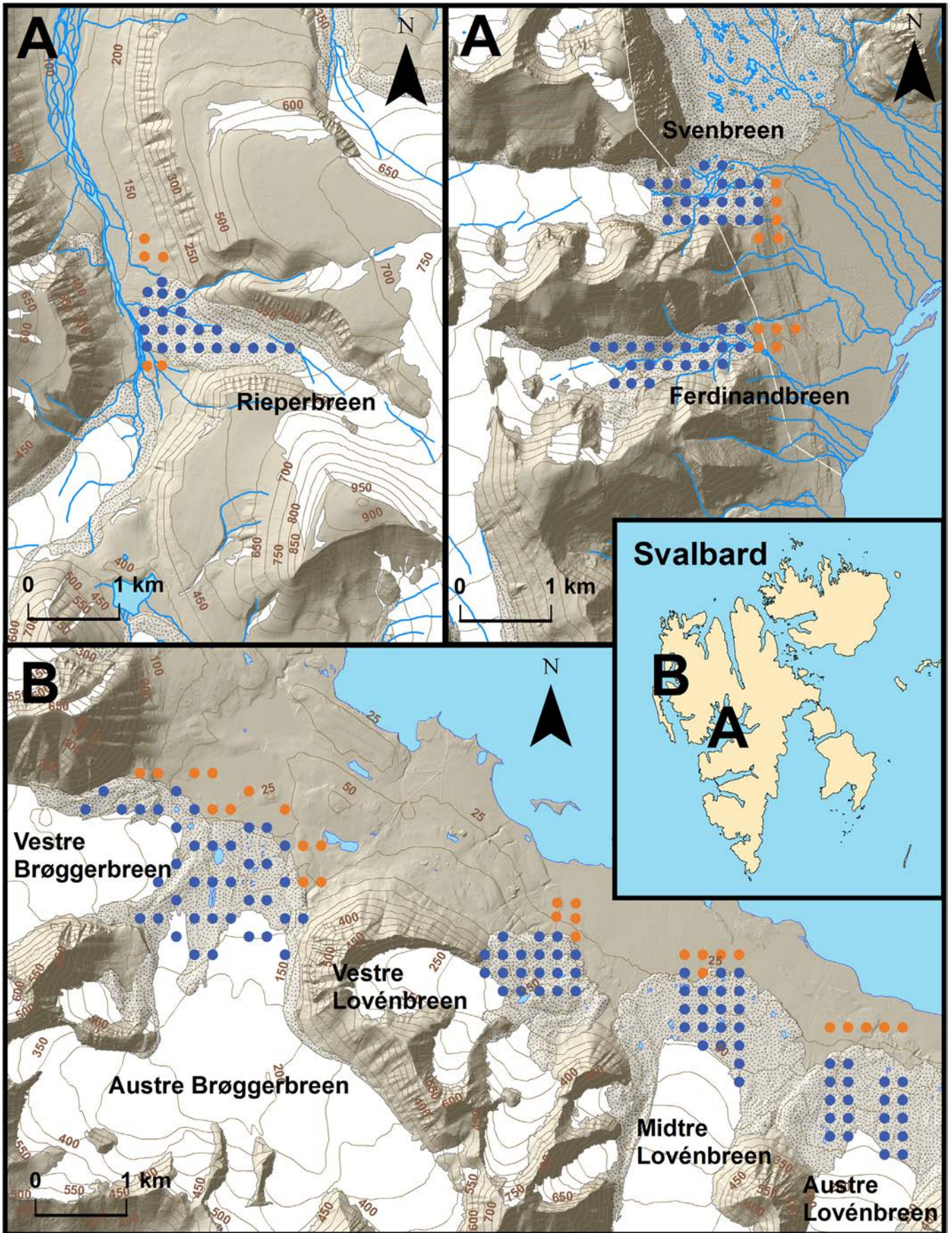
Table 1

The results of two-way ANOVA for cryptogams for the effects of habitat type (mature tundra vs glacier foreland) and geographical location (glacier) on biotic variables, with the exception of cryptogamic cover for which the results of one-way ANOVA for the effects of location in forelands and Kruskal-Wallis test for the effects of location in mature tundra are presented. Significant effects ($p < 0.05$) are provided in bold.

Variable	Location				Habitat type				Location × habitat type				Error
	F/H	p	df	Partial η^2	F	p	df	Partial η^2	F	p	df	Partial η^2	df
Cryptogams													
Cover – forelands	**9.50**	**<0.001**	7										149
Cover – mature tundra	9.09	0.247	7										
Dominance index	**2.13**	**0.043**	7	0.08	**37.20**	**<0.001**	1	0.17	0.92	0.489	7	0.03	183
Species richness	**3.74**	**0.001**	7	0.13	**115.07**	**<0.001**	1	0.39	1.09	0.371	7	0.04	183
Shannon index	**2.29**	**0.029**	7	0.08	**50.69**	**<0.001**	1	0.22	1.00	0.435	7	0.04	183

To validate the regression model, obtain reliable regression coefficients and detect the extreme cases, we performed a detailed residual analysis. Next, we calculated the Durbin-Watson statistic to evaluate the potential presence of a serial correlation of residuals. Since VIFs for sand and silt, Mg^{2+} and MgO, were >10, we only included sand and Mg^{2+} as predictor variables in the models. We performed stepwise multiple linear regression on separate data matrices for cryptogams and vascular plants. For cryptogams, 19 variables were included in the analysis (exposure of the plot, contents of Ca^{2+}, Mg^{2+}, K^+, Na^+, available P_2O_5, available K_2O, clay content, soil conductivity, distance to the glacier terminus, sand content, slope of the plot, soil pH, TOC content, TN content, time elapsed after glacier retreat, TWI, and vascular plant cover as well as geographical location as categorical variables). The same variables were included in the stepwise multiple linear regression analysis for vascular plants, except vascular plant cover. We conducted these analyses using the statistical software Statistica 13 (StatSoft, Tulsa, OK, USA).

We applied canonical correspondence analysis (CCA) to determine which environmental variables were related to species occurrence of cryptogams and vascular plants separately with the application of an automatic procedure for forward selection of the explanatory variable from the set of all available variables. For this purpose, we used CANOCO 4.5 (ter Braak and Šmilauer, 2002). Species data were square-root transformed to reduce the dominant contribution of abundant species, while rare species were down-weighted. Finally, we performed the Monte Carlo permutation test ($p < 0.05$) based on 9999 random permutations to assess the statistical significance of relationships between species and environmental factors.

3. Results

3.1. Cryptogam diversity and cover

Descriptive statistics of all environmental variables studied, including the division into geographical locations and habitat types, are presented in Supplementary file 1. Both habitat type and geographical location significantly affected cryptogamic species richness, Shannon index and dominance index ($p < 0.05$; Table 1, Fig. 2A–D). Shannon index and species richness were 1.5 times and 2.4 times higher, respectively, in the mature tundra compared to glacier forelands ($p < 0.001$; Fig. 2C, D). The opposite relationship was true for dominance index (Fig. 2B), which was always significantly lower in mature tundra than forelands. For geographical location, Rieperbreen location was characterised by the highest species richness, which was nearly two times higher than at Austre Brøggerbreen, Ferdinandbreen, Svenbreen, Vestre Brøggerbreen, and Vestre Lovénbreen locations ($p < 0.01$; Fig. 2D). Regarding the Shannon index, Austre Lovénbreen and Rieperbreen locations were ca. 1.5 times higher than at Austre Brøggerbreen and Ferdinandbreen locations ($p < 0.05$; Fig. 2C). The

remaining locations did not differ significantly from one another ($p > 0.05$). The dominance index was the highest at Austre Brøggerbreen and Ferdinandbreen locations and was significantly higher than at Austre Lovénbreen and Rieperbreen locations by two orders of magnitude (Fig. 2B). Cryptogam cover in forelands differed between particular location ($p < 0.05$), whereas within mature tundra habitat no differences between locations were found ($p > 0.05$). The highest cover was recorded at Austre Lovénbreen and Rieperbreen forelands, whereas the lowest at Austre Brøggerbreen, Ferdinandbreen and Vestre Brøggerbreen forelands (Fig. 2A). For all analysed diversity indices, habitat type accounted for more variance explained than geographical location (Table 1). For dominance index, 17% of the variation was due to habitat type, 8% due to location; for species richness, 39% of variation was due to habitat type, 18% due to location; while for Shannon index, 22% of variation was due to habitat type, 8% due to location (Table 1).

Distance to the glacier terminus, available P_2O_5 content and vascular plant cover were the only variables that significantly impacted both diversity metrics and cryptogams' cover ($p < 0.05$; Supplementary files 2–5). These predictors positively affected cryptogamic species richness, Shannon index and cover, whereas negatively impacted the dominance index ($p < 0.001$). The soil pH and electrical conductivity had a significant negative impact on cryptogamic species richness and cover (Supplementary files 2, 5). The cryptogamic species richness, Shannon index and cover were significantly and positively influenced by K^+ content (Supplementary files 2, 4, 5). Additionally, Ca^{2+} content and slope significantly affected the Shannon index, whereas clay content on species richness (Supplementary files 4, 5). Foreland location only had a significant effect on cryptogam species richness (Supplementary file 5).

