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Distinct Phototrophic Community Structure on a Central Asian Glacier: Predominance of Filamentous Cyanobacteria and Absence of Glacier Algae (*Ancylonema* spp.)

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Abstract. Cold-adapted algae and cyanobacteria are key drivers of snow and ice albedo reduction, yet their dynamics on dust-rich Central Asian glaciers remain poorly understood compared to the well-documented algal blooms in the Arctic. This study investigated the spatio-temporal distribution of phototrophic communities on Urumqi Glacier No.1, eastern Tien Shan, during a two-month melt season. Our findings reveal a distinct seasonal succession where snow-covered surfaces were dominated by snow algae *Chloromonadinia* species (Chlorophyceae), while the exposure of bare ice led to a sharp increase in biomass dominated by filamentous cyanobacteria (Oscillatoriaceae). Notably, glacier algae such as *Ancylonema* spp., which drive darkening on Arctic ice, were entirely absent, suggesting a fundamental ecological divergence. Statistical analyses indicated that cyanobacterial proliferation is closely linked to environmental factors, showing significant positive correlations with mineral-derived ions and negative correlations with inorganic nitrogen. These results, supported by recent evidence that specialized cyanobacterial taxa drive the initiation and structural development of cryoconite granules, suggest that high mineral dust deposition from surrounding arid regions facilitates a stable, nutrient-limited niche for cyanobacteria. This "cyanobacteria-mineral synergy" creates a more persistent biological darkening effect than the ephemeral algal blooms observed in polar regions. Our study highlights the necessity of integrating region-specific microbial dynamics, which is characterized by the absence of glacier algae and the dominance of mineral-buffered cyanobacterial communities,

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into glacier mass balance models to improve the accuracy of future projections for Central Asian water resources.

1 Introduction

Glacier and ice sheet surfaces constitute a distinct microbe-dominated biome within the Earth system (Anesio and Laybourn-Parry, 2012), harboring an estimated 10^{29} microbial cells (Irvine-Fynn and Edwards, 2014). The presence of liquid water, which is primarily from surface meltwater during the summer melt season, is one of key limiting factors for microbial activity (Hodson et al., 2008). Seasonal melting transforms glacier surfaces from a snow-covered landscape in winter to a mosaic of habitats in summer, with bare ice prevailing in the ablation zones and snowpack persisting in high-elevation accumulation zones (Stibal et al., 2012a). These snow and bare-ice habitats differ markedly in their physical and chemical properties, leading to distinct microbial communities (Yoshimura et al., 1997; Lutz et al., 2017). However, due to accelerated global glacier shrinkage (Hugonnet et al., 2021), the spatial extent of microbial habitats on glacier and ice sheet surfaces is rapidly diminishing. Therefore, investigating the spatial distribution and abundance of microbial taxa across icy environment is not only critical for understanding the ecological dynamics of glacier surface communities, but also for preserving a biological signature of these unique and increasingly vulnerable ecosystems.

Algae and cyanobacteria are key cold-adapted photosynthetic microorganisms that play a dominant role on biological carbon accumulation on glacier surfaces during melt season (Anesio et al., 2017). For example, eukaryotic green algae contribute up to 97% of the total photoautotrophic carbon fixation on the surface of the Midre Lovénbreen Glacier in Svalbard (Yallop et al., 2012). Cyanobacteria are the primary contributors to photosynthetic activity, accounting for approximately 75%–93% of carbon fixation within the cryoconite hole on Arctic glaciers (Stibal and Tranter, 2007).

In addition to their role in carbon cycling, these microorganisms contribute to the acceleration of snow and ice melt by reducing surface albedo. Pigmented algae, can proliferate during the melt season, leading to visible algal blooms that darken the surface of snow and ice and enhance solar radiation absorption (Williamson et al., 2018; Takeuchi, 2013). Filamentous cyanobacteria produce extracellular polymeric substances (EPS) that facilitate the aggregation of mineral particles, forming dark-colored

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cryoconite granules (Stibal et al., 2012b; Yallop et al., 2012; Musilova et al., 2016), which further lower surface albedo and enhance localized melting on glacier surfaces (Cook et al., 2016; Kohshima et al., 1993; Takeuchi et al., 2018).

The habitats of algae and cyanobacteria on glacier surfaces are heterogeneous. In cryoconite and cryoconite holes on ablation surfaces, filamentous cyanobacteria, particularly members of the order Oscillatoriales, such as *Phormidesmis priestleyi*, *Phormidium* sp., and *Leptolyngbya* sp., are typically dominant and play a crucial role in formation of cryoconite granules (Singh et al., 2021; Segawa et al., 2017; Uetake et al., 2019). On glacier ice surface, algae from the order Zygnematales, including *Ancylonema nordenskiöldii*, *Ancylonema alaskanum*, and *Cylindrocystis brébissonii*, are the predominant taxa (Remias et al., 2012; Ling and Seppelt, 1990; Uetake et al., 2010; Takeuchi et al., 2013). In contrast, snow surfaces are mainly inhabited by green and red algae belonging to the order Chlamydomonadales, such as *Chlamydomonas* sp., *Chloromonas* sp., and *Sanguina nivaloides* (Davey et al., 2019; Segawa et al., 2018). Given their patchy and heterogeneity, it is essential to investigate the altitudinal and seasonal variability of their distribution and abundance to improve our understanding of their contributions to carbon cycling and glacier mass balance.

Urumqi Glacier No.1, located in the eastern Tien Shan Mountains, is frequently subject to dust storms that derive from surrounding deserts, resulting in substantial deposition of mineral particles on its ablation surface (Nagatsuka et al., 2014). These dust inputs foster the rapid formation and enlargement of cryoconite granules. A previous investigation has reported high areal coverage and biomass of cryoconite on ablation zone of this glacier, which is far exceeding observed on many Arctic glaciers (Takeuchi and Li, 2008). Within these granules, three morphologically distinct filamentous cyanobacterial taxa have been identified (Segawa et al., 2017); each potentially plays a different role in the initiation and structural development of granules (Chen et al., 2025). Moreover, micro-scale biogeochemical analyses have revealed active nitrogen cycling processes within cryoconite (Segawa et al. 2014, 2020; Murakami et al., 2022), suggesting the presence of nutrient hotspots that sustain microbial life on the oligotrophic supraglacial environment. However, previous studies have focused almost exclusively on the single time-point observations of cryoconite and ablation zone, with limited insight into the temporal dynamics of microbial communities across snow and ice surfaces during the melt season. Furthermore, although hydrological and meteorological observations on this glacier have been conducted since the 1960s (Dong et al., 2012), continuous monitoring of microbial community

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dynamics has never been carried out, and the influence of biological processes on surface albedo has not been adequately considered. Therefore, conducting continuous observations during the biologically active melt season is essential for improving the accuracy of mass balance models and enhancing our understanding of bio-albedo feedbacks in glacier retreat.

This study has three main objectives: (1) to investigate the spatial and temporal distribution patterns of algal and cyanobacterial communities on glacial snow and ice surfaces of Urumqi Glacier No.1; (2) to identify key environmental drivers influencing variations in community structure; and (3) to evaluate the ecological role of phototrophic taxa (algae and cyanobacteria) and their potential impact on glacier surface albedo.

