Snowpack shifts cyanobacterial community in biological soil crusts postprint

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Abstract

Winter snowpack is an important source of moisture that influences the development of biological soil crusts (BSCs) in desert ecosystems. Cyanobacteria are important photosynthetic organisms in BSCs. However, the responses of the cyanobacterial community in BSCs to snowpack, snow depth and melting snow are still unknown. In this study, we investigated the cyanobacterial community composition and diversity in BSCs under different snow treatments (doubled snow, ambient snow and removed snow) and three snow stages (stage 1, snowpack; stage 2, melting snow; and stage 3, melted snow) in the Gurbantunggut Desert in China. In stages 1 and 2, Cyanobacteria were the dominant phylum in the bacterial community in the removed snow treatment, whereas Proteobacteria and Bacteroidetes were abundant in the bacterial communities in the ambient snow and doubled snow treatments. The relative abundances of Proteobacteria and Bacteroidetes increased with increasing snow depth. The relative abundances of Cyanobacteria and other bacterial taxa were affected mainly by soil temperature and irradiance. In stages 2 and 3, the relative abundance of Cyanobacteria increased quickly due to the suitable soil moisture and irradiance conditions. Oscillatoriales, Chroococcales, Nostocales, Synechococcales and unclassified Cyanobacteria were detected in all the snow treatments, and the most dominant taxa were Oscillatoriales and Chroococcales. Various cyanobacterial taxa showed different responses to snowpack. Soil moisture and irradiance were the two critical factors shaping the cyanobacterial community structure. The snowpack depth and duration altered the soil surface irradiance, soil moisture and other soil properties, which consequently were selected for different cyanobacterial communities. Thus, local microenvironmental filtering (niche selection) caused by snow conditions may be a dominant process driving shifts in the cyanobacterial community in BSCs.

Full Text

Preamble

Snowpack Shifts Cyanobacterial Community in Biological Soil Crusts

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Abstract: Winter snowpack represents a critical moisture source that influences biological soil crust (BSC) development in desert ecosystems. Cyanobacteria are key photosynthetic organisms in BSCs, yet their community responses to snowpack, snow depth, and snowmelt remain poorly understood. This study investigated cyanobacterial community composition and diversity in BSCs under different snow treatments (doubled snow, ambient snow, and removed snow) across three snow stages (stage 1: snowpack; stage 2: melting snow; stage 3: melted snow) in the Gurbantunggut Desert, China. During stages 1 and 2, Cyanobacteria dominated the bacterial community in the removed snow treatment, whereas Proteobacteria and Bacteroidetes were abundant in the ambient and doubled snow treatments. The relative abundances of Proteobacteria and Bacteroidetes increased with snow depth, while Cyanobacteria and other bacterial taxa were primarily affected by soil temperature and irradiance. During stages 2 and 3, the relative abundance of Cyanobacteria increased rapidly due to favorable soil moisture and irradiance conditions. Oscillatoriales, Chroococcales, Nostocales, Synechococcales, and unclassified Cyanobacteria were detected across all treatments, with Oscillatoriales and Chroococcales being the most dominant. Different cyanobacterial taxa exhibited distinct responses to snowpack. Soil moisture and irradiance emerged as the two critical factors shaping cyanobacterial community structure. Snowpack depth and duration altered soil surface irradiance, moisture, and other properties, thereby selecting for different cyanobacterial communities. Thus, local microenvironmental filtering (niche selection) driven by snow conditions may represent a dominant process governing shifts in BSC cyanobacterial communities.

Keywords: cyanobacterial diversity; community structure; biological soil crusts; snowpack; niche selection

1 Introduction

Winter snowfall critically regulates water and energy balance in arid and semi-arid ecosystems, which are particularly vulnerable to climate change. Small variations in temperature and precipitation can substantially alter snow cover amount and duration. While global warming is predicted to reduce snowfall and winter snowpack thickness, recent studies indicate increased snow cover in some Northern Hemisphere regions, especially post-2000. Biological soil crusts (BSCs) constitute the dominant functional vegetation unit in arid and semi-arid regions, playing vital roles in soil stabilization, structural improvement, nutrient accumulation, moisture retention, and salt stress reduction. However, BSCs are highly sensitive to precipitation changes. Winter snowfall serves as an important moisture source that influences BSC growth and development in temperate deserts, particularly in northwestern China.

