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Cryoconite: the dark biological secret of the cryosphere

Journal:	<i>Progress in Physical Geography</i>
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Keywords:	cryoconite, biogeochemistry, glaciology, albedo, nutrient cycling
Abstract:	<p>Cryoconite is granular sediment found on glacier surfaces comprising both mineral and biological material. Despite long having been recognised as an important glaciological and biological phenomenon cryoconite remains relatively poorly understood. Here, we appraise the literature on cryoconite for the first time, with the aim of synthesising and evaluating current knowledge to direct future investigations. We review the properties of cryoconite, the environments in which it is found, the biology and biogeochemistry of cryoconite, and its interactions with climate and anthropogenic pollutants. We generally focus upon cryoconite in the Arctic in summer, with Antarctic and alpine settings examined individually. We then compare the current state-of-the-science with that at the turn of the twentieth century, and suggest directions for future research including specific recommendations for studies at a range of spatial scales and a framework for integrating these into a more holistic understanding of cryoconite and its role in the cryosphere.</p>

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1 I Introduction

2 Cryoconite is granular sediment found on glacier surfaces comprising both mineral and biological
3 material. Due to its dark colour, cryoconite efficiently absorbs solar radiation and 'drills' quasi-circular
4 holes up to tens of centimetres deep into glacier ice surface. These are known as cryoconite holes, and are
5 very common features on ablating ice surfaces worldwide, although cryoconite can also be found in other
6 environments such as stream deposits and scattered on ice surfaces (Hodson et al., 2008). Despite having
7 been recognised as important glaciological and biological entities in the nineteenth century (e.g. Agassiz,
8 1846; Nordenskiöld, 1870; Nansen, 1882) cryoconite and cryoconite holes still remain poorly understood.
9 They are thought to be "ice cold hotspots" of biodiversity and microbial activity on glacier surfaces
10 (Edwards et al. 2012) and are regularly examined; however, studies have been predominantly
11 reductionist in approach and based upon assumptions of discrete habitat boundaries and simple
12 thermodynamics established by early polar explorers over a century ago. This review begins by
13 discussing the properties of cryoconite and the environments in which it is usually found, before
14 summarising current knowledge of cryoconite biology and discussing its wider significance. We generally
15 focus upon cryoconite in the Arctic in summer, with Antarctic and lower-latitude settings examined
16 individually. We conclude by comparing the current state-of-the-science with that at the turn of the
17 twentieth century, and suggest directions for future research.

18 II What is cryoconite?

19 The term 'cryoconite' (from the Greek "kryos" and "konis", meaning "cold-dust") has been used
20 interchangeably to describe the entire mass of insoluble impurities, including discrete bio-engineered
21 granules (Langford et al. 2010; Edwards et al. 2014) on glacier surfaces or the discrete granules only. In
22 this paper, particles that do not contain both biotic and abiotic components are not considered to be
23 cryoconite, being inorganic supraglacial debris or cryo-tolerant biota. We consider this distinction to be
24 important since the presence and action of biota, along with geological and hydrological processes,
25 influences the formation, morphology and biogeochemistry of cryoconite (Takeuchi et al. 2001a; Hodson
26 et al. 2008; Langford et al. 2010). In this paper, cryoconite refers to

27 *Discrete, aggregated granules of mineral and organic matter, either within cryoconite holes or elsewhere in*
28 *the supraglacial zone.*

29 Cryoconite granules are often found in quasi-cylindrical depressions on ice surfaces called 'cryoconite
30 holes'. However, cryoconite has also been identified in a range of supraglacial habitats, leading some
31 researchers to propose sub-categories of cryoconite based upon their habitat morphology. For example,
32 Hodson et al. (2007) described cryoconite-like sediment in supraglacial streams as 'hydroconite' and
33 Hodson et al. (2008) referred to thick, dry deposits of cryoconite with cracked, hummocky surfaces and
34 warm, anaerobic interiors as 'cryoconite mantles'. While separation of cryoconite into distinct classes
35 may have merit, deeper knowledge of its characteristics and variability is required before useful
36 categorisation can take place.

37 1 Composition of Granules

38 The materials comprising cryoconite can be divided into two main types: organic and inorganic. Organic
39 Matter (OM) includes living and dead microbes, their exudates, products of decomposition and
40 allochthonous biotic and biogenic matter (e.g. Takeuchi et al. 2002a, 2010; Hodson et al. 2008; Takeuchi,
41 2002; Wientjes et al. 2011; Langford et al. 2010). While there is clearly variability in OM abundance in
42 cryoconite worldwide (Table 1) it invariably represents a key component of cryoconite granules. Spatial
43 variability in OM has also been identified across individual glaciers (Stibal et al. 2010, 2012a; Langford et
44 al. 2014). The quantity and quality of OM is known to influence aggregate formation in terrestrial soils,
45 but this has rarely been examined in cryoconite (Langford et al. 2014).

46 In addition to biotic and biogenic OM, persistent organic pollutants (POPs) with carcinogenic and
47 mutagenic potential (Hodson, 2014) can be incorporated into cryoconite. These molecules resist
48 environmental degradation and might bioaccumulate in cryoconite. Whilst they likely have little impact
49 on-site, they may influence downstream ecosystems. These pollutants have been linked to industrial
50 emissions and are often deposited along with inorganic matter such as black carbon (BC) (Aamaas et al.
51 2011). BC, a product of incomplete combustion of fossil and biofuels, has attracted research attention
52 because it is an extremely effective absorber of heat, both in the atmosphere and after deposition on ice

53 and snow, possibly accelerating melt (Clark and Noone, 1985; Hansen et al. 2000; Jacobsen, 2004; Xu et al.
54 2009a). The longevity of BC on ice surfaces is probably enhanced by entrainment into cryoconite, likely
55 reducing the aggregate albedo (Xu et al. 2009b; Bøggild, 2011), although it is also possible that cryoconite
56 microbes metabolise BC and reduce its potency.

57 Inorganic matter in cryoconite is dominated by mineral fragments, often dominated by phyllosilicate,
58 tectosilicate and quartz (e.g. Stibal et al. 2008; Langford et al. 2010; Hodson et al. 2010a; Edwards et al.
59 2011); however, differences in source geology likely cause geographic variation in cryoconite mineralogy.
60 Bullard (2012) pointed out that supraglacial dusts (that presumably form cryoconite granules) generally
61 include materials from various local and distal sources, citing studies undertaken in Arctic Canada
62 (Lawrence and Neff, 2009; Zdanowicz et al. 2000), Antarctica (Bory et al. 2010), the central (Tegen and
63 Rind, 2000; Drab et al. 2002; Prospero et al. 2012) and south-west marginal zones of the Greenland Ice
64 Sheet (Wientjes et al. 2011; Bøggild et al. 2010). This was recently corroborated by Nagatsuka et al.
65 (2014) who used Sr and Nd isotopic ratios to describe contrasting origins for silicate minerals in
66 cryoconite on a selection of central Asian glaciers. Fine dusts deposited from high atmospheric
67 suspension are particularly important in the interior zones of large glaciers and ice sheets, while on
68 smaller glaciers and ice-sheet margins a greater proportion of minerals are likely derived from local
69 sources (Stibal et al. 2012a). While material can be transported from local sources (including exposed
70 valley sides and moraines) to the ice surface by gusts of wind (Oerlemans et al. 2009; Bøggild et al. 2010),
71 Porter et al. (2010) found unconsolidated morainic material to be reworked onto the surface of a
72 Svalbard glacier by debris flows. The dominant sources of cryoconite minerals can also vary across glacier
73 surfaces (Langford et al. 2011). Other possible sources include release from englacial storage by ablation
74 (MacDonnell and Fitzsimons, 2008; Wientjes et al. 2011; Atkins and Dunbar, 2009), outcropping of basal
75 tills (Stibal et al. 2012a) and deposition of micrometeorites (particularly noted on the Antarctic and
76 Greenland ice sheets). Differences in source geology and depositional regimes likely explain geographical
77 variations in the size of mineral fragments in cryoconite. For example, Takeuchi et al. (2010) found
78 mineral fragments between 1.3 and 98 μm diameter in China, while Zarsky et al. (2013) found between
79 0.02 and 2000 μm in Svalbard.

80 The mineralogy of ice surface debris (including cryoconite) might influence spatial patterns of melt. Casey
81 et al. (2013) found the mineralogy of supraglacial debris on Himalayan glaciers to correlate with surface
82 temperatures and spectral reflectance. Since cryoconite mineralogy has been shown to influence its
83 colour and reflectivity (Tedesco et al. 2013; Takeuchi et al. 2014) it may similarly influence ice surface
84 albedo (Sugiyama et al. 2014). Mineralogy might also influence cryoconite microbes (Carson et al. 2009).
85 For example, since cryoconite microbial communities are often phosphorous (P) limited (Mindl et al.
86 2007; Säwstrom et al. 2002; Stibal and Tranter, 2007), phosphates from rock debris might provide crucial
87 nutrients. Tazaki et al. (1994) found silicate clays are entrained on snow algal cell surfaces. It is likely
88 analogous to processes occurring in cryoconite, although direct evidence of mineralogical controls on
89 cryoconite microbial activity has not yet been presented. Analysis of heavy metals has indicated the
90 occurrence of mineral-microbe interactions (Nagatsuka et al. 2010) and Hodson et al. (2010a) highlighted
91 the importance of cryoconite biota for extending rock-water interactions and catalysing chemical
92 weathering. Dittrich and Luttge (2008) suggested that microbes actively control water-solid interactions.
93 Nevertheless, deep understanding of mineral-biota interactions in cryoconite is still lacking. Further
94 inorganic material in cryoconite includes heavy metals (Singh et al. 2013) and radionuclides (Tieber et al.
95 2009), the accumulation and release of which may impact supraglacial and proglacial ecosystems.

96 The literature therefore indicates geographic variations in OM (further details in section 4) and inorganic
97 matter arising from different depositional and post-depositional processes. Quantifying the relative
98 contributions of OM and inorganic matter sources and the impacts upon melt and microbial processes
99 remain important outstanding research questions.

