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Abstract

The cryosphere is one of the biomes on Earth. In recent years, studies on microorganisms in cold habitats has been mainly focused on the Earth's cryosphere, including glaciers, ice sheets, sea ice, lake ice, and permafrost. Most of the microbial groups harboring in cryosphere are cold-adapted microbes, many of which are still unknown. Psychrophiles are important strategy resources in the fields of scientific research and low temperature biotechnology. The cryosphere also seals many unknown ancient pathogenic bacteria, fungi, and virus to animals, plants, and human beings. The cold habitats and harsh conditions in the cryosphere shape the diverse microbial populations that pose unique adaptability for survival in such extreme environments. Since highly sensitive to climate changes, the cryosphere is changing as indicated by the retreat of glaciers and ice sheets as well as permafrost thawing under global warming. The habitats where the microbes of cryosphere survive on are shrinking. The release of these microbes from the cryosphere, such as the glacier and ice retreat and permafrost thawing, might be a great threat to human society. Additionally, frozen ecosystems are also of much interest as analogues of extraterrestrial habitats. Therefore, a deeply understanding of the role and potential of microbial life in cryosphere habitats has become crucial.

Keywords

cryosphere; microbes; climate change

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Microbes in Cryosphere: Opportunities and Challenges

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Abstract: The cryosphere is one of the biomes on Earth. In recent years, studies on microbes in cold habitats have been mainly focused on the Earth's cryosphere, including glaciers, ice sheets, sea ice, lake ice, and permafrost. Most of the microbial groups in cryosphere are cold-adapted microbes, many of which are still unknown. Psychrophiles are important strategy resources in the fields of scientific research and low temperature biotechnology. The cryosphere seals many unknown ancient bacteria, fungi, and viruses pathogenic to animals, plants, and human beings. The cold habitats and harsh conditions in the cryosphere shape the diverse microbial populations that pose unique adaptability for survival in such extreme environments. Since being highly sensitive to climate changes, the cryosphere is changing as indicated by the retreat of glaciers and ice sheets as well as permafrost thawing under global warming. The habitats where the microbes of cryosphere survive on are shrinking. The release of these microbes from the cryosphere might be a great threat to human society. Additionally, frozen ecosystems are also of much interest as analogues of extraterrestrial habitats. Therefore, a deeply understanding of the role and potential of microbial life in cryosphere habitats has become crucial. **DOI:** 10.16418/j.issn.1000-3045.20200228003-en

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Cryosphere, with subzero temperature, certain thickness and continuous distribution on the earth surface, is composed of glaciers (including ice sheets), snow cover, permafrost, river ice, lake ice, sea ice, ice shelf, iceberg and frozen water in the atmosphere. It is a unique and extreme habitat on the earth. The progress and integration of science and biotechnology on cryosphere have fostered the research on microbes in cryosphere, expanded the field of biotechnology and its application, and enriched the diversity of the earth ecosystem. The spectrum of microbial flora in cryosphere, especially of that in ice core, preserves the information of paleoclimate and is important biological information treasure for studying global climate change. The acceleration of global warming, the feedback effect of microbial activities on cryosphere and the role of these microbes in the emissions of greenhouse gases are major scientific issues in today's global change.

The current cryosphere, especially habitats like ice core and subglacial lake, bears slight resemblance to the earth at the early stage of life origin. The life process and characteristics of microbes in cryosphere may enlighten us on the origin and the low temperature limit of life. Cryosphere is considered to be an environment similar to Mars, Europa, Ganymede, Callisto and Himalia on the earth, and clues about microbes in cryosphere are expected to inspire the exploration of extraterrestrial life [1].

1 Review of microbes in cryosphere

The research on microbes in cryosphere began with the exploration and scientific expedition of human beings to polar regions and mountains. The research has lasted for more than 100 years [2], which has experienced three stages: morphological research, physiological research and omics research. The research scope covers the main elements including permafrost, glacier, snow and sea ice of cryosphere. Scientists have isolated a variety of microbes including archaea, bacteria and fungi from the cryosphere elements. The latest data on the number of microbial cells in cryosphere habitats are shown in Table 1 [3].

