Breaking the Ice: A Review of Phages in Polar Ecosystems

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Abstract

Bacteriophages, or phages, are viruses that infect and replicate within bacterial hosts, playing a significant role in regulating microbial populations and ecosystem dynamics. However, phages from extreme environments such as polar regions remain relatively understudied due to challenges like restricted ecosystem access and low biomass. Understanding the diversity, structure, and functions of polar phages is crucial for advancing our knowledge of the microbial ecology and biogeochemistry of these environments. In this review, we will explore the current state of knowledge on phages from the Arctic and Antarctic, focusing on insights gained from -omic studies, phage isolation, and virus-like particle abundance data. Metagenomic studies of polar environments have revealed a high diversity of phages with unique genetic characteristics, providing insights into their evolutionary and ecological roles. Phage isolation studies have identified novel phage-host interactions and contributed to the discovery of new phage species. Virus-like particle abundance and lysis rate data, on the other hand, have highlighted the importance of phages in regulating bacterial populations and nutrient cycling in polar environments. Overall, this review aims to provide a comprehensive overview of the current state of knowledge about polar phages, and by synthesizing these different sources of information, we can better understand the diversity, dynamics, and functions of polar phages in the context of ongoing climate change, which will help to predict how polar ecosystems and residing phages may respond to future environmental perturbations.

Key Words: Viruses, Antarctic, Arctic, Cryosphere, Cold adaptation, AMG, VLP, Permafrost, Cryoconite holes, Host

Introduction

This review is divided into several sections and subsections starting with a description about the peculiarities of the Arctic and Antarctic ecosystems including their general effects on microbial and viral communities (section 1). At first, we discuss challenges associated with sampling and analyzing phages from polar regions (section 2). This is followed by an overview of how culture-independent -omics approaches have improved our understanding of viral communities with a focus on *in silico* detected cold adaptations exemplified by an in-depth investigation of auxiliary metabolic genes (AMGs) detected in polar viruses (section 3). Next, we present highlights and challenges regarding phage cultivation from the Arctic and Antarctica (section 4). Then, we have an in-depth look at different polar ecosystems, namely marine, sea ice, atmosphere, freshwater (lakes and cryoconite holes), and soils/peatlands regarding their viral community structure, abundance, and diversity (section 5). Next, we discuss the ecological strategies of phages in polar ecosystems and how dispersal shapes viral community compositions at the poles (section 6). We conclude this review by addressing the major challenges and knowledge gaps in polar phage research and provide future perspectives (section 7).

1. A closer look at the Arctic and Antarctica as viral territory

1.1 Characteristics of polar environments

Both polar regions (Antarctica and the Arctic) are characterized by extreme environmental conditions, such as low temperatures, low nutrient levels, as well as dim light in winter and high ultraviolet (UV) radiation in summer [1,2]. For at least one day each year, the sun does not rise or set past the Arctic and Antarctic circles at ~66.57 ° N and S latitude. Covering approximately 4 % of the Earth's surface [3], these polar regions are defined by their unique environmental conditions (Table 1). Geographically, the two polar regions differ greatly [4]: The Arctic Ocean is largely covered in sea ice and is surrounded by the continents of Eurasia and North America/Greenland. It is connected to the North Atlantic Ocean by the Greenland-Icelandic-Norwegian seas and to the North Pacific Ocean by the narrow Bering Strait. Warm water from the North Atlantic Current enters the Arctic between Svalbard and northern Norway through these passages, while cold polar water leaves the Arctic via Fram Strait and the Canadian Arctic Archipelago. In contrast, the Antarctic is a continent almost entirely covered by a massive ice sheet that reaches a height of more than four km. Antarctica is surrounded by the Southern Ocean, which is bound by the Antarctic Circumpolar Current, an ocean current that flows clockwise. Within this band, the strong eastward flow of the Antarctic Circumpolar Current connects each of the ocean basins and permits a global overturning circulation, which in turn dominates the global transport, e.g., of heat and freshwater. The Antarctic Circumpolar Current acts as a barrier, preventing warmer waters from the north from reaching the continent. This fact is contributing to the glacial climate of Antarctica [5]. Only about 2 % of Antarctica is ice-free polar desert, while the Arctic mainland and islands are covered with polar desert, tundra, glaciers, and ice caps [3]. There is a high degree of zonality in the southern hemisphere's high latitudes except for one area, in which this pattern is markedly disrupted: the Antarctic Peninsula. Topographically and climatically, the environment on the Antarctic Peninsula is more similar to that in southern coastal Greenland with a rugged alpine topography and summer air temperatures, which exceed 0 °C at sea level [6]. The Antarctic Peninsula mountain chain forms a distinct climatic barrier [7]. The Western Antarctic Peninsula (WAP) is generally ∼7 °C warmer than at similar latitudes and elevations [8], and belongs to one of the most rapidly warming regions on the planet [9,10]. The extreme continentality in Antarctica results from the high elevation of the ice sheet and the continent’s isolation from other land masses [11,12]. Above Antarctica, the air is often poorly mixed, especially in austral winter and spring. This promotes a colder circumpolar vortex compared with that in the Arctic, and is largely responsible for the more extensive and intense stratospheric “ozone hole” of southern high latitudes [12]. The Arctic is highly azonal, with large areas of ice and cold currents off the eastern coasts of Asia and North America, and open water stretching far into Arctic latitudes around the Svalbard archipelago (80 ° N). Climate, plant cover, land ice, and permafrost differ in similar ways between the eastern and western northern continents [4]. Arctic and Antarctic marine environments have in common their high latitudes, seasonal light levels, cold air and sea temperatures, and the presence of sea ice but other physical and biological characteristics differ between both polar regions [13].

Table 1: Feature comparison between Southern and Arctic Ocean (modified from [13]).

Feature	Southern Ocean	Arctic Ocean
Area	$35–38 \times 10^6$ km^2	14.6×10^6 km^2
Extent of continental shelf	Narrow, few islands	Broad, extensive archipelagos
Depth of continental shelf	400–600 m	100–500 m
Shelf continuity with ocean	Open to oceans to the north	Open to the south at Fram and Bering Straits
Direction of currents	Circumpolar	Transpolar
Upwelling and vertical mixing	Extensive	Little
Nutrient availability	Continuously high	Seasonally depleted
Seasonality of solar illumination	Weak	Strong
Primary productivity	Moderate to high	Moderate
Fluvial input to ocean	None	Extensive
Salinity at 100–150 m	34.5–34.7 ‰	30–32 ‰
Seasonality of pack ice	High	Low
Physical disturbance of benthos by large predators	Low	Extensive
Physical disturbance of benthos by ice scour	High	Low

Differences in circulation, exchange, and transport of water masses have already influenced the movement, gene flow, and evolution of species inhabiting these systems. They have resulted in the formation of a variety of microbial and viral communities, which play a critical role in the global climate and ecological balance, as well as in the food web [14-16,13].

Diatoms are the major component of the phytoplankton assemblage, but there are regional differences in community structure and seasonal species succession [13,17]. The dominant flow of energy is driven by photosynthetic primary production at the surface, followed by sinking and breakdown of the produced biomass within the benthic microbial loop [13]. Despite seasonal fluctuations and extreme environmental conditions (i.e., large seasonal changes in light levels, cold air and sea temperatures), the polar regions contain diverse microbial species accompanied by bacteriophages, i.e., viruses that infect bacteria, building communities that are essential components of the present ecosystems [14-16,18].

1.2 A general introduction to viruses in polar ecosystems

Viruses are the most abundant biological entities on the planet (reviewed by Suttle [19]), particularly in the oceans [20,19], which cover ~70 % of the Earth’s surface. The discovery of high abundances of viruses in aquatic environments three decades ago [21] motivated scientists to understand their diversity and role in the marine environment [20].

