

Review

# Cryosphere Microbiome Biobanks for Mountain Glaciers in China

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**Abstract:** The glaciers in China have an important role as one of the most climate-sensitive constituents of the Tibetan Plateau which is known as the Asian Water Tower. Although the cryosphere is one of the most extreme environments for organisms, the soils of the glacier foreland harbor surprisingly rich microbiomes. A large amount of accelerated glacier retreat accompanied by global warming will not only raise the sea level, but it will also lead to the massive release of a considerable amount of carbon stored in these glaciers. The responses of glacier microbiomes could alter the biogeochemical cycle of carbon and have a complex impact on climate change. Thus, understanding present-day and future glacier microbiome changes is crucial to assess the feedback on climate change and the impacts on ecosystems. To this end, we discuss here the diversity and biogeochemical functions of the microbiomes in Chinese mountain glacier ecosystems.

**Keywords:** glaciers; climate warming; microbiome; microbial diversity; carbon cycle



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## 1. Introduction

Glaciers are a major component of the cryosphere, which is one of the five major spheres of the climate system [1]. Glaciers can be divided into ice caps and mountain glaciers based on their sizes and geographical characteristics [2]. Although the glacier environment is cold, nutrient-poor, and receives a large amount of UV radiation, it still harbors diverse and active microorganisms [3–5]. The microorganisms in this important ecosystem are involved in the biogeochemical cycles of various elements, including carbon, nitrogen, and sulfur [6–8]. The community structure and functions of these microorganisms are affected by the physicochemical properties of the glaciers, which are closely related to climate and environmental changes [9–13].

Current global warming is an undoubtedly trend characterized by increasingly serious temperature increase. According to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), the global surface temperature in 2011–2020 increased by 1.09 °C compared to 1850–1900 [14,15]. Under the impact of human activities and the self-reinforcing feedbacks of the Earth, this temperature increase will continue [16]. The cryosphere, which includes ice sheets, glaciers, and permafrost, is the most sensitive to these temperature changes and will be the most strongly affected. Arctic summer sea ice, the Greenland Ice Sheet, Alpine glaciers, and the west Antarctic Ice Sheet will face the threat of disappearance when the global surface temperature increases by 1–3 °C [17]. Several studies have concluded that mountain glaciers will be more easily affected by climate change, and their retreat rate is higher than those of the Arctic and Antarctic Ice Sheets [17,18]. Based on the observed global mean sea level change in 1901–2018, the retreat of mountain glaciers contributed 67.2 mm to the sea level rise [15,19].

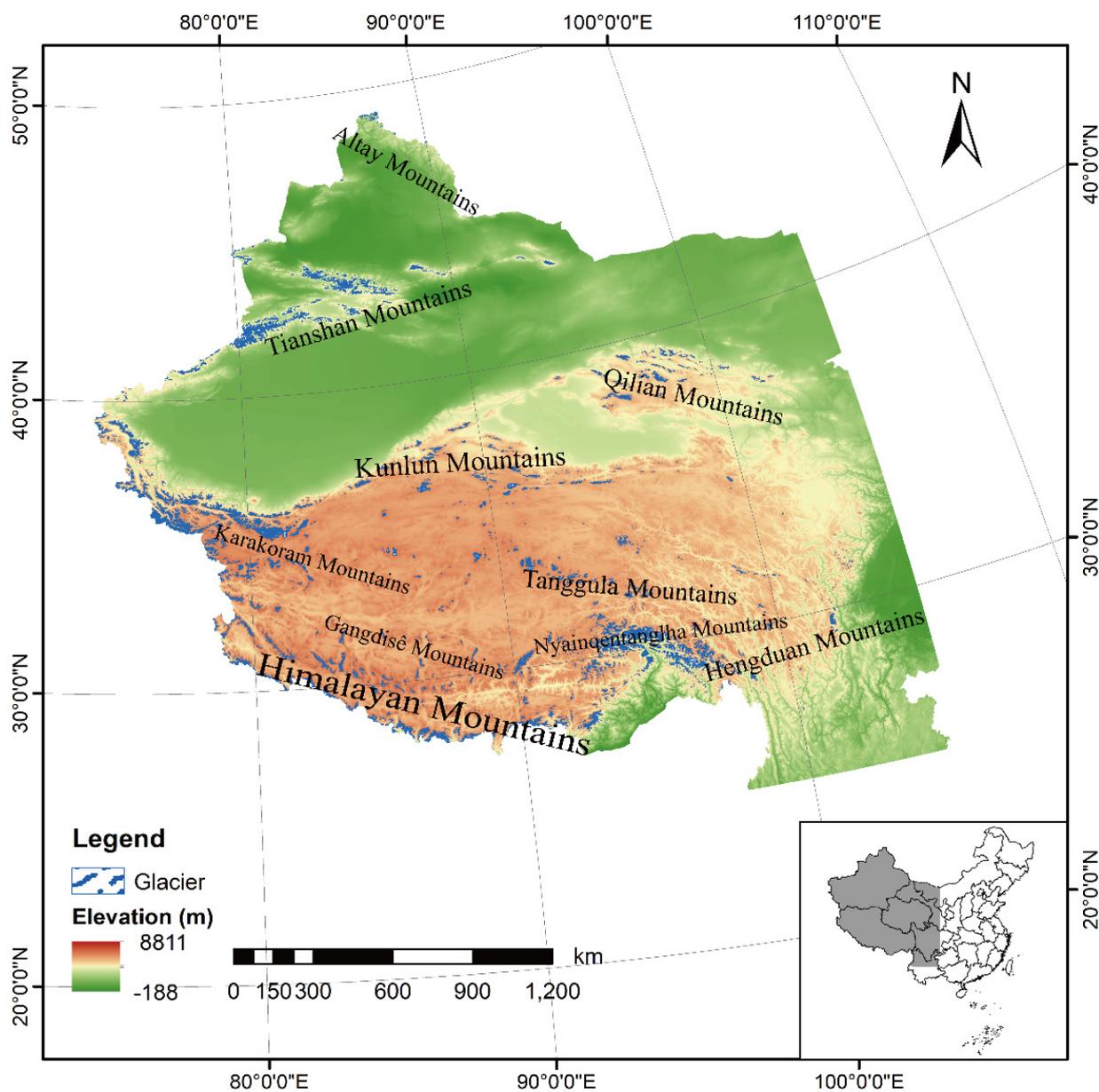
China has the largest and most numerous glaciers in the middle- and low-latitude regions of the world [20,21]. These mountain glaciers tend to melt because their temperatures are usually equal to or exceed the melting point of ice. When glacier ice melts, newly exposed habitats are formed, with diverse microbial communities. These diverse microbial communities conduct important biogeochemical processes (e.g., the microbially mediated carbon cycle), which are important aspects of glacier ecology [22,23]. Although it is difficult to culture the special glacier microorganisms using traditional cultivation methodologies, a novel technique based on uncultured methods (e.g., next-generation sequencing) provides opportunities for improving geomicrobiological studies of mountain glaciers [23,24].

