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Past and present bacterial communities in deglaciating northern latitude catchments reveal varied soil carbon sequestration potential

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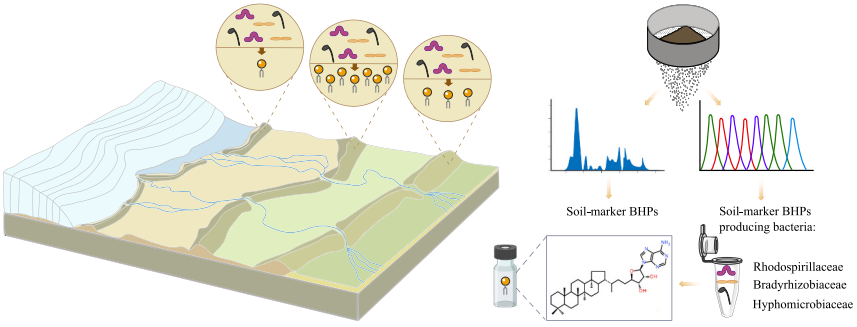
HIGHLIGHTS

- Carbon sequestration in deglaciating landscapes creates negative climate feedback.
- Bacteriohopanepolyol (BHP) biomarkers are used to assess past bacterial communities.
- Current bacterial communities were determined using 16S rRNA gene sequencing.
- Soils are gradually developing in recently deglaciated areas.
- Soil-marker BHPs were produced by Rhodospirillaceae and may have been produced by Bradyrhizobiaceae and Hyphomicrobiaceae.

GRAPHICAL ABSTRACT



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ABSTRACT

Glacier retreat in northern latitudes exposes new landscapes that may develop soils and ecosystems, which in turn may sequester carbon and serve as a negative climate change feedback. Proglacial soil development and landscape evolution were investigated using transects from three high-latitude glacial systems (Tarfala, Sweden; Vatnajökull, Iceland; Zackenberg, Greenland). Soil samples were analysed for organic carbon (OC) concentration, bacteriohopanepolyol biomarkers (BHPs, membrane lipids that trace major microbial groups), and 16S rRNA gene sequencing.

Soil and sediment samples from Sweden showed lower OC concentrations (0.27 ± 0.26 wt%) than deposits from Iceland (1.59 ± 2.12 wt%) and Greenland (1.62 ± 1.54 wt%). Highest OC concentrations were from moraines exposed for several millennia, while recently deglaciated areas in Sweden and Iceland had the lowest OC values. Higher fractional abundance of soil-specific BHPs down-valley (up to 30 % in Greenland), and matching increases in the R'_{soil} index (up to 0.37 in Greenland), suggest soils are gradually developing in recently deglaciated areas, with a stable soil microbial community observed in some soils from Iceland and Greenland.

Microbial communities stabilized quickly, adapting to the new environment. Acidobacteria, Actinobacteria, Chloroflexi, Proteobacteria, Planctomycetes, and Verrucomicrobia were the most relatively abundant phyla identified in deglaciated areas, while candidate phylum Dormibacteraeota had high concentrations in samples from Sweden. Linking organic biomarkers with bacterial communities suggests that soil-marker BHPs were

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produced by Rhodospirillaceae and may have been produced by Bradyrhizobiaceae and Hyphomicrobiaceae. However, despite some similarities in microbial communities, differences in soil development suggest that the evolution of deglaciating landscapes and their impact on the global carbon cycle may vary substantially.

1. Introduction

Glaciers cover ~10 % of Earth's land surface and are increasingly recognised as important ecosystems that are relevant in the global carbon cycle (Wadham et al., 2019; Hood et al., 2015; Lutz et al., 2015; Toubes-Rodrigo et al., 2021). Glacier and glacial ecosystem dynamics in the Arctic are of particular interest because this is a region that is experiencing especially rapid and high-magnitude warming (Rantanen et al., 2022). Over the last two decades, average air temperatures in the Arctic have increased by more than twice the global average (Meredith et al., 2019). Predicted warming through the 21st century will result in global glacier recession with exposure of new deglaciated terrains that have a potential to develop soils and ecosystems significant to the global carbon cycle (Meredith et al., 2019).

Soil development studies in deglaciating and post-glacial areas have previously focused on plant succession (e.g., Bormann and Sidle, 1990; Matthews, 1992; Chapin et al., 1994 in Schmidt et al., 2008) and recently, have expanded into investigating microbial succession along glacier foreland chronosequences (e.g., Schütte et al., 2009; Schütte et al., 2010; Mapelli et al., 2018; Wojcik et al., 2020; Venkatachalam et al., 2021). Those studies suggested that soil development in glacier forelands progresses over time as a result of bacterial succession and plant colonization of the terrain after deglaciation. Generally, organic carbon (OC) accumulation in proglacial areas is a product of chemical and mechanical weathering of organic material, bedrock material (Bhatia et al., 2013) and overridden paleosoil erosion (Lawson et al., 2014). Moreover, the availability of nutrients such as nitrogen (N) and phosphorus (P) and the nature of the bedrock are crucial for soil development (Elser et al., 2007; Burga et al., 2010).

As glaciers recede, previously inaccessible OC and bedrock material are exposed, providing an opportunity for different bacteria to colonize the newly exposed terrain (Bardgett et al., 2007; Singer et al., 2012; Vinšová et al., 2022). Some studies suggest that this OC is recalcitrant and, combined with other nutrients, enables autotrophic microorganisms to colonize deglaciated areas first, supporting nutrient cycling and organic remineralization that facilitate the establishment of heterotrophic communities (Schütte et al., 2009; Venkatachalam et al., 2021; Vinšová et al., 2022). Other studies indicate that newly exposed OC is labile and is utilized by heterotrophic microbial communities, which carry out primary succession of the deglaciated substrate before the establishment of autotrophic communities, which metabolize modern carbon derived from revegetation of deglaciated terrains that have been ice free for several decades (Bardgett et al., 2007; Singer et al., 2012). In both scenarios, microbial metabolism and decomposition of plant material in these soils accumulate OC (Vilmundardóttir et al., 2014). However, studies of soil development in deglaciating terrains do not provide information about the exact source of OC.

The utilisation and generation of OC changes over time, which is often reflected in a changing bacterial community. Some studies have focused on the succession of microbial communities along glacier chronosequences (e.g., Schütte et al., 2009; Schütte et al., 2010; Mapelli et al., 2018; Wojcik et al., 2020; Venkatachalam et al., 2021) and found that bacterial diversity increases in the initial stages of succession, with a period of stabilization in soils that have been exposed for a longer period of time. Different types of OC result in different bacterial communities, which can be determined by examining bacterial chronosequences through DNA analysis. However, since DNA is prone to rapid degradation, it can only be used to determine the current bacterial community. Alternatively, organic biomarkers can be used to determine the past bacterial community composition and original source of OC.

Bacteriohopanepolyols (BHPs) are a group of bacterial cell membrane lipids; different BHPs are produced by different bacterial groups, enabling their use as biomarkers (Cooke et al., 2008; Cooke et al., 2009; Kusch and Rush, 2022). Number, position and nature of functional groups in the side chain determine structural diversity of BHPs, which can provide taxonomic and sometimes physiological information (Rethemeyer et al., 2010; Höfle et al., 2015). Using microbial soil-specific BHPs, such as 30-(5′-adenosyl)hopane and other related structures, has an advantage of being able to distinguish between plant-derived versus soil-derived organic matter (Zhu et al., 2011; Doğrul Selver et al., 2012). Presence of soil-specific BHPs in sediment samples usually indicates terrestrial input (Cooke et al., 2009). Terrestrial BHPs have been found in ancient sediments, which proves the ability of these molecules to resist degradation (van Dongen et al., 2006). Since soil-marker BHPs, 30-(5′-adenosyl)hopane and related structures, are better preserved at lower temperatures (Rethemeyer et al., 2010; Bischoff et al., 2016), high-latitude glaciers are excellent systems for the employment of BHP analysis.

No previous studies have used BHPs to understand deglaciating catchment development. Some studies from non-glaciated catchments have successfully used microbial soil biomarkers to distinguish between OC sources (e.g., Zhu et al., 2011; Doğrul Selver et al., 2012; Doğrul Selver et al., 2015). Moreover, soils and sediments rich in OC show high concentration of soil biomarkers that can be used to trace major microbial organisms (Rethemeyer et al., 2010; Höfle et al., 2015).

In addition to using BHPs as a proxy for tracing soil biomarkers, the R_{soil} and R'_{soil} indices can be used to trace soil derived OC. These indices compare concentrations of soil-marker BHPs with bacteriohopanetetrol (BHT, a common BHP), with values close to zero indicative of non-terrestrial OC input and values from 0.5 to 0.8 indicative of primarily terrestrially sourced OC (Zhu et al., 2011; Doğrul Selver et al., 2012). Although in previous studies BHT was used as a pseudo-marine marker when calculating R_{soil} and R'_{soil} indices (Zhu et al., 2011; Doğrul Selver et al., 2012; Doğrul Selver et al., 2015), it is one of the most common BHP compounds and can be found in various environments, including soils (Cooke, 2011 and references therein). According to Doğrul Selver et al. (2012), environmental conditions in the Arctic and sub-Arctic affects the distribution of soil-marker BHPs, with methylated soil-marker BHPs showing an inconsistent presence and therefore being excluded from the R_{soil} index. Therefore the R'_{soil} index, which takes into account only non-methylated soil-marker BHPs, is more informative in cold environments compared to the R_{soil} index.