Bacteriophages play key roles in marine ecosystems by controlling microbial community dynamics, host metabolic status and biogeochemical cycles via lysis of hosts [20,22,19]. In addition, they shape the genetic diversity of their hosts through lateral gene transfer mechanisms [23-25,19]. Polar regions that are characterized by low temperature ecosystems do not hamper viral activity and their potential to infect prokaryotic populations [26,27]. In many polar ecosystems, especially the Antarctic and glacial ones, microbial communities have few species of grazers and thus, phage infection can be responsible for a large percentage of prokaryotic mortality, outcompeting grazing effects [1,28,29]. The role of viruses in ecosystem functioning is likely even greater, yet their diversity and the way in which they affect polar communities is not well understood [1], particularly in nutrient cycling [30,31].

2. Challenges related to sampling and analyzing phages from polar regions

Sampling and characterizing viruses from polar regions presents several challenges. One major challenge is the harsh environmental conditions, including extreme cold and low light levels, which can make it difficult to collect enough biomass for analyses. Additionally, the remote and isolated nature of polar regions (section 1.1) can make logistics and transportation difficult. Even for meta-omics approaches where cultivation is not required, the low biomass reduces bioinformatic analysis [32] and allows the samples to be easily contaminated by inhibitory substances making interpretation of results difficult. Other contaminating agents may be already present in the samples, which can inhibit downstream techniques such as polymerase chain reaction (PCR). For example, Northern peatlands are soil environments that have high plant biomass due to reduced microbial degradation. The plant biomass often includes humic substances and other complex carbohydrates, which co-elute with DNA, decreasing the DNA's purity and inhibiting downstream processing (section 5.5) [33,34].

Another challenge is the limited abundance of bacterial hosts in polar regions due to environmental conditions, vegetation, and available nutrients [35-37], making it difficult to identify and isolate new phages (section 4). Furthermore, the phages present in polar regions may have unique traits, e.g., surface charges, polarities [38,39], making it challenging to study them using traditional methods. Finally, phages in polar regions could be subjected to different selective pressures, which could lead to different genetic and structural characteristics, e.g., different particle sizes and infection dynamics (reviewed in Yau, Seth-Pasricha [18]). For example, viruses isolated from Antarctic sea ice were able to infect their hosts at freezing temperatures (0 and 4 °C), but not at higher temperatures [40]. These characteristics could make them difficult to isolate (section 4) and characterize bioinformatically (section 3).

3. Insights from -omics approaches to identify viruses

3.1 The benefits of -omics approaches in polar virology

While this review focuses on phages, we occasionally use the term “viruses” if results are based on -omics approaches to make clear that not only phages but also archaeal viruses or eukaryotic viruses could have been targeted by these methods. Metagenomics refers to the process of extracting genomic material from an environmental sample, revealing the base composition via sequencing that then can be bioinformatically characterized and thus has revolutionized how we think about microbes and their viruses. This is because viruses lack universal marker genes that allow interrogation of virus diversity using targeted gene amplification, instead, signature genes specific to certain viral groups are sometimes used [41]. Metagenomics captures a wide array of DNA molecules from different sources, e.g., bacteria, fungi, archaea, and mobile genetic elements including viruses. Another method critical for viral discovery is metatranscriptomics, a subfield of metagenomics that focuses on the study of RNA transcripts, i.e., mRNA, tRNA, and rRNA, rather than DNA from an environmental sample. Transcriptomic data have allowed an important expansion of the known RNA virosphere [42-44]. Over the last two decades, a targeted metagenomic approach, called a virome, has been heavily used to characterize viruses by first processing a sample before DNA extraction [45-47]. The collection of these approaches is often referred to as “omics” or “meta-omics” and aids to identify new viruses and learn more about the abundance, diversity, activity (section 5), and ecology (section 6.1) of viruses in different ecosystems. The power and value of these methods is especially apparent in hard-to-access ecosystems such as the Arctic and Antarctic posing exceptional sampling challenges (section 2) and from which microbial and viral communities are difficult to study by cultivation alone (section 4).

Notably for polar regions, these approaches can identify ancient or preserved viruses or fragments of their genomes, because the extreme conditions such as low temperatures help to preserve viral nucleic acids [48]. Meta-omics approaches are finding polar viruses becoming unearthed as temperatures rise disproportionately in northern latitudes [49,50]. Looking at AMGs from preserved viruses can moreover aid our understanding of host manipulations by viruses and the predominant metabolic processes in past times (section 3.2), and how viruses and hosts have contributed to biogeochemical regimes. Hence, exploring viruses from long-frozen samples allows us to gain insights into ancient virus-host relationships & evolution and might aid in predicting the emergence of new viruses.

3.2 AMGs & molecular adaptations of viruses in cold environments

Viruses often carry AMGs, which represent host genes picked up during previous infections and encode for proteins with important metabolic functions outside of typical viral infection. AMGs can benefit the host by enabling replication success of the phage with the most popular example being cyanophages providing more efficient photosynthetic genes to their hosts thereby promoting primary production [51]. For cold environments, different genomic studies have shown that viruses possess AMGs that aid host survival in the cold. For instance, Zhong et al. [52] identified virus-encoded fatty acid desaturase (*FAD*) genes in Arctic viral populations derived from metagenomes of sea ice, sea-ice brine, and cryopeg brine. These genes enable desaturation of cell membrane lipids thereby improving membrane fluidity [53], which allows a cell to deal with environmental challenges such as exposure to extreme cold and high salinity stress (reviewed by Beney, Gervais [54],[55]). Phylogenetic clustering of viral with microbial *FAD* genes revealed origin of these genes from Bacteroidetes and proteobacterial hosts at least for sea ice suggesting phage-host transfer for these AMGs, whereas cryopeg-derived viral *FAD* gene origin was less traceable. In addition to more *FAD* encoding viruses, a recent preprint identified a new AMG in Arctic brine viruses, namely epsG, having a role in biofilm formation and extracellular polysaccharide (EPS) production [56]. In subzero brines, microbes were previously shown to use EPS as cryo- and osmoprotectant [57,58]. According to Alarcon-Schumacher et al. [59], only few viruses from the Southern Ocean carried genes related to cold-adaptation, but among those were homologs of cold-shock proteins, genes with role in membrane fluidity, cell wall polymer or EPS production, and one antifreeze protein. Cold shock genes, efflux pump genes, and mercury resistance genes are assets for microorganisms dealing with cold environments. Relevant protein sequences were found to be carried by *Ralstonia* phages, *Aeromonas* phage (cold shock & efflux pump proteins only), *Burkholderia* phage, *Enterobacteria* phage and Bacteriophage lambda (efflux pump proteins only) from Arctic glacial ice but not soil (viral) metagenomes [60]. A study on Antarctic *Ralstonia* phages from surface snow did not find transduction of beneficial genes [61], suggesting that different environments (ice vs. snow vs. soil) might be beneficial for establishing phage-host interactions allowing AMG transfers. AMGs were also detected in Arctic peat soil [62] although this study was not focused on genes related to cold adaptation. Viral genome fragments contained AMGs related to carbon utilization, energy generation, use of organic nitrogen, transporters and miscellaneous. Most abundant were genes for carbon utilization, especially Glycosyltransferases [62], typical for viruses from Arctic peatlands [63,47]. Another recent study on an Arctic epishelf lake from Canada reported a viral community linked to several putative AMGs [64]. One was the sulfur starvation-linked gene *tauD,* which could mediate host production under a lack of sulfur, which is often limited in freshwater systems [65] and can be highly variable in Arctic lakes [66]. This is another good example that prevalence of AMGs might be very specific to a certain ecosystem. Another described AMG from this study was patatin-like phospholipase A, likely involved in phospholipid metabolism or cell signaling, therefore not necessarily a molecular adaptation to the cold but still benefiting the phage, e.g., during cell wall digestion or build-up of the phage particle [64].