2 Study sites and methods

2.1 Study sites

Urumqi Glacier No.1, located at 43°06′N and 86°49′E, lies within the Tien Shan Mountains of the Xinjiang Uyghur Autonomous Region in western China (Fig. 1a). This northeast-facing glacier spans elevations from 3,752 to 4,445 m above sea level (a.s.l.). This glacier lost approximately 20% of its volume between 1962 and 2003, and it split into eastern and western branches in 1993 as a result of its continued retreat (Ye et al., 2005). The total catchment area is approximately 1.618 km^2 (Yue et al., 2022). Mass accumulation primarily occurs during the summer months, corresponding with peak precipitation rates. Hourly meteorological data, including air temperature, downwards solar radiation, precipitation, and snowmelt (in water equivalent), were obtained from ERA5-Land (0.1° × 0.1° resolution, 2 m above surface, https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land?tab=download) for July 1 – August 31, 2013, and converted to daily means by averaging hourly values (Fig. 2). The mean annual equilibrium line altitude (ELA) in 2013 was 4240 m a.s.l. (https://wgms.ch/products_ref_glaciers/urumqi/). This region is frequently influenced by dust storm activity due to the surrounding major deserts, with dust primarily originating from the Taklimakan Desert (Takeuchi et al., 2011; Li et al., 2010; Nagatsuka et al., 2014). The glacier's ablation zone is notably characterized by the widespread presence of cryoconite granules, with a mean dry weight of 335 g m^{-2} and an organic matter content of 9.4 ± 1.6% (Takeuchi and Li, 2008). Cryoconite holes are generally absent from the glacier surface (Takeuchi and

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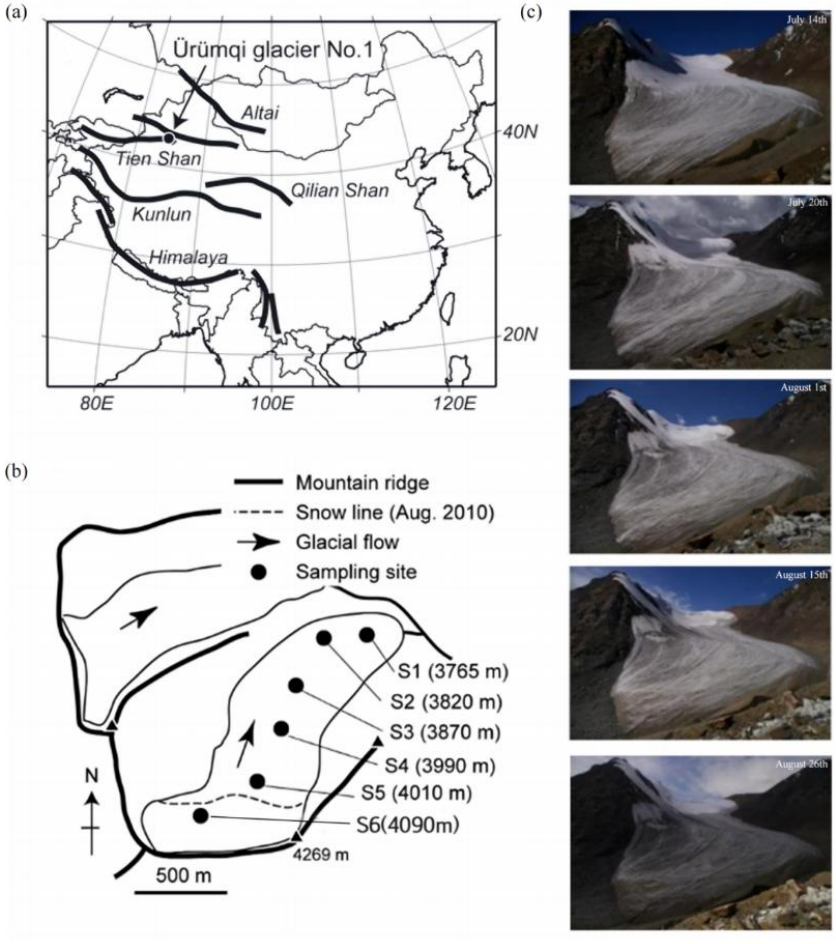
118 Li, 2008).



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120 **Figure 1: Location maps and photographs of Urumqi Glacier No.1. (a) Location of Urumqi Glacier No.1 in**
121 **the Tien Shan Mountains. (b) Map of sampling sites (S1–S6) in this study. (c) Photographs of Urumqi**
122 **Glacier No.1 across five sampling periods in 2013.**

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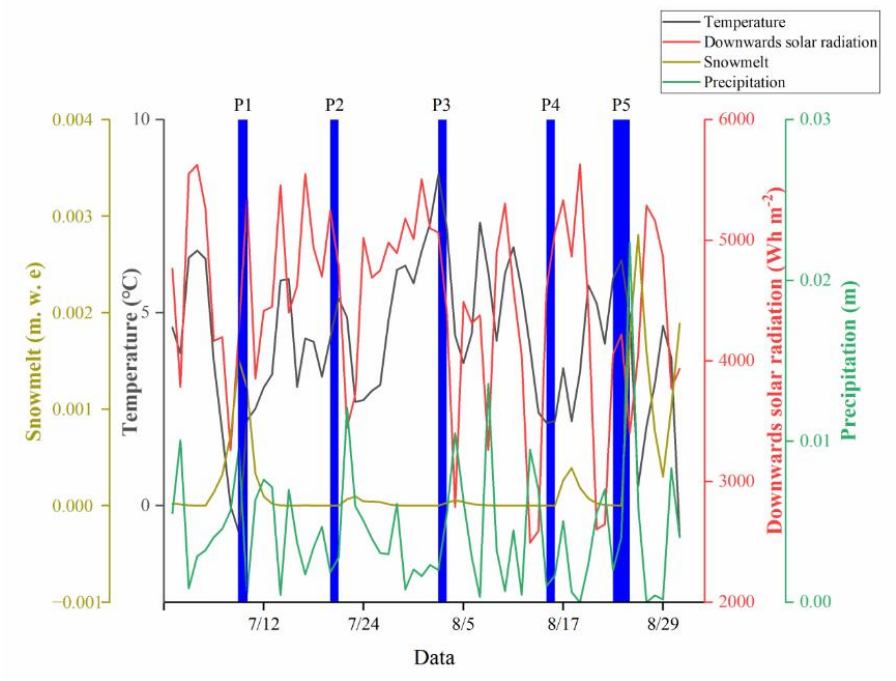

Figure 2: Meteorological datasets of Urumqi Glacier No.1 during July and August in 2013. P1-P5 denote sampling period.

2.2 Methods

2.2.1 Sampling collection

Field investigations were conducted five times in 2013, specifically on July 8–11 (P1), July 20–21 (P2), August 2–3 (P3), August 15–16 (P4), and August 24–26 (P5), across six sites on different altitudes (S1-S6, Fig. 1b). During P1, S1–S4 were characterized by exposed ice surfaces, while S5 and S6 remained snow-covered (Fig. 1c). In the subsequent four sampling periods, ice surfaces extended upslope, resulting in S1 to S5 being classified as ice surfaces, with only S6 retaining a snow cover (Fig. 1c). Surface ice and snow samples, approximately 1–2 cm in thickness, were collected along the eastern branch of Urumqi Glacier No.1 using a pre-cleaned stainless-steel scoop. For subsequent analysis, three to five samples were collected from randomly selected surface areas at each site. To preserve biological activity, samples were melted and fixed with a 3% formalin solution in sterile 30 mL polyethylene bottles (IBOY, AS ONE, Japan). Additionally, one sample per site was collected and kept frozen without fixative for taxonomic identification of algal and cyanobacterial species. All

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samples were subsequently delivered to a laboratory at Chiba University for further analysis.

2.2.2 Quantification of algal and cyanobacterial biomass

Biomass of algae and cyanobacteria at each sampling site was quantified via direct cell counting using an optical microscope. To loosen sedimentary particles, each sample was ultrasonicated for 10 minutes. A volume of 2–100 mL of meltwater was filtered through a polytetrafluoroethylene (PTFE) membrane filter (pore size 0.45 μm; JHWP01300, Merck Millipore, Germany), and cells retained on the filter were enumerated using an optical microscope (BX51, Olympus , Japan) by counting 1–3 randomly selected transects per filter. Only cells showing chlorophyll autofluorescence were considered as active cells and included in the counts. Each sample was counted in 3–5 times to ensure reproducibility. Cell concentrations (cells mL^{-1}) were calculated based on the average cell counts and the volume of water filtered. Total biomass (μL m^{-2}) of algae and cyanobacteria was then estimated by bio-volume (cell volume) per unit surface area. The biovolume was calculated from the volumes of geometric analogs of cell morphology: cyanobacterial cells were modeled as cylinders, and algal cells were represented as ellipsoids or spheres, depending on their morphology. Mean cell volume for each taxon was determined by measuring the dimensions of 50 individual cells per taxon. The morphological taxa composition (proportion) at each site was expressed as the relative abundance of each taxon to the total bio-volume. Mean values and standard deviations were calculated based on replicate samples collected from different surface areas at each site.

2.2.3 Major chemical solutes measurement

Major soluble ions in snow samples, including anions of NO_3^-, Cl^-, and SO_4^{2-} and cations of NH_4^+, K^+, Na^+, Mg^{2+}, and Ca^{2+}, were analyzed using an ion chromatography system (ICS-1100, Thermo Fisher Scientific, USA). Prior to analysis, melted samples were filtered through ion-free chromatographic discs (Chromate disk, pore size: 0.45 μm, GL Science, Japan) to eliminate particulate matter.

