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Vascular plant and cryptogam abundance as well as soil chemical properties shape microbial communities in the successional gradient of glacier foreland soils

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HIGHLIGHTS

- Vegetation, soil and microbial parameters in glacier forelands are interlinked.
- Microbial biomass was positively related to the distance from the glacier terminus.
- Low soil C and N contents contributed to limited microbial abundance.
- Microbial community structure changes with the distance from the glacier terminus.
- Distance from the glacier terminus had no impact on the fungal/bacterial PLFA.

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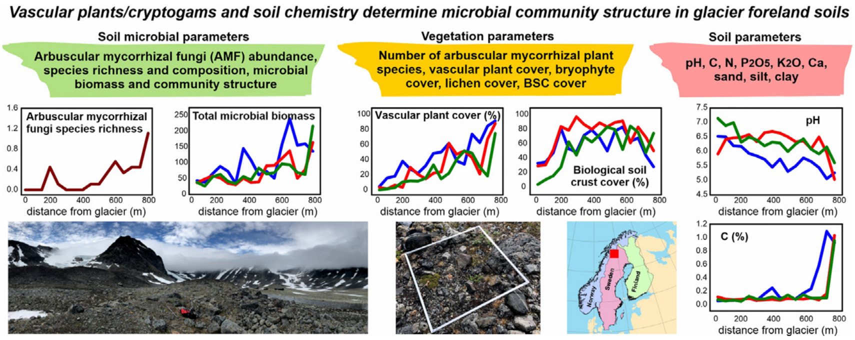
GRAPHICAL ABSTRACT



ABSTRACT

In the glacier forelands, microbes play a fundamental role in soil development and shaping the vegetation structure. Such ecosystems represent various stages of soil development and are, therefore, an excellent place to study the interrelationship between soil, plants, and microorganisms. The aim of the study was to assess the effects of vegetation and soil physicochemical properties developing after glacier retreat on soil microbial communities. Specifically, abundance, species richness and the composition of arbuscular mycorrhizal fungi (AMF), as well as microbial biomass and community structure in soils were compared between plots established in 800-meter transects of three glacier forelands in northern Sweden. The cover of vascular plants and cryptogams, soil C content, AMF spore density and species richness, AMF biomass indicators, total microbial biomass, and bacterial phospholipid fatty acids (PLFA) were significantly and positively related to the distance from the glacier terminus. On the other hand, macronutrient concentrations and pH decreased along with increasing distance. No significant impact of the distance from the glacier terminus on the ratio fungal/bacterial PLFA was observed. Moreover, we found a significant effect of both glacier and the distance from the glacier terminus on the microbial community structure. AMF species richness and spore density in the glacier forelands were generally low, which is probably due to a limited supply of inoculum in primary successional ecosystems. Most microbial biochemical markers and AMF parameters were positively associated with the number of arbuscular mycorrhizal plant species and vascular plant and lichen cover as well as C content in soil, whereas

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negatively with soil macronutrients and pH. This could be related to an increase in plant cover and a decrease in soil nutrient levels as plant succession progresses. Our results showed that vegetation, soil C content, and microbial communities are interlinked and exhibit concordant patterns along successional gradients.

1. Introduction

Arctic terrestrial ecosystems are constantly changing at an increasing rate due to global warming, and over the past 30 years, the Arctic has warmed four times faster than the entire globe (Rantanen et al., 2021). These changes are causing permafrost to melt and glaciers to retreat. As the glacier recedes, new areas are revealed that have been locked under the ice for thousands of years. This initiates the colonization and succession process of various life forms (Pendleton et al., 2019). In the glacier foreland ecosystems, microbes play a fundamental role in shaping the vegetation structure, while plants exert their influence through their own symbiotic communities through rhizospheres, which are involved in biogeochemical processes (Bai et al., 2019). In this way, microorganisms are crucial in promoting nutrient circulation involved in soil development, as well as supporting the colonization of diverse vegetation (Schuette et al., 2010; Kim et al., 2017).

Glacier forelands constitute relevant areas for primary succession studies concerning different groups of organisms due to restricted size, simple ecosystems prompted by harsh climatic conditions, and a low level of modification by environmental processes in recently deglaciated sites (Matthews, 1992). Moreover, the spatial representation of temporal changes is possible to observe along with an increasing distance from the glacier terminus and development time of the ecosystem (Bradley et al., 2014). The forelands of retreating glaciers represent various stages of soil development and are, therefore, an excellent place to study the interrelationships between soil, plants, and microorganisms. The development of such ecosystems is strongly linked to soil microbial activity. Initial areas of glacier forelands contain low levels of nutrients and are characterized by scarce vegetation; thus, it is evident that nutrient incorporation processes and the initial process of soil formation greatly depend on the activity of microorganisms (Schulz et al., 2013). Soil microbes play a significant role at different stages of soil formation and vegetation establishment. They are responsible for most biological transformations and support the development of stable and labile pools of carbon (C), nitrogen (N), and other macronutrients, which facilitate the subsequent development of plant communities (Kastovská et al., 2005; Schulz et al., 2013). The formation of microbial communities in areas after glacier retreat is a complex process, in which the main factors determining the structure of these communities include climate, topography, bedrock type, vegetation, and soil parameters (Noll and Wellinger, 2008; Lazzaro et al., 2009, 2010; Egli et al., 2011; Zeng et al., 2016; Cazzolla Gatti et al., 2018). Many studies have been carried out to recognize the patterns of vegetation and soil development in glacier forelands in the Arctic and high mountain regions (e.g., Jones and Henry, 2003; Okitsu et al., 2004; Khan et al., 2020; Wietrzyk-Pełka et al., 2020, 2021). In contrast, our knowledge on the succession pattern of soil microbial communities is limited (e.g., Hahn and Quideau, 2013; Bradley et al., 2014; Kim et al., 2017; Venkatachalam et al., 2021). Moreover, it has been shown that microbial succession can differ among glacier forelands (e.g., Sigler et al., 2002; Tscherko et al., 2003), thus recognizing the factors determining the development of soil microbial communities and their interrelationships with both abiotic and biotic factors are of great importance.

Various groups of microorganisms differ in their strategies of nutrient acquisition and trophic requirements, which should be reflected in the relationship between their abundance and nutrient content at different stages of soil development (Welc et al., 2012). Soil microorganisms are the main beneficiaries of soil organic matter decomposition. Therefore, their biomass depends on the age of the substrate and soil C content. The increasing diversity of microorganisms with soil age may be due to increasing C input to the system, and from more complex microecological interactions, including competition (Nemergut et al., 2007). In the case of arbuscular mycorrhizal fungi (AMF, Glomeromycota) and bacteria that obtain C from other sources, the main factor determining their biomass is phosphorus (P) (Jansa et al., 2009). In turn, the availability of N and other nutrients has a stimulating effect on bacterial communities (Madigan and Martinko, 2006). There have been several studies concerning microbial communities in glacier forelands with regard to abiotic factors such as soil pH, temperature and humidity, soil element concentration, soil organic matter content, soil aggregation, and vegetation cover. Quantitative aspects of microbial communities were assessed using biochemical markers, such as fatty acids, which enable the indication of which organisms dominate a given environment (Tscherko et al., 2005; Kaštovská et al., 2007). Such studies were complemented by molecular methods assessing the changes in microbial community structure (e.g., Schipper et al., 2001; Sigler and Zeyer, 2002; Sigler et al., 2002; Jumpponen, 2003; Nemergut et al., 2007; Venkatachalam et al., 2021). Acidification of soils due to C accumulation in glacier foreland ecosystems has been suggested to cause a shift in microbial communities from bacteria- to fungi-dominated (Ohtonen et al., 1999; Shanmugam and Kingery, 2018). Similarly, Bardgett (2000) found that bacterial biomass is large compared to fungal biomass in the early stages of succession in glacial forelands, but fungal biomass increases over time. On the other hand, Welc et al. (2012) reported that the ratio of fungi to bacteria remained unchanged along the soil chronosequence of alpine glacier foreland.

Arbuscular mycorrhizal fungi are the most widespread and important plant symbionts, colonizing the roots of a great majority of terrestrial plant species (Smith and Read, 2008). They increase nutrient acquisition, growth, and the vitality of plant partners, and are crucial for the protection of plants against pathogens, drought, salinity, and heavy metal stresses (Harrier and Watson, 2004; Smith and Read, 2008). Glomeromycotan fungi promote the process of soil particle aggregation and aggregate stability through the mechanical entanglement of extraradical hyphae and cementing properties of their exudates, and thus protect soils against erosion (Rillig et al., 2002; Wu et al., 2014). Regarding the occurrence of AMF in polar regions, Newsham et al. (2009) found that this type of associations is common in the roots of Poaceae, Saxifragaceae, Asteraceae, and Ranunculaceae in taiga and sub-Artic tundra areas. Moreover, arbuscular mycorrhizal association clearly decreases in abundance in polar deserts and Arctic tundra (Newsham et al., 2009). A study on the Damma glacier foreland showed that an abundance of soil fungi and bacteria were more dependent on abiotic soil parameters, i.e., pH and C content than on soil age. However, the evolution of this ecosystem progresses unevenly over time, and AMF proved to play a more important role in mineral soils, than in older, more acidified and organic soils (Welc et al., 2012).