Studying phages in frozen states can also help to reveal interesting insights into how ancient viruses manipulated microbial metabolism. For instance, Antarctic ice cores can be millions of years old and are a fund of fossil genes and microbes [67,68]. Zhong et al. [69] reported on AMGs of viruses archived in ~14,400-year-old glacier ice from Guliya ice cap in the far northwestern Tibetan Plateau. Generally, a common problem with AMGs is that their presence is often reported after *in silico* predictions but not experimentally validated nor is AMG activity confirmed, and thus the biogeochemical relevance often remains unclear. The studies compiled here, albeit being very few, point towards an important role of phage AMGs for supporting bacterial life in the cold. However, AMGs seem to occur somewhat ecosystem-specifically, e.g., AMGs found in polar ice and soil may differ.In addition, how mechanisms such as dispersal (section 6.2) or dispersal limitation mediate or preclude horizontal transfer of AMGs across Arctic and Antarctic ecosystems or even between them warrants further research.

4. Cultivation of phage from the cryosphere

4.1 Synopsis of the merits and successes of phage cultivation

In the age of increasingly powerful ‘omics to characterize phage genomes and activity, it is reasonable for phage researchers to question whether cultivating phages is worth the substantial effort required. Cultivation of an isolated phage-host pair requires additional steps to isolate a host and phage via repeated streaking of isolated plaques after the host is in culture. This may be especially time consuming for phages and hosts from the cryosphere, which may not replicate at room temperature and instead require incubation at colder temperatures [70]. However, some information cannot be inferred solely from ‘omics of environmental samples (reviewed in Trubl et al. [39]). Infection kinetics, such as adsorption rates, latent period, burst size, and the balance of lytic to lysogenic infections under different conditions, are most reliably measured in cultivation [71]. Isolation provides granular detail on phage replication physiology, which may be of particular interest for cold-adapted phages [72]. Finally, other ecological characteristics of phages such as their host ranges and their activity at varying conditions such as temperature or salinity may be directly measured in cultivation [70].

In recent years detailed genomic, structural, and infection kinetic characterization of phages have been undertaken from polar cryosphere environments, including soil from Antarctica [73,74] as well as sea ice from both the Arctic [75-77] and Antarctic [26,40] and a high Arctic lake [78]. These studies have shown that many cold-adapted phages isolated from sea ice featured siphovirus or myovirus morphotypes [76,79,75,40] and to a lesser degree short-tailed podophages [40,78] and filamentous phages, such as f327 isolated on *Pseudoalteromonas* [77]. In addition, there seems to be a bias towards successful isolation of new phages from sea ice (see above) and polar oceans [80], while phage isolates from polar freshwater environments (e.g., ponds and cryoconite holes), air, snow, melt ponds, and soils are more underrepresented or missing. Little work has also been done to isolate polar cyanophages. Isolation of Antarctic cyanophage S-EIV1 infecting polar *Synechococcus* sp. from freshwaters on Ellesmere Island (Nunavut, High Arctic Canada) however suggests that these polar phages can be very unrelated from known *Synechococcus* phages representing a new evolutionary lineage [78].

In contrast to isolating phage-host systems, it should be noted that phages may be cultured at the community level, depending on the question of interest. Community-level cultivation of phages has advantages in capturing the dynamics that arise from a diverse set of populations and their interactions in their natural environment. Furthermore, it may provide information without requiring labor-intensive and perhaps psychrophilic phage-destroying methods such as plaque streaking in a molten agar overlay. For example, community-level stable isotope probing in incubations of Arctic peat soils have demonstrated active phage-host interactions under anoxic and sub-freezing conditions over the course of months [62].

4.2 Cold-adapted phages and how to cultivate them

Cultivation of phage-host pairs from the cryosphere presents challenges unique to cold sources, including the requirements of low detection thresholds for low nutrient and biomass environments, long cultivation times, and adjustment of classic lab bench techniques for culturing phages that have traditionally relied on hot agar layers. Both hosts and phages may be inactive at or destroyed by exposure to high temperatures, and thus must be incubated at colder temperatures than phage-host pairs from other environments. For instance, one cold-adapted, well-studied phage-host system is *Colwellia psychrerythraea* strain 34H (Cp34H) and its phage Colwelliaphage 9A that was isolated from 128-m depth in Franklin Bay, Canadian Arctic, and replicates between -12 and 8 °C [70,81].

In addition to having cold incubation storage available, care must be taken not to destroy phages or their hosts with short-term exposure to hot agar in pouring a soft layer for lawns and plaques to form in. If the phage or its host cannot sufficiently tolerate the temporary heat shock of molten agar, alternative media to agar may be tried not requiring heat, or as much heat, to pour a soft layer on a petri dish. For example, one of these methods is the "silica-gel overlay" technique [70]. Alternative approaches may also be used, such as growing a phage in culture and using serial dilution in a 96-well plate, as done to isolate a cyanophage from an Arctic Lake [78].

Some bacteria and their phages found in the cryosphere may not be purely cold-adapted but merely cold-tolerant, and many may grow well at temperatures as warm as +15–20 °C with tolerance up to 45 °C, even if higher temperatures might impact infectivity [40]. These may be the low-hanging fruits in the underexplored realm of polar phage-host interactions that may yield great insight for relatively little adaptation of established and efficient polar phage isolation and cultivation methods. On the other hand, the truly unique physiology and ecology advancing science and technology may reside in the adaptations of the true extremophiles and may merit the additional effort.

5. Viral abundance and diversity of different polar ecosystems

Viral abundance, diversity and distribution are important key factors for a better understanding of ecosystem dynamics. Since bacteria are the most common host organisms in marine systems, most viruses in the oceans visualized by microscopy as virus-like particles (VLPs) are expected to be phages [82,19]. In viral ecology, the term VLPs is operationally defined by size and was established in the context of quantifying phages in environmental samples and is routinely applied for the enumeration of phages via epifluorescence microscopy [50] and flow cytometry [83]. On both a microscopic image and a cytogram, fluorescing dots of a certain intensity range are considered as VLPs. However, this definition may miss some phages such as prophages, or large viruses and may include non-virus particles such as gene-transfer agents and membrane vesicles that are erroneously counted as VLPs [84-86]. Therefore, the term VLP is applied to account for these uncertainties. Each microbial cell is a potential target for a specific viral subset. Therefore, understanding the variation in viral abundance and its relation to host abundance requires particular attention to the temporal and spatial scales of environmental variability and the interactions among viruses and hosts [87].

5.1 Viruses from marine ecosystems

Viruses have a significant impact in marine ecosystems where they often exceed bacterial abundance by one order of magnitude [19], reaching numbers of 10^5–10^7 VLPs mL^{-1}. In various marine habitats such as high-nutrient coastal waters, oligotrophic open ocean [88] and sediment traps [89], 0.8–4.3 % of bacteria were visibly phage-infected at any given time. Since phages are dependent on the presence of their host, phage abundance often correlates with microbial abundance [90,87]. For several marine environments, a relatively constant virus-to-bacteria ratio (VBR) of 5–10 VLPs per bacterial cell was observed [91]. Different studies also showed that this relationship is dependent on the type of aquatic ecosystem [92,87], and variation can be caused by multiple factors like salinity, tide, eutrophication, and temperature [93,94]. Polar ocean waters remain under-sampled compared to the temperate ocean. The polar oceans have lower bacterial production than temperate oceans due to colder temperatures and lower dissolved organic matter inputs [95], yet we know little about how phages affect their hosts and the biogeochemical cycles in the polar oceans. The few studies targeting viruses found viral abundances ranging from $1 \times 10^5 – 2.1 \times 10^7$ VLPs mL^{-1} in Antarctic waters [96-100]. For studies on the Arctic Ocean, we find a similar abundance range of $1 \times 10^5 – 2 \times 10^7$ VLPs mL^{-1} [101-104]. Seasonal studies find higher VLP abundances during the summer months [101] and in the polar oceans' surface microlayer due to increased viral activity [27].