During winter and early spring, snow cover and melt processes profoundly affect microbial community composition, activity, soil respiration, and carbon fixation and mineralization in desert BSCs. Cyanobacteria are primary colonizers and important components of photosynthetic communities in BSCs, influencing nitrogen fixation, moisture retention, soil stabilization, and organic carbon accumulation. While previous research has examined photosynthetic physiology and adaptation of BSC organisms, cyanobacterial community responses to snowpack and snowmelt remain incompletely understood.

Precipitation and temperature significantly affect BSC photoautotrophic communities. Generally, BSC net photosynthesis responds to photosynthetic photon flux density (PFD) following a typical saturation curve, with saturation occurring at or above 700 mol photons/($m^2 \cdot s$). For BSC cyanobacteria, precipitation reduction can functionally disconnect light-harvesting complexes from photosystem II reaction centers and reduce cyanobacterial biomass and diversity. Some evidence suggests that Microcoleus vaginatus polysaccharide content increases with light intensity. Net photosynthesis in BSC organisms shows strong temperature dependence. In Antarctic dry valleys, field and laboratory experiments demonstrated that Nostoc commune net carbon fixation and dark respiration rates depend strongly on irradiance and temperature, forming N. commune mats with water contents exceeding 30% saturation. Bacterial communities in developing BSCs shifted significantly from initial stages (few Cyanobacteria) to late stages (27% dominated by Nostoc, Microcoleus, and Leptolyngbya phylotypes) during 77-day incubations with daily freeze-thaw cycles.

We hypothesized that changes in snow conditions and stages (snowpack, melting snow, and melted snow) promote soil niche differentiation (e.g., in moisture, irradiance, and temperature), thereby driving variations in cyanobacterial communities. To test this hypothesis, we investigated: (1) cyanobacterial diversity in BSCs under different snow treatments and stages, and (2) key environmental factors driving cyanobacterial community structure variation in the Gurbantunggut Desert of northwestern China.

2.1 Study Area

Field experiments were conducted in the central Gurbantunggut Desert (45°03 36 N, 87°36 36 E) in Xinjiang Uygur Autonomous Region, northwestern China. The Gurbantunggut Desert is China' s largest fixed and semi-fixed desert, with extensive lichen-dominated BSC coverage. The region experiences a continental arid temperate climate with hot, dry summers and cold winters. Annual precipitation ranges from 70–160 mm, occurring primarily from April to August, while annual average potential evaporation reaches 2000–2800 mm. Despite low precipitation, stable snow cover occurs during winter and early spring, with snowmelt providing adequate moisture for BSC development. The annual average temperature is 5.0–5.7°C, with maximum temperatures exceeding 40.0°C. Natural vegetation, dominated by Haloxylon ammodendron and H. persicum, covers less than 30% of the area. Elevation ranges from 510 to 550 m above sea level.

2.2 Experimental Design

In October 2014, five fixed sample sites (10.0 m × 10.0 m) were randomly established in interdune areas among four sand dunes. Each site contained nine plots (1.5 m × 1.5 m each), with triplicate plots randomly assigned to three snow treatments: removed snow, ambient snow (natural conditions), and doubled snow [Figure 1: see original paper]. A 1-m buffer zone separated plots to prevent treatment interference. Plots were established to exclude shrubs. For removed snow plots, transparent polycarbonate (PC) sheets (2.0 m × 2.0 m) were installed 0.6 m above the surface, with >95% light transmittance (measured by LI-190 photoquantum sensors, Li-COR, USA). After each snowfall, snow on PC boards was removed and added to doubled snow treatment plots. PC boards were removed in spring when snow was absent.

