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Local-scale variability in snow chemistry drives distinct microbial communities in Alpine seasonal snowpack

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Abstract. Seasonal snowpack is a dynamic system that accumulates atmospheric particles, including dust and biological material such as microorganisms, from both local and long-distance sources. Here, we investigated the relationship between bacterial community composition and chemical properties of seasonal snowpack in mid-altitude valleys of the Swiss Alps. We characterised microbial community structure and diversity in surface snow and underlying bulk snow across three adjacent valleys (elevations 1,798-2,578 m.a.s.l.). Analysis of major ions and organic acids was used to identify key environmental factors influencing microbial community composition. While geographical location showed no clear influence on either the chemical composition or the bacterial community structure, we identified significant differences between snow layers, with surface snow showing higher diversity than bulk snow and exhibiting greater cross-site similarity. Surface snow contained twice as many bacterial genera in the core community as bulk snow, with nearly complete overlap. Total inorganic nitrogen and Ca^{2+} were key drivers of microbial community composition in the snowpack. Using Weighted Gene Co-expression Network Analysis (WGCNA), we identified modules of co-occurring bacterial taxa with distinct responses to these chemical gradients. Spore-forming genera (*Neobacillus*, *Niallia*, *Sporosarcina*) were associated with nitrogen-enriched communities, while *Brevundimonas*, *Cryobacterium*, and *Polaromonas* drove calcium-enriched communities. The distinct patterns in chemistry and microbial community structure observed within just 10-15 cm reflect differences in atmospheric sources of deposited precipitation, with additional effects from post-depositional processes. This environmental filtering decreases local diversity while selecting different species based on initial community composition and local conditions. Understanding these bacterial-physicochemical relationships offers insights into how mountain ecosystems adapt to climate-driven changes in snow cover duration and atmospheric conditions.

1 Introduction

Mountain ecosystems comprise various cryospheric elements, including glaciers, permafrost, and snow. Among these, seasonal snow is the most extensive yet ephemeral component, covering the ground for periods ranging from several weeks to months during the cold season (Barry and Gan, 2022; Vaughan et al., 2013). In the European Alps, elevations above 2,000 m.a.s.l. experience snow cover for about 6.5 months each year, although this duration is decreasing due to climate change

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(Huss and Hock, 2018; Kosolapova and Altshuler, 2024; Marty et al., 2017). This seasonal snow cover performs multiple functions in alpine ecosystems: it lowers surface albedo (Barry and Gan, 2022; Wendler and Kelley, 1988; Zhang, 2005), acts as a ground insulator (Zhang, 2005), and serves as a water reservoir (Barnett et al., 2005; Fayad et al., 2017). Furthermore, snow functions as an interface between the ground and atmosphere, collecting dust, microorganisms, and other biological particles on its surface (Xiang et al., 2009). Atmospheric deposition is the main route by which microorganisms colonise winter seasonal snowpack. In the European Alps, this relationship was demonstrated in a study comparing air and snow microbial communities during the accumulation period at Mount Sonnblick (European Alps, 3,106 m.a.s.l.) (Els et al., 2019). The origin of atmospheric microorganisms varies considerably with geography (Margesin and Miteva, 2011). In the European Alps, local microbial sources such as vegetation, fauna, and anthropogenic activities contribute more substantially to snow microbiome composition at lower elevations, while high-altitude sites receive greater inputs from long-distance transport (Sanchez-Cid et al., 2022; Segawa et al., 2005; Wunderlin et al., 2016).

Once deposited, microorganisms face the challenging conditions of the snowpack environment (Maccario et al., 2015). Snow is a dynamic oligotrophic medium where atmospheric input constitutes the primary external source of nutrients (Kuhn, 2001). Beyond nutrient limitations, snow microorganisms face low temperatures, limited water availability, and frequent structural changes in the snowpack caused by freeze-thaw cycles. At high altitudes, increased ultraviolet radiation promotes photochemical reactions that produce reactive oxygen species (ROS), which can damage cellular components and impose additional oxidative stress on microbial communities (Ezraty et al., 2017; Grannas et al., 2007). Despite these challenging conditions, some microorganisms remain metabolically active within the snowpack (Amoroso et al., 2010; Carpenter et al., 2000; Holland et al., 2020; Lopatina et al., 2013; Price and Sowers, 2004; Rivkina et al., 2000; Zhu et al., 2020), indicating that these environmental stresses act as selective pressures favouring specific microbial taxa adapted to snow environments (Hell et al., 2013; Keuschnig et al., 2023; Larose et al., 2010; Maccario et al., 2014; Segawa et al., 2005). This post-depositional selection process contributes to the differences in the composition between snowpack microbial communities and their atmospheric sources (Els et al., 2020; Hell et al., 2013), as well as between different layers within the snowpack itself.

The larger scope of research in the field of snow microbiology focuses on polar snowpack (Hell et al., 2013; Keuschnig et al., 2023; Larose et al., 2010; Lopatina et al., 2013; Maccario et al., 2014; Malard et al., 2019). However, mid-latitude alpine ecosystems, including the European Alps, differ significantly from polar regions as air temperatures are higher and frequently fluctuate around the melting point, resulting in rapid changes in snowpack structure, depth, and liquid water availability (van Herwijnen et al., 2024). In recent years, several studies focusing on snow microbial communities in the European Alps have been conducted, primarily at high-altitude sites such as Jungfraujoch (3,572 m a.s.l.) and Sonnblick (3,106 m a.s.l.) mountains (Els et al., 2020; Fillinger et al., 2021; Wunderlin et al., 2016). These studies were mostly focused on temporal (seasonal and annual) dynamics in community composition and their relation to airborne microbial communities. However, it is unknown how mountain topography impacts snow chemistry and bacterial communities at the local scale, and how these chemical-microbial patterns evolve within freshly deposited snow.

