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Spatial variation of bacterial communities in seasonal snow across northeastern and northwestern China

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Abstract. Seasonal snow is a transient microbial habitat that can contribute to nutrient cycling, yet bacterial community variation across mid-latitude seasonal snowpacks remains poorly understood. We examined bacterial diversity, community composition, environmental associations, assembly processes, niche breadth, and co-occurrence network structure using 16S rRNA gene sequencing and environmental measurements from 49 surface snow samples in northeastern (NE) and northwestern (NW) China. Our results showed that NE snow had higher bacterial richness and wider niche breadth, whereas NW snow showed greater among-site variation in community composition. Several Bacteroidia lineages were more abundant in NW snow. Community similarity declined with geographic distance in both regions, with a stronger relationship in NE. Total organic carbon's association with bacterial community composition mainly reflected regional environmental contrasts, whereas Ca^{2+} remained associated with composition after accounting for region, suggesting possible mineral dust deposition. Stochastic processes overall made a greater contribution in NE than in NW. Among the individual processes, homogeneous selection contributed more in NE, whereas heterogeneous selection was more prominent in NW, and dispersal limitation was the largest individual process in both regions. Greater environmental variation among NW sites may have contributed to stronger heterogeneous selection. The NW network was larger and denser and contained more connectors, while the NE network was more modular. Greater network complexity in NW did not increase robustness to random node removal, and both networks were most sensitive to the loss of high-degree nodes. These findings show that regional environmental variation and spatial structure jointly shape bacterial community assembly and network organisation in seasonal snow.

1 Introduction

Seasonal snow is a widespread but temporary component of the cryosphere. It stores winter precipitation, insulates the ground, and regulates exchanges between the atmosphere and land surface (Kuhn, 2001; Zhang, 2005; Miteva, 2008). Despite low temperatures and limited liquid water and nutrients, snowpacks harbour diverse microbial communities, and some members remain metabolically active below 0 °C (Amoroso et al., 2010; Hell et al., 2013; Holland et al., 2020). This

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activity contributes to nutrient transformations and can alter meltwater chemistry before the water reaches soils and surface waters (Larose et al., 2013a; Larose et al., 2013b; Segawa et al., 2014; Lazzaro et al., 2015).

Snow microbial communities are shaped first by atmospheric inputs and then by conditions within the snowpack. Snowfall and dry deposition introduce airborne microorganisms into snowpacks, including microorganisms transported over long distances (Els et al., 2019). Mineral dust also carries microorganisms into snowpacks. It can settle directly or be captured by falling snow, and the community it carries depends on air-mass origin and transport history (Chuvochina et al., 2011; Azzoni et al., 2018). After deposition, microorganisms change in response to temperature, liquid water, resources, and ionic composition, which influence persistence and relative abundance (Hauptmann et al., 2014; Lopatina et al., 2016; Maccario et al., 2019; Kosolapova et al., 2026). Atmospheric deposition provides much of the initial microbial pool, while conditions within the snowpack influence its subsequent composition. Diverse and cold-adapted bacteria have been reported from Arctic, Antarctic, and alpine snowpacks (Wunderlin et al., 2016; Bourquin et al., 2022). Their composition nevertheless varies among regions and sites, across snow layers and snowfall events, and during snowmelt (Segawa et al., 2005; Hell et al., 2013; Møller et al., 2013; Maccario et al., 2019; Kosolapova et al., 2026). Source signatures can also remain detectable. Snow over sea ice may contain marine taxa, while mineral dust can introduce soil bacteria into alpine snow (Liu et al., 2009; Maccario et al., 2019).

Research on snow microbiomes has focused mainly on polar and high-elevation environments (Bourquin et al., 2022). Many studies have tracked temporal changes within individual snowpacks or glaciers, while broader spatial surveys have often been limited to local elevation gradients (Maccario et al., 2014; Wunderlin et al., 2016; Chen et al., 2022). Less is known about short-lived seasonal snowpacks at low and moderate elevations, where temperature, physical structure, and liquid-water availability can change rapidly (Kosolapova et al., 2026). These snowpacks also receive variable terrestrial and anthropogenic inputs, yet regional patterns in their bacterial communities remain poorly documented. Previous snow studies have mainly described bacterial composition and its relationships with environmental conditions. The processes underlying regional community differences remain less well understood. Microbial community assembly is governed by deterministic selection and stochastic processes, including ecological drift and dispersal (Sloan et al., 2006; Ning et al., 2019), whose relative importance can change with environmental variation and spatial structure (Chase, 2010; Mo et al., 2021). Co-occurrence networks provide a complementary view of associations among taxa, but regional studies of seasonal snow have rarely examined network structure alongside assembly processes.

Here, we compared bacterial communities in seasonal snow collected from multiple sites across northeastern and northwestern China. We aimed to reveal (i) the spatial patterns of snow physicochemical properties and bacterial diversity composition across the two regions, (ii) the environmental variables associated with snow community composition and whether these associations remained after accounting for region, and (iii) the spatial patterns of community assembly processes and co-occurrence network structure between NE and NW snow.

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2 Materials and Methods

2.1 Site description and sampling

In January 2018, 25 snow samples were collected across Xinjiang in northwestern China. Between December 2020 and January 2021, 24 samples were collected from Heilongjiang, Jilin, and northeastern Inner Mongolia in northeastern China. At each site, the upper 0–5 cm of snow was collected with a stainless-steel scoop treated with 75% ethanol and ultraviolet light. Where snow depth was less than 5 cm, a shallower layer was sampled to avoid contact with soil. Snow was transferred to sterile plastic sampling bags (Nasco, WI, USA). Samples for microbial analysis remained frozen and protected from light until DNA extraction. Sampling dates, locations, elevations, and field measurements are provided in Table S1. Meteorological conditions included air temperature, wind speed, and relative humidity, while snowpack measurements included snow temperature and density.

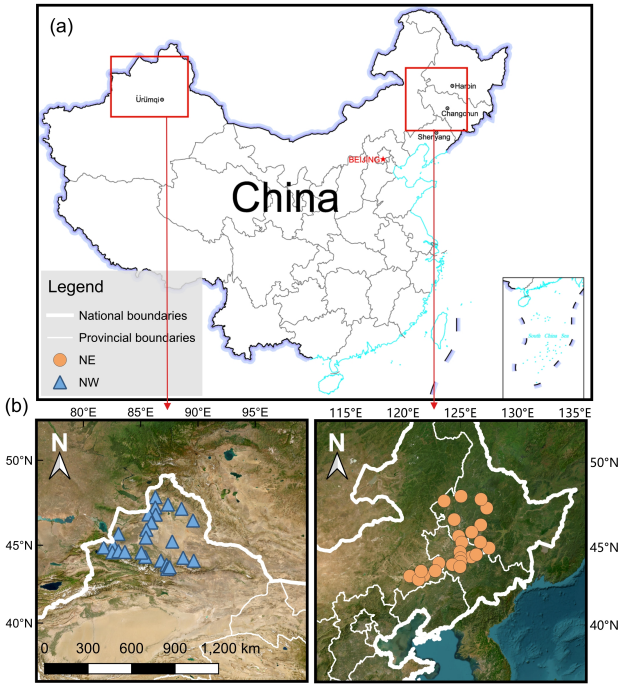


Figure 1: Geographic locations of snow sampling sites in NE and NW China. The basemap used in the sampling location map is derived from Esri World Imagery (Esri, Vantor, Earthstar Geographics, and the GIS User Community | Powered by Esri), https://server.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer. The map of China is based on the standard map from the Standard Map Service of the Ministry of Natural Resources of the People's Republic of China [No. GS(2019)1673], http://bzdt.ch.mnr.gov.cn/. Maps produced in QGIS.

