PLOS CLIMATE

REVIEW

Microbial dynamics in rapidly transforming Arctic proglacial landscapes

Grace Marsh[1]*, **Darya Chernikhova**[2], **Stefan Thiele**[3], **Ianina Altshuler**[1]

1 École Polytechnique Fédérale de Lausanne, Sion, Switzerland, **2** University of Iceland, Reykjavík, Iceland, **3** University of Bergen, Bergen, Norway

* grace.marsh@epfl.ch

Abstract

Arctic glacial environments are rapidly changing, as the Arctic warms at a rate three to four times faster than the global average (the phenomenon known as Arctic amplification). Micro-organisms are uniquely adapted to extreme glacial environments and studying how ecological and climatic feedback loops affect the diversity of these communities is crucial to the characterisation of vulnerable Arctic habitats. Glacial landscapes span a wide range of habitats, from glacier ice to marine waters, and encompass terrestrial, aquatic, and interzonal systems. While glacier shrinkage has been the focus of scientific attention, auxiliary habitats are also impacted by rapid glacier retreat. Auxiliary habitats include terrestrial systems, such as outwash plains, vegetated periglacial environments, and aquatic systems, such as glacier-fed streams, lakes, and glacier-adjacent marine environments. Glacier recession drives high-impact changes in glacier-associated habitats: rising temperatures, increased light penetration of glacial streams, changes in nitrogen-to-phosphate ratios, and increases in availability of glacier-derived organic compounds. In turn, microbial systems in these habitats may experience changes in nutrient dynamics and shifts in community structures. The exposure of new lands by retreating glaciers may also result in increased dust and microbial dispersal into the atmosphere. Here, we discuss the effects of climate change on glacial microbiomes and the feedback loops between microbial community dynamics and the large-scale climatic processes in the Arctic. We characterise aspects of vulnerable microbial ecosystems and highlight the importance of preserving unseen microbial biodiversity. We then outline current capacities for microbial conservation, focusing on cryopreservation and biobanking. Lastly, we suggest future research directions and steps that academic and governmental institutions may take to foster research and collaboration with Indigenous communities.

Competing interests: The authors have declared that no competing interests exist.

1. Introduction

The Arctic is a rapidly changing region as it warms nearly four times faster than the global average [1]. Climatic feedback loops play a central role in this Arctic amplification, contributing to increased air temperature, greater precipitation, Arctic greening, and decreased snow and ice cover [2]. Furthermore, Alaska, Arctic Canada and Greenland have

experienced decreases in Arctic glacial ice mass balance since the 1980s, in addition to decreases in land ice mass balance in the Russian High Arctic [2]. The changing glacial landscapes of the Arctic have a significant impact on life inhabiting these extreme environments [3]. Microbial life, including bacteria, archaea, fungi, protists and viruses, process nutrients and mineral substrates, affect biogeochemical cycles, primary succession, and climatic feedback loops in glacial ecosystems [4,5]. As glaciers retreat, new terrestrial and freshwater habitats are formed [3,4]. Microbiota are at the forefront of soil formation in these newly exposed habitats and contribute to the weathering of rock substrates in addition to carbon and nitrogen cycling, establishing soil for the primary succession of lichens, mosses, macrofungi and plants [6]. Similarly, newly formed freshwater aquatic habitats, such as proglacial lakes, are colonised and transformed by microbial communities [3]. In these terrestrial and aquatic environments, biogeochemical interactions occur at both local and global scales, as atmospheric carbon and nitrogen sources are sequestered within the soils, streams, rivers, and lakes [7,8].

Exploring glacial microbial diversity and microbial interactions with climate change in the Arctic are essential to modelling future microbial and environmental dynamics in this region [9]. Microbial community analyses may also enable biomonitoring of ecosystem health, as community structures may shift with environmental changes [10]. However, this sensitivity also leaves microbial communities vulnerable to dysbiosis and potential loss of taxa, emphasising the importance of capturing this diversity before it is lost [9]. This may be achieved through utilisation of biobanks and cryopreservation of entire microbiomes, which are historically focused on agriculture and human microbiome applications [11–13]. Collections of Arctic microbiota may also act as sources of raw material for biotechnological research. Arctic microbiota have unique adaptations to extreme oligotrophic and cold environments that are of interest for bioprospecting [14,15]. For example, cold-adapted enzymes are useful catalysts at low temperatures, and are applied in various industries including food technology, where products are treated at low temperatures to reduce food spoilage [16,17]. Other applications include bioremediation of cold environments, such as degradation of oil contaminates by cold-adapted lipases [16], further stressing the need of preserving such specialised microbiomes for future utilisation [14,15,18].

However, microbial research in the Arctic is challenging given the remoteness and relative inaccessibility of the region. This limits sample collection, preservation and *in situ* analysis, with further limitations surrounding the nature of extremophilic organisms, which are generally challenging to culture and isolate [14,19]. Genetic approaches are widely used for studying Arctic microbiomes, with amplicon analysis providing insight into community composition and species abundance, while metagenomics and metatranscriptomics further characterise the functional potential and active microbial members [20]. In addition, the rise of multi-omics analysis is seen in the combination of these techniques with others such as metaproteomics and meta-metabolomics, creating a multi-layered picture of biological systems [20]. However, there is considerable lack of these types of studies employing multi-omics tools in glacier-associated environments [20,21].

We outline the current knowledge of microbial diversity and dynamics in Arctic glacier-associated environments and the interaction of these microbiomes with climate change. While we briefly discuss supraglacial, englacial and subglacial systems, the scope of this review specifically focuses on microbial dynamics in proglacial terrestrial and aquatic habitats; these include glacial outwash plains, glacial aeolian dust, proglacial streams and lakes, and the immediate marine coast [4,22]. We explore the current limitations of Arctic microbial research and suggest the next steps forward to investigate changes in this region.
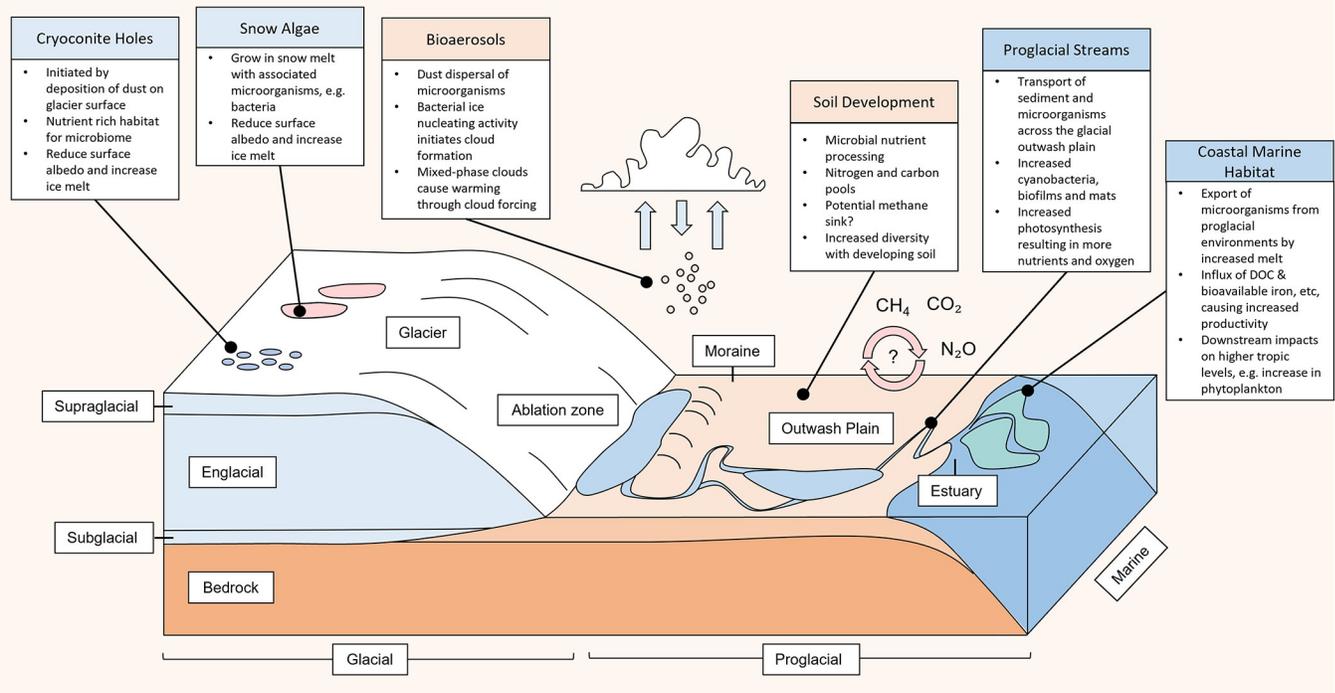
Fig 1. Ecosystem dynamics in warming glacial Arctic environments.

https://doi.org/10.1371/journal.pclm.0000337.g001

2. Glacial environments

Glaciers consist of diverse ecosystems ranging from the glacial surface (supraglacial), to the internal glacial ice mass (englacial), and the region of the glacier in contact with the underlying substrate (subglacial) [23] (Fig 1). Life in these extreme environments is limited by the availability of liquid water, nutrients, electron donor/acceptors, light, oxygen, and low temperatures [19,23]. Microbial communities inhabit surface ice, cryoconite holes, glacial snow, and englacial and subglacial habitats [19,23].

2.1 Supraglacial zone

Glacial microbial research has largely focused on supraglacial habitats which are readily accessible on the glacier surface [23]. The supraglacial zone is exposed to the atmosphere and is vulnerable to immediate climatic perturbations and solar radiation [19]. The zone contains niche environments for microbial life, such as cryoconite holes [24]. Specifically, cryoconite holes are water-filled depressions that form on the glacial surface and are sites of nutrient accumulation [23,24]. The formation of these habitats is often initiated by deposition of inorganic and organic dust particles, from sources including proglacial dust, bird nesting sites and marine aerosols, which reduce surface albedo and cause localised ice melt [24–27]. The microbial composition of cryoconite holes varies to that of glacier surface ice with a larger relative abundance of prokaryotes than eukaryotes [28]. Studies suggest the existence of core cryoconite microbiomes that may be distinct and location-specific [26,27,29]. Cryoconite holes host diverse communities of microorganisms including photosynthetic algae (eg. *Raphidonema* and *Ancylonema genera*) and cyanobacteria (eg. *Oscillatoriales* and *Nostocales* orders) which can build up organic carbon and support growth of heterotrophic bacteria, fungi, predatory protists, and higher trophic level consumers, such as tardigrades [25,28,30–33]. Microbial

activity and growth further decrease surface albedo in the cryoconite microenvironments, creating a positive feedback loop of accelerated melting [34].

Red snow is another phenomenon contributing to the accelerated surface melting via surface albedo reduction from microbial darkening [35]. Red snow describes the algae and associated microbial communities that grow in snow melt and are found across the Arctic [35]. The snow algae may appear red on the snow surface, due to the production of photoprotective pigments such as the carotenoid astaxanthin, and have also been observed in a variety of other colours, including green, golden-brown, pink, orange, and purple-grey [36–38]. Snow algae members of the genus *Chlamydomonas* and *Raphidonema* are prevalent across geographic regions, although it is only recently that species have been distinguished through genetic analysis [35,37]. Bacteria are commonly found alongside these algae and include *Cyanobacteria*, *Pseudomonadota* (prev. *Proteobacteria*), and *Bacteroidota* (prev. *Bacteriodetes*) phyla. These taxa are known to inhabit snow environments, with community compositions that are specific to geographic regions in the Arctic [35].

2.2 Englacial zone

Below the supraglacial zone the glacier grows more inhospitable with limited solar radiation, increased pressure, reduced liquid water availability and limited interstitial space within the ice interior [19]. Studies of microbial diversity in the englacial zone are restricted to ice coring techniques, with factors such as contamination posing a greater risk to results due to low microbial biomass [19]. The microorganisms in these habitats are thought to represent the historical communities deposited in the snow that formed the glacier [19]. Ice cores from Arctic glaciers and the Greenland Ice Sheet were found to consist of *Cyanobacteria*, *Alphaproteobacteria*, *Actinobacteria*, *Bacteroidetes*, *WPS-2*, *Firmicutes*, *Acidobacteria*, *Gammaproteobacteria* and *Armatimonadetes* [3,39]. However, detection of excess gases such as carbon dioxide, methane, and nitrous oxide in glacial ice cores has suggested the possibility of active microbial metabolism within the ice or recent microbial deposition through meltwater channels, implying that the microbiome composition may have changed from the initial deposited community [40–42]. This corroborates with the recovery of viable isolates from glacial ice cores, dated over 750,000 years old, in the Tibetan plateau [43]. Interestingly, a large proportion of supraglacial meltwater enters the englacial and subglacial regions which can cause altered temperatures [44] and potentially provide additional nutrients that stimulate microbial activity. Englacial meltwater channels present as cloudy ice when frozen and exhibit microbial communities less associated with glacial cold-adapted microbial taxa than communities from clear englacial ice, indicating the effect of local conditions on microbial diversity within the englacial zone [26,42].

