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Vertebrates impact on bacterial community structure of coastal Arctic snowpacks in the spring

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Abstract

Snow covers up to 35% of the Earth's surface seasonally and forms a microbial habitat despite harsh and variable conditions. While atmospheric deposition is a well-known source of microbial input, the role of vertebrates in shaping snow microbiomes remains underexplored. In Arctic ecosystems, seabirds and terrestrial mammals contribute not only nutrients but also microbial communities. Here, we explore the role of vertebrates in shaping snow microbial biodiversity of Arctic terrestrial snowpacks. The study was conducted on the northern coast of Hornsund Fjord on Spitsbergen. Fourty snow samples were collected in four transects, two established along the gradient from the centre of a seabird (*Alle alle*) colony towards non-impacted areas and two transects along the coast. We identified a total of 8,521 bacterial OTUs using short-read sequencing of the 16S rRNA gene. Samples clustered into four snow groups based on community composition, but not linked to spatial factors such as distance to colonies. Bird and terrestrial mammal faecal indicators like *Catellicoccus* or *Streptococcus* were detected in 17 out of the 40 samples and drove the formation of two distinct clusters. These findings suggest that coastal Arctic snow microbiomes are strongly shaped by biological activity, with wildlife acting as key microbial vectors.

Keywords:

snow microbial communities; snow microbial colonization; bacteria biodiversity, vertebrates impact on snow

1. Introduction

Snow is an important component of the cryosphere, hydrosphere and biosphere, regulating albedo, water resources, and biogeochemical cycles (Déry and Brown, 2007; Dong et al., 2023; Hudson,

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2006). Although seasonal snow can cover half of the Northern Hemisphere lands, most of studies on the biological diversity and ecological processes on the snow surface are focused on seasonal snow patches during summer, specifically on snow algae blooms in lower latitudes (Hoham and Remias, 2020; Lemke et al., 2007). Arctic seasonal snowpacks are now recognized as viable habitats for diverse microbial communities (Maccario et al., 2015), even outside the melting period (Amato et al., 2007; Malard et al., 2021). To colonize and thrive in cold environments like snowpacks, microorganisms must adapt to physiological stressors such as low temperatures (below 5 °C), high solar radiation, low nutrient and water availability and freeze-thaw cycles (Larose et al., 2013). These challenging conditions fluctuate both temporally and spatially, requiring significant physiological acclimation. In the Arctic, high latitudes lead to pronounced seasonality, causing gradual yet extreme shifts in photoperiod, irradiance, and temperature (Larose et al., 2013), which can lead to oxidative stress (Sanchez-Cid et al., 2023). These temporal ecosystems, whose length of existence will be increasingly impacted by global climate change, constitute extraordinary models for studying the drivers of microbial community structure and assembly mechanisms, as they form new habitats seeded by microbes from snow-free ground or the atmosphere (Keuschnig et al., 2023).

When considering potential colonization of microorganisms to snowpacks, seeding by abiotic transport factors has generally been the main focus. One of the most recognized sources for freshly developing snow habitats is the atmosphere; with microorganisms entering the snowpack via wet and dry deposition (Maccario et al., 2019). Colonization from the terrestrial surface upon which the snowpack develops might also be a factor, e.g. nunataks (Monteil et al., 2012). Keuschnig et al., (2023) revealed that microbial abundance in surface snow, but not diversity, was tightly linked to sea spray, although few marine taxa were detected in snowpacks. In contrast, biotic vectors, such as migrating animals, have been less studied as colonization routes. Vertebrates that inhabit the Arctic, such as birds, reindeers, bears and foxes, can transport and spread significant quantities of biological and chemical material with the potential to influence community structure, diversity and ecosystem function in resident habitats (Bauer and Hoye, 2014). Unlike abiotic vectors, these organisms are not limited by environmental gradients, allowing them to transport materials in diverse directions and against prevailing abiotic flow patterns (McInturf et al., 2019). For instance, migratory birds can play an important role in the spread of antibiotic resistant bacteria to snow ecosystems in remote localities (Segawa et al., 2013, 2024). As they are actively foraging, mating, and breeding, animals leave behind nutrient and potentially contaminant-rich material such as faecal matter and carcasses, among others (Stempniewicz, 1990). For example, seabird colonies have been shown to affect nutrients (C:N:P), trace elements and organic matter concentration (Souza-Kasprzyk et al., 2022).

Seabirds, key vertebrates in polar regions, enrich soils with nutrients. By feeding in the sea and breeding on land, they deliver nutrients in the form of guano, feathers and egg-shells to terrestrial ecosystems, thereby linking nutrient-rich marine ecosystems with nutrient-poor ecosystems on land

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(Zmudczyńska-Skarbek et al., 2024). Depending on their diet, either planktivorous or piscivorous, and their nesting sites, cliffs or mild mountain slopes, these birds can shape the physicochemistry of soils, the diversity of plant cover and other organisms, in addition to impacting the abundance and functional groups of different animals (Zawierucha et al., 2016, 2019; Zmudczyńska-Skarbek et al., 2024; Zwolicki et al., 2013). Areas of bird colonies in the Arctic are also attractive for other vertebrates visiting seabird colonies for feeding on grasses (barnacle goose, *Branta leucopsis*), lichens (reindeer, *Rangifer tarandus*) or hunting (polar fox, *Vulpes lagopus*) (Jakubas et al., 2008). Recent findings show that polar bears supplement the lack of nutrients during the summer by foraging on seabird eggs and feeding on surrounding plants (scurvy grass, *Cochlearia grenlandica*) (Stempniewicz, 2017). The presence and abundance of terrestrial apex predators could be the next factor that directly shapes the surrounding environment. A study near Churchill, Manitoba, found that soils on Arctic fox dens had significantly higher nutrient levels compared to nearby control sites, with an increased inorganic nitrogen and extractable phosphorus observed. Dens also supported nearly three times more vegetation biomass, highlighting the role of Arctic foxes in enhancing local nutrient cycling and productivity, shaping plant diversity and herbivore distribution on the tundra (Gharajehdaghipour et al., 2016).