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In this study, we investigated mid-altitude sites (up to 2,500 m.a.s.l.) in the Swiss Alps during spring. In contrast to previous studies, we sample across 19 closely located sites (within 25 km) along an altitudinal gradient, spanning three adjacent valleys separated by mountain ridges, but receiving the same snowfall events. This provides a unique opportunity to disentangle the impacts of geography from atmospheric deposition patterns. Additionally, we compared the chemical and bacterial community compositions between two layers of the snowpack: the surface layer and the underlying 15 cm depth layer, which allowed us to examine both atmospheric deposition differences and early-stage post-depositional selection processes at the short timescale. Finally, we distinguished the environmental factors that shaped differences in the microbial community composition and identified taxa associated with specific chemical snow gradients.

2 Methods

2.1 Study sites and sampling procedure

Snow samples were collected in late spring (18-19.04.2023) in the Western European Alps (Valais, Switzerland) at elevations between 1,798 and 2,578 m.a.s.l. (Table 1, Fig. 1).

Site	Coordinates	Elevation, m	Valley	Snow depth, cm
H1	45°54.311' 7°06.911'	1798	Val Ferret	101
H2	45°53.424' 7°06.043'	2091	Val Ferret	154
H3	45°52.385' 7°06.257'	2515	Val Ferret	>200
H4	45°52.432' 7°07.361'	2189	Val Ferret	158
H5	45°53.253' 7°07.618'	1985	Val Ferret	123
H6	45°55.671' 7°14.798'	2161	Val de Valsorey	58
H7	45°55.138' 7°15.587'	2382	Val de Valsorey	91
H8	45°55.306' 7°15.664'	2442	Val de Valsorey	132
H9	45°55.279' 7°14.646'	2323	Val de Valsorey	130
H10	45°56.010' 7°13.957'	1938	Val de Valsorey	25
H12	45°55.99' 7°24.616'	2456	Val de Bagnes	39
H13	45°57.351' 7°23.582'	2578	Val de Bagnes	49
H14	45°55.869' 7°21.408'	2387	Val de Bagnes	187
H15	45°55.493' 7°22.529'	2411	Val de Bagnes	99

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H16	45°55.120' 7°23.467'	2456	Val de Bagnes	88
H17	45°57.061' 7°21.518'	1976	Val de Bagnes	34
H11	46°00.876' 7°17.703'	2031	Peripheral	123
H18	45°58.458' 7°13.863'	2077	Peripheral	93
H19	46°00.689' 7°16.092'	2226	Peripheral	177

Table 1. List of sampling sites.

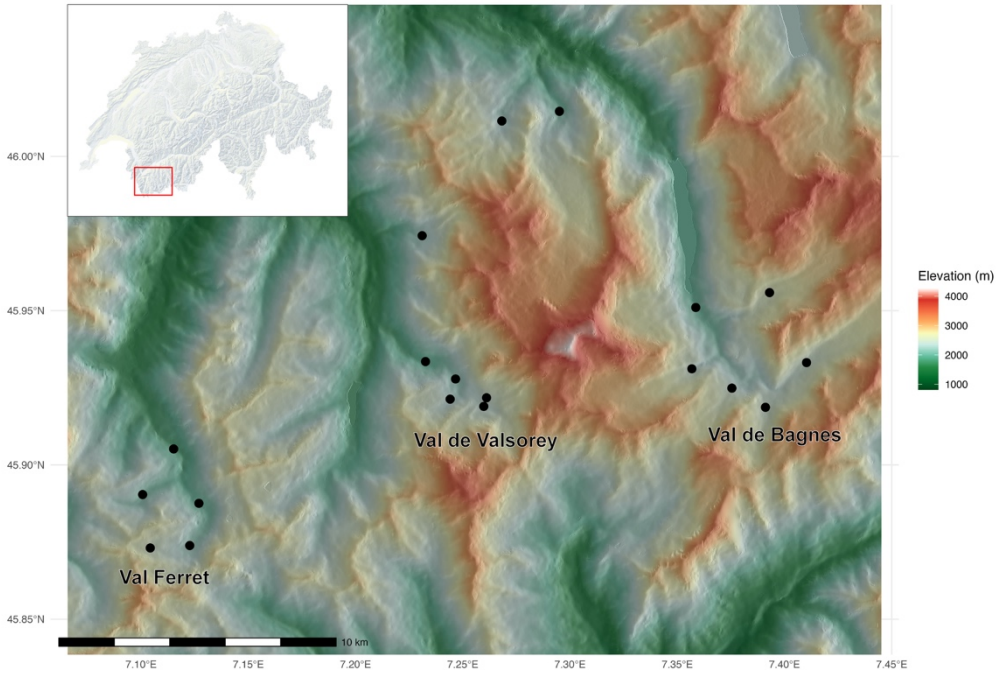

Figure 1. Location of the sampling sites. Elevation data obtained from the USGS 3D Elevation Program (3DEP).

A total of 114 samples were collected at 19 sampling sites. At each sampling site, we collected the surface snow layer (top 2 cm) and bulk snow (10-15 cm deep) in triplicate. Samples were collected with a sterile scoop into sterile whirl-pack bags. One sampling bag was damaged during transportation, resulting in a total of 113. Samples were brought to the laboratory and stored at -20°C until analysed. Before analysis, samples were thawed at 4°C. Additionally, we measured air and snow temperatures at each sampling site, as well as snow depth.

2.2 Chemical analysis

Before chemical analysis, snowmelt water samples (N=113) were filtered with Sterivex 0.22 µm filter units (EMD Millipore Corporation, USA). The anion (F^-, Cl^-, NO_2^-, NO_3^-, Br^-, SO_4^{2-}, PO_4^{3-}) and cation (Na^+, NH_4^+, K^+, Mg^{2+}, Ca^{2+}), as well as

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concentrations of several organic acids (formate, malate, lactate, butyrate, oxalate), were estimated with the use of ion chromatography (Dionex Integrion HPIC System, Thermo Scientific, USA) in the Central Environmental Laboratory (EPFL, Sion).