100 *2 Shape and size of cryoconite granules*

101 Cryoconite granules tend to be quasi-spherical, however their size and morphology is highly spatially
102 variable (Fig. 1, Table 2), likely reflecting the local balance between microbial growth, physical
103 aggregation and erosion (Irvine-Fynn et al. 2010). Variations in granule size have been reported between
104 glaciers; for example Zarsky et al. (2013) found larger granules to be more common on Aldegondabreen
105 (Svalbard) than on other glaciers, possibly due to gentle slope gradients, fine material particles, nutrient
106 input from debris avalanches and atmospheric deposition and high rates of microbial activity. Also on
107 Aldegondabreen, Langford et al. (2014) identified an "edge effect" whereby granules were generally

108 smaller towards the central areas of the glacier. This was attributed to biochemical and photophysical
109 processes including TOC and carbohydrate concentration. The strong correlation between granule size
110 and OM content (Takeuchi et al. 2010, Langford et al. 2010, Stibal et al. 2010) suggests that biota play a
111 key role in determining the shape and size of cryoconite granules.

112 Growth and proliferation of autotrophic cyanobacteria at granule peripheries has often been suggested to
113 be a driver of granule growth because their filamentous morphology enables them to entangle debris
114 (Langford et al. 2010). Heterotrophic microbes might limit this growth by decomposing OM (Hodson et al.
115 2010a). However, decomposition of OM produces 'sticky' humic substances that may enhance granule
116 cohesion (Takeuchi et al. 2001a, 2002a; Langford et al. 2011). Granule size is therefore probably co-
117 limited by the binding ability of filamentous autotrophs, the adhesion potential of other OM and rates of
118 decomposition by heterotrophs (Takeuchi et al. 2010). The potential for cryoconite microbes to control
119 granule size and morphology was demonstrated by Takeuchi et al. (2001a) who treated half a batch of
120 cryoconite with biocide (CuSO₄) before leaving them on a glacier surface over an ablation season. Algal
121 mats formed in untreated samples, whereas treated samples remained loose and disaggregated. The
122 contrasting morphologies suggest that meltwater, wind or gravity driven movement of granules might
123 influence their shapes. This is supported by the even distribution of cyanobacteria over granule surfaces
124 (e.g. Takeuchi et al. 2001a, b; Hodson et al. 2010a) despite only one side of settled grains being exposed to
125 sunlight. Irvine-Fynn et al. (2011) showed continuous hydraulic redistribution (but very little net
126 displacement) of cryoconite over a small plot on a Svalbard glacier that could be crucial for maintaining
127 homogenous growth rates over their surfaces.

128 Cryoconite granules also exhibit distinctive internal microstructures (e.g. Takeuchi et al. 2001a; Takeuchi
129 et al. 2010; Langford et al. 2010) where granule interiors are dominated by mineral fragments and
130 heterotrophic microbes, while granule surfaces are inhabited by photoautotrophs (e.g. Takeuchi et al.
131 2001a, 2002a; Langford et al. 2010). This probably results from the extinction of light within the outer
132 few mm of cryoconite granules. Indeed, Hodson et al. (2010b) showed both cyanobacterial
133 photosynthesis and photosynthetically active radiation (PAR) receipt to be concentrated at granule
134 surfaces. Thin section microscopy of Chinese cryoconite by Takeuchi et al. (2010) revealed more complex
135 internal microstructures including concentric rings of OM that may have resulted from annual biomass
136 accumulation or cycles of erosion and regrowth (Takeuchi et al. 2010). The number of rings per granule
137 ranged from 2 to 7, with a mean of 3.5. Some granules contained sub-granules with their own concentric
138 rings, suggesting amalgamation due to tight packing and rapid cyanobacterial growth. The amalgamation
139 of individual granules might explain reports of large complex granules with diameters of up to 40 mm
140 (Hodson et al. 2010a). Figure 2 shows four distinct classes of cryoconite microstructure proposed by
141 Takeuchi et al. (2010).

142 In general, larger and more stable grains exist where cyanobacteria are more abundant (Takeuchi et al.
143 2010). This is because granule growth is driven by the growth and proliferation of microbes,
144 entanglement of debris in cyanobacterial biomass and cementation by cohesive humic and extracellular
145 polymeric substances (Takeuchi et al. 2001a; Langford et al. 2010; Hodson et al. 2010b; Takeuchi et al.
146 2010; Langford et al. 2014). However, the precise biotic and abiotic processes controlling granule growth
147 and erosion are still poorly understood, and we have little knowledge of their spatio-temporal variations.
148 These are important knowledge gaps since larger granules probably have longer residence times, and
149 therefore more prolonged albedo-reducing effect on ice surfaces (Hodson et al. 2010a; Bøggild et al. 2010;
150 Irvine-Fynn et al. 2011) while also providing more microhabitats for varied microbial communities
151 (Langford et al. 2010; Zarsky et al. 2013). This suggests granule size could have important glaciological
152 and ecological implications, as well as potentially being an indicator of local biogeochemical processes
153 (Langford et al. 2014).

154 **III Cryoconite Holes**

155 *1 Formation and evolution of cryoconite holes*

156 Cryoconite exists in many several supraglacial environs (Fig 3) of which cryoconite holes are by far the
157 most common and best understood. Cryoconite holes are quasi-cylindrical depressions on ice surfaces
158 that commonly have depths and diameters ranging from millimetres to tens of centimetres. Cylindrical
159 holes are common; however, complex shapes also form and likely reflect interactions between regional
160 and local topography, aspect, ice type, hydrology and sediment dynamics (McIntyre, 1984; Cook et al.
161 2010).

1
2
3 162 Research to date has almost invariably assumed circular hole planforms, presumably to provide a
4 163 simplified model system for studying the fundamental mechanisms of hole development. It is now well
5 164 established that cryoconite holes form due to accelerated melting of ice beneath accumulations of
6 165 cryoconite (Agassiz, 1849; Nordenskiöld, 1875; Phillip, 1912; Gribbon, 1979; McIntyre, 1984; Wharton et
7 166 al. 1985). This occurs because cryoconite has low albedo relative to the surrounding ice surface, meaning
8 167 it efficiently absorbs solar radiation. Gribbon (1979) proposed a conceptual model (Equation 1, Table 3)
9 168 showing the solar radiation received by cryoconite sediment diminishing as it sinks in ice. There is,
10 169 therefore, a critical depth where the melt beneath cryoconite is equal to that of the surrounding ice
11 170 surface. This is referred to as the 'equilibrium depth'. Equilibrium depths vary over space and time
12 171 according to environmental conditions (particularly the balance between radiative and turbulent heat
13 172 fluxes in the local ice surface energy budget), the albedo of cryoconite and the extinction coefficient of
14 173 light (k) defined by Beer's Law. Beer's Law describes the exponential decay of solar radiation (I) as a
15 174 function of distance (z) through ice (Oke, 1987):

16 175
$$I_z^* = I_0^* e^{-kz} \quad (\text{Eq.1})$$

17
18 176 Coupling between equilibrium depth and environmental conditions suggests cryoconite hole depth could
19 177 be a crude indicator of synoptic energy balance (McIntyre, 1984). McIntyre (1984) used polythene
20 178 screens to shade holes and observed dramatic changes to hole shapes, confirming the role of direct solar
21 179 irradiance as a primary control on hole morphology. Microbial activity had previously been suggested to
22 180 contribute significantly to the heat balance at the hole floor (Gerdel and Drouet, 1960) but this was
23 181 discredited by the work of McIntyre (1984), Fogg (1988), Gribbon (1979) and Wharton et al. (1985).
24 182 Recent work by Hollesen et al. (2015) has shown that bioheat in organic rich permafrost can accelerate
25 183 ice-melt, but this is unlikely to occur in cryoconite unless it is extremely rich in organic matter or present
26 184 in thick deposits. There is evidence that the melt water in cryoconite holes might influence hole evolution
27 185 by acting as a radiation filter, sink of latent heat and medium for convection and advection of heat away
28 186 from hole floors (McIntyre, 1984). Sinking dark cryoconite beneath a layer of reflective water may also
29 187 raise the albedo of the ice surface, altering the local energy balance regime (McIntyre, 1984). Hydraulic
30 188 processes might therefore influence hole morphology, but this has not yet been examined in detail.

31 189 Podgorny and Grenfell (1996) provided an analytical model of radiation absorption by cryoconite that
32 190 demonstrated the importance of solar radiation and sediment albedo; however, it dealt specifically with
33 191 cryoconite holes developing on the floors of melt pools on sea ice and is probably not directly applicable
34 192 to holes on terrestrial ice. Similarly, a model for shortwave radiation-driven cryoconite hole formation
35 193 was produced by Jepsen et al. (2010) and supported by field and laboratory experiments; however, this
36 194 model considers closed holes in perennial lake ice and omitted atmospheric exchanges of sensible and
37 195 latent heat, limiting its application to cryoconite holes on Antarctic lakes. No solvable model for
38 196 cryoconite hole depth evolution on Arctic ice currently exists.

39 197 Most studies of cryoconite hole evolution have assumed that heat fluxes are exclusively vertical, although
40 198 we now know that it not the case. Cook et al. (2010) proposed a process of horizontal evolution in
41 199 response to sediment supply. Horizontal heat fluxes through thickened layers of cryoconite sediment
42 200 promote melting of hole walls, causing the hole to expand at the base and the holes walls to overhang.
43 201 Cryoconite can then fall into the newly created space at the hole periphery and the sediment layer thins. A
44 202 new equilibrium state is attained when cryoconite is spread into a layer just one grain thick (single grain
45 203 layer, 'SGL') and the widening at the hole floor has propagated upwards due to surface ablation,
46 204 producing a hole with straight walls and a wide aperture. The precise mechanism of granule
47 205 redistribution across the expanded hole floor remains uncertain, but recent observations (Cook,
48 206 unpublished data) suggest the primary mechanism is probably gravity-driven sliding of cryoconite down
49 207 sloped hole floors due to uneven solar irradiance, while redistribution driven by air bubbles escaping
50 208 from the melting hole floor may contribute (Cook et al. 2010) in areas where cryoconite granules are
51 209 small.