For anion analysis, a Dionex IonPac AS12A analytical column paired with an AG12A guard column was employed. The eluent consisted of a mixture of 2.7 mM Na_2CO_3 and 0.3 mM $NaHCO_3$, delivered at a flow rate of 1.5 mL min^{-1}. For cation analysis, a Dionex IonPac CS12A column was used with 20 mM methanesulfonic acid as the eluent, operating at a flow rate of 1.0 mL min^{-1}.

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2.2.4 Statistical data analysis

Dissimilarities in community composition of algae and cyanobacteria, as well as in ion composition across sampling period and surface status, were assessed using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis distance matrices, implemented with the adonis function in the R package "vegan" (Oksanen et al., 2010). Spearman's rank correlation analysis was conducted in OriginPro to examine relationships between algal/cyanobacterial biomass and chemical variables. Differences in total biomass and ion concentrations among sampling periods and surface conditions were evaluated using one-way analysis of variance (ANOVA) in OriginPro. Statistical significance was determined at $p < 0.05$.

3 Results

3.1 Observed algae and cyanobacteria on the glacier surface

Two taxa of algae and six taxa of cyanobacteria were identified on the glacier surface through microscopic observation (Fig. 3). The morphological characteristic of each taxon was described as follows, in conjunction with findings from previous DNA-based studies (Segawa et al., 2017; 2023). Molecular analyses previously detected a total of 20 cyanobacterial operational taxonomic units (OTUs) on the glacier surface.

Algae

(1) *Chloromonadinia* species

Cells were spherical in shape and lacked visible pyrenoids in the chloroplasts. Intracellular pigments appeared green and red, and all observed cells were in the zygote stage. Mean cell diameter was 16.0 ± 1.8 µm. Based on previously reported DNA metabarcoding data from this glacier, which showed that members of *Chloromonadinia* were highly abundant in snow samples (Segawa et al., 2023), these morphotypes were therefore assigned to *Chloromonadinia* species.

(2) *Cylindrocystis brébissonii*

Cells were cylindrical with rounded apices, containing two chloroplasts each with a central pyrenoid. However, only one chloroplast was observed in short, divided cells. Cells measured 28.3 ± 6.0 µm in length and 17.6 ± 1.9 µm in width.

Cyanobacteria

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(1) Oscillatoriaceae (Osc.) cyanobacteria 1

Trichomes lacked a sheath, and clear constrictions were visible between adjacent cells. Mean cell diameter was 1.6 ± 0.2 µm. This morphotype corresponded to OTU5 (*Pseudanabaena)* (Segawa et al., 2017).

(2) Oscillatoriaceae cyanobacteria 2

Trichome were enclosed within a colorless mucilaginous sheath. Green intracellular granules were observed within the cells. Mean cell diameter was 3.1 ± 0.5 µm. This morphotype corresponded to OTU4 (*Microcoleus*) species (Segawa et al., 2017).

(3) Oscillatoriaceae cyanobacterium 3

Trichome were surrounded by a colorless mucilaginous sheath, without conspicuous internal structures. Mean cell diameter was 1.5 ± 0.2 µm, This morphotype identified as OTUs 0 (unclassified), 8 (*Oscillatoriales*), and 9 (*Geitlerinema*) (Segawa et al., 2017).

(4) Chroococcaceae (Chr.) cyanobacterium 1

Spherical cells were surrounded by with brown or yellow mucilaginous sheaths and occurred as solitary or paired cells forming small colonies. Mean cell diameter was 3.8 ± 0.6 µm.

(5) Chroococcaceae cyanobacterium 2

Spherical paired cells without apparent colonies. Mean cell diameter was 3.9 ± 0.6 µm.

(6) Chroococcaceae cyanobacterium 3

Spherical cells with a mean diameter of 2.7 ± 1.1 µm.

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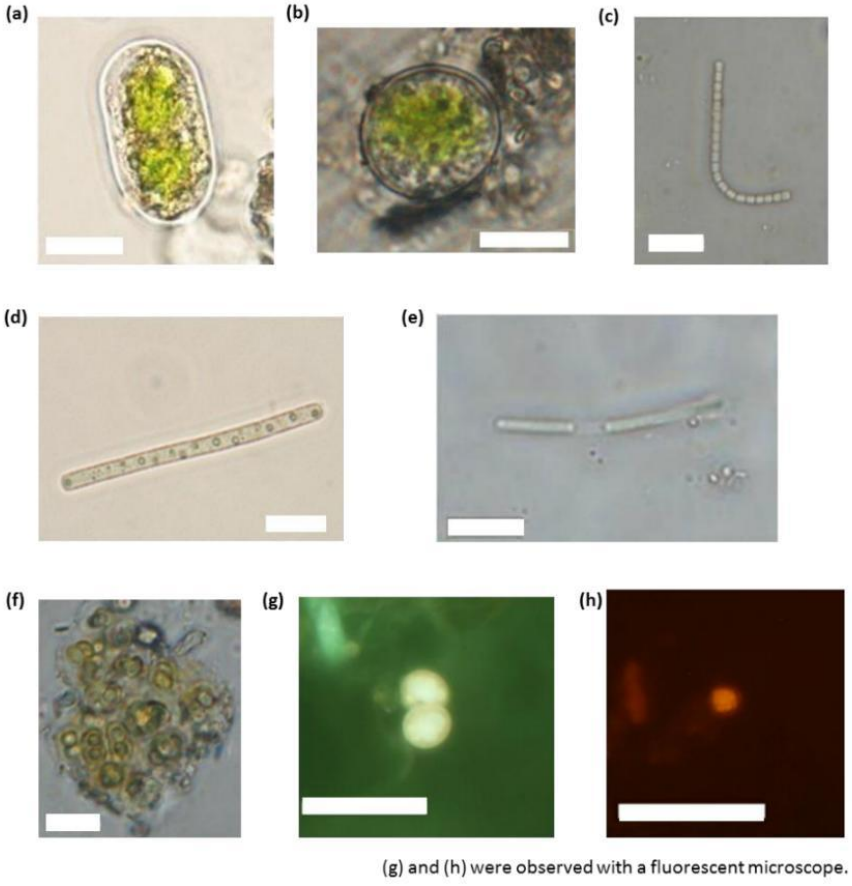

Figure 3: Photographs of algae and cyanobacteria observed on surface of Urumqi Glacier No.1. (a) *Cylindrocystis brébissonii*; (b) *Chloromonadinia* species; (c) Oscillatoriaceae cyanobacterium 1; (d) Oscillatoriaceae cyanobacterium 2; (e) Oscillatoriaceae cyanobacterium 3; (f) Chroococcaceae cyanobacterium 1; (g) Chroococcaceae cyanobacterium 2; (h) Chroococcaceae cyanobacterium 3. Scale bar = 10 μm

3.2 Seasonal and spatial variations in the total biomass of algae and cyanobacteria

The total bio-volume biomass of algae and cyanobacteria on the glacier surface remained relatively stable through the melt season (One-way ANOVA, $F = 0.007$, $p = 0.9 > 0.05$, Fig. 4). However, a marked increase in total biomass was observed when the snow surface transitioned to bare ice at the midstream sites (S4 and S5). At S4, biomass increased markedly from 4.7×10^{-3} mL m^{-2} in P1 to 0.42 mL m^{-2} in P2. At S5, although the biomass in P1 (3.7×10^{-3} mL m^{-2}) was not significantly different from that in P2 (1.2×10^{-3} mL m^{-2}), a significant increase was observed in P3, with biomass

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reaching 0.28 mL m^{-2}. Furthermore, the total biomass on the ice surface was significantly higher than that on the snow surface (One-way ANOVA, $F = 23.2$, $p < 0.01$).

