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Invited Review

Biological albedo reduction on ice sheets, glaciers, and snowfields

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ABSTRACT

The global cryosphere, Earth's frozen water, is in precipitous decline. The ongoing and predicted impacts of cryosphere loss are diverse, ranging from disappearance of entire biomes to crises of water availability. Covering approximately one-fifth of the planet, mass loss from the terrestrial cryosphere is driven primarily by a warming atmosphere but reductions in albedo (the proportion of reflected light) also contribute by increasing absorption of solar radiation. In addition to dust and other abiotic impurities, biological communities substantially reduce albedo worldwide. In this review, we provide a global synthesis of biological albedo reduction (BAR) in terrestrial snow and ice ecosystems. We first focus on known drivers—algal blooms and cryoconite (granular sediment on the ice that includes both mineral and biological material)—as they account for much of the biological albedo variability in snow and ice habitats. We then consider an array of potential drivers of BAR whose impacts may be overlooked, such as arthropod deposition, resident organisms (e.g., dark-bodied glacier ice worms), and larger vertebrates, including humans, that transiently visit the cryosphere. We consider both primary (e.g., BAR due to the presence of pigmented algal cells) and indirect (e.g., nutrient addition from arthropod deposition) effects, as well as interactions among biological groups (e.g., birds feeding on ice worms). Collectively, we highlight that in many cases, overlooked drivers and interactions among factors have considerable potential to alter BAR, perhaps rivaling the direct effects of algal blooms and cryoconite. We conclude by highlighting knowledge gaps for the field with an emphasis on the underrepresentation of genomic tools, understudied areas (particularly high-elevation glaciers at tropical latitudes), and a dearth of temporal sampling in current efforts. We detail a global framework for long-term BAR monitoring that, if implemented, would yield a tremendous amount of insight for BAR and would be particularly valuable in light of the rapid ecological and physical changes occurring in the contemporary cryosphere.

1. Introduction

The global cryosphere—the compilation of Earth's frozen water—is in rapid, accelerating decline (IPCC, 2019). Covering approximately one-fifth of the Earth's surface at present, mass loss from the terrestrial cryosphere is driven primarily by a warming atmosphere (Fountain et al., 2012; Hock et al., 2019). Over the last 50 years, spring snow cover on land in the Arctic has declined by ~13% per decade and since 2006, observed contributions to global sea level rise from glaciers and ice sheets in Antarctica, Greenland, and elsewhere, have been 0.61, 0.77,

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and 0.43 mm yr^{-1}, respectively (IPCC, 2019). Beyond physical transformation of the Earth's surface, cryosphere loss impacts climate (Groisman et al., 1994; Hansen and Nazarenko, 2003; Hu and Feng, 2002), ecology (Hotaling et al., 2017b, 2017a), hydrology (Hanzer et al., 2018; Zemp et al., 2019), and society (Milner et al., 2017).

Among the harshest ecosystems on Earth, ice sheets, glaciers, and snowfields challenge biological communities with low temperatures and limited availability of water and nutrients (Dial et al., 2018; Ganey et al., 2017; Ren et al., 2019). Cryospheric habitats also swing from extreme cold and extended darkness in winter to warm temperatures and intense solar radiation in summer, with biological communities subjected to disruptive freeze-thaw cycles, flooding, and burial by snow (even during the melt season; Hodson et al., 2008; Takeuchi et al., 2006). Nevertheless, diverse communities inhabit perennial snow and ice surfaces (Anesio et al., 2017; Hotaling et al., 2017b), including a range of viruses and microorganisms (e.g., bacteria, archaea, algae, fungi, rotifers; reviewed by Kaczmarek et al., 2015), as well as larger taxa including ice worms (Hotaling et al., 2019a) and birds (Hardy et al., 2018).

Albedo plays a critical role in the Earth's energy balance by regulating how much solar radiation is reflected or absorbed. Fresh snow has a very high albedo—reflecting >90% of visible radiation (Skiles et al., 2018)—but during melt, snow grain size and water content increase, reducing albedo and furthering melt (Wiscombe and Warren, 1980). Both abiotic (e.g., dust) and biotic (e.g., algae) contaminants can also lower snow and ice albedo, accelerating melt (Skiles et al., 2018). Topography and other aspects of the physical environment can also affect albedo, including slope, aspect, and the presence of crevasses, and/or supraglacial water (Lin et al., 2014; Ryan et al., 2018; Skiles et al., 2018; Zhang et al., 2018). Thus, albedo plays a central role in cryosphere energy balance and maintenance.

The darkening effects of particles, including dust, black carbon, algal blooms, and cryoconite, on the cryosphere can be substantial (Cook et al., 2020b; Kaspari et al., 2015; Musilova et al., 2016; Onuma et al., 2020; Painter et al., 2001, 2007; Perini et al., 2019; Takeuchi et al., 2001; Takeuchi, 2002; Takeuchi et al., 2018; Williamson et al., 2020; Yallop et al., 2012). For instance, even small amounts (~10–100 ppb) of black carbon (abiotic particles produced during hydrocarbon combustion) can decrease albedo by 1–5% (Grenfell and Light, 2002; Hadley and Kirchstetter, 2012). However, when compared to abiotic factors, the effects of biological albedo reduction (BAR)—the collective influence of biological communities on albedo—have received less attention. Before discussing the known and potential biological factors impacting albedo, we should clarify our use of BAR to define the process rather than "bio-albedo" which has been used previously (e.g., Di Mauro et al., 2020; Onuma et al., 2020). Cook et al. (2020a) argue that bio-albedo is technically incorrect from a remote sensing perspective as biological growth enhances light absorption and thus, a more correct term would be "bio-co-albedo." However, given the interdisciplinary nature of the field and the potential for confusion around the term "co-albedo", Cook et al. (2020a) recommended the field refer to these collective effects as biological albedo reduction (shortened here to BAR; Cook et al., 2020a). We echo this recommendation.

Blooms of snow and ice algae are likely the most substantial global contributor to BAR (Lutz et al., 2016b; Segawa et al., 2018a, 2018b). During the melt season, algae can dominate surfaces in the terrestrial cryosphere and dramatically reduce albedo (Cook et al., 2017b, 2017a, 2020b; Ganey et al., 2017; Lutz et al., 2016b; Ryan et al., 2018; Stibal et al., 2012, 2017; Williamson et al., 2020; Yallop et al., 2012). For instance, over a single summer, red snow algae decreased albedo in the Arctic by as much as 13% (Lutz et al., 2016b). Similarly, over 700 km^2 of an Alaskan icefield, snow algae increased melt by as much as ~21% (Ganey et al., 2017). And, on the bare ice zone of the southwestern

another global driver of BAR (Baccolo et al., 2017). Beyond algae and cryoconite, a variety of other biological factors that have received little to no attention from a BAR perspective should be considered. These range from the direct effects of dark-bodied glacier residents (e.g., ice worms) to the indirect effects of nutrients being added by, for example, passive deposition of arthropods and plant material onto snow and ice.

In this review, we consider BAR in the terrestrial cryosphere for both known (e.g., algae, cryoconite) and potential (e.g., invertebrates) drivers (Figs. 1–2). Our overarching goal is to offer a holistic perspective of BAR in the terrestrial cryosphere by considering all of its potential sources—however large or small—and going beyond direct effects (e.g., a pigmented algal cell lowering albedo *in situ*) to also consider how biological interactions may indirectly alter BAR (with an emphasis on nutrient cycling). We recognize that on a global scale, the BAR influence for the drivers we highlight varies widely, from well-known, large-scale influencers (e.g., snow and ice algal blooms) to those potentially having negligible effects (e.g., vertebrate travel on snow and ice). Our goal is not to provide a ranking of BAR impacts but rather to encourage future research by highlighting the wide potential for BAR effects. We focus on three major habitats—ice sheets, glaciers, and snowfields—but our conclusions generally apply to related habitats (e.g., seasonal snow, sea ice). Within the interdisciplinary scope of BAR research which includes biology, remote sensing, and, ultimately, physical modeling of the cryosphere and its future, we specifically focus on the biological component. We begin by synthesizing current knowledge of the known drivers of BAR: snow algae, ice algae, and cryoconite. Next, we highlight potential drivers, ranging from *in situ* viruses to vertebrate activity and assess the potential for population, community, and ecosystem-level interactions among factors to alter BAR in space and time. We then consider how the effects of climate change—from rising temperatures to altered nutrient dynamics and physical habitat change—may affect BAR. We conclude by highlighting knowledge gaps for the field and detail a framework for a long-term, global monitoring network to improve our collective knowledge of BAR.

2. Known drivers of BAR

Albedo change is a key parameter affecting glacier melt (Box et al., 2012) with various impurities—both biotic and abiotic—affecting albedo across wavelengths (Fig. 3).

With glacial ice covering ~10% of Earth's surface and permanent and seasonal snow covering up to 35% (Hell et al., 2013), clear potential exists for snow and ice algae to alter global albedo (Lutz et al., 2016b; Segawa et al., 2018a). Because the basic natural history, ecology, and physiology of snow and ice algae have been recently reviewed (Hoham and Remias, 2020; Williamson et al., 2019), here we summarize only key details in the context of BAR. We do the same for the other known BAR contributor, cryoconite, which has also been reviewed elsewhere (Cook et al., 2016).