Ten factors significantly affected cryptogam distribution (Fig. 3; Supplementary file 6) and divided species into two groups. The first group was associated with high content of TOC, K^+, Mg^{2+}, and clay, and greater distance to the glacier terminus and longer time elapsed after glacier retreat. The second group was associated with higher soil pH and electrical conductivity and higher content of Ca^{2+} and sand (Supplementary file 6). There was no clear division between lichens and bryophytes, and we recorded their presence in both distinguished groups (Fig. 3). Both the first axis and all canonical axes taken together showed statistical significance (F = 9.44, $p < 0.01$ and F = 2.18, $p < 0.01$, respectively).

3.2. Vascular plant diversity and cover

Descriptive statistics of all environmental variables studied, including the division into geographical locations and habitat types, are presented in Supplementary file 1. Both habitat type and geographical location significantly affected vascular plant cover, which was two times higher in the mature tundra than glacier forelands (Table 2;

Fig. 1. Location of study areas: (A) – Rieperbreen, Ferdinandbreen and Svenbreen; (B) – Austre Brøggerbreen, Vestre Brøggerbreen, Austre Lovénbreen, Midtre Lovénbreen, and Vestre Lovénbreen. Dots mark sampling plots: blue in glacier foreland, orange in mature tundra (Norwegian Polar Institute, 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
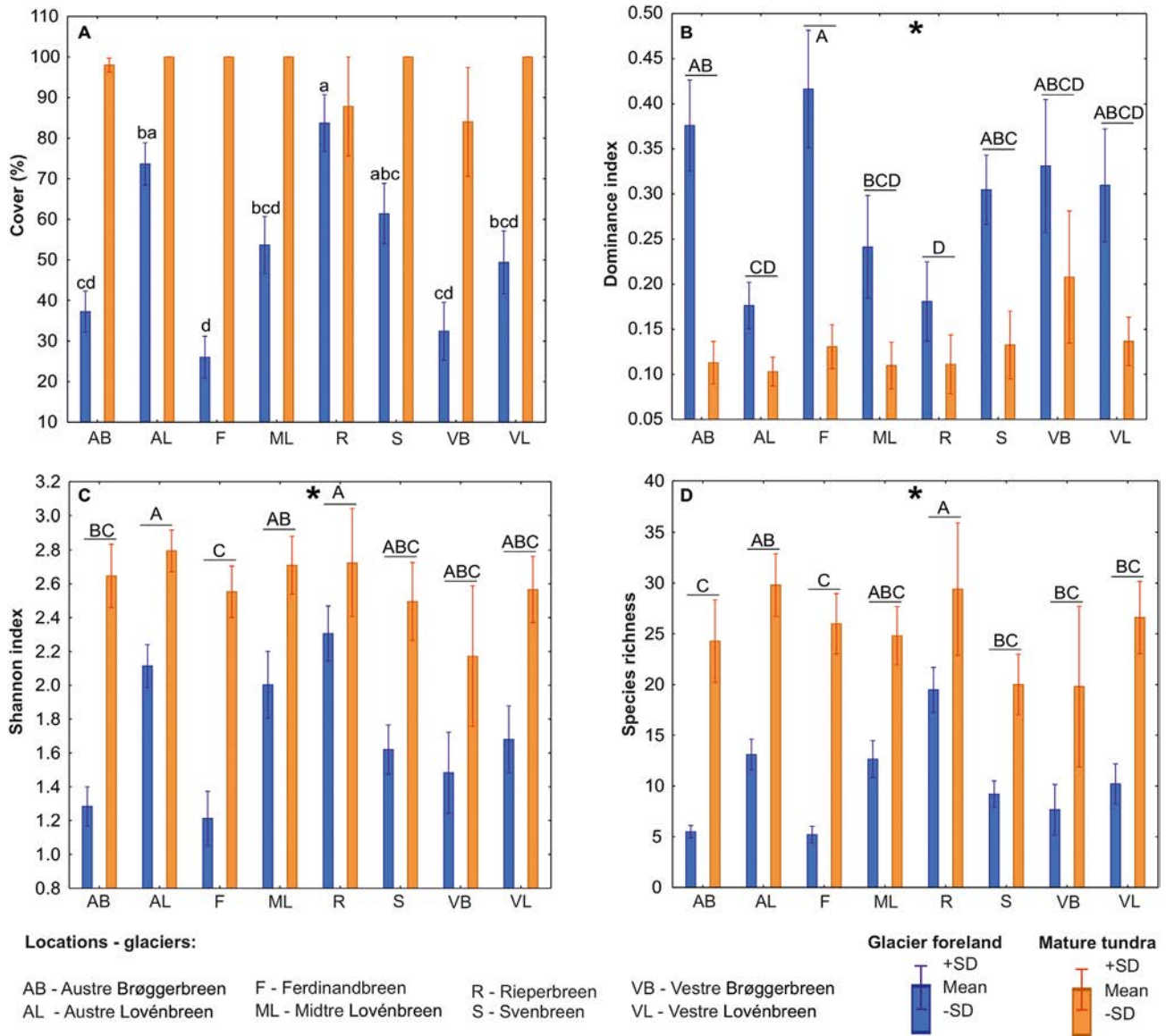
Fig. 2. Mean ± SD of cryptogam parameters including habitat type (foreland vs tundra) and location (glaciers). The results of ANOVA ($p < 0.05$) are presented graphically. The different letters above the bars indicate significant differences: the capital letters show the significant main effect of the location, while the asterisks (*) indicate the significant main effect of habitat type of two-way ANOVA. The lowercase letters correspond to one-way ANOVA results and indicate the statistically significant differences in cryptogam cover in forelands between locations (see Table 1 for detailed results).

Fig. 4A). Midtre Lovénbreen location showed the highest cover, which was 1.5 times higher than at Austre Brøggerbreen, and two times higher than at the Ferdinandbreen, Rieperbreen, and Vestre Brøggerbreen locations ($p < 0.001$; Fig. 4A). Habitat type and location also significantly affected vascular plant species richness, Shannon index and dominance index; however, there were also significant interactions between those variables (significant habitat type × location interaction) (Table 2; Fig. 4B–D). As a rule, species richness and Shannon index were higher in mature tundra than in forelands (from 0.9 times at Midtre Lovénbreen location to 4.1 times at Austre Brøggerbreen location) ($p < 0.001$). In contrast, dominance index was lower in mature tundra compared to forelands (from 0.9 times at Midtre Lovénbreen location to 2.6 times at Ferdinandbreen location) ($p < 0.001$; Fig. 4B–D).

Distance to the glacier terminus and available K_2O and/or K^+ content in soil significantly impacted species richness, cover, Shannon index, and dominance index of vascular plants (Supplementary files 7–10). Additionally, Ca^{2+} content significantly affected the cover and diversity metrics except for species richness. Available P_2O_5 content

positively affected Shannon index and species richness ($p < 0.05$; Supplementary files 9, 10), whereas clay content affected dominance index and species richness ($p < 0.01$; Supplementary files 8, 10). The highest number of significant predictor variables was included in the model for vascular plant cover. In addition to the factors mentioned above, there was a significant influence of soil pH, time elapsed after glacier retreat, content of TOC, TN and Mg^{2+} on this dependent variable (Supplementary file 7).