Soil development in deglaciating terrains in the Arctic and sub-Arctic regions will likely lead to the accumulation of OC, creating potential carbon sinks on a scale significant for the global carbon cycle (Juselius et al., 2022). Therefore, this study seeks to assess living (DNA) and dead (BHPs) soil microbial communities to understand how microbial metabolism and bioavailability of OC affects accumulation and development of soil OC along transects away from the glacier front in three actively deglaciating catchments (Tarfala in Sweden, Vatnajökull ice cap in Iceland, and Zackenberg in Greenland). This study aims to address three gaps in existing knowledge: (1) understanding accumulation of OC in deglaciated catchments using BHP analysis; (2) identifying the microbial communities within different proglacial catchments using DNA sequencing; (3) linking organic biomarkers and microbial communities in deglaciating areas. It is hypothesised that samples that have been exposed for longer (i.e., samples from catchments that have been ice free longer and samples further from the glacier front) will have (a) higher OC content and organic biomarker content due to the accumulation of OC over time; (b) an upward trend in the R'_{soil} index along the

downstream transects, indicating accumulation of soil-marker BHPs; and (c) a more abundant and more diverse bacterial community further from the glacier front.

2. Materials and methods

2.1. Study areas and sample collection

Soil development was investigated across three catchments: Tarfala valley in Sweden (67°55′N, 18°35′E), Vatnajökull ice cap in Iceland (64°00′N, 16°38′W) and Zackenberg valley in Greenland (74°30′N, 20°30′W) (Fig. 1A).

2.1.1. Tarfala, Sweden

Tarfala valley is located on the east of the Kebnekaise massif, northern Sweden (Fig. 1B). Bedrock geology of the catchment is mostly quartz- and feldspar-rich gneiss (Baird, 2005). Regional climate is mostly continental with prevailing westerly winds (Holmlund et al., 2005). The mean annual temperature at the Tarfala valley is around −3.5 °C (1965–2011) (Ingvander et al., 2013). A total of six triplicate samples were collected in 2018, with four sampling locations at the Tarfalajaure lake surroundings and two sampling locations at the Storglaciären glacier foreland (Fig. 1B, see Table 1 for sampling locations and exposure ages since the ice retreat).

2.1.2. Vatnajökull, Iceland

Vatnajökull is the largest ice cap in Iceland, situated in the south-east (Björnsson and Pálsson, 2008) (Fig. 1C). Due to the volcanic nature of the area, most of the bedrock underlying the glaciers is comprised of basaltic lava and hyaloclastite, while tephra fallout can be found in proglacial areas and on glacier surfaces (Roberts and Guðmundsson, 2015). South Iceland has mild winters and cool summers with small seasonal variations in temperature: an annual average of 5 °C at Svínafellsjökull (Vilmundardóttir et al., 2014) and around 5.5 °C at Virkisjökull (MacDonald et al., 2016). At the Vatnajökull ice cap, triplicate soil samples were collected from 11 sampling sites: three at Svínafellsjökull, three at Virkisjökull, two at Kvíárjökull and three at Fjallsjökull glacier forelands in 2018 and 2019 (Fig. 1C, see Table 1 for sampling locations and exposure ages since the ice retreat).

2.1.3. Zackenberg, Greenland

The Zackenberg River has a catchment area of 514 km^2 (Meltofte and Rasch, 2008) of which 101 km^2, or 20 %, of the total area is covered by glacier ice (Hasholt et al., 2008). An outlet glacier of the A.P. Olsen Land ice cap feeds the Zackenberg River (Fig. 1D). Tertiary igneous rocks, especially plateau basalts, comprise the coastal and outer fjord regions of East Greenland (Mowatt and Naidu, 1994). The study area is situated within a zone of continuous permafrost with an estimated depth of 200–400 m, the top 45–80 cm of which is the active layer (Christiansen et al., 2008). In 2015, annual air temperature at the Zackenberg climate station was −8.8 °C (Hansen et al., 2017). At the Zackenberg valley, a total of 13 triplicate samples were collected down the valley in 2019 (Fig. 1D, see Table 1 for sampling locations and exposure ages since the ice retreat).

2.1.4. Sample collection

Rates of glacier recession vary between the study catchments, providing an opportunity to examine potentially varying rates of soil development (Table 1). The transects have contrasting geomorphological contexts. Icelandic transects were sampled from moraines of different ages that were created by piedmont lobes emanating from the ice cap. The transects in Sweden and Greenland are from valley glaciers that are constrained by mountain slopes on either side; transects in all three study sites run along river courses with the presence of proglacial

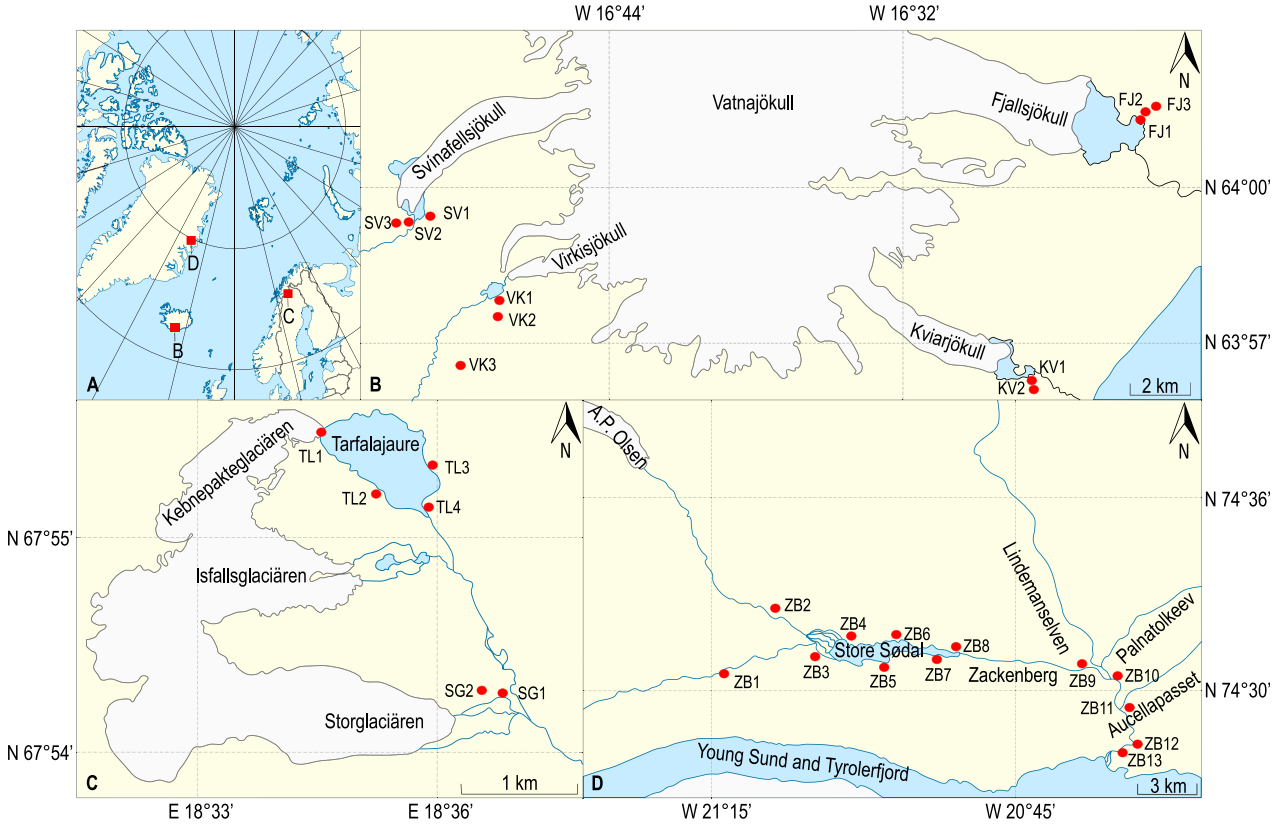

Fig. 1. (A) Overview map of study sites; (B) Tarfala valley, Sweden; (C) Vatnajökull ice cap, Iceland; (D) Zackenberg valley, Greenland. Sampling locations are indicated by red circles.

lakes.

A spatial series of triplicate samples were collected in the radius of 0.5 m from each sampling point along transects from the glacier front to moraines that have been exposed for longer. Study sites, especially Sweden, have underdeveloped thin soil layers, therefore, collected soil samples mostly represent an A-horizon (the top layer of a soil profile) (Fig. S1). The vegetated top layer was removed before taking the samples. For soil organic analysis (OC, organic biomarkers) 200 g of soil was collected in pre-combusted foil packets using a stainless-steel spatula and stored at 4 °C to avoid degradation of organic material. Additional 200 g soil samples for microbial community analysis (16S rRNA gene analysis) were collected in ziplock bags and stored at −20 °C in order to keep microbial community composition stable. Samples were transported back to the laboratory using cool bags packed with ice (gel) packs.

2.2. Organic carbon concentration analysis

Approximately 0.5 g of dried (at 40 °C), sieved (2 mm) and homogenized sample was treated with 1 mL of hydrochloric acid (37 %; Primar Plus-Trace Metal Analysis grade; Fisher Scientific) diluted with 10.6 mL of ultrapure water (18.2 MΩ, Millipore, UK), and heated for 180 min at 80 °C on a hot plate. The cleaned, dried and re-homogenized sample was analyzed using a 'Leco TruSpec®' CN analyser (2018–2019) and a Vario EL cube (Elementar) (2019–2020) for organic carbon (OC) concentrations. Approximately 0.15 g of EDTA (Ethylenediaminetetraacetic Acid) 502–092 was used as a calibration standard.

2.3. Organic biomarker extraction and separation

Soil samples were extracted using a modified Bligh-Dyer method (following Pytlak et al., 2021). Approximately 5 g of dried, sieved and homogenized sample was ultrasonically extracted (10 min at 40 °C, followed by 5 min centrifugation) using 19 mL of methanol (MeOH): dichloromethane (DCM): phosphate buffer (0.05 M solution of KH_2PO_4) (2:1:0.8, v:v:v) mixture. The remaining sample was extracted twice more. The organic phase was recovered by adding DCM and phosphate buffer (final ratio 1:1:0.9, v:v:v) to the supernatant, which was dried under a nitrogen stream. Total lipid extract was recovered using DCM: MeOH (2:1, v:v) mixture and split into three aliquots.