1.1 Bacteria and fungi in permafrost

Permafrost, with the area accounting for 25% of the land surface and main distribution in the Antarctic, the Arctic and

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Table 1 Number of microbial cells in cryosphere habitats [3]

Cryosphere habitat	Mean area ($\times 10^6 km^2$)	Mean volume ($\times 10^3 km^3$)	Cell density ($cells\cdot mL^{-1}$)	Total cells
Seasonal snow	47	2	10^2—10^5	10^{20}—10^{23}
Sea ice	25	50	10^4—10^7	10^{23}—10^{26}
Upper glacier	17	0.02	10^4—10^8	10^{23}—10^{27}
Inner glacier	17	33 000	10^1—10^3	10^{23}—10^{25}
Glacier base	17	0.02	10^3—10^5	10^{22}—10^{24}
Subglacial lake	> 0.05	16	10^2—10^5	10^{21}—10^{24}
Permafrost	23	300	10^5—10^8	10^{25}—10^{28}
Total	112	~ 33 400	10^1—10^8	10^{25}—10^{28}

high mountains, is an important habitat for microbes in cryosphere [4]. The research on microbes in permafrost has been widely valued for a long time. There are diverse microbes with a density of 10^5–10^8 $cells\cdot g^{-1}$ in permafrost [4]. As permafrost has the characteristics of chronology in depth, bacteria of different ages can be isolated from the permafrost. For example, living microbes at a density of 1×10^7 $cells\cdot g^{-1}$ were detected from the permafrost of about 100 000 years in northeastern Siberia [5], and living bacteria at a density of 10^2–10^8 $cells\cdot g^{-1}$ were detected in 1–3 million years of permafrost in the Arctic [2].

In permafrost, fungi mainly exist in the form of spores, with the number much lower than that of prokaryotic microbes. Among them, culturable yeast in Arctic permafrost has the density of 10^3–10^4 $CFU\cdot g^{-1}$, belonging to *Cryptococcus*, *Rhodotorula*, *Saccharomyces* and *Sporobolomyces*; *Geomyces*, *Cladosporium*, *Penicillium* and *Aspergillus* belonging to Ascomycota are common filamentous fungi. In contrast, the number of culturable yeast and filamentous fungi is low in the Antarctic permafrost, and *Cryptococcus* and *Mrakia* are the common fungi [6]. Diatoms are the main unicellular plants in sea ice, and more than 550 species of diatoms have been identified in the Arctic region, including 446 species of *Pinnularia* and 122 species of *Centridiatom* [4].

1.2 Bacteria and fungi in snow and ice

Scientists have carried out in-depth analysis on microbes in snow because of the easy sampling. The analysis of microbes in the Antarctic and Arctic regions and alpine snow demonstrated that the density of microbial cells in seasonal snow was 10^2–10^5 $cells\cdot mL^{-1}$ [4], while there were few new microbial species. The microbes in snow come from soil indirectly, and the source and species of microbes in snow are determined by atmospheric transport [7,8].

The ice in cryosphere is composed of glaciers, polar ice shelves and sea ice. It was first believed that there was no microbe in polar ice, whereas a large number of analyses showed that microbes grew and propagated in all types of ice, and their species and cell number decreased with the increase in ice depth. For example, the density of microbial cells in the surface ice was 10^4–10^8 $cells\cdot mL^{-1}$, while that in the glacier dropped to 10^1–10^3 $cells\cdot mL^{-1}$ [4]. Microbes in ice core were mainly from land dust, marine aerosols and volcanic dust, and the abundance is related to annual snowfall. The number of microbial cells in ice core was large in the year with heavy snowfall. Bacterial cells with the concentration of 180 $CFU\cdot mL^{-1}$ were detected in the ice core of Guliya Ice Cap of about 200 years old, and those with the concentration of 0–10 $CFU\cdot mL^{-1}$ [9] in the ice core of Antarctic Taylor Dome of about 1 800 years old. The Greenland Ice Sheet Project 2 (GISP2) drilled an ice core with a depth of 3 042.80 m and detected the microbial cells at a density of 6.1×10^7–9.1×10^7 $cells\cdot mL^{-1}$ in the meltwater [8]. Cryoconite hole is a microhabitat formed by local melting of ice on ice shelf and glacier. The microbial flora in cryoconite hole has unique characteristics: high abundance and activity, which has a marked impact on the melting and carbon cycle of glacier [10]. Although the sea ice has high salinity, the microbial density is 10^2–10^5 $cells\cdot mL^{-1}$ [4]. The subglacial lakes in the Antarctic and the Arctic, which have been sealed for hundreds of thousands of years, are more unique habitats in the cryosphere, where the microbial density is 10^2–10^5 $cells\cdot mL^{-1}$. Abundant species of fungi have been isolated from snow and ice in recent years [6]. Among them, 3×10^3–1×10^4 $CFU\cdot mL^{-1}$ yeast cells have been detected in the ice core of Svalbard Archipelago glacier [11], and many cryophilic and psychrophilic yeast have been isolated from ice in Alps glacier [12].