While these studies have focused on land during snow-free periods in the Arctic, it is likely that these nutrient additions might also impact snow microbial community structure since organic inputs have been shown to be the main drivers of bacterial diversity (Keuschnig et al., 2023) and microbial interactions (Bergk Pinto et al., 2019). In addition to contributing nutrients, vertebrates can directly introduce microorganisms, parasites, and propagules into snowpacks through excretions, facilitating their transfer and dispersal (Hayashi et al., 2018). Migrating birds have been shown to transmit the pathogenic avian influenza virus (H5Nx) (Wille et al., 2019) or antibiotic-resistant bacteria (Segawa et al., 2024). For example, the longest migratory birds, the Arctic tern (*Sterna paradisea*), migrate from pole to pole each year, crossing the world and becoming a vector of multidrug-resistant bacteria (Akhil Prakash et al., 2022). Whether these organisms are actually able to survive and colonize once they have been deposited into snowpacks has yet to be determined. The adverse abiotic factors encountered in the snow habitat, like cold temperatures and limited nutrient availability, likely hinder the survival of animal-associated microorganisms, while established snow communities might outcompete newcomers for resources.

While the influence of aerosols and snow/ice-free areas on bacterial communities in cryospheric ecosystems (e.g., snow, ice) has been well documented (Franzetti et al., 2017), the role of vertebrate activity in shaping microbial composition and function on snow remains unexplored. In this study, we assess how marine vertebrates (seabirds) and terrestrial (polar foxes, reindeer) animals alter microbial communities in coastal spring snowpacks in the vicinity of Polish Polar Station Hornsund (PPSH), Svalbard. We analyzed bacterial biodiversity along four transects: two adjacent to a little auk colony and two distanced from direct avian influence. Sampling areas exhibited clear signs of vertebrate

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activity, including reindeer herds, polar fox tracks, and biological remnants (feathers, bones). We hypothesized that seabirds and terrestrial vertebrates serve as a source of bacteria and nutrients on snowpacks. Understanding these microbial dynamics is urgent given the rapid decline of Arctic snowpacks. Our findings aim to clarify how vertebrate-driven microorganisms influence snow biodiversity and its cascading effects on Arctic terrestrial and coastal ecosystems under climate change.

2. Experimental Procedures

2.1. Study area and bird colony

Hornsund is located in the southwestern part of Spitsbergen, the biggest island of the Svalbard archipelago. It is an Arctic fjord where climate is strongly shaped by Atlantic waters, and by less saline, coastal Arctic waters from the Barents Sea. Ocean currents, geomorphology and presence of marine and land terminated glaciers sustain a high productivity and species richness in the area (Skagseth et al., 2008; Wesławski et al., 2006). Therfore, Hornsund was selected as All Taxon Biodiversity Inventory (ATBI) site (Warwick et al., 2003). Hornsund is inhabited by one of the largest worldwide concentrations of little auks (*Alle alle*) during breeding season, the total number is estimated at 592,000 pairs (Keslinka et al., 2019).

The study was conducted on the northern coast of Hornsund fjord (south-west Spitsbergen), on the slopes of the Fugleberget (569 m a.s.l.) and Ariekammen (517 m a.s.l.) mountains, which are located ca. 1 km north from the station, the latter one hosts several little auk colonies. The little auk colonies on the Ariekammen and Fuglebekken slopes are inhabited during summer season by ca 25,000 pairs (Keslinka et al., 2019). Although not investigated directly during sampling campaign, the little auk colony supplied ca. 60 tons of dry guano per km^2 of colony area during the breeding season, which shapes tundra plants, algae, invertebrates and bacterial communities (Stempniewicz, 1990; Zawierucha et al., 2019; Zielinska et al., 2016; Zwolicki et al., 2013). Apart birds, Hornsund is an important route for migration of polar bears *Ursus maritimus*, and habitat for two other mammals in Svalbard, reindeers *Rangifer tarandus platyrhunchus* and polar foxes *Vulpes lagopus* (Stempniewicz, 2017). Reindeers and foxes are known to disseminate parasites in this Arctic region (Myšková et al., 2019; Popiołek et al., 2007).

With the positive trend of mean annual temperature of +1.14 °C per decade in the last four decades (1979–2018), the climate in Hornsund is warming between 1979–2018 six times faster than the global average (Wawrzyniak and Osuch, 2020). In winter 2023/2024 snow season started in the late October. Between November and February snowpack in the catchment was stable with minor depth changes due to wind redeposition and occasional thaws. Depending on the measurement point location in the catchment maximum depth reached 111 - 127 cm at the feet of the Fugleberget slope (sample lines A and B), 70-80 cm in the middle of the Fuglebergsletta plain (sample line C), and up to 58 cm at the coast (sampling line D). In mid-May snowmelt has started, with snow patches lasting at the bottom

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of the slope till end of June, and full snow disappearance at the coast as early as first week of June 2024. The total recorded precipitation in the period 01.10.2023-31.05.2024 amounted to 209.5 mm. Of this, 152.4 mm occurred on days when the mean daily air temperature was at or below 0°C, while 57.1 mm was recorded on days with mean temperatures above 0°C. Notably, 15 days within the observation period experienced precipitation under positive temperature conditions.

2.2. Sample collection, DNA isolation and NGS sequencing

To study the effect of biotic vectors on the colonization of non-melting snowpacks, we conducted a field experiment near the PPSH in May 2024. A total of 40 surface snow samples were collected into sterile Whirl-Pak bags (equivalent to 2-3 L of melted snow) using a sterilized Teflon shovel from four transects (Line A, B, C, D) (Fig. 1). Two transects were established from the centre of a seabird colony towards non-impacted areas along an altitudinal gradient, while two other parallel transects were established closer to the coast. To reduce contamination, Tyvex® body suits, face masks and latex gloves were used during sample handling. Samples were immediately transported to the laboratory, and were left to melt at room temperature. A total of 1.5 liters of melted snow were filtered onto sterile MCE 0.22 µm 47-mm white gridded filters (Millipore) using a sterile filtration unit (Nalge Nunc International Corporation). The samples for chemistry analysis were frozen and transported for further analysis. Similarly, filters with microbial biomass for DNA isolation were stored in sterile Eppendorf tubes at -20 °C. Procedural blanks were carried out by filtering MilliQ water.

Environmental DNA was extracted from filters using the PowerWater® DNA Isolation Kit (MoBio, Carlsbad, CA, US) according to the manufacturer's instructions. The DNA purity was checked spectrophotometrically and the concentration of DNA measured using the NanoPhotometer NP80 was in the range of 2.7-9.3 ng μL^{-1}. The 16S rRNA fragment was amplified using bacterial primers 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC) spanning the V3–V4 hypervariable regions (Herlemann et al., 2011). Sequencing was performed on the MiSeq™ platform (Illumina, San Diego, USA) using paired-end reads (2 × 300 bp) by the Macrogen company (Macrogen Europe, Amsterdam, The Netherlands). Amplicon dataset was deposited at Sequence Read Archive (ID: PRJNA1277323).