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2.2 Total organic carbon and water-soluble ion analyses

Meltwater was passed through 0.45 μm polytetrafluoroethylene (PTFE) membrane filters before chemical analysis. Total organic carbon (TOC) was measured with an Aurora 1030W total carbon analyser (OI Analytical, USA). Concentrations of the cations Li^+, Na^+, NH_4^+, K^+, Mg^{2+}, and Ca^{2+} and the anions Cl^-, NO_3^-, SO_4^{2-}, F^-, and NO_2^- were quantified with an ICS 5000+ ion chromatography system (Thermo Scientific, USA) equipped with a conductivity detector and configured for a dual-channel system. Anions were separated using a Dionex IonPac AG22 guard column and a Dionex IonPac AS22 analytical column with 18 mM potassium hydroxide as the eluent. Cations were separated using a Dionex IonPac CG12A guard column and a Dionex IonPac CS12A analytical column with 20 mM methanesulfonic acid as the eluent. Both channels were operated at a flow rate of 1.0 mL min^{-1}. Ultrapure-water blanks were analysed before and after each analytical batch to monitor for potential contamination. Li^+, F^-, and NO_2^- were below their respective detection limits and were excluded from subsequent analyses.

2.3 DNA extraction, Illumina sequencing, and sequence analysis

Total genomic DNA was extracted from the snow samples with a MagPure Soil DNA LQ Kit (Magen, Guangdong, China) following the manufacturer's instructions. DNA concentration and integrity were assessed with a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, USA) and agarose gel electrophoresis, respectively. The V3–V4 region of the bacterial 16S rRNA gene was amplified in 30 μL PCR reactions using primers 343F (5′-TACGGRAGGCAGCAG-3′) and 798R (5′-AGGGTATCTAATCCT-3′). Reverse primers contained sample-specific barcodes, and both primers carried Illumina sequencing adapters. Amplicon quality was checked by agarose gel electrophoresis. PCR products were purified with Agencourt AMPure XP beads (Beckman Coulter Co., USA), quantified with a Qubit dsDNA assay kit, normalised, and sequenced on an Illumina NovaSeq 6000 platform with 2 × 250 bp paired-end reads (Illumina Inc., San Diego, CA, USA; OE Biotech Company, Shanghai, China).

Paired-end reads were preprocessed with Trimmomatic (Bolger et al., 2014) to remove ambiguous bases and low-quality sequences. Reads with a sliding-window mean quality score below 20 were discarded. The remaining reads were merged with FLASH (Reyon et al., 2012) using a minimum overlap of 10 bp, a maximum overlap of 200 bp, and a maximum mismatch rate of 20%. Reads with ambiguous bases, homologous sequences, or length shorter than 200 bp were discarded. Reads with at least 75% of bases above Q20 were retained. Chimeras were detected and removed using QIIME v1.8.0 (Caporaso et al., 2010). Clean reads were subjected to primer removal and clustered into OTUs at 97% sequence similarity using VSEARCH (Rognes et al., 2016). Representative sequences were selected in QIIME and assigned against SILVA v132 with the RDP classifier at a 70% confidence threshold (Wang et al., 2007).

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2.4 Co-occurrence network construction

Bacterial co-occurrence networks were constructed separately for NE and NW using igraph. The unrarefied OTU table was first filtered across all 49 samples and was then divided by region. OTUs were retained when their mean relative abundance was at least 0.01% and they occurred in at least 10 samples. Pairwise Spearman correlations were calculated within each region. Correlations with $|\rho| \geqslant 0.80$ and Benjamini-Hochberg adjusted $p < 0.001$ were retained. Nodes represented OTUs and edges represented retained correlations. Networks were visualised in Gephi v0.10.1, and modules were identified with the Walktrap algorithm applied to the unweighted network topology.

Network structure was described by node and edge counts, mean degree, density, diameter, mean path length, mean clustering coefficient, and modularity. Degree, betweenness centrality, and harmonic centrality were calculated for each node and compared between regions with Wilcoxon rank-sum tests. Within-module connectivity (Zi) and the participation coefficient (Pi) were used to classify nodes as network hubs (Zi > 2.5, Pi > 0.62), module hubs (Zi > 2.5, Pi ≤ 0.62), connectors (Zi ≤ 2.5, Pi > 0.62), or peripheral nodes (Zi ≤ 2.5, Pi ≤ 0.62) (Deng et al., 2012). Network hubs, module hubs, and connectors were considered potential keystone nodes.

Structural robustness was evaluated from weighted natural connectivity in igraph. Edge weights in the adjacency matrix were the absolute Spearman correlation coefficients. Nodes were removed in 1% increments until 50% of each network had been removed. Random removal used 1,000 independent removal orders. For targeted removal, nodes were ranked by degree or betweenness in the intact network and removed in descending order. Natural connectivity at each step was divided by its intact-network value, and the area under each removal curve (AUC) summarised the decline. Within each region, targeted AUCs were compared with the random-removal distribution using one-sided empirical p values. Regional differences under random removal were assessed with 1,000 Monte Carlo comparisons of NW minus NE AUC. We report the mean difference, its 95% percentile interval, and the proportion of positive differences.

2.5 Statistical analysis

For alpha-diversity analyses, the OTU table was rarefied to 23,193 reads per sample. Chao1 richness, Shannon diversity, and Simpson diversity were calculated from the rarefied table, with natural logarithms used for Shannon diversity. Sampling completeness was assessed with Good's coverage. OTU richness at 92% sample coverage ($q = 0$) was estimated with *estimateD* in iNEXT. Regional differences in environmental variables, alpha diversity, and taxon relative abundances were assessed using two-sided Wilcoxon rank-sum tests. Benjamini-Hochberg adjustment was applied separately to the 15 environmental variables, the three alpha diversity indices, and taxa at each taxonomic rank. For taxonomic comparisons, rarefied OTU counts were aggregated at class, order, family, and genus levels before analysis with ALDEx2. Unclassified taxa and taxa with fewer than 50 total reads or present in less than 10% of samples were excluded. The analysis used 128 Monte Carlo Dirichlet instances and all features as the denominator. Wilcoxon p values were adjusted using the Benjamini-Hochberg method.

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Community composition was visualised by principal coordinate analysis (PCoA) of unweighted UniFrac distances with an additive correction. Regional differences in community composition and multivariate dispersion were tested with PERMANOVA and PERMDISP using 9,999 permutations. Redundancy analysis (RDA) was performed on Hellinger-transformed OTU data from the 42 samples with complete environmental measurements. TOC and dissolved ion concentrations were log1p-transformed, and all predictors were standardised. Predictors with $|r| \geq 0.7$ were removed, and variance inflation factors (VIF) were used to assess collinearity among the remaining variables. Forward selection was performed with *ordiR2step*, using permutation significance and the adjusted R^2 of the full candidate model as stopping criteria. The selected model, constrained axes, and individual terms were tested with 9999 permutations. Contributions of the selected variables were estimated by hierarchical partitioning of adjusted R^2. Partial RDA controlled for region. Additional models assessed the effects of missing values and sample XJ.Q402 (Table S5).