2.3 Subglacial zone

The basal ice found in the deepest layer of the glacier, the subglacial zone, hosts an accumulation of nutrients transported through the preceding glacial layers by water flow [19]. The subglacial zone encompasses the basal ice of the glacier and the bedrock it grinds below, in addition to the water created from this friction, geothermal heat, and pressure [31]. This environment is predominantly anoxic, hosting methanogens and chemolithotrophs such as anaerobic nitrate reducers and sulphate reducers, while aerobic chemoheterotrophs have also been successfully cultivated from subglacial habitats [45,46]. Predominately *Proteobacteria*, *Gracilibacteria*, *Bacteroidetes*, *Actinobacteria* and *Parcubacteria* were identified from the subglacial environment via sampling of naled ice bodies in the glacier forefield [47]. Zdanowski *et al.* (2017) investigated the deposition of supraglacial cryoconites into the subglacial habitat and

identified increased abundance of anaerobic cryoconite species [31]. The study suggests that with increased climate warming, cryoconite inhabiting taxa can establish within the englacial and subglacial zones as they are flushed through the glacier [31]. Cryoconite microbial migration into the subglacial habitat is yet to be explored further but may have interesting consequences for subglacial microbial diversity.

3. Proglacial environments

Glaciers exist as part of larger landscapes and interact with the surrounding terrestrial and aquatic habitats [4,22] (Figs 1 and 2). Investigating the effects of climate change on glacial microbiomes and microbiomes influenced by deglaciation requires a holistic approach that addresses the exchange of nutrients and microorganisms between atmospheric, terrestrial, and aquatic spheres. Here we focus on the changing microbiomes of the terrestrial and aquatic proglacial environments that encompass the region beyond the glacial terminus, including the glacial outwash plains, moraines, proglacial lakes and streams, and downstream marine environments [4,22] (Fig 3).

3.1 Terrestrial environments

3.1.1 Glacial outwash plains. Glacial outwash plains are created from the sediment exposed as glaciers recede [4]. This sediment has been crushed by the weight of the glacier as it moves and contains limited nutrients, thus creating challenging conditions for life [4]. Despite this, microorganisms are capable of colonising this newly exposed oligotrophic environment [48]. Initial microbial colonisation of glacial outwash plains is derived from atmospheric sources and also extends to organisms originating from the adjacent supraglacial and subglacial environments [7], potentially from ephemeral fluvial connections. Glacial outwash plains provide a spatial study of microbial succession, known as a chronosequence, as newly exposed sediment at the glacier terminus transitions to more developed soils [49]. Colonisation by autotrophs and chemolithotrophs initiates soil development, and with time the microbial community shifts to include heterotrophic members [4,7,49]. The colonising microbes create nutrient stocks of available carbon and nitrogen, providing a mechanism of soil development, in addition to physical and chemical weathering of the exposed sediment [50]. Nitrogen fixing bacteria such as *Geobacter*, *Frankia*, *Nostoc*, *Polaromonas*, *Bradyrhizobium*, *Rivularia*, *Pseudoanabaena* and *Rhodobacter* were identified in Arctic glacier forefields [49,51]. These diazotrophs are important during early succession and can be found closer to the glacier terminus [7,49]. Overtime, this early primary succession can facilitate plant growth [52] and glacier outwash plains may become carbon sinks due to microbial and plant autotrophy resulting in accumulation of soil carbon stocks [4,53]. Further, multiple studies have identified increased methane uptake by aerobic methane-oxidising bacteria in older soils of Alpine and sub-Arctic glacier forefields, suggesting a possible methane sink in proglacial environments [54–56].

Microbial diversity and abundance tend to increase in more developed soils containing higher amounts of bioavailable nutrients [48]. Pessi *et al.* (2018) identified that cyanobacteria (predominantly filamentous) increased in abundance with soil age in multiple glacier forelands of Svalbard across the chronosequence [57]. Filamentous cyanobacteria function in soil stabilisation and can develop biological soil crusts [57]. Soil crusts have been found to facilitate initial plant establishment and are associated with greater plant density, suggesting soil stabilisation by microbial communities which aids primary succession [52,57]. While few studies focus on plant—arbuscular mycorrhizal (AM) fungi associations in the Arctic [58–61], some pioneer plants that colonize soils exposed by retreating glaciers have been found to associate with ectomycorrhizal fungi [58,62]. Studies suggest that these fungal communities in Arctic forelands will undergo taxonomic shifts with climate change [58,62].
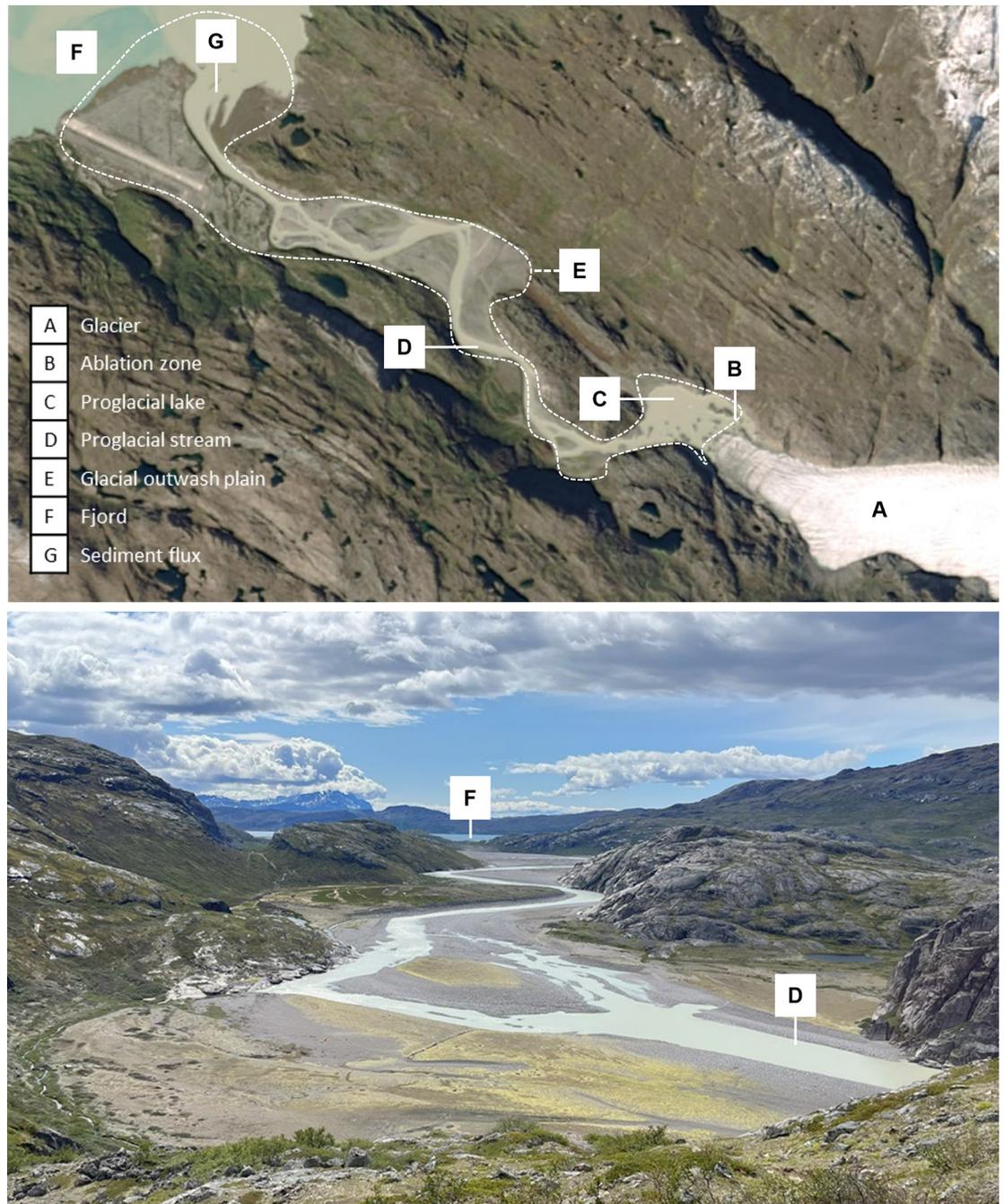
Fig 2. Features of a typical glacial outwash plain, Kiattuut Sermiat, Narsarsuaq, Greenland Base map available at: https://www.arcgis.com/home/item.html?id=7ec08e5438304dbfa1e26181503e6fa8.

https://doi.org/10.1371/journal.pclm.0000337.g002

Importantly, the diversity of microbial communities and underlying biogeochemical processes in developing outwash plains remains largely unexplored in relation to Arctic warming. Mateos-Rivera *et al.* (2016) determined that increases in surface temperature of sub-Arctic glacier forefield soils resulted in a more diverse microbial community that shifted from psychrophilic to psychrotolerant members [63]. Further, Bárcena *et al.* (2011) identified increased