52 210 Cryoconite holes can therefore evolve in three dimensions in response to changes in the local ice surface
53 211 energy budget and sediment supply. They tend towards equilibrium morphologies characterised by
54 212 maximal areal coverage and exposure of granules to solar irradiance, which promotes photosynthesis
55 213 (Cook et al. 2010). These equilibrium states are common in cryoconite holes in slow moving, low gradient
56 214 ice that is free from topographic shading during periods of shortwave radiation dominated surface energy
57 215 balance (Hodson et al. 2010a; Cook et al. 2010; 2012), although in steep, hummocky ice and in areas
58 216 where rates of sediment delivery are particularly high or during periods of turbulent heat flux-dominated

217 surface energy balance, thicker sediment layers exist. This implies that although the process of sediment
218 layer equilibration might be ubiquitous in cryoconite holes, the attainment of SGL can sometimes be
219 inhibited by synoptic conditions. The fundamental processes of vertical and lateral equilibration of
220 cryoconite holes can be summarised in a conceptual model (Fig 4) wherein thermal energy absorbed by
221 cryoconite debris is directed to the hole floor (Q_v) or transferred laterally for melting hole walls (Q_l) in
222 varying proportions according to the thickness of the debris layer (Equations 5 and 6, Table 3).

223 There are several specific challenges that must be overcome before a solvable model of cryoconite hole
224 evolution can be developed. Firstly, the mechanism of sediment redistribution on hole floors must be
225 better constrained. Second, a much deeper understanding of the thermodynamic processes operating in
226 cryoconite holes, including in the water column, is required. Furthermore, equations 5 and 6 (Table 3)
227 relate thermal fluxes to ice-debris contact area, but this assumes constant layer thickness and will
228 therefore only be applicable to holes in morphological equilibrium, which are only common on stable,
229 slow moving ice in the interior zones of large glacier and ice sheets. Elsewhere, shallow holes contain
230 thick sediment layers and granules can be dispersed directly upon the ice surface (Irvine-Fynn et al. 2011;
231 Hodson et al. 2007, 2008; Stibal et al. 2008) and understanding these may require a revised approach.
232 Current models are limited to well-developed cryoconite holes and there is a lack of research into hole
233 initiation which likely relies upon complex surface debris dynamics, microscale hydraulics and spatial
234 heterogeneities in surface melt rates. (Lancaster, 2002). Finally, these models assume an uninterrupted
235 pathway towards morphological equilibrium, whereas periods of turbulent flux dominated ice surface
236 energy balance can reduce the depths of cryoconite holes, sometimes causing them to melt out and
237 redistribute sediment onto the ice surface (Hodson et al. 2007). Similarly, natural cryoconite systems can
238 be disturbed by rainfall events. Only during extended periods of meteorological stability characterised by
239 high incident radiation receipt can cryoconite holes be expected to evolve as described by the models in
240 Table 3.

241 *Cryoconite holes and synoptic energy balance*

242 The complex interplay between synoptic energy balance conditions and cryoconite hole evolution was
243 studied by Hodson et al. (2007) who showed that frequent disruption and emptying of Svalbard
244 cryoconite holes occurred in areas of high melt rate. This was due to hydraulic mobilisation of sediment
245 from shallower holes. Hodson et al. (2010b) and Irvine-Fynn et al. (2010) both used time lapse imagery to
246 show that during sunny periods when radiative fluxes dominate ice surface energy balance, cryoconite
247 holes deepen as predicted by Gribbon (1979). This causes the albedo of the ice surface to increase locally
248 since dark sediment sinks further beneath melt water which, while still dark has greater reflectivity than
249 cryoconite. In contrast, periods of turbulent flux dominated energy balance cause cryoconite holes to
250 shallow, moving dark cryoconite closer to the ice surface and reducing the local ice surface albedo.
251 Tracking of individual cryoconite granules suggested continuous redistribution of cryoconite sediment,
252 usually in random directions and resulting in little net displacement, but occasionally melt water flow
253 caused rapid movement of cryoconite between holes (Irvine-Fynn et al. 2010). Hodson et al. (2010a)
254 further suggested frequent hydraulic redistribution of granules between cryoconite habitats and glacier
255 zones. Patterns of melt-in and melt-out of cryoconite influence the microtopography and therefore
256 roughness of the ice surface, with implications for surface albedo (Warren et al. 1998; Cutler and Munro,
257 1996) and turbulent heat fluxes (Munro and Davies, 1977). These observations imply that cryoconite hole
258 morphology is not only an indicator but may also be a driver of energy balance across melting ice
259 surfaces. In general, periods of prolonged radiative-flux dominated ice surface energy balance are
260 associated with deeper, more stable cryoconite holes.

261 *2 Feedbacks between cryoconite granules and cryoconite holes:*

262 The current model of cryoconite granule formation has been inferred from the relationships between OM
263 and granule morphology, along with observations of granule microstructures and biogeochemistry.
264 Langford et al. (2010) suggested the following mechanism: 1) Blooms of filamentous and unicellular
265 phototrophs (particularly cyanobacteria) on ice, snow and slush surfaces act as nets for wind-blown
266 debris (Fig 5A). During snow and slush melt, debris is strained through these nets, forming biofilms that
267 are deposited on ice surfaces; 2) Autotrophic activity adds sticky extracellular polymers to these nets,
268 enhancing their ability to retain particulates and prevent them from being washed down-glacier in
269 suspension in melt water (Fig 5B); 3) As these aggregations grow they become increasingly able to resist
270 entrainment into flowing meltwater and therefore settle in microtopographic lows on ice surfaces.

271 After the granules have settled, cryoconite holes can begin to form. Hole formation is primarily driven by
272 abiotic processes of radiative and turbulent heat fluxes; however, microbial activity alters the albedo of
273 cryoconite granules (Takeuchi, 2002a; Tedesco et al. 2013; Takeuchi et al. 2014). Since albedo controls
274 energy absorption and therefore thermal fluxes through cryoconite granules, accelerated melt could be
275 described as microbially mediated. Once granules reside on cryoconite hole floors, further redistribution
276 is unlikely due to the low competence of hydrologic flow through the weathering crust, unless
277 heterogeneous irradiance causes hole floors to slope (Cook et al. 2015). Hydrological monitoring by Cook
278 et al. (2015) also suggests that even if granules are entrained into flowing meltwater, granules are
279 unlikely to be evacuated onto the ice surface. Integrating this information with the well-known
280 association between stability and extended periods of net carbon fixation on Arctic ice surfaces (Hodson
281 et al. 2007; Anesio et al. 2009; Cook et al. 2012) and the tendency for cryoconite holes to widen in favour
282 of autotrophy (Cook et al. 2010) suggests that photosynthesis-driven granule growth creates and
283 maintains favourable conditions for further photosynthesis on Arctic ice surfaces. This in turn drives
284 further granule growth and stabilisation (Langford et al. 2010; Langford et al. 2014). This feedback
285 mechanism is not currently well-understood, but it does point towards the high ecological significance of
286 cryoconite autotrophs, possibly representing keystone taxa (Paine, 1969) or autogenic ecosystem
287 engineers (Jones et al. 1994).

288 In summary, cryoconite granule formation is ultimately driven by biological processes and results in the
289 formation of cryoconite holes, which further promote biological activity. However, this explanation is a
290 great oversimplification that cannot explain the complex associations between the changeable abiotic
291 environment, biological processes and hole morphology. Complex coupling exists between cryoconite
292 surface coverage, albedo, microtopography and melt processes. These processes may have implications
293 for the process of glacier and ice sheet wastage and require further investigation. What is abundantly
294 clear is that cryoconite holes should be viewed as diverse, dynamic, responsive entities on ice surfaces.

295 **IV Cryoconite Biology:**

296 *1 Microbes in cryoconite*

297 Cryoconite is an important microbial habitat and a major component of supraglacial ecosystems (Anesio
298 and Laybourn-Parry, 2011). Although recognition of this is commonly credited to Hodson et al. (2008),
299 Kohshima et al. (1984a) identified a complex microbial community in ice and snow around cryoconite
300 holes twenty-four years earlier. Kohshima's subsequent work in the Himalaya, Tien Shan and Andes
301 (Kohshima, 1984a, 1985, 1987, 1989) described abundant and diverse microbiota and meiofauna and
302 linked them with accelerated ablation via ice surface albedo reduction. Takeuchi et al. (1998) later
303 explicitly linked algal growth on a Himalayan glacier to summer mass balance. Kohshima and Takeuchi's
304 work during this period provided a crucial basis for developing our understanding of microbially-
305 mediated glacier wastage and recognition of supraglacial microbial ecology; Kohshima (1992, pg. 1)
306 stated: "Himalayan glaciers are never abiotic environments. They are simple and well closed ecosystems;
307 housing various microbes, insects and copepods", cementing a new paradigm of glacier ecology that
308 recognised the diversity and significance of life on ice.

309 In the late twentieth century, Japanese scientists made advances in the microbiology of the supraglacial
310 environment, while European and American scientists focussed specifically upon cryoconite. Wharton et
311 al. (1981) broke a twenty year hiatus in cryoconite ecology research, identifying cryoconite holes as
312 microbial niches. Wharton et al. (1985) further described them as discrete ecosystems with "distinct
313 boundaries, energy flow and nutrient cycling", establishing an ecological context with an inherent
314 reductionism that persists to the present day. Vincent (1988) further suggested that cryoconite
315 ecosystems were more complex than other glacial habitats. Despite this work, an assumption of
316 lifelessness on ice surfaces permeated cryosphere literature until at least the late 1980s with writers such
317 as Pyne (1986) stating that there was "no terrestrial ecosystem... in Antarctica". It was a further twenty-
318 five years before Anesio and Laybourn-Parry (2011) proposed the cryosphere to be one of the earth's
319 major biomes, with cryoconite holes representing important sites of concentrated microbial activity and
320 biodiversity. Between 10^{21} and 10^{26} cells have been estimated to be contained within the porous near
321 surface ice that provides the substrate for cryoconite hole formation (Irvine-Fynn and Edwards, 2014).

