Divergent Assembly and Co-Occurrence Patterns Between Bacterial and Fungal Communities on the Surface of Two Debris-Covered Glaciers from Mountain Gongga

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Abstract

Background

Microbial communities in supraglacial habitats are essential in driving the biogeochemical cycling in mountain glacial ecosystems. However, the microbial assemblage and co-occurrence pattern on the surface of the debris-covered glaciers (DCGs) remain unknown. Herein, the bacterial and fungal communities on supraglacial debris of Dagongba and Hailuoguo glacier (Mountain Gongga, southeast Tibetan Plateau, China) were investigated by high-throughput sequencing. The ecological determinants driving their distribution and diversity were also investigated.

Results

The bacterial richness showed a succession sequence on the supraglacial debris transect and positively correlated with basic nutrients content included carbon and nitrogen, but fungal richness no clear pattern and positively correlated with calcium (Ca) content ($p < 0.05$). The distribution of bacterial communities was explained more by environmental factors compared with fungal communities. The beta diversity distances of fungal communities separated better than bacterial communities, indicated that fungal communities show more variations across glaciers and sites. Interestingly, the glacier surface velocity and potassium (K) content were important in shaping microbial beta diversity. Furthermore, the bacterial co-occurrence networks were comprised of highly connected Operational Taxonomic Units (OTUs) with low modularity, particularly in Hailuoguo glacier. But fungal co-occurrence networks were less connected and tend to distribute more random.

Conclusions

The assembly processes of bacterial communities were more deterministic, but fungi communities were more stochastic in supraglacial debris. Both the co-occurrence network of bacterial and fungal communities in supraglacial debris from Dagongba glacier (higher microbial diversity) are relatively simple and more stable. This study provides insights into mechanisms that drive the establishment and early assembly of microbial communities, which provided microbial ecological basis for the biodiversity protection of glacier system.

Background

Debris cover is present on 44% of Earth's glaciers [1], particularly on high-mountain areas. The debris-covered glaciers (DCGs) are characterized by a continuous layer of debris on their tongues [2–4]. The DCGs are different from the debris-free glaciers (clean glacier) in Greenland ice sheet and Antarctica, it's typical "dirty glacier", which are considered to be one of the areas hosted a high biodiversity in the continental glaciated environment [5]. The surface of DCGs colonized by microbes included three

domains: bacteria [4], fungi and Archaea [6, 7], as well animal communities such as nematodes, rotifers [5], arthropod [8], and some plants communities included trees and shrubs [9]. Those microorganisms, particular the autotrophic microbes [10], play key roles in driving the soil development, promoting the higher trophic plants colonization, and mediating the biogeochemical cycling in supraglacial ecosystems. However, the distribution and assemblage of microbial communities in DCGs were still unexplored due to the harsh conditions, remote location, and the difficulty in sampling.

The present studies conducted on the mountain glacial ecosystems were widely focus on microbial diversity and assembling processes on the glacier forefield [11–14] and the cryoconite holes [15–18]. But remarkably, the supraglacial debris as one of the important sources of barren soil on forefield after glacier retreat and an important channel for high-altitude life migration downward, have been overlooked, it is an unexplored frontier in the cryosphere microbial studies [6]. The supraglacial debris mainly originates from englacial melt-out material, rockfalls and landslides from surrounding slopes, and wind blows dust, range from a few millimeters to more than several meters, move slowly toward the glacier terminus. Thereby, the debris layer usually is thicker [19, 20] and longer of exposure toward the glacier terminus. Evidence from the Middle Fork Toklat Glacier (Alaska, USA) [6] and Miage Glacier (Mont Blanc massif, Western Alps, Italy) [4] demonstrated that the surface of a debris-covered glacier existed a chronosequence. The arthropod, bacterial and fungal communities present a biogeographical distribution along the supraglacial transect [8], the communities change from photosynthetic to heterotrophic [6] and the community complex increased toward the glacier terminus [4]. Under the fact of rapid global glacial retreat, investigating the microbial distributions and its influenced factors on the surface of debris-covered glaciers, is essential for better excavating microbiota resources and functions, as well maintaining the stability of glaciers and surrounding ecosystems.

From the few studies refer microbes that have been done on the surface of DCGs, it only focused on the description of microbial taxa and spatial structure [4, 6, 21]. On Miage and Belvedere glacier (Alps, Italian), it found that the most abundant bacterial taxa were *Actinobacteridae*, *Sphingobacteriales* and *Burkholderiales*, and the genus *Polaromonas* has a high abundance in cold environments and contributed to rock weathering [4]. Furthermore, Environmental factors included the ice ablation rate, nitrogen availability, and organic carbon content were play important roles in driving the distribution and diversity of microbial communities on supraglacial debris ecosystems [4, 6]. Nevertheless, studies conducted by Franzetti et al. [4] and Darcy et al. [6] were involved in limited environment factors. For comprehensively understand the mechanism of how microbial communities distributed in supraglacial transect and how they maintain their diversity, it is necessary to comprehensively investigate more environmental variables included both the glaciological parameters and debris Physiochemical properties. More importantly, the positive (commensalism, mutualism) and negative (amensalism, parasitism or predation and competition) interactions among microbial communities contributed to shaping the community physiognomy [22], affecting the community dynamics [23–25].

Microbial co-occurrence network has been widely used for investigating the microbial interactions in an ecosystem [23, 26–29] and identifying the microbial keystone taxa that may not the most abundant taxa

but play roles in shaping community structure and driving ecosystem function [30, 31]. Bacterial and fungal communities are responsible for many of the biogeochemical processes that drive terrestrial ecological productivity, they are different in metabolic process [14], stress tolerance [32, 33], and substrate preferences [34]. Bacteria has a stronger dispersal capability than fungi [35], and show a wider range of physiologies than fungi [36]. Therefore, bacteria are more expected to be early colonists of the nutrient-limited, plant-free habitats, included supraglacial debris. In addition, co-occurrence network has been used to reflect microbial assembly mechanism. A more compact and connected network indicated that microbial community assembly was determined more by deterministic processes, on the contrary, a looser and separated network indicated that microbial community assembly was determined more by stochastic processes [14]. At present, the bacterial and fungal assemblage and co-occurrence pattern on the surface of the debris-covered glaciers (DCGs) has received much less attention.

The Dagongba Glacier and Hailuogou Glacier are two large and typical DCGs at Mt. Gongga. Southeast Tibetan Plateau, China. They located at the similar latitude, distinct in elevation, and both are monsoonal temperate glacier, and show niche gradient in their tongue from the upper part to the glacial terminus [37–39]. They are ideal place to compare the assemblage and co-occurrence patterns of bacterial and fungal communities. In this study, it aims to characterize the microbial communities within the supraglacial debris, which represents an under-explored extreme habitat, and aim to investigate the microbial community diversity and its driving factors, as well the intraspecific interaction of fungal and bacterial communities. Do bacterial and fungal communities assemble differently on the different supraglacial debris habitat? What environmental variables control the diversity of bacterial and fungal communities in supraglacial debris ecosystems? Previous studies found that bacterial community assembly was primarily governed by deterministic processes, while fungal communities were more determined by historical (stochastic) effects [14, 36, 40]. Therefore, it speculates that the bacterial and fungi communities were distinct across glaciers and sites, bacterial assemblage were more deterministic which driving by the environmental variables, while fungal assemblage are more stochastic which independent on environmental variables.

Methods

Site description and Debris sampling

The Mt. Gongga located on the southeastern edge of the Tibetan Plateau. Climate in this region is classic monsoon-type [41], with a mean annual precipitation of approximately 1151 mm on the western slope (3700 m a.s.l.), and 1938 mm on the eastern slope (3000 m a.s.l.). The mean annual air temperature is around 2.2°C on the western slope (3700 m a.s.l.) and 3.9°C on the eastern slope (3000 m a.s.l.) [42, 43]. The Dagongba (29°34'N, 101°48'E) glacier and Hailuogou (29°34'N, 101°59'E) Glacier are two typical DCGs, located on the western and eastern slope of Mt. Gongga (Fig. 1), respectively. The terminus elevation of Dagongba Glaciers is 3965 m a.s.l., debris-covered from about 4500 m a.s.l. downwards to the terminus. The terminus elevation of Hailuogou Glacier is 3015 m a.s.l., debris-covered from about 3700 m a.s.l. downwards to the terminus. Both Dagongba and Hailuogou Glaciers are experienced

remarkable terminus retreat [37, 38, 44]. The two glaciers significantly differ in glaciological parameters and ecological characteristics (Figure S1 and Table S1 (Supplementary Materials)). Specifically, there are higher values of glacier surface velocity (GSV) in Hailuoguo glacier than in Dagongba glaciers. The GSV was calculated by temperature-index mass balance model [45]. The debris mainly composed of crystalline rocks: gneiss, micaschists and granite. Debris thickness was evaluated by empirical models, kinetic surface temperature maps (pixel size $30 \times 30 \text{ m}^2$) acquired by the Landsat-8/TIRS on 25 August 2019[46–48], which were higher in Dagongba glacier (26.2-28.9m) than in Hailuoguo glacier (8.8-26.9m).