Phage-mediated mortality in the central Arctic Ocean ranged between <1–11 % across the central Arctic Ocean [104]. In contrast, phage infection might be more important in the Antarctic Ocean, where phage-induced mortality often accounts for more than 15 % of the bacterial production [97,105,106], and sometimes surpass bacterial production, leading to a decline in bacterial standing stocks. In the Antarctic, viral mortality strongly increases during the productive season [105,106,99], which is strongly driven by lysogeny to lytic transition following high primary productivity [105,106]. Viral lysis impacts Antarctic nano- and picophytoplankton dynamics indicating differential rates depending on community composition and size-distribution [107]. Although then phage-mediated mortality rates vary widely, several studies found evidence that a higher impact of phages can be observed in more eutrophic compared to oligotrophic waters [97,108,109,96]. This may explain the higher phage-induced mortality in the Antarctic compared to the Arctic Ocean studies.

Increasing research of viruses through metagenomics has gained more information on viral community structures in different environments around the world including different polar ecosystems [110,15,111]. Major viral metagenomic work in polar oceans has been conducted during the Tara Oceans Polar Circle expedition encompassing 25,000 km around the Arctic

Ocean in 2013 [15], revealing the Arctic Ocean to be a hotspot for viral diversity. This contrasted the common belief that the Arctic Ocean was on the lower end regarding viral diversity [112,113]. Angly et al. [112], whose work was based on pyrosequencing DNA from purified virions, specifically reported on a decrease in cyanophage numbers in the colder regions. The more recently established Nordic Sea DNA virome enhanced our understanding about prevailing phages, with the top three abundant viral populations belonging to *Caudovirales* (recently abolished order [114]) namely *Pelagibacter* phage HTVC008M, *Puniceispirillum* phage HMO-2011, and *Cellulophaga* phage phi38:1 [115]. The study investigated the influence of water masses on viral community structure and found temperature, latitude, and the flow speed between two stations being the main influencing factors for shaping viral communities in the Nordic Seas. In addition, viral abundance was primarily linked to host cell availability also depending on currents [115]. Furthermore, a comprehensive metatranscriptomic study recently reported the novel pisuviricot class 27 for Atlantic Arctic waters, likely infecting prokaryotes and thus representing RNA phages [44]. Like other freshwater ecosystems [110,116], also the ocean pelagic zone contains many single-stranded (ss) DNA viruses, as for instance reported for the Barents Sea [117]. Most found ssDNA viruses in marine ecosystems belong to the *Microviridae*, *Parvoviridae*, or *Inoviriade* family [24,117], many of them including phages capable of infecting marine hosts including those from polar environments [118,61,60]. Arctic marine viromes were further shown to contain a high abundance of prophage sequences [119].

At the other end of the world, in the Southern Ocean, where viral diversity in the pelagic upper ocean is lower compared to lower latitudes [90], a metagenomic investigation unraveled abundance of temperate viruses around the WAP leading to genetically distinct double-stranded (ds) DNA viral communities compared to Pacific Ocean viromes [105]. Analysis of viral diversity from Prydz Bay, Antarctica, found different phage in surface seawater with

Cellulophaga phages (phi38:1 and phi10:1) and *Flavobacterium* phage 11b being abundant among the dsDNA virome, but also *Pseudomonas* and *Vibrio* phages [24]. The study further detected phages including the signatures of the temperate phage isolate *Psychrobacter* phage Psymv2 [74] from the Miers Valley in the McMurdo Dry Valleys (South Victoria Land, Antarctica) in the Prydz Bay viromes, demonstrating interconnection between marine and terrestrial desert environments [24]. The surface viral community dominated by *Caudovirales* clearly differed from the bottom waters (878 m depth), where nucleocytoplasmic large DNA viruses were more dominant. Similarly, a study from South Scotia Ridge found surface waters to be dominated by *Caudovirales*. This research also identified a wide variety of unique, previously undiscovered terminase large-subunit clades, suggesting the possibility of previously unknown viral diversity in polar waters. Another study that combined Chile Bay viromes with viruses found in Southern Ocean metagenomes found Antarctic viral populations were not found in more temperate waters [59], similar to the findings for Arctic Ocean viral communities [115,15]. This means that a comprehensive pole to pole viral comparison is still missing. Southern Ocean viral communities were found to possess specific adaptations to the polar environment such as genes related to cold shock response (section 3.2) and structural changes at the protein level increasing chain flexibility of protein secondary structures at lower temperatures [59].

Due to its isolation and limiting opportunities for colonization by non-native species, the microbial communities and nutrient cycling processes in the Antarctic may be more distinct and self-contained. Thus, the ecology of organisms including phage population dynamics are rather influenced by factors stemming from the Antarctic ecosystem than from external sources. Since the Arctic is more connected to the rest of the world, with numerous land masses and shipping lanes that can introduce new species and nutrients into the marine environment, this could lead to a greater diversity of bacterial hosts in marine waters for phages to infect, as well as a wider range of nutrient sources that could influence phage populations.

5.2 Viruses in sea ice

Sea ice represents a significant proportion of polar marine ecosystems, reaching the maximum coverage during the winter of about 15 × 10^6 km^2 in the Arctic and of 18 × 10^6 km^2 in the Antarctic [120]. Yet, studies targeting viral activity and distribution in sea-ice environments remain limited. Nonetheless, some studies have detected some of the highest concentrations of viruses in the ocean in Arctic sea ice [121], with significant seasonal changes. Spring blooms show a high variation in abundances ranging from 9 × 10^6 – 1.5 × 10^8 VLPs mL^{-1} [121]. This study found that the VBR was the highest at the start of the spring bloom when bacterial production was at its highest. Viral abundances increased at a higher rate than bacteria, reaching a VBR of 72 [121], highlighting the significance of virus-induced mortality in sea-ice bacterial communities.

During the autumn freeze-up in Arctic sea ice, a sharp increase in virus numbers and a decrease in bacterial abundances compared to the underlying water was observed resulting in an extremely high VBR of 846 [122]. In contrast, a study on North Pole sea ice did not find the high viral abundances and VBRs observed at lower latitudes [123]. Antarctic sea ice showed lower virus abundances (6.3 × 10^6–1.2 × 10^8 VLPs mL^{-1}) than the underlying water and low VBR rations for Prydz Bay over a full year [124]. Yet for three latitudinal transects for the Ross Sea, viral abundances ranging from 9.0 × 10^6 – 1.5 × 10^8 VLPs mL^{-1} and higher VBRs (max 119) were found [125], indicating geographic variability of sea-ice virus activity and abundance.

Compared with phages from sea water, those from within sea ice preferentially adopted a lysogenic infection strategy [126]. The temporal freeze-thaw cycle of sea ice influences the viral abundance dramatically, making it difficult to perform spatial comparisons [40,18].

Viruses seem to be enriched in sea ice during its formation compared to the surrounding seawater, by factors of up to 100 [122,125,121]. Comparatively, many phage isolates were recovered from Arctic or Antarctic sea ice ([75,77], section 4.1), but to date, only a single study used metagenomics to investigate viruses from different sections of a sea-ice core derived from Utqiaġvik, Alaska [52]. The work described a high degree of novelty among sea-ice phages, AMGs involved in cold survival of the host (section 3.2), and *Marinobacter*, *Glaciecola*, and *Colwellia* as dominant hosts for the phages. Sea ice often melts into melt ponds, representing a pool of water that forms on the ice surface. Studies have estimated that melt ponds can cover up to 50 % of the Arctic sea-ice surface during the summer melt season [127]. However, the diversity, ecology, and fate of viruses in melt ponds is unknown [128]. Given the heterogeneity and volume of this polar environment, further research, including metagenomic and experimental approaches, is needed to unravel the complex interactions between phages and their bacterial hosts that populate the sea-ice matrix.