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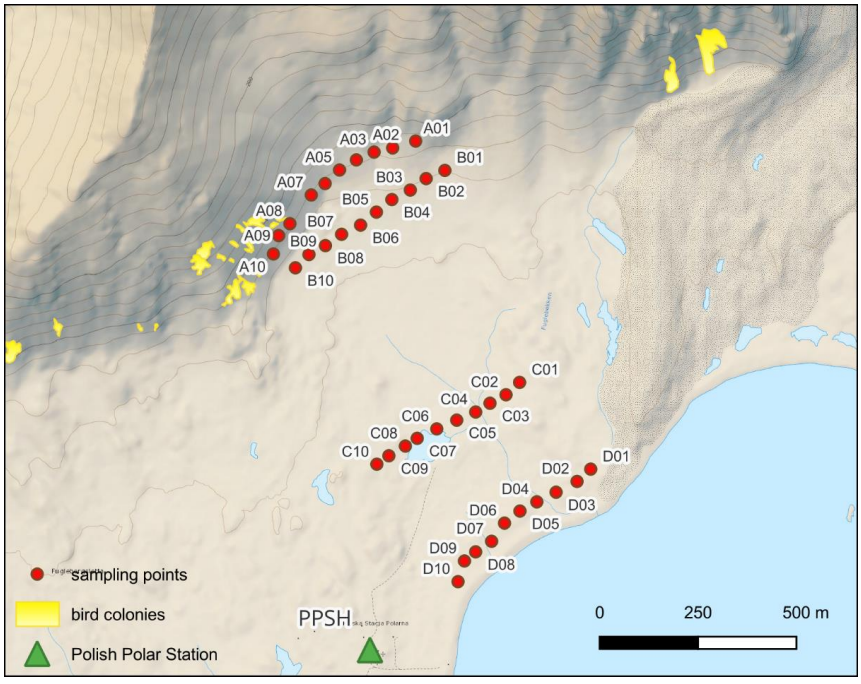

Figure 1. Transect lines A, B, C, and D where snow samples were collected (background map Norwegian Polar Institute 2014, bird colonies - Keslinka et al., 2019).

2.3. Bioinformatics and statistical analysis

Bioinformatic analysis was performed using CLC Genomic Workbench 24.0.1 and CLC Microbial Genomics Module 21.1.1 (Qiagen, USA). Raw sequence data were filtered, trimmed and merged using the default settings of *CLC tools* (Qiagen, 2024). Next, total reads were filtered from chimeric reads and assigned to operational taxonomic units (OTUs) based on the Silva SSU 99% (138.1) gene database. The *Allow creation of new OTUs* tool allowed sequences not represented at the given similarity distance in the database to form new OTUs. The default (80%) taxonomy similarity percentage was used when annotating new OTUs (Qiagen, 2024). For bacteria, the total reads of 5,172,254 were assigned to 15,812 OTUs. Next, the OTU table was filtered, and OTUs with low combined abundance (<10) were removed (*Remove OTUs with Low Abundance* tool) as well as chloroplast, mitochondrial and N/A sequences. Finally, the remaining sequences were assigned to 8,521 different OTUs (4,582 OTUs based on the database, 3,939 OTUs were created *de novo*). Coverage was calculated using Good's method (Liu et al., 2011) and was in the range of 0.994–0.999. One sample, C09, did not pass the coverage test and was excluded from the further analysis.

Next, *Estimate Alpha and Beta Diversities* workflow (Qiagen, 2024) was used to estimate relative abundance, alpha and beta diversity. Relative abundance at the family and genus level was presented as a stacked area chart. The alpha diversity was evaluated using the total number of OTUs,

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Chao1 index and Chao1 bias-corrected index as richness indices and Simpson's index *SI*, Shannon entropy *H'* and Faith's phylogenetic diversity *PD* as the diversity indices (Faith and Baker, 2006; Malandrakis et al., 2019; Qiagen, 2024). Significant changes in the alpha diversity indices between snow clusters were evaluated using pairwise Mann-Whitney U tests (P<0.05).

As for beta diversity, generalized UniFrac distance $d^{(0.5)}$ was used (Chen et al., 2012) for Principal Coordinates Analysis (PCoA). Significant changes between samples based on their transect localization (line as a main factor) or created snow clusters (cluster as factors) were detected using the *PERMANOVA analysis* tool with 99,999 permutations. From 1,137 total genera, we selected those present at >1% relative abundance in all snow clusters to identify cluster-specific taxa. Among these 56 most abundant genera, 50 showed significant differences (FDR-corrected $P < 0.05$) across clusters. We visualized these differential genera via Euclidean distance-based heatmap and compared their distribution among clusters using Venn diagrams.

2.4. Physicochemical analysis of snow properties

Samples for the determination of physicochemical parameters and major ions were collected into sterile Whirl-Pak bags using face masks, gloves and a special protective suit against contamination. Samples were transported to the Polish Polar Station Hornsund. After melting at room temperature, samples were filtered with sterile MCE 0.45 µm 47-mm white gridded filters (Millipore), and pH and conductivity were measured using calibrated EPP-1 pH and EFC-1t conductivity probes and pH/conductivity meter CPC-505 (Elmetron). As for HCO_3^- determination, samples were titrated with 0.02M HCl to pH 4.4 using a Titrino 702SM automatic titrator (Metrohm) and a pH probe (Metrohm). Ion concentrations were determined on a Metrohm 930 Compact IC Flex ion chromatograph equipped with an autosampler (Metrohm, Herisau, Switzerland). Cation samples were acidified with 2 µL of 2 mM HNO_3 per 10 mL sample prior to analysis. Cations NH_4^+, Ca^{2+}, Mg^{2+} were determined (PN EN ISO 14911, 2002) without suppression using column Metrohm 930 Compact IC Flex and eluent HNO_3 34 mM and dipicolinic acid 14 mM in water (IC eluent concentrate (20x), Supelco 61905). Anions (HCO_3^-, Br^-, Cl^-, NO_3^-, PO_4^{3-}, SO_4^{2-}) were determined (PN EN ISO 10304-1, 2009) using chemical suppression on column Metrosep A Supp 5 – 250/4.0 and eluent Na2CO3 64 mM and NaHCO3 20 mM in water (IC eluent concentrate (20x), Supelco 62414). The injection volume was 20 µL in the anion system and 100 µL in the cation system.