Here, we review the existing knowledge of microbial diversity and functions, as well as the biogeochemical interactions, in Chinese mountain glacier ecosystems. Cyanobacteria and algae, the important components of the cryosphere microbiome, are not discussed in detail due to the few related reports in Chinese glaciers. Global warming is closely related with carbon cycle, which would be greatly affected by the microorganisms. We also discuss the interactions between the microbial community of mountain glaciers and the changing climate from the involvement of microbes in carbon biogeochemical cycle, highlighting the importance of understanding the ecological implications of climate change and glacier melting.

## 2. Status of Glacier Distribution in China

According to the Second Chinese Glacier Inventory (SCGI), 48,571 glaciers were identified in Tibetan, Qinghai, Gansu, Sichuan, and Yunnan provinces, with a total area of 51,766.08 km<sup>2</sup> and an ice volume of 4494.00 ± 175.93 km<sup>3</sup> [2]. They are mainly small glaciers with areas of less than 1.0 km<sup>2</sup>, accounting for 80% of all glaciers in China [2]. Based on the development and geomorphological conditions as well as movement properties, Chinese glaciers are classified as mountain glaciers, located in the western mountains, including the Hengduan Mountains, Himalayan Mountains, Nyainqentanglha Mountains, Karakoram Mountains, Kunlun Mountains, Qilian Mountains, Tianshan Mountains, and Altay Mountains from south to north (Figure 1).

According to the development and physical properties of glaciers, Chinese glaciers can be divided into continental glaciers, sub-continental glaciers, and temperate glaciers [25–28]. Covering an area of more than 13,200 km<sup>2</sup>, with abundant summer monsoon precipitation and an annual retreat rate of 4–66 m/year [29,30], the temperate glaciers are distributed in the eastern Himalayan Mountains, the central-eastern Nyainqentanglha Mountains, and the Hengduan Mountains [28]. This type of glacier is more sensitive to air temperature than precipitation changes, and the equilibrium altitude line would rise by 153 m if the temperature increased by 1 °C [31]. Sub-continental glaciers account for 46% (about 27,200 km<sup>2</sup>) of the all glaciers in China and are mainly distributed in the Qilian Mountains, the eastern Kunlun Mountains, the eastern Tanggula Mountains, the western Nyainqentanglha Mountains, part of the Gangdise Mountains, the north slopes of the central-western Himalayas, and the north slopes of the Karakoram Mountains [28]. With an annual precipitation of 500–1000 m, they have lower retreat rates; for example, Tianshan Glacier No. 1 has retreated by about 5 m every year [32]. In comparison, continental glaciers account for one-third of the total glacier area, covering 19,000 km<sup>2</sup>, and are characterized by the lowest annual average temperature (below 0 °C). Their dry climate, with an annual precipitation of 200–500 mm, causes the ice to flow slowly. Such glaciers are located in the western Qilian Mountains, western Gangdise Mountains, western Tanggula Mountains, eastern Pamir Plateau, the central and western Kunlun Mountains, and the Qiangtang Plateau [28,31].