5.3 Viruses in the polar atmosphere

The atmosphere of polar environments has been scarcely investigated regarding its viral composition, which however applies to most environments, although dispersal potential via the atmosphere is huge (section 6.2). While marine Antarctic ecosystems are somewhat cut off (section 5.1), the input of airborne biological material from other continents is likely, e.g., Antarctica receives airborne particles including pollen and fungi from South America [129]. At the time of writing this review, < 700 uncultivated viral genomes recovered from air ecosystems are stored at the IMG/VR database [130], reflecting a big knowledge gap of viruses and especially phages from atmospheric ecosystems. This is the case despite knowledge about other microorganisms in air, and the role of aerial dispersal for their biogeography has been noticed (reviewed by [131,132]). From aquatic surfaces, mainly the surface microlayer, viruses are typically ejected to air by bursting bubbles [133] and become part of bioaerosols [134]. Since viral activity is enhanced in the surface microlayer of the Arctic and Antarctic [27], and microlayer particles from the central Arctic Ocean during summer were loaded with viral particles [135], presence of phages in the polar atmosphere near water surfaces is very likely. Phages were not only found at the air-water interface but also at the air-land interface, for instance associated with surface snow [61]. It is unknown if they were initially deposited with the snow and originate from the troposphere. Indicators that would suggest this are dsDNA and ssDNA viruses being found in clouds [136], viruses being deposited from above the atmospheric boundary layer [137], and viruses with phage hallmark genes and specific adaptations to atmospheric residence occurring in rainwater [138]. Even if phages were not (yet) recovered from the atmosphere of polar ecosystems, they could be present and influence atmospheric processes. For example, the well-characterized, cold-active *Colwellia* phage [70] was tested for ice nucleation activity at ~10^9 phage particles mL^{-1} [139]. While it was found to have little impact in this role, other viruses have ice nucleation potential [140]. Ice nucleation activity means the formation of ice crystals at temperatures above the freezing point of water, and ice nucleating particles were detected in surface microlayer and aerosols in the Arctic [141,142]. The ice nucleation process is worthwhile to study as it can influence the formation of clouds, precipitation, and thus climate-relevant processes. Because several bacteria such as *Pseudomonas syringae* and *Pseudomonas antarctica* serve as ice nucleators [143,144], phages could still influence ice formation by infecting and killing ice-nucleating bacteria, or by encoding AMGs related to ice nucleation (section 3.2), which however remains to be comprehensively investigated for polar environments.

5.4 Viral abundance and diversity in polar freshwater environments

Freshwater environments in polar regions can serve as hotspots of microbial and associated viral biomass and diversity in these environments, where low temperatures can limit liquid water available for life processes in the soils and glacier surfaces [145-147]. The limited availability of nutrients, energy, and dispersal from surrounding environments truncates food webs in many polar freshwater environments. Without higher trophic levels serving as primary sources of bacterial mortality, the role of phages may take on greater proportional significance in structuring microbial communities and accelerating their evolution [148,149,28]. Two types of polar freshwater habitats where viral abundance and diversity have been studied are lakes and cryoconite holes.

5.4.1 Viruses in polar lakes

Viral abundances measured in polar lakes range from 10^4–10^8 VLPs mL^{-1}, with higher abundances in saline lakes, in colder lakes, and at least in Antarctic lakes, with higher available phosphorus concentrations [150-152,28]. While lower temperature and UV damage reduce decay rates of viral particles, seasonal changes in viral abundance and composition demonstrate they are actively infecting and lysing hosts in these environments, and not simply a relic of dispersal from more biologically active habitats [31,29]. Lysogeny is also a prevalent strategy in polar aquatic habitats [153,154], especially during the winter, as seen in electron microscopy and induction incubation experiments [155,28]. When phages do trigger lytic replication, they require phosphorus, which is a limiting nutrient in many polar lakes [156], although in nutrient amendment experiments with Arctic lakes and cryoconite water, the phage response to phosphorus was decoupled from that of bacteria [157].

The morphological and taxonomic diversity of phages in polar lakes have often surprised researchers, given their low biomass and the isolation especially of Antarctic lakes. A metagenome of Antarctic lake water's viral fraction contained what at that time was classified as 32 different viral families. Many of these communities were more diverse than viral communities from temperate freshwater or marine sources investigated using similar methods [31]. A PCR assay for the gp23 protein of Antarctic T4 phage was furthermore conducted on these samples, and the 30 resulting sequences spanned the breadth of a phylogenetic tree constructed using sequences from cultures and environmental PCRs of other terrestrial and marine environments. A 2015 metagenomic survey of lakes and ponds in Svalbard found they contained distinctive communities of DNA viruses compared with other environments, which were most similar – especially at coarser taxonomic scales – to Antarctic lakes [110]. While most (~ 90 %) of the sequences could not be assigned to any known taxonomy, those that could were assigned to what at that time were classified as *Circoviridae*, unassigned ssDNA viruses, *Microviridae*, and *Nanoviridae*. Both studies suggested that ssDNA viruses were more abundant than dsDNA viruses, at least in certain seasons, even assuming a 100-fold bias of the Phi29 polymerase for circular ssDNA genomes. Diversity patterns of phages generally follow trends in their abundance, with greater diversity being observed with microscopy and metagenomic methods in parts of lakes with greater salinity or greater phosphorus availability [154,158].

5.4.2 Viruses in cryoconite holes

Cryoconite holes are smaller, more dynamic freshwater environments than lakes. They are meltwater features in the surface of glaciers usually less than a meter in diameter and often less than a meter in depth [159,145]. They form when sediment blows onto the surface of the glacial ice and settles into a depression, where the lower albedo of the sediment absorbs solar radiation and causes it to melt into the ice [160,161]. The sediment melts downward until the radiation passing through the ice is sufficiently attenuated that not enough warming occurs to continue melting downward. The sediment and meltwater above remain in approximate equilibrium of the glacier surface, usually tens of centimeters below the surface [162,145]. Despite their small size and dynamic conditions, cryoconite holes host actively growing microbial communities [163], and the viruses that parasitize them [148,164]. Although viral production rates in Arctic cryoconite holes have been measured as similar to other sediments around the globe, microscopy-suggested burst sizes were substantially lower (only 2-4 viruses cell^{-1}). This finding would imply a high infection rate [149] in agreement with previous results from an Arctic cryoconite hole and Arctic and Antarctic lake waters [165]. Much like polar lakes, the diversity of phages in cryoconite holes appears mostly driven by available hosts within their local environment, but they also show some signs of long-range transport. In Antarctica’s McMurdo Dry Valleys, the diversity of the major capsid proteins of ssDNA viruses in cryoconite holes across three glaciers paralleled a well-characterized gradient of biomass and diversity of microbial communities within those same environments [116]. As in other poorly characterized polar habitats, their similarity to any other published phage genomes were low overall (< 59 % amino acid pairwise identity of major capsid proteins). However, some of the phage genomes were found in holes on glaciers tens of kms away from one another. In a study on cryoconite holes in Svalbard, the major capsid proteins of T4-like phages were clustered into ten distinct groups, some of which were also found in nearby marine environments, but others represented novel sets of distinct phages [166]. Previous work had shown that although the abundance of phages in cryoconite holes in Svalbard correlated with the abundance of bacteria, transplant experiments demonstrated that cryoconite phages could also infect hosts from nearby lakes [148]. And a 2020 study of phage pangenomes in cryoconite holes across glaciers in Svalbard, Greenland, and the Alps found that of 671 virus genome and genome fragments, 257 viruses (38 %) were present in two or more of those regions, and 50 were detected in all three [167].

5.5 Viruses from soil and peatlands

Northern peatlands underlain with permafrost are structurally diverse terrestrial ecosystems that are rapidly changing due to climate change. These ecosystems are a reservoir of mostly uncharacterized microorganisms and viruses that have been shown to remain active below the freezing point in soils with both catabolic and anabolic activities observed [168-170]. Activity is likely facilitated by a portion of the water remaining liquid at temperatures below 0 °C with evidence that more than 20 % of the water can remain unfrozen in peat soils incubated between

−1 and −5 °C [171]. The water is kept in an aqueous state by the high concentration of solutes, and in peatlands the solutes are derived from organic matter, e.g., humic acids [172,173]. The environmental conditions, such as low temperatures and plant polymers, shape microbial and viral community structure, often limiting diversity and abundance compared to warmer climates. The high organic matter interacts with viruses quite differently from mineral soils and can make virus separation, enumeration, and diversity estimates difficult [39,33,34]. The few viral counts in northern peatland soils have targeted double-stranded DNA phages and estimate VLPs to be on the order of 10^8 per gram of soil, but enumeration methods of viruses from soil matrices are highly variable, costly, and laborious.