For investigating the succession patterns of microbial communities along the supraglacial debris transect, the debris samples were aseptically collected from the surface (0-15cm) of the glacier tongue at approximately constant intervals in July 2020. According to the reachability, 7 sites (D1 to D7) were set from 4018 to 4209 m a.s.l. on the Dagongba glacier, and 10 sites (H1 to H10) were set from 2998 to 3567 m a.s.l. on the Hailuoguo glacier. To avoid the new exposed debris that fall down from the slopes, all sites were distributed along the middle transect of the glacial tongue (Fig. 1). More details of the sampling sites are listed in Table S1. At each site the samples were collected from more than five plots ($1 \times 1 \text{ m}$) and mixed into one homogenized composite sample, visible plant roots and residues were removed before mixing. Overall, 17 debris samples were aseptically collected, then kept at -20°C during transport to the laboratory. The debris samples were divided into two parts: one was stored at -80°C for biological analyses and another stored at 4°C for physicochemical analyses until further processing.

Debris Physiochemical Analysis

The supraglacial debris samples were similar to barren soil, the physiochemical characteristics were determined according to the methods for soil. The particle composition (clay%, silt%, sand%) were measured using the Pipette method and characterized based on the international classification schemes (ISSS: International Soil Science Society). The pH was measured using a soil: water (1:2.5) slurry with a digital pH meter (FE20, Mettler-Toledo Instruments, China). Total nitrogen (TN), total carbon (TC) and organic matter (OM) were measured using an element analyzer (Vario TOC cube; Elementar, Langenselbold, Germany). Ammonium-N ($\text{NH}_4^+ - \text{N}$) and nitrate-N ($\text{NO}_3^- - \text{N}$) were measured using colorimetric method with a UV-vis spectrophotometer (UV-1800, Shimadzu, Japan; cuvette of Brand, Germany). Soil alkali-hydrolyzable nitrogen (AN) content was measured by alkaline hydrolysis diffusion method, Available phosphorus (AP) content was measured by Mo–Sb anti-spectrophotometer method, Available potassium (AK) content was measured by atomic absorption spectrophotometry. The elemental determination of metals included Aluminium (Al), Iron (Fe), Calcium (Ca), Potassium (K), Magnesium (Mg), Sodium (Na), Phosphorus (P), Manganese (Mn) were measured by an inductively coupled plasma optical emission spectrometer (ICP-OES, Optimal 2000 DV; Perkin-Elmer, USA). The detailed procedures for soil physiochemical analysis described by Bao [49].

DNA extraction, pyrosequencing

DNA was extracted from approximately 0.5 g debris using DNeasy® PowerSoil® Kit (Cat. No. 12888, QIAGEN GmbH, Hilden, Germany) according to the manufacturer's instructions. The purity and quantity of the DNA was verified using a NanoDrop 2000 instrument and agarose gel electrophoresis. The diluted genome DNA (1 ng/mL) was used as template for polymerase chain reaction (PCR) amplification with the barcoded primers and Tks Gflex DNA Polymerase (Cat. No. R060B, Takara Biochemicals, Beijing, China). The V3-V4 variable regions of 16S rRNA gene was amplified with universal primers 343 F and 798 R for bacterial diversity analysis [50, 51], and the ITS I variable regions was amplified with universal primers ITS1 F and ITS2 R for fungal diversity analysis as depicted by Schoch, Seifert, Huhndorf, Robert, Spouge, Levesque, Chen [52], Mukherjee, Chandra, Retuerto, Sikaroodi, Brown, Jurevic, Salata, Lederman, Gillevet, Ghannoum [53], respectively. The primer sequences are provided in Table S2(Supplementary Materials).

The first round of PCR amplification was performed with 1 µl (50 ng) template DNA in 30 µl reactions, employing an initial denaturation of 94°C for 5 min, followed by 26 cycles (30 s at 94°C, 30 s at 56°C and 20 s at 72°C), and a final extension of for 5 min at 72°C. Amplicon quality was visualized using gel electrophoresis, purified with AMPure XP beads (Beckman Coulter, Brea, CA, United States), and immediately use 1 µl products as template in 30 µl reactions for the second round of PCR (seven cycles). After purified with the AMPure XP beads again, the final amplicon was quantified using Qubit dsDNA Assay kit (Cat. No. Q32854, Life Technologies, Grand Island, NY, United States). Equal amounts of purified amplicon were pooled for subsequent sequencing [50, 54]. High-throughput sequencing of amplicons was performed on the Illumina MiSeq platform (Illumina, San Diego, CA, United States) at OEbiotech company (Shanghai, China). Sequencing data for bacterial and fungal communities were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive(<http://trace.ncbi.nlm.nih.gov/Traces/sra/>) under the accession numbers of PRJNA797905 (bacteria) and PRJNA798561 (fungi).

Sequence processing

Raw sequencing data were stored in the FASTQ format. Paired-end reads were then joined using Trimmomatic software [55]. Trimmed and assembled using FLASH software (10bp, 200bp, 20%) [56], then denoised and removed chimera using QIIME software [57]. Bacterial and fungal taxonomic assignment conducted using the RDP classifier [58] and blast [59], and clustered into operational taxonomic units using a 97% identity threshold via Vsearch software [60]. The details have been described by Guo et al [61] and Jiang et al [62]. The valid tags, mean length and OTU counts for bacteria and fungi has been listed in Table S3(Supplementary Materials).

Bioinformatic and statistical analysis

The microbial alpha diversity (α -diversity) was evaluated by observed species, good coverage, chao1, Shannon, and Simpson indices, the difference of microbial alpha diversity between two glaciers were evaluated using Wilcoxon rank sum exact test. The microbial beta diversity (β -diversity) was display by non-metric multidimensional scaling (NMDS) analyses based on the Bray-Curtis distance. The

spearman's correlation analysis was used to estimate the relationship between environmental variables and microbial alpha diversity, relative abundance, conducted by R package "vegan". And "random forest" model was used to evaluate the importance of individual environmental variables in influencing beta-diversity, the significance performed by package "rfPermute". All graphs were finished in R platform based on ggplot2 packages [63].

Network analysis

Co-occurrence networks based on all possible Spearman's rank correlations of the 100 most abundant OTUs of both bacterial and fungal. A strong and significant correlation at the threshold of Spearman's $\rho > 0.6$ and P-value < 0.01 were commonly used and recognized to be valid and robust [26, 64, 65]. The nodes and edges file calculated using package "vegan" of R platform(<http://www.r-project.org>), and visualized by Gephi software [66]. The topological features of nodes-level (including clustering coefficient, betweenness centrality), edge-level (including path percentage of positive and negative edges, average degree), and network-level (including network diameter, graph density, modularity) were calculated by Gephi [66].

Results

Debris physiochemical characteristics and dominant microbial taxa of two glaciers

The physiochemical characteristics of debris samples were significantly different in two glaciers (Figure S2, Table S3 & Table S4). Debris samples from the surface of Dagongba glacier had a higher percentage of clay, silt, and higher values of TC, TN, OM, NO_3^- -N, AN, AP, AK content, as well higher in metals content included Al, Fe, K, Na, Mn. While the debris samples from Hailuogou glacier had a higher percentage of sand, NH_4^+ -N and Ca content.

The surface habitats of the DCGs are harbored abundant bacterial and fungal communities. We obtained 1164650 high-quality bacterial 16S rRNA sequences and 1145316 high-quality fungal ITS-1 sequences. Clustered by 97% similarity to obtain a total of 18965 bacterial OUTs and 4440 fungal OTUs in 17 sites, with valid mean length of $416.91(\pm 1.75)$ bp in bacteria and $265.59(\pm 11.78)$ bp in fungi, respectively (Table S5). The common and endemic OTUs number of bacteria and fungi among sites have been shown in Figure S3 (Supplementary Materials). Bacterial OTU number showed no significant difference between Dagongba and Hailuogou glacier, while Fungal OTU number higher in Hailuogou glacier. A higher ratio of bacterial to fungal (7.79–12.74) observed in Dagongba glacier.

The top 7 bacterial phyla ($> 1\%$ of the total number of sequences) were *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, *Gemmatimonadetes*, *Acidobacteria*, *Firmicutes* and *Nitrospirae* across all the debris sites, accounting for 96.6% of the bacterial sequences (Fig. 2a, Table S6). The phylum *Proteobacteria* occupied more than half (51.5%) of the whole bacterial taxa, and negatively correlated with debris nutrients content (Supplementary Materials: Table S6 & Figure S4). The top 4 fungal phyla ($> 1\%$ of the total number of sequences) were *Ascomycota*, *Basidiomycota*, *Zygomycota*, *Chytridiomycota*, accounting for 87.6% of

the fungal sequences (Fig. 2b, Table S6). The distribution of Fungi and bacteria showed different patterns, particularly at the lower taxonomic levels: Bacterial communities were more evenness distributed across all the debris sites, while fungal communities were abundant only in specific sites, it indicated that fungi showed larger variations than bacteria among sites (Fig. 2:c&d). The *Burkholderiaceae* (*Betaproteobacteria*), *Chitinophagaceae* (*Bacteroidetes*) and *Sphingomonadaceae* (*Alphaproteobacteria*) represented the predominant bacterial family, particular in Hailuoguo glacier (Table 1). *Thelephoraceae*, *Strophariaceae* and *Sebacinaceae* represented the most abundant fungal family, all of them affiliated to the *Agaricomycetes*, which extremely abundant in Dagongba glacier (Table 1).