**Figure 1.** The distribution map of glaciers in western China based on the Second Chinese Glacier Inventory.

As a result of continued global warming, glaciers are generally exhibiting a retreating trend. Nearly all of the Chinese glaciers have retreated significantly and at an accelerated rate (Table 1). From 1960 to the beginning of the 21st century, the annual average rate of change of the glacier area in China was 0.3%, and their total area shrank by 10.1% [33]. The area of glaciers decreased by 1393.97 km<sup>2</sup> in only 10 years (2008–2018), which accounted for 3.74% of the total area of glaciers in China [34]. Based on remote sensing monitoring, 82.2% of these glaciers were found to be shrinking. The retreat size and proportion varied for each glacier, with significant regional differences [35]. In particular, the smaller glaciers were found to be more sensitive to global warming [36–38].

**Table 1.** Retreating rates of glacier areas from western China.

Location	Period	Area (km <sup>2</sup> )		Retreat Area (%) <sup>1</sup>	Retreat Rate (km <sup>2</sup> /Year) <sup>2</sup>
		Beginning	End		
Altai Mountains (Friendship Peak) [39]	1959–2008	214.04	148.94	30.41	1.33
Altai Mountains (north slope of Sawuer Mountain [40])	1959–2013	15.09	9.42	37.57	0.11
Altun Mountains [41]	1970–2016	326.02	272.95	16.28	1.15
Eastern of Gangdisê, Nyainqentanglha Mountains, eastern of Himalayas Mountains (Parlung Zangbo River) [42]	1994–2015	776.44	324.72	58.18	21.51
Gangdisê Mountains [43]	1970–2016	2160.50	1306.45	39.53	18.57
North slope of the Karakoram Mountains (Yarkant River basin) [36]	1968–2009	6341.82	5414.77	14.62	22.61
Western Karakoram Mountains (Gilgit River Basin) [44]	1993–2016	1126.77	1080.95	4.07	1.99
Eastern Pamir [45]	1960–2009	2275.8	2054.0	9.75	4.53
Qiangtang Plateau (Zangser Kangri Glacier) [46]	1971–2015	316.97	297.65	6.10	0.44
Qilian Mountains [47]	1956–2010	2000.62	1597.81	20.13	7.46
Qilian Mountains [48]	1987–2018	2080.39	1442.09	30.68	20.59
Middle Qilian Mountain [49]	1956–2003	397.41	311.02	21.74	1.84
Western Qilian Mountain [50]	1957/1966–2010	332.48	275.27	17.21	1.17
Qilian Mountain (Heihe River Basin) [51]	1990–2010	66.30	13.37	79.83	2.65
Central Qilian Mountain (Hulugou Basin) [52]	1956–2011	2.11	1.45	31.28	0.01
Qilian Mountain (Laohugou Glacier No. 12) [53]	1957–2015	21.91	20.37	7.03	0.03
Que' er Mountains (Southeastern Tibetan Plateau) [54]	1987–2016	103.63	52.82	49.03	1.75
Sawuer Mountain [55]	1977–2017	23.00	12.49	45.70	0.26
Tianshan Mountains [56]	1960–2010	8799.82	7179.77	18.41	32.40
Northern slope of Tianshan Mountains (Urumqi Basin) [57]	1964–2014	57.40	20.18	64.84	0.74
Eastern Tian Shan (Southern slope of Kalik Mountain) [58]	1972–2005	66.3	58.1	12.37	0.25
Tianshan Mountains (South slope of Sawuer Mountain [40])	1959–2013	2.60	0.71	72.69	0.04
Eastern Tianshan Mountains (Bogda regions) [59]	1990–2015	158.17	104.44	33.97	2.15
Eastern Tianshan Mountains (Karlik regions) [59]	1990–2015	158.88	107.80	32.15	2.04
Tianshan Mountains (Tomur National Nature Reserve) [60]	1992–2017	1600.56	1534.46	4.13	2.64
Tianshan Mountains (Urumqi Glacier No. 1) [61]	2012–2018	1.59	1.52	4.40	0.01
Himalayas Mountains [62]	1990–2015	23,229.27	20,676.17	10.99	102.12
Eastern Himalayas Mountains (Namjagbarwa Mountain) [63]	1980–2015	294.72	219.48	25.53	2.15
Eastern Himalayas Mountains (China and Bhutan border area) [64]	1990–2015	1779.37	1587.50	10.78	7.67
Western Himalayas Mountains (Chenab Basin) [65]	1993–2016	2847.91	2683.35	5.78	7.15
Northern Himalayas Mountains (Chema Yongdrung Glacier) [66]	1976–2019	22.98	21.37	7.01	0.04
Tanggula Mountains (Geladandong region) [67]	1986–2015	997.47	905.41	9.23	3.17

<sup>1</sup> Retreat area was the ratio of glacier area change in the time series to the glacier area of the beginning of the time series. <sup>2</sup> Retreat rate was the annual reduction of glacier area, calculated based on the change of glacier area and the corresponding time series.