Snow samples for TOC were collected in the field into HDPE 500 mL bottles, melted in them and moved directly after melting into amber glass 60 mL vials with a PTFE septum. These vials were closed airtight with no headspace stored in cool storage (+4°C) and transported to Poland. TOC (total organic carbon) was determined with a TOC-L Analyser (Shimadzu, Japan), utilizing catalytic oxidation to CO_2 by combustion at 680 °C with a platinum catalyst. CO_2 was then detected by NDIR (non-dispersive infra-red detection). TOC was determined as NPOC (non-purgeable organic carbon), which

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is a method that may lead to an underestimation of volatile organic compounds. Calibration curves achieved $R^2 \geq 0.995$, with blank offset (deionized water < 30 ppb TOC was used for all blanks). The analytical range was 0.09 – 10 mg L^{-1} (for concentrations > 10 mg L^{-1}, dilutions were applied); LOD and LOQ were 0.03 mg L^{-1} and 0.09 mg L^{-1}, respectively. Other measurement settings were: 3 out of 4 repeats accepted, CV < 2%, sparging time (with HCl) 90 seconds. Field container blanks were performed in 5 repeats and yielded results <LOQ. Comparisons of two sample storage types, i.e., samples stored in frozen conditions in polypropylene vials with the samples in amber glass, yielded consistent results.

Canonical correspondence analysis was used to identify the most important environmental factors affecting the snow clusters' microbial parameters. The CCA was performed using PAST software. Before analysis, values were normalized using log-transformation. Among 20 measured environmental factors describing snow physicochemical properties, after preliminary analysis, twelve non-correlated factors (pH, conductivity, Non-Purgeable Organic Carbon NPOC, cations: NH_4^+, Ca^{2+}, Mg^{2+} and anions: HCO_3^-, Br^-, Cl^-, NO_3^-, PO_4^{3-}, SO_4^{2-}) were used. As microbial parameters, 58 values were used (read number of 56 genera present in each cluster, which is over 1% of total read content, total number of reads, and OTU).

3. Results

3.1. Bacterial community structure - beta diversity and taxa distribution

Principal Coordinate Analysis was used to compare beta diversity profiles from different sampling sites. It showed that transects were not the most crucial factor that grouped samples (Fig. S1). Considering the transect line as a factor, PERMANOVA revealed (Table S1) the line significance (P<0.05), but the only significant difference was detected between lines A and B (P=0.039). However, based on the 2D (Fig. 2) and 3D view (Fig. S2) of principal coordinate analysis (PCoA) of bacterial 16S rRNA profiles, we identified four clusters that explained snow sample differentiation (PERMANOVA, P<0.001). This observation was supported by taxa distribution pattern in each cluster (Fig. 3A). The obtained 3,185,587 16S rRNA sequences were assigned to a total of 8,521 bacterial OTUs that were mainly classified into *Bacilli*, *Actinobacteria*, *Alphaproteobacteria*, and *Cyanobacteria* classes (Table S2). Distribution varied across samples, and bacterial markers responsible for the grouping of samples were determined. At the genus level (Fig. 3B), *Catellicoccus* (*Firmicutes* phylum) dominated samples A05–A10, B10, C07, and D08, comprising between 32.0–97.8% of reads. Other abundant genera included *Streptococcus* (*Firmicutes*; up to 35.6% in B02) and *Aliterella* (*Cyanobacteria*; up to 53% in D06). Samples with *Catellicoccus* marker created cluster number three (marked red in Fig. 2). Cluster number two was distinguished based on the higher *Streptococcus* content (orange one). These two clusters contained 17 snow samples. Other samples were classified into two additional clusters. OTUs affiliated with *Aliterella* characterized cluster number four (blue). Cluster number one, distinguished in

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the PCoA 3D view (Fig. S2, 54.48% total variability explained) was characterized by high bacterial diversity (Fig. 3B) (marked as gold).

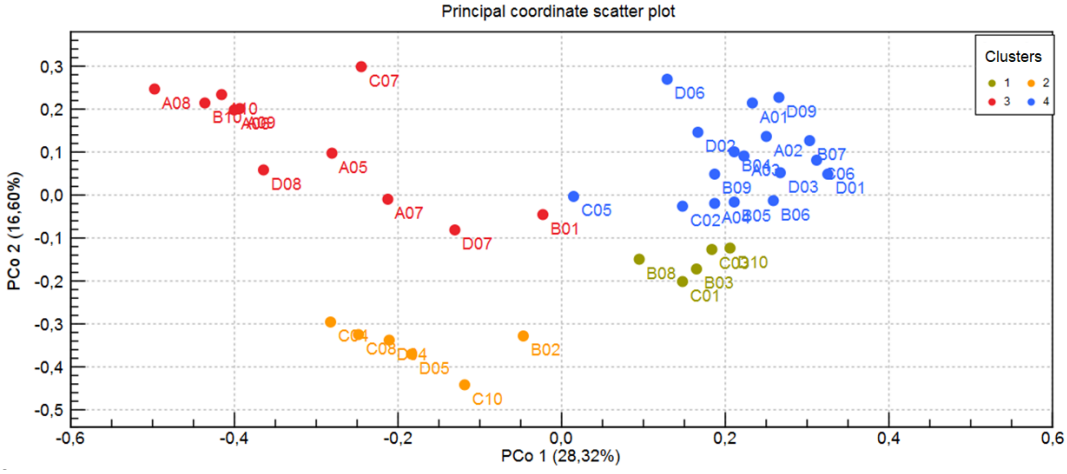

Figure 2. Principal coordinates analysis (PCoA) plot (2D view) of bacterial genetic profiles based on the generalized UniFrac distance $d^{(0.5)}$ matrix.