Distance decay relationships were examined separately for NE and NW. Unweighted UniFrac similarity was regressed against geographic distance using ordinary least squares. Similarity was calculated as $100 \times (1 - d)$, and geographic distance was obtained with the Haversine formula. Mantel tests with 9999 permutations evaluated the spatial relationships, and the two regional p values were adjusted by the Benjamini-Hochberg method. The relative contributions of five ecological processes shown in Fig. 4e were estimated by null-model analysis. The neutral community model was fitted separately for NE and NW. Confidence intervals for R^2, the immigration parameter m, and the regional difference in m were obtained from 2,000 sample-level bootstrap replicates. The modified stochasticity ratio (MST) was calculated from Bray-Curtis dissimilarity weighted by abundance using the PF null model and 1000 randomizations. A value of 0.5 separated stochastic from deterministic assembly. Confidence intervals and regional differences were estimated with *nst.boot* using 9999 bootstrap replicates. Standardized Levins niche breadth was calculated for each OTU, and sample-level values were weighted by OTU relative abundance. OTUs with a total regional relative abundance above 0.01% were retained. Analyses were repeated using OTUs shared between regions and prevalence thresholds of 5%, 10%, and 20%. Environmental dispersion was calculated for 48 complete samples from TOC, air temperature, Ca^{2+}, NO_3^-, and relative humidity. These variables were transformed and standardised as for the RDA. Euclidean distances to regional medians were calculated with *betadisper*, and regional differences were tested using 9999 permutations.

3 Results and Discussions

3.1 Regional divergence in snow bacterial diversity and composition

Several snow physicochemical properties differed between regions (Table S1, Text S1). TOC and NH_4^+concentrations were higher in NE snow than in NW snow (Wilcoxon tests, both adjusted $p < 0.05$). Mg^{2+}, K^+, and SO_4^{2-} concentrations also differed significantly between regions (Wilcoxon tests, both adjusted $p < 0.05$). Their median concentrations were higher in NE snow, but the unusually high values for XJ.Q402 raised their NW means above the NE means (Text S1). After rarefaction to 23,193 reads per sample, the 49 samples yielded 19,578 bacterial OTUs (Fig. S1). Coverage based richness

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curves for both regions are shown in Fig. S2a. Chao1 richness was higher in NE than in NW snow (3946 ± 943 vs. 2171 ± 1021, adjusted $p < 0.001$; Fig. 2a), and Shannon diversity followed the same pattern (6.30 ± 0.70 vs. 5.68 ± 0.96, adjusted $p = 0.020$; Fig. 2b). Simpson diversity did not differ between regions (0.986 ± 0.017 vs. 0.978 ± 0.035, adjusted $p = 0.653$; Fig. 2c). At a common sample coverage of 92%, $q = 0$ richness remained higher in NE snow (2165 vs. 968, adjusted $p < 0.001$, Fig. S2b). NE contained more rare and moderately abundant OTUs, while both regions contained the same number of dominant OTUs (Fig. S3, Table S2). Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes, and Gemmatimonadetes together accounted for 97.8% of sequences in NE snow and 91.6% in NW snow (Fig. 2d). The first four phyla have also been reported from alpine, Arctic, Antarctic, and Tibetan Plateau snow (Hell et al., 2013; Lopatina et al., 2013; Møller et al., 2013; Hauptmann et al., 2014; Cameron et al., 2014; Chen et al., 2022). Regional differences became clearer at lower taxonomic levels, potentially reflecting variation in deposited microbial inputs and post-depositional filtering. Cyanobacteria were rare in both regions and accounted for 0.08% of the NE community and 0.11% of the NW community. These proportions were lower than those reported for several Arctic, alpine, and Tibetan Plateau snowpacks (Møller et al., 2013; Wunderlin et al., 2016; Chen et al., 2022), but similarly low abundances were observed in other mid-latitude mountain snow (Azzoni et al., 2018). Cyanobacteria are often more abundant in wet snow, glacier ice, and cryoconite, where liquid water and light can support growth, aggregation, and nitrogen fixation (Jungblut et al., 2010; Wunderlin et al., 2016; Rozwalak et al., 2022; Wejnerowski et al., 2023). This pattern suggests that the low abundance of Cyanobacteria in our samples was associated with the characteristics of seasonal snow as a relatively dry and short-lived habitat. The limited availability of liquid water may have reduced conditions favorable for active growth, while the short duration of snow cover may further constrain the accumulation of Cyanobacteria within the snowpack.

At the class level, Bacteroidia represented 30.94% of sequences in NW snow and 13.54% in NE snow ($\log_2$FC = −1.19, adjusted $p < 0.001$; Fig. 2e). Several lineages within Bacteroidales contributed to this difference. Muribaculaceae accounted for 10.18% of sequences in NW and 1.98% in NE, and Rikenellaceae was also more abundant in NW. The genera *Alistipes* and *Alloprevotella* showed the same regional pattern (all adjusted $p < 0.01$; Table S3). These taxa were present in every sample, but their relative abundances differed between regions. Some Bacteroidales were detected in vertebrate gut communities (Grond et al., 2018; Kreisinger et al., 2017), and vertebrate inputs can affect the bacterial and chemical composition of Arctic spring snow (Sułowicz et al., 2026). Local animal inputs may therefore have contributed to the higher relative abundance of these lineages in NW snow.

At the order level, Bacteroidales, Clostridiales, Betaproteobacteriales, Sphingomonadales, Enterobacteriales, and Rhizobiales together represented about half of the bacterial sequences in both regions (Fig. S4a). Enterobacteriales accounted for 9.19% of sequences in NE snow and 1.44% in NW snow (adjusted $p < 0.001$; Fig. S4b). Members of Enterobacteriaceae (order Enterobacteriales) have been recovered from bioaerosols near wastewater treatment plants and an urban river, so anthropogenic bioaerosols could be one possible source of the higher NE abundance (Gotkowska-Płachta et al., 2013; Medina et al., 2021). Rhizobiales also differed between regions, accounting for 7.57% of sequences in NE snow and 2.46% in NW snow (adjusted $p < 0.001$; Fig. S4b). In an Arctic snowpack, Rhizobiales was abundant in the overlying atmosphere

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but declined after deposition and with increasing snow depth (Maccario et al., 2019). This observation suggests that atmospheric deposition can introduce Rhizobiales into snow, while conditions within the snowpack may alter their relative abundance after deposition. Some Rhizobiales have also been isolated from lichens (Pankratov et al., 2020). Lichen fragments transported by wind may provide another terrestrial source. Sphingomonadales was abundant in both regions but more abundant in NE (adjusted p = 0.021; Fig. S4b). Sphingomonadaceae (order Sphingomonadales) have been detected throughout alpine snowpacks, and some glacier isolates form biofilms and grow under a broad range of conditions (Wunderlin et al., 2016; Han et al., 2025). These traits may support persistence after deposition. Overall, the taxonomic composition indicates contributions from multiple sources, followed by changes within the snowpack.