2.1. Snow and ice algae

Before summarizing the role of algae in BAR, we need to again consider terminology. The term glacier algae has been proposed (e.g., Williamson et al., 2019) to differentiate algae living on terrestrial ice from algae living on sea ice (Boetius et al., 2015) and algae living on snow (Hoham and Remias, 2020). Glacier algae, however, has also been used as a collective term to refer to all algae living in glacier environments (ice and snow algae, Dial et al., 2018). Thus, a lack of clarity exists about whether "glacier algae" refers to all algae in a glacier environment or more specifically, to only algae living on glacial ice. This distinction is important because in the terrestrial realm, algae occupy both snow and portion of the Greenland ice sheet, ice algae can account for 75% of albedo variability (Cook et al., 2020b; Williamson et al., 2020). Algae, however, are not the only biological factor that alter albedo. Cryoconite, sediment-based mixtures of biotic communities and minerals, are

ice, with overlapping distributions, yet each habitat selects for distinct taxa: mainly Chlorophyceae on snow, particularly the "red" or "watermelon snow" producing genera *Chlamydomonas*, *Chloromonas* and *Sanguina* (Procházková et al., 2019; Remias et al., 2013, 2005), and

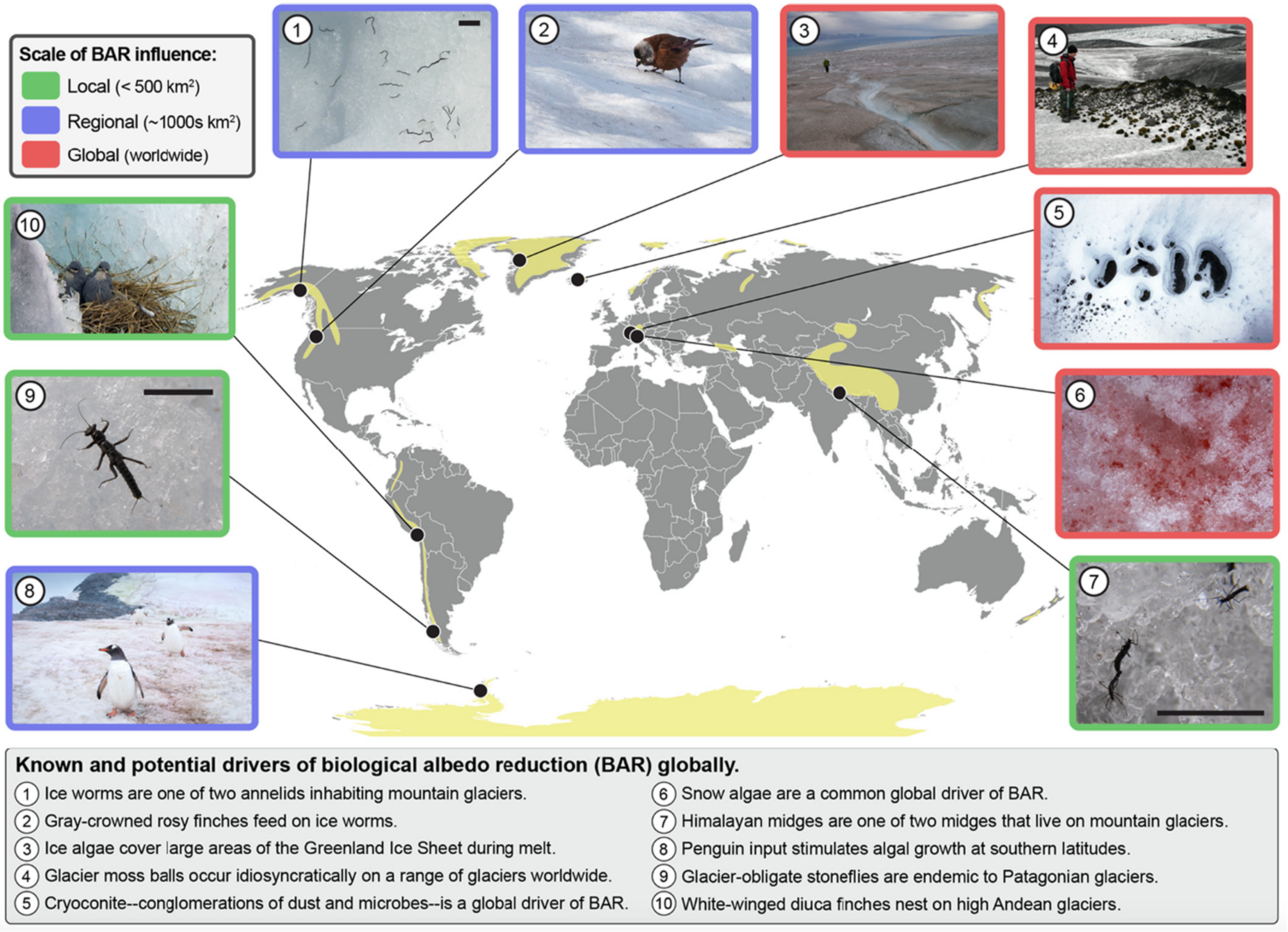


Fig. 1. Examples of known and potential drivers of biological albedo reduction (BAR) on ice sheets, glaciers, and snowfields around the world. While all albedo reduction is local in nature, the approximate geographic scale of influence for each driver—the total, non-contiguous area over which they could occur—is given as local, regional, or global. For instance, (1) North American ice worms only occur on coastal glaciers of western North America, thus their BAR influence is regional however (3) ice algae occur on glaciers and ice sheets worldwide and are a global BAR influence. The global distribution of glaciers and ice sheets is shown in yellow [outlines approximated from the Randolph Glacier Inventory (Pfeffer et al., 2014) and the well-established near complete coverage of Antarctica by ice]. The black scale bar for invertebrate images represents 1 cm. All other images are >10 cm in scale. Photo credits: (1) © Rachael Mallon, (2) © Scott Hotaling, (3) © Nozomu Takeuchi, (4) © Nicholas Midgley, (5) © Jürg Alean, (6) © Serge Ouachée/Wikimedia Commons, (7) © Shiro Koshima, (8) © Acacia Johnson, (9) © Shiro Koshima, (10) © BBC NHU. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Zygnematophyceae on ice (Remias et al., 2012, 2009). Snow and ice algae on glaciers also vary in their life-histories, surfacing strategies following winter snow accumulation, and pigmentation biochemistry (Hoham and Remias, 2020; Williamson et al., 2019). We consider it more useful to reserve glacier algae as a collective term for all algae living in glacier ecosystems, thereby differentiating these algae from those living on sea ice. In line with this recommendation, we use more specific terms to further delineate glacier algae into its two components—"snow algae" for algae living in snow (Chlorophyta) and "ice algae" for algae living in ice (Streptophyta). When needed for added clarity, "glacier" can precede either term (e.g., glacier ice algae versus sea ice algae).

Snow and ice algae pigments vary in color and reduce albedo by as much as 48% and 56%, respectively, when compared to a 'clean' surface (Table 1). Red snow algae produce astaxanthin (Remias et al., 2005), an intracellular carotenoid that colors their cells, and the snow they inhabit, red. Astaxanthin likely protects the algae's photosynthetic apparatus from damage under high UV conditions (Remias et al., 2005). red and purple pigments (astaxanthin and purpurogallin, respectively) are correlated with the largest increase in melt (Dial et al., 2018). Seasonal timing and geographic location likely control algal cell number due to the availability of water and nutrients, as evidenced by a positive correlation between algal abundance and debris (Stibal et al., 2015), an increase in algal abundance near snow-ice transitions where water is more abundant (Takeuchi et al., 2006), and decreasing algal biomass with increasing altitude (Takeuchi and Kohshima, 2004; Tanaka et al., 2016; Yoshimura et al., 1997). Increases in snow and ice algae abundance have been experimentally linked to accelerated melt (Dial et al., 2018; Ganey et al., 2017; see Box 1). For ice algae, each doubling of the population has been linked to a ~ 4% decline in albedo (Stibal et al., 2017).

Algal abundance and its BAR changes during the melt season due to growth and accumulation/removal of cells (Onuma et al., 2020; Takeuchi, 2013). For snow algae, motile cysts are typically situated below seasonal snow in older layers of hard-packed firn (the metamorphic stage between snow and glacial ice; Box 1) and resurface during melt

Ice algae produce the phenol purpurogallin, a pigment that imparts purple-gray coloring to their cells and surrounding ice surfaces (Remias et al., 2011). For both snow and ice algae, the absorption spectra of their

(Dial et al., 2018; Hoham and Duval, 2001; Hoham and Remias, 2020). The increase in astaxanthin (red color) in snow algae occurs during blooms and is concurrent with limited bioavailability of nitrogen (N;