Despite many studies on primary succession related to plant development, soil formation, and microbial diversity, the details on succession processes of newly created ecosystems are not yet fully understood. While it has been recognized that vegetation dynamics cannot be separated from the dynamics of underground soil communities and that changes in vegetation patterns coincide with soil nutrient cycling and microbial communities (Qiang et al., 2021), little is known about how the different components of the above-ground and underground systems are interrelated in glacier forelands. To gain a deeper insight into this problem, we modelled the effects of factors associated with soil and plant variables on factors represented by soil microbial biochemical markers and AMF parameters. Moreover, the changes in soil microbial communities in glacier foreland were primarily analysed by comparisons between the different succession stages along the chronosequence after glacier recession (Hahn and Quideau, 2013; Alfaro et al., 2020). On the other hand, the assessment of the changes in the abundance and composition of microbial communities in the early stage of succession is still limited. Recognition of these patterns in the early succession phase is crucial to identify the dynamics of microorganism changes along with the distance from the glacier and to determine the role of AMF in primary succession along with the identification of pioneering AMF species. The issues raised above seem to be of great importance for understanding the dynamics of microbial succession in the context of an accelerating glacial recession.

The aim of this study was to assess the effects of vegetation and soil physicochemical properties developing after glacier retreat on soil microbial communities. Specifically, AMF abundance, species richness and composition, as well as microbial biomass and community structure in soils were compared between plots established in transects in three different glacier forelands. We hypothesized that along with the distance from glaciers (1), the abundance of AMF in soil determined by spore number, concentrations of 16:1ω5 phospholipid (PLFA) and neutral (NLFA) lipid fatty acids, AMF species richness, and microbial biomass would increase, (2) the microbial parameters would also depend on habitat conditions defined by the soil physicochemical properties, vascular plant and cryptogam covers, (3) AMF species composition and microbial community structure would change, and the progressive succession of plants and cryptogams would lead to carbon accumulation in soil and would, thereby, cause a shift in microbial communities from bacteria- to fungi-dominated.

2. Materials and methods

2.1. Study sites and sample collection

The study was carried out in the glacier forelands of Isfallsglaciären (67°54′N, 18°36′E), Storglaciären (67°54′N, 18°36′E), and Rabots glaciären (67°54′N, 18°26′E) in the summer of 2019 (Fig. S1A–C). The geographic locations of the sites were placed in the region of Kebnekaise massif (2096 m a.s.l.), in northern Sweden. The regional climate of the study area is cold and humid and influenced by local topography and dominant weather patterns. The mean annual air temperature is −3.4 °C. Mean annual precipitation is 1997 mm ± 450 mm (Dahlke and Lyon, 2013). The bedrock is composed of mafic dykes, amphibolite rocks, and mylonitic augen gneiss (Andréasson and Gee, 1989). Storglaciären is a small polythermal, valley glacier covering 3 km^2, with an elevation range of 1140–1700 m a.s.l. (Holmlund and Holmlund, 2019). Isfallsglaciären is also a small, polythermal valley glacier covering ca. 1 km^2 with elevation between 1775 and 1185 m a.s.l. (Clason et al., 2021). Both glaciers are located on the eastern flanks of Kebnekaise, in the Tarfala Valley. Rabots glaciären, localized ca. 5 km west of Storglaciären, is a polythermal valley glacier with an extension of ca. 4 km^2 and elevation ranging from 1090 to 1800 m a.s.l. (Taveirne et al., 2021). The vegetation of forelands is sparse and dominated by cryptogamic organisms including lichens, bryophytes, and biological soil crust, among which vascular plants sporadically occur.

We designated 3 parallel 800-meter transects along foreland in each glacier foreland. The transects were selected so that 1) they covered areas from glacier terminus, across foreland to mature tundra, and 2) they avoided areas strongly eroded and with lakes (Fig. 1). In each transect, sampling plots were randomly located at a distance of ca. 50 m from each other (Fig. S1). Altogether we studied 144 sampling plots (Fig. S1D–E) in terms of vascular plant and cryptogam species presence and soil characteristics.

At each plot, the cover of vascular plant and cryptogam species was determined (see Section 2.5). Within each plot, 2 separate composite soil samples were collected for the purpose of (1) soil property investigation and (2) microbial analyses. After the removal of plants and organic matter, 8 soil subsamples to a depth of ca. 10 cm were randomly taken using a shovel. Subsamples were combined and homogenized in plastic bags into composite samples (4 subsamples per 1 composite sample). To prevent contamination, the shovel was carefully cleaned before digging. In total, 288 soil composite samples were collected (3 glacier forelands × 3 transects × 16 plots × 2 composite samples). Samples for microbial analyses were

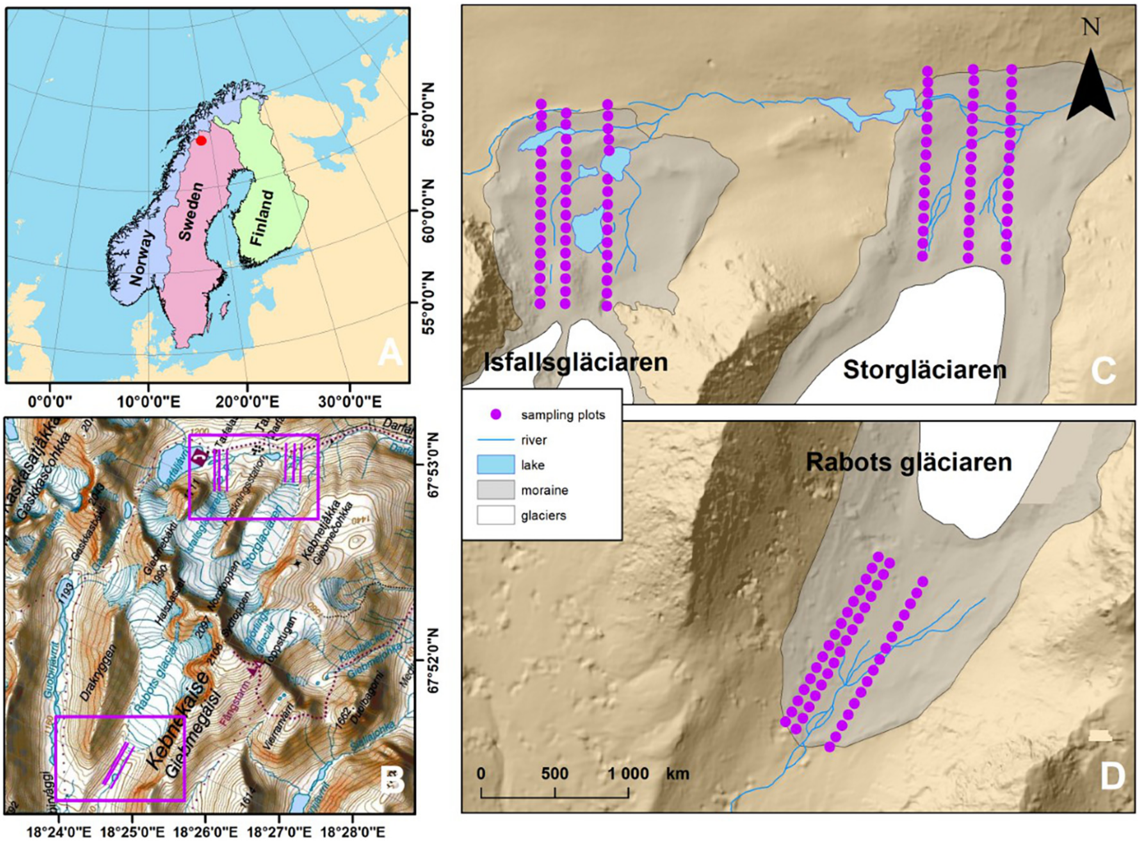

Fig. 1. Location of the study area (A) with a view on glacier forelands in the Kebnekaise region (B) and close-ups on studied forelands of Isfallsglaciären, Storglaciären, and Rabots glaciären (C–D).

stored and transported in plastic bags in a fridge. Samples for soil analyses were dried and transported in plastic bags.

2.2. Determination of AMF spore number, species richness, and species composition in soil

Soil samples for AMF spore isolations were stored at 4 °C before use. Spore extractions were performed by centrifuging 50 g of fresh soil in a 50 % sucrose solution and filtering (Brundrett et al., 1996). A sieve of 50-μm mesh size was used (Zubek et al., 2019; Rożek et al., 2020). Spores were observed and counted in Petri dishes under a dissecting microscope, and then mounted on a slide in a drop of polyvinyl alcohol/lactic acid/glycerol (PVLG) (Omar et al., 1979) and a mixture of PVLG/Melzer's reagent (1:1, v:v). The characterization of AMF spores followed Błaszkowski (2012) and was performed using an Olympus BX51 light microscope.

To further check the occurrence of AMF in the plots, particularly of the AMF species that were not sporulating in the field, laboratory cultures were established for their propagation (Błaszkowski, 2012), using soil collected from the plots. For each culture, ca. 100 g of fresh soil was placed in a plastic pot (9 × 12.5 cm; 500 ml in volume) filled with commercially available coarse-grained and autoclaved sand. *Plantago lanceolata* L. was used as a host plant. Approximately 50 seeds per pot were sown. Seeds of this species were obtained from Herbador, Poznań, Poland. The pots were positioned randomly in the plant growth room and kept in closed Sun bags to avoid contamination between treatments, at 20 °C and 345 μmol PAR photons m^{-2} s^{-1}, in a 12/12 h light regime. They were watered once every two months with 50 ml of distilled water and once every two months with 50 ml of Long Ashton nutrient solution for plants. Spore extractions were performed by centrifuging 50 g of fresh substratum of each pot after 18 months of culture establishment, using the method described above. Roots were collected from the pots at the same time as substrata and were used for staining to visualize AMF mycelia (see Section 2.3).