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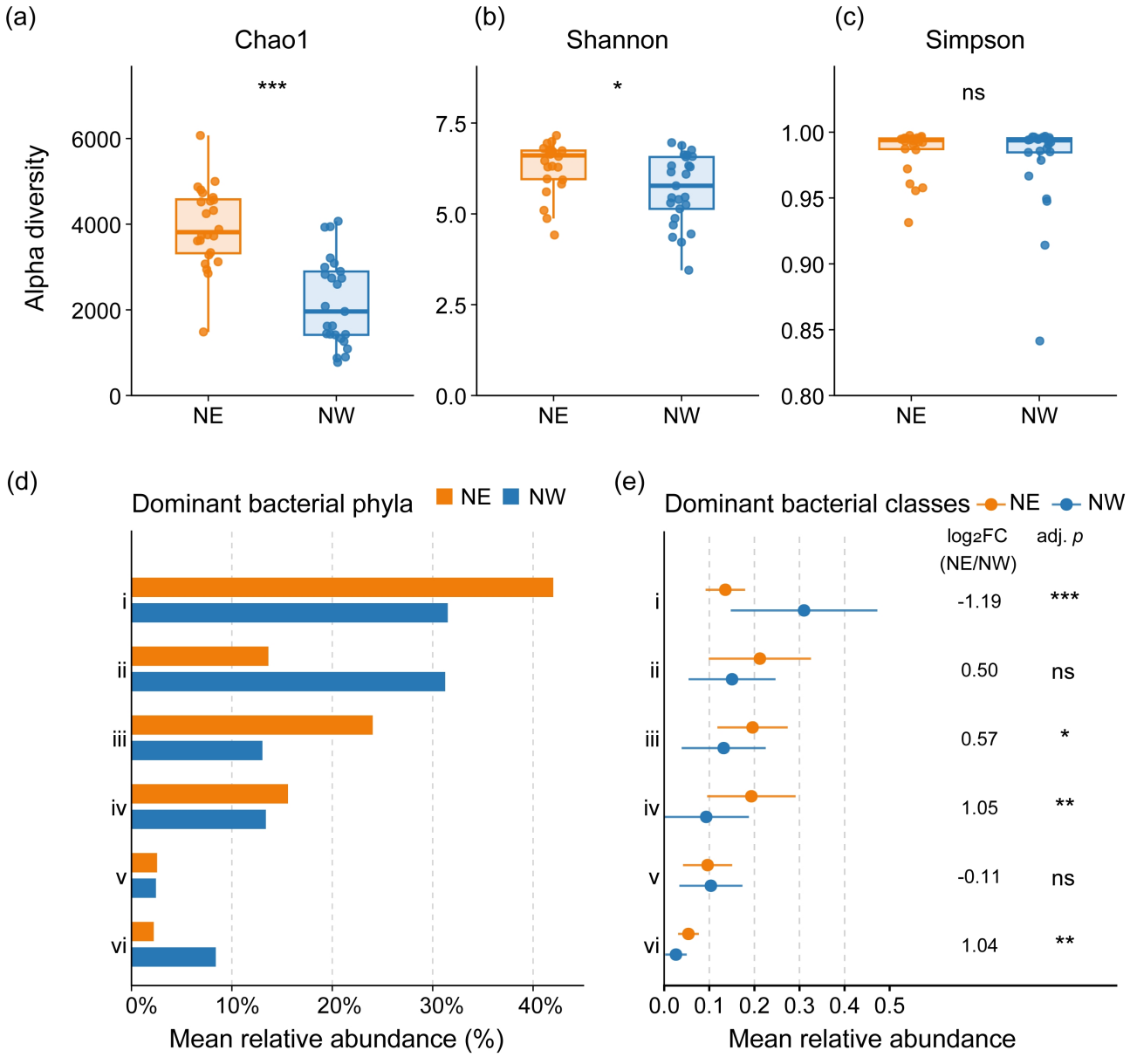


Figure 2: Bacterial alpha diversity and taxonomic composition in NE and NW snow. (a, b, c) Chao1 richness, Shannon diversity, and Simpson diversity, respectively. Boxes show medians and interquartile ranges, and points represent individual samples. (d) Mean relative abundances of five major bacterial phyla and Others, shown as paired horizontal bars. Rows i to vi represent Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes, Gemmatimonadetes and Others, respectively. (e) Mean relative abundances of the six dominant bacterial classes. Rows i to vi represent Bacteroidia, Gammaproteobacteria, Alphaproteobacteria, Actinobacteria, Clostridia and Bacilli, respectively. Points show means, and horizontal lines show mean ± SD. Orange and blue represent NE and NW, respectively. *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

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3.2 Environmental drivers of bacterial community variation

Bacterial community composition differed between NE and NW snow (PERMANOVA, pseudo-F = 6.92, R^2 = 0.128, p < 0.001; Fig. S5a), and NW samples showed greater within-region variation (PERMDISP, F = 69.26, p < 0.001; Fig. S5b). After highly correlated predictors were removed, forward selection retained TOC, air temperature, Ca^{2+}, NO_3^-, and relative humidity (Fig. 3a and b). The final RDA model explained 29.3% of the total variation in bacterial community variation (adjusted R^2 = 0.194, pseudo-F = 2.977, p < 0.001; Table S4). RDA1 and RDA2 accounted for 15.4% and 5.6% of the total variation, respectively (Fig. 3a). TOC contributed 50.5% of the constrained variation, followed by Ca^{2+} at 19.0%, air temperature at 13.6%, NO_3^- at 11.6%, and relative humidity at 5.3% (Fig. 3b). However, the marginal association of relative humidity in the full model was not significant in the full model (p = 0.055).

Partial RDA distinguished associations within regions from the broader difference between NE and NW snow. After controlling for region, the environmental variables explained 16.9% of the variation in community composition (adjusted R^2 = 0.075, pseudo-F = 1.758, p < 0.001). Air temperature, Ca^{2+}, NO_3^-, and relative humidity remained significant, while TOC was no longer significant (p = 0.724; Table S4). Thus, its association in the full RDA was mainly linked to the environmental contrast between regions, while the other four variables were also associated with variation among samples within regions. Sensitivity analyses examined the effects of missing data and unusual snow chemistry. Relative humidity was unavailable for XJ. Q427. Model fit changed little when this variable and the corresponding sample were included or excluded (n = 48 and 49, adjusted R^2 = 0.182 and 0.171, pseudo-F = 3.086 and 3.481, respectively, both p < 0.001; Table S5). XJ.Q402 had markedly higher concentrations of several major ions than the other samples (Table S1). Its removal had little effect on model fit when the same predictors were retained (adjusted R^2 = 0.197, pseudo-F = 2.962, p < 0.001). When forward selection was repeated without XJ.Q402, only TOC, air temperature, and wind speed were retained (adjusted R^2 = 0.171, pseudo-F = 3.744, p < 0.001; Table S5). The overall association between the measured environment and community composition remained, but the selection of Ca^{2+} and NO_3^- depended on the inclusion of this sample rich in ions.