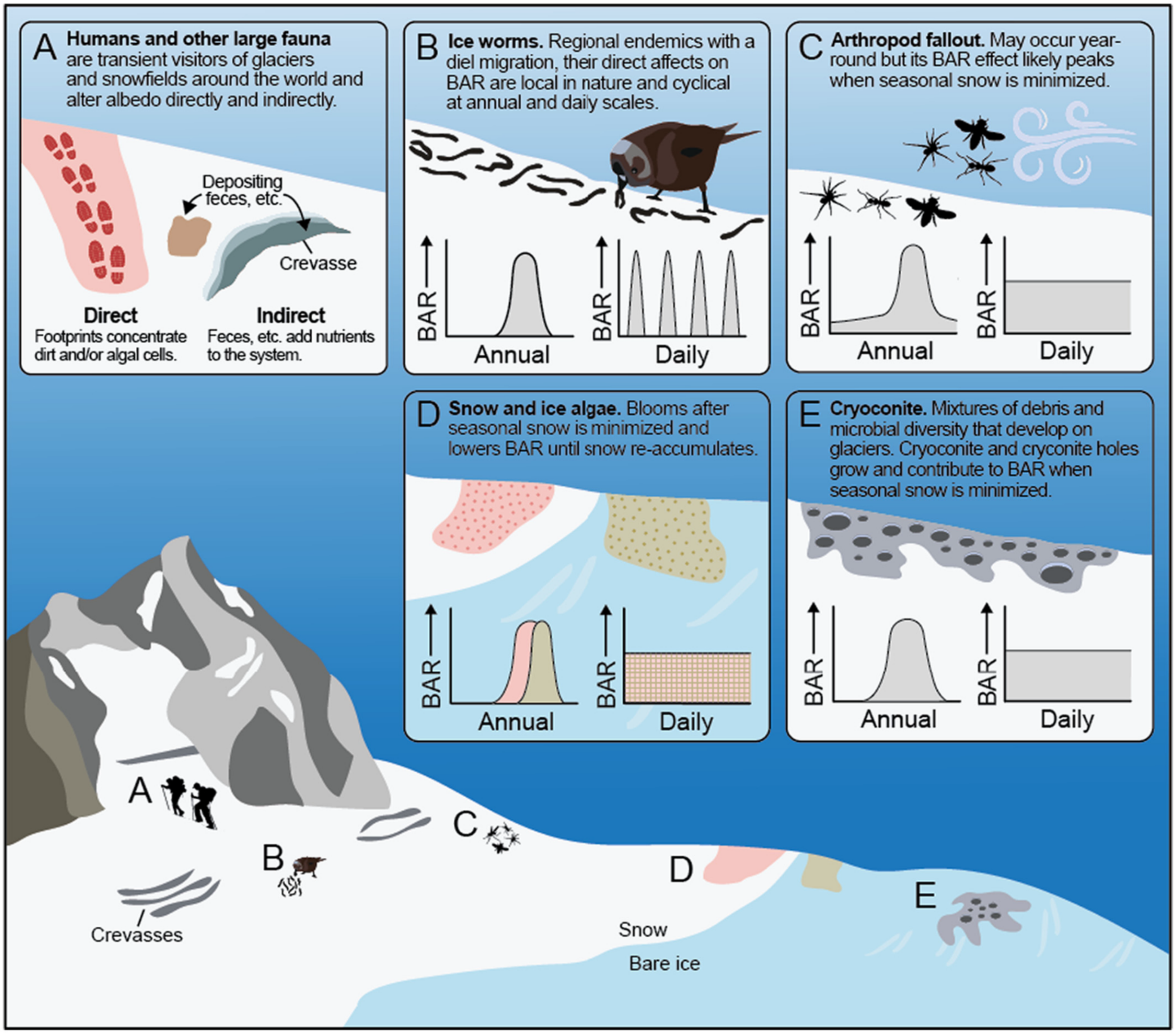


Fig. 2. Examples of biological albedo reduction (BAR) on a typical temperate glacier with theoretical plots of each factor's BAR influence on annual and daily timescales where applicable. (A) Humans and other large fauna (e.g., reindeer, birds) contribute to BAR transiently through direct impacts on the snow or ice surface and indirect additions of nutrients, often via feces. (B) Ice worms are regional endemics with diel migrations that attract foraging birds in North America. (C) Arthropods are commonly deposited on glaciers and snowfields by wind, both in regular small amounts (arthropod fallout) and in larger, mass depositions ("bug on snow" events). With limited capacity for survival, the direct effect of arthropods on BAR is constant until they are covered by new snow, consumed by a forager, or decompose. (D) Snow (pink) and ice (tan) algae also contribute to BAR, primarily during the melt season, with snow algal growth on wet snowpack peaking earlier in the season than ice algal growth on bare ice following snow clearance. (E) Cryoconite and cryoconite holes develop on ice sheets and glaciers and their BAR influence peaks when seasonal snow is cleared. Since albedo cannot be calculated at night, inset plots (B-E) only represent daylight hours. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Leya et al., 2009). Snow algae abundance tends to increase as the melt season progresses. For instance, on snowfields in northwestern Greenland, the abundance of snow algae increased from none in spring to 4.9 × 10^4 cells mL^{-1} in August (Onuma et al., 2020). When water and sunlight are no longer available due to new snow deposition, snow algae transition to dormant cysts that germinate the following spring (Remias, 2012). If snowpack is thin (e.g., on ice sheets) or melts quickly, ice algae persist for more of the melt season than snow algae. Ice algae pigment (purpurogallin) also absorbs across a broad range of wavelengths

impact of ice algae likely outweighs snow algae.

Pigment production in snow and ice algae may be under natural selection to convert solar radiation to heat (Dial et al., 2018). Heat gain through absorption of visible light allows algae to access nutrients bound within ice crystals while also producing meltwater for growth and reproduction. On the Greenland ice sheet, ice algae direct up to 65% of incident energy to surface melting compared to ~2.5% or less to photochemistry (Williamson et al., 2020). Thus, natural selection appears to favor albedo-reducing pigmentation that strikes a balance be-including UV and visible light, likely resulting in greater instantaneous albedo reduction versus snow algae (Remias et al., 2012, 2011, 2009). Thus, while both snow and ice algae decrease albedo, the net BAR

tween melt-inducing coloration and all-absorbing black that would overheat cells and disrupt their function (Dial et al., 2018). Because snow and ice algae generate meltwater, a positive feedback loop

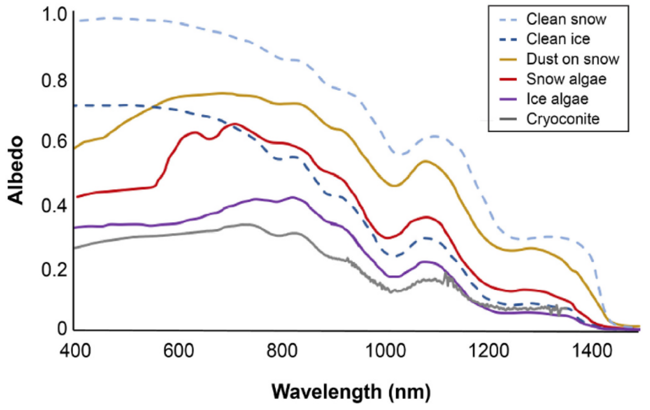


Fig. 3. Example spectral albedo profiles (400–1500 nm) for snow and ice with a variety of common cryosphere contaminants. Change in spectral shape is a useful indicator of the dominant absorber at the surface. For example, the characteristic 680 nm chlorophyll absorption feature visible in the snow algae spectra clearly differentiates it as biotic relative to abiotic dust. It also indicates snow conditions, where lower near infrared albedo indicates larger grained (older) snow and ice. Cold, dry snow is not habitable to algae, so both visible and near infrared albedo are lower when algae are present. Although these are single characteristic curves, intended as a demonstration of the variability of snow and ice albedo with abiotic and biotic darkening, the absolute magnitude of change depends on the concentration and distribution of particles across the surface as well as the age of the snow and ice surfaces. Spectra re-plotted from Aoki et al. (2003); Cook et al. (2017a); Painter et al. (2001); Skiles and Painter (2017).

between them and the ice features they inhabit may be critical to cryosphere decline (Anesio et al., 2017; Ganey et al., 2017; Hotaling et al., 2017b; Khan et al., 2020; Stibal et al., 2012; Takeuchi, 2009). However, snow and ice algae contribution to BAR is highly variable. For instance, snow algae abundance was negatively correlated with snow albedo on California snowfields but algal blooms did not meaningfully decrease albedo at the snowfield-scale due to its concentration in localized patches (Thomas and Duval, 1995). Conversely, across the southwestern Greenland ice sheet, ice algae may account for up to 75% of albedo variability (Williamson et al., 2020).

2.2. Cryoconite

Cryoconite is a granular sediment found on the surface of glaciers that typically includes biological material (Cook et al., 2016; Fountain et al., 2008). Cryoconite forms when sediment particles accumulate on an icy surface and it provides a substrate for microbial growth (organic phase; Figs. 1, 2E). The dark coloration of cryoconite stems from humic substances: residual, highly polymerized compounds remaining after bacterial decomposition of organic matter (Takeuchi, 2002). The most common primary producers associated with cryoconite are filamentous cyanobacteria (Chrismas et al., 2018, 2015; Segawa et al., 2017) which fix nitrogen (N) and provide key nutrients to other cryoconite microbiota (Telling et al., 2012, 2011). Many cyanobacteria also produce extracellular polymeric substances (EPS) that serve as a cryo- and/or UV-protectant (Tamaru et al., 2005) and an adhesive—binding particles together and facilitating biofilm formation. EPS can also be key carbon (C) source for heterotrophs (Stibal et al., 2012). Cryoconite can be abundant—exceeding 200 g/m^{-2} in dry weight—and on some glaciers, filamentous, cryoconite-associated cyanobacteria form granular mats that cover the entire ice surface (Segawa and Takeuchi, 2010). Cryoconite is a particularly strong driver of BAR on low-latitude glaciers (e.g., in Central Asia; Takeuchi et al., 2018) accelerating the local melt by formed by the acute, localized albedo reduction of the cryoconite (Figs. 1, 2E). Cryoconite holes are typically water-filled, sediment-rich, and are host to diverse assemblages of microorganisms, fungi, viruses, and invertebrates (Anesio et al., 2007; Bellas et al., 2020, 2013; Cameron et al., 2012; Cook et al., 2016; Edwards et al., 2013; Hodson et al., 2010; Lutz et al., 2019; Segawa et al., 2017; Takeuchi et al., 2001). Organic matter accumulation (leading to cryoconite hole formation) can reduce surface reflectivity from ~16% to ~31% (Musilova et al., 2016). When present, cryoconite and cryoconite holes can be rare (covering less than 1% of the surface on the Greenland ice sheet, Ryan et al., 2018) or common, covering as much 10% of a glacier's ablation zone (Anesio et al., 2009; Anesio and Laybourn-Parry, 2012; Hodson et al., 2008, 2007). In contrast to dispersed cryoconite, cryoconite holes likely have minimal effects on albedo as they are typically narrow and vertical, and thus only receive direct radiation for short periods of time (Bøggild et al., 2010). However, warm weather can collapse cryoconite holes by melting the ice surface faster than the solar-heated cryoconite can deepen the hole, thereby re-dispersing cryoconite onto the ice surface where its BAR contribution increases (Takeuchi et al., 2018).

3. Potential drivers of BAR

To date, the global study of BAR in the cryosphere has focused almost exclusively on the effects of algae and cryoconite. A focus on these drivers is reasonable given their global distribution and the near certainty that they are the dominant forces driving BAR in snow and ice ecosystems. However, the same ecosystems host many other organisms, from fungi and other microeukaryotes to invertebrates (Hotaling et al., 2017a, 2017b; Kohshima, 1984; Perini et al., 2019), often in large numbers. For instance, the darkly pigmented glacier ice worm (~2 cm long, 3 mg wet weight) can reach densities of 10–10^3 m^2 on North American glaciers (Fig. 2B; Hotaling et al., 2019a; Mann et al., 1980; Shain et al., 2001). Dozens of vertebrates, including humans, also use glaciers and perennial snow (Rosvold, 2015). Thus, non-algal biodiversity has the potential to affect BAR directly through the presence of organisms and their byproducts (e.g., fecal waste, Fig. 2A) or indirectly via nutrient inputs and interactions among organisms. In this section, we highlight the myriad of potential drivers of BAR on ice sheets, glaciers, and snowfields.

3.1. Surface microbes

Snow and ice algae co-occur with heterotrophic communities of viruses, bacteria, fungi, and other microeukaryotes (Anesio et al., 2009, 2007; Anesio and Laybourn-Parry, 2012; Hamilton and Havig, 2017; Krug et al., 2020; Lutz et al., 2015, 2016a; Perini et al., 2019; Stibal et al., 2020). In terms of abundance, the photic zone of glaciers may contain 10^{21}–10^{26} cells of bacteria and archaea (Irvine-Fynn et al., 2012; Irvine-Fynn and Edwards, 2014). Similar to algae, other microbiota also synthesize pigments for photosynthesis, to protect from UV damage, or absorb radiant energy and regulate temperature, and thus their BAR effects should be considered. For instance, on King George Island, Antarctica, phototrophic cyanobacteria can account for ~40% of the chlorophyll-a containing organisms (Tamaru et al., 2005). In addition, *Hymenobacter*, a common bacterium in ice and snow, makes at least four carotenoids that absorb light in the 475–500 nm region (Dial et al., 2018). Common cold-adapted fungi also include melanized filamentous species (Cordero et al., 2018; Perini et al., 2019) that are typically dark brown or black in color (Culka et al., 2017) and their contribution to BAR is likely similar to the humic substances in cryoconite. Fungal biomass can reach 10^4–10^5 colony forming units per 100 mL on snow and ice surfaces (de Menezes et al., 2019; Hamilton and Havig, 2017), an abundance similar to the upper limit of 1.8 × 10^5 algal cells mL^{-1}

g., in Central Asia; Takeuchi et al., 2018) accelerating the local melt by as much as 300% (Kohshima et al., 1992; Takeuchi et al., 2018).

When cryoconite is abundant, it can cluster and develop into cryoconite holes—depressions of varying depths and diameters—that are

abundance similar to the upper limit of 1.8 × 10 algal cells mL observed on the Greenland ice sheet (Perini et al., 2019).