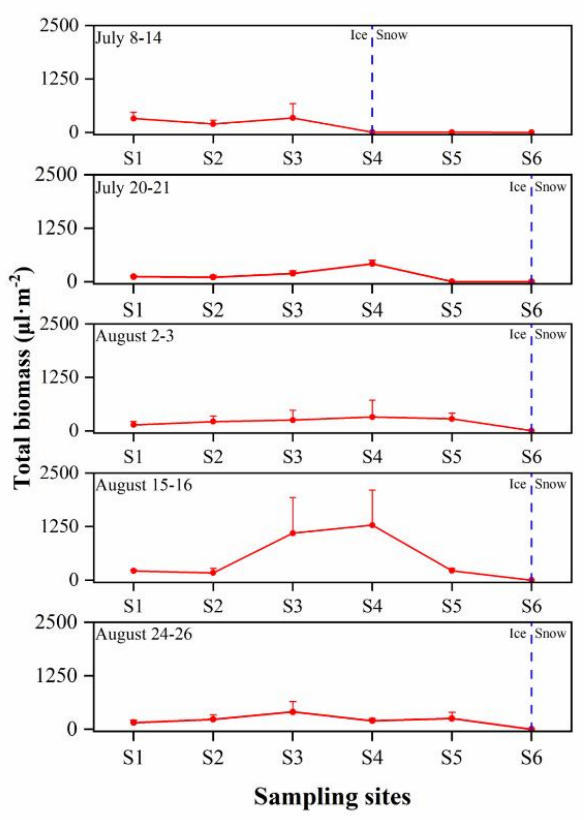

Figure 4: Seasonal and spatial variations in the total bio-volume biomass of algae and cyanobacteria on Urumqi Glacier No.1 from July to August 2013. The dashed line represents the boundary between the snow and ice surface.

3.3 Spatiotemporal changes of algal and cyanobacterial community composition on glacier surfaces

The relative dominance of algae and cyanobacteria varied with both sampling period and surface status (Fig. 5). PERMANOVA analysis indicated no significant differences ($p > 0.05$) in community composition across the different sampling periods but significant differences were found between snow and ice surfaces (PERMANOVA, $p < 0.01$). Specifically, algal taxa, primarily *Chloromonadinia* species, strongly dominated snow-covered surfaces, while cyanobacteria were consistently the dominant on bare ice surfaces throughout the study.

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In P1, filamentous cyanobacteria were dominant on ice surfaces of the downstream sites (S1 to S3), accounting for 61–75% of the total biomass, whereas the snow-covered upstream sites (S4 to S6) were prevailed by *Chloromonadinia* species, contributing 65–92% of the total biomass. By P2, the upstream expansion of bare ice was accompanied by a corresponding upstream shift in cyanobacterial dominance, leaving *Chloromonadinia* species predominant only at S5 and S6. From P3 onward, filamentous cyanobacteria consistently dominated from S1 to S5, while *Chloromonadinia* species remained dominant solely at the uppermost site, S6. For instance, in P5, filamentous cyanobacteria comprised 77–93% of the total biomass at S1 to S5, while *Chloromonadinia* species accounted for 82% at S6. An exception occurred in P4, during which filamentous cyanobacteria were dominant across all sites, comprising 61–84% of the total biomass.

Cylindrocystis brébissonii was exclusively detected on ice surfaces and was sporadically observed in one or two samples per sampling period. In P1, it was present at S2, accounting for 6% of the total biomass. In P2, the alga was observed at S3, contributing 8% of the total biomass. In P3, the taxon was detected at S2 and S4, accounting for 3% and 5% of the biomass, respectively. Its highest relative abundance was observed in P4 at S3, where it constituted 28% of the total biomass. In P5, it was present again at S2, comprising 5% of the total biomass.

Osc. cyanobacterium 1 showed a clear preference for ice surfaces, with biomass generally rising from P1 to P4, particularly at mid- to up-glacier ice sites. Its presence on snow surfaces was negligible across all periods, rarely exceeding 0.1 μL m^{-2}.

Osc. cyanobacteria 2 and 3 were the dominant cyanobacterial taxa on ice surfaces throughout the study period, constituting 65%–95% of the total cyanobacterial biomass across all ice sites and sampling periods.. Their biomass increased progressively from P1 to P4, with the highest values recorded at sites S3 and S4 during P4, where Osc. cyanobacterium 2 exceeded 300 μL m^{-2} and Osc. cyanobacterium 3 surpassed 470 μL m^{-2}. From P4 onward, a distinct spatial pattern emerged: Osc. cyanobacterium 2 dominated the downstream sites (S1–S2), whereas Osc. cyanobacterium 3 became dominant at the upstream sites (S3–S5). In contrast, both taxa were nearly absent on snow-covered surfaces, with biomass consistently below 1 μL m^{-2}.

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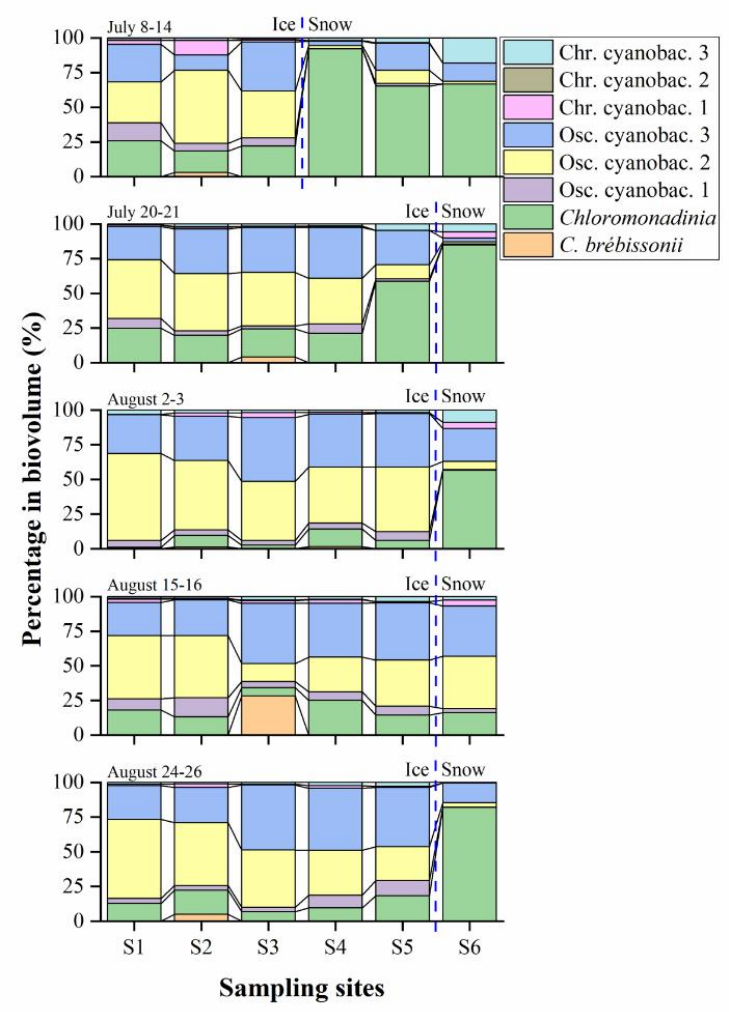

Figure 5: Seasonal and spatial variations in the morphological community structure of algae and cyanobacteria at study sites S1–S6 on Urumqi Glacier No.1 from July to August 2013. The dashed line represents the boundary between the snow and ice surface.

Among the unicellular cyanobacteria, Chr. cyanobacterium 1 showed a noticeable biomass increase by P4 on ice, reaching up to ~30 μL m^{-2} at sites S3 and S4. Chr. cyanobacteria 2 and 3 maintained relatively low abundance levels throughout all sampling sites and periods, with slight elevations observed on ice during P4. All three Chroococcaceae taxa were almost absent on snow surfaces (biomass < 0.13 μL m^{-2}) .

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3.4 Variations in chemical conditions across the sampling period and surface status

The concentrations of major ions showed notable temporal variation throughout the five sampling periods. Ca^{2+} consistently dominated the ionic composition, accounting for more than 58.3% of the total ion content, while the relative proportions of other ions fluctuated over time (Fig. 6a).

SO_4^{2-}, NO_3^-, K^+ and Mg^{2+} concentrations temporally varied significantly among sampling periods (one-way ANOVA, $p < 0.01$). SO_4^{2-} and NO_3^- both peaked in P1 (= 12.9 and = 6.8 μEq L^{-1}, respectively), declined sharply in P2, and showed secondary increases in P5. In contrast, K^+ remained stable in early periods (~5 μEq L^{-1}) before declining to its lowest level in P5 (= 1.7 μEq L^{-1}). Mg^{2+} exhibited elevated concentrations in P1 and P3 (= 20.3 and = 25.9 μEq L^{-1}), dropped markedly in P4, and partially rebounded in P5.

Significant differences in ion concentrations were also observed between surface status (ice vs. snow) (one-way ANOVA, $p < 0.01$, Fig. 6b). Ice surfaces consistently hold higher mean concentrations of crustally derived ions, including Ca^{2+} (125.5 vs. 22.6 μEq L^{-1}), Mg^{2+} (20.6 vs. 5.9 μEq L^{-1}), Na^+ (12.5 vs. 5.3 μEq L^{-1}) and K^+ (4.9 vs. 1.3 μEq L^{-1}). In contrast, snow surfaces showed higher concentrations of NO_3^- (2.3 vs. 6.0 μEq L^{-1}), SO_4^{2-} (6.3 vs. 10.1 μEq L^{-1}), and NH_4^+ (2.6 vs. 8.0 μEq L^{-1}).

