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Snow and ice ecosystems: not so extreme

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Abstract

Snow and ice environments cover up to 21% of the Earth's surface. They have been regarded as extreme environments because of their low temperatures, high UV irradiation, low nutrients and low water availability, and thus, their microbial activity has not been considered relevant from a global microbial ecology viewpoint. In this review, we focus on why snow and ice habitats might not be extreme from a microbiological perspective. Microorganisms interact closely with the abiotic conditions imposed by snow and ice habitats by having diverse adaptations, that include genetic resistance mechanisms, to different types of stresses in addition to inhabiting various niches where these potential stresses might be reduced. The microbial communities inhabiting snow and ice are not only abundant and taxonomically diverse, but complex in terms of their interactions. Altogether, snow and ice seem to be true ecosystems with a role in global biogeochemical cycles that has likely been underestimated. Future work should expand past resistance studies to understanding the function of these ecosystems.

Keywords: Snow; Ice; Extreme; Microbial ecology

1. Introduction

Extreme environments are defined as areas where one or more of the abiotic parameters, i.e. pH, temperature, water content, nutrient levels, solar irradiation, pressure, etc., reach extreme values [1]. These harsh conditions are considered to be limiting for the development of life. Nevertheless, the range of values that are considered extreme are often regarded from a macro-organism point of view, whereas the limit for the development of microbial life on Earth has not yet been fully established. The parameters cited above influence all organisms at the individual scale and could, to different extents, cause cell physiological stress. However, microorganisms harbor a remarkable capacity to adapt to a wide range of habitats. To date, no place on Earth has been shown to be sterile, and even the most "inhospitable" environments, such as deep sea hydrothermal vents, acid mine drainage and hot springs, contain many viable microorganisms. In the case of hot springs, the occurrence of a viable and active microbial community was recognized early [2]. Many studies have focused on its ecology both for fundamental and application purposes: as a model for the development of life under putative primitive Earth conditions and for enzymes with industrial interest due to their activity at high temperatures.

At the opposite end of the temperature spectrum, snow and ice have received much less attention. Over the past twenty years, microorganisms inhabiting the cryosphere have been increasingly studied for the potential discovery of enzymes with biotechnological interest and for fundamental research on the ecology of "extreme" environments [3–7]. Snow and ice have unexpectedly high microbial abundance and diversity. As main components of the cryosphere, they cover over 10^8 km^2 of the Earth's surface. Snow in the winter can cover up to 12% of the Earth's surface [8], and approximately 10% of the planet's land surface is covered by glacial ice in the form of ice caps, ice sheets or glaciers, storing 75% of the world's fresh

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water [9]. Given their coverage at a global scale, snow and ice could have a major and underestimated role in global biogeochemical cycling (Fig. 1). Therefore, the relevant knowledge and knowledge gaps concerning the microbial ecology of snow and ice ecosystems need to be evaluated for future research.

In this article, we will identify and evaluate the physical and chemical conditions in snow and ice environments and review the mechanisms used by microorganisms to survive under these conditions. We will also address the abundance and diversity of the snow and ice microbial communities, as well as the interactions that take place within the community that help them to successfully inhabit snow and ice. Given that an ecosystem is defined as the compendium of the organisms present, the physical system that hosts them and the interactions of the organisms with abiotic factors as well as the interactions between organisms [10], the available data support the idea that snow and ice are true ecosystems and actually not so extreme for these microorganisms.

2. Snow and ice environmental constraints: definition, variability and individual cell responses

Snow and ice habitats are the only ones on Earth whose matrices are partly composed of frozen water, and thus impose specific conditions on microbial life. The driving forces for microbial community structure and function might be the result of these physical–chemical conditions: low temperatures, scarcity of nutrients and water as well as high UV radiation. In this section, we compare the different abiotic attributes of snow and ice ecotypes and the related microbial adaptations (Fig. 2) in order to understand how the microbial community actively interacts with its physical–chemical environment. The objective is then to investigate whether these environmental constraints define snow and ice as extreme habitats for microorganisms.