Table 1

The dominant microbial taxa in supraglacial debris. Mean $\pm$ standard error. Different lowercase letters indicate significantly difference (Wilcoxon rank sum test) among glaciers at $p < 0.05$.

Dominant Bacteria (Top three)		Glaciers		All sites(n = 17)
		Dagongba(n = 7)	Hailuogou(n = 10)	
Phylum	<i>Proteobacteria</i>	0.409($\pm$ 0.041) b	0.59($\pm$ 0.054) a	0.515($\pm$ 0.104)
	<i>Bacteroidetes</i>	0.253($\pm$ 0.038) a	0.192($\pm$ 0.018) b	0.217($\pm$ 0.041)
	<i>Actinobacteria</i>	0.145($\pm$ 0.026) a	0.088($\pm$ 0.029) b	0.112($\pm$ 0.04)
class	<i>Gammaproteobacteria</i>	0.156($\pm$ 0.028) b	0.401($\pm$ 0.077) a	0.3($\pm$ 0.138)
	<i>Bacteroidia</i>	0.24($\pm$ 0.038) a	0.184($\pm$ 0.019) b	0.207($\pm$ 0.039)
	<i>Alphaproteobacteria</i>	0.182($\pm$ 0.016) a	0.12($\pm$ 0.031) b	0.146($\pm$ 0.04)
order	<i>Betaproteobacteriales</i>	0.127($\pm$ 0.022) b	0.33($\pm$ 0.077) a	0.246($\pm$ 0.119)
	<i>Chitinophagales</i>	0.142($\pm$ 0.014) a	0.091($\pm$ 0.011) b	0.112($\pm$ 0.028)
	<i>Sphingomonadales</i>	0.088($\pm$ 0.015) a	0.039($\pm$ 0.01) b	0.059($\pm$ 0.028)
family	<i>Burkholderiaceae</i>	0.051($\pm$ 0.01) b	0.138($\pm$ 0.051) a	0.103($\pm$ 0.059)
	<i>Chitinophagaceae</i>	0.126($\pm$ 0.016) a	0.066($\pm$ 0.011) b	0.091($\pm$ 0.033)
	<i>Sphingomonadaceae</i>	0.088($\pm$ 0.015) a	0.039($\pm$ 0.01) b	0.059($\pm$ 0.028)
genus	<i>Sphingomonas</i>	0.067($\pm$ 0.012) a	0.019($\pm$ 0.003) b	0.039($\pm$ 0.025)
	<i>Ellin6067</i>	0.012($\pm$ 0.004) b	0.04($\pm$ 0.017) a	0.029($\pm$ 0.019)
	<i>Ferruginibacter</i>	0.016($\pm$ 0.006) b	0.027($\pm$ 0.01) a	0.022($\pm$ 0.01)
Dominant Fungi (Top three)		Glaciers		All sites(n = 17)
		Dagongba(n = 7)	Hailuogou(n = 10)	
Phylum	<i>Ascomycota</i>	0.411($\pm$ 0.243)	0.558($\pm$ 0.123)	0.497($\pm$ 0.19)
	<i>Basidiomycota</i>	0.508($\pm$ 0.278) a	0.166($\pm$ 0.18) b	0.307($\pm$ 0.278)
	<i>Zygomycota</i>	0.033($\pm$ 0.045)	0.049($\pm$ 0.041)	0.042($\pm$ 0.042)
class	<i>Agaricomycetes</i>	0.503($\pm$ 0.277) a	0.157($\pm$ 0.18) b	0.3($\pm$ 0.279)
	<i>Eurotiomycetes</i>	0.076($\pm$ 0.059) a	0.028($\pm$ 0.037) b	0.048($\pm$ 0.051)
	<i>Mortierellomycotina</i>	0.033($\pm$ 0.045)	0.043($\pm$ 0.042)	0.039($\pm$ 0.042)
order	<i>Agaricales</i>	0.193($\pm$ 0.197)	0.079($\pm$ 0.147)	0.126($\pm$ 0.173)
	<i>Thelephorales</i>	0.187($\pm$ 0.251)	0.003($\pm$ 0.002)	0.079($\pm$ 0.18)

Dominant Bacteria (Top three)		Glaciers		All sites(n = 17)
		Dagongba(n = 7)	Hailuogou(n = 10)	
	<i>Sebacinales</i>	0.097(± 0.076) a	0.033(± 0.084) b	0.06(± 0.085)
family	<i>Thelephoraceae</i>	0.187(± 0.251)	0.003(± 0.002)	0.079(± 0.18)
	<i>Strophariaceae</i>	0.029(± 0.059)	0.05(± 0.135)	0.041(± 0.108)
	<i>Sebacinaceae</i>	0.089(± 0.079) a	0.005(± 0.008) b	0.04(± 0.064)
genus	<i>Tomentella</i>	0.108(± 0.16)	0.001(± 0.002)	0.045(± 0.112)
	<i>Mortierella</i>	0.032(± 0.046)	0.037(± 0.032)	0.035(± 0.037)
	<i>Lepiota</i>	0.07(± 0.156) a	0(± 0) b	0.029(± 0.102)

Diversity of microbial communities and its influencing factors

The relatively high Good's coverage values (> 0.97) suggested that both bacterial and fungal communities were well sampled owing to the high depth of Illumina sequencing (Supplementary Materials: Table S7). For investigate the alpha diversity of bacteria and fungi, the Chao1, Shannon, and Simpson indices were estimated (Table 2). For bacteria community, both the Chao1 and Shannon diversity were significantly higher in Dagongba glacier than in Hailuogou glacier. In contrast, the Chao1 and Shannon diversity of fungal communities were higher in Hailuogou glacier. Both bacterial and fungal community were showed no difference in Simpson diversity between two glaciers. The distance from the glacier terminus (DFT) were negatively ($P < 0.01$) correlated to the Bacterial alpha diversity, included the Chao1, Shannon and Simpson diversity (Fig. 3a). Precisely, the local diversity of bacterial communities was decreased as the debris samples were far from the glacial terminus (Fig. 3: b, d & f). But the local diversity of fungal communities was showed no clear pattern along the supraglacial debris transect (Fig. 3: c, e & g). Besides, more difference between bacterial and fungal communities were observed. For instance, glacier surface velocity (GSV) positively correlated with fungal Shannon diversity but negatively correlated with bacterial Shannon diversity. And the debris thickness (DT), percentage of clay (%), nutrients content (including TN, TC, TOC, NO_3^- -N), element Fe content ($P < 0.05$) were positively correlated with the bacterial alpha diversity. While only the percentage of sand (%) and Ca, P content were positively correlated with the alpha diversity of fungi ($P < 0.05$) (Fig. 3a).

Table 2
The alpha diversity of microbial communities in supraglacial debris. Mean $\pm$ standard error. Different lowercase letters indicate significantly difference (Wilcoxon rank sum test) among glaciers at $p < 0.05$.

Indices		Glaciers	
		Dagongba (n = 7)	Hailuogu (n = 10)
Bacteria	Goods coverage	0.972($\pm$ 0.003)	0.974($\pm$ 0.004)
	Observed species	5000.99($\pm$ 400.55) a	4345.87($\pm$ 697.13) b
	Chao1	6242.51($\pm$ 469.35) a	5539.69($\pm$ 812.07) b
	Shannon	10.26($\pm$ 0.3) a	9.78($\pm$ 0.5) b
	Simpson	0.9958($\pm$ 0.003)	0.9956($\pm$ 0.002)
Fungi	Goods coverage	0.9980($\pm$ 0.000)	0.9981($\pm$ 0.001)
	Observed species	491.27($\pm$ 111.02) b	692.52($\pm$ 91.43) a
	Chao1	571.92($\pm$ 107.18) b	778.13($\pm$ 99.61) a
	Shannon	4.60($\pm$ 1.31) b	5.97($\pm$ 0.66) a
	Simpson	0.83($\pm$ 0.18)	0.93($\pm$ 0.03)

The patterns of bacterial and fungal β -diversity were visualized with non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance (Fig. 4: a & b) and test significant difference between two glaciers by Analysis of Similarities (ANOSIM) (Supplementary Materials: Figure S6). For both bacterial and fungal communities, seven debris samples from Dagongba glacier were clustered together and well separated from the debris samples from Hailuogou glacier, indicated that the surface of two glaciers were harbored significantly different microbial communities. The top10 different bacterial(a) and fungal(c) genera were shown in Figure S7: a & b (Supplementary Materials). Bacteria (adjust R²: 0.65, $p < 0.01$) were explained more by environmental factors compared with fungal (adjust R²: 0.37, $p < 0.05$) (Figure S7: c & d). There were three debris samples that located at the terminus of Hailuogou glacier (H1, H2, and H3) were well separated from other samples (Fig. 4: a & b), indicated that the debris site H1, H2 and H3 were harbored significant different microbial communities with other sites from Hailuogou glacier. Interestingly, bacterial communities clustered more tightly than fungal communities, while fungal communities separated better than bacterial communities across glaciers and sites. The GSV and K content were important in shaping fungal and bacterial community beta diversity in supraglacial debris (Fig. 4: c-f).