The main contribution of non-algal surface microbiota to BAR, however, is likely through interactions with algae via nutrient

Table 1

An overview of biological albedo reduction (BAR) studies in the terrestrial cryosphere including region, methodology, habitat or organism with albedo values (if reported), and measured impact. While most studies focus on habitats that host organisms known to contribute to BAR, the measured albedo reduction or melt generation may include the effects of abiotic factors. Disentangling the effects of biotic and abiotic factors in albedo reduction remains a major challenge for the field.

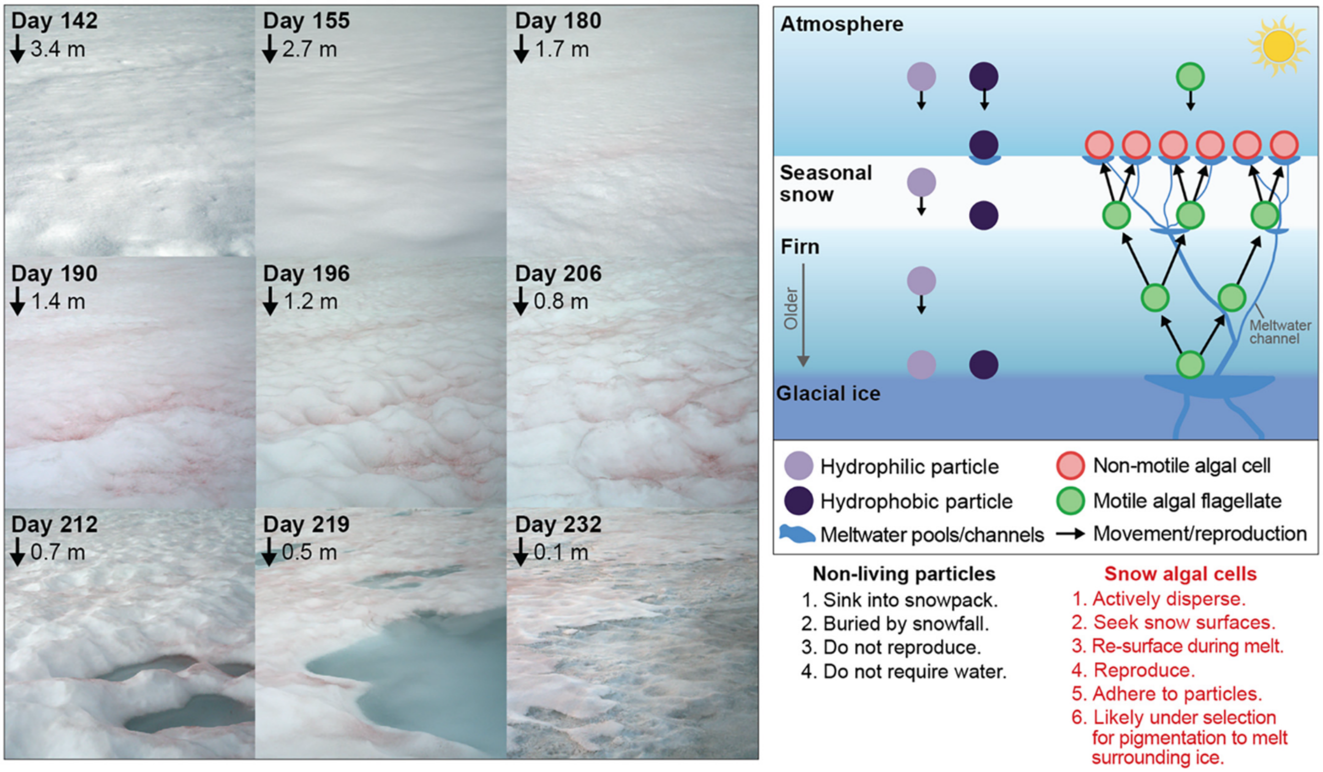
Region	Methodology	Habitat/organism: Mean albedo values (± SD where available)	Measured impact: Albedo reduction or melt generation	Study
Antarctica	Ground-based surface albedo (Analytical Spectral Devices FieldSpec® 4 hyperspectral spectroradiometer, spectral range: 350–2500 nm)	Clean snow: 0.85 ± 0.043 Red snow: 0.65 ± 0.09 Green snow: 0.44 ± 0.12	Mean albedo reduction from clean snow to: Red snow: ~24% Green snow: ~48%	Khan et al., 2020
Arctic (Svalbard, Northern Sweden, Greenland, Iceland)	Ground-based surface albedo (SolarLight, PMA2100 radiometer, spectral range: 400–700 nm)	Clean snow: 0.90 ± 0.05 Red snow: 0.50–0.75	Between ~17 and 44% reduction from clean snow to red snow ~13% reduction over one melt season	Lutz et al., 2016b
Alaska, USA	Ground-based surface albedo (Analytical Spectral Devices, FieldSpec® Pro VNIR spectrometer, spectral range: 350–1050 nm.)	Clean bare ice (cryoconite <5 g m^{-2}): 0.45 ± 0.07 Cryoconite-bearing ice: 0.32 ± 0.21	Mean albedo reduction from clean bare ice to cryoconite-bearing ice: ~29% reduction	Takeuchi, 2009
Alaska, USA	Ground-based surface albedo (cable suspended pyrometer; Kipp and Zonen Model 6B, spectral range: 0.3–2.8 mm)	Snow-buried shrubs: 0.85 Exposed shrubs: 0.60	Transition from shrub-free tundra to shrubland could produce a 69 to 75% increase in absorbed solar radiation during the snow-cover period	Sturm et al., 2005
California, USA	Ground-based surface albedo (broad band LiCor quantum sensor (Model: "Quantum", spectral range: 400–700 nm)	Clean snow: 0.58 ± 0.08 Red snow: 0.46 ± 0.11	Mean reduction of ~21% from clean to red snow	Thomas and Duval, 1995
European Alps	Ground-based surface albedo (Hand Held Analytical Spectral Devices Field Spectrometer, spectral range: 325–1075 nm)	Ice algae: 0.13–0.46 at 680 nm	Up to 72% reduction in reflectance at 680 nm* for ice hosting between 0.2 × 10^5 to 2.9 × 10^5 cells/mL	Di Mauro et al., 2020
Greenland (outlet glacier)	Ground-based surface albedo SolarLight, PMA2100 radiometer, spectral range: 400–700 nm)	Clean snow: 0.75 ± 0.05 Red snow: 0.49 ± 0.08 Green snow: 0.44 ± 0.04 Clean ice: 0.58 ± 0.08 Gray ice: 0.35 ± 0.01 Cryoconite holes: 0.23 ± 0.15	Mean reduction from clean snow to: Red snow: ~35% Green snow: ~41% Mean reduction from clean ice to: Gray ice: ~40% Cryoconite holes: ~60%	Lutz et al., 2014
Greenland Ice Sheet	Ground-based surface albedo (two opposed Apogee SP-110 pyranometers, spectral range: 300–1100 nm)	Clean ice: 0.59 ± 0.01 Cryoconite: 0.35 ± 0.01 Gray ice: 0.26 ± 0.01	Mean reduction from clean ice to: Cryoconite: ~41% Gray ice: ~56%	Yallop et al., 2012
Greenland Ice Sheet	Laboratory-based nutrient additions, surface reflectivity	Early stage cryoconite: 0.31 After carbon accumulation: 0.16	~48% reduction	Musilova et al., 2016
Greenland Ice Sheet	Ground-based surface albedo (Analytical Spectral Devices, FieldSpec® 2 with hemispheric cosine receptor, spectral range: 350–2500 nm)	Ice surface after winter snowpack ablation: decrease from 0.50 to 0.42 in 35 days	~3.8% albedo reduction per algal population doubling	Stibal et al., 2012
Greenland Ice Sheet	Field spectroscopy (Analytical Spectral Devices, FieldSpec® Pro 3 spectroradiometer with ASD cosine collector, spectral range: 350–2500 nm), radiative transfer model, UAV, satellite remote sensing, runoff modelling	Ice algae	Additional 8.8–12.2 Gt of runoff from the western Greenland ice sheet in 2016 (9–13% of total runoff)	Cook et al., 2020b
Greenland Ice Sheet	Field incubations, quantification of phytophysiological mechanisms	Ice algae	~1.86 cm water equivalent surface melt per day in patches of high algal abundance	Williamson et al., 2020
Himalaya	Ground-based surface albedo (Pyranometers)	Cryoconite: 0.09	~30% reduction	Takeuchi et al., 2001
Iceland	Ground-based surface albedo (SolarLight, PMA2100 radiometer, spectral range: 400–700 nm)	Clean snow: 0.76 ± 0.08 Red snow: 0.56 ± 0.14	Mean reduction from clean to red snow: ~26%	Lutz et al., 2015

* Albedo reduction calculated from data in the manuscript.

acquisition and cycling (Krug et al., 2020). Snow and ice algae are water-limited and potentially nutrient-limited (Anesio et al., 2017; Ganey et al., 2017; Hamilton and Havig, 2017, 2020; Lutz et al., 2015; Takeuchi et al., 2006). Algae and other psychrophilic microorganisms are also known to interact in their use of several limiting resources [e.g., C, iron (Fe), and N (Anesio et al., 2017; Harrold et al., 2018; Havig and Hamilton, 2019; Hodson et al., 2008; Phillips-Lander et al., 2020; Stibal et al., 2009; Telling et al., 2012, 2011)]. Therefore, bacteria and fungi may increase ecosystem carrying capacity, and thus the abundance of algae and algal BAR, through the liberation of phosphorus (P) and Fe

Experimental evidence supports this hypothesis; bacteria enhance the growth rate and abundance of snow algae in the presence of Fe-bearing minerals (Harrold et al., 2018; Lutz et al., 2015; Phillips-Lander et al., 2020). Viruses have not been directly linked to BAR but they may play an indirect role by regulating bacterial mortality, thereby influencing levels of dissolved organic matter (Anesio et al., 2007; Bellas et al., 2013). Thus, as in other ecosystems (Weinbauer, 2004), viruses likely impact biogeochemical cycles in snow and ice, thereby affecting the growth and abundance of organisms that propagate BAR (e.g., snow and ice algae).

(and other micronutrients) from rock flour and surface debris, while producing labile organic C that is readily consumed by heterotrophs through photosynthesis (Kellerman et al., 2020; Musilova et al., 2016).



Left panel. Seasonal progression of snow algae on Alaska's Eklutna Glacier illustrates a positive feedback in snowmelt. From the first appearance of red snow on day 180, snow with algae melts more than snow without, creating melt pools. Upper left numbers: Day of year. Numbers to the right of arrows: depth (in meters) to the permanent firn surface.