2.3 Sampling Methods

BSC samples were collected on 15 January (stage 1: snowpack), 1 March (stage 2: melting snow), and 15 March (stage 3: melted snow) in 2016. Stage 1 represented stable snowpack formation (10 December 2015–26 February 2016). Stage 2 began when daytime temperatures rose above 0.0°C (27 February–13 March). Stage 3 commenced on 13 March. To minimize spatial heterogeneity, triplicate BSC samples (0–2 cm layer) were collected from each snow treatment at each stage and pooled into one composite sample. Each treatment included five replicate samples (one per site), totaling 45 BSC samples. Samples were divided into two subsamples: one stored at -20°C for genomic DNA extraction, and one air-dried for physicochemical analysis.

2.4 Soil Physicochemical Property Analysis

Plant material was removed by sieving through 2-mm mesh. Soil organic carbon (SOC) was determined by the $K_2Cr_2O_7$ method (Walkley-Black). Total nitrogen

(N) was measured by $CuSO_4$-Se powder diffusion. Total phosphorus (P) was analyzed by NaOH fusion-Mo Te Sc colorimetry. Available P was determined by 0.5 mol/L $NaHCO_3$ leaching-Mo Te Sc colorimetry. Available N was measured by alkali hydrolyzation-diffusion. Soil pH and electrical conductivity were measured in 1:5 soil:deionized water mixtures using a PHS-3C digital pH meter and DDS-307A conductivity meter (Precision and Scientific Corp, Shanghai, China). Total salts were determined gravimetrically.

2.5 Measurements of Soil Moisture and Photosynthetic Photon Flux Density

Five soil moisture sensors (Decagon Devices, Pullman, WA, USA) were installed horizontally at 2 cm depth in each plot, connected to a Decagon EM 50 datalogger (METER, USA) that recorded volumetric water content and temperature every 15 minutes from November 2015 to March 2016. Photosynthetic photon flux density (irradiance) was measured using five LI-190 photoquantum sensors (Li-COR, USA) connected to a Li-1500 datalogger (Shenzhen AKS Technology Co., China) positioned on BSC surfaces.

2.6 Soil DNA Extraction and MiSeq Sequencing

Soil genomic DNA was extracted from 0.5 g soil using a MOBIO Power Soil DNA Isolation Kit (MOBIO Laboratories, Carlsbad, CA, USA) following standard protocols. The V4 hypervariable region of the 16S rRNA gene was amplified using universal forward primer 515F (5 -GTGCCAGCMGCCGCGGTAA-3) and reverse primer 909R (5 -CCCCGYCAATTCMTTTRAGT-3). A unique 12-bp barcode was added to the 5 end of the reverse primer for sample identification. The 25-µL PCR mixture contained 1× PCR buffer, 1.5 mM $MgCl_2$, 0.4 mM each dNTP, 1.0 µM each primer, 0.5 U Ex Taq (Takara Bio), and 10 ng soil genomic DNA. The amplification program consisted of initial denaturation at 94°C for 3 minutes, followed by 30 cycles of 94°C for 40 seconds, 56°C for 60 seconds, and 72°C for 60 seconds, with final extension at 72°C for 10 minutes. PCR products (~394 bp) were generated in duplicate for each sample, combined, purified using a SanPrep DNA Gel Extraction Kit (Sangon Biotech, China), mixed in equimolar amounts, and sequenced on an Illumina MiSeq platform using a TruSeq DNA kit.

2.7 Sequence Data Analysis

Sequence processing, clustering, taxonomic assignment, and biodiversity calculations were performed using QIIME (http://qiime.org/). Sequences were demultiplexed, and primers and barcodes were removed. High-quality sequences (>350 bp, no ambiguous ‘N’ bases, average quality score >30) were selected. For comparative analysis, 15,770 bacterial sequences per sample were randomly subsampled based on rarefaction curves. Operational taxonomic units (OTUs) were generated via open-reference OTU selection against the

Greengenes database at 97% similarity. Taxonomic assignments used the RDP Classifier (http://rdp.cme.msu.edu/) with an 80% confidence threshold. Raw sequences were deposited in NCBI (SRA accession: PRJNA490878).