Seven environmental variables significantly impacted vascular plant distribution (Fig. 5; Supplementary file 11). The CCA separated vascular plants into two groups. The first group inhabited areas characterised by flatter terrain uncovered earlier from the ice, with higher Mg^{2+} and K^+ contents and lower soil pH and Ca^{2+} content. While the second group preferred areas uncovered later from the ice, which showed an opposite trend to the above-described, more mature foreland parts (Fig. 5; Supplementary file 11). The first axis and all canonical axes taken together were statistically significant (F = 17.42, $p < 0.01$ and F = 2.87, $p < 0.01$, respectively).
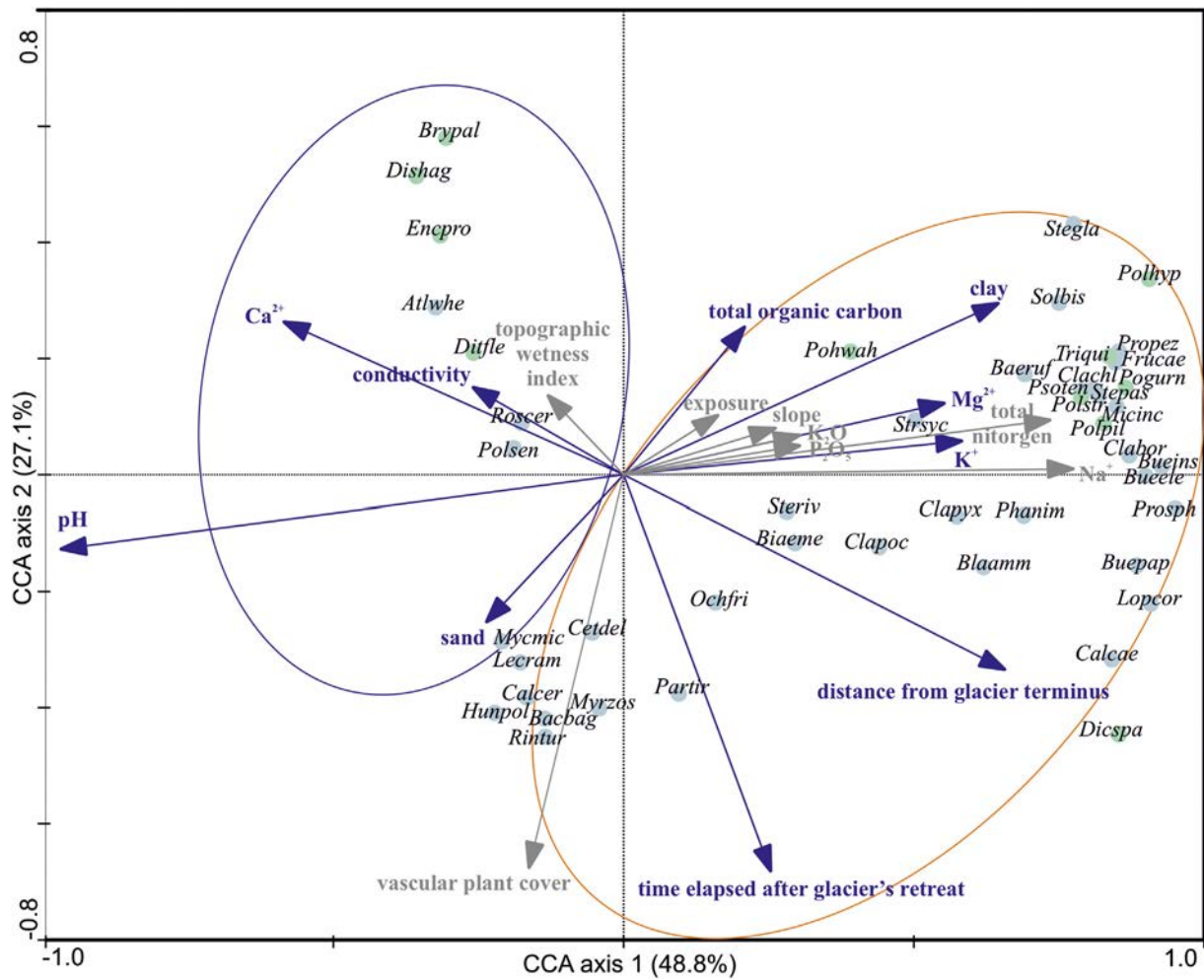
Fig. 3. CCA biplot with cryptogamic species and significant environmental variables (in blue) identified in forward selection procedure (Supplementary file 6). Species fit range is between 10% and 100% (i.e. 47 species are presented). Lichens are presented by blue dots, while bryophytes by green. Blue circle indicates younger parts of forelands, while orange circle marks older parts of forelands. Abbreviations of species names: *Atlwhe - Atla wheldonii*; *Bacbag - Bacidia bagliettoana*; *Mycmic - Mycobilimbia microcarpa*; *Baeruf - Baeomyces rufus*; *Bueele - Buellia elegans*; *Bueins - Buellia insignis*; *Buepap - Buellia papillata*; *Blaamm - Blastenia ammiospila*; *Calcae - Caloplaca caesiorufella*; *Calcer - Caloplaca cerina*; *Hunpol - Huneckia pollinii*; *Partir - Parvoplaca tiroliensis*; *Cetdel - Cetrariella delisei*; *Clabor - Cladonia borealis*; *Clachl - Cladonia chlorophaea*; *Clapoc - Cladonia pocillum*; *Clapyx - Cladonia pyxidata*; *Roscer - Rostania ceranisca*; *Frucae - Frutidella caesioatra*; *Strsyc - Strigula sychnogonoides*; *Myrzos - Myriolecis zosterae*; *Biaeme - Biatora ementiens*; *Lecram - Lecidea ramulosa*; *Lopcor - Lopadium coralloideum*; *Micinc - Micarea incrassata*; *Ochfri - Ochrolechia frigida*; *Phanim - Phaeorrhiza nimbosa*; *Polsen - Polyblastia sendtneri*; *Propez - Protopannaria pezizoides*; *Prosph - Protothelenella sphinctrinoidella*; *Psoten - Psoroma tenue*; *Rintur - Rinodina turfacea*; *Solbis - Solorina bispora*; *Stegla - Stereocaulon glareosum*; *Stepas - Stereocaulon paschale*; *Steriv - Stereocaulon rivulorum*; *Brypal - Bryum pallescens*; *Dicspa - Dicranum spadiceum*; *Dishag - Distichium hagenii*; *Ditfle - Ditrichum flexicaule*; *Encpro - Encalypta procera*; *Pogurn - Pogonatum urnigerum*; *Pohwah - Pohlia wahlenbergii*; *Polhyp - Polytrichum hyperboreum*; *Polpil - Polytrichum piliferum*; *Polstr - Polytrichum strictum*; *Triqui - Trilophozia quinquedentate*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We found several factors that significantly affected the diversity and cover of both cryptogams and vascular plants. However, we could not distinguish any single set of variables that independently impacted the diversity and cover of cryptogams and vascular plants. Also, we revealed an important influence of habitat type and geographical location on species diversity and cover of analysed plant groups. These effects were related to the individual habitat conditions of studied forelands, including different terrain features and physical and chemical characteristics of soils exposed to species succession (Mizuno, 2005; Wietrzyk-Pełka et al., 2020b). Despite the significant differences in

Table 2
The results of two-way ANOVA for vascular plants for the effects of habitat type (mature tundra vs glacier foreland) and geographical location (glacier) on biotic variables. Significant effects ($p < 0.05$) are provided in bold.

Variable	Location				Habitat type				Location × habitat type				Error
	F	p	df	Partial η^2	F	p	df	Partial η^2	F	p	df	Partial η^2	df
Vascular plants													
Cover	**7.03**	**<0.001**	7	0.22	**88.64**	**<0.001**	1	0.34	1.24	0.283	7	0.05	174
Dominance index	**3.20**	**0.003**	7	0.11	**36.16**	**<0.001**	1	0.17	**2.55**	**0.016**	7	0.09	174
Species richness	**2.35**	**0.026**	7	0.09	**63.81**	**<0.001**	1	0.27	**2.70**	**0.011**	7	0.10	174
Shannon index	**2.83**	**0.008**	7	0.10	**44.05**	**<0.001**	1	0.20	**2.73**	**0.010**	7	0.10	174
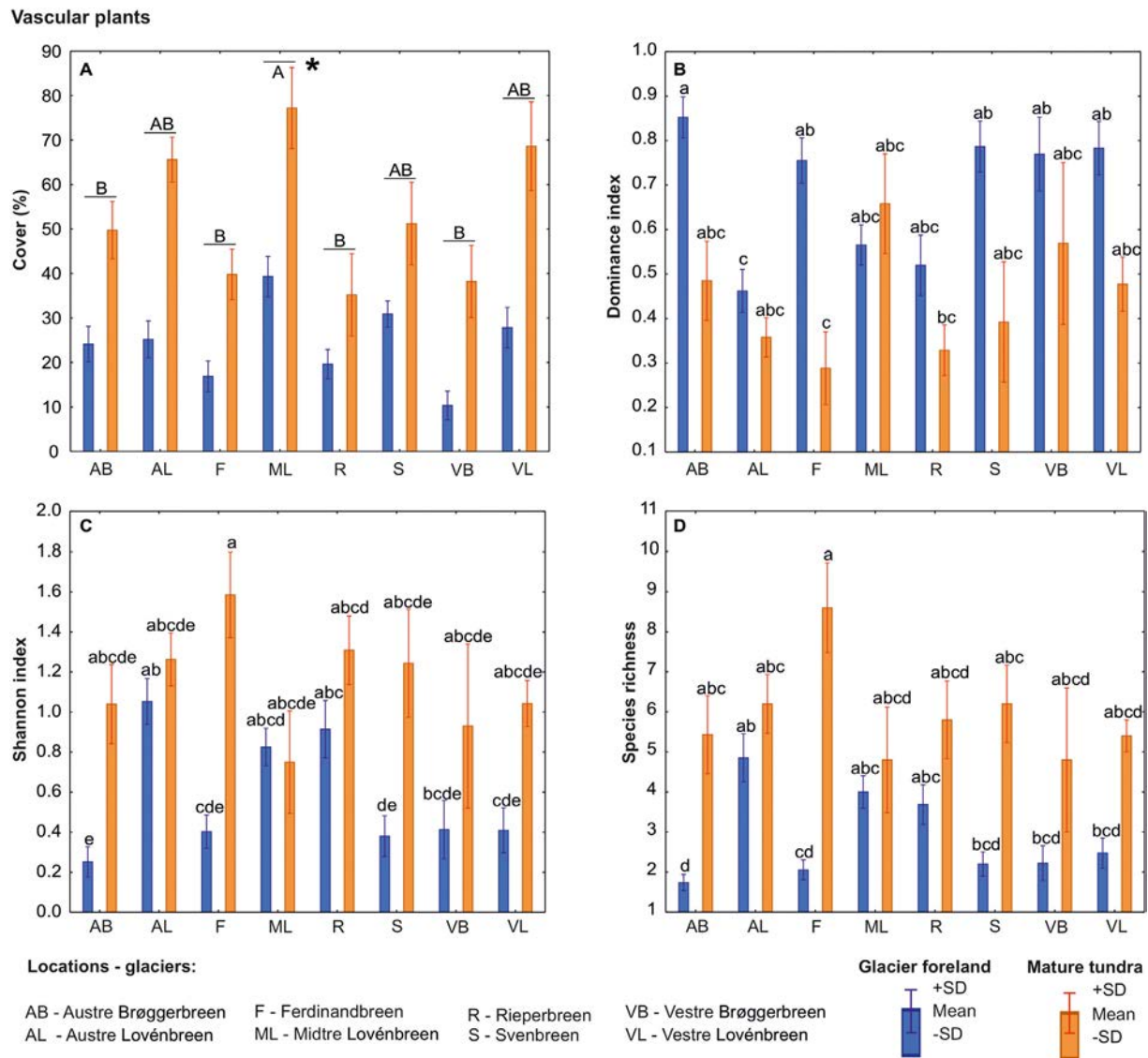
Fig. 4. Mean ± SD of vascular plant parameters including habitat type (foreland vs tundra) and location (glaciers). The results of two-way ANOVA ($p < 0.05$) are presented graphically. The different letters above the bars indicate significant differences: the capital letters show the significant main 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 2 for details on the main effects and interactions).