Antarctic soils are colder and considerably drier than Arctic soils and are devoid of higher plants. Despite these differences, high spatial heterogeneity was found among dsDNA viral communities and pH was the most significant ecological driver of the dsDNA viral communities in the ice-free surface soils [174]. Notably, calcium content was also a significant ecological driver because calcium ions are related to several essential aspects of viral life, such as entry into host cells, genome replication, and building new viruses to invade other cells [175]. Hosts predicted for dsDNA viruses were largely similar to common virus hosts in Arctic soils — Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes. The main difference from Arctic soils is the decreased abundance of Acidobacteria, which are known to be sensitive to organic content and soil pH [176].

6. Ecology of polar phages

6.1 Strategies, interactions, and impact of polar phages in the environment

6.1.1 Predominant replication modes

For replication, phages are entirely dependent on the cellular processes within a host’s cells. Reproduction predominantly occurs by lytic or lysogenic infection [177-179]. Pseudolysogeny and chronic infections are also thought to be important, although so far less-studied replication pathways in polar phages to cope with the low energy, nutrients and host availability of these ecosystems [1]. Pseudolysogeny describes a phage infection strategy, where the phage nucleic acid passively resides within a host bacterium and is asymmetrically passed down onto a daughter cell upon cell division [180,181], while during chronic infections, progeny phage particles are continuously secreted into the environment without leading to cell disruption. A lytic infection ultimately leads to the host's death and release of new virus particles besides the cellular content. By exerting top-down control, lytic phages have the most immediate impact on biomass turnover and shaping microbial community structures. A prevalent lytic lifestyle was found in various polar environments such as freshwater [64,78] or marine habitats [182]. Contrarily, temperate phages undergo lysogenic infection, i.e., integration of the viral genome into the host's chromosome, and establish long-term relationships with their host bacteria that can be mutually beneficial [183]. During lysogenic infection, phages can have an impact on their host's metabolism by regulating their genes and may even confer AMGs that may ensure the survival of both hosts and viruses ([184,185], section 3.2). Moreover, lysogenic phages can provide their hosts with immunity against infection by other viruses [186]. In the bacterial cell, they remain latent in their hosts as prophages for a prolonged period until the lytic reproduction cycle is triggered.

The lytic cycle is thought to be favored in productive systems, while lysogeny is suggested to be the preferred mode for phage propagation during adverse environmental conditions, when nutrient resources for successful phage progeny production are scarce and access to suitable hosts is restricted [187,188]. The latter strategy is therefore assumed to be prevalent in polar environments, supported by a study of Angly et al. [112] finding more prophage-like sequences in the Arctic than in the other three investigated oceanic regions. As both, the Arctic and Antarctic are characterized by strong seasonal changes in nutrient, temperature, and light regimes [101], a switch from a predominantly lysogenic to lytic replication mode was observed in some studies, when seasonal changes supported rapid microbial growth and potentially higher availability of resources promote phage progeny production [189,96,190,155]. Accordingly, the highest VBRs were observed in Austral summer, reflecting higher burst sizes and higher rates of lytic infection compared to the winter season [105]. This trend was accompanied by a shift in phage particle size towards phages with bigger capsid sizes [30]. In winter, when host abundances were lower, a shift towards lysogenic infections and lower phage production was observed [105]. However, the environmental cues and mechanisms driving the lysis-lysogeny decision remain debatable and the trend is not always that clearly decipherable in a complex environmental matrix. A study in the Arctic pelagic investigating bacterial and phage dynamics over the course of a year found a contrasting event where phage-mediated lysis was more important during polar winter when productivity and host cell abundance was low [191]. The authors however argued that the reason could be either a predominant lytic cycle or a reduction of virus decay due to diminished UV exposure in the photic zone [191], as the increase in UV radiation and constant daylight during summer in polar regions may have a strong influence on virus decay rates [192-194].

6.1.2 Growth and survival of polar phages in the environment

Despite the extreme environmental conditions at the poles (section 1.1), polar ecosystems are characterized by high infection and phage production rates [149,157] that can reach similar ranges as in productive temperate habitats [155,29] and sediments worldwide [149].

Active and dynamic phage-host interactions driving the co-evolution of both became evident by studies elucidating sophisticated defense mechanisms against phage infection for example in Antarctic hypolith bacterial communities [195] or glacial ice surfaces [196] (section 6.1.3). While the frequency of visible infected cells is higher than in temperate aquatic regions, comparatively lower burst sizes, longer latency periods and generally lower VBRs [42,197,91,190,29] appear to be typical for polar environments. Generally, VBRs ranged from mean values as low as 0.10 up to 56.9 [28], reflecting dynamic virus-to-host interactions. While specialist phages can only infect a limited number of phylogenetically close hosts, phages capable of infecting hosts from different prokaryotic phyla are considered as generalists. Typically, being a generalist can be advantageous in habitats where the presence of suitable hosts may be more limited such as at the poles. With the limited number of studies, it is difficult to draw general conclusions. The overarching trend of studies of diverse habitats however such as Antarctic lake systems [198], Arctic soil peat [62], Arctic glaciers [148] and polar oceans [81] infer that polar phages tend to have broader host ranges regarding even higher phylogenetic levels with some exceptions [40].

6.1.3 Ecological consequences of phage infections for microbial evolution, community dynamics and biogeochemical cycles

As polar systems are characterized by truncated food webs with low predation pressure from metazoans, phages are thought to have an even higher influence on bacterial dynamics than in temperate regions [14,199,200,18]. More so, the strong link between phages and their hosts that is observed in a wide range of investigated polar habitats is thought to be a key driver of the remarkably high microbial diversity in polar regions [1]. Studies conducted in various polar environments showed a major influence of phages on bacterial dynamics and carbon cycling [190,152,28,18]. In sea ice, phages and bacteria are concentrated into the brine inclusions promoting intense phage-host interactions [201]. Host organisms can build resistance to phage infections via multiple mechanisms such as cell-surface modifications ([202,203]), while phages co-evolve along with their hosts to overcome the newly emerging barriers, increasing the phenotypic and genetic diversity and driving co-evolution of both (reviewed by Koskella, Brockhurst [204]). During viral infection, host genomes can integrate pieces of invading mobile genetic elements as spacer sequences in so-called clustered regularly interspaced short palindromic repeats (CRISPR) arrays that can be gradually expanded with each new infection event [205-208]. By doing so, the CRISPR-Cas system functions as a prokaryotic immune system by providing a historical record of previous phage infections and degrading the intruding phage genetic material [209,210]. CRISPR arrays can be used as a culture-independent tool to bioinformatically investigate phage-host interactions [211,60]. However, psychrophilic and psychrotolerant microorganisms tend to disfavor CRISPR defense systems [212], which is linked to potentially higher viral diversity in colder environments [31] and to the higher fitness costs associated with maintaining these mechanisms in these very energy-restricted environments [213]. This could make the CRISPR system less suitable to study phage-host interactions in polar environments. However, the investigation of CRISPR spacers in metagenomes elucidated an enormous variety of unique CRISPR spacers in *Flavobacteria* of Antarctic snow samples [214]. Insights from CRISPR spacer-protospacer matches revealed a dynamic and ongoing interaction between host and phages of Antarctic hypolith communities during periods where ice was melted [195] and showed a history of numerous viral attacks in the genomes of Arctic cyanobacterial *Nostoc* strains, underlining their importance for nitrogen cycles [215]. Overall, these findings underline the potential that metagenomic analysis of CRISPR spacer-protospacer matches may have for understanding phage-host interactions in polar environments.