Proglacial Microbial Studies in the Arctic

	Paper	Site	Samples	Findings	Significance
Atmosphere	"Characterisation of arctic bacterial communities in the air above Svalbard" (Cuthbertson et al, 2017)	Svalbard: Billefjorden, Isfjorden, Sassenfjorden, Adventfjorden bay, Longyearbyen, Mine (Gruve) 7, Deltaneset, Gipsdalen, Bjørndalen	Airborne microbial samples from terrestrial and marine sites.	• Proteobacteria, Actinobacteria, and Firmicutes dominate atmospheric samples. • Twelve different phyla identified. • Bacterial members varied substantially between sites, suggesting higher heterogeneity.	Glacial outwash plains are a source for atmospheric dispersal of dust, containing microorganisms. Atmospheric bacterial community composition shifts depending on region and season, suggesting the influence of environmental factors. Ice-nucleating activity of bacteria can initiate cloud formation and subsequent warming.
	"Microbes in high arctic snow and implications for the cold biosphere" (Harding et al, 2011)	Canadian High Arctic: Ward Hunt Island	Airborne microbial samples from terrestrial site.	• Bacteroidetes, Acidobacteria, Firmicutes, and Proteobacteria (Alpha-, Beta-, and Gammaproteobacteria) were prominent in atmospheric samples.	
	"Glacially sourced dust as a potentially significant source of ice nucleating particles" (Tobo et al, 2019)	Svalbard: Brøggerbreen glacier	Glacial outwash sediment and ambient aerosol samples.	• High ice nucleating ability in glacial outwash dust. • Suggests ice nucleation affecting glaciation of low level clouds.	
	"Seasonal Variation of the Atmospheric Bacterial Community in the Greenlandic High Arctic Is Influenced by Weather Events and Local and Distant Sources" (Jensen et al, 2022)	Northeast Greenland: Villum Research Station	Aerosol and surface snow samples.	• Proteobacteria comprised up to 95% of the atmospheric community in spring. • The atmospheric bacterial community shifted from less than 1% Actinobacteria in spring up to 42% in summer. • Seasonal variation in atmospheric bacterial community composition. • Suggests long range transport of bacteria across the Arctic through the atmosphere.	
Soil	"Microbial dynamics in a High Arctic glacier forefield: a combined field, laboratory, and modelling approach" (Bradley et al, 2016)	Svalbard: Midtre Lovénbreen glacier	Soil sampling along chronosequence • 6 sites spanning estimated soil ages of 0-113 years	• Bacterial growth rates were impacted by soil temperature. • Modelling suggested soil development from glacially derived bacteria to mixed communities of autotrophs and heterotrophs.	Microbial nutrient processing of carbon and nitrogen, and bio-weathering, develops soil from nutrient poor deglaciated sediment. Species succession from autotrophs, chemolithotrophs and diazotrophs shifts to heterotrophs in more developed soils. This allows formation of soil crusts which can facilitate plant growth.
	"Linkages between geochemistry and microbiology in a proglacial terrain in the High Arctic" (Wojcik et al, 2019)	Svalbard: Longyearbreen glacier	Soil sampling along chronosequence • 3 sites from moraine across glacio-fluvial outwash plain	• Bacterial communities consisted of Proteobacteria, Bacteroidetes, Verrucomicrobia and Acidobacteria. • Archaeal communities dominated by Thaumarchaeota and Euryarchaeota. • Ascomycota and Basidiomycota largely constituted fungal communities. • Carbon and nitrogen processing by bacteria and archaea, and chemical weathering contributed to soil development.	
	"Bacterial diversity in a glacier forefield of the high Arctic" (Schütte et al, 2010)	Svalbard: Midtre Lovénbreen glacier	Soil sampling along chronosequence • Two parallel transects approximately 1km long	• Phylotype richness and evenness increased in older soils. • High species turnover suggests succession along outwash plain.	
	"Metagenomic insights into diazotrophic communities across Arctic glacier forefields" (Nash et al, 2018)	Sweden: Rabots glacier, Storglaciaren; Svalbard: Midtre Lovénbreen; West Greenland: Russell Glacier	Soil sampling along chronosequence • Three parallel transects	• Identified Alphaproteobacteria, Betaproteobacteria, Cyanobacteria and Firmicutes in soil samples. • Nitrogen fixing bacteria, Geobacter, Frankia, Nostoc, Polaromonas and Bradyrhizobium, were prevalent across glacier forefronts.	
	"A Taxon-Wise Insight Into Rock Weathering and Nitrogen Fixation Functional Profiles of Proglacial Systems" (Varliero et al, 2021)	Svalbard: Midtre lovénbreen; Sweden: Storglaciaren; West Greenland: Near Kangerlussuaq	Soil sampling along chronosequence • Transect up to 1,600m from glacier terminus • Sampling depth of 10cm	• Increased microbial diversity along developing outwash plain. • Autotrophs, diazotrophs and chemolithotrops dominate closest to the glacier. • Cyanobacteria, Firmicutes, Bacteroidetes, and Armatimonadetes dominant in early succession.	
	"Bacterial diversity and community structure along the glacier forefield of Midtre Lovénbreen, Svalbard, Arctic" (Venkatachalam et al, 2021)	Svalbard: Midtre Lovénbreen glacier	Soil sampling along chronosequence • 1.8km transect of approximately 1900 years deglaciation	• Proteobacteria and Actinobacteria were identified across the outwash plain, while Bacteroidota was prominent closer to the glacier in contrast to Acidobacteriota which increased in older soils. • Increased chemolithotrophic bacteria closer to the glacier terminus. • Sulfurovaceae and Sulfurimonadaceae families, associated with bio-weathering of rocks identified in glacier forefront.	
	"Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the High Arctic" (Breen & Lévesque, 2007)	Canadian High Arctic: Ellesmere Island	Soil and substrate sampling along chronosequence • 400m transect • Soil sampling depth of 5cm	• Greater plant density with biological soil crusts. • Soil crusts initiated plant establishment and growth, but later compete.	
	"Marked Succession of Cyanobacterial Communities Following Glacier Retreat in the High Arctic" (Pessi et al, 2016)	Svalbard: Ebbabreen glacier, Nørbyebreen glacier, Ragnarbreen glacier	Biological soil crust sampling along chronosequence • Transects of 0.7-1.7km from glacier terminus • Chronosequences representing up to 100 year deglaciation gradient	• Early succession by cyanobacteria sourced from nearby glacial environments. • Cyanobacteria abundance increased with soil age. • Predominantly filamentous cyanobacteria composition.	
Streams & Lakes	"Bacterial and archaeal community structure in benthic sediments from glacial lakes at the Múlajökull Glacier, central Iceland" (Lamsters et al, 2020)	Iceland: Múlajökull Glacier	Proglacial lake sediment • 5 samples 50-1750m from ice margin	• Six bacteria phyla (Proteobacteria, Cyanobacteria, Bacteroidetes, Actinobacteria, Verrucomicrobia and Planctomycetes) and one microalgae phyla (Bacillariophyta) were detected across the lake sediment. • Increased metabolic diversity but lower taxonomic diversity in oldest lake. • Decreased Cyanobacteria and Actinobacteria in the oldest lake (highest concentration of C, N and P), likely due to oligotrophy gradient.	Influences of water volume, flow, turbidity and temperature on proglacial aquatic microorganism abundance and community composition. Glacial microbial taxa are transported to proglacial streams and lakes, suggesting the impact of glacial melt on these microbiomes. Sediment flushed from the glacial outwash plain further impacts community dynamics in the immediate marine environment.
	"Bacterial community succession in an Arctic lake-stream system (Brattegg Valley, SW Spitsbergen)" (Górniak et al, 2016)	Svalbard: Brattegg Glacier	Proglacial lake water • Samples from 3 connected lakes from a lake-stream system	• Highest microbial abundance in oldest lake with well-developed microbial mats, planktonic microorganisms, fish and birds. • Bacterial succession resulted in simplification of community composition, with fewer dominant bacterial types in the oldest lake. • Increased Actinobacteria (typical colonizers of Arctic soil) and Cytophaga-Flavobacterium in older lakes, potentially sourced from surrounding soils.	
	"Patterns in Microbial Assemblages Exported From the Meltwater of Arctic and Sub-Arctic Glaciers" (Kohler et al, 2020)	West Greenland, Iceland, Svalbard, Norway, Southeast Alaska, Southwestern GrIS	Glacial meltwater streams and rivers • 24 glaciers from 6 arctic and sub-Arctic regions	• Dominance of Proteobacteria, Bacteroidetes, and Actinobacteria, with Verrucomicrobia (also common in Greenland) in meltwater. • High abundance of sulfur oxidizers, Thiobacillus and Sulfuricurvum, at high sulfide bedrock where SO4²⁻ was high. • Glacial meltwater stream dominated by Bacteria with less than 3% relative abundance of Archaea. • Diversity decreased with increasing latitude. • Most taxa were not endemic, suggesting environmental selection on transported microorganisms. • Elevation, Cl⁻, DOC, sulfate, and glacier area were factors influencing microbial community structure.	
	"Factors influencing bacterial dynamics along a transect from supraglacial runoffto proglacial lakes of a high Arctic glacier" (Mindl et al, 2006)	Svalbard: Midtre Lovénbreen glacier	Supraglacial and proglacial water • Supraglacial meltwater and cryoconite samples • Samples of two proglacial lakes	• Bacterial abundance/production was higher in the proglacial lakes compared to the glacier runoff. • Bacterial abundance positively correlated with water temperature. • Experimental incubations indicated that temperature and phosphorous largely impacted heterotrophic bacteria production. • Additional glacial flour and dissolved organic matter stimulated microbial production in lakes.	
	"Arctic bacterial diversity and connectivity in the coastal margin of the Last Ice Area" (Girard et al, 2023)	Canadian High Arctic: Thores Glacier (Ellesmere Island)	Glacier and proglacial lake-ice samples. Proglacial lake, stream and meltwater samples.	• Increased species richness from glacier. • Proglacial lake dominated by Actinobacteria, Chloroflexi, and Planctomycetota phyla with distinct communities from glacier habitat. • Few glacially sourced microorganisms in lake. • Lake phototrophs were associated with anoxygenic photosynthesis (Chloroflexi), while the glacier was associated with oxygenic photosynthesis (Cyanobacteria).	
	"Trajectories of freshwater microbial genomics and greenhouse gas saturation upon glacial retreat" (Woo et al, 2023)	Svalbard: Kongsfjorden, Longyearbyen; Norway: Finse	31 proglacial lakes • Across 5 chronosequences • 0.3-10km from the glaciers	• Lakes close to the glacier were associated with chemolithotrophic and phototrophic microbes (originating from the glacier). • Increase across the chronosequence in total bacterial cell numbers, bacterial ASV richness, methanotrophs, dissolved organic carbon, methane saturation, functional genes for methane cycling, aerobic respiration and anoxygenic photosynthesis. • Succession from heterotrophic fungi to photosynthetic algae across the chronosequence. • Cyanobacteria and Nostoc increased in proglacial lakes with birds (i.e. high nitrogen).	
	"Catchment characteristics and seasonality control the composition of microbial assemblages exported from three outlet glaciers of the Greenland Ice Sheet" (Vrbická et al, 2022)	West Greenland: Isunnguata Sermia, Leverett Glacier, Russell Glacier	Proglacial stream water.	• Increase in microbial diversity in proglacial rivers with larger proglacial catchment areas, potentially due to increasing hydrological connectivity of proglacial habitats. • Proglacial river with the smallest catchment decreased in diversity over time. • Across all samples the dominant taxa were Rhodoferax sp., Flavobacterium sp., Methylobacter sp., Polaromonas sp. and Methylophilus sp.	
	"Warming Climate's Reducing the Diversity of Dominant Microbes in the Largest High Arctic Lake" (Colby et al, 2020)	Canadian High Arctic: Lake Hazen	Proglacial lake water • Seven glacial inflow rivers (Snowgoose, Blister, Abbé, Gilman, Turnabout, Henrietta Nesmith, Very)	• Gammalphaproteobacteria, Actinobacteria, Chloroflexoto, Planctomycetota, and Acidobacteria were commonly recovered taxa across the watershed. • Increased runoff results in decreased taxonomic and functional diversity of dominant microbial communities in sediments.	
	"Freshwater microbial community diversity in a rapidly changing High Arctic watershed" (Cavaco et al, 2015)	Canadian High Arctic: Lake Hazen	Proglacial lake water, proglacial river water and snow melt samples	• The proglacial lake and glacial rivers were dominated by members of Proteobacteria, Bacteroidetes and Actinobacteria, with higher abundance of Eluvimicrobia and Chloroflexi in the lake. • Lower microbial diversity in the lake compared to the glacial rivers. • Across the spring-summer the proglacial lake microbiota correlated with turbidity and temperature, while the glacial rivers' microbiota was related with DO, major ion concentrations, and temperature. • Despite fluctuations in environmental conditions over the spring-summer season, the proglacial lake microbial communities were largely stable, suggesting resilience to future environmental changes.	
	"Upstream Freshwater and Terrestrial Sources Are Differentially Reflected in the Bacterial Community Structure along a Small Arctic River and Its Estuary" (Hauptmann et al, 2016)	Western Greenland: Red River (Disko Island)	River water • Samples from proglacial lake and stream input area • Samples from river mouth and connected estuary	• Diversity and richness decreased in sites adjacent to proglacial lake and glacier stream, and increased downstream. • Larger proportion of psychrotrophic taxa (Sporichthya, Polaribacter, Oleispira, Crocinitomix) were found in the community supplied at the proglacial lake outlet. • Influence from the terrestrial surroundings on the microbial community structure in the main river. • Presence of proglacial lake and glacial stream dominant taxa in the downstream estuary.	
	"Meltwater export of prokaryotic cells from the Greenland ice sheet" (Cameron et al, 2016)	Western Greenland: Leverett Glacier, Russell Glacier	Proglacial stream water.	• Across samples there was dominance of Proteobacteria and Bacteroidetes, followed by Actinobacteria, Verrucomicrobia, Chloroflexi, and Acidobacteria. • Biomass release from the glacier was correlated with discharged meltwater. • Increased meltwater discharge likely increased subglacial microbiota discharge into the surrounding habitats.	
	"Following the flow—Microbial ecology in surface- and groundwaters in the glacial forefield of a rapidly retreating glacier in Iceland" (Purkamo et al, 2022)	Iceland: Virkisjökull Glacier	Proglacial ground water, glacial surface water and non-glacial surface water.	• Groundwater communities varied to glacial and non-glacial surface water communities. • Increased microbial diversity in sites further from the river. • Archaeal diversity and abundance was lower in groundwater. • Bacterial abundance was lower in the groundwater and highest in the non-glacial stream. • Burkholderiales and Pseudomonadales orders were prominent in groundwater. • Higher relative abundance of Cytophagales in non-glacial stream. • Increased ammonia oxidation marker gene (amoA) in the river compared to the groundwater. • Reduced nitrate reduction marker gene (narG) from upper to lower outwash plain. • Methanogenesis genes (mcrA) identified in river and non-glacial stream, but not the groundwater.	
	"Bacterial community structure of a glacio-marine system in the Arctic (Ny-Ålesund, Svalbard)" (Thomas et al, 2020)	Svalbard: Vestrebroggerbreen glacier	Glacial snow, ice, meltwater and fjord water.	• Bacterial communities shared greater similarity between the glacial meltwater and glacial ice than the fjord water. • Glacial meltwater comprised predominantly of β and γ-proteobacteria, and Bacteroidetes. • Large environmental variability in meltwater environment (changes to stream discharge volume, temperature, sediment load and nutrient flux) challenges establishment of bacterial communities. • Stronger presence of Verrucomicrobia phyla in the fjord water than the glacial snow/ice and meltwater.	
	"Microbial communities of the Lemon Creek Glacier show subtle structural variation yet stable phylogenetic composition over space and time" (Sheik et al, 2015)	Alaska: Lemon Creek Glacier	Proglacial lake water • Input from Thomas and Lemon Creek glaciers Proglacial stream water • Lemon Creek outflow stream, and Lemon Creek subglacier terminus outflow	• Across samples, Proteobacteria and Bacteroidetes phyla were dominant. • Phyla common to anoxic systems were also present in the glacier outflow at low abundances (BD1-5, OD1, OP11, OP3, Armatimonadetes, SR1, and Methanomicrobiales). • Detected Archaea were of Euryarchaeota and Thaumarchaeota phyla. • Overall richness was higher in Lemon and glacial terminus compared to the proglacial lake. • Diversity increased over the sampling period in initial proglacial lake and stream samples.	