Co-occurrence network of bacterial and fungal communities

In supraglacial debris, bacterial and fungal communities formed significantly different co-occurrence networks across Dagongba glacier and Hailuogou glacier (Fig. 5). Specifically, bacterial networks were more connected and complex than fungal networks, as indicated by more edges and higher degree. The edges number intra-bacteria (433) were nearly double than those intra-fungi (219), but fungi networks had more positive edges, and formed by higher modularity (Fig. 5 & Table 3).

Table 3
The co-occurrence network properties of microbial communities in supraglacial debris.

Index		Bacteria		Fungi	
		Dagongba	Hailuogou	Dagongba	Hailuogou
Nodes	Nodes	71	82	58	72
	Clustering Coefficient	0.474	0.547	0.63	0.612
Edges	Edges	76	511	61	155
	Percentage of Positive	57%	49%	74%	65%
	Percentage of Negative	43%	51%	26%	35%
network	Average degree	2.141	12.463	2.103	4.306
	Graph Density	0.031	0.154	0.037	0.061
	Modularity	0.84	0.393	0.804	0.646

In a microbial network, nodes with high degree are hubs and nodes with high betweenness centrality are bridges. The genus that with the highest value of betweenness centrality (> 400) and degree (> 15) were considerate as core taxa in this study (Fig. 6). Dagongba glacier observed two highly connected keystone taxa, one from bacteria and another one from fungi (Fig. 6a & b), which were *Segetibacter* (*Chitinophagaceae*, *Bacteroidetes*, *Bacteroidetes*) and *Geopora* (*Pyronemataceae*, *Pezizomycetes*, *Ascomycota*), respectively. Hailuogou glacier observed five core OTUs from bacteria and five from bacteria (Fig. 6c & d), while the identified bacterial taxa were *Polaromonas* (*Comamonadaceae*) and *Massilia* (*Oxalobacteraceae*) both were belonged to *Burkholderiales* within *Betaproteobacteria*. And the identified fungal taxa were *Pezoloma* (*Discinellaceae*, *Leotiomyces*, *Ascomycota*) and *Hebeloma* (*Cortinariaceae*, *Agaricomycetes*, *Basidiomycota*).

Discussion

The characteristics of bacterial and fungal communities on the supraglacial debris

In some extreme environment, included the mountain glacier habitat from polar regions, microbial communities usually are the only form of life. They play important role in driving the nutrient cycling, promoting the colonization and succession of high trophic organisms. This study tried to characterize the bacterial and fungal communities on the supraglacial debris of two DCGs from Mt. Gongga (Southeast of the Tibetan plateau, China), and investigated the environmental factors shaping their diversity. It observed that the supraglacial debris of DCGs harbored abundant microbial communities. From previous studies, the Bacterial taxa from phylum Cyanobacteria that are capable of photosynthesis were described to be dominant on supraglacial debris habitats [6, 67]. But in this study, on the supraglacial debris, the phylum *Proteobacteria* occupied more than half (51.5%) of the whole bacterial taxa (Fig. 2a, Supplementary Materials: Table S6). It was a versatile phylum that have been reported common in globally glacial environments [68, 69]. They are characterized by phylogenetic, morphological, physiological and metabolic diversity [70]. Most *Proteobacteria* are mesophilic [70], it was become abundant in the cold habitats likely due to the global warming. The *Burkholderiaceae* (*Betaproteobacteria*), *Chitinophagaceae* (*Bacteroidetes*) and *Sphingomonadaceae* (*Alphaproteobacteria*) represented the predominant bacterial family, particular in Hailuoguo glacier (Table 1). Likewise, at Miage and Belvedere glaciers (Monte Bianco, Europe), the dominant microbial taxa in the supraglacial debris were also included *Sphingobacteriales* (*Alphaproteobacteria*) and *Burkholderiales* (*Betaproteobacteria*) [4]. They dominant in other glacial environments such as the cryoconite holes as well [15].

Fungal communities on the glacier forefield soils have been reported were dominant by Ascomycetous filamentous fungi and Basidiomycetous yeasts that are cold-adapted organic matter decomposers [14, 71]. Consistently, in the supraglacial debris habitat, the *Ascomycota* (60%) and *Basidiomycota* (37%) were also the mainly fungal taxa (Fig. 2b, Table 1), both them have the ability to produce large numbers of spores. Actually, rare studies focus on the microbial communities of supraglacial debris habitat, particularly the fungal communities. Before this study, it only been described in the Middle Fork Toklat Glacier (Denali National Park, Alaska, USA) [6], which found that the *Chytridiomycetes* (*Chytridiomycota*) and *Leotiomycetes* (*Ascomycota*) were the abundant fungal class on supraglacial debris. The present study found that the *Agaricomycetes* within the *Basidiomycota* being the most abundant classes of fungi, especially abundant in the supraglacial debris of Dagongba glacier. The most abundant fungal family were *Thelephoraceae*, *Strophariaceae* and *Sebacinaceae*, all of them were affiliated to the *Agaricomycetes* within *Basidiomycota* (Table 1). The *Agaricomycetes* have been observed also dominant in glacial ice and snow [72, 73], as well the soil in glacial retreat areas [74], and they usually to be more abundant at a relatively mature stages of glacial forefield soil ecosystem. Consistently, at the Damma glacier forefield (central Switzerland), Zumsteg, Luster, Göransson, Smittenberg, Brunner, Bernasconi, Zeyer, Frey [11] found that the *Basidiomycota* were more abundant in old soils, while the *Ascomycota* were more abundant in young soils. The composition of fungal communities showed larger variations among sites especially at the lower taxonomic levels (Fig. 2c & d, Supplementary Materials: Figure S5), suggesting a lower dispersal capability of fungi than bacteria, and environmental filtering selects particular fungi in those cold habitats [7, 35]. The present study further confirmed that the supraglacial habitats in different geographical locations were harbored similar microbial taxa. Because the microbial

communities from the similar habitats usually possess the similar types of strategies for survival: remaining active at low temperature on glacial habitats [68]. And the microbial communities adopted to cold and harsh habitats were usually those taxa that possess high metabolic versatility.

The assembly processes of bacterial and fungal communities on the supraglacial debris

Biodiversity is essential for supporting ecosystem functioning [75], the lower biodiversity the less stability [76]. The present study tried to understand the microbial assembly process in supraglacial habitats by evaluating both the microbial alpha and beta diversity. The lower of alpha diversity reflected the lower richness within sites [62], the closer beta diversity distances implying the taxonomic homogeneity between different sites. It observed that Dagongaba glacier harboring significantly different microbial communities from Hailuoguo glaciers (Fig. 4: a & b). And the alpha diversity (Chao1 and Shannon index) of both bacterial and fungal communities were significantly different between two glaciers ($P < 0.05$) (Table 2). It was attributable to the environmental variations between these two glacier habitats (Supplementary Materials: Figure S1 & S2). The huge population sizes, large specific area, short generation time, wide distribution, high diversity, sharp specificity and high sensitivities of microbial communities provide the advantages for them to fully interact with environmental factors. In glacial environment, the development of microbial communities has been reported limited mainly by N and P [77, 78]. In supraglacial debris habitat, besides those basic nutrients and metal ions content, the glaciological parameters such as glacier surface velocity (GSV), distance from the glacial terminus (DFT) and debris thickness (DT) also play crucial role in shaping bacterial and fungal community compositions (Fig. 3a, Fig. 4: e-f). A greater GSV represented the fast glacier shrinkage, and GSV has been demonstrated was the chief physical factor influencing vegetation cover in DCGs attributed to its influence on debris stability [9]. Likewise, the unstable habitat with frequent disturbance was not suitable for the development of microbial communities. The characteristics of microbial community and environmental condition actually can shape and reflect each other. The greater DT and lower GSV reflected that the surface of Dagongaba glacier was more stable, and the higher percentage of clay, higher values of TC, TN, OM(TOC), NO_3^- -N, CEC and metal content (Figure) of debris samples indicated that the surface habitats in Dagongaba glacier were relatively mature, with a relatively low resource stress, and more suitable for life survival when compared with Hailuoguo glacier.

Generally, in the less disturbed or relatively complex habitats, microbial communities had a higher richness with few individuals. But that doesn't seem to be the case with fungal communities in the present study. Interestingly, it found that bacteria OTU richness (Chao1, Shannon index) higher in Dagongba glacier, but fungi OTU richness higher in Hailuoguo glacier (Table 2). It should be noted that the fungi abundant and richness were positively correlated with calcium (Ca) content (Fig. 3a). Ca is important to maintain the stability of the enzymes for fungal cell survival and necessary to form fungal spores [79, 80]. When compared with Dgongba glacier, the debris samples from Hailuoguo glacier surface definitely were more abundant in Ca (Figure S2 & Table S4). In addition, it speculated that the relatively developed plant communities in Dagongba glacier will inevitably lead to the prevalence of specific plant-fungus symbiosis [81], inevitably decreased fungi local diversity. The GSV positively correlated with

fungal Shannon diversity, while negatively correlated with bacterial Shannon diversity (Fig. 3a). In all likelihood, an appropriately disturbance was beneficial for the dispersal of fungal spore and increase fungal local diversity, but is unfavorable to the maintenance of bacterial local diversity.