### 3. Diversity and Community Structure of Glacial Microbiomes in China

Despite the harsh environment with low temperatures and limited nutrients, microorganisms play important roles in the glacier forelands and have a high level of diversity, including abundant bacteria, archaea, fungi, and viruses [68]. In the early stage, microbial research mainly depended on traditional microbial isolation and culture methods, which hindered our acknowledgement of cryospheric microbes. Since the 1990s, the emergence of non-culturally microbial research methods, including cloning libraries and high-throughput sequencing, has made the study of cryospheric microbiomes more comprehensive and accurate as well as accelerating the cryospheric microbial research [69]. The glaciers in the Tibetan Plateau cover an area of 47,000 km<sup>2</sup>, accounting for 80% of the total glacier area in China [70], making this main region suitable for glacial microbial research in China. The Pamir Plateau and the Tianshan Mountains are other active regions for glacial microbial research (Table 2).

**Table 2.** Summary of the microbial diversity data for glaciers in China.

Location	Sample Type	Microbial Abundance (Cells/mL)	Culturable Bacteria Abundance (CFU/mL)	Dominant Microbial Groups
Dunde ice cap, Qilian Mountain region [71]	Ice core	$1.3 \times 10^5$ – $1.9 \times 10^6$		<i>Blastococcus</i> sp./ <i>Propionibacterium</i> , <i>Cryobacterium</i> -related, <i>Flavobacterium</i> sp., <i>Pedobacter</i> sp., <i>Polaromonas</i> sp.
Guliya ice cap, Tibetan Plateau [72]	Ice core	180		<i>Arthrobacter</i> , <i>Aureobacterium</i> , <i>Bacillus</i> , <i>Bradyrhizobium</i> , <i>Brevibacterium</i> , <i>Cellulomonas</i> , <i>Clavibacter</i> , <i>Flavobacterium</i> , <i>Frankia</i> , <i>Friedmanniella</i> , <i>Methylobacterium</i> , <i>Microbacterium</i> , <i>Micrococcus</i> , <i>Micromonospora</i> , <i>Mycobacterium</i> , <i>Nocardia</i> , <i>Nocardioidea</i> , <i>Paenibacillus</i> , <i>Planococcus</i> , <i>Propioniferax</i> , <i>Sphingomonas</i> , <i>Staphylococcus</i> , and <i>Stenotrophomonas</i>
Malan Glacier, Tibetan Plateau [73]	Ice core	50–410	0–85	<i>Micrococcus</i> , <i>Staphylococcus</i> , <i>Bacillus</i> , <i>Brevibacter</i> , <i>Achromobacter</i> , <i>Pseudomonas</i> , <i>Alcaligenes</i> , <i>Flavobacterium</i> , <i>Arthrobacter</i> , <i>Nocardia</i> , <i>Streptomyces</i>
Malan Glacier, Tibetan Plateau [74]	Ice core			Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, CFB <sup>1</sup>
Muztagata ice core, Pamir Plateau [75]	Ice core		0–127	Alphaproteobacteria, Gammaproteobacteria, Cryobacteria, CFB, HGC <sup>2</sup>
Muztagata Glacier, western margin of the Tibetan Plateau [71]	Ice core	$4.4 \times 10^4$ – $8.7 \times 10^5$		<i>Polaromonas</i> sp., <i>Enterobacter</i> sp., <i>Acinetobacter</i> sp., <i>Flexibacter</i> sp., <i>Flacvisolibacter</i> sp., <i>Thermus</i> sp., <i>Propionibacterium/Luteococcus</i> sp.
Urumqi Glacier No. 1, Tianshan Mountains [76]	Ice core	$1.4 \times 10^3$ – $1.0 \times 10^5$	0–300	Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Bacilli, Actinobacteria, Sphingobacteria, Flavobacteria
Urumqi Glacier No. 1, Tianshan Mountains [77]	Cryoconite			Oscillatoriales, Chroococcales
Yushugou Glacier, eastern Tianshan Mountains [78]	Cryoconite granules			Oscillatoriales, Chroococcales
East Rongbuk Glacier, Mount Everest [79]	Meltwater			Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Actinobacteria, Firmicutes
Laohugou Glacier No. 12, Qilian Mountains [80]	Meltwater, surface ice			Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, Verrucomicrobia, Acidobacteria, Planctomycetes, Cyanobacteria/Chloroplast
Yangbark Glacier, Muztagata [81]	Meltwater, surface ice, snow			Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Firmicutes, Actinobacteria, Bacteroidetes
Qiyi Glacier, Qilian Mountains [82]	Surface ice/snow			Oscillatoriales, Chroococcales
Qiyi Glacier, Qilian Mountains [83]	Snow pit, runoff	$9.1 \times 10^3$ (snow) $42.0 \times 10^3$ (runoff)	126.9 (snow) 271.8 (runoff)	Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Actinobacteria, Bacteroidetes, Firmicutes,
Yala Glacier, southern slope of the Himalayas [84]	Surface snow	$1.1 \times 10^4$ – $9.0 \times 10^4$		Alphaproteobacteria, Betaproteobacteria, Cyanobacteria, Actinobacteria, Bacteroidetes, Firmicutes

Table 2. Cont.