As an important and active component of polar ecosystems, phages influence microbial population dynamics and processes [216,217]. The effect of phages on the microbial communities are spatially and temporally changing and vary in the different ecosystems [218,1,105]. Besides immediately influencing community compositions via viral lysis, phages can affect their host’s ecology due to the release of host cellular material into the environment that can be substrate for growth of other microbial populations. This shortcut in the food web that channels substrate and energy in the form of lysed organic material away from higher trophic levels back to heterotrophic prokaryotes is called "viral shunt" and represents an important contributor to diversity and rapid nutrient regeneration [149,219-221]. The concomitant release of organic matter provides nutrients to the severely nutrient-restricted polar ecosystems and supports ecosystem productivity as primary production is often limited by nitrogen and phosphorus limitation in the Arctic [222] as well as iron in the Southern Ocean [223]. For example, phage-mediated lysis of bacteria was estimated to contribute up to 69 % of carbon to the dissolved organic carbon pool [29]. Released nutrients via the viral shunt fuel surrounding organisms [149,219], again influencing microbial community structures. For instance, during a shift from spring to summer, a phage-induced reduction of Gammaproteobacteria abundances was observed with a simultaneous increase of Flavobacteria due to the released nutrients around the WAP [105].

6.2 Dispersal of viruses to and from the poles

Considering the geographical isolation of the Arctic and Antarctic continents and prevailing harsh conditions, microbial dispersal can be assumed to be overall highly restricted. However, several studies demonstrated the contrary with aeolian processes mediating microbial transport even on a global scale [224], which might however work selectively for certain phyla [225,224]. It follows that biogeography and dispersal of cold-adapted phages are further interesting aspects to investigate, e.g., to understand transmission of AMGs, microbial evolution and restructuring of microbial communities in the dispersal destination of the phage. Recent work found that culturable bacterial strains with identical 16S rRNA genes were found on both poles on Earth, but despite the early hypothesis that "everything is everywhere" [226,227] invoking a lack of dispersal limitation, no fully identical bacterial genomes were detected on both poles [228]. While such dispersal limitation for marine bacteria was confirmed by modeling [229], for viruses, it is long known that nearly identical viral genomes occur in different places of the world [82,230], suggesting that viruses are widely distributed, and/or genetic exchange happens between viruses from very different environments. One study reported on the bipolar distribution of several viral lineages implying connectivity of viral communities on a global scale [110]. While Antarctic and Arctic viromes were mainly dominated by different viral species, circular contigs of highly similar (>90 % sequence similarity) ssDNA viruses were found on both poles, suggesting that viruses, compared to bacteria [228], indeed have global dispersal capacity [110]. In agreement with that, similar phage genomes with identical single-nucleotide polymorphism and related to the bacterial host *Ralstonia* were recovered from Antarctic surface snow of three stations and a seawater sample from the WAP separated by >5,000 km [61]. Their distribution indicates that air-mediated dispersal works over long distances even under the extreme conditions present on the Antarctic continent and that dispersal is probably governed by westward drift mediated by the prevailing Southern Hemisphere westerly winds. Considering the smaller sizes of viruses and their likely longer atmospheric residence times [137] and given that small aerosols remain unsettled in air for longer (reviewed by Gralton et al. [231]), widespread or even pole-to-pole viral dispersal via the atmosphere could be more probable than for prokaryotic hosts, supporting the above presented findings. DNA and RNA viruses including phage sequences were additionally found in different Antarctic animal feces [232], with most viruses including phages being detected in feces originating from migratory birds, suggesting that birds could contribute to phage distribution. Anthropogenic dispersal of phages is another likely scenario, for instance because humans invade isolated ecosystems on icebreakers, research and transport vessels, aircrafts etc., increasing the chances for transferring microbes and viruses from lower latitudes to polar ecosystems. The risk of man-made species transmission is known [233] and has for instance led to severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) outbreaks in Antarctica [234], but comprehensive investigations about the effects on phage dispersal are missing to date. Since the study of phage dispersal across the Antarctic continent as a typical extraterrestrial analogue has important implications for space exploration, forward contamination, and planetary protection measures [61] and given the growing field of astrovirology (reviewed by Trubl et al. [235],de la Higuera, Lazaro [236]), more work in this direction can be expected in the future.

7. Major challenges, knowledge gaps and future perspectives in polar phage research

7.1 Major challenges in polar phage research

The advances of knowledge on microbes and viruses from polar ecosystems is comparatively slow, mainly due to limited accessibility of these ecosystems but also due to the low biomass (Figure 1). In addition, logistical challenges result from polar regions being remote and often difficult to access, with harsh environmental conditions and limited infrastructure. Transporting equipment, personnel, and samples to and from these regions can be difficult and costly, which can limit the frequency and duration of research expeditions. Moreover, the limited cultivation success of phages and their hosts leads to few available model organisms preventing to study polar phage-host interactions in more detail. Temperatures near the surface of the Earth will rise faster in the polar regions if greenhouse gas concentrations continue to rise over the next century. In turn, these changes will have serious implications for the cryosphere, oceanic and atmospheric circulations, marine and terrestrial environments, and indigenous people in the Arctic [237,238]. It is virtually certain that global mean sea level will continue to rise over the 21st century [237]. However, there is uncertainty about the extent to which ongoing environmental changes will affect viral and microbial communities, their genomic individualities, and their implications for biogeochemical cycles and the food web [239], e.g., a study by Boras et al. [182] showed that sea-ice melt has a strong influence on bacterial carbon fluxes towards the higher trophic levels. While ice melting is progressing, the amount and type of viruses that are released into the environment as well as the chance to be further infective ("the frozen zombies") are not yet fully understood [240-243]. Research on glacial ice has confirmed that phages can maintain their stability in meltwater on the surface of glaciers, suggesting that viruses that are released during melting, may continue to function as they are carried downstream [196]. On the other hand, it is conceivable that by shifting climate zones and the resulting migration of invasive species towards the thawing poles, new phages will be introduced to these environments (reviewed by Cowan et al. [244]) and could for example carry foreign AMGs or bypass defense mechanisms of native microorganisms. In doing so, invasive phages could have an impact on the flow of biomass and energy within these systems.

Finally, polar regions are ecologically sensitive and culturally significant areas, with unique indigenous communities and delicate ecosystems. While accessing and conducting research in these regions is strictly regulated by legally binding international regulations to conserve these ecosystems, the human footprint on polar environments is detectable and expected to increase [245-247]. Major threats include habitat damage [246], pollution (reviewed by Tin et al. [248]), the introduction of invasive species [249] and the spread of antibiotic resistant microorganisms [245-247] to name a few. Expanding research efforts for example in Antarctica [247] necessitate obtaining appropriate permits and adhering to the environmental regulations to minimize the impact of research activities. Furthermore, seeking a more efficient and reciprocal communication with policy makers, effective environmental impact assessments and a continuous development of environmental protection measures as joint effort to preserve this unique yet vulnerable habitat is crucial in the face of continuous expansion of human impact and climate change [250,251].