2.3. Root staining and the assessment of AMF colonization of *Plantago lanceolata* from AMF laboratory cultures

The roots were washed in tap water to remove any remnants of soil, then stained according to the method of Phillips and Hayman (1970), with minor modifications (Zubek et al., 2022). For each sample, 30 stained root fragments approximately 1 cm long were randomly chosen, mounted on slides in glycerol: lactic acid (1:1, v/v), and pressed flat using cover slides. The fungal colonization of roots was observed using a Nikon Eclipse 80i microscope with a Nomarski interference contrast. The degree of AMF colonization was determined following the calculation of mycorrhizal frequency (F_{AMF}%), relative mycorrhizal root length (M_{AMF}%), and relative arbuscular richness (A_{AMF}%), according to the method proposed by Trouvelot et al. (1986). Estimates of F_{AMF}% represent the ratio between the number of root fragments colonized by AMF mycelium and the total number of analysed root fragments. The M_{AMF}% parameter is an estimate of the proportion of root cortex that is mycorrhizal relative to the entire analysed root system. Arbuscule abundance (A_{AMF}%) is an estimate of arbuscule richness within the entire analysed root system (Trouvelot et al., 1986).

2.4. Analysis of fatty acid concentrations in soil

Soil samples for fatty acid analyses were kept frozen at −20 °C until use. Microbial biomass was calculated on the basis of phospholipid fatty acid analysis and microbial community structure was analysed using the same PLFA method. The extraction of PLFA and neutral lipid fatty acids (NLFA) was performed according to Palojärvi (2006), with the exception of the lipid extraction, which followed Macnaughton et al. (1997). Lipids were extracted from freeze-dried (Freeze Dry System; Labconco) soil with a mixture of a methanol/chloroform/phosphate buffer (2/1/0.8, v/v/v) using an ASE 200 accelerated solvent extractor (Dionex) within two 15-min cycles at 80 °C and under 1200 PSI pressure. Following the extraction, an appropriate volume of chloroform and deionized water was added to give the correct final ratio (chloroform/methanol/phosphate buffer/water; 1/1/0.9, v/v/v) and form two phases. The chloroform layer was evaporated under N_2 gas at 40 °C. The lipids were separated into neutral-, glyco-, and phospholipids in Bakerbond conventional SPE silica gel columns (500 mg; J. T. Baker®) by eluting with chloroform, acetone, and methanol, respectively. The chloroform and methanol fractions were collected into new vials and reduced to dryness under N_2 gas at 30 °C. The lipids were subjected to mild alkaline methanolysis, and a known concentration of methyl nonadecanoate (19:0; Fluka) was added to neutral lipids and phospholipids fractions as an internal standard. The resulting fatty acid methyl esters were separated, quantified, and identified using a gas chromatography coupled with mass spectrometry (GC–MS; Varian 3900 and Saturn 2100 T), and the NIST database library. The Select FAME column (100 m × 0.25 × 0.36; Agilent Technologies) was applied for the optimal (including cis/trans isomers) separation of individual fatty acids. Helium was used as a carrier gas, and injections were made in split mode (1:10). Individual fatty acids were identified on the basis of several standards: 37-component FAME Mix (Supelco), Bacterial Acid Methyl Ester (BAME) Mix (Supelco), and a few additional one-component standards (Sigma-Aldrich, Matreya LLC).

The sum of twenty PLFAs (those with >0.5 % of the total relative abundance in most soil samples, namely: 2OH 10:0, 12:0, 14:0, 15:0, a15:0, i15:0, 16:0, i16:0, 16:1ω5, 16:1ω7, 17:0, i17:0, cy17:0, 17:1, 18:0, 18:1ω7, 18:1ω9, 18:1ω9t, 18:2ω6, 20:0), was calculated and used as an indicator of total microbial biomass. Bacteria were represented by the sum of a15:0, i15:0, i16:0, 16:1ω7, 17:0, a17:0, i17:0, cy17:0, 18:1ω7, and cy19:0. The sum of a15:0, i15:0, i16:0, a17:0, and i17:0 was an indicator of gram-positive (G+) bacteria, while the sum of 16:1ω7, cy17:0, 18:1ω7, and cy19:0 was an indicator of gram-negative (G−) bacteria. Saprotrophic fungi were represented by 18:2ω6 (Stanek et al., 2021 and references therein). Fungal/bacterial PLFA and G+/G− PLFA ratios were also calculated. The concentrations of PLFA and NLFA 16:1ω5 were used as AMF biomass indicators (Olsson et al., 1997; Olsson, 1999). PLFA 16:1ω5 was regarded as a structural lipid marker and NLFA 16:1ω5 as a storage lipid marker (Olsson et al., 1997; Olsson, 1999; Sharma and Buyer, 2015).

2.5. Assessment of vascular plant species composition and cryptogam/vascular plant cover

We investigated the cover of vascular plants and cryptogams (including lichens, bryophytes, and biological soil crusts (BSC)) using $1m^2$ plot division in 100 squares (each square represented 1 % of species presence). All vascular plant species present in the plots were identified. Vascular plants unable to be determined in the field were collected and studied using traditional taxonomy methods. Species nomenclature follows Mossberg and Stenberg (2018). Herbarium specimens were deposited in the Herbarium of the Institute of Botany of the Jagiellonian University in Kraków (KRA).

2.6. Soil physicochemical analyses

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. The C and N contents were measured in a Thermo Scientific Flash Smart CNS Analyzer (Thermo Fisher Scientific Inc., Waltham, USA) after dry combustion. The concentration of exchangeable calcium ions Ca^{2+} was measured via flame atomic absorption spectrometry (FAAS) after extraction with 1 M ammonium acetate ($C_2H_7NO_2$) (Sumner and Miller, 1996). We extracted plant available phosphorus (P_2O_5) and potassium (K_2O) according to the Egnér-Riehm protocol (Egnér et al., 1960) and determined their concentrations using the colorimetric method (Kuo, 1996) and FAAS, respectively. The soil pH was measured in distilled water (1:2.5 soil/water ratio) after 24 h when the solution was in equilibrium with the soil and, therefore, stable (Thomas, 1996). Soil particle-size distribution was determined using laser diffraction (Analysette 22, Fritsch, Germany).

2.7. Data analysis

The effect of glacier (study site) and distance from the glacier terminus on the microbial community structure (PLFA relative concentrations: 20 PLFAs with >0.5 % of the total relative abundance in most soil samples) was determined using two-way permutational multivariate analysis of variance (PERMANOVA) without replication. The analysis was based on Euclidean resemblance matrices with 999 permutations for each test (Anderson et al., 2008). The routine was run with posteriori pairwise comparisons among levels of the distance factor. To visualize the PERMANOVA results, nonmetric multidimensional scaling (NMDS) based on Euclidean distances was applied. The factors, derived from Factor analysis (described below), were fitted into ordination space. Next, the mean values of 20 PLFA concentrations for each distance on each study site were calculated and principal component analysis (PCA) was used to visualize differences in microbial community structure between particular distances from the glacier terminus.

The correlations between distance from the glacier terminus, particular plant parameters, AMF species richness and spore density, microbial biochemical markers, and soil chemical parameters were quantified with Pearson's correlation coefficients. Next, habitat properties (including soil parameters, distance from the glacier terminus, vascular plant variables, and cryptogam variables) were subjected to factor analysis (FA) to obtain uncorrelated factors. The factors with eigenvalues >1 were extracted based on Kaiser criterion and varimax-rotated to simplify their interpretation. Next, we conducted stepwise multiple linear regression analysis using forward variable selection (with a threshold of $F > 1.00$ to entry) to investigate the effect of factors derived from factor analysis on the concentration of microbial biochemical markers and AMF species richness. Prior to the analysis, the following assumptions were verified to validate the models: distribution normality of residuals was checked using the Kolmogorov-Smirnov test ($p > 0.05$), the potential multicollinearity of the predictors was verified by calculating the variance inflation factors (VIFs), and Durbin-Watson statistics were calculated to evaluate the potential presence of a serial correlation of residuals. The residual analysis was run to detect outliers and influential points.

Statistical analyses were performed using STATISTICA 13 (TIBCO Software Inc., Palo Alto, California, USA), PRIMER 7 statistical software (Primer-E, Plymouth, UK; Anderson et al., 2008), and PAST 4.06 (Hammer et al., 2001).

3. Results

3.1. Vascular plant and cryptogam cover and vascular plant species composition

In total, 43 species of vascular plants were found. Their number per plot (species richness) varied between 0 and 11 and averaged 4.51. Dominant vascular plant species included *Poa alpina*, *Luzula arcuata*, and *Salix herbacea*. Among the species of vascular plants, 21 were potentially capable of forming AM (AM species), 18 were regarded as unable to form AM (non-AM species), and 4 were of unknown mycorrhizal status (Table S1).