cryptogam and vascular plant diversity between geographical locations, the foreland location was the factor that only influenced cryptogam diversity but not vascular plant diversity. The Svalbard archipelago has low vascular plant diversity (178 species), and a limited number of the species present can colonise areas newly exposed from under the ice (Rønning, 1996; Meltofte, 2013). In contrast, cryptogams are a much more diverse group, including 742 lichen and 373 bryophyte species (Elvebakk and Prestrud, 1996; Meltofte, 2013). Their higher diversity in the archipelago and their ability to establish in harsher conditions allows for a larger variety in the species diversity of Svalbard glacier forelands.

In contrast to our hypotheses, the diversity of both cryptogam and vascular plants was generally higher in mature tundra than in foreland habitats. This difference confirmed that Svalbard foreland communities are still developing and have not yet reached the stage of mature communities (Walker and del Moral, 2003). Furthermore, this also showed that numerous species of cryptogams are adapted to coexist with vascular plants in mature communities. Contrary to our hypothesis, the results showed that competition from vascular plants did not limit the overall diversity and cover of cryptogams. The positive relationship between

diversity and cover of cryptogam and vascular plant cover was surprising as it opposed the previous findings (Cornelissen et al., 2001; Gornall et al., 2011; Belnap and Lange, 2013). Several incidences in which cryptogam diversity and cover increased with increasing plant cover exist. First, it has been shown that an herbaceous-dominated canopy can support bryophyte taxa (Longton, 1997). Second, vascular plants can take a surrogate role for some bryophyte species (Pharo et al., 1999). Third, lichens can use vascular plants as a growth substrate and a source of mineral nutrition (Favero-Longo and Piervittori, 2010). We observed all three cases in our study areas. However, the most prevalent was the lichens' presence (e.g. *Caloplaca caesiorufella*, *Caloplaca cerina*, *Parvoplaca tiroliensis*, *Phaeorrhiza nimbosa*, *Rinodina turfacea*) overgrowing vascular plants. This overgrowth was particularly common in the older parts of the glacier forelands indicating that occurrence of several cryptogam species depended on vascular plant presence.

The diversity of cryptogams and vascular plants was positively associated with increasing distance from the glacier terminus, which was in line with our hypothesis. Glacier presence produces unfavourable microclimates for non-pioneer vascular plants (Eichel, 2019). However, these conditions progressively change across the forelands and become
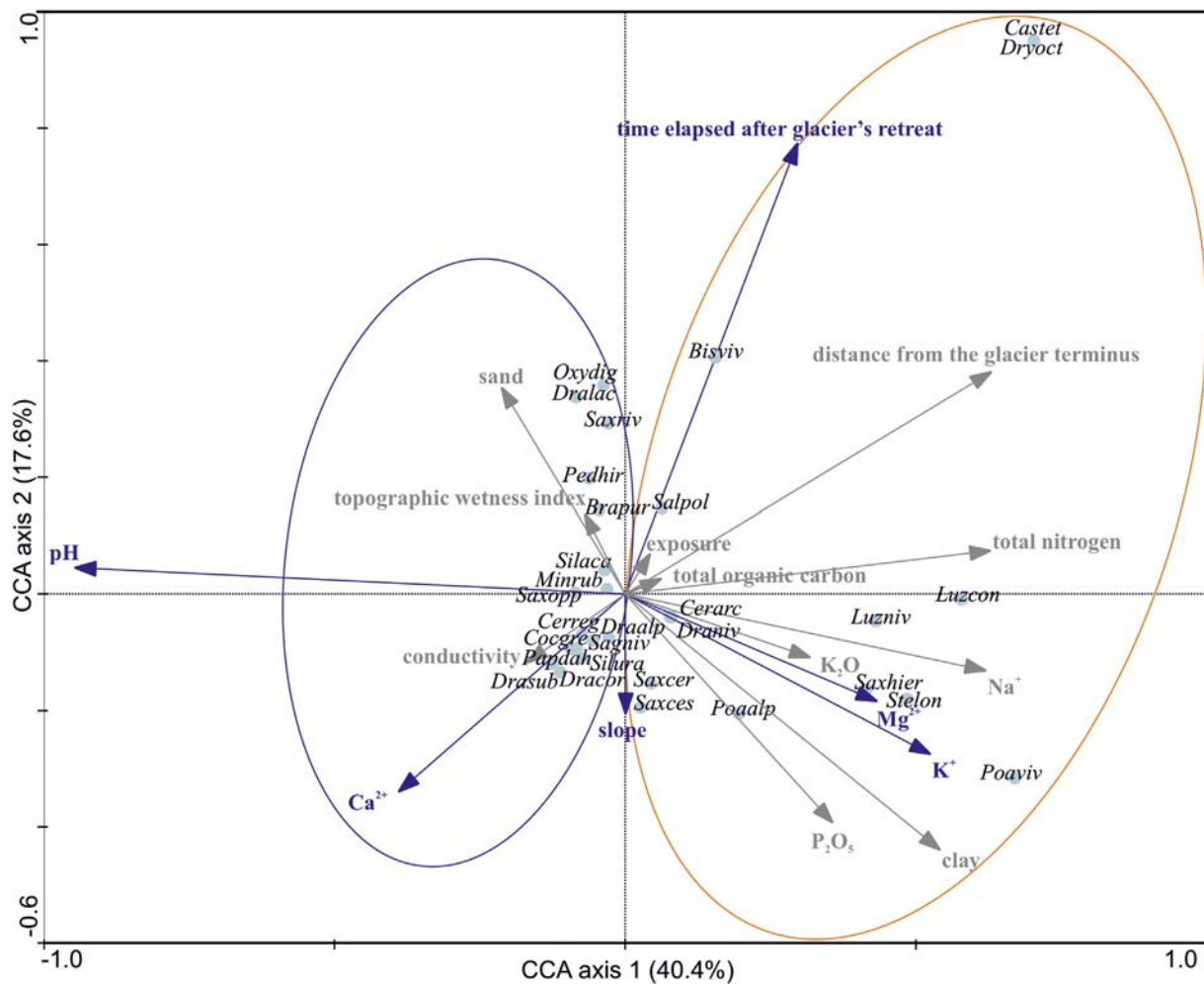
Fig. 5. CCA biplot with vascular plant species and significant environmental variables (in blue) identified in forward selection procedure (Supplementary file 11). Species fit range is between 0% and 100% (i.e. 30 species are presented). Blue circle indicates younger parts of forelands, while orange circle marks older parts of forelands. Abbreviations of species names: *Dralac - Draba lactea; Dracor - Draba corymbose; Stelon - Stellaria longipes; Brapur - Braya purpurescens; Saxopp - Saxifraga oppositifolia; Saxces - Saxifraga cespitosa; Salpol - Salix polaris; Poaalp - Poa alpina; Poaviv - Poa alpina vivipara; Saxhier - Saxifraga hieracifolia; Saxcer - Saxifraga cernua; Oxydig - Oxyria digyna; Bisviv - Bistorta vivipara; Dryoct - Dryas octopetala; Pedhir - Pedicularis hirsuta; Minrub - Minuartia rubella; Luzcon - Luzula confusa; Luzniv - Luzula nivalis; Silaca - Silene acaulis; Castet - Cassiope tetragona; Saxriv - Saxifraga rivularis; Cerarc - Cerastium arcticum; Draniv - Draba nivalis; Papdah - Papaver dahlianum; Cocgre - Cochlearia groenlandica; Draalp - Draba alpina; Sagniv - Sagina nivalis; Silura - Silene uralensis; Cerreg - Cerastium regelii; Drasub - Draba subcapitata.* (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

more favourable in the areas located further away from a glacier, supporting the highest diversity and cover of species (Mizuno, 2005; Moreau et al., 2008; Wietrzyk et al., 2016, 2018). With increasing distance from the glacier terminus, the soil gradually changes its physical and chemical properties (Burga et al., 2010). One of them is soil pH, which influenced cryptogam diversity and cover. This result confirms some species' ability to grow only within a specific narrow pH range and the presence of taxa with a broad tolerance spectrum (Longton, 1988; Saxena, 2004; Paul et al., 2009). In the studied forelands, diversity and cover of cryptogams increased with decreasing substrate pH, while vascular plant cover decreased. These findings partly align with successional soil formation and gradual decrease of pH along forelands (Burga et al., 2010; Prietzel et al., 2013). The soil development is directly linked to TOC accumulation in the substrate (Burga et al., 2010; Kabała and Zapart, 2012). In Svalbard forelands, changes in soil properties were significantly connected with biological soil crusts (formed by cryptogamic organisms) presence and cover, not vascular plants (Wietrzyk-Pełka et al., 2020b). The input of organic matter from biological soil crusts was the main factor influencing TOC accumulation and lowering soil pH along the studied forelands (Wietrzyk-Pełka et al., 2020b), even though the cover of cryptogams and vascular plants increased with increasing distance from the glacier terminus. More developed soils in