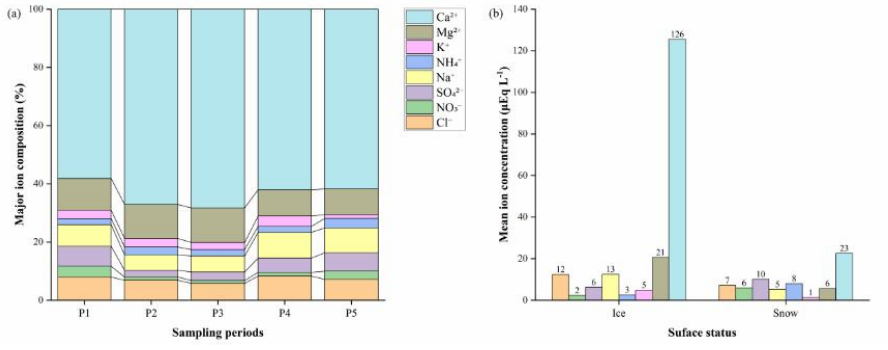

Figure 6: (a) Major ion composition in surface snow and ice at five sampling period (P1–P5). (b) Comparison of mean ion concentrations between snow and ice surfaces.

4 Discussion

4.1 Algal community dynamics in response to glacier surface transition

The algal biomass on Urumqi Glacier No.1 remained consistently low with minimal temporal variation, suggesting that algal proliferation is highly constrained in this environment. *Chloromonadinia* species

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was found on both snow and ice but showed a clear preference for snow, aligning with its classification as a snow-environment specialist (Takeuchi, 2001), similar to observations in the Himalayas (Yoshimura et al., 1997) and Altai Mountains (Takeuchi et al., 2006). Conversely, the green alga *C. brébissonii* was restricted to ice surfaces. Despite its presence, its sporadic and low abundance suggest it functions as an ice-specialist that fails to establish stable, large-scale populations on this glacier, contrasting with earlier classifications that often regard certain *Cylindrocystis* strains as opportunists with broader habitat ranges (Kol, 1942; Remias et al., 2012).

On this glacier, the role of algae in surface darkening is habitat-dependent. On snow, despite low biomass, *Chloromonadinia* species is likely the primary biological agent for albedo reduction due to the absence of cryoconite. However, on bare ice, the albedo-reducing effect of algae is negligible compared to the pronounced darkening mediated by cyanobacteria and mineral particles. This is consistent with studies suggesting that while snow algae can significantly lower albedo in the early melt season, their impact is often overshadowed by other light-absorbing particles once the ice is exposed (Lutz et al., 2016; Di Mauro et al., 2020).

4.2 Cyanobacterial dominance and its role in surface darkening

In contrast to the ephemeral nature of snow algae, the cyanobacterial community on Urumqi Glacier No. 1 exhibited remarkable temporal stability in total biomass, albeit with significant spatial and taxonomic shifts. While unicellular Chroococcaceae showed low and variable biomass, filamentous cyanobacteria (Oscillatoriaceae) maintained sustained dominance on ice surfaces throughout the melt season. This persistent presence of filamentous taxa underscores their critical role in surface darkening through two synergistic mechanisms: direct pigmentation and the structural aggregation of mineral particles into dark cryoconite granules.

The spatial distribution of these dominant filamentous cyanobacteria revealed a distinct altitudinal zonation from P4 onwards, despite the relatively uniform geochemical characteristics across the glacier. Osc. cyanobacterium 2 dominated the downstream sites (S1–S2), while Osc. cyanobacterium 3 prevailed at the mid-to-up-glacier sites (S3–S5). Given the lack of significant chemical gradients, this niche partitioning is likely driven by physical factors associated with altitude, specifically the duration of bare-ice exposure and the frequency of summer snowfall. The downstream sites (S1–S2) experience the earliest snow disappearance and the longest continuous melt season, allowing for the development

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of "mature" cryoconite communities. Osc. cyanobacterium 2 appears to be a late-successional specialist, capable of maintaining high biomass under conditions of prolonged meltwater flow and cumulative dust aggregation. Its dominance at lower altitudes suggests a high tolerance to the physical stability of older cryoconite granules in the stable, long-term habitats of the lower ablation zone. In contrast, the mid-to-up-glacier sites (S3–S5) encounter a much shorter exposure window and are frequently subjected to transient snow cover, which resets the surface temperature and temporarily halts microbial activity. The dominance of Osc. cyanobacterium 3 in these areas—marked by an explosive biomass increase exceeding 470 μL m^{-2} during P4—suggests it is a "pioneer-like" rapid colonizer. This taxon likely possesses physiological traits suited for rapid growth immediately following ice exposure or a higher resilience to the frequent freeze-thaw cycles and intermittent snow cover characteristic of higher altitudes.

This altitudinal segregation implies that the cyanobacterial community is not a monolithic assemblage but a strategically partitioned system. The presence of multiple dominant taxa with different spatio-temporal peaks ensures that the glacier surface maintains high biological biomass across a wide range of environmental conditions—from stable lower reaches to dynamic, intermittently snow-covered upper reaches. Such functional diversity within the Oscillatoriaceae ensures that the biological darkening effect is not localized or transient but remains stable and continuous across the entire ablation zone.

Unlike the ephemeral algal blooms observed on Arctic glaciers (Takeuchi, 2013), where darkening is highly sensitive to the seasonal timing of snowmelt, the biological impact on Urumqi Glacier No. 1 is stabilized by the formation and persistence of cryoconite granules. Filamentous cyanobacteria produce extracellular polymeric substances (EPS) that trap mineral dust, creating the dark, spherical aggregates characteristic of this region (Musilova et al., 2016; Segawa et al., 2017). A critical distinction is that these granules are not merely seasonal features; they can persist and grow over multiple melting seasons, effectively serving as long-term reservoirs for both mineral and organic matter. This multi-year development facilitates the accumulation of refractory organic compounds, such as humic substances, which significantly enhance the light-absorbing capacity of the granules (Takeuchi, 2002).

The structural stability provided by the cyanobacterial matrix ensures that these dark, humic-rich aggregates remain on the ice surface even during intermittent snowfall or minor scouring events. Given that such consolidated cryoconite granules exert a stronger and more localized albedo-reducing effect

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than the transient, distributed blooms of snow or ice algae (Cook et al., 2016; Hotaling et al., 2021), the "cyanobacteria-mineral synergy" driven by these specialized filamentous taxa represents the primary biological mechanism for persistent and cumulative surface darkening in Central Asian glaciers.

4.3 Environmental drivers: Nitrogen limitation and mineral-derived ions

The distinct community compositions on snow and ice surfaces suggest different environmental controls. We found significant negative correlations between inorganic nitrogen concentrations (NO_3^- and NH_4^+) and the relative abundance of dominant filamentous cyanobacteria (Oscillatoriaceae) ($p < 0.05$; Fig. 7). This suggests that nitrogen-poor ice surfaces favor these cyanobacteria, which are known to harbor metabolic pathways for efficient nitrogen utilization and recycling within the stable micro-habitats of cryoconite granules (Segawa et al., 2014; 2020; Murakami et al., 2022).

Furthermore, Oscillatoriaceae biomass positively correlated with mineral-derived ions (Ca^{2+}, Mg^{2+}, and K^+, $p < 0.05$, Fig. 7), which serve as proxies for mineral dust abundance (Li et al., 2010; Nagatsuka et al., 2014). The concentrations of these ions on Urumqi Glacier No.1 are substantially higher than those reported for Arctic glaciers, such as those in Svalbard, where mineral-derived ion concentrations are significantly lower due to limited dust input (Takeuchi et al., 2019). While the low-mineral environment of Svalbard glaciers typically favors the dominance of glacier algae on the ice surface, the high mineral availability on Urumqi Glacier No.1 provides a more suitable substrate and nutrient base for the proliferation of filamentous cyanobacteria and the subsequent development of cryoconite granules. This stark contrast in geochemical conditions explains why the primary biological drivers of albedo reduction differ so fundamentally between Central Asian and Arctic glacial systems.