322 Within cryoconite holes, biota is found both in cryoconite granules and the overlying meltwater (e.g.
323 S awstrom et al. 2002), with by far the greatest microbial abundance in the granules (Anesio et al. 2009;
324 Mieczen et al. 2013). Anesio et al. (2009) found the concentration of bacteria in cryoconite meltwater to

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3 325 be ~300× less than in debris. Nevertheless, microbes in melt water may represent important contributors
4 326 to the supraglacial ecosystem. Stratification of ciliates in the water column in cryoconite holes was
5 327 identified by Miezczen et al. (2013) in accordance with temperature and nutrient concentration gradients.
6 328 Sixteen phyla of ciliate were identified in total with algivorous and mixotrophic species inhabiting the
7 329 surface layers and bacterivores occupying the deeper water adjacent to bacteria-rich cryoconite
8 330 sediment. Suspension of microbial cells in melt water flowing through porous near-surface ice called the
9 331 “weathering crust” (Muller and Keeler, 1969) may provide an important mechanism of mixing and
10 332 redistributing microbes in the supraglacial zone. This porous ice layer likely permits admixtures of
11 333 soluble resources to be homogenised and translocated through the surface ice (Irvine-Fynn et al. 2012;
12 334 Irvine-Fynn and Edwards, 2014). Punctuating this porous ice layer are cryoconite holes, which likely act
13 335 as longer-term storage units for biomass (Hodson et al. 2008, Cook et al. 2015) and sites of enhanced
14 336 biogeochemical cycling, probably utilising resources delivered by hydrologic fluxes through the
15 337 weathering crust.

16 338 Cryoconite granules represent by far the most biodiverse supraglacial microbial habitat, harbouring
17 339 communities of several trophic levels. Food webs in cryoconite are underpinned by photoautotrophy:
18 340 primary producers use mainly solar energy to fix atmospheric CO₂ into OM, providing substrate for
19 341 heterotrophs. Of the primary producers, *Cyanobacteria* often dominates both the biomass and the C
20 342 fixation in cryoconite holes (Takeuchi et al. 2001a; Mueller et al. 2001; Christner et al. 2003; Porazinska et
21 343 al. 2004; Stibal et al. 2006; Stibal and Tranter, 2007; Hodson et al. 2010; Zarsky et al. 2013) while
22 344 simultaneously promoting the growth of granules by entangling minerals and additional OM.
23 345 Heterotrophs metabolise OM both fixed by primary producers in situ (autochthonous) and delivered from
24 346 elsewhere (allochthonous). Heterotrophic communities in cryoconite are often diverse and usually
25 347 dominated by a wide range of bacteria. This has been demonstrated using culture-dependent studies (e.g.
26 348 Margesin et al. 2002) and clone libraries (e.g. Edwards et al. 2011; Cameron et al. 2012). In Svalbard, at
27 349 least seven phyla of heterotrophic bacteria were identified in clone libraries (Edwards et al. 2011), with
28 350 their abundance varying between different glaciers. Sampling of Arctic, Antarctic and Alpine cryoconite
29 351 by Anesio et al. (2010) showed bacterial abundances ranging from 0.05×10^9 cells g⁻¹ in Antarctica to 1.40
30 352 $\times 10^9$ cells g⁻¹ in Svalbard. Rates of bacterial carbon production were not correlated to abundance and
31 353 varied greatly across the glaciers. In addition to bacteria, higher heterotrophs also inhabit cryoconite
32 354 holes, surviving by grazing upon smaller organisms. These include tardigrades, rotifers, copepods, ice
33 355 worms and midge larvae (e.g. DeSmet and Van Rompu, 1994; Zawierucha et al. 2013). Several taxa of
34 356 tardigrada and rotifera in Spitsbergen cryoconite holes were characterised by DeSmet (1988; 1990;
35 357 1993), DeSmet et al. (1988) and DeSmet and Van Rompu (1994). Ciliates usually represent the most
36 358 complex protozoa in cryoconite holes and are crucial for nutrient recycling through metabolism of
37 359 primary producers (Miezczen et al. 2013). To date, only a few studies have isolated yeasts and fungi in
38 360 cryoconite (Margesin and Fell, 2008; Singh and Singh, 2012; Edwards et al. 2013b) and only Edwards et
39 361 al. (2013b) evaluated their spatial variability, finding distinct communities on adjacent glaciers and
40 362 suggesting ice surfaces could represent reservoirs of fungal diversity.

41 363 Viruses are prominent in cryoconite holes (Anesio et al. 2004; Säwstrom et al. 2007; Hodson et al. 2008;
42 364 Bellas and Anesio, 2013; Bellas et al. 2013) and could be considered “predators” exerting top-down
43 365 controls on bacterial populations since they infect and cause the death of bacteria through viral lysis. Viral
44 366 lysis is crucial for bacterial mortality and thereby influences the recycling and export of carbon and
45 367 nutrients in cryoconite holes. Viral abundances of about 0.6×10^6 mL⁻¹ and 20×10^6 mL⁻¹ in water and
46 368 sediment have been identified (Anesio et al. 2007) in Svalbard. The frequency of virus-infected cells in
47 369 cryoconite communities (13%) was shown by Säwstrom et al. (2007) to exceed temperate freshwater
48 370 ecosystems (2%). Most recently, Bellas et al. (2015) analysed viral genomes from Arctic cryoconite
49 371 metaviromes revealed genomic signatures of unusual life strategies which are thought necessary for
50 372 longer-term interaction with their hosts. Viral shunts represent a crucial mechanism by which DOC is
51 373 recycled or made labile in cryoconite holes, thus affecting the flow of resources to higher trophic levels
52 374 and truncating the cryoconite food web (Laybourn-Parry et al. 2001).

53 375 Similarities in community structures in polar cryoconite have been illustrated using 16S rRNA gene clone
54 376 libraries (Cameron et al. 2012), implying a degree of cosmopolitanism in cryoconite microbial
55 377 assemblages. However, the abundance of particular species has been shown to vary locally (Cameron et
56 378 al. 2012), suggesting adaptation to environmental conditions at the community level. Stibal et al. (2008)
57 379 used epifluorescence microscopy to determine the abundance of phototrophs (0.25×10^3 to 8.0×10^3 cells
58 380 mg⁻¹) and heterotrophs (10×10^3 to 50×10^3 cells mg⁻¹) in cryoconite from Werenskioldbreen (Svalbard),

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3 381 finding much more biodiversity in heterotrophic communities than the cyanobacteria-dominated
4 382 autotrophic communities (further described by Stibal et al. 2006; Stibal and Tranter, 2007). At lower
5 383 latitudes and on some small polar glaciers, heterotrophs have been suggested to be more abundant than
6 384 primary producers, and may also be supported by allochthonous OC. For example, Edwards et al. (2013c)
7 385 found genes associated with *Proteobacteria* and *Bacteroidetes* to be more abundant than those associated
8 386 with *Cyanobacteria* in a metagenome of cryoconite taken from Rotmoosferner (Austrian Alps). Examining
9 387 community structures is useful for understanding microbial dynamics on glaciers, but has also been
10 388 linked to cryoconite granule morphology, perhaps indicative of biotic-abiotic feedbacks between
11 389 microhabitat structure and microbial ecology. For example, Takeuchi et al. (2001c) described poorly
12 390 aggregated, fine-grained cryoconite in Patagonia where both autochthonous and allochthonous OM were
13 391 relatively scarce, limiting granule building efficacy. In contrast, cryoconite in the Tien Shan had more
14 392 abundant biota and higher OM fractions and consequently formed larger, more stable granules.

15 393 While cryoconite hole biota can be categorised into distinct trophic levels, functionality is often shared by
16 394 various organisms throughout the community. For example, granule growth results from the production
17 395 of cyanobacterial biomass, but also through humification of OM and production of EPS by heterotrophic
18 396 bacteria, fungi and yeasts. Biogeochemistry is mediated by several organisms including nitrogen fixing
19 397 bacteria and those involved in ammonification and nitrogenation, including ammonia-oxidising Archaea
20 398 (Zarsky et al. 2013). Biological darkening of cryoconite granules (and the wider ice surface) is carried out
21 399 by organisms including algae and bacteria whose activity results in the accumulation of dark humic
22 400 material and photo-protective pigments (Takeuchi, 2002a; Takeuchi et al. 2010; Tedesco et al. 2013;
23 401 Takeuchi et al. 2014; Quesada et al. 2009).

24 402 To date, microbiological and molecular studies on glacier surfaces have been limited to snapshots, and we
25 403 await insight into temporal shifts and environmental responses in cryoconite at the community level.
26 404 However, molecular analyses are becoming increasingly affordable and accessible and are consequently
27 405 being employed more frequently. It is becoming increasingly clear that close examination of ecosystem
28 406 structure and function will be crucial for understanding biotic-abiotic processes on glacier surfaces. For a
29 407 more comprehensive review of the microbes inhabiting cryoconite holes, we direct the reader towards
30 408 Kaczmarek et al (2015).

31 409 *2 The origins of cryoconite biota:*

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33 410 The origins of cryoconite biota are currently unclear, with robust evidence in favour of any dominant
34 411 source or mode of delivery currently lacking. However, several hypotheses have emerged from the
35 412 literature, mostly linking cryoconite biota to the aeolian biome. Swan (1992) proposed the existence of an
36 413 aeolian biome based upon observations of microalgae, bacteria and spiders on high altitude and polar ice.
37 414 Active microbes have since been confirmed to survive in suspension in the atmosphere, some of which
38 415 are eventually deposited on ice surfaces (Swan, 1992; Sattler et al. 2001; Pearce et al. 2009). There, cryo-
39 416 tolerant species survive, especially under favourable conditions in cryoconite holes, whereas others
40 417 perish due to environmental and competitive stresses (Pearce et al. 2009; Anesio and Laybourn-Parry,
41 418 2011). Cryoconite biota may therefore be delivered to glacier surfaces directly from the atmosphere via
42 419 both wet and dry deposition. This may be from local or distant sources. Alternatively, biota may be
43 420 deposited onto fresh snow packs or precipitated out of atmospheric suspension in snow fall (probably
44 421 providing nuclei for ice crystallisation – Edwards et al. 2014a) and either redistributed hydrologically
45 422 following snow melt or incorporated into glacier ice in the accumulation zone. Microbes interred
46 423 englacially may be stored for 10^2 - 10^5 years, some being preferentially partitioned into water veins
47 424 (Mader et al. 2006) before being melted out in the ablation zone. Biota in basal ice and sediment may be
48 425 extruded onto the ice surface by thrust faulting or via pressure ridges and subsequently blown upglacier.
49 426 There may also be biota blown or simply dropped onto glaciers from local valley sides.