the studied forelands were usually characterised by higher content of TOC, lower pH, higher biological soil crust cover and simultaneously lower vascular plant cover (Wietrzyk-Pełka et al., 2020b). In the forelands, vascular plants usually appear in the form of isolated patches or single scattered individuals, while cryptogams form more or less continuous and more compacted biological soil crusts (Fig. 6; Wietrzyk et al., 2016; Wietrzyk-Pełka et al., 2020b; Yoshitake et al., 2018). Therefore, the contribution of cryptogams in the supply of organic matter to the soil is most likely higher than vascular plants' contribution. Furthermore, the higher supply of organic matter to the soil from cryptogams decreases soil pH much more than the supply of organic matter originating from vascular plants. In addition, vascular plants are more susceptible to microbial decomposition than cryptogams (Dorrepaal et al., 2005; Lang et al., 2009). This susceptibility may indicate that the vascular plant input into the soil TOC is marginal because they are predominantly decomposed by microorganisms occurring in foreland soils (Górniak et al., 2017). It is also worth noting that, in our research, we did not apply the traditional chronosequence method involving the selection of only undisturbed areas in terms of vegetation (Walker and del Moral, 2003). We studied both disturbed and undisturbed plots along forelands, which may affect our results. With our approach, the plots' location further from the glacier terminus did not always prevent their
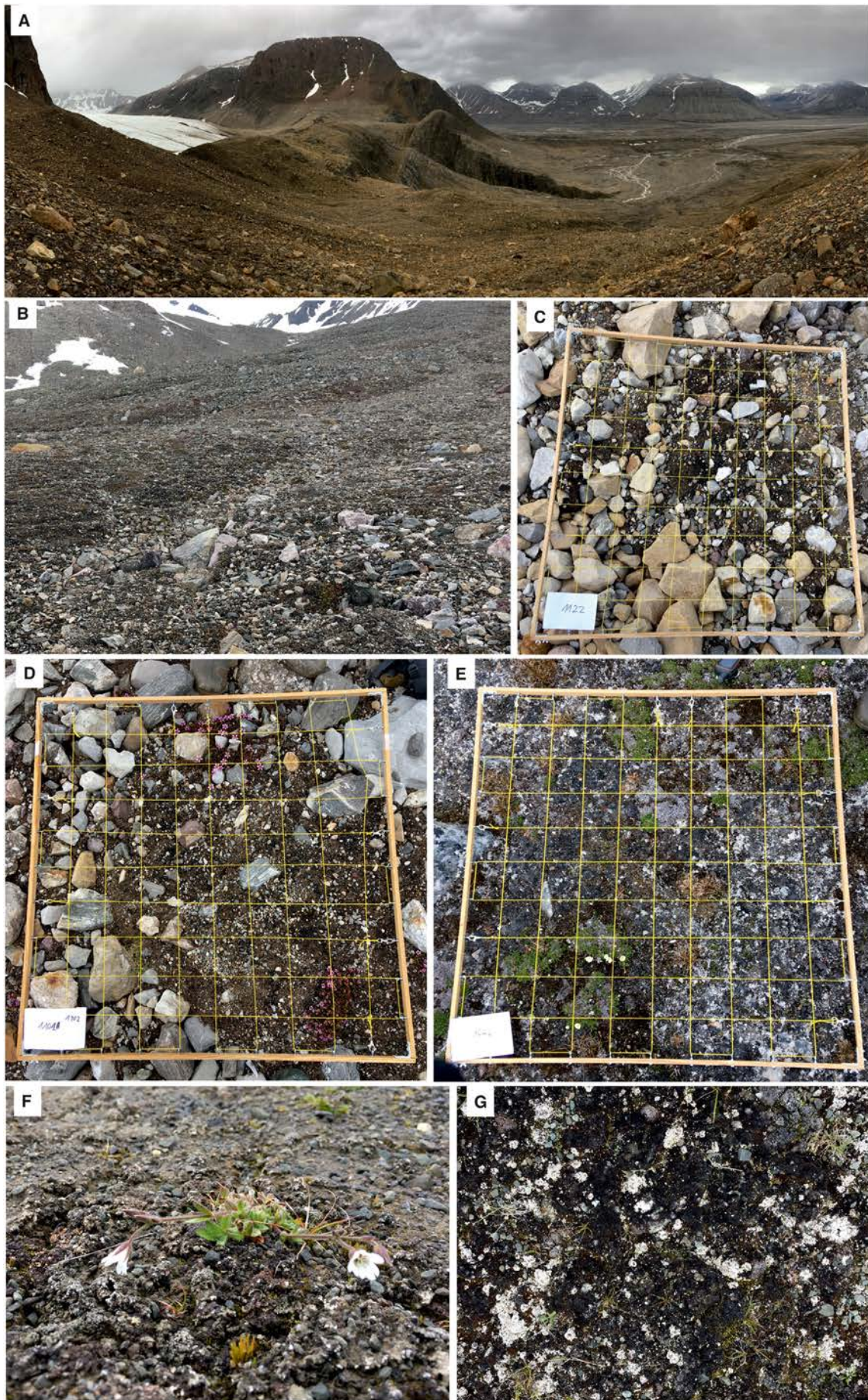
disturbance by geomorphological processes. As vascular plants usually grow on an undisturbed substrate (Cannone et al., 2004; Eichel, 2019), the method we applied might also cause contrasting results with previous studies concerning the associations between vascular plants and soil TOC and pH.

Cryptogams forming biological soil crusts usually occupy all initial soil surfaces, which are not previously colonised by vascular plants (Belnap and Lange, 2013). They facilitate vascular plant growth by significantly contributing to organic matter content and other soil elements (Breen and Lévesque, 2008; Pushkareva et al., 2017; Wietrzyk-Pełka et al., 2020b). Thanks to cyanobacterial components capable of atmospheric nitrogen fixation, cryptogams are major sources of nitrogen in the barren and nitrogen-limited soil of forelands (Sancho et al., 2011; Pushkareva et al., 2017). For vascular plant growth, low nitrogen content in soil is one of the main limiting factors. Consequently, we observed a positive relationship between TN content and the development of vascular plant cover.

We hypothesised nutrient content to be the most essential for vascular plants. However, our hypothesis was not entirely supported since the soil nutrient content significantly impacted species diversity and cover of both cryptogams and vascular plants. Cryptogams lack a typical root system compared to vascular plants (Longton, 1988). Despite that, they are still able to take up nutrients from the soil solution using root-like structures called rhizines (lichens) or rhizoids (bryophytes), and also through the lower part of lichen thallus adjacent to the below substrate (Longton, 1988; Mallen-Cooper et al., 2020). Although they can obtain nutrients from precipitation and other forms of aerial deposition (Longton, 1988; Cornelissen et al., 2007), our results highlight the importance of soil nutrient contents for cryptogam presence in the forelands.

We observed a soil Ca^{2+} gradient ranging from high at the glacier terminus to low in the mature tundra. Despite the important role of Ca^{2+} in plant nutrition (Meriño-Gergichevich et al., 2010), we found a negative relationship between the soil's Ca^{2+} content and diversity of cryptogams and vascular plants, as well as vascular plant cover. Three phenomena might explain this negative relationship. The first is that Ca^{2+} in foreland soils mainly comes from carbonates, which dissolve and are leached from the soil relatively quickly with increasing distance from the glacier terminus (He and Tang, 2008; Burga et al., 2010; Kabała and Zapart, 2012; Prietzel et al., 2013; Wietrzyk-Pełka et al., 2020b). The second is that the plant uptake along the foreland also increases, lowering Ca^{2+} content in soil (He and Tang, 2008). The third is that Ca^{2+}-rich soils are located in the closest vicinity of glaciers, where harsh microclimatic conditions do not favour vegetation development (Kabała and Zapart, 2012). In contrast to Ca^{2+}, Mg^{2+} content in soil gradually increased with increasing distance from the glacier terminus and time after glacier retreat. This pattern may be due to minerals weathering for a longer time, releasing Mg^{2+} from the crystal lattice, which subsequently may be sorbed in older soils and is therefore chemically extracted in greater amounts. A similar pattern was recorded in the forelands of Hailuogou (He and Tang, 2008) and Quaternary (Douglass and Bockheim, 2006) glaciers. We found that soils poor in Mg^{2+} supported greater vascular plant cover. Magnesium is a macronutrient that is closely involved in plant nutrition, and its content in foreland soils depends on vegetation type (Parkinson and Gellatly, 1991). Therefore, the observed negative impact of Mg^{2+} might be related to higher uptake of Mg^{2+} by vascular plants, resulting in a substantial decrease of Mg^{2+} content in soils with high vascular plant cover. Alternatively, high magnesium content in soil might be phytotoxic (Brooks, 1988; D'Amico et al., 2008). Assuming foreland vascular plants as pioneer

species with low Mg^{2+} requirement, soils with high Mg^{2+} content might limit their growth. Nevertheless, further research should be conducted to determine the cause of the observed negative impact of soil Ca^{2+} and Mg^{2+} on plant growth.