2.3 Metabarcoding

Bacterial community composition was assessed with sequencing of the full-length 16S rRNA gene. In brief, 150-200 mL of snowmelt water (N=113) was filtered with sterile Sterivex 0.22 µm filter units. DNA was extracted from filters with the DNeasy PowerWater Sterivex kit (Qiagen, Germany) according to the manufacturer's protocol. DNA concentrations were assessed with the Qubit HS DNA kit (Thermo Fisher Scientific, USA). For amplification of the full-length 16S rRNA gene, we used primer set 27f (AGAGTTTGATCMTGGCTCAG) and 1427r (CGGTTACCTTGTTACGACTT) (Zorz et al., 2023). The target sequence was amplified with KAPA HiFi HotStart ReadyMix polymerase (Roche, Switzerland). PCR products were cleaned up with AMPure beads (Beckman Coulter, USA) according to the manufacturer's protocol. DNA concentrations were estimated with the Qubit HS DNA kit. The amplicon DNA was barcoded using the Native Barcoding Kit 96 v14 (SQK-NBD114.96, Oxford Nanopore Technologies, UK). Samples were separated into two batches. Long-read sequencing was performed on a MinION Mk1C device (Oxford Nanopore Technologies, UK) using R10.4.1 flow cells (FLO-MIN114).

2.4 Bioinformatic analysis

Basecalling was performed using Dorado v0.7.2 in super accuracy (sup) mode. Adapter sequences were removed using Porechop v.0.2.4. Quality filtering (Q > 12) and size selection (1300–1800 bp) were performed with Chopper v.0.9.0. Sequences were then dereplicated and clustered into OTUs using Vsearch v.2.22.1 with 97% as the threshold for clustering (cluster_size function) (Rognes et al., 2016). Taxonomic classification of ASVs was carried out on the centroid sequences of the OTUs in QIIME 2 v.2024.10.1 (Bolyen et al., 2019) using the Greengenes2 database (McDonald et al., 2024). The phylogenetic tree was built with QIIME 2 using MAFFT alignment. The resulting OTU and taxonomy tables, along with the phylogenetic tree and metadata table, were then analysed with R (v.4.2.2) and were handled as a phyloseq object (package phyloseq v.1.42.0) (McMurdie and Holmes, 2013). Before statistical analysis, we removed all non-bacterial sequences and blank-related contaminants (package decontam v.1.18.0) (Davis et al., 2018). The OTU table was filtered so that each OTU must be present in at least two samples with a total count of at least 10. The rarefaction curve was created with the microeco package (v.1.14.0) (Supp. Fig. S1) (Liu et al., 2021).

2.5 Statistical analysis

For statistical analysis, we summed concentrations of nitrogen species (NO_2^-, NO_3^-, NH_4^+) as total inorganic nitrogen (TIN) and combined formate, malate, lactate, butyrate, and oxalate as organic acids. Paired comparisons of chemical composition between snow layers were performed using log-transformed chemical data with the Wilcoxon signed-rank test (package stats

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v 4.2.2), p-values were adjusted using the Benjamini–Hochberg procedure to control the false discovery rate (FDR). Spearman's correlation (rcorr function, package Hmisc v.5.2-3) and PCA (rda function, vegan package v.2.6-10) were calculated for log-transformed and scaled chemical variables and elevation. Correlation matrices were visualised with the corrplot function (corrplot v.0.95). PCA plot was visualised with ggplot2 package (v.3.5.2.).

Bacterial community composition was analysed with the phyloseq package. Before analysis, the OTU table was Hellinger transformed. Alpha-diversity metrics were calculated using the phyloseq function estimate_richness. Faith's phylogenetic diversity index was calculated with the calculatePD function (package biomeUtils v.0.022). Bray-Curtis dissimilarity matrix was calculated with vegdist function from vegan package (v.2.6-10), and weighted UniFrac distances were calculated with UniFrac function (phyloseq v.1.42.0). Hierarchical clustering was performed with the agnes function (method = "flexible", par.method = 0.625; package cluster v.2.1.8.2.).

Distance-based redundancy analysis was performed with the capscale function (package vegan v.2.6-10). The best models were selected with an automatic stepwise model selection procedure with the ordistep function (vegan v.2.6-10). Differential abundance analysis at the genus level was performed in relation to TIN and Ca^{2+} concentrations with ANCOM-BC2 (package ANCOMBC v.2.0.3) with p-values adjusted for multiple comparisons using the Holm method. For differential analysis, we used the following parameters: a prevalence threshold of 0.1, a library size cutoff of 1,000 reads per sample, and a smoothing parameter of 0.05. Weighted gene co-expression network analysis (WGCNA) was performed with the package WGCNA (v.1.73) (Langfelder and Horvath, 2008). Before analysis, the OTU table was additionally filtered by removing OTUs whose total abundance across all samples was lower than 0.05. The soft thresholding power was set to 9 based on scale-free topology criteria (R^2 = 0.907), and the minimal module size was set to 100 OTUs. To identify genera enriched within each WGCNA module, we performed a hypergeometric test (phyper function, package stats v. 4.2.2). P-values were adjusted for multiple comparisons using the Benjamini-Hochberg method.

3 Results

3.1 Chemical composition of the alpine seasonal snowpack

To assess the vertical variability in snowpack chemistry, we measured the concentrations of ions, organic acids, and pH in two layers of seasonal snow samples collected from 19 alpine sampling sites in the late spring: the surface snow (top 0-2 cm; n = 57) and the bulk snow (10-15 cm deep; n = 56). The last precipitation events in the area occurred a day before (with air masses transported from the east, over Central Europe) and three days before sampling (with the air masses originating from the Atlantic Ocean and transported from the west) (Supp. Fig. S2, S3).

Paired comparisons of samples from the same sites showed significant differences in chemical composition between surface and bulk snow (Wilcoxon test, $p < 0.05$; Fig. 2a). Total inorganic nitrogen (TIN) was higher in the surface layer, while

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organic acids, Ca^{2+}, PO_4^{3-}, Mg^{2+}, Na^+ and K^+ were higher in the bulk layer. No significant differences were found for pH and SO_4^{2-} (Fig. 2a).