50 427 Suspension of microbes in the high atmosphere may pre-select microbial communities for survival on
51 428 glacier surfaces. Evidence suggests long term survival in the atmosphere requires similar adaptation to
52 429 survival on ice surfaces (tolerance to UV, cold and dessication; Pearce et al. 2009) and viable communities
53 430 may therefore be shaped to some degree prior to deposition. However, there are commonalities in species
54 431 abundance between cryoconite holes, soils, freshwater, marine, frozen lake and activated sludge habitats
55 432 (Edwards et al. 2011) that indicate wide cosmopolitanism of many cryoconite microbes. Furthermore,
56 433 post-depositional structuring of communities has been suggested to be dynamic over short time scales,
57 434 responding rapidly to local biotic and abiotic stresses (Edwards et al. 2014b; Priscu and Christner, 2004).
58 435 There is most likely a fine balance between cosmopolitanism and endemism that reflects complex

436 associations of sources and modes of delivery of biota, post-depositional ecological dynamics and local
 437 environmental regimes that collectively shape cryoconite microbial communities. Amplicon
 438 pyrosequencing of cryoconite bacterial 16S rRNA genes from six Arctic and Alpine glaciers and the
 439 southwestern margin of the Greenland Ice Sheet (Edwards 2014b) reveals that cosmopolitan generalist
 440 taxa (c.f. Barberan et al. 2012) are predominant in cryoconite bacterial communities (Fig 6). This is
 441 consistent with the notion that priority effects may be important in colonization of nascent cryoconite
 442 granules by bacteria, first indicated by Edwards et al. (2013c) as a result of phylotype abundance
 443 distribution models supporting deterministic community assembly as a result of several stages of
 444 succession. To an extent, environmental variability may buffer against priority effects (c.f. Tucker &
 445 Fukami, 2014) promoting species richness and evenness as insurance against fluctuating environmental
 446 conditions. Indeed, varying levels of bacterial community evenness correlated with ecosystem function
 447 measurements in Svalbard cryoconite (Edwards et al. 2011). By these means, perturbations at the ice
 448 surface may trigger reconfiguration of cryoconite associated microbiota. Further support that cryoconite
 449 granules are formed as a result of microbial succession is provided by the striking negative correlation in
 450 the relative abundance of taxa assigned to *r*-selected, early-colonizing *Betaproteobacteria* versus
 451 typically *K*-selected, late-colonizing *Alphaproteobacteria* (Fig 6; Edwards et al. 2014b). It is clear that the
 452 processes of microbial succession in supraglacial habitats such as cryoconite not only require, but merit
 453 further study as currently, our understanding of these processes is basic yet the implications for the
 454 development of biodiverse communities as a result of glacier melting are considerable. In short, the
 455 question of whether microbial succession interacts with glacier atrophy prior to the development of the
 456 glacier forefield is raised.

457 *3 Cryoconite Biogeochemistry*

458 Biogeochemical cycling in cryoconite holes has been intensely researched over the past decade due to the
 459 potential for storage, transformation and export of nutrients. Cryoconite ecosystems have been found to
 460 be colimited by temperature and nutrient stress (S awstrom et al. 2002), meaning knowledge of hole
 461 biogeochemistry is crucial for understanding cryoconite hole microbiology. Research has concentrated
 462 upon three main elements: Carbon (C), Nitrogen (N) and Phosphorous (P), with a particular focus upon C.
 463 These nutrients will be studied individually here.

464 *Carbon.* Cryoconite holes represent particularly active sites of C fixation (autotrophy) and oxidation
 465 (heterotrophy) in the supraglacial zone (Hodson et al. 2010a,b), with rates comparable to warm, nutrient
 466 rich environments being measured in cryoconite (Hodson et al. 2007, 2008; Anesio et al. 2009, 2010). C
 467 transformations may determine glacier albedo through aggregation and darkening of cryoconite
 468 (Kohshima et al. 1993; Takeuchi et al. 2001 a, b, c; Takeuchi, 2009; and B oggild et al. 2010; Hodson et al.
 469 2010a, b) and influence the quality and quantity of C exported to extraglacial environments (e.g. Hood et
 470 al. 2009).

471 *Net Ecosystem Production.* NEP describes the balance between autotrophy (fixation of CO₂ into organic
 472 molecules) and heterotrophy (metabolism of organic molecules back into atmospheric CO₂) (Eq.7).

$$473 \quad \text{NEP} = \text{PP} - \text{R} \quad (\text{Eq.7})$$

474 *Where PP = primary production and R = community respiration (Hodson et al. 2010)*

475 This has been a particular focus for glacier microbiologists because NEP determines whether a
 476 community represents a C sink or a C source (e.g. Stibal et al. 2008a; Hodson et al. 2010b; Cook et al.
 477 2012), and also whether there is an overall increase in dark OM on a glacier surface. In cryoconite holes
 478 autotrophy is opposed by heterotrophy, perhaps providing biotic control on granule morphology and
 479 glacier ablation (e.g. Hodson et al. 2008). NEP both drives and indicates community structure and
 480 function and hole biogeochemistry. For example, C fixation increases the pH of cryoconite hole melt water
 481 (Stibal and Tranter, 2007; Stibal et al. 2010), particularly important in Antarctic systems where
 482 cryoconite holes are decoupled from surface and atmospheric exchanges by thick ice lids. Several crucial
 483 abiotic controls upon NEP have been identified, including sediment arrangement (Cook et al. 2010;
 484 Telling et al. 2012a), PAR, N and P availability, solar angle and hydrologic regime (e.g. Mindl et al. 2007;
 485 Hodson et al. 2007; Stibal et al. 2008b; Hodson et al. 2010b; Irvine-Fynn et al. 2011; Telling et al. 2012a;
 486 Stibal et al. 2012b). Cook et al. (2010) and Telling et al. (2012a) suggested a threshold thickness of 3 mm

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3 487 above which systems are net heterotrophic, below which net autotrophic, and at which NEP is balanced.
4 488 Telling et al. (2012) found sediment thickness to explain more than half the variation in NEP in Arctic
5 489 cryoconite due to the increased surface area of cryoconite exposed to PAR. Cook et al.'s (2010)
6 490 mechanism of lateral equilibration suggests that given low gradient, slow moving ice and moderate
7 491 sediment delivery, cryoconite holes evolve towards robust net autotrophy. Where ice surface are steeper
8 492 or faster moving thick, net heterotrophic layers are more likely to form. Therefore, although rates of
9 493 microbial activity in cryoconite holes are broadly similar to aquatic ecosystems (e.g. Anesio et al. 2009)
10 494 NEP varies considerably over both space and time (Table 4). This has been further corroborated by
11 495 various Greenland (Stibal et al. 2010; 2012b; Cook et al. 2012; Yallop et al. 2012) and Svalbard (Langford
12 496 et al. 2014) transect studies which have found spatial patterns of NEP controlled primarily by granule size
13 497 limits imposed by disaggregation and removal of biomass by melt water, while nutrient and PAR
14 498 availability are also important. Under seasonal snow, photosynthesis probably ceases and systems
15 499 become net heterotrophic; however, this remains untested. Outside of cryoconite holes, thick, net
16 500 heterotrophic accumulations of cryoconite can develop under distinct redox and hydrological conditions
17 501 (Hodson et al. 2008).

18 502 NEP in cryoconite holes is impacted by bacterial activity (Foreman et al. 2007; Hodson et al. 2007; Mindl
19 503 et al. 2007) predominantly via heterotrophic C oxidation, much of the energy from which drives bacterial
20 504 growth and production. Anesio et al. (2010) examined bacterial production in Antarctic, Arctic and Alpine
21 505 cryoconite, finding rates between $0.13 \text{ ng C g}^{-1} \text{ h}^{-1}$ (Stubacher Sonnbliekees, Austria) and $39.7 \text{ ng C g}^{-1} \text{ h}^{-1}$
22 506 (Midtre Lovenbreen, Svalbard). The same study found bacterial doubling times to usually be < 5 days
23 507 (where > 60 days was suggested to signify negligible contribution to cryoconite biogeochemistry) apart
24 508 from in Antarctic melt water and radioactive cryoconite on Stubacher Sonnbliekees (Austria). However,
25 509 bacterial production only represents transformation of OC into biomass, omitting growth and respiration
26 510 (Hodson et al. 2007; Anesio et al. 2010). To characterise bacterial C fluxes, bacterial growth efficiency
27 511 (BGE) and respiration rates are also required (Hodson et al. 2007). Anesio et al. (2010) estimated bacteria
28 512 in Arctic cryoconite to use only 0.4 – 2.4% of available OC (1.2 – 7% in Antarctica), suggesting
29 513 autochthonous production alone was more than sufficient to sustain bacterial production. Low rates of
30 514 production were therefore unlikely to be due to OC limitation. Temperature, P, viral lysis, and grazing of
31 515 bacteria by ciliates were identified as much more likely limiting factors, although on Stubacher
32 516 Sonnbliekees, rates were probably also limited by radioactivity ($\sim 140,000\text{Bq}$) persisting from the 1984
33 517 Chernobyl disaster and bomb tests in the 1950s and 1960s (Tieber et al. 2009).

34 518 Recognising the need for standardised reporting of NEP, PP and R, Telling et al. (2010) evaluated various
35 519 measurement techniques. Measuring changes in dissolved inorganic C (ΔTDIC) consistently outperformed
36 520 radiolabel incorporation and dissolved O_2 methods. A standard procedure was proposed by Hodson et al.
37 521 (2010b) and Telling et al. (2010) whereby ΔTDIC incubations last for whole days and results normalised
38 522 for dry mass. Rates of PP, R and NEP previously reported in the literature are shown in Table 4.

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40 523 *Allochthonous and Autochthonous Carbon.* Cryoconite microbes utilise OC synthesised *in*
41 524 *situ* (autochthonous) and delivered from elsewhere (allochthonous). Autochthonous production involves
42 525 fixation of atmospheric CO_2 into organic molecules predominantly by photosynthesis. Allochthonous OC is
43 526 primarily deposited by wind and comprises fragments of flora, mineral dusts, microbes, BC and
44 527 anthropogenic pollutants from local and distant sources (e.g. Swan, 1992; Stibal et al. 2012b; Hodson,
45 528 2014). Englacial OC can be released by melt out and provides a significant source of ancient bioavailable
46 529 OC for downstream ecosystems (Stubbins et al. 2012) and likely provides an energy source for cryoconite
47 530 microbes. Subglacial OC might also be delivered to the supraglacial zone by thrust faulting (Stibal et al.
48 531 2012b), supplementing allochthonous OC in cryoconite holes in some locations.