A BHP aliquot was redissolved in 200 μL DCM and passed through a pre-conditioned NH_2 solid phase extraction cartridge (Supelclean™ LC-NH2 SPE Tube, Merck Life Science UK Limited), pre-conditioned using 6 mL of Hexane. Non-polar and acidic compounds were washed out using 6 mL of diethyl ether: acetic acid (98:2), while 10 mL of MeOH was passed through the column yielding a fraction that contains the BHPs, including soil-marker BHPs. 200 μL of an internal standard 5α-pregnane-3β,20β-diol (Tokyo Chemical Industry UK Ltd.) was added to the BHP fraction and acetylated using 250 μL of pyridine: acetic anhydride (1:1, v:v). Dried sample was redissolved in propan-2-ol: MeOH (60: 40) and filtered through a 0.2 μm PTFE syringe filter.

2.4. HPLC-Q-TOF-MS determination of organic biomarkers

BHPs were identified using reverse phase high-performance liquid chromatography/atmospheric pressure chemical ionisation – mass spectrometry (HPLC/APCI-MS) following the method described in Pytlak et al. (2021). MassHunter Acquisition Software (Agilent, US) was used to determine BHPs. BHP structures (Fig. S2) were identified based on previously published spectra or by comparison of absolute and relative retention times, major ions and MS^2 ions (Cooke et al., 2008) using MassHunter Qualitative Analysis Software (Agilent, US). Comparison between the base peak area of the internal standard 5α-pregnane-3β,20β-diol (Tokyo Chemical Industry UK Ltd.) at *m/z* 345 and the area of individual BHPs was used to determine the concentration of each compound. The reproducibility of repeat (duplicate or triplicate) injections was 6 %. The BHPs were grouped into five main classifications: BHT, amino, sugar, aminosugar and soil-markers (specified in Table S1, S2 and S3).

BHP based R'_{soil} index values were calculated as described in Doğrul Selver et al. (2012), using eq. (1).

$$R'_{soil} = \frac{G1 + G2 + G3}{G1 + G2 + G3 + BHT} \quad (1)$$

G1 corresponds to 30-(5′-adenosyl)hopane, G2 – N1-methylinosylhopane and G3 – adenosylhopane$_{HG\text{-}Me}$ (Kusch and Rush, 2022).

2.5. Microbial DNA extraction and sequencing

Genomic DNA was isolated using DNeasy PowerSoil Kit (Qiagen, Hilden, Germany). In order to ensure sufficient DNA yield, 0.4 g of soil (wet weight, c.f. the standard 0.25 g) was extracted in a bead beating tube, and DNA eluted in 50 μL of 10 mM Tris (c.f. 100 μL). The isolated DNA was quantified using Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, CA 92008 USA). DNA was amplified using the Q5 Hot Start High-Fidelity DNA Polymerase (New England Biolabs, Ipswich, MA, USA), targeting the V4 region (Illumina, 2020). PCR conditions for DNA amplification using a SimpliAmp Thermal Cycler (ThermoFisher Scientific, Waltham, MA, USA) were: initial denaturation at 98 °C for 2 min, followed by 25 cycles of denaturation at 95 °C for 20 min, annealing at 65 °C for 15 min and extension at 70 °C for 20 min, with a final extension at 72 °C for 5 min. PCR products were run on agarose gel (2 %) electrophoresis to ensure successful amplification. Quality checked samples were sent to the NERC Biomolecular Analysis Facility at the University of Liverpool for sequencing of the V4 region of the 16S rRNA gene using the Illumina© sequencing platform (Illumina, San Diego, CA, United States).

Sequencing data were processed using the QIIME2 software package version 2020.8 (Bolyen et al., 2019). Raw amplicon sequencing data were processed using the DADA2 pipeline to create operational taxonomic unit (OTU) (Callahan et al., 2016). Sequences below 220 bp in length, and those with an average quality score below 30 on a window of 20 bases were discarded. OTUs were assigned to taxa using the GreenGenes database (DeSantis et al., 2006). The sequence datasets were deposited in the National Center for Biotechnology Information (Project accession number: PRJNA1037499). Non–metric multidimensional scaling (NMDS) ordination plots of family-level bacterial communities were plotted using the 'vegan' package (v2.5–7), while alpha diversity (Shannon) and richness (Chao1) were calculated and plotted using the 'phyloseq' package (v1.36.0) running on R 4.10R.

3. Results

3.1. Total organic carbon concentration

Table 1 provides data about OC, as well as exposure ages of soils and sediments since deglaciation. Mean OC concentration of field triplicates was lowest in Sweden (0.27 ± 0.26 wt%), followed by Iceland (1.59 ± 2.12 wt%) and Greenland (1.62 ± 1.54 wt%). The sampling locations closer to the glacier front in Sweden and Iceland had lower OC concentrations compared to the ones away from the glacier margin (Fig. 2A and Fig. 3A), which was not observed in Greenland (Fig. 4A). In Sweden, samples from the Tarfalajaure system, which has been ice free for 9000–8500 BP (Karlen, 1979), had higher OC values, while Storglaciären (ice free for <100 years, Kirchner et al., 2019) had lower OC values (Table 1). In Iceland, samples from Svínafellsjökull and Virkisjökull had the highest OC concentrations, followed by Fjallsjökull and Kvíárjökull (Table 1).

3.2. Abundance and distribution of BHPs

All samples except sample SG1 from Storglaciären contained

Table 1
Sampling locations, linear distance from a glacier front, age since deglaciation (as of 2024), organic carbon concentration, total relative concentration of BHPs and R'$_{soil}$ values of samples from Tarfala valley, Vatnajökull ice cap and Zackenberg valley.

Sample name	Glacier/ Transect	Latitude, Longitude	Linear distance from a glacier front (m)	Age (years)	Source	OC[a] (wt%)	Σ BHPs[a] (μg/g OC)	R'$_{soil}$[a]
TL1	Tarfalajaure	67°55′32"N 18°34′30"E	50	ca. 84	Kirchner et al., 2019	0.01 ± 0.01	2929 ±661	0.12 ± 0.03
TL2	Tarfalajaure	67°55′14"N 18°35′20"E	858	9000–8500 BP	Karlen, 1979	0.44 ± 0.18	4940 ± 862	0.23 ± 0.02
TL3	Tarfalajaure	67°55′20"N 18°35′60"E	1156	9000–8500 BP	Karlen, 1979	0.65 ± 0.14	6109 ± 1053	0.26 ± 0.01
TL4	Tarfalajaure	67°55′10"N 18°35′52"E	1226	9000–8500 BP	Karlen, 1979	0.29 ± 0.21	7184 ± 3243	0.34 ± 0.02
SG1	Storglaciären	67°54′10"N 18°37′02"E	439	114	Holmlund et al., 2005	0.08 ± 0.12	BDL[c]	
SG2	Storglaciären	67°54′19"N 18°36′45"E	350	114	Holmlund et al., 2005	0.13 ± 0.11	8736	0.21
SV1	Svínafellsjökull	63°59′27"N 16°51′37"W	353	21	Cook et al., 2011	0.54 ± 0.19	2510 ± 1423	0.27 ± 0.07
SV2	Svínafellsjökull	63°59′12"N 16°52′11"W	617	LIA[b]	Björnsson and Pálsson, 2008; Lee, 2016	5.24 ± 2.68	950 ± 125	0.34 ± 0.01
SV3	Svínafellsjökull	63°59′29"N 16°53′29"W	738	2500	Guðmundsson et al., 2002	2.97 ± 1.80	1366 ± 688	0.35 ± 0.05
VK1	Virkisjökull	63°57′49"N 16°48′44"W	785	ca. 34	Dochartaigh et al., 2019	0.07 ± 0.02	4477	0.15
VK2	Virkisjökull	63°58′15"N 16°48′08"W	1542	LIA[b]	Everest et al., 2017	0.58 ± 0.36	3816	0.24
VK3	Virkisjökull	63°57′01"N 16°51′17"W	3298	5000-6000	Guðmundsson, 1998	4.71 ± 3.07	2352	0.11
KV1	Kvíárjökull	63°56′15"N 16°27′20"W	838	LIA[b]	Bennett et al., 2010	0.18 ± 0.02	3232	0.15
KV2	Kvíárjökull	63°56′18"N 16°26′27"W	1516	3200 BP	Guðmundsson, 1997; Bennett et al., 2010	0.59 ± 0.12	4864	0.09
FJ1	Fjallsjökull	64°01′08"N 16°22′16"W	2349	59	Rose et al., 1997	0.14 ± 0.06	1062	0.15
FJ2	Fjallsjökull	64°00′36"N 16°22′20"W	2615	LIA[b]	Thorarinsson, 1943	0.86 ± 0.59	1435	0.17
FJ3	Fjallsjökull	64°00′16"N 16°22′24"W	2917	4500 s BP	Rose et al., 1997	1.44 ± 0.43	1227	0.10
ZB1	Zackenberg	74°30′56"N 21°10′50"W	12,401	not known	Garcia-Oteyza et al., 2022	2.33 ± 1.52	6195	0.14
ZB2	Zackenberg	74°32′03"N 21°07′11"W	11,603	not known	Garcia-Oteyza et al., 2022	0.30 ± 0.15	2535	0.28
ZB3	Zackenberg	74°31′17"N 21°04′48"W	13,445	not known	Garcia-Oteyza et al., 2022	1.27 ± 0.26	4934	0.23
ZB4	Zackenberg	74°31′28"N 21°00′07"W	14,742	not known	Garcia-Oteyza et al., 2022	4.88 ± 3.56	5875 ± 1978	0.18 ± 0.13
ZB5	Zackenberg	74°31′07"N 20°55′17"W	16,981	not known	Garcia-Oteyza et al., 2022	1.28 ± 1.04	6986	0.17
ZB6	Zackenberg	74°31′20"N 20°52′33"W	17,833	not known	Garcia-Oteyza et al., 2022	1.92 ± 0.46	5743	0.16
ZB7	Zackenberg	74°31′08"N 20°50′17"W	18,929	not known	Garcia-Oteyza et al., 2022	1.76 ± 0.66	9486	0.13
ZB8	Zackenberg	74°30′57"N 20°45′17"W	21,232	not known	Garcia-Oteyza et al., 2022	0.56 ± 0.07	6687	0.11
ZB9	Zackenberg	74°30′41"N 20°38′48"W	24,268	ca. 10.5 ka	Garcia-Oteyza et al., 2022	3.05 ± 0.6	3738	0.37
ZB10	Zackenberg	74°30′12"N 20°34′54"W	26,348	ca. 10.5 ka	Garcia-Oteyza et al., 2022	2.17 ± 0.31	3667	0.12
ZB11	Zackenberg	74°29′41"N 20°35′24"W	26,629	ca. 10.5 ka	Garcia-Oteyza et al., 2022	0.45 ± 0.07	3201	0.12
ZB12	Zackenberg	74°28′32"N 20°34′01"W	28,323	ca. 10.5 ka	Garcia-Oteyza et al., 2022	1.55 ± 0.78	5339	0.22
ZB13	Zackenberg	74°28′15"N 20°34′43"W	28,377	ca. 10.5 ka	Garcia-Oteyza et al., 2022	0.89 ± 0.11	4021	0.20