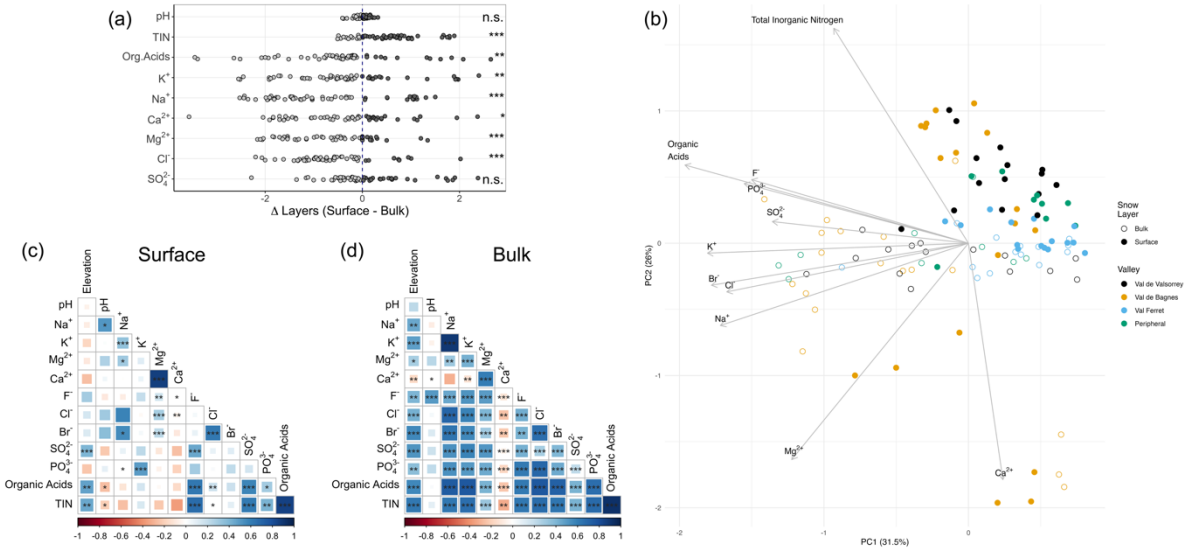

Figure 2. Chemical composition comparison between surface and bulk snow layers. (a) Paired differences in chemical concentrations between surface and bulk snow layers. Positive values indicate higher concentrations in surface snow, and negative values indicate higher concentrations in bulk snow. Statistical significance determined by Wilcoxon signed-rank test with FDR correction. (b) Principal Component Analysis biplot of chemical composition data. Filled circles represent surface snow samples, empty circles represent bulk snow samples, with colours indicating the valley of origin. The *** p < 0.001, ** p < 0.01, * p < 0.05 indicate significance; n.s. indicates not significant. (c, d) Spearman correlations among chemical compounds for surface and bulk layers, respectively. Colour intensity and size indicate correlation strength.

To assess broader patterns in chemical composition, we performed a Principal Component Analysis (PCA) (Fig. 2b). The first two principal components explained 56.78% of the total variance. Samples were separated by snow layer, with differences primarily driven by total inorganic nitrogen (TIN) content. In contrast, no distinct clustering was observed based on the valley of origin. Notably, six samples from a single site, characterised by high calcium concentrations, formed a separate cluster.

To further explore the relationships among chemical compounds in the seasonal snowpack, we performed Spearman rank correlation analysis separately for each snow layer (Fig. 2c and 2d). In the bulk snow, most chemical compounds showed positive correlations with one another and with elevation. Total inorganic nitrogen (TIN) and organic acids were positively correlated with each other, as well as with SO_4^{2-}, PO_4^{3-}, F^-, and elevation in both layers. Calcium exhibited a positive correlation exclusively with Mg^{2+} in both layers, whereas in the bulk snow, it was negatively correlated with most other compounds and with elevation.

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3.2 Bacterial community composition of the seasonal snowpack

To investigate microbial community composition and diversity patterns across snow layers, we performed full-length 16S rRNA sequencing. After quality filtering (see Methods), which removed low-abundance and potentially erroneous sequences, we detected 16,050 OTUs across all samples.

To characterise the overall microbial community composition, we analysed the relative abundances of taxonomic groups across both snow layers (Fig. 3). Five phyla comprised over 90% of the total community in both surface and bulk snow layers, with nearly identical relative abundances: *Pseudomonadota* (mean ± SE: 45.5 ± 1.8%, n = 57 in surface; 45.3 ± 2.68%, n = 56 in bulk), *Bacillota I* (20.4 ± 2.57% in surface, 24.0 ± 3.3% in bulk), *Bacteroidota* (11.5 ± 1.36% in surface, 10.4 ± 1.69% in bulk), *Acidobacteriota* (11.3 ± 1.11% in surface, 10.2 ± 1.34% in bulk), *Actinomycetota* (5.06 ± 0.66% in surface, 6.43 ± 1.28% in bulk).