Following the negative impact of Ca^{2+} and Mg^{2+} contents, we found that electrical conductivity was also negatively associated with the diversity of both vascular plants and cryptogams and cryptogam cover. Electrical conductivity is an indicator of the amount of plant-available nutrients in soil; the higher the nutrient content, the higher its electrical conductivity (Heiniger et al., 2003). However, plant-available nutrients can also be indirectly affected by soil texture, as usually more developed, fine-grained soil possesses a higher conductivity level (Heiniger et al., 2003). The observed negative relationship may relate to the disappearance of pioneer species in more nutrient-rich areas with higher clay content and major development of cryptogams on substrates low in nutrients.

Contrastingly, K^+, and available P_2O_5 contents positively affected the diversity of both groups and cryptogam cover, confirming these elements' vital roles for both cryptogams and vascular plants. K^+ is a fundamental cation in living plants and plays a crucial role in many processes, i.e. enzyme activation, membrane transport, and osmoregulation (Wang and Wu, 2013). Phosphorus is an essential nutrient for plant growth and ecosystem development, and it is the primary limiting nutrient in polar ecosystems (Seastedt and Vaccaro, 2001; Vitousek et al., 2010; Zhou et al., 2013). Its availability is closely associated with the ribosomal RNA processes connected to protein synthesis (Elser et al., 2007; Bracken et al., 2015). Moreover, phosphorus is an essential element in biological N fixation, carried out by nitrogen-fixing cryptogams (Vance, 2001). Biological N fixation is crucial during primary plant succession in glacier forelands as newly uncovered soils are N-limited.

Despite the studies indicating that soil age can affect vegetation development (e.g. Haugland and Beatty, 2005; Moreau et al., 2008, 2009; Robbins and Matthews, 2010; Glausen and Tanner, 2019; Fickert, 2020), we found that the time elapsed after glacier retreat only positively impacted vascular plant cover in the forelands. This factor also affected the distribution of some species of vascular plants and cryptogams, along with other variables, such as nutrient content and soil pH, which is in agreement with several other studies (e.g. Burga et al., 2010; Kabała and Zapart, 2012; Wang and Wu, 2013; Bracken et al., 2015; Wietrzyk et al., 2016, 2018). Species distribution of both plant groups across studied forelands showed similar patterns. We distinguished early and late colonisers in both cryptogam and vascular plants (Wietrzyk et al., 2016; Fickert, 2020). Early colonisers of cryptogams (e.g. *Atla wheldonii*, *Rostania ceranisca*, *Polyblastia sendtneri*, and *Ditrichum flexicaule*) and vascular plants (e.g. *Papaver dahlianum*, *Cochlearia groenlandica*, and *Draba subcapitata*) inhabited areas relatively newly exposed, characterised by higher soil pH and Ca^{2+} content, and lower K^+ content. In addition, pioneer cryptogams overgrowth areas near the glacier terminus, with lower clay and TOC contents, and lower soil conductivity, while pioneer vascular plants inhabited hillier foreland parts. These patterns were reflected by the dominance index of both cryptogams and vascular plants, which was higher in foreland than mature tundra. Although, the species diversity of mature tundra was higher, and there were few dominant species that consistently commonly occurred in forelands. The earlier stages of primary succession in forelands are characterised by the sporadic occurrence of various species, which increases species diversity; however, they usually form an initial community, which is thought to be more heterogeneous than mature tundra (Mizuno, 2005; Mori et al., 2008; Robbins and

Fig. 6. Images of selected study sites presenting their heterogeneity: (A) – view on Svenbreen foreland; (B) – example of initial community; (C) – example of plot located near to the glacier terminus where only cryptogams are present; (D) – example of plot located further from the glacier terminus where apart with cryptogams also *Saxifraga oppositifolia* is present; (E) – example of plot located furthest from the glacier terminus where cryptogams and vascular plants are present; (F) – single *Cerastium arcticum* overgrowing biological soil crusts; (G) – foreland community dominated by biological soil crusts.

Matthews, 2010). As the ecosystem develops, the heterogeneous community is believed to evolve into a more structured vegetation, leading to a homogenous tundra community (del Moral and Jones, 2002; Fickert, 2020). Our results did not confirm this pattern; instead, they revealed significant differences in diversity and cover of cryptogams and vascular plants between the studied habitats indicating the on-going development of foreland communities and the more heterogeneous character of mature tundra communities.

5. Conclusions

The diversity and cover of cryptogams and vascular plants differed between locations and habitat types except for cryptogam cover in mature tundra in terms of location. In addition, different sets of factors affected diversity, cover and distribution of both groups, including distance to the glacier terminus, selected physio-chemical substrate properties, and time elapsed after glacier retreat. In the glacier forelands, the overall diversity and cover of cryptogams were not limited by competition from vascular plants. Vascular plant cover positively influenced the diversity and cover of cryptogams, which indicates the existence of complex species relationships and the coexistence of species dependent on each other between these distinct groups even in initial and relatively simple communities of Svalbard forelands. These relationships are particularly important in the aspect of climate change's impact on tundra species as our research suggested that some cryptogam species might benefit from vascular plant expansion. Future research should explore vascular plant and cryptogam dynamics in more detail to properly assess the directions of changes in tundra communities. Due to high cryptogam diversity in the polar and alpine areas, future ecological studies on climate change's impact on vegetation should also consider the more taxonomical challenging organisms such as cryptogams. The inclusion of cryptogams is the only approach to better understand the full impact of climate change on Arctic plant diversity.

CRediT authorship contribution statement

Paulina Wietrzyk-Pełka: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Project administration, Writing – original draft, Writing – review & editing, Funding acquisition. **Kaja Rola:** Formal analysis, Validation, Writing – review & editing. **Aurora Patchett:** Writing – review & editing. **Wojciech Szymański:** Methodology, Writing – review & editing, Supervision. **Michał H. Węgrzyn:** Methodology, Investigation. **Robert G. Björk:** Writing – review & editing, Supervision.

Declaration of competing interest

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

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Appendix A. Supplementary data

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References

Bates, J.W., Farmer, A.M., 1992. Bryophytes and Lichens in a Changing Environment. Clarendon Press, Oxford.

Belnap, J., Lange, O.L., 2013. Biological Soil Crusts: Structure, Function, and Management. Springer Science & Business Media, Berlin, Heidelberg.

Bracken, M.E., Hillebrand, H., Borer, E.T., Seabloom, E.W., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner, D.S., Harpole, W.S., Ngai, J.T., Smith, J.E., 2015. Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. Oikos 124 (2), 113–121. https://doi.org/10.1111/oik.01215.

Breen, K., Lévesque, E., 2008. The influence of biological soil crusts on soil characteristics along a High Arctic glacier foreland, Nunavut, Canada. Arct. Antarct. Alp. Res. 40 (2), 287–297. https://doi.org/10.1657/1523-0430(06-098)[BREEN]2.0.CO;2.

Brooks, R.R., 1988. Serpentine and its vegetation: a multidisciplinary approach. Brittonia 40, 268. https://doi.org/10.2307/2807470.

Burga, C.A., Krüsi, B., Egli, M., Wernli, M., Elsener, S., Ziefle, M., Fischer, T., Mavris, C., 2010. Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): straight forward or chaotic? Flora 205, 561–576. https://doi.org/10.1016/j.flora.2009.10.001.

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Jónsdóttir, I.S., Laine, K., Taulavuori, K., Taulavuori, E., Zöckler, C., 2004. Responses to projected changes in climate and UV-B at the species level. Ambio 33, 418–435. https://doi.org/10.1579/0044-7447-33.7.418.

Cannone, N., Guglielmin, M., Gerdol, R., 2004. Relationships between vegetation patterns and periglacial landforms in northwestern Svalbard. Polar Biol. 27, 562–571. https://doi.org/10.1007/s00300-004-0622-4.

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

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for automated geoscientific analyses (SAGA) v. 2.1. 4. Geosci. Model Dev. Discuss. 8 (2), 2271–2312. https://doi.org/10.5194/gmdd-8-2271-2015.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Gwynn Jones, D., Jonasson, S., Chapin III, F.S., Molau, U., Neill, C., Lee, J.A., Melillo, J.M., Sveinbjörnsson, B., Aerts, R., 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? J. Ecol. 89, 984–994. https://doi.org/10.1111/j.1365-2745.2001.00625.x.

Cornelissen, J.H., Lang, S.I., Soudzilovskaia, N.A., During, H.J., 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Ann. Bot. 99 (5), 987–1001. https://doi.org/10.1093/aob/mcm030.

Dallmann, W.K., 1999. Lithostratigraphic Lexicon of Svalbard: Upper Palaeozoic to Quaternary Bedrock: Review and Recommendations for Nomenclature Use. Review and Recommendations for Nomenclature Use. Committee on the Stratigraphy of Svalbard, Tromsø, p. 318.

Dallmann, W.K., Kjærnet, T., Nøttvedt, A., 2001. Geological map of Svalbard 1:100000. Sheet C9Q Adventdalen. Temakart 31/32. Norwegian Polar Institute, Tromsø.

Dallmann, W.K., Ohta, Y., Birjukov, A.S., Karnoušenko, E.P., Sirotkin, A.N., Piepjohn, K., 2004. Geological map of Svalbard, 1:100 000. Sheet C7G Dicksonfjorden. Temakart 35. Norwegian Polar Institute, Tromsø.