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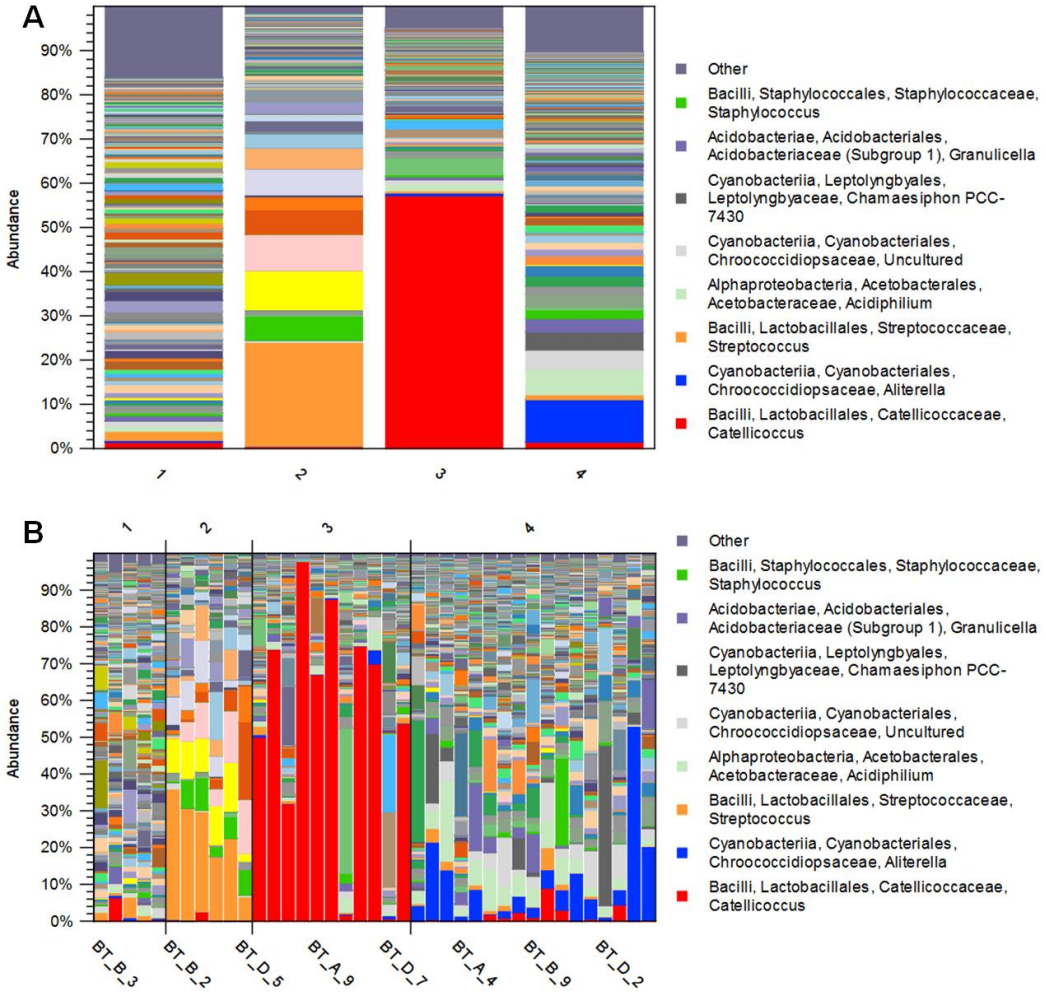

Figure 3. Stacked bar of the microbial community at the genus level in snow clusters (A) and for each individual samples (B). The taxonomic affiliation of the most abundant genera are provided in the legend.

3.2. Microbial taxons that differentiate snow clusters

A heat map of the 50 genera that significantly differentiated samples was used to identify key taxa in each cluster (Fig. 4). In cluster three, OTUs affiliated with *Catellicoccus* and genus 1174-901-12 (*Alphaproteobacteri*a class) were significantly higher than in other clusters. OTUs classified as *Psychrobacter and Arthrobacter* were significantly higher in cluster three than in clusters two and four, and *Sporosarcina* sequences were more abundant in cluster three than in cluster two. Cluster number two contained significantly more OTUs affiliated with *Streptococcus*, *Veillonella* and *Actinomyces*

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genera than other clusters. Cluster number four had significantly higher proportions of *Aliterella*, *Cyanobacteria*: *Chamaesiphon* PCC-7430 and *Tychonema* CCAP 1459-11B, as well as *Spirosoma* (*Bacteroidia* class), and *Massilia* (*Gammaproteobacteria* class) genera. In cluster one, sequences affiliated with *Sanguibacter-Flavimobilis*, *Homoserinimonas* and *Cryobacterium* (all *Actionobacteria* class), as well as *Cellvibrio* and *Luteimonas* (*Gammaproteobacteria* class) and *Pricia* (*Bacteroidia* class) were significantly more abundant than in other clusters.

Based on Venn diagram analysis (Fig. S3), the most significant differences at genera level were observed between cluster number two and the other snow clusters. Among 50 genera considered, 43 significantly differentiated this cluster from cluster four, and 41 and 34 with clusters three and one, respectively. It is worth mentioning that 18 different genera significantly differentiated clusters one and four, confirming the relevance of separating the cluster one from cluster four.

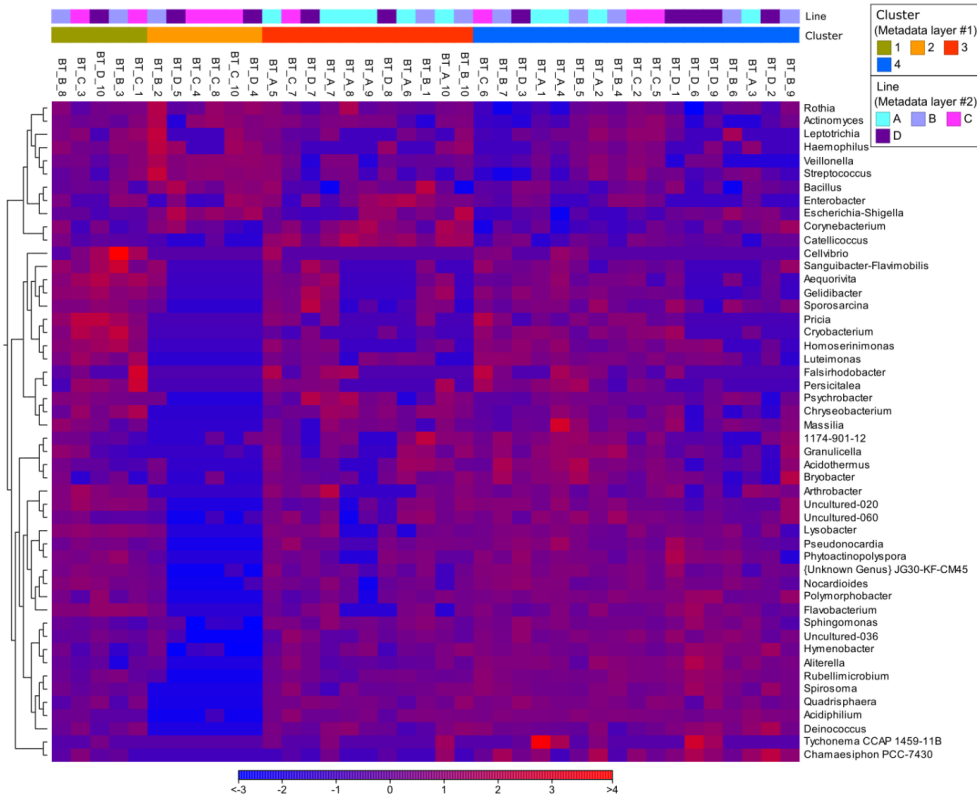

Figure 4. Normalized distribution of the 50 most abundant genera that significantly (P<0.05) differentiated snow clusters. Samples are ordered based on clusters derived from PCoA, while transect information is provided in the top bar (line).