Fig 3. Proglacial microbial studies in the Arctic.

methane consumption in sub-Arctic glacier foreland soil incubated at 22°C compared to 10°C, indicating increased temperature influencing microbial function and highlighting the importance of investigating temperature effects in Arctic proglacial regions [56].

In addition, rapidly changing fluvial systems shape Arctic glacial outwash plains into a dynamic environment for life, an aspect which has not been explored in the literature. Of particular interest are glacier flooding events known as *jökulhlaups*, which are caused by geothermal or volcanic activity under the glacier or from the bursting of an ice-dammed supraglacial lake [64]. The ensuing flood passes around or through the glacier to the outwash plain where water levels are greatly increased for the span of a few days and large amounts of sediment are transported [64]. The flooding events can cause significant morphological changes to the proglacial landscape but currently the effects on terrestrial and aquatic biology are unknown. As *jökulhlaup* flooding events are becoming more frequent in regions such as Greenland, as a consequence of warmer temperatures [64], the effects of these floods on soil development and outflow forefield microbiomes warrants investigation.

3.1.2 Glacial aeolian dust. The fine sediments of glacial outwash plains can be emitted into the atmosphere as dust containing bioaerosols which may be transported across large distances through atmospheric dispersal [5,65]. Proglacial environments are a significant source of dust at high latitudes and contribute to dust deposition on glacial surfaces, which reduces albedo and drives increased melt [66]. The dust can include viable cells and spores which in turn can potentially colonise new areas despite exposure to intense UV, low nutrients and extreme temperatures during atmospheric transport [67]. Few studies have focused on aerial microbial diversity in the Arctic specifically, with a study in Svalbard by Cuthbertson *et al.* (2017) observing predominantly *Pseudomonadota*, *Actinobacteria*, and *Firmicutes* in accordance with findings from other aerial bacterial studies in both polar and nonpolar regions [67,68].

Further, bioaerosols in aeolian dust can have ice nucleating properties by initiating water crystallisation at higher temperatures [5]. This phenomenon is observed in gram-negative bacteria from *Gammaproteobacteria* (e.g. *Pseudomonas*), and less commonly in gram-positive bacteria from certain species of *Lysinibacillus* [69,70]. The biologically induced freezing is attributed to ice nucleating activity (INA) proteins which bind water molecules in a specific structure favourable to ice crystallisation [69]. The ability of bacteria to induce freezing at higher temperatures may have developed as a way to cause frost damage to plants, resulting in the release of plant nutrients [71]. While the role of ice nucleation in bacterial species originating from the Arctic is largely unknown, it likely plays a role in reducing atmospheric residence time via precipitation [72,73].

Increased glacial dust from newly exposed proglacial outwash plains has climatic ramifications as ice nucleation from bioaerosols encourages cloud formation via glaciation of low-level clouds [5]. Specifically, Arctic mixed-phase clouds can form, which contribute to warming effects through cloud forcing [74]. Warming occurs as long-wave radiation emitted by the Earth is absorbed by mixed-phase clouds and partly emitted back to the Earth surface [74]. Cloud forcing takes place at high latitudes, including the Arctic, where incoming solar (short-wave) radiation is reduced [74]. Hence, the ice nucleating activity of glacially sourced bioaerosols can contribute to the changing climate of the Arctic.

3.2 Aquatic environments

Besides influencing the surrounding terrestrial environments, glacial retreat also affects a variety of proglacial freshwater and marine habitats [75,76]. Freshwater environments include both proglacial streams/rivers, which are formed by glacial meltwater release into the glacier

forefield, as well as proglacial lakes, which can be formed when glacial meltwater is dammed by moraines or the bedrock [22]. Furthermore, freshwater from proglacial streams, lakes, and direct glacial run offs can reach the ocean and influence marine environments [76–78]. Warming in the Arctic increases glacial melting, leading to changes in water volume, flow velocity, turbidity, sediment and microbial transport, nutrient concentrations, salinity, and temperature, all of which influence the bacterial and archaeal communities in glacial streams, lakes, and the connected marine environments [79–82].

3.2.1 Freshwater proglacial streams and lakes. Proglacial freshwater environments can consist of interconnected networks of glacial meltwater streams/rivers and proglacial lakes [3]. As there are few studies on microbial dynamics in Arctic proglacial freshwater ecosystems, currently knowledge is also supplemented with mid-latitude Alpine systems [83]. Glacial streams originate from glacial meltwater and are variable in their geochemical and geographical settings, which influences the bacterial and archaeal community of these environments, resulting in endemism [83]. Due to the low salinity, the communities found in glacial streams mostly consist of freshwater associated taxa and are often similar but distinct to those found in glaciers [78,84]. The main phyla found in glacial streams in various Arctic environments including Svalbard, Greenland, and Alaska, are *Pseudomonadota*, *Bacteroidia*, and *Actinobacteria*, with lower abundances of *Verrucomicrobia*, *Acidobacteria*, *Planctomycetota* [78,83,85,86]. While the common genera in these environments are *Polaromonas*, *Methylotenera*, *Methylophilus*, *Nitrotoga*, and *Rhodoferax*, this is variable between different environments [83,85,87]. The initial community of such streams is seeded mostly from the subglacial run off [77,88]. However, diversity of the community often increases downstream, which in a space-for-time approach may imply that glacial retreat and changes in the physicochemical parameters is followed by a succession in the bacterial and archaeal community, based on their metabolic capabilities and preferences, as an effect of climate change or from increased connectivity with the surrounding terrestrial environments [84,87]. The microbial communities in downstream areas of proglacial rivers are likely more influenced by the surrounding soils (e.g. *Actinobacteria*) and groundwater [86] compared to upstream areas closer to the glacier source [84,88,89]. This increased influence of the surrounding soil microbiota on the glacial river microbiome is also true for glacial rivers with larger catchment sizes compared to smaller ones [87]. In benthic biofilms of proglacial streams, *Pseudomonadota* and *Bacteroidia*, together with *Patescibacteria* and *Planctomycetota*, are the most dominant phyla [90,91]. While *Cyanobacteria* can be found in stream biofilms and microbial mats, their abundance and photosynthesis rates partially depend on the outflow volume and turbidity of glacial discharge, due to the effect of shear forces on light permeability [82,84,92]. The similarity of benthic biofilm communities to the glacial stream water communities might be due to the constant mixing of sediment particles into the water and the corresponding dispersal of microbes [93].

Groundwater microbiomes are the least studied of glacial-associated ecosystems [86]. These microbiomes are influenced by glacial runoff, specifically, community compositions depend on the type of aquifer, the source of the water, flow dynamics, and the distance to the glacier [86,94,95]. Importantly, groundwater provides an interphase between surface water and surrounding soil microbiomes [86], however this dynamic may be altered with increased glacial melt causing a shift from confined to unconfined aquifers [95]. While the groundwater and glacial river are hydrologically interconnected, they host distinct microbial communities [86,96]. Purkamo *et al.* (2022) found a dominance of *Burkholderiales* and *Pseudomonadales* in Icelandic glacial groundwater, but relatively low abundance of *Candidatus Yanofskybacteria* in comparison to glacial river water [86]. Bacterial and archaeal diversity were greater in groundwater sites with increasing distance from the river, indicating the influence of the unique environmental pressures between these glacial sub-habitats [86,96]. While no archaea were

detected in the river, the groundwater archaeal communities were dominated by *Woesearch-aeales*, highlighting the distinction between interconnected groundwater and river micro-biomes [86]. Furthermore, presence of anaerobic microorganisms in groundwater was supported by Bomberg *et al* (2019), who detected methanogenic archaea and iron reducing bacteria in deeper groundwater [96]. However, seasonal environmental conditions impact the dynamics between shallow and deep groundwater ecosystems [97]. For example, in the summer, shallow oxygenated groundwater mixes with deeper anaerobic groundwater, driving seasonal microbial methane oxidation [97,98]. In the winter, this dynamic shifts, shallow groundwater freezes while deeper methane-rich groundwater remains active, potentially resulting in greater methane emissions [97,98]. This is corroborated by identification of methanogens in deep anaerobic groundwater (such as *Bathyarchaeota*) [96].

Proglacial lakes reside in the glacial forefield and are formed by, in-contact with, or directly influenced by the glacier ice margin and glacial meltwater [22]. Proglacial lakes are variable in physicochemical characteristics (although generally characterised by oligotrophy) and microbial diversity, as they often depend on the influx of glacial streams and meltwater [8,22,78]. Consequently, the microbial taxa often found in glacial lakes are similar to those in streams, characterised by the presence of *Pseudomonadota*, *Bacteroidia*, *Actinobacteria*, *Planctomycetes*, *Verrucomicrobia*, *Chloroflexi*, and at times *Acidobacteria*, *Patescibacteria*, *Elusimicrobia*, and *Cyanobacteria*, as well as microalgae and diatoms, in addition to overall low abundances of archaea [78,99–104].

Arctic proglacial lakes are increasing in numbers and extent as glaciers retreat [105]. These proglacial lakes can interrupt the delivery of meltwater and sediment to oceans and potentially act as partial freshwater reserves in place of glaciers [22]. Microbial succession in Arctic proglacial fluvio-lacustrine systems depends on gradients of environmental conditions acting on the microorganisms originating from the glacier, as well as new colonisation from the surrounding habitats (e.g., soils) [84,88,100]. While there is interconnection and sourcing of microbial taxa across the glacier and the proglacial freshwater environments, there appears to be strong taxonomic sorting across the habitats despite hydrological connectivity across environments [77,78,100]. For example, the study by Girard *et al.* (2023) demonstrated that while the surface of glacial ice was dominated by *Cyanobacteria*, the adjacent proglacial lake was dominated by an assemblage of *Chloroflexi*, *Actinobacteriota*, and *Planctomycetota* [78]. Interestingly, this study detected *Polaromonas*, a psychrophilic bacteria, across all sampled habitats (e.g. glacial and lake ice, proglacial lake and stream waters) but with unique phylotype assemblages in each habitat [78], suggesting strong sorting even at lower taxonomic levels.

Distance from the glacier and age of the proglacial lakes appear to be driving factors in microbial abundance and diversity, although without a consistent pattern. The study by Górniak *et al.* (2016) in an Arctic fluvio-lacustrine system (Svalbard) demonstrated that shifts in physicochemical parameters result in selective pressure on microorganisms across the proglacial field chronosequence, with higher diversity but lower biomass in the younger colder lake, closer to the glacier, compared to an older warmer downstream lake [100,106]. This was followed by increased abundance of *Actinobacteria* and *Bacteroidota* and decreased abundance of *Alphaproteobacteria* [100]. A similar pattern of reduced diversity with distance from the glacier was demonstrated in sediments of Icelandic proglacial lakes, Lamsters *et al.* (2020) showed that the oldest, least oligotrophic, furthest lake from the glacier had a considerably different community assemblage and lower taxonomic diversity compared to the younger lake that was still hydrologically connected to the glacier [102]. Contrary to these studies, a more recent analysis of five proglacial chronosequences demonstrated an increase in both bacterial cell number and diversity in older lakes, further from the glacier [8], suggesting no universal trend in proglacial lake succession. However, this could be due to differences in hydrological

connectivity of the lakes or the influences of bird-driven nutrient fertilization and pH changes across the different studies [8]. Hydrological connectivity across the glacier habitats in the context of increased melt can also be important in the context of viral control of ecological dynamics. Viruses originating from glacier cryoconite holes are able to infect microbiota in downstream proglacial ponds, with increased viral abundance associated with higher host availability and higher temperatures in proglacial ponds [107].

Based on Alpine systems, turbidity seems to be a main driving factor for the bacterial and archaeal community, and the loss of turbidity due to climate change in glacial streams and connected lakes may lead to a shift in the autotrophic and heterotrophic bacterial diversity [108]. These differences between glacier fed and disconnected proglacial lakes suggest that with increased glacial retreat the proglacial lake communities may shift from chemohetero-trophic processes in connected lakes to photoautotrophy in disconnected lakes, which can result in shifts of ecosystem functions [109].