TOC explained the largest share of constrained variation in the full RDA but was no longer significant after region was taken into account. Its association was therefore linked mainly to the broad environmental contrast between NE and NW snow. Organic carbon may originate from atmospheric deposition, nearby terrestrial sources, or biological production within snow and ice (Maccario et al., 2014). Organic carbon, particularly its labile fractions, can serve as carbon and energy sources for heterotrophic microorganisms, potentially influencing their abundance, diversity, and community composition in glacial environments (Smith et al., 2017). Higher TOC in NE may reflect greater organic-matter inputs or availability, which could favor heterotrophic taxa and contribute to the regional differences in community composition. Yet TOC was not associated with community composition within a region in the partial RDA. Its apparent effect in the full RDA probably came from regional covariation. Ca^{2+} remained associated with bacterial community composition after controlling for region. In Alpine seasonal snow, Ca^{2+} was also among the chemical variables most strongly associated with bacterial community composition (Kosolapova et al., 2026). Calcium has been used as an indicator of mineral dust deposition in snow and glacier

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environments (Liu et al., 2009; Chuvochina et al., 2011). Mineral particles can carry microbial cells and nutrients into snowpacks (Chuvochina et al., 2011; Stibal et al., 2015). On the Mont Blanc glacier, three Saharan dust events carried different dominant bacterial phylotypes, including two events that occurred within a month of each other (Chuvochina et al., 2011). The bacteria deposited with dust may vary with the source and atmospheric transport history of individual events. In our study, the association between Ca^{2+} and community composition is consistent with a possible contribution from transport associated with minerals. However, Ca^{2+} can also have other sources, and its selection changed when XJ.Q402 was removed, so in this study it serves as an indicator of a possible gradient associated with particles. This observation is consistent with previous findings that many OTUs were positively correlated with Ca^{2+}, which may reflect the diversity of bacteria deposited together with dust particles (Kosolapova et al., 2026). This limitation also applies to our study, because we did not assess the particulate fraction and measured only dissolved Ca^{2+}, so dissolved Ca^{2+} cannot be used to directly infer biological processes associated with particles.

Air temperature and relative humidity describe atmospheric conditions that can affect the microorganisms available for deposition. Temperature also influences snow metamorphism and meltwater production, which can redistribute soluble ions and microbial cells within snowpacks (Hell et al., 2013; Lazzaro et al., 2015). Bacterial populations can increase during seasonal melt, showing that communities continue to change after deposition when liquid water and resources become available (Segawa et al., 2005). In southwest Greenland, airborne bacterial diversity was positively correlated with air temperature and negatively correlated with relative humidity. Lower relative humidity was associated with greater aerosolization of bacteria from local terrestrial sources (Šantl-Temkiv et al., 2018). Relative humidity contributed less constrained variation than the other selected variables, but it remained significant in the partial RDA. NO_3^- concentrations did not differ significantly between NE and NW snow on average. After controlling for region, variation in NO_3^- among samples remained associated with bacterial community composition. Nitrogen in snow can be affected by atmospheric deposition, photochemical reactions, and microbial transformation (Hell et al., 2013; Maccario et al., 2014; Chen et al., 2022). Following snowfall on the Tibetan Plateau, changes in NO_3^- and NH_4^+ coincided with changes in bacterial diversity, community composition, and predicted nitrogen cycling functions (Chen et al., 2022). In a melting High Arctic snowpack, nitrate and other soluble ions were also associated with differences among bacterial communities in snow, slush, and ice (Hell et al., 2013).

Collectively, the selected variables represent several processes that shape snow microbial communities. These communities receive inputs from the atmosphere and surrounding environments, and after deposition, redistribution and selection can further alter their composition (Harding et al., 2011; Maccario et al., 2014; Lazzaro et al., 2015; Els et al., 2019).

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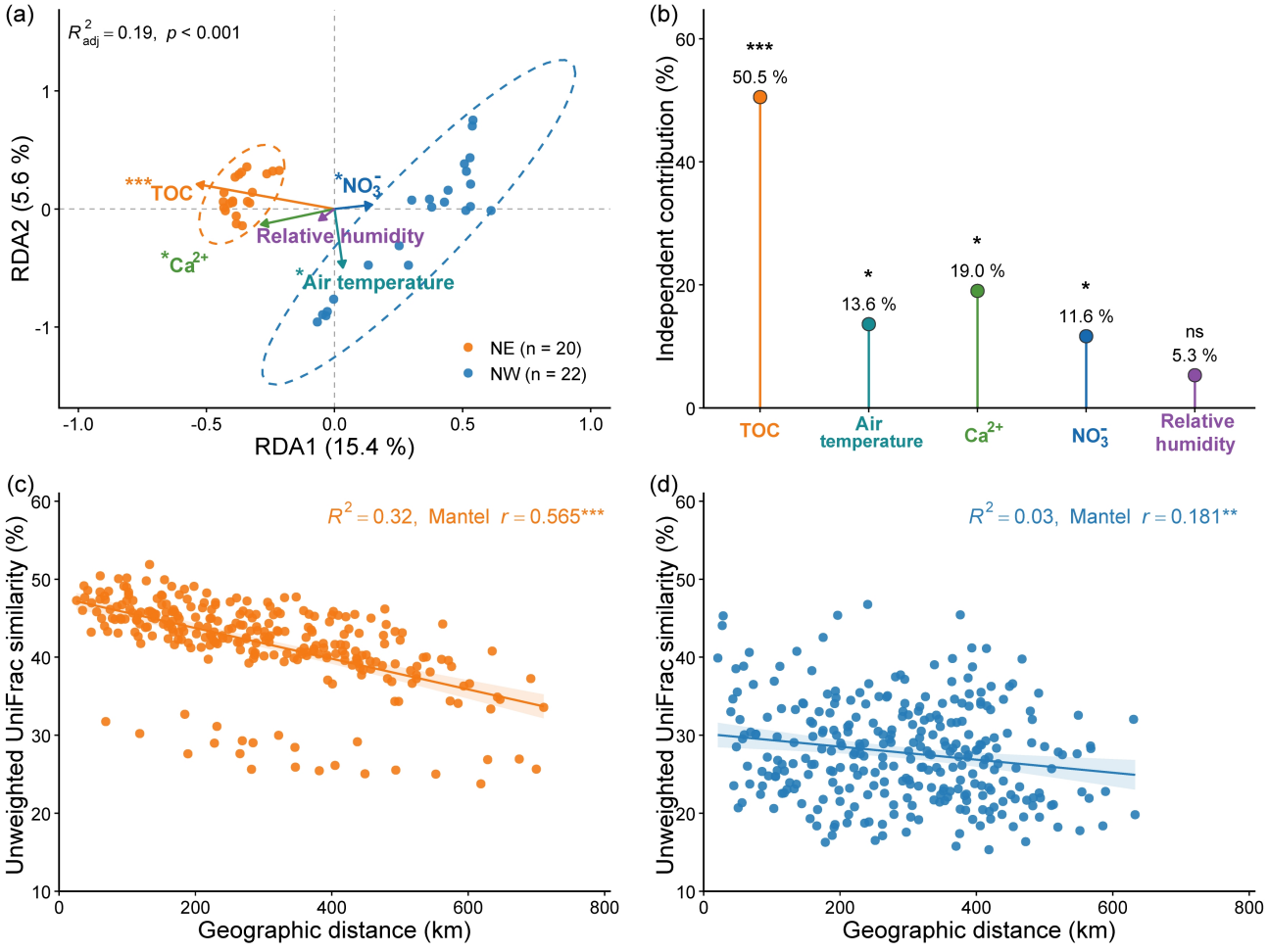