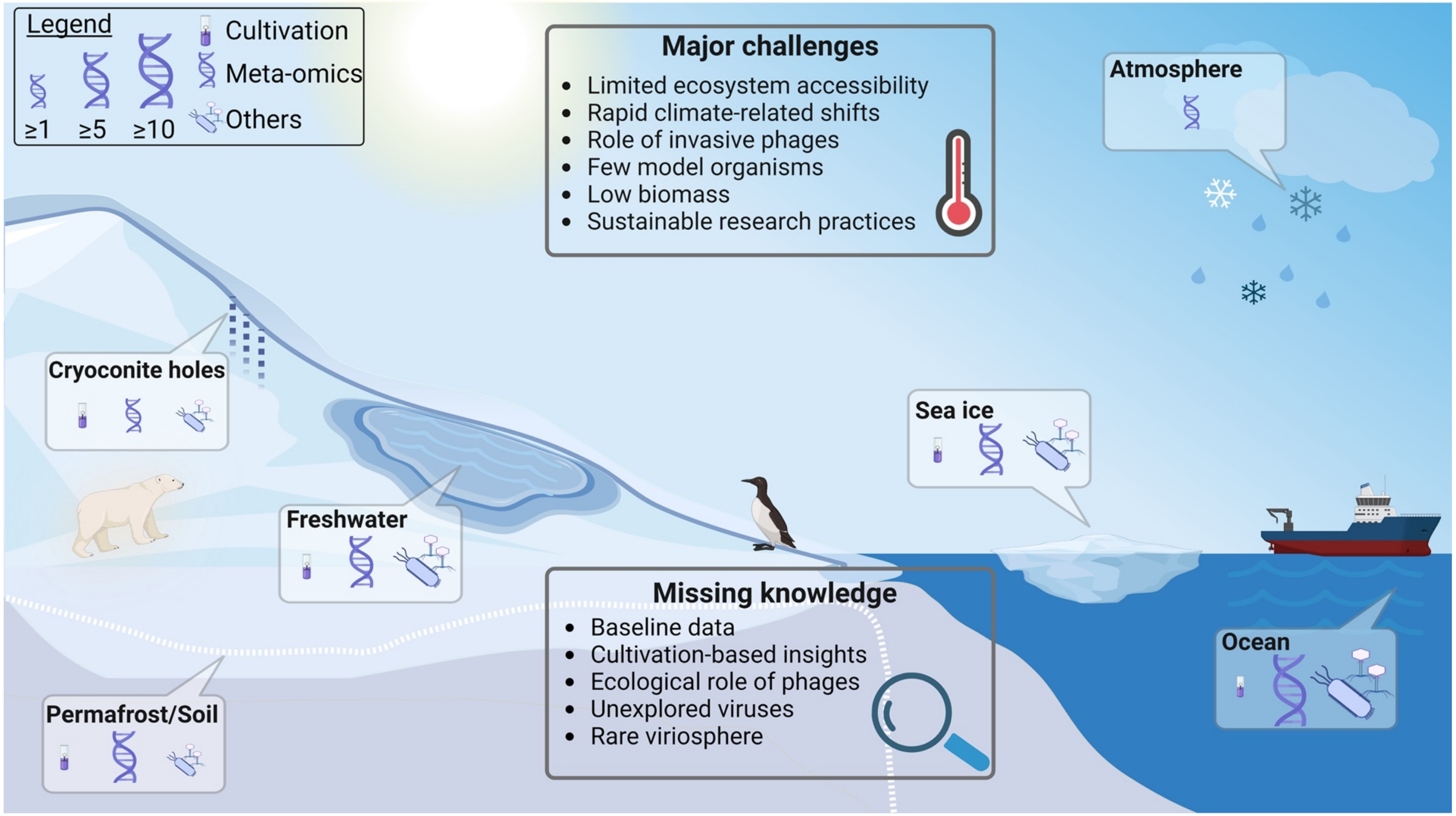

Figure 1: Summary figure on phage studies from six different polar ecosystems of the Arctic and Antarctic. Depicted are the ocean, freshwater, sea ice, cryoconite holes, soils/permafrost, and the atmosphere. Symbols represent studies involving polar phage isolates/cultivation (test tube), genomic analyses (DNA helix), and other studies (viral abundance, infection, and induced mortality). The symbols show the minimum number of studies published per ecosystem with three different size categories: small icon: ≥ 1 study, medium size: ≥ 5 studies, large size: ≥ 10 studies. Icon size was

based on combined findings from independent literature research conducted by two of the authors. Two boxes point out the major challenges and knowledge gaps in polar phage research as further addressed in section 7.1 and section 7.2, respectively. The penguin and polar bear represent the Antarctic and Arctic, respectively, and normally do not live together in the same environment.

7.2 Major knowledge gaps in polar phage research

While conducting literature research for this review, we identified several major knowledge gaps in polar phage research (Figure 1). Climate change and associated ecosystem loss is threatening the definition of the status quo, i.e., the generation of a baseline understanding of current phage abundance, diversity, and activity. This makes it also difficult to establish meaningful comparisons and interpret results. Long-term monitoring efforts and comprehensive baseline data collection are necessary to understand the dynamics of phage populations in polar regions. Today, there are several ocean time series data, collected from Arctic regions by the FRAM Observatory project [252], allowing us to describe the dynamics of prokaryotes over time regarding changing environmental conditions [253,254], but such monitoring projects are generally sparse for viruses, especially in polar regions. We also found that several ecosystems are particularly understudied regarding their viral content (Figure 1), with most insights being derived from aquatic ecosystems and least from the atmosphere.

Due to the many challenges mentioned in section 7.1 and Figure 1, interactions between phages and their host bacteria in polar regions are not well characterized. Understanding the dynamics of phage-host interactions in polar ecosystems, including the factors that influence phage infection rates, host resistance mechanisms, and the role of phages in shaping bacterial communities, is crucial to elucidate the ecological and evolutionary impacts of phages in these extreme environments. More comprehensive genomic studies, including viral metagenomics and comparative genomics, could provide valuable insights into the genetic makeup and functional potential of phages in polar regions. One major problem is the high number of unexplored viruses representing a vast reservoir of genetic information that remains largely unknown and poorly understood, e.g., due to missing reference genomes in public databases, which limits our understanding of viral diversity, ecology, and evolution. Besides missing insights from -omics, the lack of information comprehends capturing the extensive diversity of viruses that have not yet been identified, cultured, or characterized using traditional laboratory methods due to the many challenges associated with cultivation as mentioned above. Especially the rare virosphere, to which we count psychrophilic viruses, viruses of low abundance, viruses with novel genetic features and limited representatives in public databases, rare or endemic viral species need more attention by using state-of-the-art molecular tools, metagenomics, single-virus genomics, and other advanced techniques. Further research is needed to fully characterize and understand phages in polar regions and their ecological roles in these unique but extreme ecosystems.

7.3. Future perspectives

Our review shows that phage investigations from the Arctic and Antarctic are overall scarce. This includes regions, which are completely unexplored such as the Central Arctic Ocean and large parts of the Southern Ocean (not covered by the Tara Oceans Polar Circle expedition [15]) but also long-term monitoring could be improved. Recent expeditions such as the MOSAiC expedition between September 2019 and October 2020 as well as Synaptic Arctic Survey 2021 conducted sampling for (viral) metagenomics in the Central Arctic Ocean up to the North Pole [255,256] and will hopefully extend our knowledge about phages from these remote regions in the near future.

The Arctic region is warmer and more accessible compared to the Antarctic, and therefore easier to monitor and sample. Likewise, as global temperatures and the human population continue to rise, the Arctic will likely become prime land for mining, agriculture, and urban development [257,50]. These human influences will change the Arctic landscape further increasing permafrost thaw, altering native vegetation, and native microbial and viral community structures. Although disease outbreaks caused by viruses from thawing permafrost have not occurred yet, these viruses are detectable in permafrost [258], and there have been outbreaks from other human pathogens, e.g., anthrax [259]. There will likely be increased outbreaks of viral plant pathogens [260,261], as we introduce non-native plants, and these changes will extend to soil communities. There is already evidence of increased microbial and phage diversity with thaw [63,262,47,37], and virus-host dynamics will continue to change with global warming [263]. In polar regions, it was shown that the predominant life cycle of temperate phages switches to a more lytic one with increasing temperatures and more favorable environmental conditions (section 6.1). Global warming may extenuate the dominance of the lysogenic phage cycle towards the lytic mediated one, with consequences for the full ecosystem. In section 3.2, we summarized work describing AMGs being related to cryosurvival. If environmental conditions at the poles become more moderate with climate change, AMGs involved in cold adaptation could lose their function and be replaced. Warmer temperatures and increased precipitation frequency and volume could also influence phage dispersal and migration patterns, potentially resulting in shifts in phage distribution across polar ecosystems and enhanced dispersal to temperate regions. This could impact the overall phage community structure and function in these regions and around the globe. In addition, bacterial populations may shift with warming, leading to changes in the availability and composition of phage hosts. This could result in changes in phage diversity, host specificity, and infection dynamics, which may impact phage populations in polar regions.

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