This relationship highlights the critical importance of mineral availability for cyanobacterial colonization and granule formation. Our results mirror observations from the Greenland Ice Sheet, where phosphorus and mineral availability are key drivers of cyanobacterial growth (Uetake et al., 2019; McCutcheon et al., 2021), but this effect is likely amplified on Urumqi Glacier No.1 due to the extreme dust deposition characteristic of Central Asian mountains. In contrast, algal taxa showed no such correlations, suggesting their distribution may be driven by stochastic colonization or micro-scale physical factors like meltwater flow rather than macro-scale chemical parameters (Stibal et al., 2012a).

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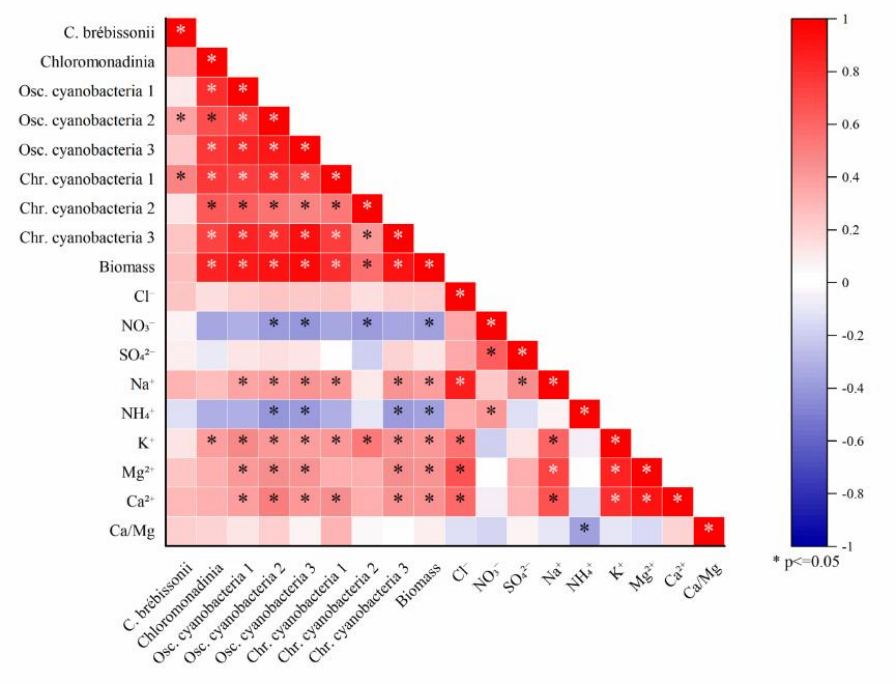

Figure 7: Correlation between major ion concentration and bio-volume of each algal and cyanobacterial taxa.

4.4 Ecological Implications and comparison with Arctic glaciers

One of the most significant ecological findings of this study is the complete absence of glacier algae, such as *Ancylonema* spp., which are the primary drivers of ice darkening on Arctic glaciers (e.g., Alaska, Svalbard) (Takeuchi 2013; Takeuchi et al., 2019). In polar regions, these Zygnematalean algae bloom on the ice surface, producing dark purple pigments that significantly reduce albedo (Williamson et al., 2018; Remias et al., 2012). However, on Urumqi Glacier No.1, this niche is entirely occupied by a stable, cyanobacteria-dominated community.

The absence of *Ancylonema* and the corresponding dominance of filamentous cyanobacteria (Oscillatoriaceae) are likely attributable to the unique geochemical and physical environment of Central Asia. Takeuchi et al. (2019) demonstrated that Arctic glaciers in Svalbard are characterized by extremely low mineral ion concentrations, a condition that appears to favor the proliferation of free-living glacier algae. In contrast, the high dust flux on Urumqi Glacier No.1 provides an abundance of mineral cations, resulting in substantially elevated ionic concentrations. For example, mean Mg^{2+}

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and Ca^{2+} concentrations on Urumqi Glacier No. 1 are approximately 13 and 59 times higher, respectively, than those reported for Svalbard (Mg^{2+}: 20.6 vs. 1.6 μEq L^{-1}; Ca^{2+}: 125.5 vs. 2.1 μEq L^{-1}). These elevated mineral inputs not only raises the ionic strength but may also maintain a higher pH on the ice surface. Central Asian glaciers are characterized by a high influx of mineral dust containing abundant carbonate minerals, particularly calcite ($CaCO_3$), from the surrounding arid regions (Li et al., 2010; Nagatsuka et al., 2014). The dissolution of these carbonate-rich particles consumes protons and releases bicarbonate (HCO_3^-), acting as a powerful geochemical buffer that maintains the meltwater pH in a neutral to alkaline range (typically pH 7.5–8.5), as documented in hydrochemical studies of Urumqi Glacier No. 1 (Li et al., 2007; Wu et al., 2012). Such alkaline and mineral-rich conditions may be physiologically inhibitory to *Ancylonema*, which typically thrives in the more acidic, ultra-oligotrophic environments characteristic of polar ice (Remias et al., 2012; McCutcheon et al., 2021).

Furthermore, the physical presence of massive mineral dust promotes the formation of cryoconite granules. As revealed by Segawa and Takeuchi (2010) on Qiyi Glacier and further elucidated by Chen et al. (2025) on Urumqi Glacier No.1, filamentous cyanobacteria act as "ecosystem engineers," trapping mineral particles to form stable, spherical aggregates. This process may physically exclude glacier algae by reducing the availability of "clean" ice surfaces required for their colonization.

These results suggest that the biological darkening of Central Asian glaciers follows a fundamentally different mechanism—a "cyanobacteria-mineral synergy"—compared to the "algal bloom" model of the Arctic. While Arctic darkening is often ephemeral and sensitive to seasonal snowmelt timing, the darkening on Urumqi Glacier No.1 is more persistent due to the structural stability of cyanobacterial cryoconite. Therefore, applying Arctic-based bio-albedo models to Central Asian glaciers may lead to significant errors, highlighting the need for region-specific models that account for high mineral loading and its role in shaping microbial community structures.

5 Conclusion

This study characterized the spatiotemporal dynamics of phototrophic communities on Urumqi Glacier No. 1, revealing an ecological structure fundamentally distinct from those of better-studied polar glacial systems. The primary finding of this research is the clear biological succession driven by the seasonal transition of the glacier surface. As the snowpack recedes, the community shifts from the

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dominance of the snow alga *Chloromonadinia* species to a massive proliferation of filamentous cyanobacteria (Oscillatoriaceae) on the exposed bare ice. This transition is marked by a significant increase in total biomass and the establishment of a stable microbial community that persists throughout the ablation period.

Crucially, this study highlights the complete absence of glacier algae such as *Ancylonema* spp., which are the primary drivers of ice darkening on Arctic glaciers. Instead, the biological darkening on Urumqi Glacier No.1 is governed by a specialized "cyanobacteria-mineral synergy." Our results demonstrate that the proliferation of dominant filamentous cyanobacteria is closely linked to high concentrations of mineral-derived ions and low inorganic nitrogen levels. This geochemical environment, shaped by high dust input from surrounding arid regions, appears to provide a specialized niche that favors cyanobacterial colonization and the structural development of cryoconite granules over the growth of eukaryotic glacier algae. Furthermore, we identified an altitudinal niche partitioning within the Oscillatoriaceae, where different taxa (e.g., Osc. cyanobacterium 2 and 3) dominate based on the duration of ice exposure and snowfall frequency. This functional diversity ensures that a high biological biomass is maintained across the entire ablation zone, regardless of altitudinal gradients.

The ecological implications of these findings are essential for predicting the future of alpine glaciers in a changing climate. Unlike the ephemeral algal blooms observed in Arctic regions, the darkening on Urumqi Glacier No. 1 is driven by structurally stable cryoconite granules that can persist and grow over multiple melt seasons. This multi-year development facilitates the accumulation of refractory humic substances, creating a more constant, cumulative, and resilient bio-albedo feedback mechanism. Under projected warming scenarios, including extended melt seasons and increased dust deposition, the expansion of these cyanobacterial communities may further accelerate glacier mass loss. Therefore, it is imperative to integrate region-specific microbial dynamics—characterized by the absence of glacier algae and the dominance of mineral-buffered, long-lived cyanobacterial aggregates—into global glacier melt models to improve the accuracy of water resource projections in Central Asia.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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Author contributions

YC and NT designed the study. YC and NT wrote and revised the manuscript with supports of XH and WZ. ST collected samples and quantified biomass of algae and cyanobacteria. NT measured ion concentration. YC and SL statistically analyzed data and draw Figs. ZL organized the field investigation.