Cyanobacterial sequences were resampled from bacterial sequences. To determine cyanobacterial species composition, representative sequences from the top 125 OTUs were BLASTed against NCBI. We selected 158 reference cyanobacterial sequences from desert BSCs and aligned them with our OTU representatives using CLUSTALX (1.83), trimming to uniform length. A neighbor-joining tree was constructed using the maximum composite likelihood model in MEGA 5.0. Based on the phylogenetic tree (Fig. S1), we assigned taxonomy using the highest BLAST match to reference species.

2.8 Statistical Analysis

Cyanobacterial community dissimilarity was calculated using Bray-Curtis distance from OTU tables. Alpha diversity metrics (Observed species, Chao 1) were generated in QIIME. Relative abundances were calculated as percentages of cyanobacterial sequences relative to total bacterial reads. Repeated-measures ANOVA (SPSS 13.0) tested differences in soil physicochemical properties, diversity indices, and relative abundances among treatments and stages, with LSD post-hoc comparisons. Pearson correlations (two-tailed) were calculated prior to redundancy analysis (RDA) to eliminate autocorrelated variables ($P<0.01$). Based on correlation analysis, organic C and total K represented nutrients, while pH, total salts, and electrical conductivity represented salinity. Soil moisture, temperature, and irradiance were included as meteorological factors. Cyanobacterial relative abundances were square-root transformed. PERMANOVA based on Bray-Curtis distances tested community composition differences among treatments and stages using PAST (http://folk.uio.no/ohammer/past/). Mantel tests evaluated correlations between community dissimilarity and environmental variables using PASSaGE (http://www.passagesoftware.net/). RDA explored relationships between cyanobacterial communities (OTU data) and environmental factors using the vegan package in R, with significance determined by the envfit function.

3.1 Soil Physicochemical Properties Under Different Snow Treatments

The ambient snow treatment received approximately 250 ($±$50) mm of snowfall during winter 2015–early spring 2016. Stage 1 (10 December 2015–26 February 2016) had soil temperatures ranging from -6.3 to -2.9°C (doubled snow), -7.5 to -2.8°C (ambient snow), and -22.7 to 5.4°C (removed snow), with no freeze-thaw cycles. January snow depths were ~250 mm (ambient) and 500 mm (doubled), while the removed snow treatment received minimal snow. Stage 2 (27 February–13 March 2016) had soil temperatures of -5.5 to 11.9°C (doubled), -4.9 to 8.5°C (ambient), and -8.5 to 22.1°C (removed), with 10, 6, and 15 freeze-

thaw cycles, respectively. Stage 3 (beginning 13 March) had no snow cover or freeze-thaw cycles.

Soil moisture, temperature, and irradiance were significantly affected by snow treatments, stages, and their interactions ($P<0.01$). In stages 1 and 2, soil moisture in doubled and ambient snow treatments was significantly higher than in the removed snow treatment ($P<0.001$). Moisture in doubled and ambient treatments was significantly higher in stage 2 than in stages 1 and 3 ($P<0.05$). Soil temperature and irradiance increased significantly from stage 1 to stages 2 and 3 ($P<0.001$). In stage 1, soil temperature in doubled and ambient treatments was significantly higher than in the removed treatment. Irradiance in stages 1 and 2 increased significantly with decreasing snow depth ($P<0.001$). Snow treatments significantly affected SOC ($P<0.05$), total N ($P<0.05$), available K ($P<0.01$), and pH ($P<0.001$), while stages significantly influenced SOC ($P<0.001$), total N ($P<0.05$), and electrical conductivity ($P<0.001$). Available P was significantly affected by treatment-stage interactions .

SOC and total N in ambient and removed treatments increased from stage 1 to stages 2 and 3. In stage 1, available P in ambient snow was significantly higher than in removed snow ($P<0.05$). In stages 2 and 3, electrical conductivity in ambient snow was higher than in doubled snow but lower than in removed snow . These results demonstrate that snow depth and stage influenced soil nutrients, pH, and electrical conductivity by altering moisture and temperature, creating different niches for cyanobacteria.

Pearson correlation analysis revealed SOC was significantly positively correlated with total N ($r=0.817$, $P<0.01$), total P ($r=0.357$, $P<0.05$), available P ($r=0.490$, $P<0.01$), available K ($r=0.661$, $P<0.01$), and soil temperature ($r=0.430$, $P<0.01$). Total N correlated positively with available P ($r=0.364$, $P<0.05$) and soil temperature ($r=0.387$, $P<0.01$), but negatively with available K ($r=-0.525$, $P<0.01$) (Table S1).