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50 532 Autochthonous and allochthonous OC together (TOC) provide crucial substrates for heterotrophy. It is
51 533 uncertain whether OC demands in cryoconite holes are met by autochthonous production, or whether
52 534 heterotrophy is sustained primarily by OC from allochthonous sources (Stibal et al. 2008a; Stibal et al.
53 535 2010; Telling et al. 2012a; Edwards et al. 2013b). It has emerged that in general, the interiors of large ice
54 536 sheets and glaciers are characterised by autochthonous OC accumulation and allochthonous OC from
55 537 distant sources whereas ice sheet margins and small glaciers are dominated by local allochthonous OC
56 538 (Stibal et al. 2012a; Telling et al. 2012a). However, variations in topographic shading, incident radiation,
57 539 sediment layer thicknesses, allochthonous OC and nutrient supply and ice type likely establish local

540 heterogeneity and dynamism in cryoconite carbon budgets. For further information on allochthonous and
541 autochthonous OC dynamics we suggest Stibal et al.'s (2012a) review.

542 *Carbon Export.* OC produced or transformed in cryoconite holes can be redistributed by meltwater and
543 ultimately provide a source of labile C for nearby terrestrial, marine or lacustrine ecosystems (Wharton et
544 al. 1985; Swan, 1992; Hood et al. 2009; Lawson et al. 2014). This is usually by entrainment into
545 supraglacial streams or possibly transport in solution through the low density ice comprising the
546 weathering crust (top ~2m of ice surface; Irvine-Fynn and Edwards, 2014). Whole cells and organic
547 molecules dissolved in water (Dissolved Organic Carbon: DOC) are probably transferred between habitats
548 within the supraglacial zone and other glacial and extra-glacial environments, although no measurements
549 of either dissolved or particulate OC exported from cryoconite holes have yet been made. This pathway
550 might be important for seeding proglacial streams, glacier fed lakes and subglacial sediments, as well as
551 providing nutrients and energy sources for pre-existing downstream ecosystems, and requires research,
552 although the stark contrast in microbial abundance between cryoconite sediment and overlying
553 meltwater suggests robust binding of OM to cryoconite debris and limited transfer into suspension or
554 solution. This indicates that cryoconite currently provides POC storage in the supraglacial environment.
555 Nevertheless, cryoconite and other supraglacial habitats have recently been suggested to be important
556 metacommunities influencing downstream biodiversity and community structure (Wilhelm et al. 2013).
557 For further information regarding DOC and POC export to rivers and oceans, we suggest consulting Stibal
558 et al. 2012's review.

559 *Carbon Cycle Models.* In situ measurements of NEP, PP and R in cryoconite holes have informed models of
560 regional and global C cycling. Anesio et al. (2009) upscaled local measurements of NEP to all glaciated
561 areas outside of Antarctica, suggesting net C fixation of ~64 Gg a⁻¹. Their analysis assumed rates of NEP in
562 cryoconite obtained from a small number of sites in Svalbard, Greenland and European Alps were globally
563 representative and temporally constant. Further, the extent of the summer ablation zone was assumed
564 constant, compensated for using a conservative melt duration. This approach overlooks seasonal shifts in
565 irradiance, temperature, ice and sediment dynamics that may significantly impact rates of C cycling.
566 Furthermore, Anesio et al.'s (2009) spot measurements of NEP were 10 – 100 times greater than
567 subsequent measurements made on some of the same glaciers, possibly due to methodological issues
568 (Anesio et al. 2010). Hodson et al. (2010a) estimated C fluxes on the Greenland ice sheet based upon
569 cryoconite alone. Spatio-temporal evolution of the ablation zone was incorporated, where PP was limited
570 to the bare ice area while R occurred in both bare ice and slush. Mass per unit area of cryoconite and rates
571 of PP and R (derived from short transects from the ice margin near Kangerlussuaq, Greenland) were
572 assumed spatially uniform. Later, Cook et al. (2012) showed the assumption of spatial uniformity was not
573 justified, and in fact the greatest mass loading, spatial coverage and rates of biological activity for
574 cryoconite occurred further inland than the end of Hodson et al.'s (2010a) transects. Furthermore,
575 Hodson et al. (2010a) measured late-season communities approaching acquiescence. Cook et al. (2012)
576 obtained measurements from a 79 km transect (the entire ablation zone) to estimate C fluxes from a 1600
577 km² area of the Greenland ice sheet, suggesting additional transects would be required to upscale further.
578 Their model incorporated spatially variable coverage, mass loading and rates of PP and R, as well as
579 including surface algal blooms. Spatial variability in cryoconite distribution and rates of activity had a
580 strong influence on C-flux estimates, and the inclusion of surface-dwelling algae potentially greatly
581 increased C fixation along the transect. However, that model is fundamentally limited in a number of
582 ways: First, there remains an assumption that there are only two discrete ecosystems that contribute to
583 supraglacial C fluxes; Second, it assumes microbial activity, spatial coverage and mass loading are
584 constant throughout a melt season and that there is no redistribution of debris or biomass. Third, it
585 assumes no changes in albedo, hydrology or other abiotic factors occur during the melt season and makes
586 no attempt to model any associated feedbacks. Fourth, rates of algal productivity were based upon 14C
587 incubations and loosely constrained estimates of algal respiration. Finally, deriving cryoconite
588 distribution in photographs by calibrating against measurements made in small quadrats is unlikely to be
589 accurate (recently corroborated by Chandler et al. 2015 who found high spatial and temporal variability
590 in cryoconite coverage and productivity on the Greenland Ice Sheet). Nevertheless, these papers
591 encouraged appreciation of the supraglacial biome and its significance for global atmospheric exchanges.

592 *Nitrogen.* Despite Bayley (1891) identifying nitrogenous material on ice surfaces, and abundant studies of
593 N cycling in polar oceans (Dittmar, 2004), ice cores (Olivier et al. 2006), soils (Nordin et al. 2004), rivers
594 (Tockner et al. 2002), subglacial sediments (Wynn et al. 2007) and snowpacks (Williams et al. 1996; Jones

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3 595 et al. 1999; Hodson et al. 2005; Hodson, 2006), supraglacial N cycling was only recently considered in
4 596 detail. Tranter et al. (2004) found high inorganic : organic N ratios in Antarctic cryoconite holes, implying
5 597 recycling rather than fixation of nitrogenous compounds, likely due to isolation by thick ice lids. In
6 598 contrast, holes in Svalbard showed net NH_3 production, indicating fixation of N_2 by cyanobacteria
7 599 (Hodson et al. 2008). Telling et al. (2012b) showed N fixation to be energy demanding and only
8 600 undertaken by N fixers when allochthonous bio-available N is scarce. Therefore, active fixation indicates
9 601 insufficient allochthonous bio-available N and may limit growth. Säwstrom et al. (2002) showed Svalbard
10 602 cryoconite communities were not N limited, highlighting the influence of N-fixing bacteria on ecosystem
11 603 function. Telling et al. (2011, 2012b) investigated N cycling across the ablation zones of Svalbard glaciers
12 604 and the Greenland ice sheet. N_2 fixation was active in cryoconite holes in both regions, implying
13 605 insufficient allochthonous bio-available N to sustain microbial production. Evidence of denitrification and
14 606 ammonification was also identified in Greenland (Telling et al. 2011) and *nifH* genes have been detected
15 607 across the south-west Greenland Ice Sheet (Telling et al. 2012). Allochthonous sources included
16 608 anthropogenic N compounds and guano from bird colonies (guano was corroborated as a source of
17 609 bioavailable N by Zarsky et al. 2013; Hodson et al. 2006; Hodson et al. 2008). Other stages of N cycling
18 610 including microbial ammonium assimilation (Zarsky et al. 2013) and nitrification (Wynn et al. 2007;
19 611 Hodson et al. 2010c; Ansari et al. 2013) have been observed on Svalbard glaciers. Amplification of *nifH*
20 612 genes indicated genetic potential for nitrogen fixation by bacteria (Cameron et al. 2012) and Archaea
21 613 (Zarsky et al. 2013) in Svalbard cryoconite. Catalysis of nitrification (Hodson et al. 2005; Wynn et al.
22 614 2007) and N_2 fixation (Telling et al. 2011) in cryoconite communities might contribute organic N
23 615 substrates to subglacial and proglacial ecosystems. The nutrient demands of cryoconite holes and wet
24 616 snowpacks account for most of the annual NH_4^+ deposition on Midtre Lovénbréen (Svalbard) (Säwstrom
25 617 et al. 2002; Hodson et al. 2005; Anesio et al. 2009; Hodson et al. 2010c). N-addition experiments have
26 618 shown N availability not to be a limiting factor in Svalbard cryoconite, suggesting that N-cycling microbes
27 619 contribute significantly to cryoconite communities (Hodson et al. 2008). Recently, Edwards et al.'s
28 620 (2013b) cryoconite metagenome showed an abundance of functional genes related to N, Fe, S and P
29 621 cycling that suggested efficient nitrogen recycling on Rotmoosferner (Austria). Rates of N fixation have
30 622 been shown to increase in late summer once bioavailable N stores have depleted (Anesio and Laybourn-
31 623 Parry, 2011). Supraglacial N cycling remains poorly understood, although recent work by Segawa et al.
32 624 (2014) used isotopic and RNA evidence to directly trace N cycling on a glacier surface in central Asia,
33 625 showing that intense N cycling supports abundant microbial life on glaciers.

34 626 *Anthropogenic Nitrogen.* Allochthonous N deposition down-regulates N_2 fixation, increasing available
35 627 energy for microbial growth and proliferation, although Telling et al. (2011) showed N limitation is
36 628 unlikely to primarily control biomass production in cryoconite holes. Anthropogenic pollutants have
37 629 increased the concentration of bioavailable N in polar snowpacks such that cryoconite microbes no longer
38 630 need to fix atmospheric N_2 , since activity can be sustained by allochthonous inputs (Telling et al. 2011).
39 631 Hodson et al. (2010c) monitored nutrient budgets in Svalbard after a period of pollutant deposition and
40 632 observed shifts in nutrient cycling that impacted the entire glacier catchment. Anthropogenic industrial
41 633 activity produces nitrogenous compounds that can be suspended in the atmosphere and deposited on
42 634 glacier surfaces (Kozak et al. 2013), possibly influencing nutrient cycling, community dynamics and NEP
43 635 in these areas. Heavy metals have also been found to accumulate in cryoconite in the Arctic (Singh et al.
44 636 2013). It is well known that in extraglacial areas nitrogenous inputs from industrial emissions, road
45 637 vehicles and agricultural fertilisers have a strong influence upon ecosystem dynamics.