Competing interests

The authors have declared that they have no competing interests in relation to this study.

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Preprint. Discussion started: 20 March 2026
© Author(s) 2026. CC BY 4.0 License.

References

Anesio, A.M. and Laybourn-Parry, J.: Glaciers and ice sheets as a biome, Trends Ecol. Evol., 27, 219-225, https://doi.org/10.1016/j.tree.2011.09.012, 2012.

Anesio, A.M., Lutz, S., Chrismas, N.A. and Benning, L.G.: The microbiome of glaciers and ice sheets, npj Biofilms Microbi., 3, 10. https://doi.org/10.1038/s41522-017-0019-0, 2017.

Chen, Y., Takeuchi, N., Tanaka, S. and Li, Z.:. Aggregation of mineral particles in cryoconite granules by multiple species of cyanobacteria on Urumqi Glacier No. 1, China, Front. Earth Sci., 13, 1596472, https://doi.org/10.3389/feart.2025.1596472, 2025.

Cook, J., Edwards, A., Takeuchi, N. and Irvine-Fynn, T.: Cryoconite: the dark biological secret of the cryosphere, Prog. Phys. Geog., 40, 66-111, https://doi.org/10.1177/0309133315616574, 2016.

Davey, M.P., Norman, L., Sterk, P., Huete-Ortega, M., Bunbury, F., Loh, B.K.W., Stockton, S., Peck, L.S., Convey, P., Newsham, K.K. and Smith, A.G.: Snow algae communities in Antarctica: metabolic and taxonomic composition, New Phytologist., 222, 1242-1255, https://doi.org/10.1111/nph.15701, 2019.

Di Mauro, B., Garzonio, R., Baccolo, G., Franzetti, A., Pittino, F., Leoni, B., Remias, D., Colombo, R. and Rossini, M.: Glacier algae foster ice-albedo feedback in the European Alps, Sci. Rep., 10, 4739, https://doi.org/10.1038/s41598-020-61762-0, 2020.

Dong, Z., Qin, D., Ren, J., Li, K. and Li, Z., Variations in the equilibrium line altitude of Urumqi Glacier No. 1, Tianshan Mountains, over the past 50 years, Chinese Sci. Bull., 57, 4776-4783, https://doi.org/10.1007/s11434-012-5524-1, 2012.

Hodson, A., Anesio, A.M., Tranter, M., Fountain, A., Osborn, M., Priscu, J., Laybourn-Parry, J. and Sattler, B.: Glacial ecosystems, Ecol. Monogr., 78, 41-67, https://doi.org/10.1890/07-0187.1, 2008.

Hotaling, S., Lutz, S., Dial, R.J., Anesio, A.M., Benning, L.G., Fountain, A.G., Kelley, J.L., McCutcheon, J., Skiles, S.M., Takeuchi, N. and Hamilton, T.L.: Biological albedo reduction on ice sheets, glaciers, and snowfields. Earth-sci. Rev., 220, 103728, https://doi.org/10.1016/j.earscirev.2021.103728, 2021.

Hugonnet, R., McNabb, R., Berthier, E., Menounos, B., Nuth, C., Girod, L., Farinotti, D., Huss, M., Dussaillant, I., Brun, F. and Kääb, A.: Accelerated global glacier mass loss in the early twenty-first century, Nature, 592, 726-731, https://doi.org/10.1038/s41586-021-03436-z, 2021.

https://doi.org/10.5194/egusphere-2026-1281
Preprint. Discussion started: 20 March 2026
© Author(s) 2026. CC BY 4.0 License.

Irvine-Fynn, T.D. and Edwards, A.: A frozen asset: the potential of flow cytometry in constraining the glacial biome, Cytom. Part A, 85, 3-7, https://doi.org/10.1002/cyto.a.22411, 2014.

Kol, E. and Taylor, W.R.: The snow and ice algae of Alaska, Smithsonian Miscellaneous Collections, 101, Smithsonian Institution, 36 pp., 1942.

Koshima, S., Seko, K., Yoshimura, Y.: Biotic acceleration of glacier melting in Yala glacier, Langtang region, Nepal Himalaya, IAHS Publ., 218, 309-319, 1993.

Li, X., Li, Z., Ding, Y., Liu, S., Zhao, Z., Luo, L., Pang, H., Li, C., Li, H., You, X. and Wang, F.: Seasonal variations of pH and electrical conductivity in a snow-firn pack on Glacier No. 1, eastern Tianshan, China, Cold Reg. Sci. Technol., 48, 55-63, https://doi.org/10.1016/j.coldregions.2006.09.006, 2007.

Li, Z., Li, H., Dong, Z. and Zhang, M.: Chemical characteristics and environmental significance of fresh snow deposition on Urumqi Glacier No. 1 of Tianshan Mountains, China, Chinese Geogr. Sci., 20, 389-397, https://doi.org/10.1007/s11769-010-0412-6, 2010.

Ling, H.U. and Seppelt, R.D.: Snow algae of the Windmill Islands, continental Antarctica. Mesotaenium berggrenii (Zygnematales, Chlorophyta) the alga of grey snow, Antarct. Sci., 2, 143-148, https://doi.org/10.1017/s0954102090000189, 1990.

Lutz, S., Anesio, A.M., Edwards, A. and Benning, L.G.: Linking microbial diversity and functionality of arctic glacial surface habitats, Enviro. Microbiol., 19, 551-565, https://doi.org/10.1111/1462-2920.13494, 2017.

Lutz, S., Anesio, A.M., Raiswell, R., Edwards, A., Newton, R.J., Gill, F. and Benning, L.G.: The biogeography of red snow microbiomes and their role in melting arctic glaciers, Nat. Comm., 7, 11968, https://doi.org/10.1038/ncomms11968, 2016.

McCutcheon, J., Lutz, S., Williamson, C., Cook, J.M., Tedstone, A.J., Vanderstraeten, A., Wilson, S., Stockdale, A., Bonneville, S., Anesio, A.M. and Yallop, M.L.: Mineral phosphorus drives glacier algal blooms on the Greenland Ice Sheet, Nat. Comm., 12, 570, https://doi.org/10.1038/s41467-020-20627-w, 2021.

Murakami, T., Takeuchi, N., Mori, H., Hirose, Y., Edwards, A., Irvine-Fynn, T., Li, Z., Ishii, S. and Segawa, T.: Metagenomics reveals global-scale contrasts in nitrogen cycling and cyanobacterial light-harvesting mechanisms in glacier cryoconite, Microbiome, 10, 1-14, https://doi.org/10.1186/s40168-022-01238-7, 2022.

https://doi.org/10.5194/egusphere-2026-1281
Preprint. Discussion started: 20 March 2026
© Author(s) 2026. CC BY 4.0 License.

538 Musilova, M., Tranter, M., Bamber, J.L., Takeuchi, N. and Anesio, A.M.: Experimental evidence that
539 microbial activity lowers the albedo of glaciers. Geochem, Perspect. Lett., 2, 106-116,
540 https://doi.org/10.7185/geochemlet.1611, 2016.
541 Nagatsuka, N., Takeuchi, N., Nakano, T., Shin, K. and Kokado, E.: Geographical variations in Sr and
542 Nd isotopic ratios of cryoconite on Asian glaciers, Environ. Res. Lett., 9, 045007,
543 https://doi.org/10.1088/1748-9326/9/4/045007, 2014.
544 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'hara, R., Simpson, G. L., Solymos, P., Stevens,
545 M. H. H., and Wagner, H.: vegan: Community Ecology Package. R package version 1.17-2,
546 https://cran.r-project.org/web/packages/vegan/index.html, 23, 2010.
547 Remias, D., Holzinger, A., Aigner, S. and Lütz, C.: Ecophysiology and ultrastructure of Ancylonema
548 nordenskiöldii (Zygnematales, Streptophyta), causing brown ice on glaciers in Svalbard (high arctic),
549 Polar Biol., 35, 899-908, https://doi.org/10.1007/s00300-011-1135-6, 2012.
550 Segawa, T. and Takeuchi, N., Cyanobacterial communities on Qiyi glacier, Qilian Shan, China. Ann.
551 Glaciol., 51, 135-144, https://doi.org/10.3189/172756411795932047, 2010.
552 Segawa, T., Ishii, S., Ohte, N., Akiyoshi, A., Yamada, A., Maruyama, F., Li, Z., Hongoh, Y. and
553 Takeuchi, N.: The nitrogen cycle in cryoconites: naturally occurring nitrification-denitrification
554 granules on a glacier, Environ. Microbiol., 16, 3250-3262, https://doi.org/10.1111/1462-2920.12543,
555 2014.
556 Segawa, T., Matsuzaki, R., Takeuchi, N., Akiyoshi, A., Navarro, F., Sugiyama, S., Yonezawa, T. and
557 Mori, H.: Bipolar dispersal of red-snow algae, Nat. Commun., 9, 3094,
558 https://doi.org/10.1038/s41467-018-05521-w, 2018.
559 Segawa, T., Takeuchi, N., Mori, H., Rathnayake, R.M., Li, Z., Akiyoshi, A., Satoh, H. and Ishii, S.,
560 Redox stratification within cryoconite granules influences the nitrogen cycle on glaciers, FEMS
561 Microbiol. Ecol., 96, fiaa199, https://doi.org/10.1093/femsec/fiaa199, 2020.
562 Segawa, T., Yonezawa, T., Edwards, A., Akiyoshi, A., Tanaka, S., Uetake, J., Irvine-Fynn, T., Fukui,
563 K., Li, Z. and Takeuchi, N.: Biogeography of cryoconite forming cyanobacteria on polar and Asian
564 glaciers, J. Biogeogr., 44, 2849-2861, https://doi.org/10.1111/jbi.13089, 2017.
565 Segawa, T., Yonezawa, T., Matsuzaki, R., Mori, H., Akiyoshi, A., Navarro, F., Fujita, K., Aizen, V.B.,
566 Li, Z., Mano, S. and Takeuchi, N.: Evolution of snow algae, from cosmopolitans to endemics, revealed

