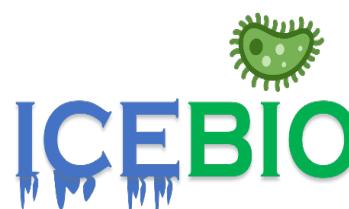


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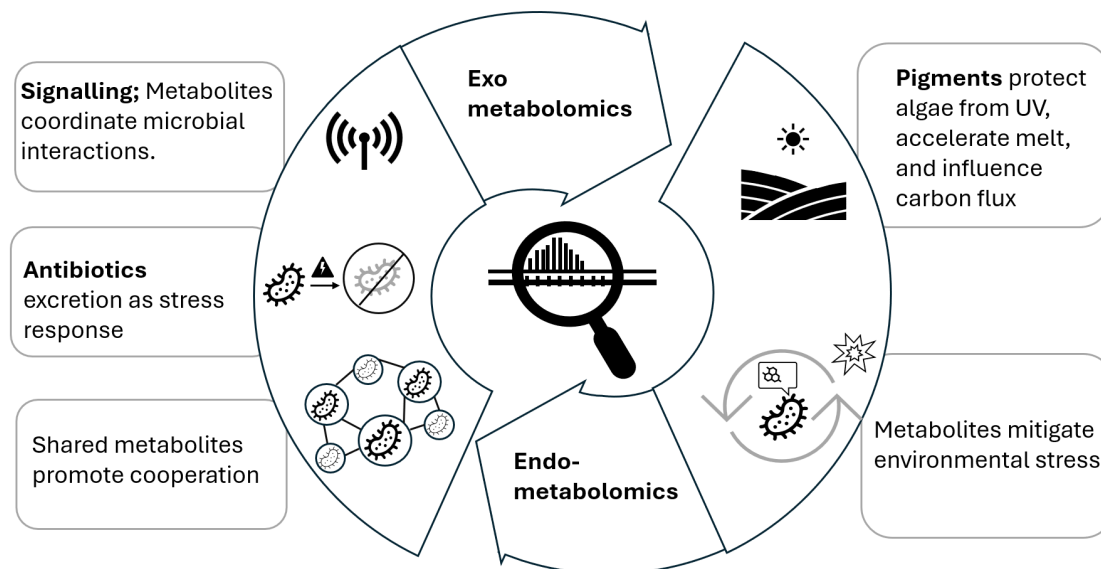
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Metabolite production in glacial surfaces:

Exploring the metabolic signatures of surface ice microbial communities highlights diverse adaptation strategies to extreme environments

Graphical Abstract



Abstract

Glacier surfaces, once considered barren, encompass diverse microbial communities that shape and are shaped by their extreme environment through metabolic processes. The production of secondary metabolites, including pigments, antibiotics, and signalling molecules, likely plays a crucial role in microbial adaptation, community dynamics, and environmental feedback such as ice melt and carbon fluxes. Endometabolomic analyses provide insights into microbial stress responses and metabolic trade-offs, while exometabolomes influence ecosystem interactions by modulating competition and cooperation. However, much of the glacier metabolome remains uncharacterized, limiting our understanding of microbial survival strategies and biogeochemical impacts. Advanced analytical techniques, including nuclear magnetic resonance (NMR) and mass spectrometry (MS), are essential to uncover the full extent of metabolic diversity and its ecological role. Exploring these metabolomes offers a unique opportunity to understand microbial-environment interactions in extreme ecosystems and their broader implications for global biogeochemical cycles.

Surface ice metabolomic studies and their role in assessing ecosystem response

Glaciers, once perceived as barren landscapes, are home to a diverse array of microorganisms, including bacteria, archaea, fungi, viruses, and most notably, ice algae (Anesio & Laybourn-Parry, 2012; Anesio et al., 2017). This microbial diversity is mirrored by their significant metabolic potential (Jaarsma et al., 2023). The unique metabolic profiles of glacier-inhabiting microorganisms reflect their remarkable ability to adapt to extreme and rapidly changing environmental conditions (Jaarsma et al., 2023). Secondary metabolites, distinct from primary metabolites essential for basic cellular functions, are produced as adaptive responses to environmental stresses and include antibiotics, public goods, and signalling molecules (Reshi et al., 2023). These metabolites play pivotal roles in facilitating microbial survival and interactions, with antibiotics providing protection against competitors and public goods promoting cooperative growth and resilience within microbial communities (O'Brien & Wright, 2011; Petersen et al., 2020; Morris et al., 2012). Ice algae, which dominate bare ice surfaces, form extensive blooms that significantly accelerate ice melt and influence carbon fluxes (Anesio & Laybourn-Parry, 2012; Anesio et al., 2017; Cook et al., 2020). Given that glaciers and ice sheets cover roughly 10% of Earth's land surface, their potential contributions to global biogeochemical cycles are immense. (Ali et al., 2020) Understanding the controls on bloom composition and spatial extent, likely mediated by microbially produced metabolites, is crucial for predicting ecosystem responses to environmental change. The unique environment of glacier surfaces offers an unparalleled opportunity (Doting et al., 2024; Halbach et al., 2022) to study the intricate interplay between microbial activity, environmental dynamics, and carbon cycling on a global scale.