3.2 Cyanobacterial Composition of BSCs

Bacterial OTUs ranged from 18,619 to 18,810 per sample. Bacterial communities were dominated by Proteobacteria and Cyanobacteria, followed by Actinobacteria, Bacteroidetes, and Acidobacteria (Fig. S2). In stages 1 and 2, Cyanobacteria predominated in removed snow treatments but were less abundant in doubled and ambient treatments. Proteobacteria abundance was significantly higher ($P<0.05$) in ambient and doubled snow than in removed snow. Bacteroidetes were most abundant in doubled snow, followed by ambient snow, and rare in removed snow. In stage 3, Cyanobacteria dominated all treatments, while Bacteroidetes constituted a very small proportion, suggesting irradiance-mediated filtering.

At the order level, cyanobacterial communities comprised Oscillatoriales (212 OTUs), Chroococcales (167 OTUs), Nostocales (32 OTUs), Synechococcales (11 OTUs), and unclassified Cyanobacteria (165 OTUs) across all treatments.

Oscillatoriales and Chroococcales were dominant, representing 31.1%–48.7% and 22.9%–38.3% of cyanobacterial sequences, respectively.

At the OTU level, 796 cyanobacterial OTUs were detected. Dominant OTUs were assigned to Microcoleaceae, Coleofasciculaceae, Phormidaceae, Chroococcidiopsidaceae, Chroococcaceae, Nostocaceae, Scytonemataceae, Tolypothrichaceae, and Leptolynbyaceae. Sequences related to *M. vaginatus* and *Chroococcidiopsis* sp. dominated, followed by *M. steenstrupii*, *Chroococcidiopsis thermalis*, and *Trichodesmium contortum* (Table S2). Some OTUs related to Streptophyta were found among Cyanobacteria, and many sequences could not be confidently classified at the genus level.

3.3 Effects of Snowpack on Cyanobacterial Diversity and Relative Abundance

Shannon-Wiener diversity did not differ significantly among treatments ($P>0.05$) or stages ($P>0.05$). In stage 1, Cyanobacteria relative abundance was significantly higher in removed snow than in ambient and doubled snow ($P<0.05$), while cyanobacterial OTU numbers were significantly lower in doubled snow than in removed snow ($P<0.05$; [Figure 2: see original paper]). During spring snowmelt, cyanobacterial OTUs increased significantly in doubled snow, and relative abundance increased significantly in ambient snow ($P<0.05$). After complete snowmelt, Cyanobacteria abundance in doubled snow increased from stage 2 to stage 3, with no significant differences among treatments in stage 3 ($P>0.05$; [Figure 2: see original paper]).

Repeated-measures ANOVA showed that relative abundances of Oscillatoriales ($P<0.05$), Chroococcales ($P<0.01$), Synechococcales ($P<0.05$), and unclassified Cyanobacteria ($P<0.05$) differed significantly among treatments. Nostocales ($P<0.05$) and Oscillatoriales ($P<0.01$) abundances were significantly influenced by snow stage. Treatment-stage interactions significantly affected Oscillatoriales ($P<0.01$) and unclassified Cyanobacteria ($P<0.01$) .

In stage 1, relative abundances of Oscillatoriales, Chroococcales, Nostocales, and unclassified Cyanobacteria in removed snow increased significantly ($P<0.05$) with decreasing snow depth. In stage 2, Oscillatoriales and Chroococcales abundances increased significantly across treatments. In stage 3, most cyanobacterial orders showed no significant treatment differences, though Chroococcales abundance in removed snow remained significantly higher than in doubled and ambient snow. Oscillatoriales abundances in doubled and ambient snow increased from stage 1 to stages 2 and 3, while other orders showed no significant stage-related changes .