Dallmann, W.K., Piepjohn, K., Blomeier, D., Elvevold, S., 2009. Geological map of Svalbard, 1:100 000. Sheet C8G Billefjorden. Temakart 43. Norwegian Polar Institute, Tromsø.

D'Amico, M., Julitta, F., Previtali, F., Cantelli, D., 2008. Podzolization over ophiolitic materials in the western Alps (Natural Park of Mont Avic, Aosta Valley, Italy). Geoderma 146 (1–2), 129–137. https://doi.org/10.1016/j.geoderma.2008.05.025.

del Moral, R., Jones, C., 2002. Vegetation development on pumice at Mount St. Helens, USA. Plant Ecol. 162 (1), 9–22. https://doi.org/10.1023/A:1020316503967.

Dorrepaal, E., Cornelissen, J.H., Aerts, R., Wallen, B.O., Van Logtestijn, R.S., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? J. Ecol. 93 (4), 817–828. https://doi.org/10.1111/j.1365-2745.2005.01024.x.

Douglass, D.C., Bockheim, J.G., 2006. Soil-forming rates and processes on Quaternary moraines near Lago Buenos Aires, Argentina. Quat. Res. 65 (2), 293–307. https://doi.org/10.1016/j.yqres.2005.08.027.

Egner, H., Riehm, H., Domingo, W.R., 1960. Untersuchungen über die chemische Boden-Analyse als grundlage für die beurteilung des Nährstoffzustandes der Böden. II. Chemische Extraktionsmetoden zu Phosphor – und Kaliumbestimmung. Kungliga Lantbrukshügskolans Annaler 26, 199–215.

Eichel, J., 2019. Vegetation succession and biogeomorphic interactions in glacier forelands. In: Heckmann, T., Morche, D. (Eds.), Geomorphology of Proglacial Systems. Landform and Sediment Dynamics in Recently Deglaciated Alpine Landscapes. Springer, Cham, pp. 327–349 https://doi.org/10.1007/978-3-319-94184-4_19.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10 (12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x.

Elvebakk, A., Prestrud, P., 1996. A Catalogue of Svalbard Plants, Fungi, Algae and Cyanobacteria. Norsk Polarinstitutt, Oslo.

Favero-Longo, S.E., Piervittori, R., 2010. Lichen-plant interactions. J. Plant Interact. 5 (3), 163–177. https://doi.org/10.1080/17429145.2010.492917.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Fickert, T., 2020. Common patterns and diverging trajectories in primary succession of plants in eastern alpine glacier forelands. Diversity 12 (5), 191. https://doi.org/10.3390/d12050191.

Garcia-Pichel, F., Wojciechowski, M.F., 2009. The evolution of a capacity to build supra-cellular ropes enabled filamentous cyanobacteria to colonize highly erodible substrates. PLoS One 4, e7801. https://doi.org/10.1371/journal.pone.0007801.

Glausen, T.G., Tanner, L.H., 2019. Successional trends and processes on a glacial foreland in Southern Iceland studied by repeated species counts. Ecol. Process. 8, 11. https://doi.org/10.1186/s13717-019-0165-9.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J., van der Wal, R., 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia 153, 931–941. https://doi.org/10.1007/s00442-007-0785-0.

Gornall, J.L., Woodin, S.J., Jónsdóttir, I.S., van der Wal, R., 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. Oecologia 166 (3), 769–782. https://doi.org/10.1007/s00442-011-1911-6.

Górniak, D., Marszałek, H., Kwaśniak-Kominek, M., Rzepa, G., Manecki, M., 2017. Soil formation and initial microbiological activity on a foreland of an Arctic glacier (SW Svalbard). App. Soil Ecol. 114, 34–44. https://doi.org/10.1016/j.apsoil.2017.02.017.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1–9.

Haugland, J.E., Beatty, S.W., 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. J. Biogeogr. 32 (1), 145–153. https://doi.org/10.1111/j.1365-2699.2004.01175.x.

He, L., Tang, Y., 2008. Soil development along primary succession sequences on moraines of Hailuogou Glacier, Gongga Mountain, Sichuan, China. Catena 72 (2), 259–269. https://doi.org/10.1016/j.catena.2007.05.010.

Heiniger, R.W., McBride, R.G., Clay, D.E., 2003. Using soil electrical conductivity to improve nutrient management. Agron. J. 95 (3), 508–519. https://doi.org/10.2134/agronj2003.5080.

Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS One 12 (2), e0169748. https://doi.org/10.1371/journal.pone.0169748.

Huntington, H., Fox, S., 2005. The changing Arctic: indigenous perspectives. In: Berner, J., Heal, O.W. (Eds.), Arctic Climate Impact Assessment-Scientific Report. Cambridge University Press, Cambridge, pp. 61–98.

Jones, C.C., del Moral, R., 2005. Patterns of primary succession on the foreland of Coleman Glacier, Washington, USA. Plant Ecol. 180 (1), 105–116. https://doi.org/10.1007/s11258-005-2843-1.

Jónsdóttir, I.S., 2005. Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. Biol. Environ. 105 (3), 155–165. https://doi.org/10.3318/bioe.2005.105.3.155.

Jung, P., Briegel-Williams, L., Simon, A., Thyssen, A., Büdel, B., 2018. Uncovering biological soil crusts: carbon content and structure of intact Arctic, Antarctic and alpine biological soil crusts. Biogeosciences 15, 1149–1160. https://doi.org/10.5194/bg-15-1149-2018.

Kabała, C., Zapart, J., 2012. Initaiil soil development and carbon accumulation on moraines of the rapidly retreating Wernskiold Gleacier, SW Spitsbergen, Svalbard archipelago. Geoderma 175–176, 9–20. https://doi.org/10.1016/j.geoderma.2012.01.025.

Kuo, S., 1996. Phosphorus. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. SSSA Book Series vol. 5. SSSA and ASA, Madison, Wisconsin, pp. 869–920.

Landsat, 2020. Landsat image courtesy of the U.S. Geological Survey. https://www.usgs.gov/core-science-systems/nli/landsat (accessed 15 March 2020).

Lang, S.I., Cornelissen, J.H., Klahn, T., Van Logtestijn, R.S., Broekman, R., Schweikert, W., Aerts, R., 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. J. Ecol. 97 (5), 886–900.

Loeppert, R.H., Suarez, D.L., 1996. Carbonate and gypsum. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. SSSA Book Series vol. 5. SSSA and ASA, Madison, Wisconsin, pp. 437–474.

Longton, R.E., 1988. Biology of polar bryophytes and lichens. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511565212.

Longton, R.E., 1997. The role of bryophytes and lichens in polar ecosystems. In: Woodin, S.J., Marquiss, M. (Eds.), Ecology of Arctic Environments: 13th Special Symposium of the British Ecological Society. Cambridge University Press, pp. 69–96 https://doi.org/10.1016/j.flora.2009.10.001.

Mallen-Cooper, M., Bowker, M.A., Antoninka, A.J., Eldridge, D.J., 2020. A practical guide to measuring functional indicators and traits in biocrusts. Restor. Ecol. 28, S56–S66. https://doi.org/10.1111/rec.12974.

Matthews, J.A., Whittaker, R.J., 1987. Vegetation succession on the Storbreen glacier foreland, Jotunheimen. Norway: A review. Arctic Alpine Res. 19, 385–395. https://doi.org/10.2307/1551403.

Mattivi, P., Franci, F., Lambertini, A., Bitelli, G., 2019. TWI computation: a comparison of different open source GISs. Open Geospat. Data, Softw. Stand. 4 (6), 1–12. https://doi.org/10.1186/s40965-019-0066-y.

Meltofte, H., 2013. Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity. Akureyri, Conservation of Arctic Flora and Fauna, Akureyri.

Meriño-Gergichevich, C., Alberdi, M., Ivanov, A.G., Reyes-Díaz, M., 2010. Al^{3+}-Ca^{2+} interaction in plants growing in acid soils: al-phytotoxicity response to calcareous amendments. J. Soil Sci. Plant Nutr. 10 (3), 217–243.

Mizuno, K., 2005. Glacial fluctuation and vegetation succession on Tyndall Glacier. Mt Kenya. Mt. Res. Dev. 25 (1), 68–76. https://doi.org/10.1659/0276-4741(2005)025[0068:GFAVSO]2.0.CO;2.

Modified Copernicus Sentinel, 2020. Modified Copernicus Sentinel data from Sentinel Hub. https://www.sentinel-hub.com/ (accessed 15 March 2020).

Moreau, M., Mercier, D., Laffly, D., 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. https://doi.org/10.1016/j.geomorph.2006.07.031.

Moreau, M., Laffly, D., Brossard, T., 2009. Recent spatial development of Svalbard strand flat vegetation over a period of 31 years. Polar Res. 28, 364–375. https://doi.org/10.1111/j.1751-8369.2009.00119.x.

Mori, A.S., Osono, T., Uchida, M., Kanda, H., 2008. Changes in the structure and heterogeneity of vegetation and microsite environments with the chronosequence of primary succession on a glacier foreland in Ellesmere Island, high arctic Canada. Ecol. Res. 23 (2), 363–370. https://doi.org/10.1007/s11284-007-0388-6.