1.3 Viruses in cryosphere

Because of the poor nutrients and short food chain in the cryosphere, viruses play a vital role in the ecosystem and material circulation of the cryosphere. Viruses regulate the diversity and richness of bacteria and fungi by disrupting host cells which then release organic substances into the environment. Moreover, through horizontal gene transfer, they affect the evolution of host bacteria [13]. In recent years, with the advancement of metagenomic technology, the research on viruses in cryosphere has become a hot spot, especially for glaciers [14], ice shelf, lake water [15], soil [16] and sea ice [17] in the Antarctic and the Arctic. So far, abundant and diverse viruses have been detected in various habitats in the Antarctic and the Arctic, including bacteriophages, circular ssDNA viruses, dsDNA viruses, phycoDNAviruses and virophages that would infect algae, as well as RNA viruses including *Picornavirales* [18]. DNA viruses belonging to the *Microviridae* family were identified in the Taylor Valley cryoconite hole in the Antarctic [19]. According to the computer analysis, it is estimated that there are about 10 000 viruses in Antarctic ice lakes, much more than the 800 viruses in North American lakes [20]. The virus-like particles have the density of 10^5–10^8 particles·mL^{-1} in the Antarctic and Arctic sea ice [17], and the mean abundance of 10.9×10^5 particles·mL^{-1} and the mean viruses-to-bacteria ratio of 5.3 in the Antarctic sea ice core [21,22]. The mean viruses-to-bacteria ratio is an indicator for understanding the abundance of viruses in the cryosphere and its relationship with the host. Despite the large differences in different habitats, the collected data show that the viruses-to-bacteria ratio is high in the ice and cryoconite hole in the Antarctic and the Arctic (Table 2).

Table 2 Viruses-to-bacteria ratio in cryosphere habitats [20]

Cryosphere habitat	Mean viruses-to-bacteria ratio
Antarctic sea ice core	5.3
Antarctic cryoconite hole	< 10
Antarctic freshwater lake	< 10
Arctic glacier	7.5
Arctic cryoconite hole	136
Arctic glacial lake	30.6—80.0
North Atlantic Ocean	0.5—5
Mediterranean	0.3—138
Seawater	10

With the expansion of research scope in recent years, the knowledge on viruses in cryosphere has been enriched. The genomic sequencing of viruses in the ice cores of Guliya Ice Cap (northwestern Tibetan Plateau, China) 520 years ago and 15 000 years ago identified 33 viral populations (i.e., species-level designations) that represented four known genera and likely 28 novel viral genera (assessed by gene-sharing networks). The results of gene prediction show that 18 virus species are closely associated with the number of bacteria in ice core, which indicates that the virus hosts are diverse within the ice cores [23]. The giant virus isolated from Siberian permafrost 30 000 years old still has the activity of infecting the target host [24]. A large number of viruses have been found in Alaskan permafrost, which mainly exist in unfrozen water of permafrost [25].

2 Microbial resources in cryosphere

2.1 New microbes in cryosphere

The evolution of microbes in cryosphere is affected by the unique environment, and the microbial species and groups with strong adaptability gradually become dominant in each cryosphere element. After thousands or even millions of years of evolution, stable microbial community and ecosystems are formed. In recent 100 years, a large number of new microbial species or groups were isolated from the cryosphere, including new archaea, bacteria and fungi. With the development of molecular biotechnology, the isolation and identification of new microbial species in cryosphere are speeding up, and more and more new species will be reported. The task we are facing is to isolate and preserve the new microbes as much as possible for research and utilization before a certain cryosphere habitat disappears.

The extreme living conditions of cryosphere not only shape the microbial groups but also change their metabolic pathways, which strengthens the environmental adaptability of microbes during evolution. The new metabolites of microbes provide the possibility for human to obtain new bioactive compounds, such as antibiotics. Our team has isolated several new strains of methicillin-resistant *Staphylococcus aureus* (MRSA) from the permafrost on the Tibetan Plateau. Some secondary metabolites of these strains are new compounds with the potential of being applied as antibiotics. At present, this research is in progress [26,27].