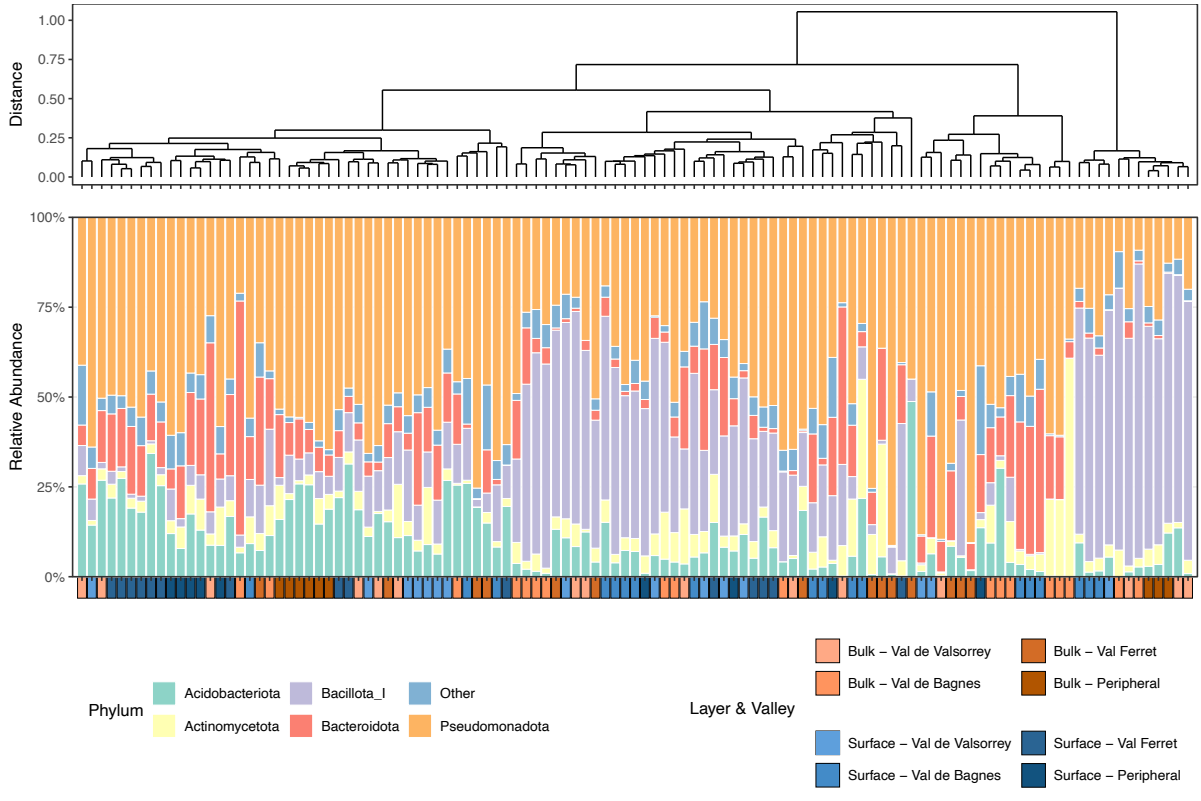

Figure 3. Microbial community composition across alpine snow samples. Top - Hierarchical cluster analysis using weighted UniFrac distances with flexible linkage method; bottom - Relative abundance of major bacterial phyla in surface and bulk snow samples.

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Core microbiome analysis at the genus level revealed greater community specificity, identifying 17 genera in surface snow and 9 genera in bulk snow that were present in at least 50% of samples with a minimum 0.5% relative abundance (Supp. Fig. S4). The core microbiomes of surface and bulk snow largely overlapped, with *Domibacillus* emerging as the only genus exclusive to the bulk snow core microbiome. These core genera exhibited ecological adaptations consistent with survival strategies expected in snow, including several cold-adapted (e.g., *Hymenobacter*, *Sphingomonas*) (Tighe et al., 2025), lichen-associated (e.g., *Lichenibacterium*, *Lichenicola*) (Touchette et al., 2023), and spore-forming taxa (e.g., *Sporosarcina*, *Domibacillus*) (Bauer et al., 2002).

Within-sample diversity analysis revealed systematic differences between snow layers (Fig. 4). Surface snow consistently exhibited higher microbial diversity than bulk snow across multiple metrics. Shannon diversity index was 13% higher in the surface snow layer (mean ± SE: 4.90 ± 0.12) than in the bulk snow layer (mean ± SE: 4.34 ± 0.12; Wilcoxon test, $p < 0.01$). Similarly, inverse Simpson diversity showed a significant difference (surface: 47.04 ± 4.53; bulk: 30.16 ± 3.09; Wilcoxon test, $p = 0.003$), indicating that surface snow not only contains more species but also has more even abundance distributions. At the same time, the differences in Faith's phylogenetic diversity were statistically nonsignificant ($p = 0.06$), suggesting that while surface snow has more species, the evolutionary diversity of communities is similar.

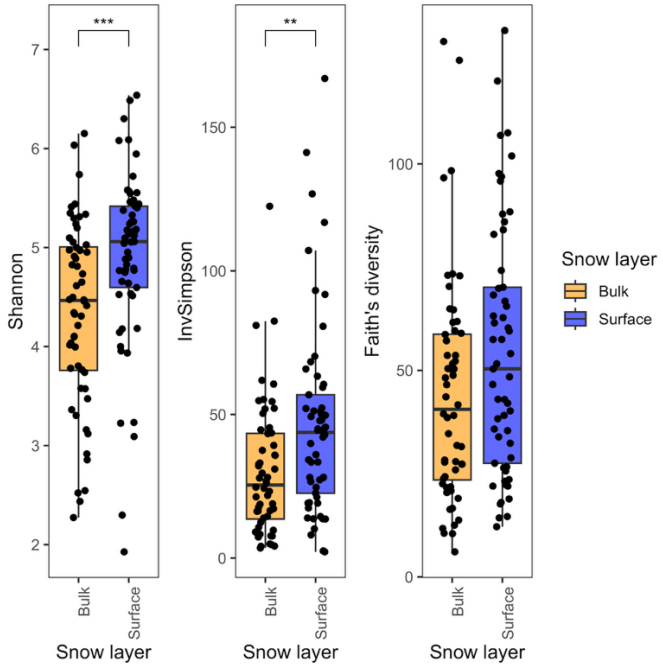

Figure 4. Alpha diversity metrics in surface and bulk snow layers. Boxplots comparing Shannon diversity, inverse Simpson diversity, and Faith's phylogenetic diversity between surface and bulk snow samples. Statistical significance determined by the Wilcoxon signed-rank test (* $p < 0.001$, ** $p < 0.01$).**

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To compare beta-diversity patterns between snow layers, we analysed Bray-Curtis dissimilarity distributions within surface and bulk snow samples. Microbial community dissimilarity was significantly higher between the bulk samples compared to the surface samples (Wilcoxon test, $p < 0.001$), indicating that while surface samples are similar to each other, bulk samples are more dissimilar from one another. Analogous comparison of weighted UniFrac distances confirmed this pattern ($p < 0.001$), indicating greater homogeneity in surface snow communities. Despite these structural differences, cluster analysis using both Bray-Curtis and weighted UniFrac distances did not reveal distinct clusters associated with snow layer or valley of origin (weighted UniFrac, Fig. 3).