Figure 3: Environmental associations and distance decay of bacterial communities. (a) RDA ordination of OTU-level community composition and selected environmental variables. Arrows denote environmental variables, and dashed ellipses distinguish regions. (b) Relative contributions of selected variables to constrained variation. (c, d) Pairwise unweighted UniFrac similarity plotted against geographic distance in NE and NW snow, respectively. Solid lines show ordinary least-squares regressions, shaded bands show 95% confidence intervals, and R^2 values denote model fit. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

3.3 Regional differences in bacterial community assembly

Bacterial community similarity declined with increasing geographic distance within both regions, but the relationship was stronger in NE snow (Mantel $r = 0.57$, adjusted $p < 0.001$) than in NW snow (Mantel $r = 0.18$, adjusted $p = 0.0085$; Fig. 3c and d). These relationships indicated spatial structuring of bacterial community composition within each region. Distance decay describes the spatial pattern of community turnover, while assembly processes help explain how that pattern is maintained. The modified stochasticity ratio (MST) was also higher in NE than in NW (MST = 0.663 and 0.443, respectively, bootstrap $p = 0.0011$; Fig. 4b). Its bootstrap confidence interval remained above 0.5 in NE but crossed this threshold in NW, indicating stochastic predominance only in NE (Ning et al., 2019; Liang et al., 2020). The null model also estimated a

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greater contribution of stochastic processes in NE than in NW, but the regional difference was smaller than that indicated by the MST. Stochastic processes accounted for 62.7% of pairwise community turnover in NE and 57.3% in NW snow (Fig. 4e). Dispersal limitation was the largest individual process in both regions, accounting for 47.1% in NE and 48.3% in NW. Homogeneous selection contributed more in NE (24.6% vs. 19.7%), whereas heterogeneous selection contributed more in NW (23.0% vs. 12.7%). The neutral community model (NCM) fitted the relationship between OTU occurrence frequency and mean relative abundance more closely in NE snow (R^2 = 0.785) than in NW snow (R^2 = 0.409; Fig. 4c and d). The estimated migration parameter m was 0.271 in NE and 0.020 in NW. In snow habitats, the migration rate m describes the strength of microbial input into local snow communities, reflecting the contribution of external immigration to snow microbial community assembly (Sloan et al., 2006; Liu et al., 2021). Mean Levins niche breadth was also greater in NE than in NW snow (0.44 ± 0.08 vs. 0.15 ± 0.04, $p < 0.001$; Fig. 4a). This difference remained when analyses were restricted to shared OTUs and when prevalence thresholds of 5%, 10%, and 20% were applied (Fig. S6a). In addition, the five measured environmental variables were more dispersed among NW samples (PERMDISP, F = 9.048, p = 0.0024; Fig. S6b).

Stochastic processes accounted for more than half of community assembly in both regions. Snow microbial communities are not generated in situ but are primarily assembled from atmospheric deposition, which is inherently stochastic because local air bacteria are carried by airborne particles and deposited during snowfall (Harding et al., 2011; Azzoni et al., 2018). Source environments, air mass histories, and deposition events vary among widely separated sites, so the species pool arriving at any given snowpack represents a random sample of the atmospheric community at that time. Among the stochastic processes, dispersal limitation made the largest individual contribution to community assembly in both regions. In the null model, dispersal limitation was inferred when selection was not strong and pairwise compositional turnover exceeded the random expectation (Stegen et al., 2013; Ning et al., 2019). Meltwater may redistribute cells within an individual snowpack, but this local movement does not connect separate sampling sites (Lazzaro et al., 2015). The importance of dispersal limitation in both regions therefore suggests that microbial exchange among spatially separated snowpacks was limited or uneven. Assembly also varies among snow habitats and stages. High stochastic contributions have been reported in Tibetan glacier surface snow and connected glacier-fed aquatic communities (Liu et al., 2021; Chen et al., 2022). In contrast, homogeneous selection governed bacterial community assembly during Antarctic snow algae blooms (Soto et al., 2023). Homogeneous selection also accounted for 59.3% of assembly in Tibetan supraglacial snow (Xing et al., 2024). Although dispersal limitation was the largest contributor in both regions, these findings indicate that snow microbial community assembly is habitat-dependent and is not governed by a universal assembly rule. Nevertheless, deterministic processes differed between the two regions. Homogeneous selection was more important in NE, where environmental conditions varied less among sites. Similar conditions may select for phylogenetically similar groups after deposition (Fillinger et al., 2021). Heterogeneous selection contributed more in NW, where environmental variation among sites was greater. Lower niche breadth indicates a community with greater sensitivity to local conditions and higher spatial turnover (Levins, 1968; Xu et al., 2022).

Community similarity declined more clearly with geographic distance in NE, while dispersal limitation contributed similarly to pairwise turnover in both regions. Distance decay describes the spatial pattern of community similarity. The null model

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then attributes this pattern to specific assembly processes. A clear geographic pattern can still emerge when stochastic processes contribute substantially to assembly. A study of river microeukaryotic communities also found distance decay, where stochastic processes made a substantial contribution to assembly (Li et al., 2025). The clearer distance decay in NE may reflect local environmental conditions that varied more consistently across space, potentially combined with more spatially structured microbial inputs. In NW, community differences were less closely related to geographic distance, and the measured environmental conditions were more dispersed. Environmental variation may thus have contributed to the weaker relationship between community similarity and geographic distance in NW. Atmospheric microorganisms were not measured, so their contribution to the regional spatial patterns remains uncertain.