[a] mean ± 1 standard deviation ($n = 3$).
[b] Little Ice Age.
[c] Below detection limit.

measurable BHPs. Analysis revealed up to 33 individual BHPs in samples from Sweden, Iceland and Greenland (Table S1, S2 and S3). Generally, absolute BHP concentration was lowest in Sweden, followed by Iceland and Greenland (Table 2).

Up to 28, 28 and 31 individual BHPs were identified in samples from the Tarfala valley, Vatnajökull ice cap and Zackenberg valley respectively, with the relative concentration of total BHPs ranging from below the instrumental detection limit (BDL) (sample SG1) to 8736 (sample SG2) μg/g OC, 950 ± 125 (sample SV2) to 4864 (sample KV2) μg/g OC and 2535 (sample ZB2) to 9486 (sample ZB7) μg/g OC (Table 2). Mean relative concentration of total BHPs was highest in Sweden, followed by Iceland and Greenland (Table 2). Conversely, in Sweden, mean absolute concentration of total BHPs was low. Mean absolute concentration of total BHPs was lower in Iceland compared to Greenland despite similar OC concentrations (Table 2). The BHPs were grouped in five main classifications: BHT, amino, sugar, aminosugar and soil-marker BHPs (specified in Table S1, S2 and S3). Across the three study sites, BHT was the most abundant single BHP, contributing to 37–61 % of total BHPs, followed by methylated BHT (1–21 %), 30-(5′-adenosyl)hopane (3–20 %), BHT cyclitol ether (1–15 %), aminotriol (1–10 %) and adenosylhopane$_{HG\text{-}Me}$ (BDL-9 %) (see Table S1, S2 and S3 for details).

At Tarfalajaure, R'$_{soil}$ index increased from 0.12 ± 0.03 to 0.34 ± 0.02, indicative of accumulation of soil-marker BHPs, while SG2 from Storglaciären had a value of 0.21, having some soil-specific BHPs (Table 1, Fig. 2A). Along the downstream transects at the Vatnajökull ice cap, R'$_{soil}$ followed a trend of initial increase, followed by decrease in the moraine exposed for a longer period (Fig. 3A). R'$_{soil}$ was highest at Svínafellsjökull (0.27 ± 0.07 to 0.35 ± 0.05) and Virkisjökull (0.11 to 0.24) and lowest at Fjallsjökull (0.10 to 0.17) and Kvíárjökull (0.09 to 0.15) (Table 1). At the Zackenberg valley, R'$_{soil}$ had similar values to sites in Sweden and Iceland, ranging from 0.11 to 0.37 (Table 1) and had a downward trend along the Store Sø (Fig. 4A).

3.3. Microbial community structure

A total of 7,077,544 sequence reads were obtained from 16S rRNA V3-V4 region of 69 samples, yielding 9589 to 169,325 OTUs per sample. In general, samples from Greenland exhibited fewer OTUs, followed by Iceland and Sweden. Approximately 4 % of the sequences could not be assigned to any phylum, while 53 % could not be classified into family (see Fig. S3), and 87 % remained unclassified at the genus level.

A two-dimensional NMDS ordination plot (Fig. S4) did not exhibit clear clustering of bacterial family-level distribution of samples by transect. Although overlapping, samples from Zackenberg valley were predominantly grouped in the centre of the cluster, with Tarfalajaure samples to the right and Svínafellsjökull samples to the left. While not evident in NMDS plots, PERMANOVA analysis demonstrated a statistically significant difference between samples from each site (p-value <0.05).

The alpha diversity indices (Shannon–Weiner diversity index and Chao1 species richness estimate), derived from family-level data indicated that samples from Iceland were the most diverse ones. Samples from Sweden had lower diversity compared to samples from Iceland and Greenland (Fig. S5).

The sequences were assigned to 50 phyla. The most relatively abundant phyla identified in samples from Sweden, Iceland and Greenland were Acidobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, Proteobacteria, Planctomycetes and Verrucomicrobia, all of which appeared consistently in all samples (Table 3, Fig. 2B, Fig. 3B and Fig. 4B). Candidate phylum Dormibacteraeota (previously AD3) was

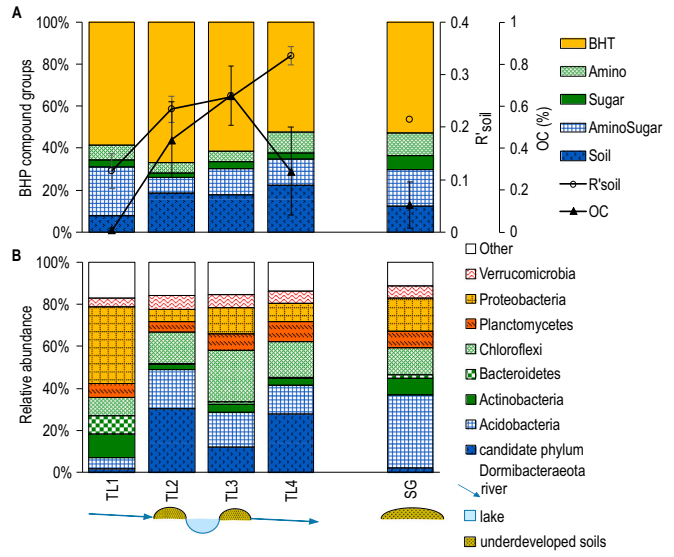

Fig. 2. (A) Fractional abundance of BHP compound groups, R'$_{soil}$ and total organic carbon in samples from Tarfala valley. Error bars represent ± one standard deviation of three field replicate samples collected from individual sampling locations. Only one field replicate per sampling location from Storglaciären was analysed for organic biomarkers. (B) Relative abundance of all assigned bacterial taxa at phylum level where possible. Charts at the bottom of the graph show downstream (left to right) transect profiles. Samples TL2 and TL3 are collected from either side of the Tarfalajaure lake and representative of similar exposure time since glacier retreat.

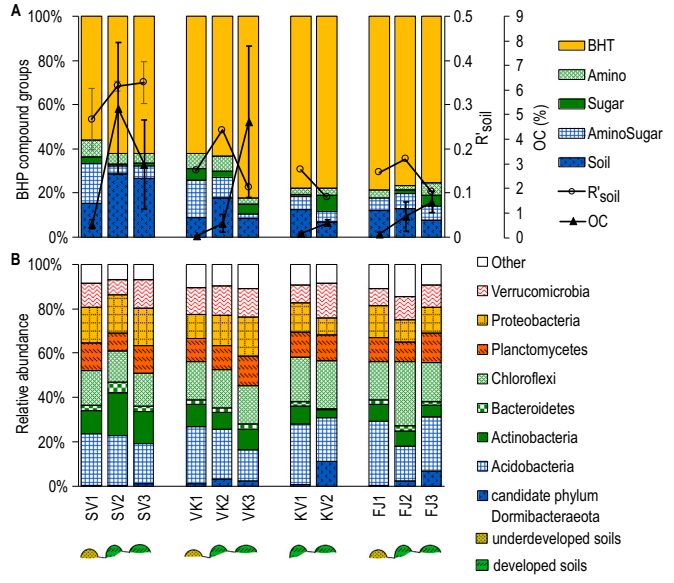

Fig. 3. (A) Fractional abundance of BHP compound groups, R'$_{soil}$ and total organic carbon in samples from Vatnajökull ice cap. Error bars represent ± one standard deviation of three field replicate samples collected from individual sampling locations. Only one field replicate per sampling location from Virkisjökull, Fjallsjökull and Kvíárjökull was analysed for organic biomarkers. (B) Relative abundance of all assigned bacterial taxa at phylum level where possible. Charts at the bottom of the graph show downstream (left to right) transect profiles.

also one of the major phyla at the Tarfala valley. Relative abundance of Proteobacteria, Bacteroidetes and Actinobacteria decreased from TL1 to TL2, while candidate phylum Dormibacteraeota and Actinobacteria increased. Meanwhile, Acidobacteria was the most prevalent phylum at