46 638 *Phosphorous.* Little is known about P cycling in the supraglacial zone, although cryoconite communities
47 639 are likely P-limited (Stibal and Tranter, 2007; Säwstrom et al. 2002; Mindl et al. 2007; Hodson et al. 2008;
48 640 Stibal et al. 2008b; Stibal et al. 2009). Typical P concentrations on Arctic ice surfaces have been estimated
49 641 at $< 0.1\mu\text{M}$ (Stibal et al. 2009). Säwstrom et al. (2002) showed bacterial production in cryoconite to
50 642 increase following P addition, but only above 12°C , suggesting that cryoconite communities may be co-
51 643 limited by P availability and temperature. In Svalbard, Stibal et al. (2008b) reported P deficiency in
52 644 cryoconite melt water relative to cryoconite sediment, indicating that the majority of P in the supraglacial
53 645 zone was bound to cryoconite debris. Mueller et al. (2001) suggested that P demand likely exceeds P
54 646 supply in the supraglacial zone because atmospheric deposition is very low and there are no mechanisms
55 647 of biotic P generation that can compensate. Stibal et al. (2009) agreed that inorganic P is probably scarce
56 648 and rapidly depleted in cryoconite, but found that microbes respond by recycling P from OM using
57 649 phosphatase (an enzyme used to scavenge P from organic complexes). The efficiency of this process is
58 650 uncertain. Adding bioavailable P to cryoconite incubations resulted in the inhibition of phosphatase

651 activity, indicating insufficient allochthonous P supply in natural cryoconite systems. Importantly, Stibal
652 et al. (2009) identified several difficulties with measuring P concentrations in cryoconite, in particular
653 only a fraction of the total bioavailable P present seems to be accessible to microbes, meaning basic
654 chemical extraction techniques are not suitable for assessing the amount of P available for cryoconite
655 microbes.

656 **V Antarctic and lower-latitude cryoconite**

657 Much of the current knowledge about cryoconite has come from work in the Arctic; however, there is a
658 significant body of literature concerning cryoconite in Antarctica and on low-latitude glaciers. Antarctica
659 is generally much colder and drier than the Arctic, meaning cryoconite phenomena contrast greatly with
660 those described in section 2. Antarctic holes form by upwards melting from entombed sediment in
661 summer (Fountain et al. 2008), retaining a thick ice lid that decouples debris and melt-water from
662 atmospheric and ice surface exchanges. This reduces flushing of cryoconite holes and facilitates the
663 accumulation of solutes leached from surrounding ice and produced by microbial activity. Concentrations
664 of Cl⁻ ions in Antarctic cryoconite holes have suggested continuous periods of isolation from atmospheric
665 exchanged of up to 11 years (Fountain et al. 2004, Tranter et al. 2004, Bagshaw et al. 2007). This can
666 result in extreme hydrochemical conditions within cryoconite holes that are unique to Antarctica
667 (Tranter et al. 2004; Hodson et al. 2008). This probably explains the contrasts in biota between Antarctic
668 and Arctic cryoconite. Antarctic cryoconite generally contains little OM (Table 1) and bacterial
669 abundance, productivity and bacterial doubling times have been suggested to be much lower in Antarctic
670 cryoconite than in the Arctic (Anesio et al. 2010). Nutrient limitation arises due to the isolation of
671 Antarctic cryoconite holes, necessitating recycling (Tranter et al. 2004). This increases the concentrations
672 of ammonia, nitrate and dissolved P concentrations and lowers the pH of cryoconite melt water (Meuller
673 et al. 2001) and causes modes of biogeochemical cycling in Antarctic cryoconite holes to contrast with
674 that in the Arctic. In particular, contrasts in nitrogen cycling have been identified between Arctic and
675 Antarctic cryoconite due to inhibited transfer of atmospheric N₂ to cyanobacteria in Antarctic holes
676 (Tranter et al. 2004). The OM in Antarctic cryoconite was found to be less heterogeneous than in Arctic
677 cryoconite (Pautler et al. 2013) probably due to ice lidding and remoteness limiting allochthonous inputs
678 from plants, mosses and sphagnum from deglaciated land. Similarly, Bagshaw et al. (2013) described
679 clear disparities between cryoconite and valley-floor OC in the McMurdo Dry Valleys, showing cryoconite
680 to support net autochthonous OC production. Antarctic cryoconite is therefore probably more reliant
681 upon autochthonous production of OC to support microbial activity. The different conditions in Arctic and
682 Arctic cryoconite holes has been shown to generate contrasts in microbial community structures. Meuller
683 and Pollard (2004) showed that inter-hole mixing in open Arctic cryoconite holes resets community
684 structures and homogenises ecosystems, whereas hydrologic and atmospheric isolation in Antarctica
685 establishes more optimised communities in areas of different environmental pressures. Microbial
686 communities are less cosmopolitan in the Antarctic because the more extreme environmental stresses
687 promote endemism. An additional cryoconite habitat has been identified in Antarctic blue ice areas
688 (Hodson et al. 2013). These regions of smooth, wind-polished ice contain entombed cryoconite that
689 absorbs solar radiation and melts a subsurface layer of liquid water, supporting microbial activity. The
690 biogeochemistry of these habitats is characterised by low rates of PP, R and melt water replenishment
691 due to low temperature and solar irradiance. These habitats require very low temperatures and
692 persistent strong winds to form and are therefore unique to Antarctica.

693 Despite being isolated from surface hydrologic and atmospheric exchanges, cryoconite holes are
694 important components of Antarctic glacier hydrology. About a third of all supraglacial melt on Wright
695 Lower glacier was attributed to the formation of cryoconite holes which then stored up to 47,000 m³ of
696 water (MacDonnell and Fitzsimons, 2008). Furthermore, Antarctic cryoconite holes can interconnect and
697 link with supraglacial streams and lakes via discrete conduits (Fountain et al. 1998; Fountain et al. 2004;
698 Tranter et al. 2005; Bagshaw et al. 2007; MacDonnell and Fitzsimons, 2008). Up to 56% of cryoconite
699 holes on Canada Glacier were estimated to be hydrologically connected (Fountain et al. 2004), providing a
700 subsurface drainage mechanism that is likely unique to cold Antarctic glaciers. Periodic 'stripping events'
701 have also been reported in Antarctica, where the upper layer of glacier surface is suddenly removed by
702 rapid melt (Fountain et al. 2004; MacDonnell and Fitzsimons, 2008). This probably provides the primary
703 mechanism of cryoconite redistribution on Antarctic glaciers (Fountain et al. 2004). These events occur
704 roughly decadal on Antarctic glaciers (Bagshaw et al. 2013), whereas they may be annual in the Arctic.
705 Seasonal evolution from hydrologic isolation to interconnectedness was proposed by MacDonnell and
706 Fitzsimons (2012), who also suggested that all cryoconite holes are ultimately erased by ablation,

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3 707 dependent upon water supply, ablation rate and local topography. Telling et al (2014) also showed that
4 708 periodic melt events provide nutrient fluxes into cryoconite holes that stimulate biological activity
5 709 including nitrification, phosphorous uptake and bacterial production. Antarctic cryoconite holes have
6 710 additional importance as analogs for microbial habitats on other icy planets including Mars (e.g. McKay
7 711 and Stoker, 1989; Priscu et al. 1998; Priscu et al. 1999a,b; Paerl and Priscu, 1998; MacClune et al. 2003;
8 712 Schulze-Makuch and Grinspoon, 2005; Wentworth et al. 2005; Tranter et al. 2010). Understanding
9 713 microbial processes in Antarctic cryoconite holes may therefore have wider reaching implications than
10 714 our own planet and contemporary timescale.

11 715 Cryoconite on low-latitude mountain glaciers is distinct from cryoconite on polar glaciers and ice sheets.
12 716 This is primarily due to local glaciological and meteorological conditions. Low-latitude glaciers are
13 717 generally small, fast flowing and subject to large diurnal fluctuations in energy balance. Solar radiation is
14 718 more intense during the day at lower latitudes; however dark nights and variable cloud cover can
15 719 produce complex melt dynamics. Due to the abundance of deglaciated land in close proximity to most
16 720 low-latitude glaciers there is greater deposition of aeolian dusts and soluble ions from terrestrial and
17 721 anthropogenic sources. Takeuchi and Li (2008) showed that this causes rapid microbial production and
18 722 high cryoconite coverage on Asian glaciers. High melt rates on low-latitude glaciers tend to produce
19 723 shallower cryoconite holes with shorter life spans than those on polar ice (Takeuchi et al. 2000), and
20 724 more frequent redistribution across ice surfaces might therefore be expected. High microbial production
21 725 and abundant inorganic impurities encourage diverse microfauna and meiofauna to inhabit the glacier
22 726 surface. These include glacial midges, copepods, collembolan, tardigrada and rotifers. Contrasting
23 727 organisational taxonomic units and metabolite profiles has revealed different microbial community
24 728 structures and functions in cryoconite from Arctic and Alpine glaciers (Edwards et al. 2014b). Cryoconite
25 729 biogeochemistry on low-latitude glaciers is probably similar to that of ice sheet margins, where fast
26 730 flowing and rapidly melting ice favours net heterotrophy (Stibal et al. 2012a). Edwards et al. (2014b)
27 731 suggested a latitudinal control upon NEP whereby lower latitudes are associated with net heterotrophy
28 732 and high northern latitudes associated with net autotrophy. There is a geographical bias in the literature
29 733 that favours polar over mountain glaciers, despite mountain glaciers being very sensitive to albedo shifts
30 734 (Oerlemans et al. 2009; Ming et al. 2013), important for water security (Edwards et al. 2014a) and
31 735 particularly poorly understood in terms of their response to climate change (IPCC, 2013).

32 736 There are therefore stark geographical contrasts in cryoconite morphodynamics, biogeochemistry and
33 737 microbial ecology. However, these seem to arise from variations in the physical environment in which the
34 738 cryoconite exists rather than from different processes. This suggests commonalities in the fundamental
35 739 mechanisms governing cryoconite and cryoconite habitat properties that require elucidation, and
36 740 indicates the potential for general, widely applicable cryoconite models to be developed.