3.3 Environmental drivers of bacterial communities in the seasonal snowpack

To identify environmental drivers of microbial community composition, we performed distance-based redundancy analysis (dbRDA) using both weighted UniFrac and Bray-Curtis dissimilarities. For weighted UniFrac distances, stepwise model selection identified TIN, Ca^{2+}, and Mg^{2+} as chemical drivers, explaining 17.5% of phylogenetic variation, with TIN showing the strongest effect (pseudo-F = 9.71, p = 0.001). Including elevation as a candidate predictor significantly enhanced the model, with TIN, Ca^{2+}, elevation, and organic acids explaining 24.0% of the variation (Fig. 5a). For Bray-Curtis distances, models were more complex, with the chemical-only model including six predictors (Ca^{2+}, SO_4^{2-}, PO_4^{3-}, TIN, pH, organic acids) explaining 12.5% of variation, while adding elevation improved model performance to 14.5% (Fig. 5b). Marginal effects analysis of the Bray-Curtis model revealed Ca^{2+}, elevation, and TIN as the strongest predictors (pseudo-F = 2.99, 2.79, and 2.65, respectively, all p = 0.001). Together, these results highlight Ca^{2+} and TIN as important environmental drivers of bacterial community composition in seasonal snow, consistently showing strong influence across both phylogenetic and taxonomic analyses. Elevation also plays a notable role, particularly in shaping the phylogenetic structure of microbial communities (Fig. 5a).

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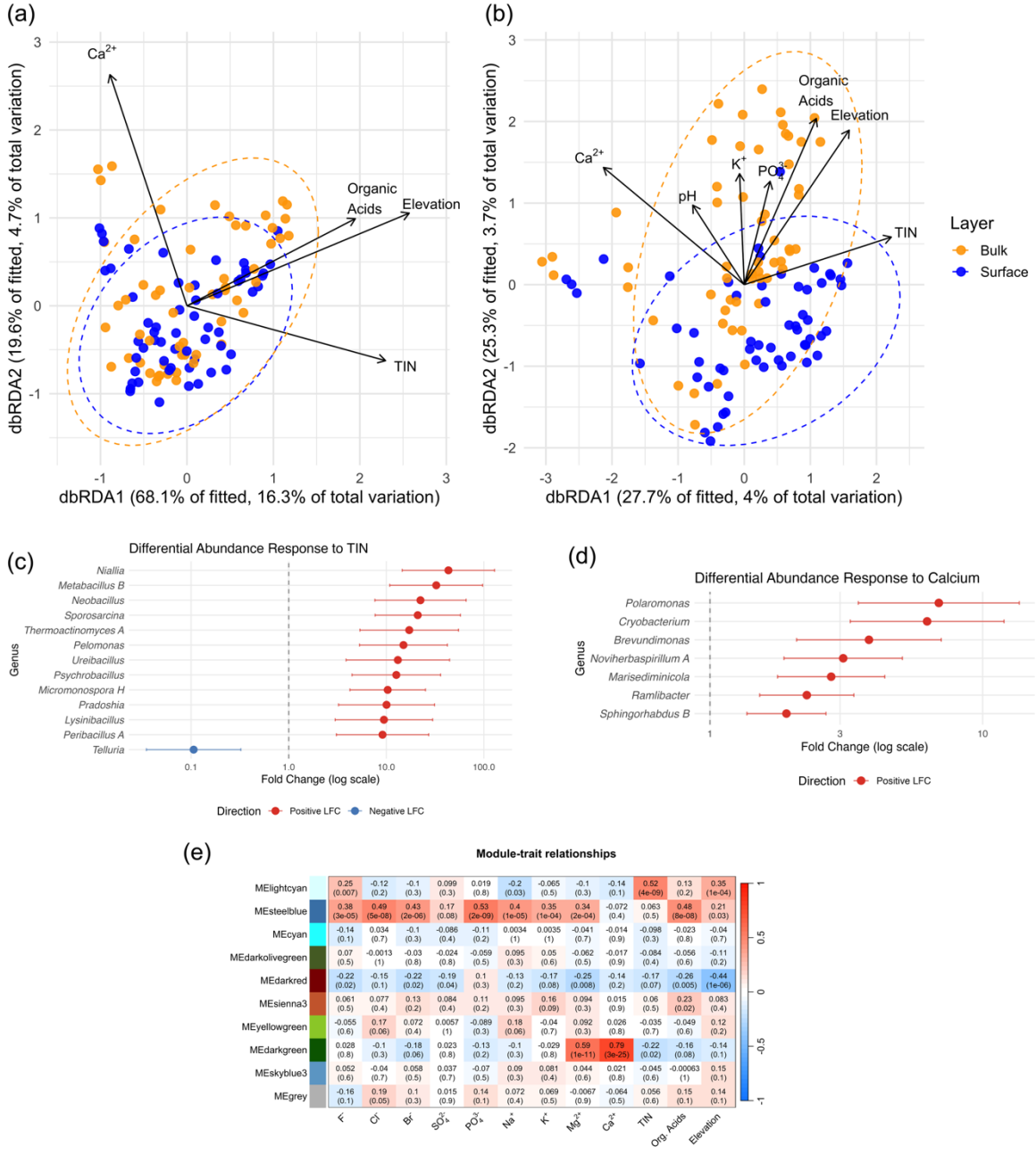

Figure 5. Environmental drivers of microbial community variation. (a, b) Distance-based redundancy analysis (dbRDA) ordination plots using weighted UniFrac (a) and Bray-Curtis (b) distances. (c, d) Fold-change in genus-level abundance associated with total inorganic nitrogen (TIN) and calcium concentrations (ANCOM-BC2 analysis). (e) Weighted gene co-expression network analysis (WGCNA) heatmap showing correlations between microbial modules and environmental factors, values show Pearson correlation coefficients with p-values in parentheses.