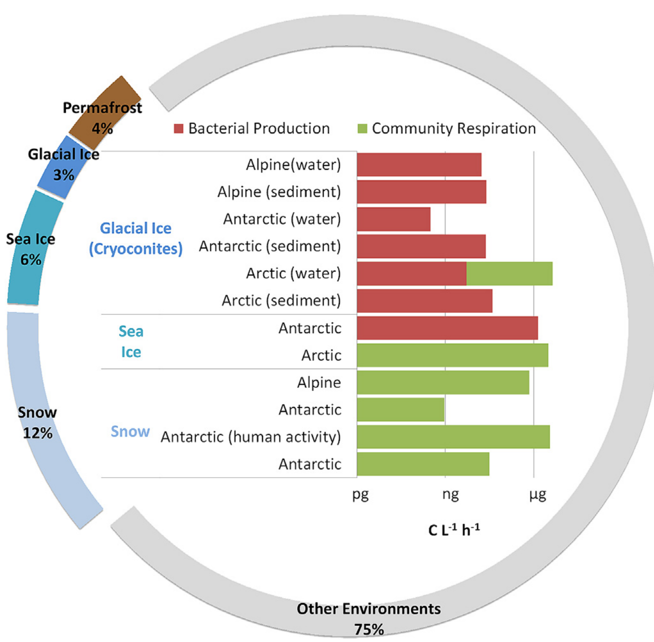

Fig. 1. Coverage and microbial productivity of snow and ice. The graph on the outer ring depicts the percentage of the surface of the Earth covered by the different environments of the cryosphere. The bar chart shows bacterial production and community respiration rates (in carbon per liter per h) found in the literature for these environments. Sediment or water represent the different parts of cryoconite. Human activity refers to snow samples taken near a scientific station and potentially impacted by human activity.

2.1. Cold temperature and low water availability

Snow and ice are found in the coldest places on the planet and fall within group E of the Köppen climate classification or in polar and alpine climates, which are characterized by monthly mean temperatures below 10 °C [11]. The term “cryosphere”, first introduced by Dobrowolski in 1923 [12], derives from the Greek *cryos*, which means “cold” or “ice” and refers to areas where water is in a frozen state [5]. Mean temperatures observed in snow and ice environments can be highly variable at different depths, sites or seasons. For example, surfaces directly exposed to wind are influenced by air temperature (as low as −50 °C and −70 °C during the winter in the Arctic and Antarctic, respectively, and can be as warm as 0 °C during the melt period in summer) and therefore exhibit the coldest and most variable temperature. Top snow layers work as insulators leading to an increase in temperatures in the layers below. The low temperatures can be deleterious for cells due to increases in membrane rigidity that will limit substrate exchange, reduce enzyme activity and damage cells with cytoplasmic water crystal formation. Many studies on microbial life in the cryosphere have focused on understanding how microorganisms can adapt to the cold. The term “psychrophiles” refers to cold-adapted microorganisms with optimal growth temperatures below 15 °C, and “psychrotolerants” are organisms able to survive below 0 °C, but with optimal growth temperatures between 20 and 25 °C [13]. They use strategies at different levels of cell physiology, including increased membrane fluidity (unsaturated fatty acid synthesis, desaturases), freeze protection (compatible solutes, anti-freeze and ice-binding proteins synthesis), and maintenance of protein catalytic efficiency (reduction of internal hydrophobic interaction, proline and arginine content, increased length of external loops and accessibility to active sites) (see detailed reviews on psychrophilic adaptations [14,15]), and recently highlighted by sequencing technologies [16]. Sequences associated with cold-adapted organisms have been systematically detected in snow and ice sequence datasets [17–20]. The psychrophilic lifestyle of some snow and ice microorganisms has been confirmed via isolates cultivated at low temperature [21,22]. In addition, the possibility that this icy lifestyle could have a remote or ancient origin cannot be discarded. Although the origin of life and the emergence of microorganisms on Earth remain unknown, some proposals for a cold origin of life have been made [23,24]. This hypothesis is supported by various studies including assays on prebiotic polymerization in an icy matrix [25–28] and bacterial phylogeny [29]. If this were to be the case, then native conditions at the origin of microbial development should not be considered as extreme.