On the ecological succession of glacier retreat area, the distance from the glacier terminus (DFT) is usually regarded as a proxy for exposure time [82]. In this study, we observed that bacterial alpha diversity increased from the upper towards the glacial terminus, moreover, microbial communities on the three sites (H1, H2, H3) near the glacial terminus of Hailuoguo glacier were separated from other sites (Fig. 4: a & b). It suggested that there was a succession sequence of bacterial community on the supraglacial debris transect. Actually, there were two chronosequences on mountain glacial ecosystem, glacier forefield chronosequence and supraglacial chronosequence, but the latter has been overlooked for a long time. When compared with the upper part, the debris habitat near the glacier terminus usually are more superior for microorganisms to live, because of the older and thicker debris layer near the glacier terminus tend to be more stable and less nutrient-limited. Evidence from the Middle Fork Toklat Glacier (Alaska, USA) [6] and Miage Glacier (Mont Blanc massif, Western Alps, Italy) [4] also demonstrated that the surface of a debris-covered glacier existed a chronosequence. The arthropod [8], bacterial and fungal communities present a biogeographical distribution along the supraglacial transect, the communities change from photosynthetic to heterotrophic [6] and the community complex increased toward the glacier terminus [4]. But it should be noted that supraglacial chronosequence was mainly appeared in the middle transect of the glacier surface, because the two sides are frequently disturbed by the collapse of lateral moraines and surrounding rocks. The supraglacial debris covered on mountain glacier surface is the important sources of barren soil on glacial forefield after glacial retreat, as well an important channel for high-altitude life migration downward. Therefore, the ecosystem succession and development process in the glacial forefield must be different between the DCGs and debris-free glaciers [21]. In the study of ecological succession of glacial forefield soil of a DCG, it cannot ignore the supraglacial debris as an important source of initial microbial colonizers.

The co-occurrence patterns of bacterial and fungal communities on the supraglacial debris

The microbial co-occurrence network provides a pathway to better predict the ecosystem functional stability when response to environmental change [22]. In this study, it evaluated the microbial co-occurrence network patterns at two DCGs. The complexity and stability of co-occurrence network can be assessed by network topological properties such as edges properties, degree, modularity [83]. A higher number of edges and average degree indicated more frequent interactions between taxa [84]. The positive edge in a network implies a mutualistic interaction (commensalism, synergism or mutualism) between two nodes(taxa), while the negative edge implies an antagonistic interaction (amensalism, parasitism, competition or predation) [85, 86]. The complex and connected network in Hailuoguo glacier, especially with more positive interactions (Fig. 5 & Table 3), it indicative of an overlap in the niches among microbial taxa [84], which result in interspecific cooperation or competition of microbes for the limited resources. A recent study has also found that there was high frequency of positive interactions between bacteria and fungi of permafrost ecosystem in a rock glacier where was nutrients-limited [87]. Comparing with

Dagongba glacier, Hailuoguo glacier were more limited by nutrients (Supplementary Materials: Figure S2 & Table S4), hence, bacterial and fungal communities will inevitably compete for the resources distributed in patches, passively enhancing the intraspecific interactions.

The value of modularity indices > 0.4 indicated that the network has a modular structure [88]. A higher values of modularity indices indicate that the co-occurrence networks had a strong modular structure. For both the bacterial and Fungal network, the modularity indices typically higher in Dagongba glacier than in Hailuoguo glacier (Fig. 5 & Table 3). Indicating that the microbial co-occurrence networks are relatively simple (less edges, lower degree) but more stable (higher modularity) in Dagongba glacier. The relatively stronger disturbance due to natural (high GSV, fluctuated air temperature and precipitation) and artificial (tourist attractions with high intensity of human activities) interference on the surface Hailuoguo glacier may resulted in increased interactions within microbial community. Especially, the disturbances may reduce the stability of co-occurrence network by increasing the positive interactions between microbial communities, such networks were actually unstable [89]. By the way, the development of microbial community promoted the colonization of high-trophic organisms such as plants and Protozoa, and the high-trophic organisms colonized on the supraglacial debris will benefit to pedogenesis, and further promote the development and evolution of ecosystems. But it inhibits the colonization of high trophic organisms when the surface of DCGs were insufficiently stable [9].

The keystone taxa in a network hold the network stability, they may not the most abundant but play key roles in shaping community structure and driving ecosystem functions [22, 30, 31]. In Dagongba glacier, *Segetibacter* (*Chitinophagaceae*, *Bacteroidetes*, *Bacteroidetes*) and *Geopora* (*Pyronemataceae*, *Pezizomycetes*, *Ascomycota*) were the keystone bacteria and fungi taxa, respectively. In Hailuoguo glacier, the keystone bacteria were *Polaromonas* and *Massilia*, both belong to *Burkholderiales* within *Betaproteobacteria*, both can degrade the labile compound [90]. The identified keystone fungal taxa were *Pezoloma* (*Discinellaceae*, *Leotiomyces*, *Ascomycota*) and *Hebeloma* (*Agaricomycetes*, *Basidiomycota*) (Figure, Table S), some species within them were mycorrhizal fungus of plants [91–93]. The genus *Polaromonas* were particularly dominant on the upper part of the Hailuoguo glacier (Figure S8: c). The consistent results were reported by Darcy et al [6], who found that the *Polaromonas* were less abundant near the terminus of Middle Fork Toklat Glacier (Alaskan, USA). In addition, the genus *Polaromonas* has been reported was dominant on supraglacial habitats worldwide, such as the glacial ice, sediments, debris and cryoconite holes [4, 15, 94]. Evidence showed that the *Polaromonas* has a highly successful dispersal capacity, and they can capture organic carbon energy directly from the atmosphere rely on the carbon monoxide dehydrogenase genes [15, 94]. A good ability to adopt cold habitats with low nutrition makes them the earliest-successional bacteria. As well, the pioneers of a new habitat usually are photoautotrophs, heterotrophs or chemoautotrophs that can fix atmospheric N [36], and some species of the *Polaromonas* have been demonstrated can fix N from atmosphere [95].

Divergent assembly and co-occurrence patterns between Bacterial and Fungal Communities

The mechanisms to form and maintain microbial biodiversity, which are the microbial community assembly, have been studied extensively in many types of ecosystems but still inconclusive and lack of mature theories [14, 28, 96]. At present, the stochastic and deterministic processes were widely studied the microbial community assembly [97–101]. The assembly strategy between bacterial and fungal communities showed great difference. On the glacial ecosystem, the divergent assemblage patterns have been widely described in glacial forefield succession [14, 36, 40]. Consistently, the present study showed that bacteria and fungi showed distinct assembly and co-occurrence patterns across different glaciers and sites (Fig. 2, Fig. 3, Fig. 4, Fig. 5). It can be explained by their morphological and physiological difference, including the body size, metabolic process, stress tolerance, and substrate preferences [34, 36]. Compared with bacteria, fungi have larger body size which might be dispersal more constrained [14], fungi have stronger tolerance to environmental change [32, 34, 102], and most fungi are regarded as the main lignin and Cellulose decomposers, bacteria are more competitive to degrade easily available carbon sources, such as simple carbohydrates [103]. Previous study conducted in globally alpine glacier ecosystem by [7] indicated that the difference in dispersal ability between bacteria and fungi likely was the main factors in driving their divergent distribution patterns.

Specifically, the bacterial communities clustered more tightly than fungal communities as indicated by non-metric multi-dimensional scaling plots (Fig. 4: a & b). One likely explanation was that fungi may be more dispersal limited than bacteria, therefore more prone to historical (stochastic) effects [36, 81, 102]. The fungal communities within a glacier or among glaciers were highly diverse and spatially heterogenous [104]. Evidence from the Lyman Glacier (Washington, USA) forefield demonstrated that the assembly trajectories and processes of fungal communities are complex, even more than plant communities [82]. Study from the same area also demonstrated that the assemblage processes of fungal community tend to be more stochastic than bacterial community [14]. The colonization of plants communities at the supraglacial debris may strongly influence on the fungal communities. The presence of plants had a stronger effect in shaping bacterial communities than fungal communities has been reported in retreating glacier succession [40] and other ecological succession [34], because of the more commonly specific relationships (symbiotic) of fungi-plants. Bacteria adapted better than fungi in some newly exposed substrate and barren soil, and exhibit a broader range of physiologies. Besides, only some bacteria taxa can fix N and C from the atmosphere for survival [36], such as the *Polaromonas* (*Burkholderiaceae*).

In this study, bacterial communities network properties were obviously different from fungal communities, particularly at Hailuoguo glacier (Table 3, Fig. 5 & Fig. 6). The interactions intra-bacteria (edges number: 433) were nearly double than those intra-fungi (edges number: 219). Indicating bacterial network was more complex. Consistent with this study, the different co-occurrence patterns between bacterial and fungal communities were also found in glacier-fed streams ecosystem [89]. And at Hailuoguo glacier forefield soil, Jiang, Lei, Yang, Korpelainen, Niinemets, Li [14] found a more compact and connected network in bacterial communities (as indicated by the lower clustering coefficients and higher edge numbers), but a looser clustering in fungal communities. Indicated that bacterial assemblage dominant by deterministic processes, whereas fungal assembly dominant by stochastic processes [14].