Right panel. Even in an ecosystem of snow and ice, organisms still require liquid water for survival and reproduction. Thus natural selection in snow and ice algae has led to adaptations to promote melt and acquire nutrients bound within ice crystals. By absorbing overabundant solar radiation on the surface of the cryosphere, organisms that drive BAR differ from abiotic light absorbing particles in key ways. Living cells reproduce, sometimes exponentially, as during an algal bloom. Living organisms also actively remain surficial, even returning to the surface after burial beneath snowfall. In contrast, abiotic particles neither actively resurface nor reproduce. Moreover, because abiotic particles offer islands of resources to life and harbor nutrients bound to their surfaces, as well as absorbing light—photosynthetic organisms like algae and cyanobacteria bind abiotic and organic particles, creating habitat for other microbiota.

Box 1. Snow algae progression, movement, and comparison to non-living (abiotic) particles that reduce albedo. Photo credits: © G.Q. Ganey.

3.2. *Invertebrates*

A variety of invertebrates—ranging from microscopic rotifers to macroscopic ice worms—live in glacier and snowfield ecosystems (Hotaling et al., 2019b; Shain et al., 2016; Zawierucha et al., 2018) and even more are marooned there via atmospheric deposition as "arthropod fallout" (Fig. 4; Edwards, 1987). Arthropod fallout occurs on glaciers and snowfield globally (reviewed by Edwards, 1987), likely on any ice or snow surface that is relatively close (perhaps less than 50 km) to ice-free habitat. Even portions of the Greenland ice sheet likely see some amount of arthropod fallout as a diverse invertebrate community containing many winged species has been described just 2 km from its margin (Hansen et al., 2016). The presence of invertebrates on glaciers and snowfields raises three BAR-related hypotheses: (1) If sufficient invertebrate densities are reached (with dark enough pigmentation), *in situ* communities or atmospheric depositions may meaningfully lower albedo, driving "bug on snow" events (Fig. 4) that are akin to well-known "dust on snow" events (Painter et al., 2007; Skiles et al., 2015; Zhang et al., 2018). (2) Macroinvertebrates may attract other organisms (e.g., birds) to glacial ecosystems, whose activity reduces albedo. (3) 1800s (von Humboldt, 1808), and diverse, mostly arthropod communities have been described from cryosphere habitats worldwide (Durbin, 1975; Edwards, 1987; Edwards and Banko, 1976; Kohshima, 1984; Mann et al., 1980; Masutti and Covassi, 1978; Swan, 1963). Invertebrates delivered by wind to cold, high-UV glacial ecosystems typically find the environment to be lethal (Edwards, 1987; Edwards and Banko, 1976; Heinrich and Bell, 1995; Swan, 1963). However, resident metazoans in the cryosphere do occur, including nematodes (Azzoni et al., 2015), rotifers (Shain et al., 2016), tardigrades (Zawierucha and Shain, 2019), and glacier ice worms (Dial et al., 2012; Hotaling et al., 2019a). Resident invertebrates are often present at high densities (hundreds to thousands per m^2 (Goodman, 1971; Mann et al., 1980) and tend to be highly melanized (see Fig. 1; Mani, 1968). Thus, like snow algae and other pigmented taxa, their presence on the surface alone likely drives BAR.

However, not all invertebrates are present at the surface continuously (Fig. 2B). For instance, on coastal glaciers of North America, a daily migration of heavily pigmented glacier ice worms occurs during summer, with worms typically congregating at densities $>100\ m^2$ (wet mass $\sim$ 0.31 g) on the snow surface 4–6 h before sunset and retreating

Arthropod fallout meaningfully alters the nutrient dynamics of the cryosphere, thereby affecting known BAR drivers (e.g., algal blooms).

Invertebrates on glaciers and snowfields were first recorded in the

back into the ice before dawn (Fig. 2B; Goodman, 1971; Mann et al., 1980). Ice worms may also affect BAR indirectly by exerting top-down control on algae abundance through grazing (and thus decreasing

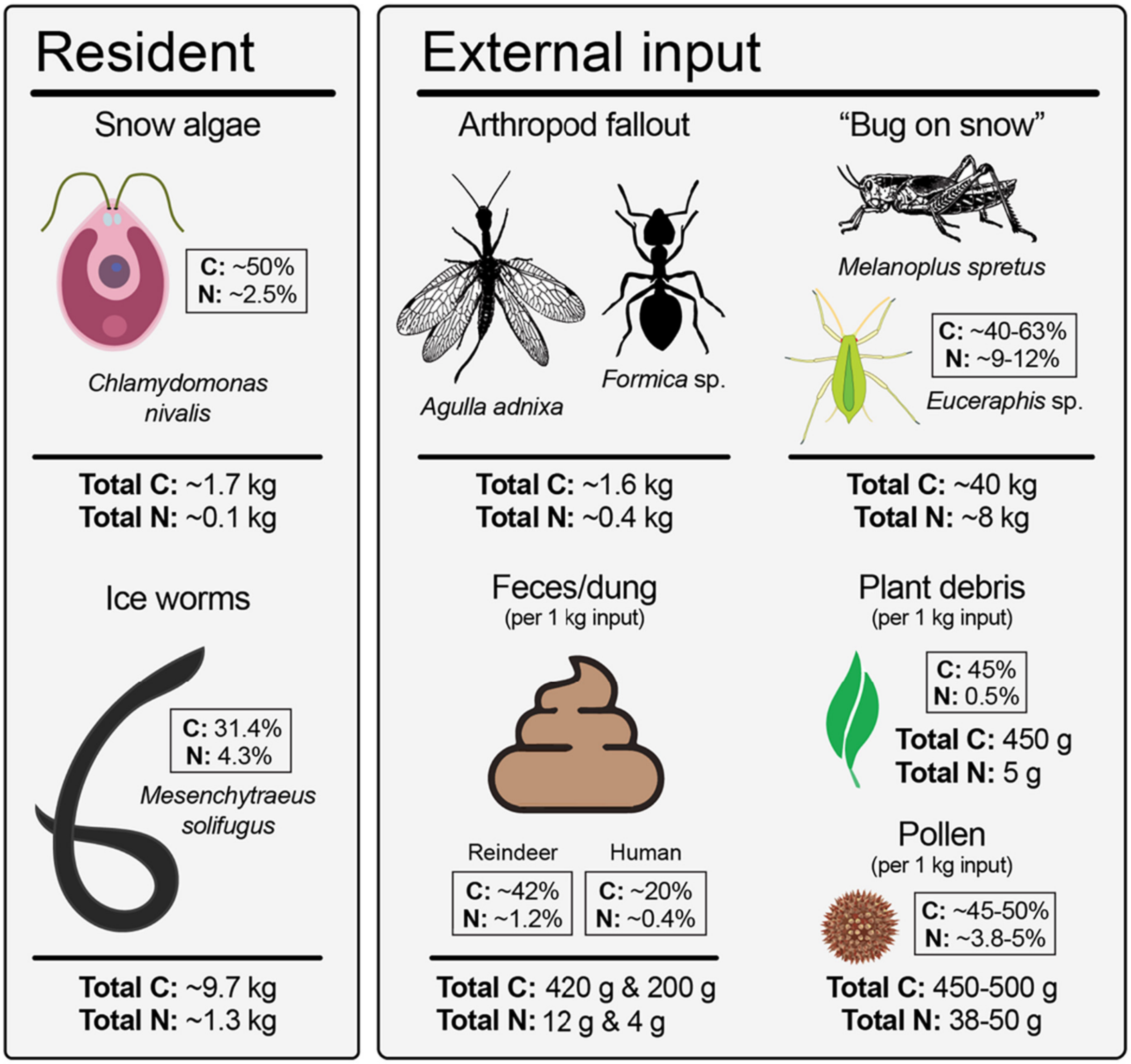


Fig. 4. Contribution of biomass from resident and external sources to the nutrient composition of ice sheets, glaciers, and snowfields. Total carbon (C) and nitrogen (N) estimates are for a 0.1 km^2 area and are calculated from empirical observations of abundances and C:N ratios of representative biomass (except where noted as "per 1 kg input"). Since no empirical estimates exist for input of feces/dung, plant debris, and pollen to the cryosphere, these numbers are calculated on a per kg basis. C and N data are based on elemental analysis of different sources of biomass from Hughes and Bazzaz, 2001; Pramanik et al., 2007; Spijkerman et al., 2012; Small et al., 2013; Fiera, 2014; Hayashi et al., 2014; Filipiak, 2016; Hamilton and Havig, 2017; Havig and Hamilton, 2019; Gray et al., 2020. The values, reported in %C and %N, were then applied to biomass deposition rates to estimate the amount (in g or kg) of total C and N deposition.

BAR), adding bioavailable nutrients that stimulate algal growth through feeding, and by attracting foragers (Hotaling et al., 2019b). Ice worms consume algae (Goodman, 1971; Murakami et al., 2015) but it is currently unknown if their grazing substantially impacts algal abundance. Future studies should compare algae abundance on glaciers with and without ice worms (e.g., in southeast Alaska; Dial et al., 2012; Hartzell et al., 2005) to investigate this relationship. Another dark-bodied invertebrate—springtails (subclass Collembola)—are much smaller than ice worms but can be present at densities >5000 m^2 during daylight (Mann et al., 1980). In terms of nutrient mass, C and N content of ice worms is 31.4% C and 4.3% N (Havig and Hamilton, 2019) which would add 9.7 kg of C and 1.3 kg of N over a 0.1 km^2 glacier assuming a conservative density of 100 worms m^2 (Fig. 4). Springtail C and N content ranges from 15 to 47% and 5–14%, respectively and individual matrix, wind-blown invertebrates are mostly static and reduce albedo on extremely localized scales (Fig. 2C). However, large-scale depositions, where one taxon is heavily deposited do occur and may induce "bug on snow" events (see below, Fig. 4). During summer on an Alaskan snowfield (Edwards, 1987; Edwards and Banko, 1976), biomass added via arthropod fallout was highest from mid-June to early July and declined to nearly zero by early September. A similar temporal decline was observed from July to August in the White Mountains, California, USA (Spalding, 1979). At its peak, approximately 1.5 mg m^{-2} per day of dry invertebrate biomass was added. Although this is low relative to dust events, which can deposit ~100 to ~25,000 mg m^{-2} over 1–2 days, dust events are episodic (Edwards and Banko, 1976) whereas arthropod fallout appears more consistent. If we consider peak arthropod deposition to be from mid-June to early July and use a minimum area of 0.1

springtails range in weight from ~10 to 100 s of μg (Fiera, 2014), thus their C and N contribution may be similar to ice worms.

While resident invertebrates actively move throughout the ice

km^2, arthropod additions would add 3.2 kg of biomass to the system. For comparison, snow algal biomass has been estimated at 1.2–3.3 kg over a similar area (0.1 km^2; Painter et al., 2001; Takeuchi et al., 2006).