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3.3. Variability in alpha diversity among clusters

Richness (total number of OTUs, Faith's phylogenetic diversity PD, Chao1 index and Chao1 bias-corrected index) and diversity indices (Shannon entropy H' and Simpson's index SI,) were used to evaluate the changes in the alpha diversity of snow clusters (Fig. 5). The cluster factor was significant (P<0.001) for each index. The highest richness indices values were detected in cluster one and the lowest in cluster two. Generally, the richness indices values differed significantly between snow clusters, except between clusters one and four. Additionally, no significant differences were observed in the PD index values between clusters one and three. As for diversity indices, the highest Shannon and Simpson index values were measured for cluster one, and these values were significantly different compared to other snow clusters. In contrast to richness indices, the lowest values were detected in cluster three.

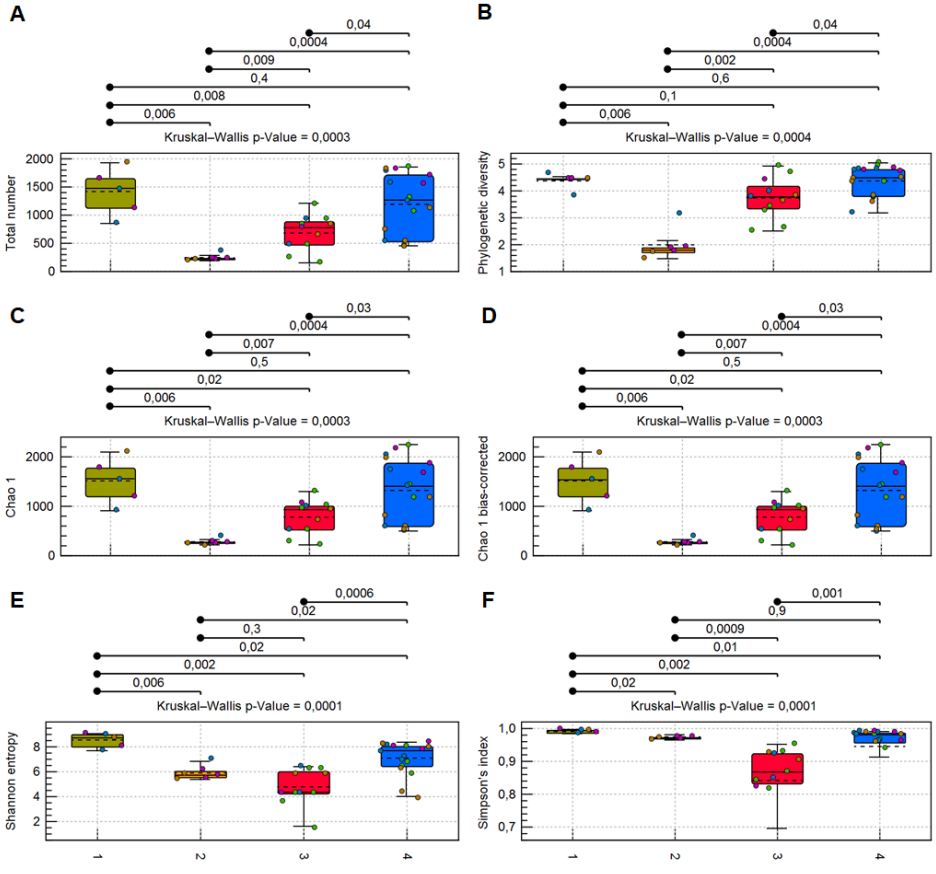

Figure 5. Comparison of alpha diversity indices between snow clusters: A: total number of reads; B: phylogenetic diversity; C: Chao 1; D: Chao 1 bias-corrected; E: Shannon entropy; F: Simpson's index. Legend: dashed line presents mean value; continuous line – median value; box borders define 25 percentile.

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3.4. Associating variations in bacterial community structure with snow environmental variables - canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) was used to associate variation in bacterial community structure with snow physicochemical variables (Fig. 6, Fig. S4). The top two axes (Axis 1 and 2) were included and accounted for 28.2% and 20.4% of microbial genera sequence structure variation, respectively.

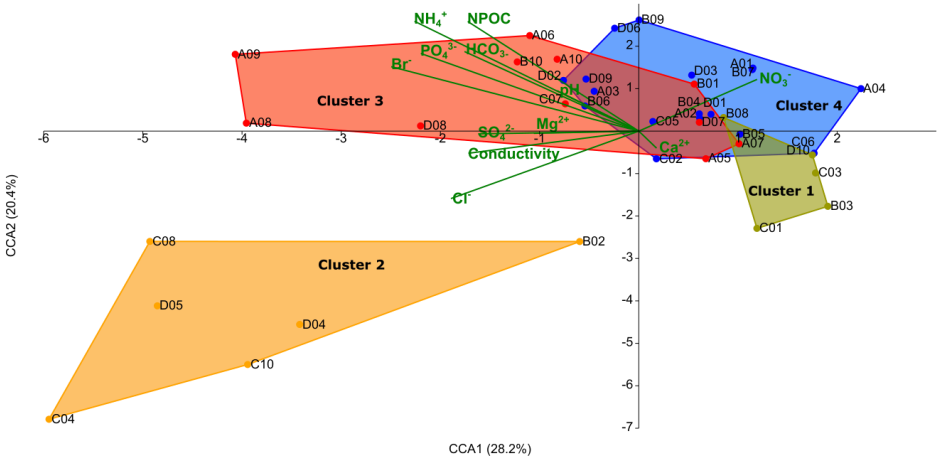

Figure 6. Canonical correspondence analysis of bacterial profiles at the genera level in snow clusters. The biplot presents the effect of the physicochemical properties of snow on the microbial community structure. Green lines represent the physicochemical parameters; the line length indicates which physicochemical parameters most strongly determine the cluster genera distribution. Four snow clusters are marked by gold, orange, red and blue colours.