Location	Sample Type	Microbial Abundance (Cells/mL)	Culturable Bacteria Abundance (CFU/mL)	Dominant Microbial Groups
Meikuang Glacier, Tibetan Plateau [85]	Surface snow, snow pit		58.07	Bacteroidetes, Actinobacteria, Firmicutes, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria
Xiao-Dongkemadi Glacier, Tibetan Plateau [85]	Surface snow, snow pit		18.54	Actinobacteria, Firmicutes, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria
Yuzhufeng Glacier, Tibetan Plateau [85]	Surface snow, snow pit,		35.53	Firmicutes, Actinobacteria, Alphaproteobacteria, Betaproteobacteria
DongRongbu Glacier, Qomolangma region [86]	Snow pit	$5.7 \times 10^3$ – $2.3 \times 10^4$		Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Actinobacteria, Firmicutes, CFB, Cyanobacteria, Eukaryotic chloroplast, TM7 candidate phylum
Glaciers, Yulong Mountain regions [87]	Snow pit	$1.4 \times 10^3$ – $3.9 \times 10^3$	8–96	Alphaproteobacteria, Actinobacteria, Firmicutes
Miaoergou glacier, East Tianshan Mountains [88]	Sonw pit	$1.03 \times 10^4$ – $1.74 \times 10^4$	$1.18 \times 10^2$ – $4.96 \times 10^2$	Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, CFB, HGC, LGC <sup>3</sup>
ZhuoAoyou Peak, Tibetan Plateau [89]	Sonw pit			<i>Caulobacter</i> , <i>Ralstonia</i> , <i>Cupriavidus</i> , <i>Pelomonas</i> , <i>Pseudomonas</i>
Chongce Ice Cap, West Kunlun Mountains [90]	Glacial snow, exposed soil			Actinobacteria, Proteobacteria, Deinococcus-Thermus, Acidobacteria, Armatimonadetes, Bacteroidetes, Chloroflexi, Cyanobacteria, Candidate division FBP, Gemmatimonadetes, Planctomycetes, Verrucomicrobia
Hailuogou glacier retreat area, Gongga Mountain [91]	Exposed soil			Proteobacteria, Acidobacteria, Bacteroidetes, Actinobacteria
Laohugou Glacier No. 12, Qilian Mountains [92]	Exposed soil			Proteobacteria, Cyanobacteria, Actinobacteria.
Mingyong Glacier, Yunnan Province [93]	Exposed soil			<i>Pseudomonas</i> , <i>Yersinia</i> , <i>Stenotrophomonas</i> , <i>Bacillus</i> , <i>Brevibacterium</i> , <i>Streptomyce</i> , <i>Flavobacterium</i>

<sup>1</sup> CFB denotes the bacterial group of Fibrobacterium, Flavobacterium, and Proteobacteria (CFB). <sup>2</sup> HGC denotes bacterial group whose DNA has higher G and C DNA bases than A and T bases, as compared to other bacteria. <sup>3</sup> LGC denotes the bacterial group whose DNA typically has fewer G and C DNA bases than A and T bases in comparison with other bacteria.

### 3.1. Bacteria and Archaea

At the end of the 19th century, Christner [72] analyzed the Guliya ice cores from the Tibetan Plateau glaciers and found that the number of bacteria in them reached 180 cells/mL. Microbial diversity research was also subsequently conducted on Malan Glacier, Urumqi Glacier No. 1 in Tianshan Mountains and Dongkemadi Glacier on the Tibetan Plateau [72,75,84]. The number and major groups of bacteria in the ice cores varied in the different glaciers. The microorganisms in the Malan ice core were mainly Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, and Fibrobacterium/Flavobacterium/Proteobacteria (CFB), with a total amount of 50–410 cells/mL, and the culturable microorganisms were 0–85 CFU/mL [73]. Tianshan Glacier No. 1 had a higher total number of microorganisms ( $10^3$ – $10^5$  cells/mL) compared to Malan Glacier [76]. The dominant taxa were found to be Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, CFB, high G+C% bacteria (HGC), and low G+C Gram-positive bacteria (LGC) [76,88]. The culturable microorganisms in the Muztagata ice cores from the Pamir Plateau ranged from 9 to 96 CFU/mL with main taxa of Alphaproteobacteria, Betaproteobacteria, Cryobacteria, CFB, and HGC [75]. It can be seen that although there are differences in the microorganisms in the different glacial ice cores, there are also commonalities, which may be because microorganisms in ice cores mainly originate from atmospheric deposition. The atmospheric deposition in different periods may drive the different bacterial abundances and community structures at different ice core depths. For example, the composition of the bacterial taxa varied at four depths in the Malan ice core: Alphaproteobacteria, Betaproteobacteria, and Gammaproteobacteria (35 m); Betaproteobacteria (64 m); Gammaproteobacteria, CFB, Marinobacter, and agricultural soil bacterium (70 m); and Betaproteobacteria (82 m) [74]. The number of culturable bacteria in the Muztagata ice cores also varied with depth in the cores, and the variations were few and small at depths of 0–2.7, 3.0–5.5, 12.5–14.7, and 16.0–17.7 m, while the number of culturable bacteria (2 to 56 CFU/mL) was greater at depths of 8–9.2 m [75].