3.2.2 Marine environments. Glacial meltwater is not only released into terrestrial environments, but also shed into marine systems, thus transporting nutrients, sediment, freshwater, and microorganisms into the coastal ocean with effects for the marine bacterial and archaeal communities and potential downstream impacts on higher trophic levels [110,111]. These glacial runoff influxes are more pronounced in the melting season and might increase with ongoing climate warming, while affecting the water column and pelagic ecosystem structure within fjords [110–112]. The transport of macro- and micro- nutrients from both land and marine terminating glaciers can include nitrogen, phosphorus, silicic acid, manganese and bioessential iron; these can increase marine productivity, and therefore zooplankton and downstream ecosystem dynamics [113–117]. Though for marine terminating glaciers, the nutrient influx dynamics into the marine photic zone depends on the glacier grounding line depth and induced upwelling of deeper nutrient-rich marine water [113,118].

The glacial runoff also creates gradients in salinity and turbidity, with turbidity sometimes causing decreases in phytoplankton productivity and tipping the system to net heterotrophy in the inner fjord compared to coastal shelf waters [119,120]. During high influx times, the microbial communities found in glacial meltwater persist in the freshwater layer and mix with marine communities, which continues until mixing and eventual lower influx lead to a homogenisation of the marine community and a disappearance of glacial derived microbiota [120]. Dissolved organic carbon (DOC) transported with the glacial meltwater may stimulate bacterial and archaeal production, while nutrients can stimulate phytoplankton production, which may have a secondary effect on the bacterial and archaeal community by additional carbon source availability [76,121,122]. However, the stimulation of phytoplankton growth again seems to be largely dependent on the turbidity of the water [121,122]. The origin of the water, whether directly from the glacier or from glacier influenced terrestrial sources, seems to be a key factor for the influx of nutrients and sediments [76]. With increased melt, the high influx of sediments with glacial runoffs can lead to a burial of glacial stream bacteria in the marine sedimentation zones [123,124]. This burial can then have implications for the oxygenation and consequently the sulfur- and iron cycling in the glacial influenced marine sediments [123,124].

4. Future perspectives

Overall research on microbiomes in Arctic glacial forefields is generally limited to phylogenetic identification [6,85,102], although some recent studies are expanding upon this with greater metagenomic insights [7,8,51]. While there are Arctic centric studies that utilise multiomics, these are not focused on proglacial environments [21,125]. Therefore, it would be beneficial to analyse microbial function and active taxa through combinations of multi-omic

technologies, including metagenomics, metatranscriptomics, metaproteomics and meta-metabolomics [20], to better understand microbial dynamics and succession in developing proglacial environments. Furthermore, while there is evidence for future carbon sequestration in proglacial terrestrial and aquatic environments [7,126], there is a lack of nuanced understanding of microbially mediated production and sequestration of greenhouse gases (carbon dioxide, methane, and nitrous dioxide) in Arctic proglacial fields. Recent innovations regarding *in situ* metagenomic analysis will aid the study of these extreme environments [127–129], for example metagenomic analysis was demonstrated in the field using a Nanopore MinION device and flow cell in a solar powered offline system, across a remote Icelandic ice cap [129].

While there is hydrological, nutrient, and microbial interconnectivity between supra-, en-, and sub-glacial zones [3,26,45,78,98,130], few studies approach this in a holistic way. For example, glacial microbiomes interact with the microbial systems in groundwater [95], glacier-fed streams, and lakes [78,86] –ecosystems with direct impacts on the human communities in the Arctic. Thus, research to gain better understanding of those interactions is a priority to establish baselines for future monitoring [10]. For example, future research could focus on interconnectedness of these environments (e.g. proglacial fields and cryoconites) in relation to seasonality, biogeochemical cycles, and climate change-related disturbances.

As Indigenous communities are the key stakeholders in Arctic research, researchers working in Indigenous lands should strive to avoid colonial parachute science, and work in partnerships with local communities [131]. For meaningful collaborations, it is important to consider the historical interactions of western science initiatives in the Arctic, and to ensure equitable benefit sharing between stakeholders [132]. Collaborative research can be co-productive or Indigenous-led [133], where all parties participate in writing research proposals, project planning, selection of priorities, local training (skill sharing), iterative co-managing, and co-assessing [134,135] (reference). Co-production is an inherently interdisciplinary paradigm that lends itself well to ecosystem-centred science [133,136]. These community partnerships should extend beyond the data gathering–community members should be acknowledged in publications and study results delivered back to the community. Moreover, Arctic communities have already developed recommendations for researchers to meaningfully engage with indigenous communities (e.g. ScIQ framework) [137] and online resources/databases of existing community-based monitoring (CBM) and Indigenous Knowledge (IK) projects [138,139]. Lastly, involving indigenous communities in research can also be a more sustainable approach with potential decrease in field work-associated carbon footprint [140].

As Arctic environments are rapidly changing it is important to preserve samples of current microbial diversity as baselines for future studies, environmental monitoring, conservation management and restoration of biomes, and as a bioprospecting resource for future industrial and medical applications [14,141,142]. Future basic environmental research would also benefit from reliable preservation, archival, and sharing of raw environmental samples (reference specimens) and samples in preservation solutions (e.g. ethanol, DNA/RNA ShieldTM, RNAlater®) [141,143]. This may be especially true for Arctic studies with challenging and expensive campaigns that rely on non-reproducible samples from a limited set of locations and timepoints [28,144]. Furthermore, availability of samples for reanalysis with novel techniques would facilitate reproducibility and new avenues of inquiry that were not part of the original focus (for example looking at the virome of a proglacial soil sample that was previously used solely for prokaryotic analysis) [143].

Database collections of multi-omic data are useful resources for research, lend themselves well to public access (e.g. NCBI) [145], and allow comparison between different studies. However, as sequencing and molecular techniques continue to advance, it may become increasingly difficult to compare newly generated research with older studies without access to the original

source material [143,146]. Microbial domain biological resource centres (mBRCs), also known as culture collections, store and distribute microorganisms and replicable genetic and viral material, with ~790 mBRCs worldwide, holding over three million strains [147]. Government-supported initiatives to interlink mBRCs and other biodiversity archives are building international networks to support research and democratise access [148,149]. Cryopreservation can maintain bacterial diversity in phylogenetically complex samples [150]. Two common temperature options are -80˚C and -196˚C [151,152]. For long-term storage (over 5 years), preservation in liquid nitrogen at -196˚C is recommended to avoid degradation [152–154]. Cryopreservation damage may be assessed with viability PCR, utilising the DNA-binding dye propidium monoazide (PMA) to prevent amplification of extracellular (from dead cells) and relic DNA [155]. Cryopreservation also allows mBRCs to efficiently hold large microbial inventories, which can be recovered upon thaw, and reduces the risks of genetic drift inherent in long-term sub-culturing [151–153,156]. However, most mBRC collections are confined to culturable axenic isolates and do not generally include whole microbiomes, which limits environmental microbiome research [13]. Hence, there are calls for the creation of biobanks (based on adapted mBRC infrastructure) of cryopreserved complex microbial communities, representing whole ecological microbiomes [13,141,147,157], as done for medical stool biobanks, which may aid environmental research [13]. However, more research is needed on cryopreservation protocols, to optimise microbial survival and preservation of community structures [143].

As oligotrophic Arctic samples have low microbial biomass, microbiome molecular analysis is susceptible to contamination during sample gathering and transport, and from extraction kits which can be contaminated with oligotrophic and extremophile taxa [19,142]. This can be mediated with the use of cryopreserved reference samples that can be standardised and included across different studies to enhance reproducibility and reduce impact of contaminants. Additionally, a PMA-treated field sample aliquot (immediately after collection and before cryopreserving) can help identify contaminants introduced during downstream processing [158]. Publicly funded repositories could be a future source of these shared reference samples and their associated metadata, processing history, and storage protocols [13,159,160].

Author Contributions

Conceptualization: Ianina Altshuler.

Supervision: Ianina Altshuler.

Visualization: Grace Marsh.

Writing – original draft: Grace Marsh, Darya Chernikhova, Stefan Thiele, Ianina Altshuler.

Writing – review & editing: Grace Marsh, Darya Chernikhova, Ianina Altshuler.

References

1. Rantanen Mika. The Arctic has warmed nearly four times faster than the globe since 1979. Nature. 2022; 3(168).

2. Box JE, Colgan WT, Christensen TR, Schmidt NM, Lund M, Parmentier FJW, et al. Key indicators of Arctic climate change: 1971–2017. Vol. 14, Environmental Research Letters. 2019.

3. Varliero G, Lebre PH, Frey B, Fountain AG, Anesio AM, Cowan DA. Glacial Water: A Dynamic Microbial Medium. Vol. 11, Microorganisms. 2023.

4. Bradley JA, Singarayer JS, Anesio AM. Microbial community dynamics in the forefield of glaciers. Vol. 281, Proceedings of the Royal Society B: Biological Sciences. 2014. https://doi.org/10.1098/rspb.2014.0882 PMID: 25274358

5. Tobo Y, Adachi K, DeMott PJ, Hill TCJ, Hamilton DS, Mahowald NM, et al. Glacially sourced dust as a potentially significant source of ice nucleating particles. Nat Geosci. 2019; 12(4).

6. Venkatachalam S, Kannan VM, Saritha VN, Loganathachetti DS, Mohan M, Krishnan KP. Bacterial diversity and community structure along the glacier foreland of Midtre Lovénbreen, Svalbard, Arctic. Ecol Indic. 2021; 126.

7. Varliero G, Anesio AM, Barker GLA. A Taxon-Wise Insight Into Rock Weathering and Nitrogen Fixation Functional Profiles of Proglacial Systems. Front Microbiol. 2021; 12. https://doi.org/10.3389/fmicb.2021.627437 PMID: 34621246

8. Wei J, Fontaine L, Valiente N, Dörsch P, Hessen DO, Eiler A. Trajectories of freshwater microbial genomics and greenhouse gas saturation upon glacial retreat. Nat Commun. 2023; 14(1). https://doi.org/10.1038/s41467-023-38806-w PMID: 37270637

9. Blaud A, Lerch TZ, Phoenix GK, Osborn AM. Arctic soil microbial diversity in a changing world. Res Microbiol. 2015; 166(10).

10. Ribas MP, García-Ulloa M, Espunyes J, Cabezón O. Improving the assessment of ecosystem and wildlife health: microbiome as an early indicator. Vol. 81, Current Opinion in Biotechnology. 2023. https://doi.org/10.1016/j.copbio.2023.102923 PMID: 36996728

11. Bhattacharjee A, Dubey S, Sharma S. Storage of soil microbiome for application in sustainable agriculture: prospects and challenges. Vol. 29, Environmental Science and Pollution Research. 2022. https://doi.org/10.1007/s11356-021-17164-4 PMID: 34718953

12. Biclot A, Huys GRB, Bacigalupe R, D'hoe K, Vandeputte D, Falony G, et al. Effect of cryopreservation medium conditions on growth and isolation of gut anaerobes from human faecal samples. Microbiome. 2022; 10(1). https://doi.org/10.1186/s40168-022-01267-2 PMID: 35644616

13. Ryan MJ, Schloter M, Berg G, Kostic T, Kinkel LL, Eversole K, et al. Development of Microbiome Biobanks–Challenges and Opportunities. Vol. 29, Trends in Microbiology. 2021.

14. Hoag H. The cold rush. Vol. 27, Nature Biotechnology. 2009. https://doi.org/10.1038/nbt0809-690 PMID: 19668168

15. Liu Y, Ji M, Yu T, Zaugg J, Anesio AM, Zhang Z, et al. A genome and gene catalog of glacier microbiomes. Nat Biotechnol. 2022. https://doi.org/10.1038/s41587-022-01367-2 PMID: 35760913

16. Kumar A, Mukhia S, Kumar R. Industrial applications of cold-adapted enzymes: challenges, innovations and future perspective. Vol. 11, 3 Biotech. 2021. https://doi.org/10.1007/s13205-021-02929-y PMID: 34567931

17. Białkowska A, Majewska E, Olczak A, Twarda-clapa A. Ice binding proteins: Diverse biological roles and applications in different types of industry. Vol. 10, Biomolecules. 2020. https://doi.org/10.3390/biom10020274 PMID: 32053888

18. Williams W, Chilton A, Schneemilch M, Williams S, Neilan B, Driscoll C. Microbial biobanking—Cyanobacteria-rich topsoil facilitates mine rehabilitation. Biogeosciences. 2019; 16(10).