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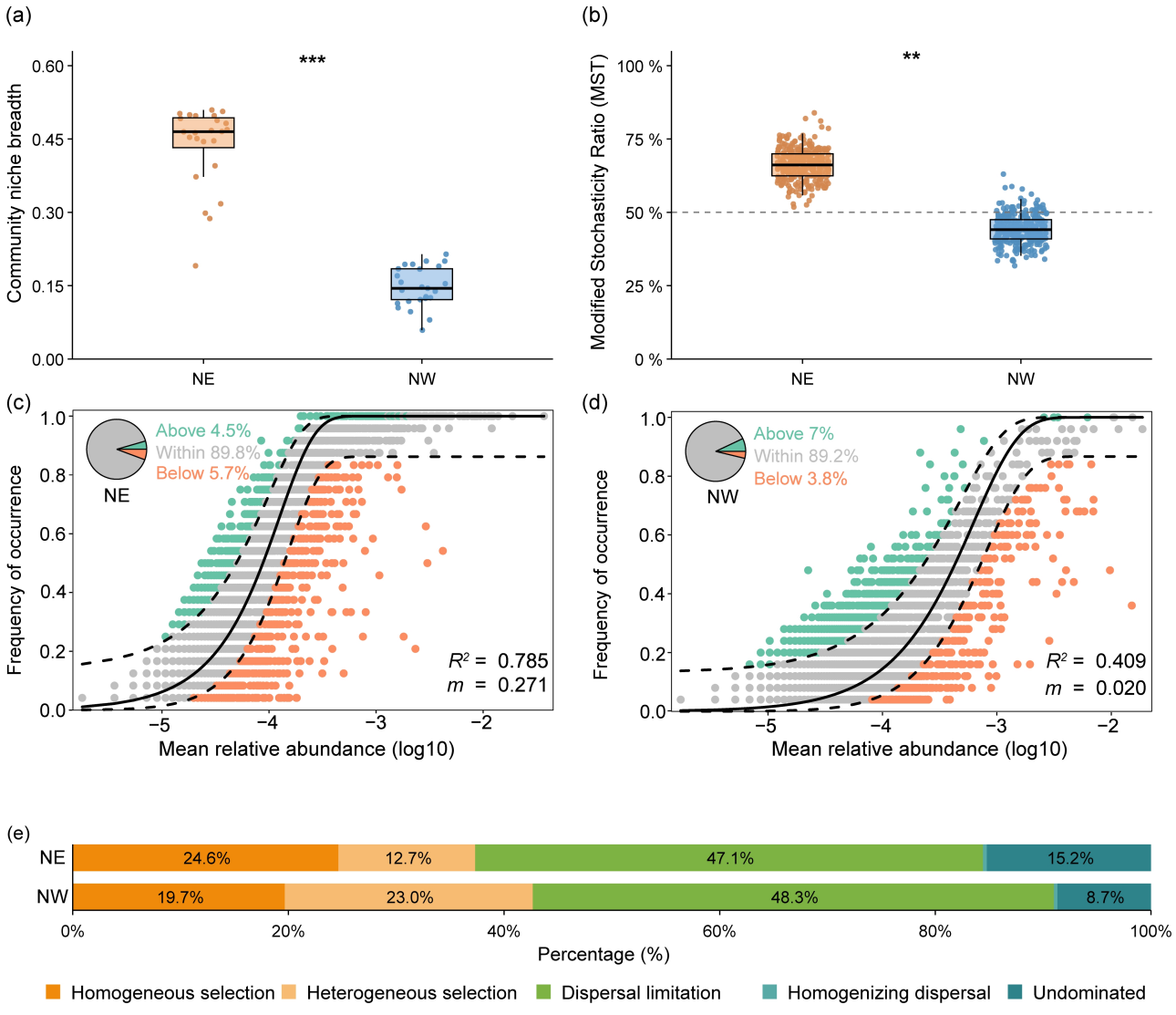


Figure 4: Bacterial community assembly in NE and NW snow. (a) Mean Levins niche breadth. Boxes show medians and interquartile ranges, and points denote samples. (b) Bootstrap distributions of the modified stochasticity ratio (MST). The dashed line marks MST = 0.5. (c, d) Neutral community models for NE and NW. Green, grey, and orange points denote OTUs above, within, and below the 95% prediction limits. Solid and dashed black lines show model fits and prediction limits. *m* is the migration parameter, and R^2 is the model fit. (e) Relative contributions of ecological processes from null-model analysis. Significance in (a) was assessed using a two-sided Wilcoxon rank-sum test, and that in (b) used bootstrap inference. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

3.4 Co-occurrence network of the NE and NW regions

The regional co-occurrence networks differed in size and topology (Fig. 5g and h, Table S6). The NW network contained 669 nodes and 11,616 edges, compared with 290 nodes and 533 edges in the NE. Mean degree was 34.73 in NW and 3.68 in

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NE, and network density was 0.052 and 0.013, respectively. Modularity showed the reverse pattern and was higher in NE (0.78 vs. 0.14). Although NE snow contained more OTUs overall, fewer were retained as connected nodes in the network. Node degree was generally higher in NW (Fig. 5a). Betweenness centrality was low for most nodes in both regions, but several high values increased the NE mean to 0.0045 ± 0.0156, compared with 0.0022 ± 0.0031 in NW. Mean harmonic centrality was 0.309 ± 0.144 in NW and 0.062 ± 0.053 in NE (Fig. 5c).

Zi and Pi values were used to classify nodes according to their positions within the modular structure (Fig. 5e, Fig. S7). Of the 290 NE nodes, 288 were peripherals (99.3%). The other two were module hubs affiliated with *Ruminococcaceae UCG-005* and *Skermanella*. No connectors or network hubs were detected. In NW, 421 nodes were peripherals (62.9%) and 248 were connectors (37.1%). No module hubs or network hubs were identified. Actinobacteria, Proteobacteria, and Bacteroidetes represented 38.7%, 35.5%, and 18.1% of the NW connectors, respectively. Among identified genera, 14 connector OTUs belonged to *Sphingomonas*, 13 to *Hymenobacter*, and 11 to *Nocardioides*. The corresponding numbers were 8 for *Massilia*, 7 for *Acidiphilium*, and 6 for *Pseudonocardia*. Network robustness was assessed by random removal and targeted removal based on degree and betweenness. Under random removal, natural connectivity declined more slowly in NW than in NE, and mean AUC was 73.03 and 63.36, respectively (Fig. 5d). The regional AUC comparison did not clearly support a difference. Targeted removal caused a faster decline in natural connectivity in both networks (Fig. S8). Compared with random removal, removal based on degree reduced AUC by 80.1% in NE and 74.5% in NW. Removal based on betweenness reduced AUC by 49.8% and 46.7%, respectively. Degree based removal produced the largest reduction in both regions.

The two networks differed in their node role composition. Module hubs and connectors occupy central positions within or among modules and are often treated as putative keystone nodes in microbial networks (Yuan et al., 2021). In NE, the two module hubs had many associations within their respective modules. NW had 248 connectors whose associations extended across modules, which was consistent with the lower modularity of NW. Several NW connectors were affiliated with genera previously reported from snow. *Sphingomonas* isolates from Antarctic snow showed cellulolytic and lignolytic activities, suggesting the potential to metabolize cellulose and lignin (Antony et al., 2016). *Hymenobacter* has been reported in alpine surface snow (Fillinger et al., 2021). *Hymenobacter* produces extracellular polymeric substances (EPS) and tolerates UV radiation and oxidative stress (Koo, 2014; Bourquin et al., 2022). The genus also metabolizes a broad range of carbohydrates. A *Hymenobacter* strain isolated from Antarctic red snow utilizes glycogen, D-galactose, maltose, and sucrose (Kojima et al., 2016), and polar *Hymenobacter* strains carry multiple hemicellulose degradation genes (Ghimire et al., 2020).