Assuming a similar contribution to BAR, at these deposition rates the contribution of arthropod biomass to albedo reduction could rise to the level of algae. However, this estimate oversimplifies the concentrated nature of arthropod biomass and does not account for the added melt-inducing physiology of algae.

"Bug on snow" events differ quantitatively and qualitatively from regular fallout. For instance, in July 1966 on the ~3.9 km^2 Gulkana Glacier in Alaska, live aphid weight was approximately 83 kg after a major deposition (Edwards, 1987). In Montana, grasshoppers are entombed in at least five glaciers, and tell the legacy of widespread, recurring depositions (Lockwood et al., 1992, 1991). First reported as "billions of grasshopper carcasses" (Henderson, 1933), grasshoppers were observed at densities up to 100 m^2 across a swath of the Rocky Mountains and were so abundant that two glaciers within ~25 km have been named "Grasshopper Glacier" (Lockwood et al., 1992). Large-scale grasshopper deposits happened iteratively from 140 to 800 years ago (Lockwood et al., 1991, 1992, 1994) and were dominated by the now extinct Rocky Mountain locust (*Melanoplus spretus*; Lockwood et al., 1991).

No measures of albedo reductions for single invertebrates, much less before and after major "bug on snow" events, have been published. Furthermore, the global biogeography of "bug on snow" events, including their spatial and temporal variability, remains unknown. The latter is likely because the major foci of modern biological research on permanent ice have been in Greenland and Antarctica, two isolated areas where arthropod deposition is rare or non-existent. Moreover, documentation of real-time "bug on snow" events like the July 1966 observation in Alaska require a unique combination of a skilled mountaineer with the biological expertise to record and publish such an event. Looking ahead, however, there is reason to predict that the frequency of "bug on snow" events is in decline due to the extinction of species like *M. spretus* in North America and contemporary global declines in insect diversity (Hallmann et al., 2017; Sanchez-Bayo and Wyckhuys, 2019).

Arthropod biomass, particularly insect biomass, is typically of high quality and labile (i.e., with a low C:N ratio; Yang and Gratton, 2014). Estimates of C and N in arthropod biomass range from ~40–63% and 9–12%, respectively (Havig and Hamilton, 2019; Hughes and Bazzaz, 2001; Small et al., 2013). Thus, the 3.2 kg of arthropod biomass calculated above would add ~1.6 kg of C and ~0.4 kg of N to the surface of a small (0.1 km^2) glacier during peak deposition from mid-June to early July (Fig. 4). For larger "bug on snow'" events, over 40 kg of C and ~8 kg of N could be added (Fig. 4). In contrast, ice and snow algae contribute a range of biomass values, from 1.2 kg km^{-2} on ice sheets in Alaska (Takeuchi, 2013) to 33 kg km^{-2} in California (Painter et al., 2001). Assuming the same 0.1 km^2 glacier area and algal biomass that is ~50% C and 2.5% N (Gray et al., 2020; Hamilton and Havig, 2017; Havig and Hamilton, 2019; Spijkerman et al., 2012), snow and ice algae would contribute ~1.7 kg of C and ~0.1 kg of N. These comparisons suggest arthropod biomass can substantially influence biogeochemical cycles on snow and ice surfaces but presumably, surface primary productivity would provide more readily available C.

While studies are needed to characterize the bioavailability of nutrients, particularly C and N, in arthropod biomass and subsequent effects on snow and ice microbiota, the deposition of invertebrates may impact BAR in another indirect way. Invertebrates on glaciers are a key resource for other organisms, including invertebrates (Mann et al., 1980) and birds (Edwards and Banko, 1976; Hotaling et al., 2019a; Vera et al., 2012). By attracting larger organisms to the cryosphere, invertebrates likely increase the net biological activity of the cryosphere. And, by also attracting their waste products (e.g., bird feces), invertebrates may influence BAR. In this context, the potential for BAR hinges on two factors. First, that larger organisms like birds are being attracted from outside the cryosphere to feed on invertebrates. This is

on the cryosphere surface—primarily through fecal and related inputs—outweighs the removal of a local contaminant (the invertebrate) and its nutrients.

3.3. Vertebrates

Many mammals and birds, ranging from songbirds to ungulates and felids transiently use glaciers and snowfields (Rosvold, 2015) for relief from abiotic or biotic factors (Hagemoen and Reimers, 2002), foraging (Stevens, 1979), nesting (Hardy and Hardy, 2008; Hardy et al., 2018), recreation (Reckin, 2013), and travel (Koshkarev, 1984). For BAR, the key aspect of vertebrates on glaciers and snowfields are their inputs, whether feces, blood and other byproducts of predation, or their own hair and feathers (Fig. 2A). For example, 60% of algal blooms along the Antarctic Peninsula are within 5 km of penguin colonies and blooms are larger near bird or seal colonies (Gray et al., 2020).

Worldwide, birds are the most diverse vertebrate group on glaciers and snowfields and are therefore likely the vertebrate group that contributes the most to BAR. Birds forage on glaciers and snowfields (Antor, 1995; Hardy et al., 2018; Hotaling et al., 2019a; Resano-Mayor et al., 2019) with latitudinal variation in their rates (higher foraging rates at lower latitudes; Edwards and Banko, 1976; Verbeek, 1970). For BAR, birds may control arthropod abundance on glacier and snowfield surfaces, effectively limiting biomass accumulation through time. At high-latitudes, coastal glaciers and snowfields are heavily used by seabirds (and seals) and algal blooms have been linked to penguin colonies (Remias et al., 2013), predatory bird prey (Fujii et al., 2009), and seal carcasses (Ishikawa et al., 1986). In mountain ecosystems, birds play a role in dispersal of glacier biota, as implicated in the genetic biogeography of ice worms (Dial et al., 2012; Hotaling et al., 2019a). Some birds even nest on glaciers (Hardy and Hardy, 2008), thereby attracting mammalian predators and increasing opportunities for fecal input. Larger organisms can also be major sources of feces to glaciers and snowfields (Figs. 2A, 4). Ungulates, particularly reindeer, migrate to snow- or ice-covered land daily in the summer as a reprieve from heat and to escape flies (Rosvold, 2015). In Norway, ~1200 reindeer have been observed spending hours on snow (Hagemoen and Reimers, 2002) and their dung stains snowfields over large areas (Rosvold, 2015). Brown bears and snow leopards also travel on ice or snow (French et al., 1994; Koshkarev, 1984) but not in herds and thus likely have little to no impact on BAR.

Vertebrate "input" (feces, feathers, blood) altering snowfield albedo in maritime environments is well-known (Fujii et al., 2009) and similar effects likely occur on inland glaciers and snowfields. For instance, fecal staining by emperor penguin colonies can be detected with satellite imagery (Fretwell and Trathan, 2009). While the albedo of animal products remain to be quantified, it is reasonable to assume they are similar to bare ground (~15% reflectance), and thus much lower than the ~90% reflectance of fresh snow (Skiles et al., 2018). Humans, possibly the most widespread vertebrate on glaciers and snowfields worldwide, also contribute to BAR. For example, ~1000 people attempt the most popular mountaineering route on Denali, the tallest peak in North America, each year (Denali National Park and Preserve, 2019). In addition to footprints altering the physical snow surface (Fig. 2A), climbers generate ~2 metric tons of fecal waste on this single route, and the bulk of it is typically disposed of in crevasses (Goodwin et al., 2012; Pickering and Barros, 2015). While these feces may flow through the glacier and be exported to lower elevations, fecal contamination of snow near camps and climbing routes has been observed (Goodwin et al., 2012; McLaughlin et al., 2005) highlighting that camps, and their methods for waste disposal, can still impact BAR at higher elevations.

Nutrient inputs by vertebrates to cryosphere habitats may be substantial, particularly in high use areas (e.g., near a popular mountain attracted from outside the cryosphere to feed on invertebrates. This is certainly true in the case of ice worms in North America as none of their vertebrate predators nest directly on glaciers and snowfields (Hotaling et al., 2019a). Second, that the net effect of increasing biological activity

stantial, particularly in high-use areas (e.g., near a popular mountaineering route or large herd of reindeer). For instance, reindeer feces contain 420 mg C/g and 12 mg N/g (dry mass; Hayashi et al., 2014). While nutrient content of human fecal waste can vary with diet, as an example, solid waste from Kolkata, India contained 200 mg C/g and 3.7 mg N/g (Pramanik et al., 2007). Assuming 1 kg of fecal deposition on a 0.1 km^2 glacier, reindeer feces add 420 g of carbon and 12 g of nitrogen while human feces adds 200 g of C and 3.7 g of N (Fig. 4). Bird fecal deposition may provide a uniquely important source of bioavailable N. For instance, seabird guano is used in high N fertilizer and can be ~11% N of which only 0.8% is inorganic (mainly NH_4-N; Hartz and Johnstone, 2006).

Assuming the loss of permanent snow and ice does not drive a corresponding decline in vertebrate population densities, the BAR effects of vertebrates on the cryosphere is likely to increase as snow and ice area declines and use is concentrated in ever smaller areas. Moreover, the full suite of glacier and snowfield usage by vertebrate is likely underreported as the remains of moose, African wild dogs, leopards, snowshoe hare, wolves, and various rodents have melted out of glaciers and snowfields from North America to Africa (Andrews et al., 2012; Farnell et al., 2004; Guest and Leedal, 1954; Hare et al., 2012; Lee, 2012; Mizuno, 2005; Thesiger, 1970). High-altitude discoveries of extinct megafauna (Madsen, 2000) also highlights the potential for a legacy of organic debris in extant snowfields which, when exposed, will further BAR.

3.4. Plants

Plants and plant matter are common on ice sheets, glaciers, and snowfields. The most well-known floral resident of glaciers are "glacier mice" (Fig. 1)—balls of moss that are not attached to the ice surface and "move" across it on glaciers worldwide (Coulson and Midgley, 2012; Hotaling et al., 2020). Glacier mice are typically ~8–10 cm in diameter and harbor invertebrate communities (Coulson and Midgley, 2012). In central Africa, moss colonizes the termini of disappearing glaciers in the Rwenzori Mountains, Uganda (Uetake et al., 2014). Unlike glacier mice, African moss aggregations are not formed by moss shoots but rather by dense aggregations of gemmae. On average, moss aggregates are ~19 x ~ 13 mm with a broad distribution up to 46 × 32 mm. The aggregations experience daily freeze-thaw cycles, with internal temperatures reaching 10 °C, and penetrate several millimeters into the ice due to radiative warming (Uetake et al., 2014).