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To identify specific taxa driving the observed associations with TIN and Ca^{2+} concentrations, we performed differential abundance analysis using ANCOM-BC2. For TIN concentration, we identified 13 significantly differentially abundant genera (Fig. 5c), with 12 genera showing positive associations and only 1 genus showing a negative association. The positively associated taxa included several genera previously identified as core taxa in surface snow (*Neobacillus*, *Sporosarcina*, *Thermoactinomyces_A*) or both snow layers (*Niallia_299899* and *Pelomonas*). At the same time, *Telluria_571537* was the only genus negatively associated with nitrogen concentration. Similarly, seven bacterial genera showed increased abundance in calcium-rich snow samples (Fig. 5d).

While differential abundance analysis identified individual taxa responding to chemical gradients, we next explored how these taxa are organised into co-occurring groups within the community. To capture these complex environmental interactions, we applied Weighted Gene Co-expression Network Analysis (WGCNA) to identify modules of co-occurring bacterial taxa and their collective responses to chemical variation. The analysis identified nine co-occurrence modules, ranging in size from 105 to 3,952 OTUs, with 56 OTUs remaining unassigned to a module (Table 2). Three modules showed strong and significant correlations with chemical compounds ($|r| > 0.5$, $p < 0.05$; Fig. 5e). Notably, the darkgreen (#5) module (n = 3,626 OTUs) was positively correlated with Ca^{2+} (r = 0.79, p = 3e-25) and was significantly enriched for 19 genera, including three (*Brevundimonas*, *Cryobacterium_381841*, and *Polaromonas*) previously identified in the differential abundance analysis (Table 2). The lightcyan (#1) module (n = 964 OTUs) exhibited the strongest association with TIN (r = 0.52, p = 4e-09) and was enriched in five genera, including three (*Neobacillus*, *Niallia_299899*, and *Sporosarcina*), also detected through the differential abundance analysis (Table 2). Interestingly, the largest module, darkred (#5), showed a significant but weaker negative correlation with elevation (r = -0.44, p = 1e-06) and several chemical compounds, including organic acids (r = -0.26, p = 0.005) (Fig. 5e). This module was enriched in 16 genera, including seven members of the core microbiome, such as *Granulicella_C_415415*, *Terriglobus_A*, as well as lichen-associated genera *Lichenibacterium_504423* and *Lichenicola* (Table 2).

Module	n OTUs	Correlation with environmental factors (r>0.5, p <0.05)	Enriched genera in module (p<0.05)
MElightcyan (#1)	964	TIN (r = 0.52, p = 4e-09)	*Planifilum, Sporosarcina, Neobacillus, Niallia_299899, Lichenicola*
MEsteelblue (#2)	1328	PO_4^{3-} (r = 0.53, p = 2e-09)	*Symbiobacterium, Oceanobacillus_287537, Ureibacillus, Bacillus_BA, Neobacillus, Domibacillus, Niallia_299899*
MEcyan (#3)	224	NA	*Niallia_299899, Hymenobacter_910554*

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MEdarkolivegreen (#4)	126	NA	NA
MEdarkred (#5)	3952	NA	*Sphingomonas_N_483429; Sphingomonas_I, EB88, Friedmanniella, UBA2421, Granulicella_C_416163; LMUY01, Novosphingobium, Polymorphobacter_A_486815, Lichenibacterium_504423, Granulicella_C_416634, Mucilaginibacter_A, Capsulimonas, Granulicella_C_415415, Terriglobus_A, Lichenicola*
MEsienna3 (#6)	115	NA	NA
MEyellowgreen (#7)	114	NA	NA
MEdarkgreen (#8)	3626	Mg^{2+} (r = 0.59, p = 1e-11), Ca^{2+} (r = 0.79, p = 3e-25)	*Telluria_571537, Pedobacter_B_887417, Nocardioides_A_392796, Variovorax, Niastella, Armatimonas, Brevundimonas, Rubellimicrobium, Methylobacterium, Deinococcus_B, Jatrophihabitans_A_372606, Cryobacterium_381841, Chioneia, Sphingomonas_O_486718, Polaromonas, Abditibacterium, Spirosoma, Sphingomonas_L_486704, Hymenobacter_910554*

Table 2. Co-occurrence modules identified by WGCNA with associated environmental factors and enriched genera.

4 Discussion

In this study, we investigated the relationship between bacterial community composition and chemical content of the seasonal snowpack in mid-altitude valleys in the European Alps. To examine how chemical differences between snow layers influence microbial communities, we compared the surface snow layer to the underlying 15 cm depth layer. We demonstrated that both chemical content and bacterial community composition differed between layers, with total inorganic nitrogen (TIN) and calcium concentrations serving as key drivers of both chemical and microbial community differentiation

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between these layers. These findings suggest strong linkages between snowpack chemistry and bacterial community composition in alpine environments.

Analysis of the major ions and several organic acids concentrations in spring snowpack revealed no clear association between snow chemistry and the valley of origin. This suggests that atmospheric transport of air masses from different sources over medium to long distances plays the predominant role in determining snow chemistry at our study sites. However, one site formed a distinct cluster in the PCA analysis due to elevated calcium concentrations, likely reflecting short-range transport of dust eroded from surrounding exposed slopes (Nickus et al., 1998). In contrast, elevation emerged as a significant driver of chemical composition, with higher concentrations of organic acids, sulfate, and TIN at higher elevation sites. This pattern may result from the warmer daytime temperatures at lower elevations that may promote melting that redistributes solutes downward through the snowpack, resulting in lower concentrations compared to high-elevation sites. For comparison, a study analysing complete snowpit profiles in the French Alps (1100-3300 m a.s.l.) found the opposite relationship between elevation and concentrations of nitrate and ammonium; however, this trend was not consistent as the Southern Alps did not follow that pattern (Dambrine et al., 2018).