The vascular plant cover gradually increased with the distance from the terminus of the glaciers and reached the highest values at a distance of 800 m. A similar rising trend was observed for the number of AM plant species (Fig. 2). With regard to bryophyte and BSC cover, their values increased with the distance from the terminus of glaciers, but at the final distances decreased. Generally, in the case of lichen cover, initial low values increased and then remained at a level of 70 % upwards with increasing distance (Fig. 2).

3.2. Soil physicochemical properties

With regard to macronutrients, i.e., P_2O_5, K_2O, and Ca, as well as pH, the initial high values decreased with distance from the terminus of glaciers (Fig. 3). The contents of N in most distances were close to zero in Storglaciären and Isfallsglaciären, and reached higher values in the last two distances, while in Rabots glaciären this parameter varied independently of the distance (Fig. 3). A similar trend was observed for C contents, but considerably higher values were recorded from the distance of 600 m to the end of the transects (Fig. 3).

3.3. Arbuscular mycorrhizal fungi abundance, species richness, and species composition

In total, the spores of 8 AMF species were isolated from all sites. The spores representing the genus *Glomus* were not identified to the species level. The spores of *Acaulospora cavernata* were most frequently isolated, being found in 12 (Storglaciären), 1 (Isfallsglaciären), and 5 (Rabots glaciären) plots, respectively. The number of AMF species per sample ranged from 0 to 3 and averaged 0.25. From the field soil, 4 species were

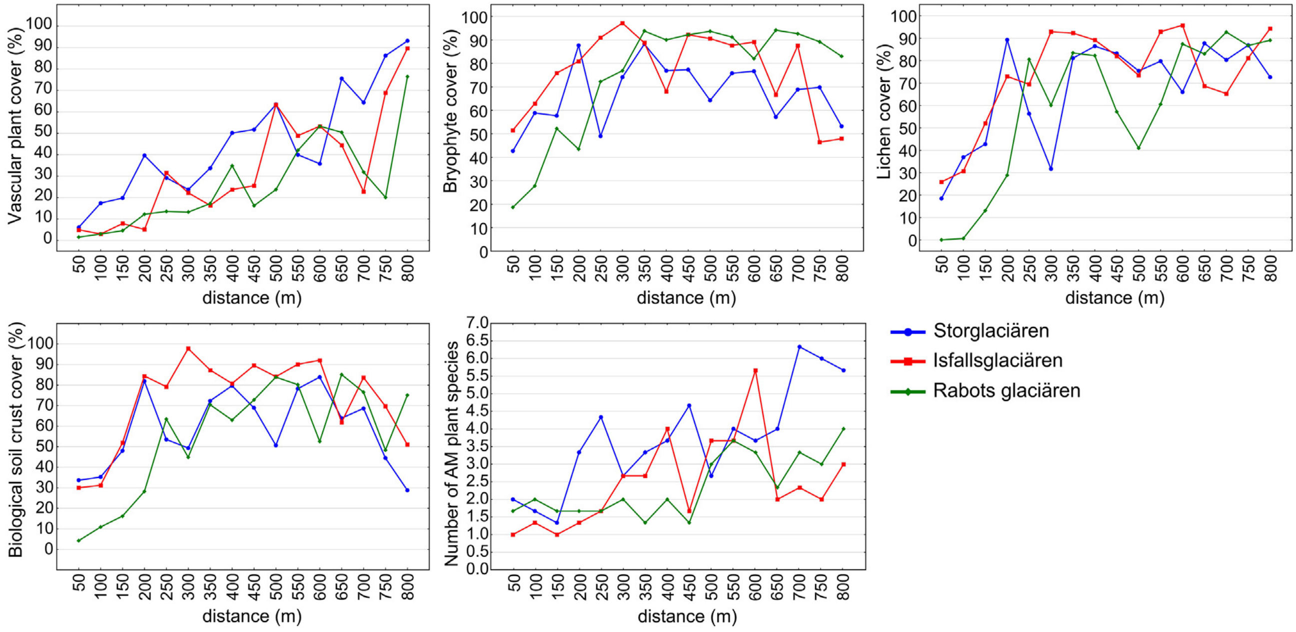

Fig. 2. Mean values (n = 3) of vascular plant and cryptogam parameters at individual distances from the terminus of three glaciers in northern Sweden. A list of arbuscular mycorrhizal (AM) plant species is presented in Table S1. Detailed statistics are provided in Table S2.

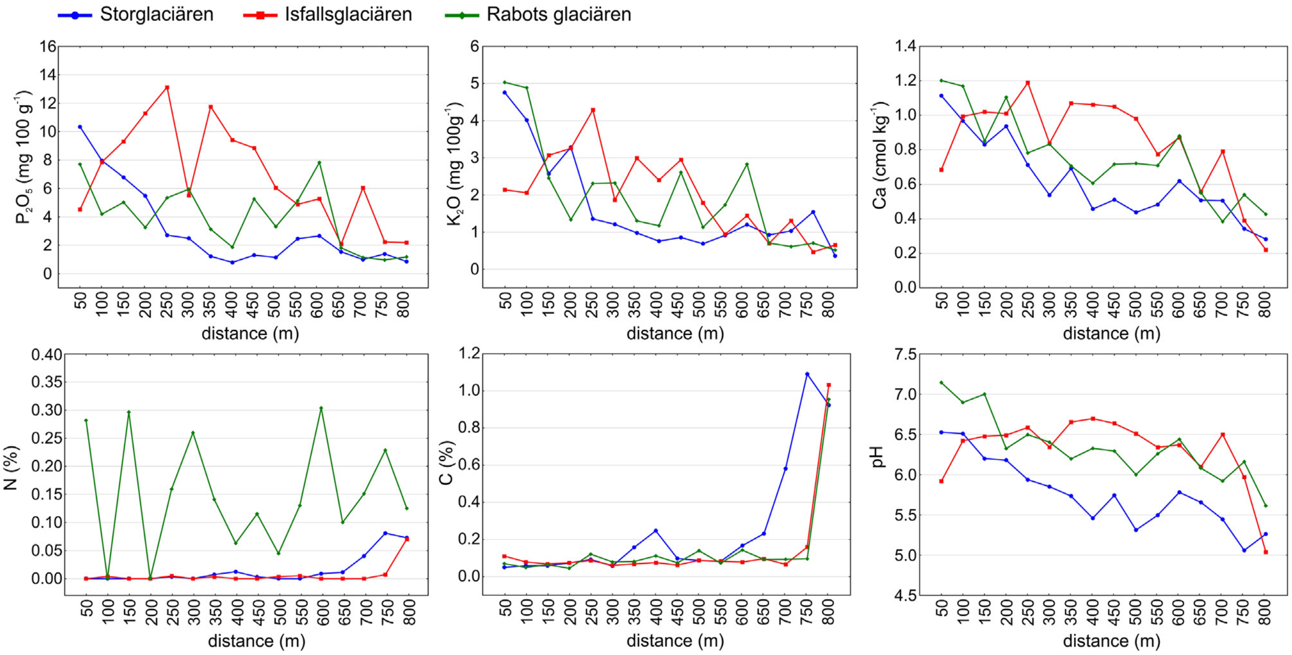

Fig. 3. Mean values (n = 3) of soil parameters at individual distances from the terminus of three glaciers in northern Sweden. Detailed statistics are provided in Table S3.

isolated, namely *Acaulospora cavernata*, *A. capsicula*, *A. laevis*, and *Diversispora epigaea*; 4 species were also recorded from laboratory cultures, i.e., *Acaulospora paulinae*, *Entrophospora glacialis*, *Rhizoglomus irregulare*, and *Glomus* sp. *Plantago lanceolata* colonization was detected in 59 pots and indicated the presence of AMF mycelia in soils from 59 plots (Fig. S2).

At distances close to the terminus of three glaciers up to 400 m, the AMF species richness equalled zero or was close to zero, with the exception of the distance 200 m, where mean AMF species richness increased to 0.4 (Fig. 4). Generally, from the distance of 400 m AMF species richness increased with increasing distance from the terminus of three glaciers, reaching the highest value at a distance of 800 m (Fig. 4). In the case of AMF spore density, at distances from 50 m to 500 m, the values were close to zero. Next, the value temporarily increased, and then reached its highest (100) at a distance of 750 m (Fig. 4).

Generally, in the case of three glaciers, the pattern of AMF occurrence in soil samples in their foreland was similar. The greatest number of species was recorded at distances between 450 m and 800 m, the most common AMF species was *A. cavernata* (Fig. 5). In addition, spores of *Endogone* sp., were observed only at 8 distances in the Rabots glaciären glacier and only at the two final distances (650 m and 800 m) at Storglaciären glacier (Fig. 5).

Mycorrhizal colonization of *P. lanceolata* was recorded in laboratory cultures established on soil samples from different distances in each of three glaciers, but was most commonly recorded in soils from the Storglaciären (Fig. 5).