With the continuous development of biomolecular information technology, microbial studies of glacier surface ice and snow have gradually developed, and the bacterial taxa present have been identified, including Alphaproteobacteria, Betaproteobacteria, Actinobacteria, Bacteroidetes, Firmicutes, Flavobacterium, and Cyanobacteria [81,85]. As the important autotrophic microbes, Oscillatoriales and Chroococcales were the main orders of cyanobacteria in the glacial surface, which could be found in the cryoconites of Urumqi Glacier No.1 and Yushugou Glacier [77,78]. The CFB and Proteobacteria taxa were dominant in the snow pits of the Miaoergou glacier in the Tianshan Mountains, while Actinobacteria was the dominant bacterial group in the snow samples from ZhuoAoyou on the Tibetan Plateau [88,89]. Alphaproteobacteria was the dominant culturable bacterial group, accounting for 52%, isolated from the snow pits on Yulong Snow Mountain [87]. However, the dominant taxon in the surface snow and meltwater from Qiyi Glacier in the Qilian Mountains was Bacteroidetes [88]. This shows that the geographic location of the glacier has an impact on the bacterial community structure because of the distinctly different climatic and nutritional conditions [94,95]. In addition, the seasons also led to changes in the number of bacteria and the community's structure; e.g., the number of bacteria in snow deposited in summer ( $2.3 \times 10^4$  cells/mL) was much higher than that in the snow deposited in winter ( $6.9 \times 10^3$  cells/mL) in Rongbuk Glacier on Mt. Qomolangma [86]. Archaea have a lower diversity in glacier forelands and have received more research attention because of their important role in biogeochemical cycles, especially that of methane [96]. Euryarchaeota, Crenarchaeota, and Thaumarchaeota are the three dominant archaea phyla in glacier forelands, and they can withstand the low temperatures and remain active, but reports of archaea in glacial ice and snow environments in China are still rare [97–99].

Microbial activity and diversity are closely related to climatic factors such as temperature. Environmental changes induced by glacial retreat due to global warming are the main cause of the varied distribution of microbial communities in glacial retreat areas [100]. The microbial community in the glacier retreat area is dominated by bacterial communities, and

archaea only account for a very small proportion [101]. Yue et al. reported that there was no correlation between the culturable bacteria and retreat time in the Zadang glacier foreland in the Nianqing Tanggula Mountains [102], while the number of culturable bacteria in the Tanggula Dongkemadi Glacier and Tianshan Glacier No. 1 increased with increasing glacier retreat time [103,104]. Focusing on Tianshan Glacier No. 1, we found that the copy number and microbial  $\alpha$ -diversity of the soil bacteria and archaea increased with increasing retreat age, and the relative abundance of the Bacillus phylum was found to increase, as well [105]. The abundances and community structure of the microorganisms shifted due to climate warming, and they generally exhibited positive correlations with the retreat time. However, because of the climate and environmental heterogeneity, there are some exceptions [106]. Further study is needed to clarify the underlying reasons for the specific successional changes in glacier microbiomes.

### 3.2. Fungi

Compared with bacteria and archaea, fungi are rare in the glacier surface and can be more easily found in the glacier forelands [107]. The dominant fungal phyla in the retreat area are Ascomycota and Basidiomycota [90,108,109]. There are also geographical differences in the community structure of glacial fungi; for example, the fungi in Himalayan glaciers include the genus *Lemonniera* and species *Tetracladium nainitalense* (Sati and P. Arya) and *Thelebolus microsporus* (Berk. and Broome) [69,108]; those in the Tibetan Plateau glaciers include *Phoma sclerotoides* (Preuss ex Sacc.), *Pseudogymnoascus pannorum* (Minnis and D.L. Lindner), *Psychrophila antarctica* (M.M. Wang and Xing Z. Liu), *P. lutea* (M.M. Wang and Xing Z. Liu), *P. olivacea* (M.M. Wang and Xing Z. Liu), *Tetracladium ellipsoideum* (M.M. Wang and Xing Z. Liu), *T. globosum* (M.M. Wang and Xing Z. Liu), and *T. psychrophilum* (M.M. Wang and Xing Z. Liu) [69,109]. In addition, differences in the structure of the fungal communities have been observed in different locations in the same glacier. The dominance of Basidiomycota and Ascomycota in Tianshan Glacier No. 1 is consistent with the dominant fungal taxa in the Hailuoguo Glacier [91]. At the genus level, *Rhodotorula* and *Leucosporidium* dominate the glacier surface, but the unique genus *Cladosporium* also exists here. The genus *Aureobasidium* is unique to the sediment layer at the bottom of the glacier, and the dominant genera are *Aspergillus* and *Simplicillium* [110].