In stages 1 and 2, most cyanobacterial OTU abundances in removed snow were significantly higher than in doubled and ambient snow ($P<0.05$), increasing with decreasing snow depth (e.g., *Microcoleus vaginatus*, *M. steenstrupii*, *T. contortum*, *Symplocastrum torsivum*, *S. californicum*, Phormidiaceae cyanobacterium, *Chroococcidiopsis* sp. CC1, *C. thermalis*, *Chroococcidiopsis* sp. CC3) (Table

S2). In stage 3, no significant OTU differences occurred among treatments. Snow stages significantly affected some species: *M. vaginatus* and unknown Cyanobacteria in doubled snow increased significantly from stage 1 to stages 2 and 3, while *Coleofasciculus chthonoplastes* in removed snow was significantly more abundant in stage 2 than stage 1 (Table S2).

3.4 Relationships Between Cyanobacterial Community Composition and Environmental Factors

PERMANOVA analysis revealed significant differences in cyanobacterial community composition between doubled and removed snow treatments in stage 1 ($P=0.025$), but no differences among treatments in stage 3. The stage 1 doubled snow community differed significantly from removed snow in stage 2 ($P<0.05$) and all stage 3 treatments ($P<0.01$).

RDA explained 34.86% of cumulative community variation, with axes 1 and 2 accounting for 18.47% and 10.03%, respectively [Figure 3: see original paper]. Axis 1 correlated significantly with soil moisture ($R^2=0.261$, $P=0.001$) and irradiance ($R^2=0.184$, $P=0.005$), while axis 2 correlated with SOC ($R^2=0.180$, $P=0.001$) and pH ($R^2=0.114$, $P=0.016$). In stage 1, snow depth effects on community composition were evident across treatments and correlated with irradiance, moisture, and pH. In stage 2, removed snow samples separated from doubled snow samples, with communities correlating with moisture and irradiance. Most doubled and ambient snow samples in stage 2 associated positively with SOC and total K, highlighting Cyanobacteria' s role in C fixation and nutrient accumulation. Immediately post-melt, ambient and removed snow communities were similar but differed from doubled snow. Mantel tests confirmed positive associations between cyanobacterial communities and both soil moisture ($P=0.00060$) and irradiance ($P=0.00087$).

4 Discussion

Cyanobacteria are important autotrophic microorganisms and primary producers of organic carbon and nitrogen in BSCs. Snowpack alters environmental conditions including soil moisture, temperature, irradiance, and other properties. This study revealed how BSC cyanobacteria respond to snowpack, identifying moisture, irradiance, and temperature as critical factors shaping community structure.

4.1 Role of Soil Moisture in Determining the Cyanobacterial Community in BSCs

Snow directly affects soil moisture content during melt in desert ecosystems. Soil moisture declined significantly with reduced snow depth in stages 1 and 2, and differed significantly between stages in doubled and ambient snow treatments . In arid and semi-arid regions, BSC CO_2 fixation efficiency remains constant at optimal or supra-optimal moisture but declines rapidly at lower moisture levels.

For cyanobacteria, hydration triggers photosynthetic activity, with hydration thresholds determining growth. *M. vaginatus* exhibits hydrotaxis, migrating to the crust surface during rainfall events. In stage 2, melting snow increased water availability, promoting cyanobacterial growth. Consequently, dominant species abundances (e.g., *M. vaginatus* and *Chroococcidiopsis* sp. CC1) in doubled and ambient snow were significantly higher in stage 2 than stage 1 (Table S2). Many other OTUs showed similar patterns, though not significantly. This contributed to significant increases in Oscillatoriales abundances in doubled and ambient snow from stage 1 to stage 2 , partially explained by remarkable moisture differences among treatments and stages. Although desert cyanobacteria generally tolerate desiccation, our data indicate taxon-specific responses to moisture changes from varying snow depths and stages, resulting in increased or decreased relative abundances under different snow conditions.