3.4. The concentration of microbial biochemical markers in soils

The concentrations of AMF biochemical markers ranged between 0 and 14.45 nmol g^{-1}, averaging 1.53 nmol g^{-1} (16:1ω5 PLFA), and between 0 and 4.73 nmol g^{-1}, averaging 0.54 nmol g^{-1} (16:1ω5 NLFA). The values of these parameters increased from the distance of 400 m and reached the highest values at the distance of 800 m. The exception was the Storglaciären, where high concentrations were recorded at several distances (Fig. 6). As regards total microbial biomass, values ranged between 11.26 and 425.84 nmol g^{-1}, averaging 81.01 nmol g^{-1}, and for three glaciers gradually increased to the highest values at the farthest distances. Fungal PLFA parameter ranged between 0 and 12.48 nmol g^{-1}, averaging

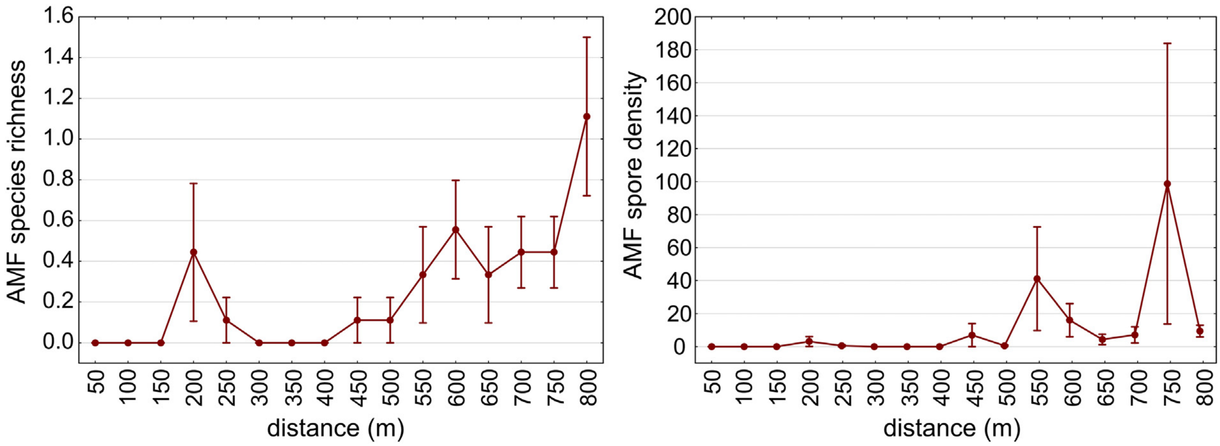

Fig. 4. Arbuscular mycorrhizal fungi (AMF) species richness and AMF spore density (mean values ± SE; n = 9) at individual distances from the terminus of three glaciers in northern Sweden. Detailed statistics are provided in Table S4.

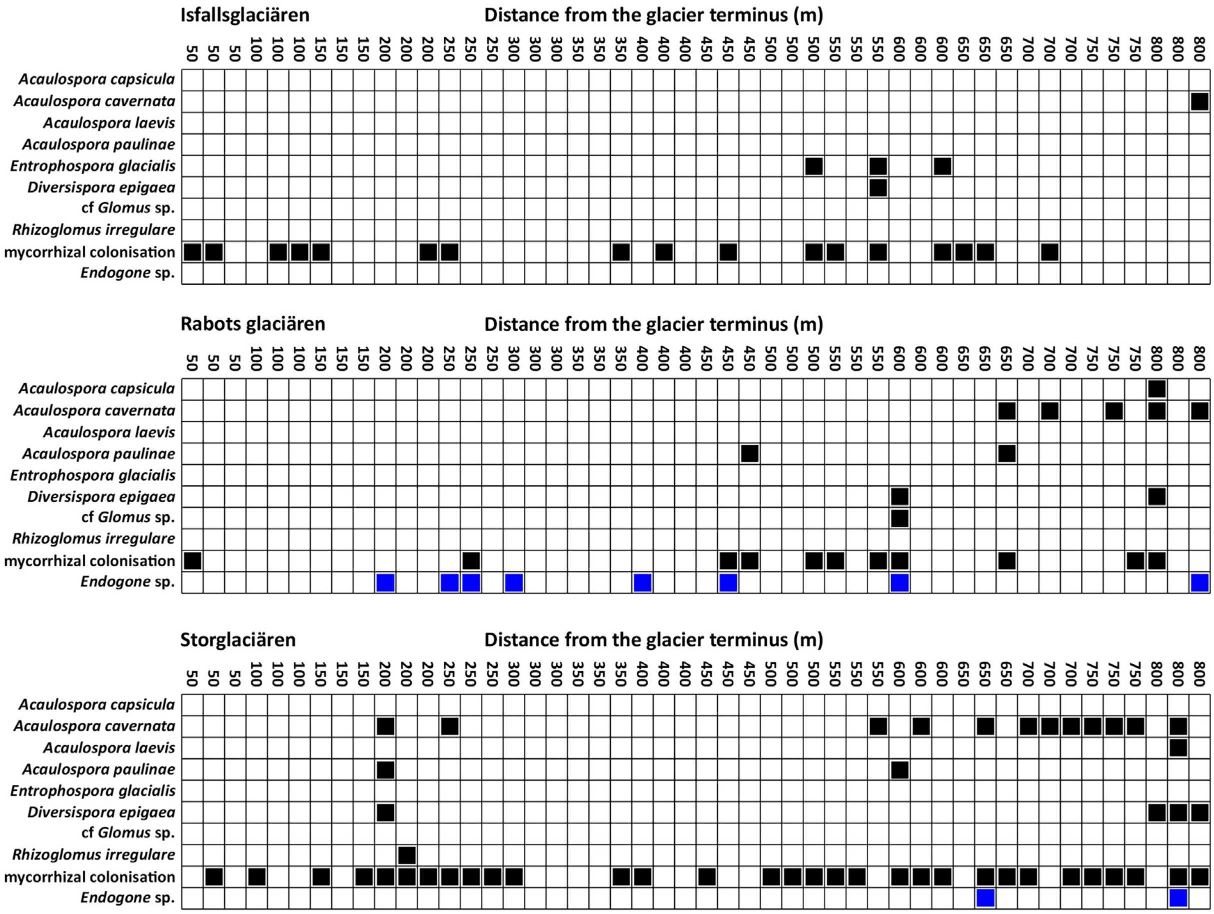

Fig. 5. Pattern of arbuscular mycorrhizal fungi (AMF) occurrence in soil samples in the foreland of three glaciers in northern Sweden along the distance from the glacier terminus, mycorrhizal colonization of *Plantago lanceolata* from laboratory cultures established with soil samples collected from the three glaciers, and the presence of *Endogone* sp. spores in soil samples.

1.49 nmol g^{-1}, and its values remained relatively constant at all distances for each glacier (Fig. 6). Regarding bacterial parameters, the concentrations fluctuated between 8.51 and 59.95 nmol g^{-1}, averaging 38.03 nmol g^{-1} (Bacterial PLFA), between 5.03 and 39.21 nmol g^{-1}, averaging 22.92 nmol g^{-1} (G+ PLFA), and between 1.94 and 27.24 nmol g^{-1}, averaging 14.74 nmol g^{-1} (G− PLFA). The values of these three parameters gradually increased with a distance from the terminus of three glaciers (Fig. 6). With regard to G+/G− PLFA, the values ranged between 0.49 and 5.57, averaging 1.75 (G+/G− PLFA), no clear trend of changes in this parameter with a distance from the glacier terminus was observed. The exception was the Isfallsglaciären glacier, where high values were observed at middle distances (350 m and 450 m) (Fig. 6). A similar trend was recorded for the fungal/bacterial PLFA, which showed no clear trend with distance from the glacier, the ratio ranged between 0 and 0.32, averaging 0.04; however, the highest values were observed for Rabots glaciären at distances of 200 m and 800 m.

3.5. Microbial community structure

Two-way PERMANOVA revealed a significant effect of both glacier ($p = 0.002$) and the distance from the glacier terminus ($p = 0.001$) on the microbial community structure (Table S6); the interaction between both factors was not significant ($p > 0.05$). Regarding the effect of glacier, Storglaciären significantly differed from the remaining glaciers. Pairwise comparisons among particular distances revealed that, generally, the most significant differences in community structure were observed between the distances close to the glaciers (50 to 150 m) and the last 5 distance intervals. The exception was the distance of 300 m, which differs significantly from most distances ($p < 0.05$). Moreover, the values obtained at a distance of 800 m differed significantly from almost all other distances (Table S7).

The differences in microbial community structure between the individual plots are visualized on the NMDS diagram (Fig. S3). The plots located near Isfallsglaciären and Rabots glaciären showed a relatively similar pattern of microbial community structure and are mainly associated with high values of Factors 1, 3 and 4 that are represented by soil nutrient levels and cryptogamic species cover. The Storglaciären was most strongly linked with Factor 2 that is mainly represented by C content and vascular plant cover (Table 1; Fig. S3).

Regarding the differences in microbial community structure between particular distances from the glacier terminus, as a rule, the soil from plots located at distances from 600 m to 800 m were the most outstanding from the plots located near the glacier. This differentiation was mainly due to a greater abundance of PLFAs located on the left side of the diagram in soils at further distances and a greater abundance of 18:2ω6 (biomarker of saprotrophic fungi) in the initial soils close to the glacier (Fig. S4).