Similar to arthropods, plant fallout also occurs and may alter BAR directly and indirectly. In the western USA, vegetation on snow and ice surfaces includes pine needles, grass, and lupine, and contain ~45% C and ~0.5% N while mosses are ~8% C and ~0.2% N (Havig and Hamilton, 2019). Over 5000 pollen grains/L have been observed in arctic snow (Bourgeois et al., 2001) and in southern Greenland, pollen deposition has been estimated at ~0.7 grains cm^2 per year (Bourgeois, 1990). Pollen C and N content ranges from ~45–50% C and ~ 2–5% N (dry mass; Filipiak, 2016). Assuming 1 kg of deposition on a 0.1 km^2 glacier, plant debris add ~450 g of C and 5 g of N, moss add 80 g of C and 2 g of N, and pollen add ~450–500 g of C and ~ 38–50 g of N (Fig. 4). However, accumulation rates of plant debris, moss, and pollen on most glaciers and snowfields are largely unknown and likely vary by location and season.

4. Biological shading

While many biological factors may contribute to BAR and further melt, some might instead shade the surface, thereby insulating it and preventing melt. This biological shading is similar—albeit on a much smaller scale—to how debris-cover on glaciers and other ice forms can limit ablation (Anderson et al., 2018). For example, the "movement" of glacier mice stems from biological shading as the moss conglomerations protect the ice below from solar radiation and warm ambient temperatures while surrounding ice melts away. Eventually, this creates a pedestal that the glacier mouse rests upon before tumbling off and

depths of fecal masses have been observed up to ~30 cm, well beyond the amount needed to protect ice (Rosvold, 2015). Although likely negligible on large spatial scales except in rare, short-term cases (e.g., tents in human mountaineering camps), larger-bodied animals on snow and ice surfaces (particularly birds and mammals) may also cause local, transient shading.

5. Climate change and anthropogenic effects

Climate change is predicted to raise temperatures (Hansen et al., 2010), alter patterns of wind and solar radiation (Hofer et al., 2017; Sydeman et al., 2014), increase meltwater run off (Huss and Hock, 2018), and influence the population dynamics of biota around the world (Cavicchioli et al., 2019; Parmesan, 2006). Thus, potential exists for climate change to enhance BAR. However, the alternative—climate change mitigating BAR—perhaps through increased rainfall washing away more biological particles should also be considered. Below, we consider both perspectives, primarily in the context of the most pressing question for BAR: how will climate change alter the timing, scale, and duration of snow and ice algae blooms?

5.1. Temperature and precipitation

Climate change has resulted in decreased snowfall versus rain in many locations and, in general, this trend is expected to continue with increasing temperature (Diffenbaugh et al., 2013; Knowles et al., 2006; Krasting et al., 2013; Thackeray et al., 2019). However, changes will not be uniform with snow amounts actually increasing in some areas (e.g., The Alaska Range, Winski et al., 2017). At present, the strongest correlation between air temperature and snow cover extent occurs between April and June in the northern hemisphere. Extended melt seasons due to rising temperatures should increase microbial growth by adding meltwater earlier in the season (and likely at higher quantities throughout). In field experiments, the addition of 250 mL of water to a 2 m^2 increased snow algal cell counts by 50% (Ganey et al., 2017). And, due to added water and more algae in plots treated with excess water, bare ice was exposed earlier in the melt season (Ganey et al., 2017). However, rainfall may limit the growth of ice algal blooms by flushing algal cells from the ice surface or redistributing algal cells elsewhere (Stibal et al., 2017). A positive correlation ($R^2 = 0.51, p < 0.01$) between darkening of ice during summer and the timing of snow clearance from ice surfaces has been observed with earlier snow clearance in spring leading to darker ice in summer (Tedstone et al., 2017). If snow algae are "annuals" dispersing to snowfields each year from elsewhere (Onuma et al., 2018), then snow depth may have no impact on their abundance and distribution. If, however, they are "perennials" as current evidence suggests (Box 1; Hoham and Remias, 2020), then altered snow depth may alter their distribution and abundance. If snow depths increase, snow algae may fail to germinate due to a lack of meltwater reaching dormant cysts. If snow depths decrease, germination will occur increasingly earlier until there is insufficient habitat available for their growth and reproduction.

5.2. Nutrient change

Greater availability of resources (e.g., water) may underlie the trophically expanded food webs observed on some glaciers around the world. For instance, in addition to a standard microbial assemblage, the Paradise Glacier, Mount Rainier, USA, also supports ice worm macroconsumers which are preyed upon by birds (Hotaling et al., 2019b). Though it is unclear if more trophic levels on a glacier lead to an increase in BAR, a link seems plausible as it could create more net biological activity on snow and ice surfaces. Thus, an increase in pedestal that the glacier mouse rests upon before tumbling off and restarting the process (Hotaling et al., 2020). Similarly, reindeer fecal deposits can be deep enough that they transition from driving melt through reduced albedo to actively insulating snow and ice. In Norway,

activity on snow and ice surfaces. Thus, an increase in nutrients—perhaps from expanded algal blooms, storm frequency, or wildfire (see below)—could lead to tropic expansions in the cryosphere. This potential is particularly clear given the evidence that increased availability of key nutrients (e.g., C and N) can expand algal blooms.

Ongoing recession of glaciers may also increase local nutrient input. Glacier retreat contributes fine dust particles to adjacent landscapes through bedrock grinding (Bullard et al., 2016) and exposure of unconsolidated sediments may increase local addition of dust, typically rich in Fe and P, to nearby snow and ice. Added mineral dust will also increase mineral-microbe aggregates that affect the surface architecture of snow and ice, provide opportunities for nutrient biomining by microbial communities, and reduce albedo (leading to increased availability of water). For instance, ice algae in southwestern Greenland show a positive photophysiological response to increased P availability, with P in this region likely sourced locally from mineral dust (McCutcheon et al., 2021).

Global circulation models predict an increase in storms and other extreme weather events (IPCC, 2019). In North America, the Arctic, and along the Antarctic Peninsula, cyclonic storms deposit marine-derived aerosols containing N, P, potassium (K), and Fe onto coastal glaciers and icefields (Quinn et al., 2015). If storms increase in frequency, duration, or magnitude, then cryospheric ecosystems enriched by deposition of marine-derived nutrients may see more extensive algal blooms and thus increased BAR.

Anthropogenic activities may also affect nutrient delivery to snow and ice ecosystems. Agricultural dust carries N, P, and K which can expand algal blooms on snowfields (Ganey et al., 2017). Increases in temperature and drought will lead to an increase in fuel aridity, forest fires, and corresponding increases in black carbon delivery to snow and ice (Kaspari et al., 2015; Keegan et al., 2014; Kim et al., 2005; Stevens-Rumann et al., 2018). While addition of soot from forest fires will lower albedo and increase melt directly, it can also serve as a nutrient source. Finally, higher levels of atmospheric CO_2 will likely increase snow algae primary productivity and further a positive feedback loop between rising atmospheric CO_2, algal abundance, and BAR (Hamilton and Havig, 2020).

6. Research gaps

Below, we highlight gaps in our understanding of BAR in the cryosphere. Recent reviews have highlighted research priorities for BAR studies including establishing algae culture collections and sequencing algal genomes, measuring single cell reflectance spectra to facilitate remote sensing, and improving modeling of BAR effects over increasing spatial scales (Edwards et al., 2020; Hoham and Remias, 2020; Williamson et al., 2019). Here, we focus on gaps that have either not been covered by previous efforts or we extend their points. We conclude by highlighting one of the most valuable research gaps that remains to be filled: establishing a long-term, global monitoring network for BAR.

6.1. *Genomics*

Biogeographic analyses of snow and ice algae have revealed similarities in population structure across spatial and temporal scales (Lutz et al., 2018; Segawa et al., 2018a, 2018b). Connecting genes to function in these communities, however, remains largely unexplored. Until recently, cutting-edge genomic tools—such as long-read sequencing (Hotaling and Kelley, 2019)—have not been applied to the cryosphere (Edwards et al., 2020; Williamson et al., 2019) although they likely hold considerable potential for understanding the genomic basis of life in snow and ice, including phenotypic variation directly related to BAR (e.g., pigment production). The first genome of a cryophilic algae was recently reported from a green algae—*Chlamydomonas* sp. ICE-L—that lives in brine channels on Antarctic sea ice (Zhang et al., 2020). The genome of *Chlamydomonas* sp. ICE-L includes expanded gene families related to DNA repair, likely in response to the high UV radiation it

could be integrated into a comparative framework as future BAR-related genomes become available. Similarly, integrating transcriptomics, for instance, into a developmental time-series of algal growth may aid in the identification of key genes underlying the transition from green flagellates to red cysts (and associated pigment production) in snow algae and purple pigmentation in ice algae.

Another genomic realm that remains underexplored is the use of temporal sampling from ice or sediment cores to understand the historical population dynamics of BAR-related taxa. For instance, Segawa et al. (2018a, 2018b) recovered ancient DNA for cryoconite-forming cyanobacteria from a ~ 12,500-year ice core in central Asia and used these ancient sequences to estimate a key evolutionary parameter—mutation rate—by comparing them to modern sequences. In a related study, Chen et al. (2016) used shallow ice cores from a high mountain glacier to characterize bacterial abundance and community shifts over a 40-year contemporary record. Both studies highlight the potential for gaining historical inference into microbial population dynamics on mountain glaciers. For BAR, an ice core-based climate reconstruction paired with presence and abundance of key taxa (e.g., snow and ice algae) could shed light on how algal blooms, for instance, have been historically influenced by changing atmospheric conditions. When designing ice core-based historical studies, the most critical limitation may be the residence time of ice. Sediment cores from proglacial lakes could provide another option for reconstructing BAR history for glaciers and ice sheets of interest (e.g., Larsen et al., 2020). Relative to ice cores, sediment cores would be advantageous as they are not constrained by ice presence nor movement. However, target biomarkers (e.g. DNA, pigments, carotenoids) are likely to degrade more rapidly in sediments relative to englacial ice.

6.2. *Understudied regions*

The location, seasonality, and global extent of permanent snow and ice ecosystems means vast areas remain understudied, especially for BAR. Understudied high-latitude areas include (but are not limited to) the Russian Arctic, most of Antarctica, and northwestern and eastern Greenland. A variety of temperate regions have also been overlooked, including subranges of the Rocky Mountains in North America (e.g., Teton Range, USA), the Caucasus Mountains in eastern Europe (e.g., Makowska et al., 2020), and similar localities. Rapidly receding tropical glaciers are also urgent targets for ecological studies (Veettil and Kamp, 2019; Zawierucha and Shain, 2019). Tropical glaciers, for instance, show far greater variability in terms of climate sensitivity (Kaser, 2001; Kaser et al., 2004) compared to mid- and high-latitude glaciers and differ from higher latitude glaciers by the absence of seasonal temperature cycles (monthly mean temperatures vary by less than 5 °C) and extended periods of freezing (Lentini et al., 2011). Due to their high altitude, tropical glaciers receive higher levels of energy forcing and are particularly susceptible to increasing temperatures and shifting precipitation regimes (Chevallier et al., 2011). Typical snow and ice algae have been reported from equatorial glaciers and are likely contributing to BAR in analogous ways to other snow and ice ecosystems. However, the absence of seasonal temperature cycles and extended periods of freezing may allow biota to be active, and in the case of algae, even bloom throughout the year. Thus, unlike higher latitude glaciers, algal impact on BAR in equatorial regions may not be restricted to melt seasons.