4.2 Effects of Irradiance on the Cyanobacterial Community in BSCs

In stage 1, most cyanobacterial OTU abundances in removed snow were significantly higher than in ambient and doubled snow ($P<0.05$). Some OTUs showed similar trends in stage 2 (Table S2). Irradiance critically enhances cyanobacterial growth under extremely dry conditions. Since the photic zone is limited to a few millimeters below the surface, cyanobacteria are significantly more abundant in BSCs than deeper soil layers. In stage 1, irradiance increased with decreasing snow depth ($P<0.05$;), promoting cyanobacterial growth and reproduction in removed snow. Conversely, cyanobacteria in ambient and doubled snow received little light (<55.8 $\mathrm{mol}/(\mathrm{m}^2 \cdot \mathrm{s})$) in winter, severely inhibiting growth and resulting in lower abundances compared to removed snow in stages 1 and 2.

In other ecosystems (Tibetan Plateau, wetlands), Proteobacteria and Bacteroidetes dominate bacterial communities across soil depths, with Proteobacteria abundance (23–29%) negatively correlating with depth and Bacteroidetes positively correlating with snow depth in alpine meadows. In our study, Proteobacteria and Bacteroidetes dominated doubled and ambient snow bacterial communities in stages 1 and 2, but declined sharply in stage 3 after complete snowmelt, indicating that irradiance is not essential for their growth.

4.3 Regulatory Effect of Temperature on the Microbial Community

Snow insulation moderates soil temperature regimes relative to air temperature. Our results showed snow cover increased winter soil temperatures. During spring melt, soil temperature in doubled and ambient snow was significantly lower than in removed snow . Temperature drives microbial biomass, abundance, and community structure. In stages 1 and 2, higher temperatures and lower irradiance in doubled and ambient snow may have created unique niches favoring Proteobacteria and Bacteroidetes over other taxa. Low temperatures and freezing can cause microbial dormancy or death. The removed snow treatment had very low soil temperatures in stage 1 ($-11.06°C \pm 0.15°C$), potentially restricting Proteobacteria and Bacteroidetes growth. However, cyanobacteria

tolerate extremely low temperatures, remaining viable in permafrost and polar desert rocks. Continental-scale BSC surveys indicate *M. vaginatus* is more thermotolerant than *M. steenstrupii*. This cold tolerance partially explains why cyanobacterial abundance in removed snow exceeded that in doubled and ambient snow in stage 1 [Figure 2: see original paper]. In stage 3, increased soil temperature and non-limiting irradiance allowed cyanobacteria to dominate bacterial communities across all treatments.

Climate warming alters precipitation patterns, increases temperatures, and reduces snow cover. Snow cover changes can directly or indirectly affect soil bacterial communities, promoting either heterotrophic Proteobacteria and Bacteroidetes dominance or autotrophic Cyanobacteria dominance. We speculate that long-term snow cover changes may alter microbial population dynamics and functions, ultimately affecting carbon and nitrogen processes by increasing heterotrophic respiration and reducing carbon sequestration. Further research is needed to understand long-term snow cover effects on microbial communities and functions in BSCs.

5 Conclusions

This study demonstrated that snowpack changes significantly altered BSC bacterial community structures in desert ecosystems. Cyanobacteria dominated BSC bacterial communities under snow removal, while Proteobacteria and Bacteroidetes were relatively abundant under snow cover. Soil moisture, temperature, and irradiance were critical factors shaping cyanobacterial community structure, with cyanobacterial abundance increasing rapidly under adequate moisture and irradiance during snowmelt and post-melt stages.

Variations in snow depth across stages promoted new niche formation by influencing soil physicochemical properties (moisture, nutrients, temperature, pH) and irradiance, driving changes in BSC cyanobacterial communities. Thus, local microenvironmental filtering (niche selection) caused by snow conditions may constitute a dominant process driving cyanobacterial community variation in BSCs.

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Appendix

Fig. S1 Phylogenetic trees based on 16S rRNA gene representative sequences of cyanobacterial operational taxonomic units (OTUs) from biological soil crusts (BSCs) samples and reference sequences using maximum likelihood method.

Fig. S2 Bacterial community compositions in different snow treatments and snow stages. Stage 1, snowpack; Stage 2, melting snow; Stage 3, melted snow; DS, double snow; AS, ambient snow; RS, removed snow. Data represent mean relative abundances of five replicate samples. Values at the top of each bar indicate total bacterial OTU numbers.

Note: Figure translations are in progress. See original paper for figures.