3.6. Relationships between plant, soil, microbial biochemical markers, and AMF parameters

All of the plant parameters were significantly and positively related to the distance from the glacier terminus (Fig. 7). Similarly, soil C content, AMF spore density and species richness, AMF biomass indicators, total microbial biomass, and bacterial PLFA significantly increased with the distance from the glacier terminus. On the other hand, macronutrient concentrations and pH decreased along with increasing distance. Most microbial biochemical markers and AMF parameters were positively associated

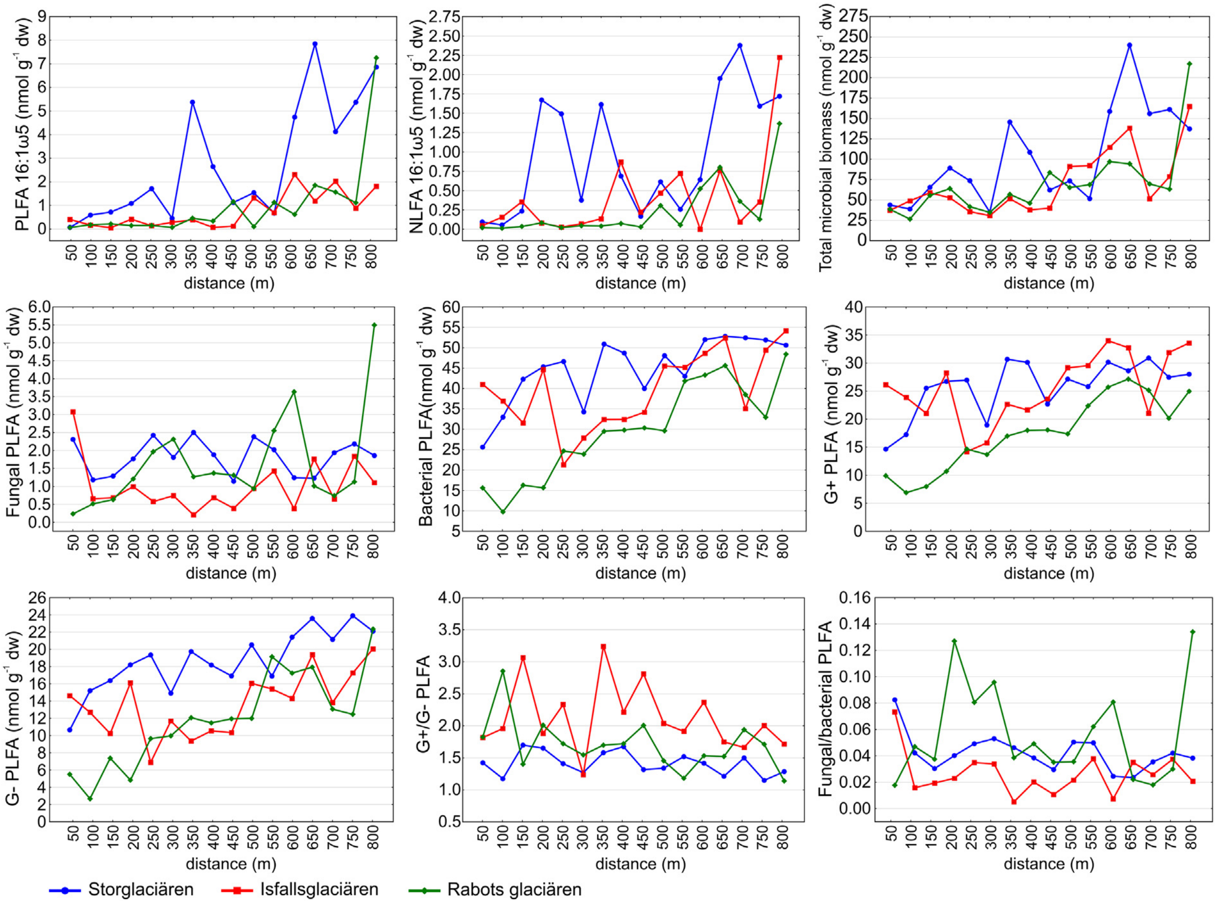

Fig. 6. Mean values (n = 3) of microbial biochemical marker parameters at individual distances from the terminus of three glaciers in northern Sweden. Detailed statistics are provided in Table S5.

with the number of AM plant species and vascular plant and lichen cover as well as C content in soil, whereas negatively with soil macronutrients and pH (Fig. 7).

3.7. Factors affecting the concentration of microbial biochemical markers and AMF species richness

Based on the entire data matrix, factor analysis reduced 16 variables to four factors with eigenvalues >1 that jointly explained 77.01 % of the total variation (Table 1). Factor 1 explained 30.33 % of variance and related to P_2O_5 (0.84), K_2O (0.75), Ca (0.78), sand (−0.93), silt (0.9), and clay (0.94). Factor 2 explained 22.11 % of variance and was associated with the distance (0.74), number of AM plant species (0.66), the vascular plant cover (0.86), and C (0.81). Factor 3 explained 15.52 % of variance and was related to the bryophyte cover (0.9), the lichen cover (0.75), and the BSC cover (0.88). Factor 4 explained 9.05 % of variance and correlated with N (0.83).

Multiple stepwise regression analysis with a forward stepwise procedure with four Factors derived from factor analysis as predictor factors and microbial biochemical markers and AMF species richness as the dependent variables revealed that, in most cases, Factors 1, 2, and 4 were included in the models (Table 2). As regards AMF species richness, Factors 2 and 4 were included in the model. Both the distance from the glacier terminus, the number of AM plant species, the vascular plant cover, as well as C and N contents in soil positively affected AMF species richness. As regards PLFA 16:1ω5, bacterial PLFA and G+ PLFA, Factors 2, 1, and 4 were included in the model; however, only the first two factors showed a significant effect. In this case, the distance from the glacier terminus, the number of AM plant species, the vascular plant cover, C and sand had a positive influence, while macronutrient concentrations, silt and clay negatively affected these parameters. Regarding NFLA 16:1ω5 and total microbial biomass, fungal PLFA and G- PLFA, only Factors 2 and 1 were included in the model. Factor 2 showed a significant effect in each case, but Factor 1 showed a significant effect only in the case of total microbial biomass and G- PLFA. In relation to these parameters, the distance to the glacier terminus, the number of AM plant species, the vascular plant cover, C, and sand showed a positive effect. On the contrary, the concentration of macronutrients, silt, and clay had a negative effect. As regards G+/G− PLFA, Factors 2 and 1 were included in the model, but, in this case, the distance, the number of AM plant species, the vascular plant cover, C and sand negatively influenced G+/G− PLFA, while macronutrients, silt, and clay showed a positive but not significant impact. In the case of fungal/bacterial PLFA, Factors 4 and 3 were included in the model. N content was positively related to this parameter, while the bryophyte cover, the lichen cover, and

Table 1
Factors derived from habitat properties of glacier forelands in northern Sweden (including soil parameters, vascular plant variables, cryptogam variables, and the distance from the glacier terminus). Factor loadings are given in parentheses; only variables with factor loadings >0.65 are listed. The percentage of explained variance for each factor is provided.

Factor no	Variables (factor loadings)	Variance explained (%)
Factor 1	P_2O_5 (0.84), K_2O (0.75), Ca (0.78), sand (−0.93), silt (0.90), clay (0.94)	30.33
Factor 2	Distance (0.74), number of AM plant species (0.66), vascular plant cover (0.86), C (0.81)	22.11
Factor 3	Bryophyte cover (0.90), lichen cover (0.75), BSC cover (0.88)	15.52
Factor 4	N (0.83)	9.05

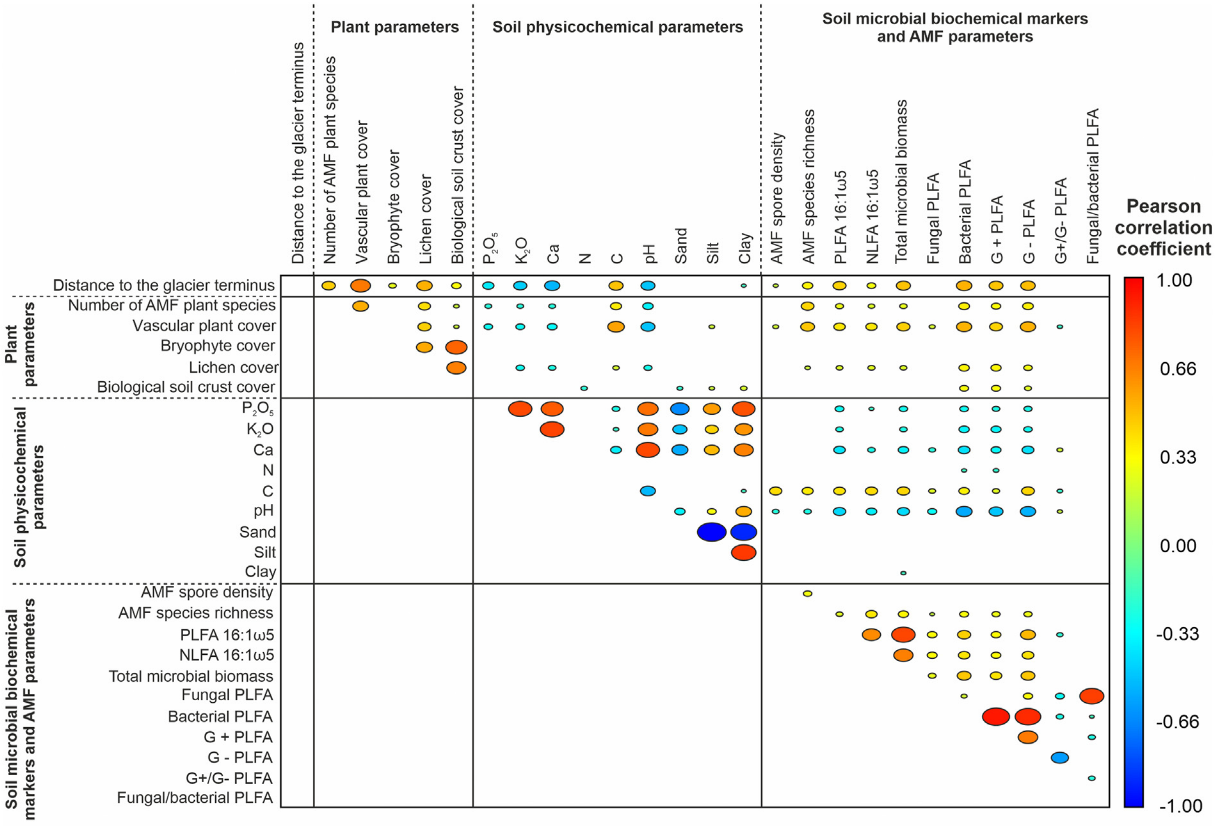

Fig. 7. Exploratory heatmap showing Pearson correlation coefficients for plant, soil physicochemical and soil microbial biochemical markers, and arbuscular mycorrhizal fungi (AMF) parameters in soils of glacier forelands in northern Sweden. Only statistically significant ($p < 0.05$) correlations are shown.