### 3.3. Viruses

Viruses are not only important drivers of microbial evolution due to their unique mode of survival and reproduction, but they also play important roles in the cycling of nutrients and organic matter in ecosystems. Because of the fragile, low biodiversity, and short biological chains in glacial ecosystems, viruses in glaciers have a more significant impact on their material cycles and microbial community survival [111]. Viruses have been found in relatively high abundances and diversity in the South and Arctic glaciers and the Greenland glaciers, and a high virus-to-bacteria ratio has been reported [112]. Analysis of their genetic information has revealed that there were 33 different viral species, including four known genera and 28 unknown genera, in the ice cores from Guria Glacier on the Tibetan Plateau. In addition, genetic prediction analysis revealed that 18 viral species were closely related to the number of multiple bacteria in the ice cores [113]. Viruses in the cryosphere may be released due to climate change, permafrost thawing, and glacier retreat. Based on an average glacier virus-to-bacteria ratio of 30 to 1, the amount of viruses released from Arctic glaciers into the downstream environment could be up to approximately  $10^{23}$ , which has a significant impact on downstream ecosystems [114,115]. The study of cryosphere viruses in China and around the world is still in its infancy. The impacts of these released viruses and how to cope with the possible threat under climate warming are important research directions for the future.

#### 4. Involvement of Glacier Microbes in Carbon Cycle

According to statistics, approximately 6 Pg of organic carbon is stored in glaciers worldwide, which could be released after glacier retreat due to the increased temperature and increased microbial activity [116]. The impacts on the ecosystems and the feedback on climate change due to the increased carbon release from the glacier ecosystem must be assessed. It is estimated that  $0.58 \pm 0.07$  Tg of dissolved organic carbon would be released from meltwater of mountain glaciers, which would account for about 56% of dissolved organic carbon loss from all glaciers in the world [116–118]. In addition, as glaciers melt, subglacial sediments are gradually exposed and large amounts of carbon are released in different forms, further influencing the balance of the original global carbon cycle [119].

Glacier forelands provide an ideal study area and are a spatial representative of the temporal changes in important biogeochemical processes such as the accumulation of soil organic carbon (SOC) [120,121]. Except for external input such as supraglacial input and aerial deposition, biological activity is the major source of the nutrients in glacier forelands [120,122]. Thus, there are three distinct carbon sources in glacier forelands: the ancient organic pools originating from under the glacier, exogenous deposition such as soot particles, and the primary production of vegetation and autotrophic microorganisms [122]. Soil development requires the accumulation of SOC, but the speed of soil development is significantly affected by the climate conditions and regional geographic environment. The microbial biogenic carbon content varies significantly with successional age, ranging from 4.78 to 145.53 mg/kg in the soils exposed by the retreat of Hailuoguo Glacier, which is a typical temperate glacier in China [123]. Shrubs appeared in less than 30 years in the foreland of Hailuoguo Glacier [124]. Meadow vegetation began to colonize the area after the soil had been exposed for about 20 years in the forelands of Tianshan Glacier No. 1, and in more than 10 years for the Laohugou Glacier [125].

As the dominant undertaker of life activities in the fragile glacier ecosystem, microorganisms are the main contributors to the carbon cycles, and they have various metabolism and fixation capacities, which determine the dynamic storage of the carbon pool before the emergence of vegetation [8,126]. Traditionally, detection of enzyme activity and microbial culture methods have been used to study the biogeochemical processes mediated by microbial communities [127–129]. With the development of high-throughput sequencing and the microarray-based metabolic Geochip, a better understanding of the relationships between element biogeochemical cycles and microorganisms can be obtained from the microbial community's composition, as well as the diversity and abundance of the functional genes [130].

Under the low temperature, high UV exposure, and unstable water conditions of the glacier ecosystem, microorganisms, including fungi, bacteria, and archaea, in glacier forelands are characterized by strong carbon metabolism abilities [131]. Zhu et al. [92] determined that the microbial community in the Laohugou Glacier can use amino acids, carbohydrates, carboxylic acids, and amines as metabolic substrates using the BiologEco microporous plate method. By detecting the soil enzymes, such as urease, sucrase, protease, polyphenol oxidase, catalase, and dehydrogenase, Wu et al. [127] found that the enzyme activity increased as the exposure time increased in the foreland of Tianshan Glacier No. 1, indicating active microbial metabolism. This is consistent with the increased microbial activity during the soil chronosequence of the foreland of Tianshan Glacier No. 1 [132]. Sanyal et al. [133] found that the microbial communities in the Himalayan region are able to utilize more diverse types of carbonaceous substrates compared to those in the Antarctic region. The effects of the heterogeneity of mountain glaciers on the responses and feedback of microbial communities must be studied further.

Nearly all microorganisms need to decompose carbon nutrients to survive; only photoautotrophs such as Cyanobacteria and chemoautotrophs and some members of Alphaproteobacteria can synthesize carbon compounds independently through utilization of inorganic carbon such as CO<sub>2</sub> and bicarbonate [121,134,135]. Cyanobacteria are important contributors to the carbon in glacier forelands and cryconite [76,133,136]. For example,