https://doi.org/10.5194/egusphere-2026-1281
Preprint. Discussion started: 20 March 2026
© Author(s) 2026. CC BY 4.0 License.

by DNA analysis of ancient ice, ISME J., 17, 491-501, https://doi.org/10.1038/s41396-023-01359-3, 2023.

Singh, P., Kumar, N. and Pal, S.: Chapter 10 - Cyanobacteria in the polar regions: diversity, adaptation, and taxonomic problems, Understanding Present and Past Arctic Environments, 189-212, ISBN 9780128228692, https://doi.org/10.1016/B978-0-12-822869-2.00013-X，2021.

Stibal, M. and Tranter, M.: Laboratory investigation of inorganic carbon uptake by cryoconite debris from Werenskioldbreen, Svalbard, J. Geophys. Res-Biogeo., 112, https://doi.org/10.1029/2007JG000429, 2007.

Stibal, M., Šabacká, M. and Žárský, J.: Biological processes on glacier and ice sheet surfaces, Nat. Geosci., 5, 771-774, https://doi.org/10.1038/ngeo1611, 2012a.

Stibal, M., Telling, J., Cook, J., Mak, K.M., Hodson, A. and Anesio, A.M.: Environmental controls on microbial abundance and activity on the Greenland ice sheet: a multivariate analysis approach, Micro. Ecol., 63, 74-84. https://doi.org/10.1007/s00248-011-9935-3, 2012b.

Takeuchi, N. and Li, Z.: Characteristics of surface dust on Ürümqi glacier No. 1 in the Tien Shan mountains, China, Arct. Antarct. Alp. Res., 40, 744-750, https://doi.org/10.1657/1523-0430(07-094)[takeuchi]2.0.co;2, 2008.

Takeuchi, N., Ishida, Y. and Li, Z.: Microscopic analyses of insoluble particles in an ice core of Ürümqi Glacier No. 1: Quantification of mineral and organic particles, J. Earth Sci., 22, 431-440, https://doi.org/10.1007/s12583-011-0197-2, 2011.

Takeuchi, N., Sakaki, R., Uetake, J., Nagatsuka, N., Shimada, R., Niwano, M. and Aoki, T.: Temporal variations of cryoconite holes and cryoconite coverage on the ablation ice surface of Qaanaaq Glacier in northwest Greenland, Ann. Glaciol., 59, 21-30, https://doi.org/10.1017/aog.2018.19, 2018.

Takeuchi, N., Tanaka, S., Konno, Y., Irvine-Fynn, T.D., Rassner, S.M. and Edwards, A.: Variations in phototroph communities on the ablating bare-ice surface of glaciers on Brøggerhalvøya, Svalbard, Front. Earth Sci., 7, 4, https://doi.org/10.3389/feart.2019.00004, 2019.

Takeuchi, N., Uetake, J., Fujita, K., Aizen, V.B. and Nikitin, S.D.: A snow algal community on Akkem glacier in the Russian Altai mountains, Ann. Glaciology, 43, 378-384, https://doi.org/10.3189/172756406781812113, 2006.

https://doi.org/10.5194/egusphere-2026-1281
Preprint. Discussion started: 20 March 2026
© Author(s) 2026. CC BY 4.0 License.

595 Takeuchi, N.: Optical characteristics of cryoconite (surface dust) on glaciers: the relationship between
596 light absorbency and the property of organic matter contained in the cryoconite, Ann. Glaciology, 34,
597 409-414, https://doi.org/10.3189/172756402781817743, 2002.
598 Takeuchi, N.: Seasonal and altitudinal variations in snow algal communities on an Alaskan glacier
599 (Gulkana glacier in the Alaska range), Environ. Res. Lett., 8, 035002,
600 https://doi.org/10.1088/1748-9326/8/3/035002, 2013.
601 Takeuchi, N.: The altitudinal distribution of snow algae on an Alaska glacier (Gulkana Glacier in the
602 Alaska Range), Hydrol. Process., 15, 3447-3459, https://doi.org/10.1002/hyp.1040, 2001.
603 Uetake, J., Naganuma, T., Hebsgaard, M.B., Kanda, H. and Kohshima, S.: Communities of algae and
604 cyanobacteria on glaciers in west Greenland, Polar Sci., 4, pp.71-80,
605 https://doi.org/10.1016/j.polar.2010.03.002, 2010.
606 Uetake, J., Nagatsuka, N., Onuma, Y., Takeuchi, N., Motoyama, H. and Aoki, T.: Bacterial community
607 changes with granule size in cryoconite and their susceptibility to exogenous nutrients on NW
608 Greenland glaciers, FEMS Microbiol. Ecol., 95, fiz075, https://doi.org/10.1093/femsec/fiz075, 2019.
609 Williamson, C.J., Anesio, A.M., Cook, J., Tedstone, A., Poniecka, E., Holland, A., Fagan, D., Tranter,
610 M. and Yallop, M.L.: Ice algal bloom development on the surface of the Greenland Ice Sheet, FEMS
611 Microbiol. Ecol., 94, fiy025, https://doi.org/10.1093/femsec/fiy025, 2018.
612 Wu, G., Zhang, C., Li, Z., Zhang, X. and Gao, S.: Iron content and solubility in dust from high-alpine
613 snow along a north-south transect of High Asia, Tellus B, 64, 17735,
614 https://doi.org/10.3402/tellusb.v64i0.17735, 2012.
615 Yallop, M.L., Anesio, A.M., Perkins, R.G., Cook, J., Telling, J., Fagan, D., MacFarlane, J., Stibal, M.,
616 Barker, G., Bellas, C. and Hodson, A.: Photophysiology and albedo-changing potential of the ice algal
617 community on the surface of the Greenland ice sheet, ISME J., 6, 2302-2313,
618 https://doi.org/10.1038/ismej.2012.107, 2012.
619 Ye, B., Yang, D., Jiao, K., Han, T., Jin, Z., Yang, H. and Li, Z.: The Urumqi River source glacier No. 1,
620 Tianshan, China: changes over the past 45 years, Geophys. Res. Lett., 32,
621 https://doi.org/10.1029/2005gl024178, 2005.
622 Yoshimura, Y., Kohshima, S. and Ohtani, S.: A community of snow algae on a Himalayan glacier:
623 change of algal biomass and community structure with altitude, Arct. Antarct. Alp. Res., 29, 126-137,
624 https://doi.org/10.1080/00040851.1997.12003222, 1997.

https://doi.org/10.5194/egusphere-2026-1281
Preprint. Discussion started: 20 March 2026
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625 Yue, X., Li, Z., Li, H., Wang, F. and Jin, S.: Multi-temporal variations in surface albedo on Urumqi
626 glacier No. 1 in Tien Shan, under arid and semi-arid environment, Remote Sens., 14, 808,
627 https://doi.org/10.3390/rs14040808, 2022.