BSC cover showed a negative effect; however, these effects proved not to be significant.

4. Discussion

4.1. Changes in microbial communities versus the distance from the glacier terminus

Habitats created by glacier retreat are the perfect ecosystems to test interactions between bacteria and fungi with biotic and abiotic components of the environment. As a rule, soil microbial communities on recently deglaciated areas differed considerably from those of later successional stages (Bardgett et al., 2007). Our results showed that total microbial biomass increased along with the distance from the terminus of the glacier which, in turn, was positively related to the vascular plant cover, the number of AM plant species, and soil C content. This confirms that plant communities, soil C content, and microbial communities are interlinked and exhibit concordant patterns along environmental gradients. A similar trend of increased microbial biomass over successional stages was also observed in the foreland of other glaciers (e.g., Ohtonen et al., 1999; Welc et al., 2012; Brown and Jumpponen, 2014; Jiang et al., 2019). Our results correspond with the conclusions of other authors in that the abundance of bacterial communities could be related to the availability of organic matter in soils that, as a rule, increase with the distance from glaciers (Kastovská et al., 2005; Eskelinen et al., 2009; Li et al., 2017). In our study, the increasing trend was most evident in the case of bacteria, both G+ and G−. To a lesser extent it also concerned saprotrophic fungi. Interestingly, we found no significant impact of the distance from the glacier terminus on fungal/bacterial PLFA. In contrast, Ohtonen et al. (1999) found that the microbial community shifted from bacteria-dominated to fungi-dominated over the successional gradient on the foreland of Lyman Glacier in the USA. Such a trend was suggested to be linked with the acidification of soils due to C accumulation (Bardgett, 2000). However, in accordance with our results, Welc et al. (2012) reported a rather constant proportion of bacteria to fungi along soil chronosequence in the Alpine Damma glacier. Therefore, it can be concluded that the decrease of fungal/bacterial PLFA along with the distance gradient is not a constant pattern in the succession process on glacier forelands, and other factors, such as soil disturbances, different tolerance of soil microbial communities in relation to soil pH, or the availability of nutrients, may also play an important role.

The distance from the glacier terminus also had a significant impact on the structure of microbial communities. The most important variables affecting the PLFA profile were organic C, nutrient contents and vascular plant/cryptogamic species covers, and thus the soil spatial heterogeneity related to edaphic properties played a crucial role in shaping the structure of microbial communities across larger spatial scales (distance), while the abundance of vascular plant/cryptogam species determined the structure of plant-associated microbiomes on a smaller scale. In our study, significant differences in microbiome structure were observed between the various distances close to the glaciers; however, the distances of 300 and 800 m differed significantly from almost all of the others. This could be explained by the fact that, in close proximity to glaciers, the initial stage of successional processes is observed, therefore only highly specialized organisms can inhabit ecosystems in relatively extreme environments (Rime et al., 2016). However, further away from the glacier terminus, in the later stages of succession, more stable environments arise with more niches created by the greater quantity and quality of vascular plant species. Subsequently, some root-associated fungi and other bacteria, capable of degrading various sources of organic C, prevail (Sun et al., 2016; Jiang et al., 2019), contributing to significant changes in the microbial community structure along with the distance. We found that saprotrophic fungi predominate in initial soil at close proximity to the glaciers, which is congruent with the findings of previous studies of glacial environments (Zumsteg et al., 2012; Edwards et al., 2013; Gutiérrez et al., 2015). This leads to the assumption that

Table 2
The result of forward stepwise multiple regression analysis for the effect of factors related to habitat properties of glacier forelands in northern Sweden derived from factor analysis on microbial biochemical markers and arbuscular mycorrhizal fungi (AMF) species richness (for factor characteristics see Table 1). Standardized β coefficients follow from the standardization of variables to a mean of 0 and a standard deviation of 1. Coefficients of determination (R^2) of the whole model are provided. Factors are listed according to the *p* value. Significant effects are provided in bold ($p < 0.05$).

	Standardized β coefficient	SE for β coefficient	t	p	Model R^2
AMF species richness					
Constant			6.18	<0.001	0.33
Factor 2	0.56	0.07	8.06	**<0.001**	
Factor 4	0.13	0.07	1.87	0.054	
PLFA 16:1ω5					
Constant			9.06	<0.001	0.27
Factor 2	0.49	0.07	6.67	**<0.001**	
Factor 1	−0.15	0.07	−2.00	**0.047**	
Factor 4	−0.09	0.07	−1.25	0.215	
NLFA 16:1ω5					
Constant			6.98	<0.001	0.19
Factor 2	0.43	0.08	5.68	**<0.001**	
Factor 1	−0.08	0.08	−1.04	0.300	
Total microbial biomass					
Constant			21.86	<0.001	0.42
Factor 2	0.63	0.06	9.64	**<0.001**	
Factor 1	−0.17	0.06	−2.63	**0.009**	
Fungal PLFA					
Constant			9.08	<0.001	0.19
Factor 2	0.42	0.08	5.53	**<0.001**	
Factor 1	−0.08	0.08	−1.07	0.285	
Bacterial PLFA					
Constant			17.27	<0.001	0.46
Factor 2	0.66	0.06	10.44	**<0.001**	
Factor 1	−0.15	0.06	−2.33	**0.021**	
Factor 4	−0.08	0.06	−1.26	0.209	
G+ PLFA					
Constant			17.37	<0.001	0.42
Factor 2	0.62	0.06	9.57	**<0.001**	
Factor 1	−0.15	0.06	−2.29	**0.023**	
Factor 4	−0.11	0.06	−1.71	0.090	
G− PLFA					
Constant			16.06	<0.001	0.47
Factor 2	0.68	0.06	10.98	**<0.001**	
Factor 1	−0.14	0.06	−2.23	**0.027**	
G+/G− PLFA					
Constant			30.81	<0.001	0.05
Factor 2	−0.20	0.08	−2.37	**0.019**	
Factor 1	0.10	0.08	1.20	0.233	
Fungal/bacterial PLFA					
Constant			13.92	<0.001	0.02
Factor 4	0.09	0.08	1.09	0.280	
Factor 3	−0.08	0.08	−1.01	0.317	

recently deglaciated environments may be a significant source of certain saprotrophic fungi.

Overall, we found low AMF species richness and spore density in glacier forelands. The main reason for such a trend is probably the fact that the supply of inoculum may be limited in primary successional ecosystems, such as the forelands of receding glaciers. However, they increased along with the distance from the glacier terminus. Arbuscular mycorrhizal fungi species found in our study can be considered pioneer species in the glacier foreland, and their small size of spores (e.g., *Acaulospora paulinae*) will potentially promote their occurrence in the early stages of succession due to their facilitated dispersal by wind (Wilkinson, 1998). Arbuscular mycorrhizal symbiosis may constitute vital help for plant species facilitating them to take up water and nutrients, even from solid inorganic particles in initial soils, which is important for sustaining plant growth in harsh conditions of glacier forelands (Cripps and Eddington, 2005). Moreover, many studies of mycorrhizal plant colonization patterns indicated that AMF play an important role in primary succession ecosystems (Cázares et al., 2005; Kikvidze et al., 2010). The increasing abundance of AMF was also evidenced by PLFA 16:1ω5 and NLFA 16:1ω5, which clearly increased with the distance. When considering the presence of AMF, the influence of plant species forming AM cannot be ignored. In the foreland of all three glaciers, the share of these species increases with the distance from the glacier terminus. This phenomenon also occurs in the forelands of other glaciers, where it was found that nonmycorrhizal plants predominated in the earlier successional sites, whereas the proportion of mycorrhizal plants generally increases with the age of the substrate (e.g., Cázares et al., 2005).