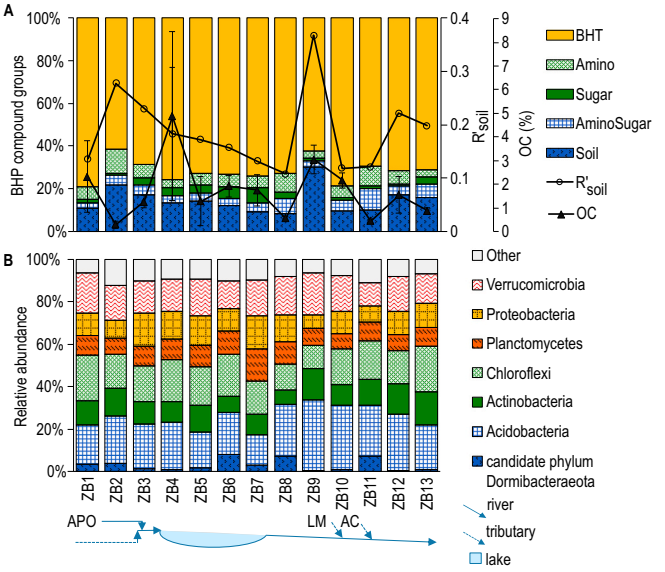

Fig. 4. (A) Fractional abundance of BHP compound groups, R'$_{soil}$ and total organic carbon in samples from Zackenberg valley. Error bars represent ± one standard deviation of three field replicate samples collected from individual sampling locations. Only one field replicate per sampling location, except sample ZB4, was analysed for organic biomarkers. (B) Relative abundance of all assigned bacterial taxa at phylum level where possible. Charts at the bottom of the graph show downstream (left to right) transect profiles. APO stands for glacier runoff from A.P. Olsen Land ice cap, LM - Lindemanselven and Palnatokeelv rivers and AC - Aucellaelv river.

Storglaciären (Fig. 2B). No particular pattern of distribution of the relative abundance of phyla across the transects in Iceland and Greenland was observed (Fig. 3B and Fig. 4B) and the relative abundance of phyla between the two countries was similar (Table 3).

Table 3 shows relative abundances of potentially BHP-producing family-level bacteria. Some family-level bacteria belonging to Proteobacteria, such as Rhodospirillaceae, Bradyrhizobiaceae and Hyphomicrobiaceae, are of particular interest as potentially soil-marker BHPs-producing bacteria. All three were detected across the three study sites: Hyphomicrobiaceae had the highest relative abundance, followed by Bradyrhizobiaceae and Rhodospirillaceae (Table 3). Minute traces of Nitrosomonadaceae were detected in a few samples from Tarfalajaure (0.01 ± 0.01 %), Zackenberg (0.02 %) and a Little Ice Age (LIA) moraine samples from Svínafellsjökull (0.03 ± 0.02 %). Other potentially BHP-producing family-level bacteria from the Proteobacteria phylum were also detected across the sampling sites (Table 3).

4. Discussion

The aim of this study was to understand accumulation of soil OC along downstream transects in deglaciating catchments in Sweden, Iceland and Greenland using a combination of organic biomarkers and microbial community composition of proglacial soils. It was hypothesised that soils that have developed on surfaces that have been exposed for longer periods of time would have higher OC, higher BHP concentrations, particularly soil-marker BHPs, and a more abundant and diverse microbial community.

4.1. Relationship between organic carbon and soil development

Wietrzyk et al. (2018) suggested that OC concentration is a function of time and distance from the glacier margin, i.e., time of exposure after deglaciation. In line with this, OC concentration was lower in samples closer to glacier front in Sweden (Fig. 2A) and Iceland (Fig. 3A) compared to samples that have been ice free for longer (Table 1). In

Table 2
OC, total BHPs, fractional abundance of soil-marker BHPs and R'$_{soil}$ values in this study compared to literature.

	OC, wt%		Σ BHPs, relative concentration, μg/g OC		Σ BHPs, absolute concentration, μg/g sediment		Fractional abundance of soil-marker BHPs, %		R'$_{soil}$	
	min	max	min	max	min	max	min	max	min	max
Sweden [a]	0.01 ± 0.01[h]	0.65 ± 0.14[h]	BDL	8736	BDL	41±13[h]	8	22	0.12 ± 0.03[h]	0.34 ± 0.02[h]
Iceland [a]	0.07 ± 0.02[h]	5.24 ± 2.68[h]	950±125[h]	4864	2	79	7	29	0.09	0.35 ± 0.05[h]
Greenland [a]	0.30 ± 0.15[h]	4.88 ± 3.56[h]	2535	9486	9	303±46[h]	8	30	0.11	0.37
Arctic Rivers [b]			89	613				37		
Yenisei River [c]			180	2300					0.07	0.62
Sweden [d]			72	89					0.08	0.30
Kolyma River [e]	8	13.6	138	281	1.2	3.4	5	44	0.07	0.57
Siberian permafrost [f]	1.5	28.4	84	1111						
Siberian Yedoma [e]	1.5	1.6	97	110			67	78	0.69	0.80
Svalbard [g]	0.1	28.4	7	660			20	73		

[a] Data from this study.
[b] Data from Cooke et al., 2009.
[c] Data from De Jonge et al., 2016.
[d] Data from Doğrul Selver et al., 2012.
[e] Data from Doğrul Selver et al., 2015, Bischoff et al., 2016.
[f] Data from Höfle et al., 2015.
[g] Data from Rethemeyer et al., 2010.
[h] mean ± standard deviation (n = 3).

other studies investigating deglaciating sites, OC concentrations also increased in samples that had been exposed for longer, i.e., from 0.69 % in samples that had been ice free for less than a year to 3.81 % in samples exposed for 96 years in Svalbard (Wietrzyk et al., 2018), and from 0.15 to 7.97 % in Switzerland, 15–700 years after glacier retreat (Prietzel et al., 2013). This was not observed in Greenland, where soil development might be controlled to a greater extent by local geomorphological activity, topo-climatic and micro-climatic conditions, or bedrock lithology conducive to soil development, along with exposure time since ice retreat. For instance, Prietzel et al. (2013), who observed that OC concentrations were smaller in some of the soils further away from the glacier front compared to soils closer to the glacier margin from the Hailuogou glacier, China, suggested that OC content is dependent on local differences of soil-forming moraine material and the physical exposure processes (i.e., glaci-fluvial erosion, transport and re-sedimentation) that these moraines experience. This suggests that many factors, including time of exposure, significantly contribute to OC accumulation in deglaciating systems, which is evident when comparing three study areas in this study. To better understand soil development, we investigated organic biomarkers across these sites.

Table 3
Relative abundance (mean ± standard deviation, %) of the dominant phyla and potentially BHP-producing bacteria in samples from Sweden, Iceland, and Greenland.

Bacteria	Country					
	Sweden		Iceland		Greenland	
Dominant phylum						
candidate phylum AD3	18.1	±13.3	1.9	±3.2	2.6	±3.4
Acidobacteria	18.4	±9.9	22.3	±5.3	23.2	±11.7
Actinobacteria	4.7	±2.9	10.8	±5.3	11.7	±3.2
Chloroflexi	16.9	±5.5	17.1	±4.7	17.1	±3.8
Planctomycetes	7.5	±3.2	11.1	±2.3	9.3	±2.3
Proteobacteria	12.4	±8.4	14.4	±4.3	11.1	±3.1
Verrucomicrobia	5.9	±1.3	11	±3.2	16	±3.0
Potentially BHP-producing bacteria						
Phylum						
Cyanobacteria	0.5	±0.8	0.3	±0.4	0.3	±0.6
Class (Phylum)						
Methylacidiphilae (Verrucomicrobia)	0.22	±0.36	0.56	±0.67	0.32	±0.31
Family (Phylum)						
Rhodospirillaceae (Proteobacteria)	0.29	±0.14	0.62	±0.44	0.59	±0.39
Bradyrhizobiaceae (Proteobacteria)	0.74	±0.38	1.57	±1.24	1.39	±0.76
Hyphomicrobiaceae (Proteobacteria)	0.82	±0.38	1.48	±0.53	1.54	±0.55
Xanthomonadaceae (Proteobacteria)	0.53	±0.85	0.43	±0.88	0.18	±0.14
Sphingomonadaceae (Proteobacteria)	0.37	±0.97	0.72	±1.17	0.41	±0.30
Beijerinckiaceae (Proteobacteria)	0	±0.00	0.01	±0.02	0.03	±0.06
Burkholderiaceae (Proteobacteria)	0.01	±0.02	0.11	±0.20	0.02	±0.02
Acetobacteraceae (Proteobacteria)	0.48	±1.22	0.4	±0.43	0.27	±0.26
Methylocystaceae (Proteobacteria)	0.05	±0.08	0.11	±0.13	0.05	±0.07
Pseudomonadaceae (Proteobacteria)	0.02	±0.02	0.12	±0.33	0.03	±0.06
Nostocaceae (Cyanobacteria)	0	±0.01	0.08	±0.39	0.06	±0.24
Phormidiaceae (Cyanobacteria)	0	±0.01	0	±0.00	0.05	±0.11
Frankiaceae (Actinobacteria)	0.08	±0.10	0.15	±0.12	0.42	±0.32

4.2. Composition and distribution of soil specific BHPs in Sweden, Iceland and Greenland

Soil-marker BHPs are abundant in soils but not aquatic sediments (Cooke et al., 2008; Doğrul Selver et al., 2012; Höfle et al., 2015), and therefore, in this study they are used as indicators of soil development in deglaciated areas. Literature indicates that this is the first study to examine the distribution of soil-marker BHPs along downstream transects across proglacial systems, with previous studies looking into soil-marker BHPs to trace terrestrial OC along land-to-ocean transects (e.g., Bischoff et al., 2016; De Jonge et al., 2016; Doğrul Selver et al., 2012; Doğrul Selver et al., 2015).