2.2 Psychrophiles in cryosphere

The low-temperature environment of cryosphere drives the microbes evolve toward cold adaptation. Both psychrophiles and psychrotrophs that have been isolated and studied have been obtained from cryosphere. Among them, the deeply studied psychrophiles include *Colwellia psychrerythraea* 34H isolated from the Arctic Ocean sediments, *Psychromonas ingrahamii* from the Arctic sea ice, *Methanococcoides burtonii* DSM 6242 from the Arctic lake ice, *Planococcus halocryophilus* of the Arctic permafrost, and *Arthrobacter* sp. TAD20 and *Arthrobacter psychrolactophilus* F2 from the Antarctic soil [28]. Many psychrotolerant fungi and yeast have been isolated from habitats in cryosphere.

The isolation, culture, research and utilization of psychrophiles provide important strain resources for the development of microbes in cryosphere. The research on psychrophiles makes us deeply understand the various mechanisms of microbial adaptation to cold environment and provides us with a variety of psychrophilic bacteria and cold-active enzymes and proteins. These strains, enzymes and proteins have been applied to various fields such as industry, agriculture, medical treatment and environmental protection, which have achieved great economic and social benefits. Some cold-adaptive microorganisms have been applied in the field of bioenergy and show a bright development prospect. For example, the lipid accumulation of *Chlamydomonas* sp. ICE-L isolated from the Antarctic ice is higher at 0 °C and 5 °C than that at 15 °C and reached 84 $\mu L \cdot L^{-1}$ at 6 °C [29]. *Mrakia blollopsis* SK-4 can efficiently convert lignocellulose to ethanol at 10 °C [30]. The integration of these psychrophiles and cold-adaptation genes with biotechnology is fostering the development of new biotechnology industries [31].

2.3 Genetic resources in cryosphere

Although there may be a large number of microbial species with promising application prospects in cryosphere, only a small proportion of microbes can be isolated and cultured in the laboratory, which limits the research and utilization of microbes in cryosphere. The metagenomics technology provides a new strategy. The assembly of genomes and genes obtained by sequencing of the environmental samples can reveal the systematics, metabolic diversity and environmental adaptation of microbes. Moreover, the related functional genes and their functions can be studied, and then heterologous expression can be conducted to produce corresponding proteins. For example, metagenomic sequencing revealed that there were genes related to cold adaptation in Schneeferner glacier ice in Germany, including the genes related to the synthesis of cryoprotectants and polyunsaturated fatty acids [32].

3 Challenges from a changing cryosphere

3.1 Global warming is changing the cryosphere

Global warming is one of the biggest challenges in front of human beings. Cryosphere is the most sensitive sphere on the earth to global change. Global warming is leading to rapid shrinkage of cryosphere (including glacial retreat and permafrost thawing) [33]. However, the impact of such change on the microbial biodiversity, the downstream ecosystem and its biodiversity remains unknown. Permafrost, with the area accounting for about 1/4 of the land area on the earth, is an important carbon pool. Global warming will accelerate the microbial transformation of organic carbon and nutrients stored in the permafrost, resulting in the release of greenhouse gases CO_2, CH_4 and N_2O [34]. Glaciers account for about 10% of the earth's land area, and the glacial retreat will directly lead to the release of inorganic and organic substances (including pollutants) stored in them for a long time. The release of nutrients sealed in ice will affect the downstream water system, terrestrial ecosystem and biodiversity.

3.2 Cryosphere shrinkage accelerates the disappearance of habitats of microbes in cryosphere

The long-term low temperature makes cryophilic microbes survive in cryosphere, which has led to the unique microbe groups in cryosphere. Most of these microbial species can only survive in the cryosphere habitats. The melting of cryosphere will have a disastrous impact on them, and some endemic species will disappear. A study has shown that of all the organisms facing glacial retreat, about 6%–11% of the species become extinct, while 19%–26% survive. Most of the former are endemic to glacial habitats, some of which can only survive in glacial ecosystem. The latter is the widespread or invasive, which can usually settle in the downstream habitat of the glacier [33]. The permafrost seals microbes which have been dormant for thousands or even millions of years, and a large number of them are unknown species [35,36]. Permafrost thawing will lead to the change of their habitats, and these unknown microbial species will disappear before they are known.