In Hailuoguo glacier (greater surface velocity and more tourist activity), more bacteria-bacteria interactions were observed. But fungal network in Hailuoguo glacier seem to be more stable than bacteria, as noted elsewhere [32]. Knowledge about the divergent assemblage of bacterial and fungal communities, and how they co-occurred on the newly exposed habitats is essential for understanding the ecosystem functions and evolution process. Further studies were urgently needed.

Conclusions

The compositions, diversity, community assembly processes, and co-occurrence patterns of bacterial and fungal communities in supraglacial debris habitat of Hailuoguo and Dagongba glacier (Mt. Gongga, Southeast Tibetan Plateau, China) were investigated. It found that the supraglacial debris harbored abundant bacterial and fungal communities. And the microbial communities adopted well to cold and harsh habitats were those taxa that possess high metabolic versatility. The composition and diversity of fungal communities showed great variations than bacteria communities across glaciers and sites, and influenced more by environmental factors, which means the assembly process of bacterial communities were more deterministic, but fungi communities were more stochastic. Both the co-occurrence network of both bacterial and fungal communities in Dagongba glacier (higher microbial diversity) are relatively simple and more stable. This study provides insights into mechanisms that drive the establishment and early assembly of microbial communities. It provided microbial ecological basis for the biodiversity protection of glacier system and the surrounding natural environment.

Abbreviations

DCGs: Debris-covered glaciers. Mt.: mountain, PCR: polymerase chain reaction, α -diversity: alpha diversity, β -diversity: beta diversity, OTUs: Operational Taxonomic Units, NMDS: non-metric multidimensional scaling, NCBI: National Center for Biotechnology Information. E: elevation(m), AT: average annual temperature($^{\circ}$ C), DT: debris thickness(m), GSV: glacier surface velocity($\text{m}\cdot\text{a}^{-1}$), DFT: distance from the glacier terminus(m). TN: total nitrogen, TC: total carbon, OM: organic matter, NH_4^{+} -N: Ammonium nitrogen, NO_3^{-} -N: nitrate nitrogen, AN: available nitrogen, AP: available phosphorus; AK: available potassium. Al: Aluminium, Fe: Iron, Ca: Calcium, K: Potassium, Mg: Magnesium, Na: Sodium, P: Phosphorus, Mn: Manganese.

Declarations

Ethics approval and consent to participate

Not applicable as there were no human, animal or pathogen subjects involved.

Consent for publication

Not applicable.

Availability of data and materials

Sequencing data for bacterial and fungal communities were deposited in the National Center for Biotechnology Information (NCBI) Sequence Read Archive(<http://trace.ncbi.nlm.nih.gov/Traces/sra/>) under the accession numbers of PRJNA797905 (bacteria) and PRJNA798561 (fungi).

Competing interests

The authors declare no conflict of interest.

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Authors' contributions

X.L. and Q.L. contributed to the implementation of the research, conceived the ideas. Y.H. analyzed the data and wrote the manuscript. H.J., H.L. and Y.Z. assisted in sample collection in field and environmental data collection, Z.W. and B.D. assisted in data analysis and conceived the ideas. All authors have contributed substantially to the revisions.

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References

1. Herreid S, Pellicciotti F. The state of rock debris covering Earth's glaciers. *Nature Geoscience*. 2020;13(9):621–627.
2. Scherler D, Wulf H, Gorelick N. Global Assessment of Supraglacial Debris-Cover Extents. *Geophysical Research Letters*. 2018;45(21):11,798 – 711,805.

3. Compagno L, Huss M, Miles E, et al. Modelling supraglacial debris-cover evolution from the single glacier to the regional scale: an application to High Mountain Asia. *The Cryosphere Discuss.* In review, 2021, [preprint]; doi.org/10.5194/tc-2021-233.
4. Franzetti A, Tatangelo V, Gandolfi I, et al. Bacterial community structure on two alpine debris-covered glaciers and biogeography of *Polaromonas* phylotypes. *The ISME Journal*. 2013;7(8):1483–1492.
5. Azzoni R, Franzetti A, Fontaneto D, Zullini A, Ambrosini R. Nematodes and rotifers on two Alpine debris-covered glaciers. *Italian Journal of Zoology*. 2015;82.
6. Darcy JL, King AJ, Gendron EMS, Schmidt SK. Spatial autocorrelation of microbial communities atop a debris-covered glacier is evidence of a supraglacial chronosequence. *Fems Microbiol Ecol*. 2017;93(8).
7. Rime T, Hartmann M, Frey B. Potential sources of microbial colonizers in an initial soil ecosystem after retreat of an alpine glacier. *ISME J*. 2016;10(7):1625–1641.
8. Gobbi M, Isaia M, De Bernardi F. Arthropod colonisation of a debris-covered glacier. *The Holocene*. 2010;21(2):343–349.
9. Caccianiga M, Andreis C, Diolaiuti G, D'Agata C, Mihalcea C, Smiraglia C. Alpine debris-covered glaciers as a habitat for plant life. *The Holocene*. 2011;21(6):1011–1020.
10. Kong W, Liu J, Ji M, Yue L, Kang S, Morgan-Kiss RM. Autotrophic microbial community succession from glacier terminus to downstream waters on the Tibetan Plateau. *Fems Microbiol Ecol*. 2019;95(6).
11. Zumsteg A, Luster J, Göransson H, et al. Bacterial, Archaeal and Fungal Succession in the Forefield of a Receding Glacier. *Microb Ecol*. 2012;63(3):552–564.
12. Pessi IS, Osorio-Forero C, Galvez EJ, et al. Distinct composition signatures of archaeal and bacterial phylotypes in the Wanda Glacier forefield, Antarctic Peninsula. *Fems Microbiol Ecol*. 2015;91(1):1–10.
13. Rime T, Hartmann M, Brunner I, Widmer F, Zeyer J, Frey B. Vertical distribution of the soil microbiota along a successional gradient in a glacier forefield. *Mol Ecol*. 2015;24(5):1091–1108.
14. Jiang Y, Lei Y, Yang Y, Korpelainen H, Niinemets Ü, Li C. Divergent assemblage patterns and driving forces for bacterial and fungal communities along a glacier forefield chronosequence. *Soil Biology and Biochemistry*. 2018;118:207–216.
15. Ambrosini R, Musitelli F, Navarra F, et al. Diversity and Assembling Processes of Bacterial Communities in Cryoconite Holes of a Karakoram Glacier. *Microb Ecol*. 2017;73(4):827–837.
16. Stibal M, Sabacka M, Kastovska K. Microbial communities on glacier surfaces in Svalbard: impact of physical and chemical properties on abundance and structure of cyanobacteria and algae. *Microb Ecol*. 2006;52(4):644–654.
17. Smith HJ, Dieser M, McKnight DM, SanClements MD, Foreman CM. Relationship between dissolved organic matter quality and microbial community composition across polar glacial environments. *Fems Microbiol Ecol*. 2018;94(7).

18. Edwards A, Anesio AM, Rassner SM, et al. Possible interactions between bacterial diversity, microbial activity and supraglacial hydrology of cryoconite holes in Svalbard. *ISME J.* 2011;5(1):150–160.
19. Miles KE, Hubbard B, Irvine-Fynn TDL, Miles ES, Quincey DJ, Rowan AV. Hydrology of debris-covered glaciers in High Mountain Asia. *Earth-Science Reviews.* 2020;207:103212.
20. Kirkbride MP. Debris-Covered Glaciers. In: Singh VP, Singh P, Haritashya UK, eds. *Encyclopedia of Snow, Ice and Glaciers.* Dordrecht: Springer Netherlands; 2011:180–182.
21. Sherpa MT, Najar IN, Das S, Thakur N. Bacterial Diversity in an Alpine Debris-Free and Debris-Cover Accumulation Zone Glacier Ice, North Sikkim, India. *Indian J Microbiol.* 2018;58(4):470–478.
22. Ma B, Wang Y, Ye S, et al. Earth microbial co-occurrence network reveals interconnection pattern across microbiomes. *Microbiome.* 2020;8(1):82.
23. de Menezes AB, Richardson AE, Thrall PH. Linking fungal–bacterial co-occurrences to soil ecosystem function. *Current Opinion in Microbiology.* 2017;37:135–141.
24. Wagg C, Schlaeppi K, Banerjee S, Kuramae EE, van der Heijden MGA. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nature Communications.* 2019;10(1):4841.
25. Zheng W, Zhao Z, Gong Q, Zhai B, Li Z. Responses of fungal–bacterial community and network to organic inputs vary among different spatial habitats in soil. *Soil Biology and Biochemistry.* 2018;125:54–63.
26. Barberán A, Bates ST, Casamayor EO, Fierer N. Using network analysis to explore co-occurrence patterns in soil microbial communities. *The ISME Journal.* 2012;6(2):343–351.
27. Williams RJ, Howe A, Hofmockel KS. Demonstrating microbial co-occurrence pattern analyses within and between ecosystems. 2014;5(358).
28. Zhu B, Li C, Wang J, Li J, Li X. Elevation rather than season determines the assembly and co-occurrence patterns of soil bacterial communities in forest ecosystems of Mount Gongga. *Appl Microbiol Biotechnol.* 2020;104(17):7589–7602.
29. Li J, Li C, Kou Y, Yao M, He Z, Li X. Distinct mechanisms shape soil bacterial and fungal co-occurrence networks in a mountain ecosystem. *FEMS Microbiol Ecol.* 2020;96(4): fiae030; doi: 10.1093/femsec/fiae030.
30. Banerjee S, Schlaeppi K, van der Heijden MGA. Keystone taxa as drivers of microbiome structure and functioning. *Nature Reviews Microbiology.* 2018;16(9):567–576.
31. Mikhailov IS, Zakharova YR, Bukin YS, et al. Co-occurrence Networks Among Bacteria and Microbial Eukaryotes of Lake Baikal During a Spring Phytoplankton Bloom. *Microb Ecol.* 2019;77(1):96–109.
32. de Vries FT, Griffiths RI, Bailey M, et al. Soil bacterial networks are less stable under drought than fungal networks. *Nature Communications.* 2018;9(1):3033.
33. Shen C, Gunina A, Luo Y, et al. Contrasting patterns and drivers of soil bacterial and fungal diversity across a mountain gradient. *Environ Microbiol.* 2020;22(8):3287–3301.
34. Sun S, Li S, Avera BN, Strahm BD, Badgley BD. Soil Bacterial and Fungal Communities Show Distinct Recovery Patterns during Forest Ecosystem Restoration. *Appl Environ Microbiol.* 2017;83(14).