In cluster one the variation of the most abundant genera from *Actinobacteria*, *Gammaproteobacteria* or *Bacteroidia* classes (Fig. S4, marked by gold) was mainly explained by higher Ca^{2+} concentration and lower values of physicochemical snow properties like organic matter, NH_4^+, Br^-, PO_4^{3-}, HCO_3^- and pH values (Fig. 6). As for markers of cluster two, *Streptococcus*, *Actinomyces, and Veillonella* (Fig. S4, marked by orange), their appearance in the snow was mainly associated with higher Cl^- and SO_4^{2-} concentrations and conductivity values and was negatively correlated with NO_3^- anions. In cluster three, the presence of *Catellicoccus* marker (Fig. S4, red) was highly influenced by a higher concentration of organic carbon (non-purgeable organic carbon NPOC), NH_4^+, and anions: Br^-, PO_4^{3-}, HCO_3^- and pH values. The same environmental variables were correlated with the higher abundance of markers from cluster four: *Aliterella* and *Spirosoma*. In contrast, three other the most abundant genera from cluster four (*Chamaesiphon* PCC-7430, *Massilia and Tychonema* CCAP 1459-11B), as well as

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three different genera, which had the highest abundance in cluster two (1174-901-12, *Sporosarcina*, and *Arthrobacter*), were influenced by the higher NO_3^- concentration.

4. Discussion

Snowpacks are complex ecosystems populated by diverse microorganisms, and their community composition is linked to the specific physicochemical properties of snow and the nutrients that snow provides (Maccario et al., 2015). As newly formed habitats, seasonal terrestrial snowpacks are colonized from the terrestrial surface upon which the snowpack develops or microorganisms from aerosols (Keuschnig et al., 2023; Maccario et al., 2019). In this study, we focus on the effects of vertebrates on the snow surface microbiome during early spring in the High Arctic.

4.1. Vertebrates as Key Contributors to Snow Microbial Communities

We determined that wild animals significantly contribute to seeding surface snow samples, with bacteria of animal origin identified in almost half of our samples (clusters two and three). Cluster three was dominated by the Gram-positive bacteria *Catellicoccus* of the *Lactobacillales* order, a ubiquitous organism in the gut microbiome of many avian species that is used as a bird faecal indicator (Grond et al., 2018; Kreisinger et al., 2017). *Catellicoccus* genus is also a dominant bacteria in the gut microbiome of thick-billed murres (*Uria lomvia*) (Góngora et al., 2021), and was detected in the microbiome of ruddy turnstone (*Arenaria interpres*) (Grond et al., 2014). These bacteria indicate that birds were the primary source of microorganisms on the snow surface in samples classified into cluster three. Moreover, *Psychrobacter*, a cold-adapted Gram-negative aerobic bacteria commonly identified in ice, snow and frozen soils (Rodrigues et al., 2009; Zeng et al., 2013) was also detected in higher abundance in cluster three. These cold-adapted bacteria were also found in Arctic and Antarctic ornithogenic soils, which are derived from the deposition of the faecal matter of birds (Bowman et al., 1996; Lasek et al., 2017). Interestingly, *Psychrobacter* strains were isolated from the guano of little auks collected in the vicinity of the Polish Polar Station Hornsund on Spitsbergen, too (Dziewit et al., 2013), which is consistent with our assumption that the snow surface in this cluster was colonized mainly by bird-origin microbes. This hypothesis is further supported by the chemical data that showed that the relative abundance of *Catellicoccus* was linked to higher concentrations of carbon, nitrogen, and phosphorus species and higher pH values, which points to their joint origin in bird droppings, as *Catellicoccus* has been found in faecal matter of e.g. gulls (Koskey et al., 2014; Yao et al., 2023), while the enrichment of the Arctic tundra in nutrients by birds has been shown in multiple locations, including the little auk colony in question (Finne et al., 2024; Skrzypek et al., 2015; Zwolicki et al., 2016). The spatial variability in these variable levels confirms their likely origin in little auk colony, which could be a direct source of C, N and P, while elevated pH is likely an additional effect of ammonia-containing faeces.

Cluster two had the lowest diversity of all clusters, which could be explained by the presence of a few dominant organisms. Genera detected in higher abundance in this cluster were markers of the bird

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or animal microbiome (including human). The prevalence of animal-derived genera, corroborated by heatmap and Venn diagram results, confirmed cluster two as the most unique grouping within the snow microbiome. For instance, *Streptococcus*, another *Lactobacillales* member common in migratory bird guts (Kreisinger et al., 2017) as well as animals like reindeer (Aagnes et al., 1995; Sundset et al., 2007) or fish (Ringø et al., 2018), was correlated with a strict anaerobic bacteria *Veillonella* (Fig. S4). Both bacterial genera were also described as frequently co-occurring members of the human and animal gut microbiome (van den Bogert et al., 2013; Lu et al., 2020) or were detected in birds that live in Svalbard like snow bunting (*Plectrophenax nivalis*), sanderling (*Calidris alba*) (Cho and Young, 2020) or all-season rock ptarmigans (Ushida et al., 2016). *Veillonella* were also observed in a small proportion in the tundra river system in Svalbard (Kosek et al., 2018), glacial snow and soil (Yang et al., 2016) or in the inner fjord Kongsfjorden (Jain and Krishnan, 2017). Another significantly more abundant genus was *Actinomyces*, often identified within the oral human microbiome (Könönen, 2024; Tsuneishi et al., 2006). A similar situation was noted for *Rothia*, previously observed in samples from the oral and gut microbiome of birds (Abolnik et al., 2021; Cho and Young, 2020) or humans (Buetas et al., 2024; Yamane et al., 2010). These genera were mainly associated with higher salinity indices and negatively correlated with NO_3^- anions. Indeed, they show a high tolerance for saline stress, which supports their survival in harsh environments (Zhang et al., 2021). From the point of view of the spatial distribution of the collected samples, the elevated salinity of snow may be due to the sea spray impact, which is very typical for snowpacks in the Hornsund area of Svalbard (Barbaro et al., 2021). While the community composition of these groups was mostly driven by vertebrates, other colonization sources were also likely. For example, in cluster three, the high relative abundance of 1174-901-12 genus (*Alphaproteobacteri*a class), which is often linked with lichen-associated *Rhizobiales*, suggests a lichen origin (Hodkinson et al., 2012; Pankratov et al., 2020), while *Arthrobacter* is a widely distributed genus most frequently found in soil due to its ability to degrade different carbon sources and tolerate environmental challenges (Karmacharya et al., 2022; Teng et al., 2021).