Nakatsubo, T., Fujiyoshi, M., Yoshitake, S., Koizumi, H., Uchida, M., 2010. Colonization of the polar willow Salix polaris on the early stage of succession after glacier retreat in the High Arctic, Ny-Ålesund. Svalbard. Polar Res. 29, 385–390. https://doi.org/10.3402/polar.v29i3.6078.

Norwegian Polar Institute, 2020. Norwegian Polar Institute Map Data and Services. https://geodata.npolar.no (accessed 20 September 2020).

Parkinson, R., Gellatly, A., 1991. Soil formation on Holocene moraines in the Cirque de Troumouse, Pyrenees. Pirineos 138, 69–82. https://doi.org/10.3989/pirineos.1991.v138.190.

Paul, A., Hauck, M., Leuschner, C., 2009. Iron and phosphate uptake explains the calcifuge-calcicole behavior of the terricolous lichens Cladonia furcata subsp. furcata and C. rangiformis. Plant Soil 319, 49. https://doi.org/10.1007/s11104-008-9848-1.

Pharo, E.J., Beattie, A.J., Binns, D., 1999. Vascular plant diversity as a surrogate for bryophyte and lichen diversity. Conserv. Biol. 13 (2), 282–292. https://doi.org/10.1046/j.1523-1739.1999.013002282.x.

Pointing, S.B., Büdel, B., Convey, P., Gillman, L.N., Körner, C., Leuzinger, S., Vincent, W.F., 2015. Biogeography of photoautotrophs in the high polar biome. Front. Plant Sci. 6, 692. https://doi.org/10.3389/fpls.2015.00692.

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 Jr., M., Williamson, C., Bauer, G., Enos, J., Arnold, G., Kramer, W., Becker, P., Doshi, A., D'Souza, C., Cummens, P., Laurier, F., Bojesen, M., 2018. ArcticDEM. Harvard Dataverse. https://doi.org/10.7910/DVN/OHHUKH.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M., Aastrup, P., 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325 (5946), 1355–1358. https://doi.org/10.1126/science.1173113.

Prach, K., Rachlewicz, G., 2012. Succession of vascular plants in front of retreating glaciers in central Spitsbergen. Pol. Polar Res. 33, 319–328. https://doi.org/10.2478/v10183-012-0022-3.

Prietzel, J., Dümig, A., Wu, Y., Zhou, J., Klysubun, W., 2013. Synchrotron-based P K-edge XANES spectroscopy reveals rapid changes of phosphorus speciation in the topsoil of two glacier foreland chronosequences. Geochim. Cosmochim. Acta 108, 154–171. https://doi.org/10.1016/j.gca.2013.01.029.

Pushkareva, E., Kvíderová, J., Šimek, M., Elster, J., 2017. Nitrogen fixation and diurnal changes of photosynthetic activity in Arctic soil crusts at different development stage. Eur. J. Soil Biol. 79, 21–30. https://doi.org/10.1016/j.ejsobi.2017.02.002.

Rippin, M., Lange, S., Sausen, N., Becker, B., 2018. Biodiversity of biological soil crusts from the Polar Regions revealed by metabarcoding. FEMS Microbiol. Ecol. 94 (4), fiy036. https://doi.org/10.1093/femsec/fiy036.

Robbins, J.A., Matthews, J.A., 2010. Regional variation in successional trajectories and rates of vegetation change on glacier forelands in south-central Norway. Arct. Antarct. Alp. Res. 42, 351–361. https://doi.org/10.1657/1938-4246-42.3.351.

Rodriguez, J.M., Passo, A., Chiapella, J.O., 2018. Lichen species assemblage gradient in South Shetlands Islands, Antarctica: relationship to deglaciation and microsite conditions. Polar Biol. 41 (12), 2523–2531. https://doi.org/10.1007/s00300-018-2388-0.

Rønning, O.I., 1996. The Flora of Svalbard. Norsk Polarinstitutt, Tromsø.

Roos, R.E., van Zuijlen, K., Birkemoe, T., Klanderud, K., Lang, S.I., Bokhorst, S., Wardle, D.A., Asplund, J., 2019. Contrasting drivers of community-level trait variation for vascular

plants, lichens and bryophytes across an elevational gradient. Funct. Ecol. 33 (12), 2430–2446. https://doi.org/10.1111/1365-2435.13454.

Rydgren, K., Halvorsen, R., Töpper, J.P., Njøs, J.M., 2014. Glacier foreland succession and the fading effect of terrain age. J. Veg. Sci. 25, 1367–1380. https://doi.org/10.1111/jvs.12184.

Saalmann, K., Thiedig, F., 2000. Structural evolution of the Tertiary West Spitsbergen fold-and-thrust belt on Broggerhalvoya, NW-Spitsbergen. Polarforschung 68, 111–119.

Sancho, L.G., Palacios, D., Green, A.T.G., Vivas, M., Pintado, A., 2011. Extreme high lichen growth rates detected in recently deglaciated areas in Tierra del Fuego. Polar Biol. 34, 813–822. https://doi.org/10.1007/s00300-010-0935-4.

Saxena, D., 2004. Uses of bryophytes. Reson. 9, 56–65. https://doi.org/10.1007/BF02839221.

Schachtschabel, P., 1954. Das pflanzenverfügbare Magnesium des Boden und seine Bestimmung. Zeitschrift für Pflanzenernährung, Düngung, Bodenkunde 67, 9–23.

Seastedt, T.R., Vaccaro, L., 2001. Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, USA. Arct. Antarct. Alp. Res. 33 (1), 100–106. https://doi.org/10.1080/15230430.2001.12003410.

Shively, J.M., English, R.S., Baker, S.H., Cannon, G.C., 2001. Carbon cycling: the prokaryotic contribution. Curr. Opin. Microbiol. 4, 301–306. https://doi.org/10.1016/S1369-5274(00)00207-1.

Skre, O., 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. https://doi.org/10.1007/BF00346987.

Sumner, M.E., Miller, W.P., 1996. Cation exchange capacity and exchange coefficients. In: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. SSSA Book Series vol. 5. SSSA and ASA, Madison, Wisconsin, pp. 1201–1229.

ter Braak, C.J.F., 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: Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. SSSA Book Series vol. 5. SSSA and ASA, Madison, Wisconsin, pp. 475–490.

Vance, C.P., 2001. Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. Plant Physiol. 127 (2), 390–397. https://doi.org/10.1104/pp.010331.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol. Appl. 20 (1), 5–15. https://doi.org/10.1890/08-0127.1.

Walker, L.R., del Moral, R., 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, Cambridge.

Wang, Y., Wu, W.H., 2013. Potassium transport and signalling in higher plants. Annu. Rev. Plant Biol. 64, 451–476. https://doi.org/10.1146/annurev-arplant-050312-120153.

Wietrzyk, P., Węgrzyn, M., Lisowska, M., 2016. Vegetation diversity and selected abiotic factors influencing the primary succession process on the foreland of Gåsbreen. Svalbard. Pol. Polar Res. 37 (4), 493–509. https://doi.org/10.1515/popore-2016-0026.

Wietrzyk, P., Rola, K., Osyczka, P., Nicia, P., Szymański, W., 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 Soil 428 (1–2), 195–211. https://doi.org/10.1007/s11104-018-3660-3.

Wietrzyk-Pełka, P., Otte, V., Węgrzyn, M.H., Olech, M., 2018. From barren substrate to mature tundra-lichen colonization in the forelands of Svalbard glaciers. Acta Soc. Bot. Pol. 87 (4), 3599. https://doi.org/10.5586/asbp.3599.

Wietrzyk-Pełka, P., Cykowska-Marzencka, B., Maruo, F., Szymański, W., Węgrzyn, M.H., 2020a. Mosses and liverworts in the glacier forelands and mature tundra of Svalbard (High Arctic): diversity, ecology, and community composition. Pol. Polar Res. 41(2), 151–186. doi: 10.24425/ppr.2020.132571.

Wietrzyk-Pełka, P., Rola, K., Szymański, W., Węgrzyn, M.H., 2020b. Organic carbon accumulation in the glacier forelands with regard to variability of environmental conditions in different ecogenesis stages of High Arctic ecosystems. Sci. Total Environ. 717, 135151. https://doi.org/10.1016/j.scitotenv.2019.135151.

Wojtuń, B., Matuła, J., Pereyma, J., 2008. Kolonizacja przedpola lodowca Werenskiolda (Spitsbergen Zachodni) przez sinice i rośliny. In: Kowalska, A., Latocha, A., Maszałek, H., Pereyma, J. (Eds.), Środowisko przyrodnicze obszarów polarnych. University of Wroclaw, Wrocław, pp. 228–236.

Yoshitake, S., Uchida, M., Iimura, Y., Ohtsuka, T., Nakatsubo, T., 2018. Soil microbial succession along a chronosequence on a High Arctic glacier foreland, Ny-Ålesund, Svalbard: 10 years' change. Polar Sci. 16, 59–67. https://doi.org/10.1016/j.polar.2018.03.003.

Zhou, J., Wu, Y., Prietzel, J., Bing, H., Yu, D., Sun, S., Luo, J., Sun, H., 2013. Changes of soil phosphorus speciation along a 120-year soil chronosequence in the Hailuogou Glacier retreat area (Gongga Mountain, SW China). Geoderma 195, 251–259. https://doi.org/10.1016/j.geoderma.2012.12.010.