6.3. *Temporal sampling*

Given the degree that seasonal variation can influence BAR, temporal sampling for full, explicitly defined, melt seasons are conspicuously lacking. Ideally, temporal perspectives during melt seasons should be complemented by year-round sampling of snow and ice to generate related to DNA repair, likely in response to the high UV radiation it encounters on sea ice (Zhang et al., 2020). While pigment production was not a focus of the study, pigment-related genes (e.g., carotenogenesis genes; Takaichi, 2011) in the *Chlamydomonas* sp. ICE-L genome

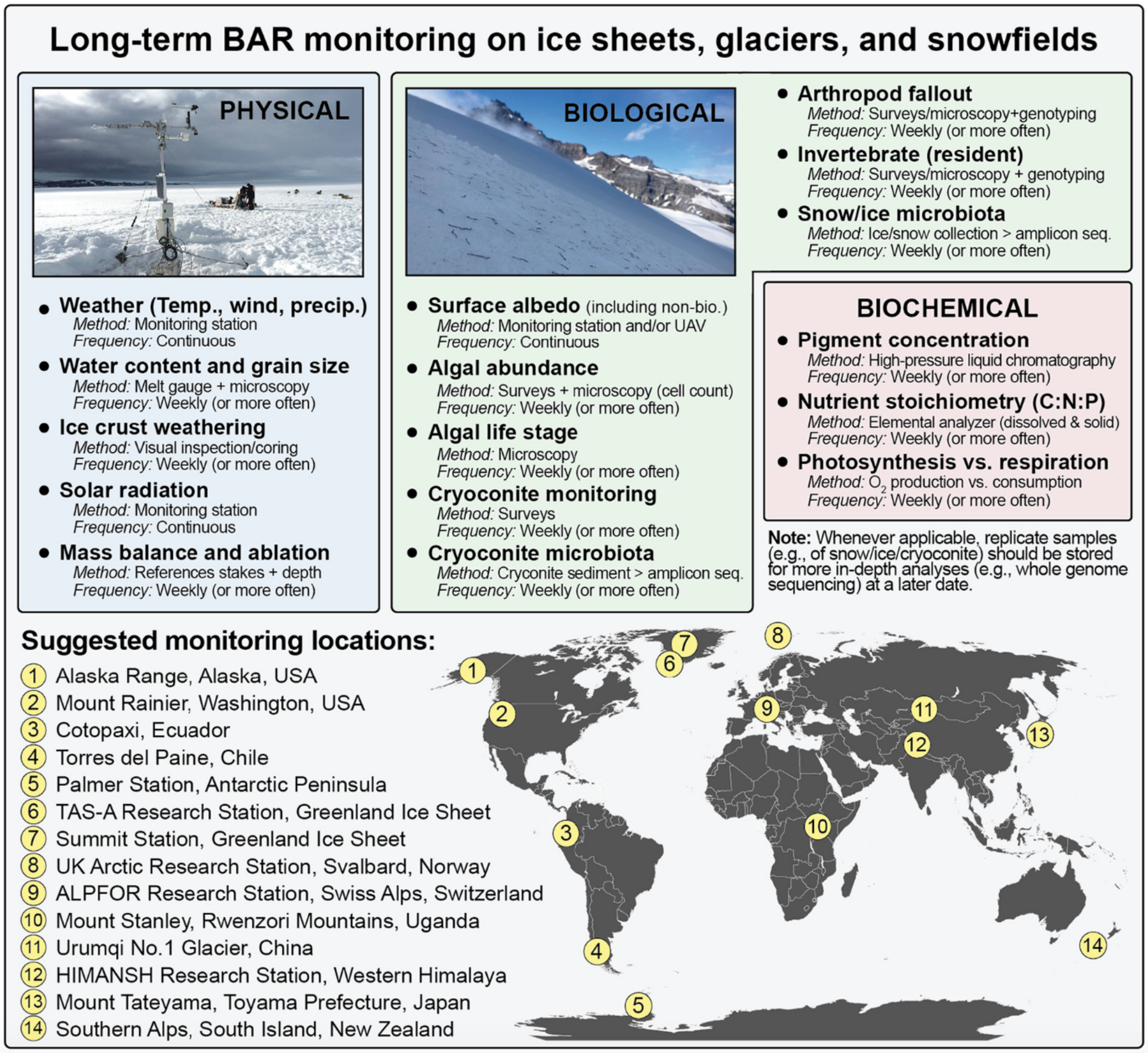
be complemented by year-round sampling of snow and ice to generate reference information about dominant winter processes and associated biotic communities. Similarly, latitudinal comparisons of seasonality across a gradient of day lengths from temperate to polar regions will shed important information on how light availability and related factors may influence melt season processes and ultimately BAR.

6.4. *Long-term BAR monitoring*

Our ability to monitor the feedbacks between BAR and climate change is limited by the fact that no glacier biology monitoring programs exist. Long-term environmental data are collected by weather stations on some glaciers and ice sheets (e.g., PROMICE on the Greenland ice sheet) and if linked to data associated with abiotic and biotic drivers of albedo reduction, they could provide a key data set for monitoring and quantifying BAR. However, environmental data alone, especially from a single location, will not substantially improve global understanding of BAR nor provide an opportunity to track changes. A global call for collaboration, including existing networks (e.g., International Network for Terrestrial Research and Monitoring in the Arctic, INTERACT), could be used to bring the necessary partners together. Here, we propose a global framework (outlined in Fig. 5) for long-term monitoring of BAR that integrates 16 environmental variables spanning the physical, biological, and biochemical sciences to be collected at 14 locations around the world. A global, and thus representative, data set can only be gained through coordinated effort. Such a program could begin with one or several select sites, in particular those that are staffed year-round. As part of this effort, protocols should be established, refined, and published. The effort could then be expanded to new sites as resources allow.

7. Towards a global comparative framework

One overarching goal for BAR research in the cryosphere—testing and quantifying the effects of all potential drivers, from microbes to humans—will always be challenging due to the many unknowns discussed in this review, the complexity of interactions between biotic and abiotic factors, and the difficulty of comparing results at different spatial and temporal scales. However, one major challenge for the field—the difficulty of making comparisons among studies—is largely an issue of coordination and can be improved more easily. The development of an integrative monitoring program with protocols developed through collaboration and shared across research groups would greatly improve comparability of results (see Fig. 5). Similarly, standardizing approaches



Long-term BAR monitoring on ice sheets, glaciers, and snowfields

PHYSICAL

- **Weather (Temp., wind, precip.)**
  Method: Monitoring station
  Frequency: Continuous
- **Water content and grain size**
  Method: Melt gauge + microscopy
  Frequency: Weekly (or more often)
- **Ice crust weathering**
  Method: Visual inspection/coring
  Frequency: Weekly (or more often)
- **Solar radiation**
  Method: Monitoring station
  Frequency: Continuous
- **Mass balance and ablation**
  Method: References stakes + depth
  Frequency: Weekly (or more often)

BIOLOGICAL

- **Arthropod fallout**
  Method: Surveys/microscopy+genotyping
  Frequency: Weekly (or more often)
- **Invertebrate (resident)**
  Method: Surveys/microscopy + genotyping
  Frequency: Weekly (or more often)
- **Snow/ice microbiota**
  Method: Ice/snow collection > amplicon seq.
  Frequency: Weekly (or more often)
- **Surface albedo** (including non-bio.)
  Method: Monitoring station and/or UAV
  Frequency: Continuous
- **Algal abundance**
  Method: Surveys + microscopy (cell count)
  Frequency: Weekly (or more often)
- **Algal life stage**
  Method: Microscopy
  Frequency: Weekly (or more often)
- **Cryoconite monitoring**
  Method: Surveys
  Frequency: Weekly (or more often)
- **Cryoconite microbiota**
  Method: Cryconite sediment > amplicon seq.
  Frequency: Weekly (or more often)

BIOCHEMICAL

- **Pigment concentration**
  Method: High-pressure liquid chromatography
  Frequency: Weekly (or more often)
- **Nutrient stoichiometry (C:N:P)**
  Method: Elemental analyzer (dissolved & solid)
  Frequency: Weekly (or more often)
- **Photosynthesis vs. respiration**
  Method: O_2 production vs. consumption
  Frequency: Weekly (or more often)

Note: Whenever applicable, replicate samples (e.g., of snow/ice/cryoconite) should be stored for more in-depth analyses (e.g., whole genome sequencing) at a later date.

Suggested monitoring locations:

① Alaska Range, Alaska, USA
② Mount Rainier, Washington, USA
③ Cotopaxi, Ecuador
④ Torres del Paine, Chile
⑤ Palmer Station, Antarctic Peninsula
⑥ TAS-A Research Station, Greenland Ice Sheet
⑦ Summit Station, Greenland Ice Sheet
⑧ UK Arctic Research Station, Svalbard, Norway
⑨ ALPFOR Research Station, Swiss Alps, Switzerland
⑩ Mount Stanley, Rwenzori Mountains, Uganda
⑪ Urumqi No.1 Glacier, China
⑫ HIMANSH Research Station, Western Himalaya
⑬ Mount Tateyama, Toyama Prefecture, Japan
⑭ Southern Alps, South Island, New Zealand

Fig. 5. A proposed global framework for long-term monitoring of biological albedo reduction (BAR) on ice sheets, glaciers, and snowfields. Recommended focal variables and frequency of data collection are were selected to strike a balance between the value of the inference and often limited resources and minimal research infrastructure where monitoring is most needed. Proposed monitoring locations span a global gradient of elevation, latitude, and longitude, while also being in close proximity to existing research stations or long-term projects where possible. Photo credits: © Andres Ahlstrøm/GEUS (left) and © Scott Hotaling (right).

for measuring albedo, including instrument configuration, are key and have been discussed previously (Cook et al., 2017a). Finally, greater consistency in the terminology used to refer to both the phenomenon and taxa being discussed is needed. To this end, we recommend that the effects of biotic factors on albedo reduction be referred to as biological albedo reduction (BAR; Cook et al., 2020a). Researchers should also take care to specify if their focus is on terrestrial or marine algae. In the terrestrial realm, we recommend the phrase "glacier algae" be reserved for collectively referring to all algae inhabiting glacier snow and ice habitats with specific groups differentiated by "ice algae" and "snow algae" therein.

Author contributions

S.H. and T.L.H. conceived of the review and defined its framework. All authors contributed content, editing, and approved the final version for submission.

Declaration of Competing Interest

The authors declare no competing interests.

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