4.2. Bacterial taxa distribution in non-animal impacted snow

Clusters one and four exhibited minimal animal influence, instead reflecting microbial communities typical of Arctic snow environments. These clusters displayed the highest species diversity (Shannon H' = 4.76–8.47; Fig. 5), significantly exceeding values reported for other Spitsbergen snow samples (Keuschnig et al., 2023; Thomas et al., 2020), likely due to atmospheric deposition as the primary colonization pathway. Dominant taxa included cold-adapted genera such as *Aliterella* (cluster four's key indicator), a cyanobacterium previously documented in Antarctic seawater (Rigonato et al., 2016), Atacama Desert rocks (Jung et al., 2020), and lichen photobionts (Jung et al., 2021). Additional cyanobacteria in cluster four (*Chamaesiphon*, *Tychonema*) are known from polar lake microbial mats (de los Ríos et al., 2015; Pessi et al., 2023) and riverine rocks (Aigner et al., 2018; Nemergut et al., 2007), suggesting wind dispersal from local terrestrial or aquatic habitats (Harding et al., 2011; Jensen

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et al., 2022). Other cluster four taxa, including *Spirosoma*, *Hymenobacter*, and the psychrophile *Massilia*, are characteristic of cryospheric environments—detected in subglacial ice (Perini et al., 2019), Svalbard glaciers (Garcia-Lopez et al., 2019), Svalbard snowpacks (Keuschnig et al., 2023) and Svalbard soil (Peeters et al., 2012; Son et al., 2021; Wang et al., 2018).

Cluster four's microbial composition showed strong correlation with elevated nitrate levels. While cyanobacteria (*Aliterella*, *Chamaesiphon*, *Tychonema*) dominated this cluster, their presence in nitrate-rich snow likely reflects atmospheric nitrogen (N_2) fixation rather than nitrate utilization (Cho and Young, 2020; Jungblut et al., 2010). As key nitrogen fixers in Arctic ecosystems (Liengen and Olsen, 1997; Solheim et al., 1996), cyanobacteria play critical roles in soil formation, biocrust development, and aquatic primary production (Patova et al., 2016; Rousk et al., 2017), while also serving as ecosystem engineers through bioaggregate formation on glaciers (Rozwalak et al., 2022; Wejnerowski et al., 2023). The cluster also contained nitrate-reducing *Massilia* (*Gammaproteobacteria*) (Mukhia et al., 2024) and nitrogen-associated *Spirosoma* (*Bacteroidia*) (Valdespino-Castillo et al., 2018), along with Arctic soil-dwelling *Arthrobacter* and *Sporosarcina* (Kim et al., 2010; Singh et al., 2017). Collectively, these patterns suggest cluster four represents a characteristic snow microbiome shaped by wind-dispersed tundra materials containing nitrogen-cycling taxa.

Cluster one differed from cluster four due to a higher relative abundance of *Actinobacteria*, including *Sanguibacter-Flavimobilis* genus, which members were previously isolated from Antarctic sea sand (Hong et al., 2008) and bovine blood (Ivanova et al., 2009), along with the some airborne *Homoserinimonas* genus members (Kim et al., 2012) and psychrophilic *Cryobacterium*, often identified in cryoconite holes from Ny-Ålesund glaciers (Singh et al., 2014) and ice cores (Liu et al., 2020). The cluster also contained *Gammaproteobacteria* such as *Cellvibrio* (frequent in spring/winter air samples) (González-Martín et al., 2021) and *Luteimonas* detected in migratory bird microbiota (Kreisinger et al., 2017) and hydrocarbon-contaminated soils (Hemala et al., 2014; Zhang et al., 2010), as well as *Pricia* members (*Bacteroidia*), that were originally isolated from Antarctic intertidal sediments (Yu et al., 2012). These cold-adapted taxa suggest aerosol deposition as the primary colonization mechanism, mirroring cluster four. The abundance of *Actinobacteria*, *Gammaproteobacteria* and *Bacteroidia* was mainly explained by lower nutrient and pH levels (Fig. 6, Fig. S4), suggesting tolerance to oligotrophic conditions. While these phyla are well-documented in Arctic tundra soils (Kosek et al., 2017; Nissinen et al., 2012) and Hornsund river systems (Kosek et al., 2019), their ecological roles appear habitat-dependent. For instance, the Bacteroidia genus *Pricia* thrives in nutrient-poor, oxygen-limited settings (Liu et al., 2021), whereas *Gammaproteobacteria* and *Bacteroidia* typically dominate carbon-rich marine ecosystems (Francis et al., 2021; Thiele et al., 2022). Furthermore, *Cellvibrio* (*Gammaproteobacteria*) is a copiotrophic bacteria that decomposes complex carbohydrates (Spring et al., 2015). Therefore, the composition of this cluster is not entirely indicative of oligotrophic environments, yet some of its components are connected to Arctic environments. Reindeer feces may

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represent an additional source, as several genera (*Cryobacterium, Sanguibacter, Nocardioides, Massilia*, and *Bacteroidia* members) have been identified in fecal samples from Ny-Ålesund (Fang et al., 2024) and Hornsund (Zielińska et al., 2016).

5. Conclusions

Our study shows that vertebrates influence the bacterial community structure of coastal Arctic snowpacks in the spring. In addition to typical for psychrophilic environments cold-adapted microorganisms that are usually considered as primary sources of microbial colonization, we detected vertebrate origin microbes. They are mainly linked to the gut microbiome of birds and terrestrial mammal, including humans. Sequences classified to *Catellicoccus*, *Streptococcus* and *Actinomyces* genus indicated vertebrate activity and nutrient enrichment. Interaction of environmental parameters, especially salinity, pH, and nutrient content dependent on vertebrates and marine aerosols, likely influenced the snow microbiome, enabling the coexistence of oligotrophic and copiotrophic bacterial taxa. Our study indicated that compared to previously considered areas, animals are an important source of microorganisms colonizing the snow surface. Overall, our findings indicated that in addition to transport factors such as atmospheric deposition and wind-transported materials from snow-free terrestrial, microbial colonization in Arctic coastal snowpacks is more dependent on wildlife than assumed. Additionally, activity of scientists could also affect the snowpack. Both abiotic and biotic transport factors should be considered when assessing microbial ecosystem dynamics in polar regions.

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Author Contributions Statement

S.S.: Conceptualization, Formal analysis, Investigation, Resources, Data Curation, Writing - Original Draft, Visualization; **K. Z.**: Conceptualization, Investigation, Resources, Writing - Original Draft; **A. M.**: Investigation, Writing - Review & Editing; **K. K.**: Conceptualization, Investigation, Resources, Writing - Review & Editing; **W. Z.**: Investigation, Writing - Review & Editing; **A. N.**: Conceptualization, Investigation; **K. T.**: Investigation; **B. L.**: Conceptualization, Visualization, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition; **C. L.**: Conceptualization, Formal analysis, Investigation, Resources, Writing - Original Draft.

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