19. Kim S, Lee H, Hur S Do, Sul WJ, Kim OS. Glaciers as microbial habitats: current knowledge and implication. Vol. 60, Journal of Microbiology. 2022. https://doi.org/10.1007/s12275-022-2275-9 PMID: 35904688

20. Arıkan M, Muth T. Integrated multi-omics analyses of microbial communities: a review of the current state and future directions. Mol Omics [Internet]. 2023; Available from: http://xlink.rsc.org/?DOI=D3MO00089C. https://doi.org/10.1039/d3mo00089c PMID: 37417894

21. Lutz S, Anesio AM, Field K, Benning LG. Integrated "Omics", targeted metabolite and single-cell analyses of arctic snow algae functionality and adaptability. Front Microbiol. 2015; 6(NOV). https://doi.org/10.3389/fmicb.2015.01323 PMID: 26635781

22. Carrivick JL, Tweed FS. Proglacial Lakes: Character, behaviour and geological importance. Quat Sci Rev. 2013; 78.

23. Boetius A, Anesio AM, Deming JW, Mikucki JA, Rapp JZ. Microbial ecology of the cryosphere: Sea ice and glacial habitats. Vol. 13, Nature Reviews Microbiology. 2015. https://doi.org/10.1038/nrmicro3522 PMID: 26344407

24. Musilova M, Tranter M, Bennett SA, Wadham J, Anesio AM. Stable microbial community composition on the Greenland Ice Sheet. Front Microbiol. 2015; 6(MAR). https://doi.org/10.3389/fmicb.2015.00193 PMID: 25852658

25. Lutz S, Anesio AM, Edwards A, Benning LG. Linking microbial diversity and functionality of arctic glacial surface habitats. Environ Microbiol. 2017; 19(2). https://doi.org/10.1111/1462-2920.13494 PMID: 27511455

26. Cook J, Edwards A, Takeuchi N, Irvine-Fynn T. Cryoconite: The dark biological secret of the cryosphere. Prog Phys Geogr. 2016; 40(1).

27. Grzesiak J, Górniak D, Świątecki A, Aleksandrzak-Piekarczyk T, Szatraj K, Zdanowski MK. Microbial community development on the surface of Hans and Werenskiold Glaciers (Svalbard, Arctic): a comparison. Extremophiles. 2015; 19(5). https://doi.org/10.1007/s00792-015-0764-z PMID: 26104673

28. Jaarsma AH, Sipes K, Zervas A, Jiménez FC, Ellegaard-Jensen L, Thøgersen MS, et al. Exploring microbial diversity in Greenland Ice Sheet supraglacial habitats through culturing-dependent and -independent approaches. FEMS Microbiol Ecol. 2023; 99(11). https://doi.org/10.1093/femsec/fiad119 PMID: 37791411

29. Millar JL, Bagshaw EA, Edwards A, Poniecka EA, Jungblut AD. Polar Cryoconite Associated Microbiota Is Dominated by Hemispheric Specialist Genera. Front Microbiol. 2021; 12. https://doi.org/10.3389/fmicb.2021.738451 PMID: 34899626

30. Kaczmarek Ł, Jakubowska N, Celewicz-Gołdyn S, Zawierucha K. The microorganisms of cryoconite holes (algae, Archaea, bacteria, cyanobacteria, fungi, and Protista): A review. Vol. 52, Polar Record. 2016.

31. Zdanowski MK, Bogdanowicz A, Gawor J, Gromadka R, Wolicka D, Grzesiak J. Enrichment of Cryoconite Hole Anaerobes: Implications for the Subglacial Microbiome. Microb Ecol. 2017; 73(3). https://doi.org/10.1007/s00248-016-0886-6 PMID: 27822618

32. Cameron KA, Hodson AJ, Osborn AM. Structure and diversity of bacterial, eukaryotic and archaeal communities in glacial cryoconite holes from the Arctic and the Antarctic. FEMS Microbiol Ecol. 2012; 82(2). https://doi.org/10.1111/j.1574-6941.2011.01277.x PMID: 22168226

33. Zawierucha K, Kolicka M, Takeuchi N, Kaczmarek L. What animals can live in cryoconite holes? A faunal review. J Zool. 2015; 295(3).

34. Edwards A, Mur LAJ, Girdwood SE, Anesio AM, Stibal M, Rassner SME, et al. Coupled cryoconite ecosystem structure-function relationships are revealed by comparing bacterial communities in alpine and Arctic glaciers. FEMS Microbiol Ecol. 2014; 89(2). https://doi.org/10.1111/1574-6941.12283 PMID: 24433483

35. Lutz S, Anesio AM, Raiswell R, Edwards A, Newton RJ, Gill F, et al. The biogeography of red snow microbiomes and their role in melting arctic glaciers. Nat Commun. 2016; 7. https://doi.org/10.1038/ncomms11968 PMID: 27329445

36. Segawa T, Matsuzaki R, Takeuchi N, Akiyoshi A, Navarro F, Sugiyama S, et al. Bipolar dispersal of red-snow algae. Nat Commun. 2018; 9(1). https://doi.org/10.1038/s41467-018-05521-w PMID: 30082897

37. Hoham RW, Remias D. Snow and Glacial Algae: A Review1. Vol. 56, Journal of Phycology. 2020. https://doi.org/10.1111/jpy.12952 PMID: 31825096

38. Procházková L, Remias D, Suzuki H, Kociánová M, Nedbalová L. Chloromonas rubrosalmonea sp. nov. (Chlorophyta) causes blooms of salmon-red snow due to high astaxanthin and low chlorophyll content. Bot Lett. 2024.

39. Miteva V, Teacher C, Sowers T, Brenchley J. Comparison of the microbial diversity at different depths of the GISP2 Greenland ice core in relationship to deposition climates. Environ Microbiol. 2009; 11(3). https://doi.org/10.1111/j.1462-2920.2008.01835.x PMID: 19278450

40. Zhong ZP, Tian F, Roux S, Gazitúa MC, Solonenko NE, Li YF, et al. Glacier ice archives nearly 15,000-year-old microbes and phages. Microbiome. 2021; 9(1). https://doi.org/10.1186/s40168-021-01106-w PMID: 34281625

41. Miteva V, Sowers T, Schüpbach S, Fischer H, Brenchley J. Geochemical and Microbiological Studies of Nitrous Oxide Variations within the New NEEM Greenland Ice Core during the Last Glacial Period. Geomicrobiol J. 2016; 33(8).

42. Varliero G, Holland A, Barker GLA, Yallop ML, Fountain AG, Anesio AM. Glacier clear ice bands indicate englacial channel microbial distribution. Journal of Glaciology. 2021; 67(265).

43. Christner BC, Mosley-Thompson E, Thompson LG, Reeve JN. Bacterial recovery from ancient glacial ice. Environ Microbiol. 2003; 5(5). https://doi.org/10.1046/j.1462-2920.2003.00422.x PMID: 12713469

44. Phillips T, Raiaram H, Steffen K. Melt water influence on englacial temperature distribution. IOP Conf Ser Earth Environ Sci. 2009; 6(1).

45. Skidmore ML, Foght JM, Sharp MJ. Microbial life beneath a high Arctic glacier. Appl Environ Microbiol. 2000; 66(8). https://doi.org/10.1128/AEM.66.8.3214-3220.2000 PMID: 10919772

46. Toubes-Rodrigo M, Potgieter-Vermaak S, Sen R, Oddsdóttir ES, Elliott D, Cook S. Active microbial ecosystem in glacier basal ice fuelled by iron and silicate comminution-derived hydrogen. Microbiologyopen. 2021; 10(4). https://doi.org/10.1002/mbo3.1200 PMID: 34459543

47. Sułowicz S, Bondarczuk K, Ignatiuk D, Jania JA, Piotrowska-Seget Z. Microbial communities from subglacial water of naled ice bodies in the forefield of Werenskioldbreen, Svalbard. Science of the Total Environment. 2020;723. https://doi.org/10.1016/j.scitotenv.2020.138025 PMID: 32213417

48. Schütte UME, Abdo Z, Foster J, Ravel J, Bunge J, Solheim B, et al. Bacterial diversity in a glacier fore-land of the high Arctic. Mol Ecol. 2010; 19(SUPPL. 1).

49. Bradley JA, Arndt S, Šabacká M, Benning LG, Barker GL, Blacker JJ, et al. Microbial dynamics in a High Arctic glacier forefield: A combined field, laboratory, and modelling approach. Biogeosciences. 2016; 13(19).

50. Wojcik R, Donhauser J, Frey B, Holm S, Holland A, Anesio AM, et al. Linkages between geochemistry and microbiology in a proglacial terrain in the High Arctic. Ann Glaciol. 2018; 59(77).

51. Nash M V., Anesio AM, Barker G, Tranter M, Varliero G, Eloe-Fadrosh EA, et al. Metagenomic insights into diazotrophic communities across Arctic glacier forefields. FEMS Microbiol Ecol. 2018; 94(9). https://doi.org/10.1093/femsec/fiy114 PMID: 29901729

52. Breen K, Lévesque E. Proglacial succession of biological soil crusts and vascular plants: Biotic interac-tions in the High Arctic. Canadian Journal of Botany. 2006; 84(11).

53. John Anderson N, Saros JE, Bullard JE, Cahoon SMP, McGowan S, Bagshaw EA, et al. The arctic in the twenty-first century: Changing biogeochemical linkages across a paraglacial landscape of Green-land. Vol. 67, BioScience. 2017. https://doi.org/10.1093/biosci/biw158 PMID: 28596614

54. Chiri E, Nauer PA, Rainer EM, Zeyer J, Schroth MH. High temporal and spatial variability of atmo-spheric-methane oxidation in Alpine glacier forefield soils. Appl Environ Microbiol. 2017; 83(18). https://doi.org/10.1128/AEM.01139-17 PMID: 28687652

55. Mateos-Rivera A, Øvreås L, Wilson B, Yde JC, Finster KW. Activity and diversity of methane-oxidizing bacteria along a Norwegian sub-Arctic glacier forefield. FEMS Microbiol Ecol. 2018; 94(5). https://doi.org/10.1093/femsec/fiy059 PMID: 29617984

56. Bárcena TG, Finster KW, Yde JC. Spatial patterns of soil development, methane oxidation, and methanotrophic diversity along a receding Glacier forefield, Southeast Greenland. Arct Antarct Alp Res. 2011; 43(2).

57. Pessi IS, Pushkareva E, Lara Y, Borderie F, Wilmotte A, Elster J. Marked Succession of Cyanobacter-ial Communities Following Glacier Retreat in the High Arctic. Microb Ecol. 2019; 77(1). https://doi.org/10.1007/s00248-018-1203-3 PMID: 29796758

58. Botnen SS, Mundra S, Kauserud H, Eidesen PB. Glacier retreat in the High Arctic: opportunity or threat for ectomycorrhizal diversity? FEMS Microbiol Ecol. 2020; 96(12). https://doi.org/10.1093/femsec/fiaa171 PMID: 32816005

59. Botnen SS, Thoen E, Eidesen PB, Krabberød AK, Kauserud H. Community composition of arctic root-associated fungi mirrors host plant phylogeny. FEMS Microbiol Ecol. 2020; 96(11). https://doi.org/10.1093/femsec/fiaa185 PMID: 32918451

60. Yarzábal LA. Perspectives for using glacial and periglacial microorganisms for plant growth promotion at low temperatures. Vol. 104, Applied Microbiology and Biotechnology. 2020. https://doi.org/10.1007/s00253-020-10468-4 PMID: 32076773

61. Backer R, Rokem JS, Ilangumaran G, Lamont J, Praslickova D, Ricci E, et al. Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Vol. 871, Frontiers in Plant Science. 2018. https://doi.org/10.3389/fpls.2018.01473 PMID: 30405652

62. Parisy B, Schmidt NM, Wirta H, Stewart L, Pellissier L, Holben WE, et al. Ecological signals of arctic plant-microbe associations are consistent across eDNA and vegetation surveys. Metabarcoding Meta-genom. 2023; 7.

63. Mateos-Rivera A, Yde JC, Wilson B, Finster KW, Reigstad LJ, Øvreås L. The effect of temperature change on the microbial diversity and community structure along the chronosequence of the sub-arctic glacier forefield of Styggedalsbreen (Norway). FEMS Microbiol Ecol. 2016; 92(4). https://doi.org/10.1093/femsec/fiw038 PMID: 26902803

64. Carrivick JL, Tweed FS. A review of glacier outburst floods in Iceland and Greenland with a mega-floods perspective. Vol. 196, Earth-Science Reviews. 2019.