35. Rime T, Hartmann M, Stierli B, Anesio AM, Frey B. Assimilation of microbial and plant carbon by active prokaryotic and fungal populations in glacial forefields. *Soil Biology and Biochemistry*. 2016;98:30–41.
36. Schmidt SK, Nemergut DR, Darcy JL, Lynch R. Do bacterial and fungal communities assemble differently during primary succession? *Mol Ecol*. 2014;23(2):254–258.
37. Liu Q, Liu S, Zhang Y, et al. Recent Shrinkage and Hydrological Response of Hailuoguo Glacier, A Monsoon Temperate Glacier on the East Slope of Mount Gongga, China. *Journal of Glaciology*. 2010;56:215–224.
38. Liao H, Liu Q, Zhong Y, Lu X. Landsat-Based Estimation of the Glacier Surface Temperature of Hailuoguo Glacier, Southeastern Tibetan Plateau, Between 1990 and 2018. *Remote Sensing*. 2020;12(13).
39. Fu Y, Liu Q, Liu G, et al. Seasonal ice dynamics in the lower ablation zone of Dagongba Glacier, southeastern Tibetan Plateau, from multitemporal UAV images. *Journal of Glaciology*. 2021; 10.1017/jog.2021.123:1–15.
40. Brown SP, Jumpponen A. Contrasting primary successional trajectories of fungi and bacteria in retreating glacier soils. *Mol Ecol*. 2014;23(2):481–497.
41. Li Z, He Y, Yang X, et al. Changes of the Hailuoguo glacier, Mt. Gongga, China, against the background of climate change during the Holocene. *Quaternary International*. 2010;218(1):166–175.
42. Su z, Liang D, Hong M. Developing Conditions, Amounts and Distributions of glaciers in Gongga Mountains. *Journal of Glaciology and Geocryology*. 1993;15:551–558(in Chinese).
43. Su Z, Song G, Cao Z. Maritime characteristics of Hailuoguo glacier in the Gongga Mountains. *Journal of Glaciology and Geocryology*. 1996;S1:51–59(in Chinese).
44. Zhang G, Pan B, Cao B, Wang J, Cui H, Cao X. Elevation changes measured during 1966–2010 on the monsoonal temperate glaciers' ablation region, Gongga Mountains, China. *Quaternary International*. 2015;371:49–57.
45. Liu Q, Liu S. Response of glacier mass balance to climate change in the Tianshan Mountains during the second half of the twentieth century. *Climate Dynamics*. 2015;46(1–2):303–316.
46. Schauwecker S, Rohrer M, Huggel C, et al. Remotely sensed debris thickness mapping of Bara Shigri Glacier, Indian Himalaya. *Journal of Glaciology*. 2015;61(228):675–688.
47. Zhang Y, Fujita K, Liu S, Liu Q, Nuimura T. Distribution of debris thickness and its effect on ice melt at Hailuoguo Glacier, southeastern Tibetan Plateau, using in situ surveys and ASTER imagery. *Journal of Glaciology*. 2011;57:1147–1157.
48. Zhang Y, Liu S, Liu Q, Wang X, Jiang Z, Junfeng W. The Role of Debris Cover in Catchment Runoff: A Case Study of the Hailuoguo Catchment, South-Eastern Tibetan Plateau. *Water-Sui*. 2019;11:2601.
49. Bao S. *Soil and Agricultural Chemistry Analysis*. 3 ed. Beijing: China Agriculture Press; 2000
50. Nossa CW, Oberdorf WE, Yang L, et al. Design of 16S rRNA gene primers for 454 pyrosequencing of the human foregut microbiome. *World J Gastroenterol*. 2010;16(33):4135–4144.

51. Wu X, Zhang H, Chen J, et al. Comparison of the fecal microbiota of dholes high-throughput Illumina sequencing of the V3–V4 region of the 16S rRNA gene. *Applied Microbiology and Biotechnology*. 2016;100(8):3577–3586.
52. Schoch CL, Seifert KA, Huhndorf S, et al. Nuclear ribosomal internal transcribed spacer (ITS) region as a universal DNA barcode marker for Fungi. *Proc Natl Acad Sci U S A*. 2012;109(16):6241–6246.
53. Mukherjee PK, Chandra J, Retuerto M, et al. Oral mycobiome analysis of HIV-infected patients: identification of *Pichia* as an antagonist of opportunistic fungi. *PLoS Pathog*. 2014;10(3):e1003996–e1003996.
54. Wu L, Wen C, Qin Y, et al. Phasing amplicon sequencing on Illumina Miseq for robust environmental microbial community analysis. *BMC Microbiology*. 2015;15(1):125.
55. Bolger AM, Lohse M, Usadel B. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics (Oxford, England)*. 2014;30(15):2114–2120.
56. Reyon D, Tsai SQ, Khayter C, Foden JA, Sander JD, Joung JK. FLASH assembly of TALENs for high-throughput genome editing. *Nature Biotechnology*. 2012;30(5):460–465.
57. Caporaso JG, Kuczynski J, Stombaugh J, et al. QIIME allows analysis of high-throughput community sequencing data. *Nature methods*. 2010;7(5):335–336.
58. Wang Q, Garrity GM, Tiedje JM, Cole JR. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl Environ Microbiol*. 2007;73(16):5261–5267.
59. Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ. Basic local alignment search tool. *Journal of molecular biology*. 1990;215(3):403–410.
60. Rognes T, Flouri T, Nichols B, Quince C, Mahé F. VSEARCH: a versatile open source tool for metagenomics. *PeerJ*. 2016;4:e2584; doi: 10.7717/peerj.2584.
61. Guo J, Xiong Y, Shi C, et al. Characteristics of airborne bacterial communities in indoor and outdoor environments during continuous haze events in Beijing: Implications for health care. *Environ Int*. 2020;139:105721.
62. Jiang H, Chen Y, Hu Y, Wang Z, Lu X. Soil Bacterial Communities and Diversity in Alpine Grasslands on the Tibetan Plateau Based on 16S rRNA Gene Sequencing. 2021;9(45).
63. Wickham H. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag; 2016
64. Steinhauser D, Krall L, Müssig C, Büssis D, Usadel B. Correlation Networks. *Analysis of Biological Networks*. 2008; doi.org/10.1002/9780470253489.
65. Ma L, Li B, Jiang XT, et al. Catalogue of antibiotic resistome and host-tracking in drinking water deciphered by a large scale survey. *Microbiome*. 2017;5(1):154.
66. Bastian M, Heymann S, Jacomy M. Gephi: An Open Source Software for Exploring and Manipulating Networks. *Proceedings of the International AAAI Conference on Web and Social Media*, 2009; 3(1), 361–362.
67. Anesio AM, Lutz S, Christmas NAM, Benning LG. The microbiome of glaciers and ice sheets. *NPJ Biofilms Microbiomes*. 2017;3:10.