The two regions also differed in network connectivity, which may reflect distinct assembly processes and environmental variation. The NE network had fewer associations, most of its nodes were peripheral, and no connectors were identified. Measured environmental variables varied less among NE samples (Fig. S6b). At the same time, homogeneous selection accounted for a larger share of community turnover than in NW (Fig. 4e). When snow conditions vary less among sites, taxa responding to those conditions may show less variation together across samples. This may have contributed to the smaller number of retained correlations in NE. Its high modularity further shows that the associations that remained were more

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strongly separated among modules. NW snow had greater environmental dispersion, a larger contribution of heterogeneous selection, and narrower mean niche breadth. Taxa contributing more strongly to local NW communities were more restricted or unevenly distributed among samples. Across the more variable NW conditions, taxa with similar responses may have varied together, contributing to the larger number of retained associations. Co-occurrence patterns may arise from biotic interactions, environmental filtering, or dispersal limitation (Yuan et al., 2021). A study of Tibetan glacier snow similarly linked greater network connectivity and a shorter path length in subsurface snow to stronger environmental filtering (Chen et al., 2022). Random removal did not clearly distinguish the structural robustness of the two regions. Targeted removal caused a much greater loss of natural connectivity in both networks, particularly when nodes were removed by degree. Natural connectivity reflects the redundancy of alternative paths within a network (Peng and Wu, 2016). Removing high-degree nodes eliminates many associations at once, and natural connectivity declines steeply. Removal based on betweenness had a smaller structural effect. High-betweenness nodes connect modules but have fewer direct edges, and their removal leads to a smaller drop in natural connectivity.

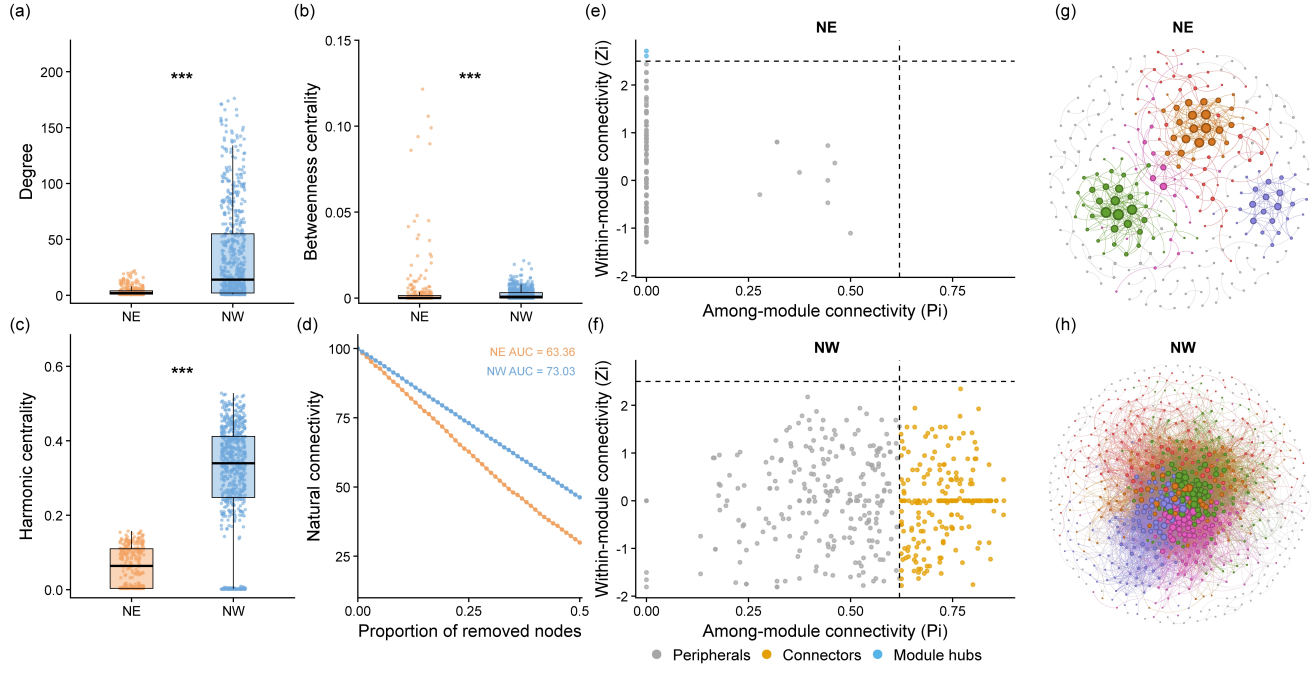


Figure 5: Co-occurrence network patterns of bacterial communities in NE and NW snow. (a, b, c) Node-level topological properties. Boxes show medians and interquartile ranges, and points represent nodes. (d) Network robustness based on weighted natural connectivity during random node removal. AUC represents the area under the curve. (e, f) Node topological roles classified by Zi and Pi. (g, h) Co-occurrence networks for NE and NW, respectively. Nodes are colored by modules and sized by degree, and edges represent significant correlations. *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$.

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4 Conclusions

In this study, we compared bacterial diversity, community composition, assembly processes, and co-occurrence networks in seasonal snow from northeastern and northwestern China. NE snow had higher bacterial richness and wider niche breadth. The wider niche breadth indicated that taxa contributing more strongly to NE communities were distributed more broadly or evenly among samples. Community composition was more variable among NW sites. The measured environmental variables were also more dispersed in NW, consistent with the larger contribution of heterogeneous selection. Environmental differences among NW sites may have contributed to community differentiation. TOC was primarily associated with the broader environmental contrast between regions. Ca^{2+} remained associated with community composition after conditioning on region, suggesting a possible contribution from mineral dust deposition. Community similarity declined with geographic distance in both regions, indicating spatial structuring of bacterial community composition. Stochastic processes accounted for more than half of community assembly in both regions. Within the stochastic processes, dispersal limitation made the largest individual contribution in both regions, indicating that dispersal among sites was too limited or uneven to homogenize community composition. The overall stochastic contribution was greater in NE than in NW. Within the deterministic processes, heterogeneous selection contributed more in NW, whereas homogeneous selection contributed more in NE. Network organization also differed between regions. The NW network was densely connected and contained numerous connectors that linked different modules. The NE network contained fewer associations and showed clearer separation among modules. Random removal showed no significant regional difference in structural robustness. Degree-based removal caused the largest decline in natural connectivity in both networks, indicating that nodes with high degree were important for maintaining network connectivity.

Together, these findings show that seasonal snow in NE and NW China supported distinct patterns of bacterial community assembly and network organization. The present spatial survey did not resolve whether these patterns persist through the snow season or between years. Future studies could follow individual snowpacks over time and collect air samples during the same periods. Such sampling would help distinguish variation introduced during atmospheric deposition from changes occurring within the snowpack after deposition.

Data availability

Raw 16S rRNA sequencing data are available in the European Nucleotide Archive (PRJEB128220), and all other data are provided in the manuscript and its supplementary information. The basemap used in the sampling location map is derived from Esri World Imagery (Esri, Vantor, Earthstar Geographics, and the GIS User Community), https://server.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer. The map of China is based on the standard map provided by the Standard Map Service of the Ministry of Natural Resources of the People's Republic of China [No. GS(2019)1673], http://bzdt.ch.mnr.gov.cn/.

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Author contributions

RG and XW led Conceptualization. RG conducted Data curation, Formal analysis, Investigation, Methodology, Validation, and Visualization. XW handled Funding acquisition, Project administration, Resources, and Supervision. RG and ZM wrote the original draft (Writing – original draft). RG, ZM, HX, DX, YL, GS, WX, and XW contributed to Writing – review & editing.

Competing interests

The authors declare that they have no competing interests.

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