*Cyanobium* (*Synechococcales*), *Trichormus*, and *Nostoc* (*Nostocales*) can fix CO<sub>2</sub> into organic carbon compounds using light energy via the Calvin cycle (CBB cycle). This typical carbon fixation pathway utilizes one molecule of CO<sub>2</sub> and ribulose 1, 5-disphosphate to synthesize three molecules of triose phosphate [137,138]. Some members of Cyanobacteria can upregulate the carbon concentration to improve the carbon fixation ability [134]. Chemoautotrophs such as sulfate-reducing bacteria and Chlorobiales have been found in Antarctic soils [135], and they can utilize organic carbon through the reductive tricarboxylic acid cycle (rTCA cycle). This pathway converts four molecules of CO<sub>2</sub> into one molecule of oxalacetate [137]. The reductive acetyl-CoA pathway (WL cycle) and the hydroxypropionate bicycle (3HP cycle) convert two molecules of CO<sub>2</sub> into acetic acid or glyoxylate [136], and they have been found to occur in Antarctica based on detection of *Chloroflexi*, *Armatimonadetes*, and *Nitrospirae* [119,139]. Generally, the Calvin cycle is the main pathway in the surface environments of mountain glaciers, such as in the glacial runoff of Qiangyong and Satrundi glaciers on the Tibetan Plateau [140,141]. Based on bioinformatics analysis, Actinobacteria, Cyanobacteria, and Proteobacteria, which are also the main microbial groups found in Chinese glaciers, are the dominant carbon sequestration microbial groups [140,142–144]. The mean relative abundance of Actinobacteria, Cyanobacteria, and Proteobacteria was found to be higher in Tibetan Plateau glaciers than in the South and Arctic glaciers, which implies a higher carbon fixation ability in this area [119]. The assessment of the rate of carbon sequestration is key to understanding the carbon cycle; however, few relevant studies have been conducted on the Chinese glacier ecosystem.

## 5. Concluding Remarks

At present, climate change has accelerated glacier ablation, accompanied by a large amount of glacier foreland exposure. With the abundant carbon storage and more intense microbial activities, not only have microbial succession and soil development received wide attention, but changes in the carbon cycle in glacier forelands have also been intensively studied, such as carbon sources [8,122], the carbon release rate [145], and the dynamic processes involving carbon [146,147].

Climate warming will have direct and indirect effects on microbial communities, including changes in the microbial community structures, the accelerated release of CO<sub>2</sub>, and the indirect impact of changes in the soil properties [148]. Based on field experiments and indoor simulation experiments, the carbon loss would be intensified as the temperature increases due to the more active microbial activities [149–151]. Higher carbon fluxes have been detected in short-term warming experiments compared with long-term warming experiments [152], which is related to the lack of labile carbon [153], the low carbon utilization rate [154], and changes in the thermal adaptability of microorganisms [155,156].

Furthermore, the biogeochemical cycle in the glacier ecosystem is mediated by microorganisms, which are affected by the environmental conditions, such as nutrient limitations [157]. Jiang et al. [158] investigated the microbial processes and nutrient limitations and also found that carbon and nitrogen are the main limiting nutrients in the early succession stage in Hailuoguo Glacier, followed by a shift to phosphorus in the later stages. Climate warming and the retreat time affect the soil properties and microbial community, which can result in positive or negative feedback.

As one of the indicators of climate change, glacier microbiomes and their response to climate warming can provide a better understanding of glacier ecosystems and the effects of climate warming. At present, although a series of results have been achieved regarding microbial diversity and community structure, research on Chinese glacial microbiomes still needs to be strengthened. Under the context of climate change, future sustained research, including the following topics, is required.

### 1. Response of glacial microbes to climate change

Microbial responses to climate change are complex. The microbial response to climate warming varies in the different types of glaciers. In particular, mountain glaciers have a higher environmental heterogeneity, so enhancing the research on these glaciers may

improve our understanding of global glacier microbes. In addition, ancient viruses that lie dormant in glaciers may be gradually released with the melting of glaciers. Whether they are still infectious and pose a great threat to glacial ecosystems locally or globally is an issue that needs to be explored.

## 2. Evolutionary and biogeographical studies of glacial microbiomes

Many studies have found that glacial microorganisms mostly originate from atmospheric deposition, and they subsequently undergo gradual adaptation over time to become glacier-specific, but there are different opinions on this subject. Therefore, where and how glacial microbes originate, how they colonize, and their environmental and evolutionary drivers need to be studied further. The microbial diversity in the glaciers in China has both uniqueness and similarities compared to glaciers elsewhere in the world. Whether there is a certain pattern in the distribution of glacial microbes across the country or even globally must be determined. All of these issues are related to the origin and evolution of glacial microorganisms and biogeography.

## 3. Glacial microbes and geochemical cycles

At present, research on the mediation of the geochemical cycles by glacial microbiomes in China is in the preliminary stage. More attention is devoted to the carbon and nitrogen cycles, while other elements, such as sulfur, phosphorus, and metals, have been studied less. With the retreat of glaciers, various elements contained in the glaciers are gradually being released, and their effects on glacial microorganisms and the underlying mechanisms of these effects need to be studied further.

## 4. Glacial microbial diversity and microbial resources

Glacier microorganisms often have their own unique metabolic characteristics and products, such as protease producing low-temperature resistant bacteria, low-temperature amylase-producing strains, and purple pigment synthesized strains [159–161]. The diversity of glacier microorganisms is rapidly decreasing as a result of climate warming, which suggests that the biodiversity of the environment-specific microorganisms in glaciers will also decrease. We recognize the effects of climate change on glacier microbiomes and their feedback; however, we know far less about this issue. It is urgent to strengthen research on glacier microbiomes to conserve the biodiversity and these unique microbial resources.

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