OC and BHP concentrations are strongly correlated (Pearson correlation = 0.70), supporting theories that biomarker content and composition in soils is dependent on carbon content (Höfle et al., 2015). Mean relative concentration of total BHPs (μg/g OC) observed in this study were much higher compared to the values recorded in other studies in high-latitude areas, e.g., in estuary and open bay sediment samples from Northern Sweden (Doğrul Selver et al., 2012), in river mouth sediments from Siberia (Doğrul Selver et al., 2015), sediment and soil samples from the Bayelva River catchment in Svalbard (Rethemeyer et al., 2010) and even Siberian permafrost soils (Höfle et al., 2015) (Table 2). These difference in values could be due to higher OC content in other studies, i.e., high relative BHP concentrations in this study were driven by low soil OC values rather than high absolute BHP concentrations, suggesting that BHP concentrations increase faster than the bulk OC.

Soil marker BHPs are less dominant than in other Arctic sites, as shown by both their fractional abundance and the R'_{soil} index (Table 2). Soil specific BHP concentrations (per gram of sediment) in this study increase with exposure age since deglaciation, but fractional abundance values are typically lower than samples from Arctic and sub-Arctic estuaries (e.g., Cooke et al., 2009; Doğrul Selver et al., 2012) and Svalbard soils (e.g., Rethemeyer et al., 2010), and much lower than organic-rich Arctic permafrost permafrost sites (e.g., De Jonge et al., 2016; Doğrul Selver et al., 2015). Soils in this study with higher OC content also have higher fractional abundance of soil marker BHPs and R'_{soil}, suggesting that soil-marker BHPs can be used to trace the rise in soil OC, which demonstrates the potential of using soil-specific BHPs to understand soil development.

4.3. Down-valley soil development

Soil-marker BHPs increase with depth in the soil profiles in soils from Spitsbergen (Rethemeyer et al., 2010), suggesting preservation of these compounds in soils. Therefore, it was expected that soil-marker BHPs accumulate over time after proglacial areas are exposed by glacier retreat, with concentrations of soil-marker BHPs and R'_{soil} index increasing along the down-valley transects away from the glacier. There is a clear pattern of increase in R'_{soil} along the Tarfalajaure transect with soil-marker BHPs increasing as well (Fig. 2), suggesting that more biomarkers have accumulated with the age of exposure after deglaciation. However, in Iceland, despite an upward trend in OC concentration with distance from the glacier, an initial increase in R'_{soil} is followed by a subsequent decrease in the most established moraines. Similarly, while OC is somewhat stable along the lake transect in Greenland, the R'_{soil} index indicated that there is a downward trend along the transect of the Store Sø Lake. This suggests that even though soils develop after being exposed, this development is non-linear over time. This can be explained either by (1) development of soil-marker BHPs plateaus after reaching a certain stage; (2) other BHP compounds, such as BHT, methylated BHT, aminotriol and BHT cyclitol ether, overtake and mask soil-marker BHPs; and/or (3) differences in the soil-forming material and physical exposures could override any obvious patterns downstream along the transect. This summary emphasizes the importance of studying different deglaciating areas across multiple sites to gain a broader understanding of the processes in these catchments. To further improve our knowledge, we investigated the microbial communities in the soils and their distribution patterns along the down-valley transects.

4.4. Microbial community diversity and bacterial taxa

While organic biomarkers function as a signal of past changes, it is also important to investigate the current microbial communities inhabiting deglaciated areas. Nutrients such as N and P are essential for the establishment of microbial communities (Elser et al., 2007). P availability influences primary productivity, decomposition, and N fixation (Porder and Ramachandran, 2013). N, a limiting nutrient, can originate from both atmospheric and rock sources (Houlton et al., 2018). Consequently, bedrock type may impact bacterial community composition, as different lithologies offer varying nutrient availability (Dong et al., 2023). Furthermore, P availability tends to be lower in older soils due to mineral transformations, whereas N availability is expected to increase in older soils due to the greater turnover of organic N (Göransson et al., 2016).

Each site in this study has a distinct bedrock type. For example, gneiss as exposed in Sweden is lower in P (mean concentration of 867 ppm), while basalt, bedrock in Iceland and Greenland, contains higher values of P (1304 ppm) (Porder and Ramachandran, 2013). Likewise, gneiss has been reported to have lower N (25 to 82 ppm) levels compared to basalt (56 and 105 ppm) (Holloway and Dahlgren, 2002). Volcanic activity (Iceland) has also been shown to increase nutrient availability (Holloway and Dahlgren, 2002; Porder and Ramachandran, 2013). Consequently, microbial communities are expected to differ between these sites, with Sweden likely having a distinct composition due to its lower nutrient (N and P) bedrock. Alpha diversity analysis revealed distinct family-level microbial composition in samples from Sweden, Iceland, and Greenland (Fig. S5). This is in line with findings in other studies (i.e., Mapelli et al., 2018; Khan et al., 2020; Franzetti et al., 2020), who reported variations in bacterial community composition across soil development stages.

The dominant phyla identified in catchments in this study are comparable to the findings of other similar studies. For instance, Acidobacteria, Actinobacteria, Bacteroidetes, and Proteobacteria, major phyla in our samples, were also prevalent in soils across the Arctic tundra (Chu et al., 2010). Similarly, our findings align with studies in Spitsbergen and Svalbard glacier forelands, suggesting microbial communities in Sweden, Iceland and Greenland resemble those in other cold catchments (Schütte et al., 2010; Seok et al., 2016; Venkatachalam et al., 2021).

The relative abundance of Acidobacteria corresponds to its prevalence in soils with low nutrient availability, particularly in the Tarfala Valley, where oligotrophic conditions favour its adaptation (Janssen et al., 2002; Kielak et al., 2016). Conversely, its lower relative abundance in more carbon-rich soils from the Vatnajökull ice cap suggests a decrease with increasing carbon content, supporting previous studies (Fierer et al., 2005; Delgado-Balbuena et al., 2016). At the Zackenberg valley, Acidobacteria distribution lacked a clear pattern, possibly attributed to the longer exposure age since deglaciation (Schütte et al., 2010), allowing for the phylum to adapt and homogenise over time.

Most Actinobacteria are aerobic, can be either heterotrophic or chemoautotrophic, and can be found in different environments, including aquatic and terrestrial habitats (Barka et al., 2016). Relative abundance of Actinobacteria decreased along downstream transects at the Tarfala valley and Kvíárjökull glacier foreland, suggesting that this phylum prefers to inhabit low carbon environments, suggesting chemoautotrophic nature.

Unlike other studies (Mateos-Rivera et al., 2016; Nemergut et al., 2007), no distinct pattern in variation of Proteobacteria with the age of exposure was observed, suggesting homogenization. Sphingomonadaceae was one of the dominant family members of Proteobacteria in Iceland. Sphingomonadaceae are usually chemoorganotrophic and can

be found in different environments, including soils and cryoconite (Glaeser and Kämpfer, 2014). Species of this family, *Zymomonas mobilis*, was reported to produce BHT and BHT cyclitol ether (Table 4), which are abundant BHP compounds in samples from Iceland. Likewise, Bradyrhizobiaceae, a family belonging to the Proteobacteria phylum, was abundant in samples from Sweden, Iceland and Greenland. This nitrogen-fixing bacterium can be found in different environments, including soils (Marcondes de Souza et al., 2014). *Bradyrhizobium japonicum* that produces soil-marker BHPs and *Rhodopseudomonas palustris* that produces Me-BHT, and *Rhodopseudomonas acdophila*, which produces BHT are species of this family-level bacteria (Table 4). This suggests that members of Proteobacteria are responsible for producing the abovementioned BHP compounds, allowing us to potentially link the current microbes with the biomarkers.

Chloroflexi reported in various environments, including cold regions (Costello and Schmidt, 2006), exhibited higher relative abundance in more developed soils in Sweden, aligning with findings suggesting its increased presence with the age of exposure (Mateos-Rivera et al., 2016) and potentially performing photosynthesis in soil (Ji et al., 2016). One of the abundant family-level members of Chloroflexi across all three catchments was Ellin6529, which fixes N_2, contributing to the enrichment of deglaciated soils in labile N (Lopes et al., 2015), fostering the growth of vegetation and soil development.

Planctomycetes is usually found in different environments, including freshwater, soil (Fuerst and Sagulenko, 2011) and polar and alpine environments (Costello and Schmidt, 2006; Ji et al., 2016; Mateos-Rivera et al., 2016). According to Schlesner et al. (2006), Verrucomicrobia has a moderate degree of relationship with Planctomycetes. Relative abundance of Planctomycetes and Verrucomicrobia did not follow a pattern along the chronosequence of glacier forelands, potentially stabilising over time as Schütte et al. (2010) suggested. Verrucomicrobia is found in various aquatic and terrestrial habitats (Schlesner et al., 2006). For instance, it was one of the abundant phyla in a glacier foreland in Norway (Mateos-Rivera et al., 2016) and Svalbard (Venkatachalam et al., 2021).

Bacteroidetes predominant in polar soils (Chu et al., 2010) grows in anoxic environments, fermenting inorganic material of subglacial origin (Sheik et al., 2015), explaining its relative abundance in samples collected from carbon-poor soils in this study. Similarly, Venkatachalam et al. (2021) reported that Bacteroidetes was mainly identified in samples from recently deglaciated areas, its relative abundance drastically decreasing in carbon-rich samples exposed for longer periods. This suggests that the distribution of this heterotrophic organism in this study points toward lability of the OC in recently deglaciated soils.