3.3 Cryosphere melting releases unknown microbes

As mentioned above, there are many unknown microbes in cryosphere, which will inevitably impact the downstream ecosystem and even human society. It remains unclear that whether the cryosphere harbors microbes pathogenic to animals, plants and human beings. Especially, the impact of viruses released from cryosphere melting may impose serious challenges. Obviously, this issue is barely concerned. A study on viruses in cryosphere demonstrated that about 3.15×10^{21} bacterial and archaeal cells are released from the Arctic glacier ice to the downstream environment every year [37]. According to the mean viruses-to-bacteria ratio of 30:1 in the glacier, 10^{23} viruses will be released from the Arctic glacier to the downstream environment every year [38]. In this process, bacteria and viruses trapped in the cryosphere for tens of thousands to hundreds of thousands of years will be directly released into the environment, which has potential harm to human survival. In 2016, an outbreak of anthrax in Siberia killed more than 2 000 reindeers and hospitalized 96 people. Relevant studies indicated that the epidemic was caused by the thawing of a deer infected with anthrax pathogen in the permafrost. In addition, a giant virus with a history of 30 000 years from the permafrost of Siberia was revived in relevant studies, and the result showed that this virus can still infect its target—amoeba [24]. As global warming intensifies, the release of unknown microbes from the cryosphere will speed up, and more viruses will enter the downstream oceans and rivers with the melting water of polar region and alpine glaciers. Such a huge amount of virus particles may spread and survive in the new ecosystem and have the possibility of infecting completely different hosts, which will pose serious impact on the new host ecosystem.

4 Prospects

Microbes in cryosphere, especially those in glaciers and permafrost, have attracted more and more attention. The sensitivity of cryosphere to climate change makes us realize the urgency of understanding the microbes in cryosphere and their roles. The rapid emergence of new technologies and their combination and complementation with traditional technologies have greatly fostered the research on microbes in cryosphere, especially on microbial genes and potential functional genes and their expression, as well as metabolic activity of microbes *in situ*. The reduction of DNA sequencing cost and the improvement of comparative genome analysis methods facilitate the revealing of the cold adaptation characteristics and the evolution of microbes in cryosphere, as well as the identification of the specific cold adaptation characteristics and mechanisms of microbial groups. These studies will promote the application of cold-adapted microbes and their cell components [31]. The accelerated global change requires us to speed up the research on microbes in cryosphere and their responses to global change. Therefore, it is essential to carry out in-depth work in the following four aspects.

(1) We should strengthen the ecological research on microbes in cryosphere in the context of global change. The available studies on microbes in cryosphere still give priority to laboratory studies. There are few studies predicting the dynamics of microbial community and the response of their function to global change by utilizing ecological mathematical models. Therefore, strengthening the combination of multi-disciplinary theory and experimental study will be a research focus. Climate change threatens the diversity of microbes in cryosphere, and thus it is urgent to understand the links of the diversity of microbes in cryosphere with climate and function. How the functions and behaviors of cold-adapted microbes that are associated with climate warming (glacial retreat and permafrost melting) will respond to climate change should also be learned. The interaction and feedback among chemical, physical, biological and environmental factors should be studied from a multidisciplinary perspective in terms of time and space dimensions.

(2) Viruses in cryosphere are another topic gaining attention. The available research data on virus community in cryosphere and their adaptation to extreme environment are still limited. Metagenomic sequencing can be employed to identify the biological functions of virus genes and further reveal the relationship between the biological functions and the adaptability of virus to extreme environment, thereby unveiling the role of viruses in cryosphere.

(3) There is an urgent need to strengthen the culture and research of microbes in cryosphere, which can provide as many culturable microbial resources as possible for subsequent research and utilization. In addition, it is an important task in the future to learn the microbes with potential pathogenicity to animals and plants in various cryosphere habitats, especially the old and undiscovered new pathogenic microbes sealed in them.

(4) The Tibetan Plateau is one of the regions worthy of special attention in the research on microbes in cryosphere. China has the largest area and the largest number of glaciers and permafrost in the middle-latitude zone of the globe, and the Tibetan Plateau is the largest cryosphere habitat outside the Antarctic and the Arctic. In recent years, Chinese scientists have carried out a large number of microbiological studies on the Tibetan Plateau, whereas these studies are mainly concentrated on microbial ecology and microbial physical geography [39,40]. It is the mission of Chinese scientists to strengthen the research on the correlation of microbes in cryosphere with climate and environment in the context of global change.

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