65. Jensen LZ, Glasius M, Gryning SE, Massling A, Finster K, Šantl-Temkiv T. Seasonal Variation of the Atmospheric Bacterial Community in the Greenlandic High Arctic Is Influenced by Weather Events and Local and Distant Sources. Front Microbiol. 2022; 13. https://doi.org/10.3389/fmicb.2022.909980 PMID: 35879956

66. Bullard JE, Baddock M, Bradwell T, Crusius J, Darlington E, Gaiero D, et al. High-latitude dust in the Earth system. Vol. 54, Reviews of Geophysics. 2016.

67. Cuthbertson L, Amores-Arrocha H, Malard LA, Els N, Sattler B, Pearce DA. Characterisation of arctic bacterial communities in the air above svalbard. Biology (Basel). 2017; 6(2). https://doi.org/10.3390/biology6020029 PMID: 28481257

68. Harding T, Jungblut AD, Lovejoy C, Vincent WF. Microbes in high arctic snow and implications for the cold biosphere. Appl Environ Microbiol. 2011; 77(10). https://doi.org/10.1128/AEM.02611-10 PMID: 21460114

69. Failor KC, Schmale DG, Vinatzer BA, Monteil CL. Ice nucleation active bacteria in precipitation are genetically diverse and nucleate ice by employing different mechanisms. ISME Journal. 2017; 11(12). https://doi.org/10.1038/ismej.2017.124 PMID: 28753208

70. Huang S, Hu W, Chen J, Wu Z, Zhang D, Fu P. Overview of biological ice nucleating particles in the atmosphere. Vol. 146, Environment International. 2021. https://doi.org/10.1016/j.envint.2020.106197 PMID: 33271442

71. Lukas M, Schwidetzky R, Eufemio RJ, Bonn M, Meister K. Toward Understanding Bacterial Ice Nucleation. Vol. 126, Journal of Physical Chemistry B. 2022. https://doi.org/10.1021/acs.jpcb.1c09342 PMID: 35084861

72. Roeters SJ, Golbek TW, Bregnhøj M, Drace T, Alamdari S, Roseboom W, et al. Ice-nucleating proteins are activated by low temperatures to control the structure of interfacial water. Nat Commun. 2021; 12(1). https://doi.org/10.1038/s41467-021-21349-3 PMID: 33608518

73. Amato P, Joly M, Schaupp C, Attard E, Möhler O, Morris CE, et al. Survival and ice nucleation activity of bacteria as aerosols in a cloud simulation chamber. Atmos Chem Phys. 2015; 15(11).

74. Solomon A, De Boer G, Creamean JM, McComiskey A, Shupe MD, Maahn M, et al. The relative impact of cloud condensation nuclei and ice nucleating particle concentrations on phase partitioning in Arctic mixed-phase stratocumulus clouds. Atmos Chem Phys. 2018; 18(23).

75. Žárský JD, Kohler TJ, Yde JC, Falteisek L, Lamarche-Gagnon G, Hawkings JR, et al. Prokaryotic assemblages in suspended and subglacial sediments within a glacierized catchment on Qeqertarsuaq (Disko Island), west Greenland. FEMS Microbiol Ecol. 2018; 94(7). https://doi.org/10.1093/femsec/fiy100 PMID: 29846587

76. Hopwood MJ, Carroll D, Dunse T, Hodson A, Holding JM, Iriarte JL, et al. Review article: How does glacier discharge affect marine biogeochemistry and primary production in the Arctic? Vol. 14, Cryosphere. 2020.

77. Cameron KA, Stibal M, Hawkings JR, Mikkelsen AB, Telling J, Kohler TJ, et al. Meltwater export of prokaryotic cells from the Greenland ice sheet. Environ Microbiol. 2017; 19(2). https://doi.org/10.1111/1462-2920.13483 PMID: 27489963

78. Girard C, Vincent WF, Culley AI. Arctic bacterial diversity and connectivity in the coastal margin of the Last Ice Area. ISME Communications. 2023 Sep 26; 3(1):105. https://doi.org/10.1038/s43705-023-00313-w PMID: 37752298

79. Hood E, Berner L. Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in southeastern Alaska. J Geophys Res Biogeosci. 2009; 114(3).

80. Uehlinger U, Robinson CT, Hieber M, Zah R. The physico-chemical habitat template for periphyton in alpine glacial streams under a changing climate. Hydrobiologia. 2010; 657(1).

81. Koch JC, McKnight DM, Neupauer RM. Simulating unsteady flow, anabranching, and hyporheic dynamics in a glacial meltwater stream using a coupled surface water routing and groundwater flow model. Water Resour Res. 2011; 47(5).

82. Weinbauer MG, Bettarel Y, Cattaneo R, Luef B, Maier C, Motegi C, et al. Viral ecology of organic and inorganic particles in aquatic systems: Avenues for further research. Aquatic Microbial Ecology. 2009; 57(3). https://doi.org/10.3354/ame01363 PMID: 27478304

83. Battin TJ, Ezzat L, Peter H, Bourquin M, Michoud G, Fodelianakis S, et al. Towards a global biogeography of the glacier-fed stream benthic microbiome. 2023.

84. Wilhelm L, Singer GA, Fasching C, Battin TJ, Besemer K. Microbial biodiversity in glacier-fed streams. ISME Journal. 2013; 7(8). https://doi.org/10.1038/ismej.2013.44 PMID: 23486246

85. Kohler TJ, Vinšová P, Falteisek L, Žárský JD, Yde JC, Hatton JE, et al. Patterns in Microbial Assemblages Exported From the Meltwater of Arctic and Sub-Arctic Glaciers. Front Microbiol. 2020; 11. https://doi.org/10.3389/fmicb.2020.00669 PMID: 32351489

86. Purkamo L, Ó Dochartaigh B, MacDonald A, Cousins C. Following the flow—Microbial ecology in surface- and groundwaters in the glacial forefield of a rapidly retreating glacier in Iceland. Environ Microbiol. 2022; 24(12). https://doi.org/10.1111/1462-2920.16104 PMID: 35706139

87. Vrbická K, Kohler TJ, Falteisek L, Hawkings JR, Vinšová P, Bulínová M, et al. Catchment characteristics and seasonality control the composition of microbial assemblages exported from three outlet glaciers of the Greenland Ice Sheet. Front Microbiol. 2022; 13. https://doi.org/10.3389/fmicb.2022.1035197 PMID: 36523833

88. Hotaling S, Hood E, Hamilton TL. Microbial ecology of mountain glacier ecosystems: biodiversity, ecological connections and implications of a warming climate. Vol. 19, Environmental Microbiology. 2017. https://doi.org/10.1111/1462-2920.13766 PMID: 28419666

89. Hauptmann AL, Markussen TN, Stibal M, Olsen NS, Elberling B, Bælum J, et al. Upstream freshwater and terrestrial sources are differentially reflected in the bacterial community structure along a small Arctic river and its estuary. Front Microbiol. 2016; 7(SEP). https://doi.org/10.3389/fmicb.2016.01474 PMID: 27708629

90. Brandani J, Peter H, Busi SB, Kohler TJ, Fodelianakis S, Ezzat L, et al. Spatial patterns of benthic biofilm diversity among streams draining proglacial floodplains. Front Microbiol. 2022; 13. https://doi.org/10.3389/fmicb.2022.948165 PMID: 36003939

91. Ezzat L, Fodelianakis S, Kohler TJ, Bourquin M, Brandani J, Busi SB, et al. Benthic Biofilms in Glacier-Fed Streams from Scandinavia to the Himalayas Host Distinct Bacterial Communities Compared with the Streamwater. Appl Environ Microbiol. 2022; 88(12).

92. Sudlow K, Tremblay SS, Vinebrooke RD. Glacial stream ecosystems and epilithic algal communities under a warming climate. Vol. 31, Environmental Reviews. 2023.

93. Dubnick A, Kazemi S, Sharp M, Wadham J, Hawkings J, Beaton A, et al. Hydrological controls on glacially exported microbial assemblages. J Geophys Res Biogeosci. 2017; 122(5).

94. Miller JB, Frisbee MD, Hamilton TL, Murugapiran SK. Recharge from glacial meltwater is critical for alpine springs and their microbiomes. Environmental Research Letters. 2021; 16(6).

95. Retter A, Karwautz C, Griebler C. Groundwater microbial communities in times of climate change. Curr Issues Mol Biol. 2021;41.

96. Bomberg M, Liljedahl LC, Lamminmäki T, Kontula A. Highly diverse aquatic microbial communities separated by permafrost in Greenland show distinct features according to environmental niches. Front Microbiol. 2019; 10(JULY). https://doi.org/10.3389/fmicb.2019.01583 PMID: 31354674

97. Kleber GE, Magerl L, Turchyn A V., Redeker K, Thiele S, Liira M, et al. Shallow and deep groundwater moderate methane dynamics in a high Arctic glacial catchment. Front Earth Sci (Lausanne). 2024; 12.

98. Kleber GE, Hodson AJ, Magerl L, Mannerfelt ES, Bradbury HJ, Zhu Y, et al. Groundwater springs formed during glacial retreat are a large source of methane in the high Arctic. Nat Geosci. 2023; 16(7).

99. Liu Y, Yao T, Jiao N, Kang S, Zeng Y, Huang S. Microbial community structure in moraine lakes and glacial meltwaters, Mount Everest. FEMS Microbiol Lett. 2006; 265(1). https://doi.org/10.1111/j.1574-6968.2006.00477.x PMID: 17107422

100. Górniak D, Marszałek H, Jankowska K, Dunalska J. Bacterial community succession in an arctic lake-stream system (Brattegg valley, SW Spitsbergen). Boreal Environment Research. 2016; 21(1–2).

101. Dindhoria K, Kumar S, Kumar R. Taxonomic and functional analysis of proglacial water bodies of Triloknath glacier ecosystem from North-Western Himalayas. Ecol Inform. 2021; 64.

102. Lamsters K, Ustinova M, Birzniece L, Silamiķelis I, Gaidelene J, Karušs J, et al. Bacterial and archaeal community structure in benthic sediments from glacial lakes at the Múlajökull Glacier, central Iceland. Polar Biol. 2020; 43(12).

103. Colby GA, Ruuskanen MO, St.Pierre KA, St.Louis VL, Poulain AJ, Aris-Brosou S. Warming Climate Is Reducing the Diversity of Dominant Microbes in the Largest High Arctic Lake. Front Microbiol. 2020; 11. https://doi.org/10.3389/fmicb.2020.561194 PMID: 33133035

104. Cavaco MA, St. Louis VL, Engel K, St. Pierre KA, Schiff SL, Stibal M, et al. Freshwater microbial community diversity in a rapidly changing High Arctic watershed. FEMS Microbiol Ecol. 2019; 95(11).

105. Dye A, Bryant R, Rippin D. Proglacial lake expansion and glacier retreat in Arctic Sweden. Geografiska Annaler, Series A: Physical Geography. 2022; 104(4).

106. Marszałek H, Górniak D. Changes in water chemistry along the newly formed High Arctic fluvial–lacustrine system of the Brattegg Valley (SW Spitsbergen, Svalbard). Environ Earth Sci. 2017; 76(13).

107. Anesio AM, Mindl B, Laybourn-Parry J, Hodson AJ, Sattler B. Viral dynamics in cryoconite holes on a high Arctic glacier (Svalbard). J Geophys Res Biogeosci. 2007; 112(4).

108. Peter H, Sommaruga R. Shifts in diversity and function of lake bacterial communities upon glacier retreat. ISME Journal. 2016; 10(7). https://doi.org/10.1038/ismej.2015.245 PMID: 26771929

109. Kleinteich J, Hanselmann K, Hildebrand F, Kappler A, Zarfl C. Glacier melt-down changes habitat characteristics and unique microbial community composition and physiology in alpine lake sediments. FEMS Microbiol Ecol. 2022; 98(7). https://doi.org/10.1093/femsec/fiac075 PMID: 35749563

110. Mortensen J, Bendtsen J, Motyka RJ, Lennert K, Truffer M, Fahnestock M, et al. On the seasonal freshwater stratification in the proximity of fast-flowing tidewater outlet glaciers in a sub-Arctic sill fjord. J Geophys Res Oceans. 2013; 118(3).

111. Meire L, Mortensen J, Rysgaard S, Bendtsen J, Boone W, Meire P, et al. Spring bloom dynamics in a subarctic fjord influenced by tidewater outlet glaciers (Godthåbsfjord, SW Greenland). J Geophys Res Biogeosci. 2016; 121(6).

112. Arendt KE, Agersted MD, Sejr MK, Juul-Pedersen T. Glacial meltwater influences on plankton community structure and the importance of top-down control (of primary production) in a NE Greenland fjord. Vol. 183, Estuarine, Coastal and Shelf Science. 2016.