The metabolome of the glacier microbial community is forged by extremes

Endometabolomic research on glacier surfaces is crucial for probing microbial adaptation mechanisms and understanding their immediate metabolic responses to environmental changes. By profiling intracellular metabolites, researchers can gain insights into the physiological state of glacier-inhabiting microorganisms, revealing stress responses, nutrient utilization, and metabolic trade-offs. Given the central role of pigments in mediating ice melt rates, locally increasing biological radiative forcing by 13%, studying intracellular pigment composition is vital for assessing the future of glacial habitats (Cook et al., 2020). Furthermore, Glacier and snow algae exhibit distinct pigment signatures, with glacier ice algae predominantly producing purpurogallin and snow algae synthesizing astaxanthin esters (Halbach et al., 2022). These photoprotective pigments not only play a key role in energy absorption but are also likely integral in shielding cells from intense solar radiation, directly influencing algal survival, bloom dynamics, and the associated biogeochemical processes in these rapidly changing ecosystems (Jensen et al., 2024; Upadhyay et al., 2024).

Changes in light conditions or nutrient regimes significantly impact pigment signatures across glacier surfaces, highlighting the dynamic interplay between environmental drivers and microbial metabolomes. In turn, microorganisms actively shape their environment by releasing a diverse array of metabolites, collectively forming the exometabolome. Compounds such as riboflavin, lumichrome, tryptophan, and azelaic acid are involved in microbial growth, signalling,

community dynamics, and stress mitigation (Doting et al., 2024). Stress on microorganism often reflects in the production of metabolites with ecological function, such as antimicrobial compounds. These stress-induced metabolites not only protect the producers but also affect the broader microbial community structure (Amaranth et al., 2023). The potential for antimicrobial compounds to alleviate environmental stress is particularly relevant to glacier surface microorganisms as ice algae are sensitive to irradiance levels exhibiting reduced photophysiological performance under increased light conditions (Jensen et al. 2024). Antibiotics with aromatic structures may offer protection against oxidative stress induced by intense UV radiation. These compounds act as antioxidants, mitigating the harmful effects of reactive oxygen species and enhancing microbial survival in the face of UV exposure (Wienhausen et al., 2017). The production of such compounds not only aids in individual survival but also shapes the microbial community by mediating competition and cooperation. Thus, production of compounds with antimicrobial properties like indol-derivates serve as ecological adaptations to glaciers extreme conditions (Doting et al., 2024). Stress-induced metabolites not only protect the producers but also affect the broader microbial community structure (Amaranth et al., 2023) promoting ecosystem stability (Upadhyay et al., 2024; Zark & Dittmar, 2018)

In addition to antibiotic production, glacier microbial communities likely produce other secondary metabolites such as carotenoid pigments, siderophores, and osmoprotectants, which are critical for withstanding the extreme conditions of glacier habitats (Jaarsma et al., 2023). These metabolites foster complex metabolic dependencies that contribute to microbial community resilience and ecosystem. Nonetheless, despite the advancements in metabolomics, much of the data collected remains as "dark matter," with biological mechanisms often being inferred from just 2-3% of the metabolome (MohammadiPeyhani et al., 2022). On glacier surfaces, a large proportion of metabolites detected through profiling remain unidentified, pointing to biochemical pathways and ecological roles that are yet to be understood. The glacier microbial metabolome holds untapped potential, with unknown metabolites hinting at novel biochemical processes that could reshape our understanding of microbial adaptation in extreme environments. Combining metagenomic analyses with microbial culturing could enhance the discovery of new compounds by tapping into the complementary genetic and chemical diversity of these ecosystems. However, the absence of comprehensive knowledge surrounding "dark matter metabolites" continues to impede our ability to fully appreciate the metabolic complexity of these environments (da Silva et al., 2015). The structural complexity of metabolites, often characterized by multiple functional groups, stereoisomers, and rare building blocks, poses significant challenges in their isolation, identification, and characterization (DiBello et al., 2023). To overcome these challenges, advanced analytical techniques, such as nuclear magnetic resonance (NMR) and mass spectrometry (MS), are essential for providing more accurate and comprehensive profiles of the glacier surface metabolome, thus unlocking the potential of these elusive compounds (Bauermeister et al., 2022). Unravelling the mystery of these unknown metabolites remains a crucial frontier in metabolomic research, offering exciting prospects for discovering new compounds with ecological and biotechnological significance.

In conclusion, glaciers are far more than lifeless and frozen expanses. The microbial communities on glacier surfaces contribute to the multiple functions of these ecosystems through their metabolic activities, including the production of secondary metabolites that support microbial survival, community interactions and ecosystem resilience. Investigating the glacier microbial metabolome, including both the exometabolome and endometabolome, is essential for understanding how these communities adapt to extreme environmental conditions,

influence biogeochemical processes, and contribute to global carbon fluxes. The findings from recent metabolomic studies provide valuable insights into the metabolic diversity and ecological significance of these unique environments, revealing the intricate relationship between microorganisms and their icy habitats (Halbach et al., 2022; Jensen et al., 2024). The metabolome of glacier surfaces reflects the resilience and adaptability of microbial communities in extreme environments (Isah, 2019; Jensen et al., 2024). Light is a likely dominant driver of metabolic shifts, with stress-induced compounds playing critical roles in survival and ecological interactions (Isah, 2019; Upadhyay et al., 2024). The high diversity of metabolites, including those with antimicrobial and stress-regulating functions, underscores the ecological complexity of glacier ecosystems. Understanding the metabolic responses of glacier microbes to abiotic stresses is vital for predicting how these communities will respond to climate change. Furthermore, the suggested high potential for discovery of novel metabolites opens avenues for biotechnological applications, emphasizing the importance of continued research in these fragile ecosystems.

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