While the aforementioned phyla were prominent in other samples from similar cold environments (e.g., Chu et al., 2010; Costello and Schmidt, 2006; Ji et al., 2016; Mateos-Rivera et al., 2016; Schütte et al., 2010; Seok et al., 2016; Venkatachalam et al., 2021), the bacterial communities identified at the Tarfala valley exhibited an unusually high relative abundance of the candidate phylum Dormibacteraeota, a unique feature not commonly observed. From previous studies, soils with such high relative abundance of candidate phylum Dormibacteraeota have only been reported once (Mitchell Peninsula, Ji et al., 2016). Moreover, candidate phylum Dormibacteraeota was present only in mature soils (LIA) from the Styggedalsbreen glacier foreland in Norway (Mateos-Rivera et al., 2016), in line with the age of exposure of soil samples collected along the Tarfalajaure transect. The observed relatively high relative abundance of the candidate phylum Dormibacteraeota highlights the uniqueness of this system and calls for further investigation. Similar to the findings in Sweden candidate phylum Dormibacteraeota had higher concentration in soils that have been exposed for longer in Kviárjökull and Fjallsjökull.

Contrary to some studies (e.g., Schütte et al., 2009; Venkatachalam et al., 2021), no clear pattern of microbial community changes along the transects was observed, suggesting bacterial community stabilization over time. This aligns with the concept that bacterial communities adapt

Table 4
Major BHPs, their source organism and environment they are found in (adapted from Cooke, 2011).

BHP	Source organism	Environment
30-(5′-adenosyl) hopane and related structures	Purple non-sulfur bacteria[1], *Nitrosomonas europaea*[1], *Bradyrhizobium japonicum*[1]	Sediment[2], soils[2], peats[2]
BHT	*Acetobacter*[18], *Acetobacter xylinum*[17], *Anabaena cylindrica*[28], *Azotobacter vinelandii*[29], *Bacillus acidocaldarius*[17], *Beijerinckia indica*[29], *Beijerinckia mobilis*[29], *Burkholderia* spp.[7], *Calothrix*[28], *Chlorogloeopsis fritschii*[28], *Chroococcidiopsis*[28], Cyanobacteria[24,28], *Cyanothece*[28], *Desulfovibrio*[5], *Frankia*[3,20], *Frateuria aurantia*[11], *Gloeocapsa* sp.[28], *Gluconacetobacter*[26], methylotrophs[24], *Methylobacterium organophilum*[4,8,12,19,27], *Methylocystis parvus*[23], *Methylosinus trichosporium*[15], *Microcystis aeruginosa*[28], *Nostoc muscorum*[4,28], *Oscillatoria amphigranulata*[28], *Phormidium* sp.[28], *Prochlorothrix hollandica*[22], Purple non-sulfur bacteria[24], *Purple non-sulfur bacterium Rhodomicrobium vannielii*[14], *Rhodopseudomonas acidophila*[8], some gram-positive and gram-negative bacteria[24], *Zymomonas mobilis*[8,9,13]	Sediment[2], soils[2], water column[2], peat[2], hot springs[2]
BHT cyclitol ether	*Acetobacter xylinum*[10], *Anacystis montana*[28], *Azotobacter vinelandii*[29], *Burkholderia cepacia*[26], *Chlorogloeopsis*[25,28], *Chroococcidiopsis*[28], *Desulfovibrio*[5], *Frateuria aurantia*[11], *Gloeocapsa* sp.[28], *Methylobacterium organophilum*[16,19], *Trichodesmium erythraeum*[28], *Zymomonas mobilis*[16,23]	Sediments[2], soils[2], water column[2], peat[2]
Aminotriol	*Anacystis montana*[28], *Beijerinckiaceae*[29], *Bradyrhizobium japonicum*[6], *cyanobacteria: Microcystis* sp.[28], *Chroococcidiopsis* sp.[28], *Desulfovibrio*[5], *Methylomicrobium album*[23], *Methylocystis parvus*[23], *Methylosinus trichosporium*[23], *Microcystis aeruginosa*[28], *Nitrosomonas europaea*[21]	Sediments[2], soils[2], water column[2], hot springs[2]
Me-BHT	Cyanobacteria[1], *Rhodopseudomonas palustris*[1], *Methylobacterium organophilum*[1]	Sediments[2], soils[2], water column[2], hot springs[2]
Aminotetrol	Methanotrophs[1]	Sediments[2], soils[2], water column[2], peat[2], hot springs[2]
Me-aminopentol	Methanotrophs[1]	Sediments[2], hot springs[2]

References:
[1] as cited in Table 2.2a, Cooke, 2011.
[2] as cited in Table 2.2b, Cooke, 2011.
[3] Berry et al., 1991.
[4] Bisseret et al., 1985.
[5] Blumenberg et al., 2006.
[6] Bravo et al., 2001.
[7] Cvejic et al., 2000.
[8] Flesch and Rohmer, 1988.
[9] Flesch and Rohmer, 1989.
[10] Herrmann et al., 1996.
[11] Joyeux et al., 2004.
[12] Knani et al., 1994.
[13] Moreau et al., 1997.

[14] Neunlist and Rohmer, 1985.
[15] Neunlist et al., 1985.
[16] Neunlist et al., 1988.
[17] Ourisson and Rohmer, 1992.
[18] Peiseler and Rohmer, 1992.
[19] Renoux and Rohmer, 1985.
[20] Rosa-Putra et al., 2001.
[21] Seemann et al., 1999.
[22] Simonin et al., 1996.
[23] Talbot et al., 2001.
[24] Talbot et al., 2003b.
[25] Talbot et al., 2003a.
[26] Talbot et al., 2007a.
[27] Talbot et al., 2007b.
[28] Talbot et al., 2008.
[29] Vilcheze et al., 1994.

to new environments and become homogeneous in soils exposed for longer, as observed in the surroundings of the Tarfalajaure lake, Vatnajökull ice cap glacier forelands and the Zackenberg valley (Schütte et al., 2009, 2010). Investigating microbial communities in deglaciating areas across the three study sites has revealed the similarities and differences between and within the catchments, showing us that these communities stabilize over time. Additionally, to better understand soil development, we examined which bacteria produce specific biomarkers.

4.5. Source and nature of organic biomarkers

Individual BHPs are produced by specific bacteria and, therefore, can be used as biomarkers characteristic of certain environments (Kusch and Rush, 2022). Despite variations in chemical compositions and the time of exposure, samples from different catchments exhibited similar main BHP compounds. For instance, 30-(5′-adenosyl)hopane and adenosylhopane$_{HG\text{-}Me}$ were the main soil-marker BHPs detected in samples from Sweden, Iceland and Greenland. Soil-marker BHPs, 30-(5′-adenosyl)hopane and related structures are produced by purple non-sulfur bacteria, *Nitrosomonas europaea*, and *Bradyrhizobium japonicum* (as cited in Cooke, 2011). Some of the bacteria are known to produce more than one BHP compound: purple non-sulfur bacteria produce BHT (Talbot et al., 2003b), while *Nitrosomonas europaea* and *Bradyrhizobium japonicum* produce aminotriol (Seemann et al., 1999; Bravo et al., 2001). Therefore, even when detected, it is challenging to pinpoint which bacteria produced specific BHP compounds. Though BHT is a common compound and used to describe both aquatic (Doğrul Selver et al., 2012, and references therein) and terrestrial environments (Doğrul Selver et al., 2012, and references therein), most likely it has a terrestrial origin in samples collected from glacier forelands. BHT, aminotriol and BHT cyclitol ether are produced by various organisms and can be found in different environments (Table 4), therefore, presence of these BHP compounds in samples in this study is not surprising. Interestingly, some of the bacteria producing Me-BHT also produce BHT, aminotriol and BHT cyclitol ether. When detected, these bacteria (e.g., Cyanobacteria and *Methylobacterium organophilum*) may be responsible for production of more than one BHP compound. There is also a small amount of aminotetrol and methylated aminopentol, likely produced by methanotrophs (Table 4). Methylated aminopentol has previously been reported in sediments (Table 4, as cited in Cooke, 2011), but is also present in soil samples in this study, expanding the range of environments (soils) where this compound has been observed.

Understanding the source and nature of BHPs provides new insights into soil development mechanisms in deglaciating high-latitude areas. Next, we attempted to link the bacteria detected in this study to the organic biomarkers they might have produced.

4.6. Relationship between microbial community and organic biomarkers

BHPs produced by microbial communities are resistant to degradation and accumulate in soils over time. These biomarkers reflect microbial presence and activity, providing insights into past communities and potentially indicating long-term OC sequestration in deglaciating areas. BHPs, including soil-marker BHPs, were detected in all analysed samples, with 30-(5′-adenosyl)hopane and adenosylhopane$_{HG\text{-}Me}$ being the most abundant. Soil-marker BHPs are generally abundant in terrestrial environments (Cooke et al., 2008; Doğrul Selver et al., 2012; Höfle et al., 2015) and, in this study, are used as indicators of soil development in glacier forelands. Identifying the specific microbial sources of these BHPs allows for a closer examination of their potential roles in OC cycling and soil development. While species-level identifications are not available, several bacterial families – including photosynthetic bacteria such as purple non-sulfur bacteria, nitrogen fixers, methanotrophs, and cyanobacteria – are plausible producers of the detected biomarkers (Table 4).

The presence of 30-(5′-adenosyl)hopane-producing photosynthetic bacterium Rhodospirillaceae (Proteobacteria), also known as purple non-sulfur bacteria (as cited in Cooke, 2011), and potentially soil-marker BHPs-producing family Hyphomicrobiaceae (photosynthetic bacterium species *Rhodomicrobium vannielii*, purple non-sulfur bacteria, Proteobacteria; Neunlist et al., 1985) and nitrogen fixing bacterium Bradyrhizobiaceae (species *Bradyrhizobium japonicum*, Proteobacteria; as cited in Cooke, 2011), detected in Sweden, Iceland and Greenland, suggests that these bacteria might contribute not only to soil-marker BHP production but also to nitrogen cycling within these catchments, potentially enhancing OC accumulation in soils over time. Carbon and nitrogen fixation by these microbes may enhance OC accumulation in soils over time by increasing nutrient availability for plant and microbial communities, thereby promoting biomass production and soil stabilization.