68. Sherpa MT, Najar IN, Das S, Thakur N. Exploration of Microbial Diversity of Himalayan Glacier Moraine Soil Using 16S Amplicon Sequencing and Phospholipid Fatty Acid Analysis Approaches. *Current Microbiology*. 2021;78(1):78–85.
69. Sajjad W, Ali B, Bahadur A, Ghimire PS, Kang S. Bacterial Diversity and Communities Structural Dynamics in Soil and Meltwater Runoff at the Frontier of Baishui Glacier No.1, China. *Microb Ecol*. 2021;81(2):370–384.
70. Kersters K, De Vos P, Gillis M, Swings J, Vandamme P, Stackebrandt E. Introduction to the Proteobacteria. In: Dworkin M, Falkow S, Rosenberg E, Schleifer K-H, Stackebrandt E, eds. *The Prokaryotes: Volume 5: Proteobacteria: Alpha and Beta Subclasses*. New York, NY: Springer New York; 2006:3–37.
71. Franzetti A, Pittino F, Gandolfi I, et al. Early ecological succession patterns of bacterial, fungal and plant communities along a chronosequence in a recently deglaciated area of the Italian Alps. *Fems Microbiol Ecol*. 2020;96(10).
72. Perini L, Gostinčar C, Gunde-Cimerman N. Fungal and bacterial diversity of Svalbard subglacial ice. *Sci Rep-Uk*. 2019;9(1):20230.
73. Perini L, Gostinčar C, Anesio AM, Williamson C, Tranter M, Gunde-Cimerman N. Darkening of the Greenland Ice Sheet: Fungal Abundance and Diversity Are Associated With Algal Bloom. *Front Microbiol*. 2019;10:557–557.
74. Fernández-Martínez MA, Pérez-Ortega S, Pointing SB, et al. Microbial succession dynamics along glacier forefield chronosequences in Tierra del Fuego (Chile). *Polar Biology*. 2017;40(10):1939–1957.
75. Duffy JE. Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*. 2009;7(8):437–444.
76. van Moorsel SJ, Hahl T, Petchey OL, et al. Co-occurrence history increases ecosystem stability and resilience in experimental plant communities. *Ecology*. 2021;102(1):e03205.
77. Darcy JL, Schmidt SK. Nutrient limitation of microbial phototrophs on a debris-covered glacier. *Soil Biology and Biochemistry*. 2016;95:156–163.
78. Schmidt SK, Porazinska D, Concienne BL, Darcy JL, King AJ, Nemergut DR. Biogeochemical Stoichiometry Reveals P and N Limitation Across the Post-glacial Landscape of Denali National Park, Alaska. *Ecosystems*. 2016;19(7):1164–1177.
79. Liu S, Yinglong H, Liu W, Lu C, Wang W, Sun S. Components of the Calcium-Calcieneurin Signaling Pathway in Fungal Cells and Their Potential as Antifungal Targets. *Eukaryotic cell*. 2015;14.
80. Dzurendova S, Zimmermann B, Kohler A, et al. Calcium Affects Polyphosphate and Lipid Accumulation in Mucoromycota Fungi. *J Fungi (Basel)*. 2021;7(4):300.
81. Jiang S, Xing Y, Liu G, et al. Changes in soil bacterial and fungal community composition and functional groups during the succession of boreal forests. *Soil Biology and Biochemistry*. 2021;161:108393.
82. Jumpponen A, Brown SP, Trappe JM, Cázares E, Strömmer R. Twenty years of research on fungal–plant interactions on Lyman Glacier forefront – lessons learned and questions yet unanswered.

- Fungal Ecol. 2012;5(4):430–442.
83. Qiu L, Zhang Q, Zhu H, et al. Erosion reduces soil microbial diversity, network complexity and multifunctionality. *The ISME Journal*. 2021;15(8):2474–2489.
 84. Hernandez DJ, David AS, Menges ES, Searcy CA, Afkhami ME. Environmental stress destabilizes microbial networks. *The ISME Journal*. 2021;15(6):1722–1734.
 85. Wan X, Gao Q, Zhao J, et al. Biogeographic patterns of microbial association networks in paddy soil within Eastern China. *Soil Biology and Biochemistry*. 2020;142.
 86. Faust K, Raes J. Microbial interactions: from networks to models. *Nature Reviews Microbiology*. 2012;10(8):538–550.
 87. Sannino C, Borruso L, Mezzasoma A, et al. Abiotic factors affecting the bacterial and fungal diversity of permafrost in a rock glacier in the Stelvio Pass (Italian Central Alps). *Applied Soil Ecology*. 2021;166:104079.
 88. Newman ME. Modularity and community structure in networks. *Proc Natl Acad Sci U S A*. 2006;103(23):8577–8582.
 89. Ren Z, Gao H. Ecological networks reveal contrasting patterns of bacterial and fungal communities in glacier-fed streams in Central Asia. *PeerJ*. 2019;7:e7715.
 90. Coenye T. The Family Burkholderiaceae. In: Rosenberg E., DeLong E.F., Lory S., Stackebrandt E., Thompson F. (eds) *The Prokaryotes*. Springer, Berlin, Heidelberg; 2014. p.759–765.
 91. Kowal J, Pressel S, Duckett JG, Bidartondo MI. Liverworts to the rescue: an investigation of their efficacy as mycorrhizal inoculum for vascular plants. *Functional Ecology*. 2016;30(6):1014–1023.
 92. Peintner U, Bougher N, Castellano M, et al. Multiple Origins of Sequestrate Fungi Related to *Cortinarius* (Cortinariaceae). *American journal of botany*. 2001;88:2168–2179.
 93. Becquer A, Garcia K, Amenc L, et al. The *Hebeloma cylindrosporum* HcPT2 Pi transporter plays a key role in ectomycorrhizal symbiosis. *New Phytologist*. 2018;220(4):1185–1199.
 94. Gawor J, Grzesiak J, Sasin-Kurowska J, et al. Evidence of adaptation, niche separation and microevolution within the genus *Polaromonas* on Arctic and Antarctic glacial surfaces. *Extremophiles: life under extreme conditions*. 2016;20(4):403–413.
 95. Hanson B, Yagi J, Jeon C, Madsen E. Role of nitrogen fixation in the autecology of *Polaromonas naphthalenivorans* in contaminated sediments. *Environ Microbiol*. 2012;14:1544–1557.
 96. Chen W, Wen D. Archaeal and bacterial communities assembly and co-occurrence networks in subtropical mangrove sediments under *Spartina alterniflora* invasion. *Environmental Microbiome*. 2021;16(1):10.
 97. Gibbons SM, Gilbert JA. Microbial diversity—exploration of natural ecosystems and microbiomes. *Curr Opin Genet Dev*. 2015;35:66–72.
 98. Caruso T, Chan Y, Lacap DC, Lau MCY, McKay CP, Pointing SB. Stochastic and deterministic processes interact in the assembly of desert microbial communities on a global scale. *The ISME Journal*. 2011;5(9):1406–1413.

99. Stegen JC, Lin X, Konopka AE, Fredrickson JK. Stochastic and deterministic assembly processes in subsurface microbial communities. *The ISME Journal*. 2012;6(9):1653–1664.
100. Dini-Andreote F, Stegen JC, van Elsas JD, Salles JF. Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. *PNAS*. 2015;112(11):E1326-1332.
101. Liu W, Graham EB, Dong Y, et al. Balanced stochastic versus deterministic assembly processes benefit diverse yet uneven ecosystem functions in representative agroecosystems. *Environ Microbiol*. 2021;23(1):391–404.
102. Li J, Li C, Kou Y, Yao M, He Z, Li X. Distinct mechanisms shape soil bacterial and fungal co-occurrence networks in a mountain ecosystem. *Fems Microbiol Ecol*. 2020;96(4).
103. Meidute S, Demoling F, Bååth E. Antagonistic and synergistic effects of fungal and bacterial growth in soil after adding different carbon and nitrogen sources. *Soil Biology and Biochemistry*. 2008;40(9):2334–2343.
104. Perini L, Gostinčar C, Gunde-Cimerman N. Fungal and bacterial diversity of Svalbard subglacial ice. *Sci Rep*. 2019;9(1):20230.

Figures

Figure 1

The Hailuogou(a) and Dagongba(b) glacier with sampling sites. D: Dagongba glacier, H: Hailuogou glacier.

Figure 2

The relative abundance of dominant bacterial and fungal taxa in phylum (a, b), family (c, d) level across supraglacial debris samples. Figure S5 in Supplementary Materials showed the relative abundance of dominant bacterial and fungal taxa in class (a, b), order (c, d), and genus (e, f) level across supraglacial debris samples.

Figure 3

Relationship between microbial alpha diversity and environmental variables. E: elevation(m), AT: average annual temperature($^{\circ}\text{C}$), DT: debris thickness(m), GSV: glacier surface velocity($\text{m}\cdot\text{a}^{-1}$), DFT: distance from the glacier terminus(m). TN: total nitrogen, TC: total carbon, OM: organic matter, NH_4^+-N : Ammonium nitrogen, NO_3^--N : nitrate nitrogen, AN: available nitrogen, AP: available phosphorus; AK: available potassium. The Al, Fe, Ca, K, Mg, Na, P and Mn were the elemental metals included Al: Aluminium, Fe: Iron, Ca: Calcium, K: Potassium, Mg: Magnesium, Na: Sodium, P: Phosphorus, Mn: Manganese. “*”, indicate significant difference at the level of “ $P < 0.01$ ”, respectively.

Figure 4

The NMDS for bacterial(a) and fungi(b) communities and environmental factors (c-d). NMDS: non-metric multidimensional scaling, ANOSIM: Analysis of similarities. E: elevation(m), AT: average annual temperature($^{\circ}\text{C}$), DT: debris thickness(m), GSV: glacier surface velocity($\text{m}\cdot\text{a}^{-1}$), DFT: distance from the glacier terminus(m). TN: total nitrogen, TC: total carbon, OM: organic matter, NH_4^+-N : Ammonium

Figure 6

The keystone bacterial(a&b) and fungal(c&d) networks of Dagongba(left) and Hailuogou(right) glacier. Nodes with high betweenness centrality and high degree values are considered to be keystone taxa in the networks.

Supplementary Files

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