4.2. Effect of soil chemistry on microbial communities

Generally, the C content in glacial foreland is typically low. The content of C, as a rule, rises with the distance from the glacier terminus due to the increase of biological activity (Guelland et al., 2013; Wietrzyk et al., 2018). We found that soil C content was positively associated with both microbial biomass and AMF species richness and spore density. In recently deglaciated soils, microbial organisms drive soil transformation by increasing C and N resources, while depleting available P, thus improving plant colonization and soil development (Alfaro et al., 2020). C-fixing autotrophic microorganisms and free-living N-fixing groups are crucial for soil development as these organisms increase the C and N content of the soil (Nemergut et al., 2007). The fixation of N and soil C increases with the diversity of cyanobacteria, which further promotes the abundance of heterotrophic groups of bacteria and fungi (Chapin et al., 1994). Some of these microbial heterotrophs are decomposers and their activity enhances the further accumulation of organic C and soil formation (Bardgett et al., 2007). Wietrzyk-Pełka et al. (2020) showed that the SOC content of soil is strongly related to the C content of BSC, showing that BSCs are an important source of SOC. Nevertheless, a variety of heterotrophic microbial communities occur on newly exposed glacial substrates prior to the formation of autotrophic communities (Tscherko et al., 2003). These initial microbial communities were shown to primarily use ancient and recalcitrant C as an energy source, whereas in the later stages of succession, soil microbial communities change into one that is mainly supported by modern C, most likely from recent plant production (Bardgett et al., 2007). The use of ancient and recalcitrant C by microorganisms in the early stages of succession is likely to occur in the studied glacier forelands, as evidenced by the initial sparse plant and BSC cover. On the other hand, at further distances from the glacier terminus, there is probably a shift to the use of C from recent plant production and BSC, thereby driving the accumulation of organic matter in young soils and inducing the observed change in the structure of microbial communities with the increasing distance from the glacier. Arbuscular mycorrhizal fungi lack any substantial saprotrophic capability; however, Hodge (2014) suggested that they can preferentially associate with organic substrates and respond by hyphal proliferation, indicating that they derive a benefit from these substrates. Alternatively, the enhanced abundance of AMF may be related to the increased number of plant species rather than higher C contents in the plots.

The negative effect of macronutrient soil contents on microbial abundance revealed in our study can be explained by the decrease of macronutrient content in soil with the distance from the glacier terminus, which is related to ongoing succession and a shift to competition for macronutrients (Vitousek and Farrington, 1997), while, in the most initial soils, microbial activity might accelerate the release of such elements from the bedrock to supply other living organisms (Ragot et al., 2013). Low C and N contents, despite the relatively high availability of macronutrients in the soil near the glacier terminus, certainly contributed to a limited microbial abundance. Low AMF abundance in the soils of glacier foreland found in our study may also be associated with a deficiency of bioavailable phosphate that could favour ecto- and ericoid mycorrhizal associations (Bernasconi et al., 2011). Our results showed that microbial biomass and community structure also depend on the soil granulometric composition. Soil aggregation is a significant factor affecting microbial structure and functions (Schulz et al., 2013). The weathered fractions in the studied glacier forelands include sand, silt and clay, with sand as a dominant fraction. This allows for good gas diffusion and bacterial mobility, as well as a high ion exchange capacity and water retention in the soil (Schulz et al., 2013). In particular, clay is often found in glacier forelands (Kobierska et al., 2011; Mavris et al., 2011), and this is essential for the formation of aggregates and the stabilization of soil organic matter (Paul and Clark, 1996). In our study, the content of all fractions fluctuated considerably throughout the entire length of the transects, but a high contribution of clay was mainly recorded at initial distances.

4.3. Effect of cryptogam and vascular plant succession on microbial communities

Changes in soil chemistry in glacier forelands can be directly caused by microbial organisms in plant-free soils and in the later stages of succession by the presence and abundance of vascular plants and cryptogams (Bardgett et al., 2007). Plant species established in nutrient-poor ecosystems have a significant influence on the chemical properties of soil (Kuramae et al., 2011). Moreover, BSC proved to have a significant influence on the process of soil development in the forelands of Svalbard glaciers (Wietrzyk-Pełka et al., 2020). BSCs did not only enhance the soil nutrient status, but also improved the physical conditions for plant establishment (Schulz et al., 2013). During early succession, fast-growing plants inhabit the glacier foreland, thus promoting rapid nutrient exchange. As primary succession progresses, nutrients become less available due to leaching, and a slower circulation of nutrients in the ecosystem leads to their immobilization (Williamson et al., 2005). The significant negative effect of soil macronutrients on microbial abundance in soil observed in our study could be indirectly related to increasing vegetation cover. As plant succession progresses, vegetation cover increases, and soil nutrient levels decline. Although plants compete with microbes for limited nutrients such as N, they contribute to an increase in the amount of organic C, which promotes an increase in microbial biomass (Brankatschk et al., 2011; Duc et al., 2009; Sigler and Zeyer, 2002). Ohtonen et al. (1999) reported that microbial biomass increased with progressing succession and PLFA analysis showed that it was higher under plant canopies than in the unvegetated soils. Additionally, the high contribution of dead plant material provides a broad spectrum of nutrients for decomposing microbes (Schulz et al., 2013). Moreover, the high abundance and activity of microbes were commonly recorded in the rhizosphere of pioneer plants (Schulz et al., 2013). This phenomenon of enhanced microbial abundance in plant rhizosphere is known as the “rhizosphere effect” (Butler et al., 2003; Hartmann et al., 2008); however, this dependency proved to be generally more pronounced at initial sites as compared to developed ones (Edwards et al., 2006).

It is known that plant vegetation is a predictor of the soil microbial community structure, but also the diversity and activity of microbial communities can significantly influence plant community dynamics (Paul and Clark, 1996). Our results showed that vascular plant cover is one of the main factors influencing microbial abundance and community structure in the studied glacier forelands. These plant-mediated differences could result both from plant species composition and the quality of organic matter inputs to the soil (Paul and Clark, 1996). Knelman et al. (2012) also found that the absence or presence of vegetation and the composition of plant communities influenced the structure of soil microbial community. Although Tscherko et al. (2005) suggested that in the early stages of succession plants or soil age does not play a crucial role in the determination of microbial biomass, in more advanced stages of succession, the improvement in soil conditions enhanced the effects of plants on the soil microbial community.

4.4. AMF diversity

Of the seven identified species of AMF in the glacier forelands, *A. cavernata* spores were most frequently found. Although this species is acknowledged as rare (Gai et al., 2006), it was recently found in several stands in temperate forests of Poland (Rożek et al., 2019, 2020; Zubek et al., 2022). In addition, among others, Stürmer and Kemmelmeier (2021) reported 16 records of this species in the Neotropics. *Acaulospora paulinae* and *A. capsicula* are also rare AMF, but the sites of their findings are located in different regions of the world (Błaszkowski, 1988, 1990; Cofré et al., 2019; Maia et al., 2020; Stürmer and Kemmelmeier, 2021). Also, *A. laevis*, *D. epigaea* and *R. irregulare* occur worldwide, but these species are classified as frequent AMF (Schüßler et al., 2011; Błaszkowski, 2012, unpubl. data). In Poland, *A. laevis* and *D. epigaea* were found in one and several sites, respectively, in temperate forests (Rożek et al., 2019, 2020; Zubek et al., 2021, 2022), and *R. irregulare* occurred in many cultivated and non-cultivated sites (Błaszkowski, 2012; unpubl. data). In contrast, the three stands in the foreland of Isfallsglaciären are the only known habitats of *E. glacialis* in the world; this species was recently newly described in Glomeromycota (Błaszkowski et al., 2022). The dominance of *Acaulospora* species in glacier forelands confirms the conclusion of Vasar et al. (2022) that Acaulosporaceae is a cold tolerant family of Glomeromycota.

5. Conclusions

Microbial biomass increased with the distance from the glacier terminus, which could be related to the increased availability of organic matter in soils as plant and cryptogam succession progress. Generally, AMF species richness and abundance in glacier forelands were low, which could be related to the limited supply of inoculum in primary successional ecosystems, such as the forelands of receding glaciers; however, AMF abundance also increased with the distance. Soil spatial heterogeneity related to edaphic properties played a crucial role in shaping the structure of microbial communities across larger spatial scales (distance), while the abundance of vascular plant/cryptogam species determined the structure of plant-associated microbiomes on a smaller scale. The observed negative influence of soil macronutrient on microbial abundance may result from increasing vegetation cover, since when plant succession progresses, plant cover increases, and soil nutrient levels decline. In conclusion, vegetation, soil properties, and microbial communities are interlinked and exhibit concordant patterns along the successional gradient.

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CRediT authorship contribution statement

Kaja Rola: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. **Katarzyna Rożek:** Investigation, Writing – review & editing. **Karolina Chowaniec:** Formal analysis, Visualization, Writing – original draft. **Janusz Błaszkowski:** Investigation, Writing – review & editing. **Igor Gielas:** Investigation, Writing – review & editing. **Małgorzata Stanek:** Investigation, Writing – review & editing. **Paulina Wietrzyk-Pełka:** Investigation, Funding acquisition, Writing – review & editing. **Michał Węgrzyn:** Investigation, Writing – review & editing. **Patrycja Fałowska:** Investigation, Writing – review & editing. **Patrycja Dziurowicz:** Investigation, Writing – review & editing. **Paweł Nicia:** Investigation, Writing – review & editing. **Romualda Bejger:** Investigation, Writing – review & editing. **Paweł Zadrożny:** Investigation, Writing – review & editing. **Artur Pliszko:** Investigation, Writing – review & editing. **Joanna Zalewska-Gałosz:** Investigation, Writing – review &

editing. **Szymon Zubek:** Conceptualization, Methodology, Investigation, Funding acquisition, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160550.

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