The presence of potentially 30-(5′-adenosyl)hopane-producing family Nitrosomonadaceae (species *Nitrosomonas europaea* (as cited in Cooke, 2011; Seemann et al., 1999)), detected in LIA moraine samples from Svínafellsjökull (SV2), suggests that the moraine is inhabited by bacteria that are not common in other sites in Iceland. The moraine is the only site within our sampled locations where the invasive nitrogen-fixing plant species *Lupinus nootkatensis* is present, though the distribution of this species is currently expanding in Iceland (Hiltbrunner et al., 2014; Vetter et al., 2018; Lehnhart-Barnett and Waldron, 2020). Both the plant and the bacteria contribute to the nitrogen cycle: *Lupinus nootkatensis* increases nitrogen input in soils, while Nitrosomonadaceae are ammonia-oxidizing bacteria (Chain et al., 2003), convert ammonia into nitrates, which are more readily assimilated by soil and plant systems. This interaction may influence the nitrogen cycle and contribute to soil fertility, thereby supporting OC accumulation.

BHPs from other nitrogen-fixing bacteria in this study: families Frankiaceae (*Frankia* (Berry et al., 1991; Rosa-Putra et al., 2001)), Pseudomonadaceae (specie *Azotobacter vinelandii* (Vilcheze et al., 1994)) and Beijerinckiaceae ((*Beijerinckia indica* and *Beijerinckia mobilis* (Vilcheze et al., 1994)), may contribute to soil fertility, supporting OC accumulation by providing essential nitrogen to soil microbes and plants.

Similarly, cyanobacteria, known for nitrogen fixation and photosynthesis, contribute significantly to soil development by enhancing carbon and nitrogen availability. Certain cyanobacteria, including *Anabaena cylindrica* (Talbot et al., 2008) and *Nostoc muscorum (*Bisseret et al., 1985; Talbot et al., 2008) from the Nostocaceae family, and *Phormidium* species (Talbot et al., 2008) from Phormidiaceae, produce BHPs like BHT and Me-BHT. These compounds are among the most abundant found in the soils in this study. By adding essential nutrients, cyanobacteria play a crucial role in fostering soil formation and development in glacier forelands, further supporting the OC accumulation.

In addition, BHPs derived from methanotrophs (Desulfovibrionaceae (*Desulfovibrio* (Blumenberg et al., 2006)); Methylacidiphilae (Verrucomicrobia); Methylocystaceae: *Methylocystis parvus* (Talbot et al., 2001) and *Methylosinus trichosporium* (Neunlist and Rohmer, 1985)) were

detected in low abundance across the sites. Methanotrophic bacteria play an essential role in methane oxidation within soils, potentially impacting OC dynamics by converting methane, a potent greenhouse gas, into more stable forms, such as OC (Lau et al., 2007). The presence of Me-aminopentol and aminotetrol, that can be used as markers of methanotrophic activity along with aminopentol (Zhu et al., 2011), aligns with the presence of this bacteria.

Across all three catchments, the microbial community profile includes bacteria likely responsible for producing multiple BHP compounds. For example, species belonging to family Bradyrhizobiaceae are responsible for producing BHP compounds other than soil-marker BHPs: *Bradyrhizobium japonicum* also produces aminotriol (Bravo et al., 2001), *Rhodopseudomonas palustris* produces Me-BHT (as cited in Cooke, 2011), and *Rhodopseudomonas acidophila* produces BHT (Flesch and Rohmer, 1988). Similarly, *Nitrosomonas europaea* (Nitrosomonadaceae) responsible for production of soil-marker BHPs also produces aminotriol (Seemann et al., 1999). *Rhodomicrobium vannielii* (Neunlist et al., 1985) produces soil-marker BHPs, BHT and aminotriol. Rhodospirillaceae produces BHT, as well as 30-(5′-adenosyl)hopane (as cited in Cooke, 2011).

The presence of BHP-producing bacteria associated with multiple ecological functions suggests that these compounds are not solely indicators of specific bacteria but also reflect adaptive responses to environmental stresses. For instance, *Rhodopseudomonas palustris* produces 2-Me BHPs under pH stress, underscoring the role of BHPs in membrane integrity and resilience under variable pH conditions (Welander et al., 2009). Similarly, *Frateuria aurantia* (Xanthomonadaceae), which modifies BHP composition in response to temperature changes, demonstrates the role of BHPs in maintaining membrane fluidity and stability (Joyeux et al., 2004). These mechanisms highlight that BHPs not only serve as biomarkers but also play protective and stabilizing functions within microbial membranes, which may facilitate OC preservation in soils by adapting to environmental stresses under extreme conditions typical of glacier forelands.

BHP-producing microbial communities, particularly those with nitrogen-fixing and photosynthetic functions are likely to contribute to OC accumulation and soil stabilization in glacier forelands. These microbial functions enrich the soil with essential nutrients and produce BHPs that may aid in OC retention, supporting the gradual development of stable soil ecosystems in deglaciating areas. However, given that bacteria detected in this study potentially produce multiple BHP compounds, pinpointing the original source of the biomarkers remains challenging. We suggest that soil-marker BHPs in samples from Sweden, Iceland and Greenland were produced by Rhodospirillaceae (Proteobacteria) and might have been produced by Bradyrhizobiaceae (Proteobacteria) and Hyphomicrobiaceae (Proteobacteria). Although results indicate that most of the detected BHP-producing bacteria have low relative abundances, they may still have produced organic biomarkers detected in the samples, especially considering that organic biomarkers accumulate over a long period of time. On the other hand, as biomarkers accumulate over time, the microbial community present now might not be representative of the biomarkers produced by different bacteria in the past. This introduces functional uncertainty, as some BHP production may reflect past environmental conditions rather than current microbial activity.

Findings suggests that processes taking place in catchments in this study and perhaps in other catchments in the Arctic and sub-Arctic regions are complex, and more environmental studies aimed at establishing the link between bacteria and specific organic biomarkers should be carried out. Moreover, further investigation is necessary to confirm bacteria responsible for the production of BHP compounds from these catchments. This study was the first attempt to link BHPs and microbial communities in environmental samples, using their combination to understand soil development in deglaciating areas in northern latitudes.

This study highlights how microbial community composition influences organic carbon accumulation in newly forming soils. BHPs provide insight into past microbial activity and their role in recalcitrant carbon storage. By linking microbial functions to biomarker profiles, this approach enhances our understanding of soil development in deglaciating landscapes, emphasizing the importance of microbial communities in early soil formation and carbon sequestration processes.

5. Conclusion

This study investigated bacterial community establishment and subsequent accumulation of BHPs across three deglaciating areas in northern latitudes, providing a broader understanding of OC accumulation and soil development in these newly exposed landscapes. To our knowledge, this is the first study to employ organic biomarkers to elucidate soil development in deglaciating catchments, a highly perturbed part of the global carbon cycle. Combined with microbial community analysis, this study investigated the relationship between the current bacterial population and the former population, as indicated by bacteriohopanepolyols, in deglaciated areas.

Among the studied catchments, Sweden exhibited the lowest OC content, while OC concentrations in Iceland and Greenland were comparable. Our analysis indicated that soil marker BHPs accumulate in recently deglaciated areas along the glacier chronosequence, followed by stabilization in soils that have been exposed for longer. Interestingly, exposure time since deglaciation did not appear to be a primary control on microbial community composition. Bacterial community compositions were similar in Iceland and Greenland, while a distinct bacterial community has been established in Sweden.

Analysis of the relationship between bacterial community and organic biomarkers indicated that while some bacteria could have been responsible for production of certain organic biomarkers, most bacteria had low relative abundance. It may be that some bacteria, even in low relative abundance, produced organic biomarkers that accumulated over time, or that the bacterial community in the catchments changed as the environment developed. The latter suggests that the contemporary bacterial community is not responsible for the historical production of organic biomarkers.

The main findings of this study are as follows:

1. Recently deglaciated areas rapidly accumulate OC, as well as soil-marker BHPs, subsequently stabilising over time.
2. Microbial communities detected in this study are generally representative of other Arctic catchments and consist of members of Acidobacteria, Actinobacteria, Chloroflexi, Planctomycetes, Proteobacteria and Verrucomicrobia. Microbial community is different in Sweden, having high relative abundance of candidate phylum Dormibacteraeota.
3. Soil-marker BHPs in Sweden, Iceland and Greenland are produced by Rhodospirillaceae (Proteobacteria) and may be produced by Bradyrhizobiaceae (Proteobacteria) and Hyphomicrobiaceae (Proteobacteria).

Despite some similarities in bacterial communities (Iceland and Greenland) and similar R'_{soil} values across the three sites, soil development varied between and within the sites. Comparing different ecosystems, ranging from recently deglaciated (Storglaciären) to those that have been ice-free for several millennia (Tarfalajaure, Zackenberg) allowed us to understand soil development over time, although these catchments are still relatively carbon-poor on the global scale. In conclusion, glacial recession due to climate warming will establish new soils in which bacterial communities will develop and organic carbon will rapidly accumulate, before stabilising.

CRediT authorship contribution statement

Saule Akhmetkaliyeva: Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis. **Andrew P. Dean:**

Writing – review & editing, Supervision, Funding acquisition. **Leon J. Clarke:** Writing – review & editing, Supervision, Funding acquisition. **Simon J. Cook:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Sharon Ruiz Lopez:** Writing – review & editing, Investigation, Formal analysis. **Robert B. Sparkes:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Saule Akhmetkaliyeva reports travel was provided by EU INTERACT. Andrew Dean, Robert Sparkes, Saule Akhmetkaliyeva reports financial support and equipment, drugs, or supplies were provided by NERC Biomolecular Analysis Facility in Liverpool. If there are other authors, they 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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.178723.

Data availability

The sequence datasets were deposited in the National Center for Biotechnology Information (Project accession number: PRJNA1037499). The biomarker data is provided in supplementary material. Raw biomarker data is available on request.

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