113. Hopwood MJ, Carroll D, Browning TJ, Meire L, Mortensen J, Krisch S, et al. Non-linear response of summertime marine productivity to increased meltwater discharge around Greenland. Nat Commun. 2018; 9(1). https://doi.org/10.1038/s41467-018-05488-8 PMID: 30108210

114. Bhatia MP, Waterman S, Burgess DO, Williams PL, Bundy RM, Mellett T, et al. Glaciers and Nutrients in the Canadian Arctic Archipelago Marine System. Global Biogeochem Cycles. 2021; 35(8).

115. Hawkings JR, Wadham JL, Tranter M, Lawson E, Sole A, Cowton T, et al. The effect of warming climate on nutrient and solute export from the Greenland Ice Sheet. Geochem Perspect Lett. 2015; 1(1).

116. Bhatia MP, Kujawinski EB, Das SB, Breier CF, Henderson PB, Charette MA. Greenland meltwater as a significant and potentially bioavailable source of iron to the ocean. Nat Geosci. 2013; 6(4).

117. Juul-Pedersen T, Arendt KE, Mortensen J, Blicher ME, Søgaard DH, Rysgaard S. Seasonal and interannual phytoplankton production in a sub-Arctic tidewater outlet glacier fjord, SW Greenland. Mar Ecol Prog Ser. 2015; 524.

118. Williams PL, Burgess DO, Waterman S, Roberts M, Bertrand EM, Bhatia MP. Nutrient and Carbon Export From a Tidewater Glacier to the Coastal Ocean in the Canadian Arctic Archipelago. J Geophys Res Biogeosci. 2021; 126(9).

119. Sejr MK, Bruhn A, Dalsgaard T, Juul-Pedersen T, Stedmon CA, Blicher M, et al. Glacial meltwater determines the balance between autotrophic and heterotrophic processes in a Greenland fjord. Proc Natl Acad Sci U S A. 2022; 119(52).

120. Gutiérrez MH, Galand PE, Moffat C, Pantoja S. Melting glacier impacts community structure of Bacteria, Archaea and Fungi in a Chilean Patagonia fjord. Environ Microbiol. 2015; 17(10).

121. Meire L, Mortensen J, Meire P, Juul-Pedersen T, Sejr MK, Rysgaard S, et al. Marine-terminating glaciers sustain high productivity in Greenland fjords. Glob Chang Biol. 2017; 23(12). https://doi.org/10.1111/gcb.13801 PMID: 28776870

122. Maselli M, Meire L, Meire P, Hansen PJ. Effects of Glacial Flour on Marine Micro-plankton: Evidences from Natural Communities of Greenlandic Fjords and Experimental Studies. Protist. 2023; 174(1). https://doi.org/10.1016/j.protis.2022.125928 PMID: 36442289

123. Pelikan C, Jaussi M, Wasmund K, Seidenkrantz MS, Pearce C, Kuzyk ZZA, et al. Glacial Runoff Promotes Deep Burial of Sulfur Cycling-Associated Microorganisms in Marine Sediments. Front Microbiol. 2019; 10. https://doi.org/10.3389/fmicb.2019.02558 PMID: 31787951

124. Michaud AB, Laufer K, Findlay A, Pellerin A, Antler G, Turchyn A V., et al. Glacial influence on the iron and sulfur cycles in Arctic fjord sediments (Svalbard). Geochim Cosmochim Acta. 2020; 280.

125. Mikan MP, Harvey HR, Timmins-Schiffman E, Riffle M, May DH, Salter I, et al. Metaproteomics reveal that rapid perturbations in organic matter prioritize functional restructuring over taxonomy in western Arctic Ocean microbiomes. ISME Journal. 2020; 14(1). https://doi.org/10.1038/s41396-019-0503-z PMID: 31492961

126. John Anderson N, Saros JE, Bullard JE, Cahoon SMP, McGowan S, Bagshaw EA, et al. The arctic in the twenty-first century: Changing biogeochemical linkages across a paraglacial landscape of Greenland. Vol. 67, BioScience. 2017. https://doi.org/10.1093/biosci/biw158 PMID: 28596614

127. Tamames J, Jiménez-Lalana D, Redondo Á, Martínez-García S, de los Rios A. In situ metagenomics: A platform for rapid sequencing and analysis of metagenomes in less than one day. Mol Ecol Resour. 2024; 24(2).

128. Goordial J, Altshuler I, Hindson K, Chan-Yam K, Marcolefas E, Whyte LG. In situ field sequencing and life detection in remote (79˚26'N) Canadian high arctic permafrost ice wedge microbial communities. Front Microbiol. 2017; 8(DEC).

129. Gowers GOF, Vince O, Charles JH, Klarenberg I, Ellis T, Edwards A. Entirely off-grid and solar-powered DNA sequencing of microbial communities during an ice cap traverse expedition. Genes (Basel). 2019; 10(11). https://doi.org/10.3390/genes10110902 PMID: 31703372

130. Bhatia M, Sharp M, Foght J. Distinct bacterial communities exist beneath a high arctic polythermal Glacier. Appl Environ Microbiol. 2006; 72(9). https://doi.org/10.1128/AEM.00595-06 PMID: 16957202

131. Odeny B, Bosurgi R. Time to end parachute science. Vol. 19, PLoS Medicine. 2022. https://doi.org/10.1371/journal.pmed.1004099 PMID: 36067221

132. Merrild Hansen A, Ren C. Collaborative research methods in the Arctic: Why and how? In: Collaborative Research Methods in the Arctic. 2020.

133. Wheeler HC, Danielsen F, Fidel M, Hausner V, Horstkotte T, Johnson N, et al. The need for transformative changes in the use of Indigenous knowledge along with science for environmental decision-making in the Arctic. People and Nature. 2020; 2(3).

134. Buschman VQ. Framing co-productive conservation in partnership with Arctic Indigenous peoples. Conservation Biology. 2022; 36(6). https://doi.org/10.1111/cobi.13972 PMID: 35775098

135. Arctic Council. PAME:Meaningful Engagement of Indigenous Peoples and Local Communities in Marine Activities: A Reference Guide. Akureyri, Iceland: Protection of the Arctice Marine Environment (PAME); 2021. 1–15 p.

136. Jessen TD, Ban NC, Claxton NXEMOLTW, Darimont CT. Contributions of Indigenous Knowledge to ecological and evolutionary understanding. Vol. 20, Frontiers in Ecology and the Environment. 2022.

137. Pedersen C, Otokiak M, Koonoo I, Milton J, Maktar E, Anaviapik A, et al. ScIQ: An invitation and recommendations to combine science and Inuit Qaujimajatuqangit for meaningful engagement of inuit communities in research. Arct Sci. 2020; 6(3).

138. Johnson N, Behe C, Danielsen F, Krümmel EM, Nickels S, Pulsifer PL. Community-Based Monitoring and Indigenous Knowledge in a Changing Arctic: A Review for the Sustaining Arctic Observing Networks. Final Report to Sustaining Arctic Observing Networks. 2016; 1(1).

139. Carlo N. Arctic Observing: Indigenous Peoples' History, Perspectives, and Approaches for Partnership. Fairbanks: Center for Arctic Policy Studies; 2020. 1–25 p.

140. Sonne C, Alstrup AKO, Dietz R, Ok YS, Ciesielski TM, Jenssen BM. Aviation, melting sea-ice and polar bears. Environ Int. 2019;133. https://doi.org/10.1016/j.envint.2019.105279 PMID: 31671313

141. Prakash O, Nimonkar Y, Desai D. A Recent Overview of Microbes and Microbiome Preservation. Vol. 60, Indian Journal of Microbiology. 2020. https://doi.org/10.1007/s12088-020-00880-9 PMID: 32655197

142. Edwards A, Cameron KA, Cook JM, Debbonaire AR, Furness E, Hay MC, et al. Microbial genomics amidst the arctic crisis. Vol. 6, Microbial Genomics. 2020. https://doi.org/10.1099/mgen.0.000375 PMID: 32392124

143. Cary SC, Fierer N. The importance of sample archiving in microbial ecology. Vol. 12, Nature Reviews Microbiology. 2014. https://doi.org/10.1038/nrmicro3382 PMID: 25564681

144. Metcalfe DB, Hermans TDG, Ahlstrand J, Becker M, Berggren M, Björk RG, et al. Patchy field sampling biases understanding of climate change impacts across the Arctic. Nat Ecol Evol. 2018; 2(9). https://doi.org/10.1038/s41559-018-0612-5 PMID: 30013133

145. Pruitt KD, Tatusova T, Maglott DR. NCBI Reference Sequence (RefSeq): A curated non-redundant sequence database of genomes, transcripts and proteins. Nucleic Acids Res. 2005; 33(DATABASE ISS.). https://doi.org/10.1093/nar/gki025 PMID: 15608248

146. Nissimov JI, Campbell CN, Probert I, Wilson WH. Aquatic virus culture collection: an absent (but necessary) safety net for environmental microbiologists. Applied Phycology. 2022; 3(1).

147. Smith D, Kermode A, Cafà G, Buddie AG, Caine TS, Ryan MJ. Strengthening mycology research through coordinated access to microbial culture collection strains. Vol. 1, CABI Agriculture and Bioscience. 2020.

148. Stackebrandt E, Schüngel M, Martin D, Smith D. The microbial resource research infrastructure mirri: Strength through coordination. Microorganisms. 2015; 3(4). https://doi.org/10.3390/microorganisms3040890 PMID: 27682123

149. Becker P, Bosschaerts M, Chaerle P, Daniel HM, Hellemans A, Olbrechts A, et al. Public microbial resource centers: Key hubs for findable, accessible, interoperable, and reusable (FAIR) microorganisms and genetic materials. Vol. 85, Applied and Environmental Microbiology. 2019.

150. Carroll IM, Ringel-Kulka T, Siddle JP, Klaenhammer TR, Ringel Y. Characterization of the Fecal Microbiota Using High-Throughput Sequencing Reveals a Stable Microbial Community during Storage. PLoS One. 2012; 7(10). https://doi.org/10.1371/journal.pone.0046953 PMID: 23071673

151. Müller J, Day JG, Harding K, Hepperle D, Lorenz M, Friedl T. Assessing genetic stability of a range of terrestrial microalgae after cryopreservation using amplified fragment length polymorphism (AFLP). Am J Bot. 2007; 94(5). https://doi.org/10.3732/ajb.94.5.799 PMID: 21636449

152. Rain-Franco A, de Moraes GP, Beier S. Cryopreservation and Resuscitation of Natural Aquatic Prokaryotic Communities. Front Microbiol. 2021; 11. https://doi.org/10.3389/fmicb.2020.597653 PMID: 33584565

153. Nakanishi K, Deuchi K, Kuwano K. Cryopreservation of four valuable strains of microalgae, including viability and characteristics during 15 years of cryostorage. J Appl Phycol. 2012; 24(6).

154. Heylen K, Hoefman S, Vekeman B, Peiren J, De Vos P. Safeguarding bacterial resources promotes biotechnological innovation. Vol. 94, Applied Microbiology and Biotechnology. 2012. https://doi.org/10.1007/s00253-011-3797-y PMID: 22410740

155. Emerson JB, Adams RI, Román CMB, Brooks B, Coil DA, Dahlhausen K, et al. Schrödinger's microbes: Tools for distinguishing the living from the dead in microbial ecosystems. Vol. 5, Microbiome. 2017.

156. Ali P, Fucich D, Shah AA, Hasan F, Chen F. Cryopreservation of cyanobacteria and eukaryotic microalgae using exopolysaccharide extracted from a glacier bacterium. Microorganisms. 2021; 9(2). https://doi.org/10.3390/microorganisms9020395 PMID: 33671910

157. Dubilier N, Mcfall-Ngai M, Zhao L. Microbiology: Create a global microbiome effort. Vol. 526, Nature. 2015. https://doi.org/10.1038/526631a PMID: 26511562

158. Bairoliya S, Zhi Xiang JK, Cao B. Extracellular DNA in Environmental Samples: Occurrence, Extraction, Quantification, and Impact on Microbial Biodiversity Assessment. Vol. 88, Applied and Environmental Microbiology. 2022. https://doi.org/10.1128/AEM.01845-21 PMID: 34818108

159. Fagorzi C, Passeri I, Cangioli L, Vaccaro F, Mengoni A. When biodiversity preservation meets biotechnology: The challenge of developing synthetic microbiota for resilient sustainable crop production. Vol. 2, Journal of Sustainable Agriculture and Environment. 2023.

160. Caenazzo L, Tozzo P. The future of biobanking: What is next? Vol. 9, High-Throughput. 2020. https://doi.org/10.3390/biotech9040023 PMID: 35822826