Comparison between surface and 15 cm depth snow layers revealed significant differences in chemical composition. Surface snow was enriched in TIN but had significantly lower concentrations of most other measured compounds. The differences between snow layers likely originate from the differences in chemical composition of different snowfall events characterised by different air mass sources. Surface snow was influenced by air masses coming from Central Europe's industrialised and densely populated areas (Suppl. Fig. S3). This explains the higher concentrations of nitrogen species, which correlated positively with sulphate, as both nitrogen and sulphate compounds are commonly associated with anthropogenic pollution (Filippa et al., 2010; Greilinger et al., 2016; Novak et al., 2025). In contrast, the bulk snow layer is probably linked to earlier snowfall events related to air masses transported over the Atlantic Ocean and Western Europe, with higher levels of calcium, chloride, and potassium often associated with marine sources (Suppl. Fig. S3) (Filippa et al., 2010; Möller, 1990). Additionally, the variation in the concentrations may be conditioned not only by the differences in the chemical content of the initially deposited snow but also be associated with processes occurring after the deposition. For example, the lower TIN concentrations in the 15 cm depth snow layer may reflect losses of nitrogen species through photolysis and volatilisation caused by prolonged UV exposure (Jacobi and Hilker, 2007; Trachsel et al., 2019), as well as biological uptake of TIN. The strong positive correlation between major ions and organic acids in the deeper snow layer may reflect post-depositional redistribution processes occurring in the snowpack (Raben and Theakstone, 1994).

Similar to the chemical composition patterns, the valley of origin did not influence bacterial community composition, while differences between snow layers were pronounced. Surface snow contained twice as many bacterial genera in the core community as bulk snow, with nearly complete overlap, showing higher diversity and greater cross-site similarity. The reduced diversity and increased between-site variability in bulk snow suggest that post-depositional selection reduces local diversity while selecting for different species based on variations in initial community composition and local conditions.

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Post-depositional selection towards snow-specific communities was previously demonstrated for Greenland snow-ice communities, accompanied by changes in the functional profile of the communities (Maccario et al., 2019).

We consistently identified calcium and TIN as key drivers of microbial community composition and structure. We identified 964 OTUs associated with elevated TIN levels, with the genera *Neobacillus*, *Niallia*, and *Sporosarcina* being identified as drivers of these nitrogen-enriched bacterial communities. All three genera are spore-forming bacteria, an adaptation that enables them to survive in the harsh environmental conditions associated with aerial transport and subsequent deposition in the snowpack (Maccario et al., 2015). Additionally, the genus *Sporosarcina* includes psychophilic species that remain active in cold environments (e.g., ice), which may explain their positive correlation with TIN, necessary for metabolic activity under such challenging conditions (Bakermans and Skidmore, 2011; Yadav et al., 2016). In Arctic snowpack, nitrogen was shown to be the limiting factor for bacterial growth and activity, with assimilation serving as the primary N cycling pathway (Larose et al., 2013).

A much larger set of OTUs (3,626 OTUs) was associated with high calcium levels, as well as magnesium. These ions are associated with the mineral particles, the concentration of which is positively correlated with the bacterial deposition from the atmosphere to the snowpack (Keuschnig et al., 2023). The high number of OTUs positively associated with calcium may reflect the diversity of bacteria that were deposited together with the dust particles. A positive correlation between calcium and bacterial abundance was demonstrated previously in melted snow (Margesin and Miteva, 2011). We identified three genera that were consistently identified as drivers of these calcium-enriched microbial communities: *Brevundimonas*, *Cryobacterium*, and *Polaromonas* – all previously identified in snow communities (Harding et al., 2011; Hell et al., 2013; Segawa et al., 2005; Yan et al., 2012; Zhang et al., 2010, 2012). Notably, *Brevundimonas* species have been identified as most abundant in microbial communities from alpine ice caves, a habitat characterised by constant low temperatures and high calcium concentrations, where these bacteria remain metabolically active and participate in the precipitation of calcium carbonate (Lange-Enyedi et al., 2024).

5 Conclusions

Seasonal snowpack serves as a dynamic medium that accumulates atmospheric particles and microorganisms, creating unique microbial habitats in alpine environments. In this study, we examined bacterial community composition and chemical properties in seasonal snowpack across 19 sites in three adjacent Swiss Alpine valleys. Our findings demonstrate that snow layer differences, rather than geographic location, drive both chemical composition and bacterial community structure within alpine snowpack. Surface snow exhibited higher bacterial diversity and greater cross-site similarity compared to bulk snow at 15 cm depth, reflecting distinct atmospheric sources and post-depositional selection processes that operate at centimetre scales. Total inorganic nitrogen and calcium emerged as key environmental drivers of community structure, with spore-

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forming genera (*Neobacillus*, *Niallia*, *Sporosarcina*) associated with nitrogen-enriched surface communities and cold-adapted genera (*Brevundimonas*, *Cryobacterium*, *Polaromonas*) linked to calcium-rich environments.

Future research incorporating functional annotation and assessment of the community's activity may improve our understanding of post-depositional selection and reveal differences and similarities in bacterial activity in alpine snowpack compared to the more extensively studied snowpack of polar regions. Additionally, inclusion of fungi, non-fungal eukaryotes such as protists and algae, and viruses could provide a more comprehensive understanding of microbial diversity and ecological interactions within alpine snowpack ecosystems.

Code availability

The code is available on the GitHub repository (https://github.com/a-kosolapova/alpine-snow-microbiome-2023) and was published on Zenodo (10.5281/zenodo.17249709).

Data availability

The 16S rRNA sequencing data used in this study are uploaded to the European Nucleotide Archive (Project PRJEB94184).

Author contribution

Conceptualisation: AK, IA; funding acquisition: IA; investigation: AK, RC, CL, IA; data analysis and visualisation: AK, FR; writing – original draft: AK; writing – review and editing: AK, RC, FR, CL, IA.

Competing interests

The authors declare that they have no conflict of interest.

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