37 741 **VI Cryoconite, climate change and anthropogenic pollution**

38 742 The response of Earth's ice to climate warming can be broadly characterised by increasingly negative
39 743 mass balance, retreat or acceleration towards lower elevations. Since ice masses store ~70% of Earth's
40 744 freshwater, this threatens to destabilise a crucial domestic, agricultural and industrial resource relied
41 745 upon by over a billion people (Hodson, 2014) and a crucial biome harbouring unique microbial
42 746 assemblages (Anesio and Laybourn Parry, 2011).

43 747 Glacier and ice sheet wastage is strongly influenced by ice surface albedo, which may in turn be
44 748 influenced by supraglacial ecology. Ice albedo can be lowered by algal blooms on ice surfaces (Yallop et al,
45 749 2012), dust deposition (Bøggild et al. 2010), melt water production (Gruell, 2000) and also the
46 750 aggregation of cryoconite granules. Once aggregated the growth and proliferation of microbes,
47 751 entanglement of allochthonous debris, production of humic substances and photo-protective
48 752 pigmentation further decrease granule albedo (Takeuchi, 2002a; Takeuchi et al. 1998, 2001a, 2010;
49 753 Hodson et al. 2008, 2010a, b; Irvine-Fynn et al. 2010; Yallop et al. 2012). Aggregation of cryoconite also
50 754 enhances the longevity of minerals and OM on ice surfaces, therefore prolonging their albedo lowering
51 755 effect. For example Hodson et al. (2010b) found cryoconite distribution to explain 53% of the albedo
52 756 variance on Longyearbreen (Svalbard), although complex interactions between cryoconite coverage, hole
53 757 evolution, microtopography, surface roughness and energy balance (e.g. Hodson et al. 2007; Irvine-Fynn
54 758 et al. 2010, 2011; Cook et al. 2010; Hodson et al. 2010b) imply complex relationships exist between
55 759 cryoconite morphodynamics and ice surface melt rate. Increased temperature might cause more frequent
56 760 melt-out and enhanced hydraulic redistribution of cryoconite over ice surfaces (Hodson et al. 2008) and

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3 761 therefore alter supraglacial melt patterns. As identified by Hodson et al. (2007, 2010a) and Cook et al.
4 762 (2012), longer ablation seasons due to climate warming will likely extend annual periods of
5 763 photoautotrophy, possibly promoting growth of cryoconite granules and proliferation of surface dwelling
6 764 algae, further reducing ice surface albedo. On the Greenland ice sheet, warming was estimated to
7 765 strengthen net autotrophy and increase atmospheric C fixation (Cook et al. 2012); however, albedo and
8 766 melt feedbacks were not considered, and increased snowfall in a warmer climate could promote
9 767 heterotrophy (Jones, 1999). Given recent suggestions of melt-water disruption mobilising cells and
10 768 partially disaggregating cryoconite granules (Langford et al. 2014), climate-forced changes to glacier
11 769 hydrologic regimes will likely impact cryoconite morphology and alter environmental stresses on
12 770 incumbent organisms, with unknown impacts upon ice surface albedo and melt rates. It is currently
13 771 unclear whether additional melt will enhance nutrient delivery and therefore cohesive OM production
14 772 promoting cryoconite growth, or enhance disturbance and disaggregation of granules promoting
15 773 redistribution. In a palaeoglaciological context, Abbot and Pierrehumbert (2010) suggested cryoconite
16 774 might contribute to albedo-driven deglaciation from 'Snowball Earth' events, implying its significance as a
17 775 melt catalyst over geologic timescales.

18 776 As well as being a potential melt catalyst, cryoconite is a store of nutrients and biodiversity in otherwise
19 777 depauperate or ultra-oligotrophic environments. For example, nutrient concentrations in Antarctic
20 778 cryoconite holes have been found to be much higher than in surrounding ice and sediments (Tranter et al.
21 779 2004; Bagshaw et al. 2013). Since cryoconite holes contribute to supraglacial hydraulic regimes (Fountain
22 780 et al. 2004; Hodson et al. 2008) the transformation and accumulation of nutrients within them influences
23 781 the geochemistry of melt waters exported to nearby valley ecosystems via ephemeral streams. Export of
24 782 nutrients and biota from ice surfaces to deglaciated areas will be sensitive to climatic changes because
25 783 warmer temperatures ultimately transform glacial zones into proglacial zones (Prowse et al. 2006),
26 784 accompanied by release of glacier-stored nutrients and changes to mechanisms of nutrient cycling (Stibal
27 785 et al. 2012b). Glacier hydrologic regimes are vulnerable to dramatic changes due to increased
28 786 temperature, with mass loss leading to greater isolation of the supraglacial zone due to basal refreezing
29 787 or, where refreezing does not occur, increased melt could tightly couple the supraglacial, subglacial and
30 788 extraglacial zones (Hodson et al. 2008), impacting biogeochemical transformations and export to
31 789 forefields. In the Arctic, Wilhelm et al. (2013) showed that cryoconite contributes to ecological succession
32 790 in glacier fed streams, particularly following glacier retreat. Cryoconite has also been suggested to be an
33 791 important source of microbes that recolonize freshly exposed land following glacier retreat (Kaštovská et
34 792 al. 2005). Increased summer snowmelt might increase the delivery of nutrients and biota to glacier
35 793 surface habitats and also the extraglacial zones (Hodson et al. 2008). Glaciers have been shown to provide
36 794 sources of ancient, bioavailable OC to marine, riverine and lacustrine ecosystems and cryoconite may
37 795 therefore play an important role in defining the carbon cycling regime in diverse environments (e.g. Mindl
38 796 et al. 2007; Hood et al. 2009; Stubbins et al. 2012; Singer et al. 2012). The role of cryoconite in this
39 797 process is not currently well understood.

40 798 The role of cryoconite granules for contaminant dynamics on glacier surfaces is also uncertain. Hodson et
41 799 al. (2010b) suggested cryoconite to catalyse supraglacial chemical weathering by extending rock-water
42 800 interactions, with implications for both glacial and extraglacial geochemistry. Other impurities that
43 801 influence glacier albedo (e.g. BC, mineral dust) or are ecologically damaging (e.g. POPs, heavy metals,
44 802 pesticides) may have their residence on glacier surfaces prolonged, and therefore their impact
45 803 exacerbated, by incorporation into cryoconite. Several types of POP were identified in cryoconite in the
46 804 European Alps by Lee et al. (2011), particularly on glaciers used for recreation. Genes for antibiotic
47 805 resistance have been identified in cryoconite in a range of non-Antarctic glaciers, indicating widespread
48 806 contamination by anthropogenic antibiotics (Segawa et al. 2013). Incorporation into cryoconite might
49 807 cause bioaccumulation of contaminants. Alternatively, burial of dark particulates under brighter biomass
50 808 at granule surfaces and metabolism of pollutants might decrease their potency (Hodson, 2014).
51 809 Potentially harmful radionuclide concentrations have been identified in Alpine cryoconite (Tieber et al.
52 810 2009) originating from the 1984 Chernobyl disaster and the bomb tests of the 1950s and 1960s,
53 811 illustrating the potential for cryoconite contaminant storage. The potential for increased delivery and
54 812 export of supraglacial contaminants in a warmer climate has not yet been studied in detail. However, the
55 813 role of supraglacial BC as an amplifier of climatic change has recently been recognised (Casey et al. 2013;
56 814 Hodson, 2014). There remains great uncertainty about the role of cryoconite in remediating the climate
57 815 impacts of BC on ice surfaces. Incorporation of BC into cryoconite may prolong its residence, but may
58 816 reduce its impact by covering it in lighter-coloured biomass. BC may also provide an allochthonous source

817 of bioavailable OC to be metabolised by cryoconite heterotrophs, diminishing its potency (Hodson, 2014).
818 Further studies are required to uncover the role of cryoconite in BC dynamics in the supraglacial zone.

819 Cryoconite therefore plays a complex and as yet uncertain role in supraglacial climate processes. The
820 properties of cryoconite and cryoconite habitats will likely respond to shifts in climate, while potentially
821 amplifying climate changes through albedo feedbacks. The role of cryoconite in bioremediating or
822 exacerbating the impacts of contaminants and anthropogenic pollutants is still unknown. Furthermore,
823 biogeochemical exports from ice surfaces will likely respond to climate changes and have far-reaching
824 impacts for polar ecosystems. However, these processes are poorly understood and require urgent
825 attention.

826 **VII Is cryoconite science back to where it started?**

827 The history of glacial microbiology could arguably start with the work of Kohshima (1984) and Wharton
828 et al. (1985); certainly appreciation of supraglacial ecosystems has only become widespread since.
829 However, microbial life on ice was hypothesised by ancient Greeks (Sattler et al. 2002) several thousand
830 years previously. In 1818 James Ross described 'crimson cliffs' of biologically inoculated ice in Greenland,
831 and soon after cryoconite holes were documented by Agassiz (1846) who suggested that their formation
832 was related to energy balance. The microbiological significance was recognised by Nordenskiöld (1875),
833 and the association between cryoconite and albedo-driven melt dynamics was established by
834 Nordenskiöld (1875) and Nansen (1906). In fact, many of the fundamental principles underpinning
835 modern supraglacial ecology had already been established by the early 1900s, and the major questions
836 facing cryoconite scientists at the end of the 19th century were the same as those we face in the second
837 decade of the twenty-first century. It is therefore crucial to look back to the "prehistory" of cryoconite
838 research, both to direct future research and to appreciate the remarkable insights of the early polar
839 scientists.

840 A.E. Nordenskiöld coined the term "cryoconite" to describe cylindrical 'ice pipes' containing 'remarkable
841 powder' that hampered his crossing of Greenland in 1870 (Leslie, 1879). The term originates from the
842 Greek "kryos" (cold) and "konis" (dust). The holes he documented were "a foot or two deep, from a couple
843 of lines to a foot in diameter, and so close together that it was impossible to find between them room for
844 the foot, much less a sleeping sack" (Leslie, 1879). Nordenskiöld postulated that these holes formed by
845 solar heating of dark cryoconite debris and this was corroborated by several of his contemporaries,
846 notably Drygalski (1897), who further suggested that stable, low gradient ice and multiple melt seasons
847 as prerequisites for hole formation, and subsequently Hobbs (1910), Phillip (1912), Kayser (1928),
848 Wegener (1930) and Poser (1934). Some debate surrounded the relative importance of diffuse and direct
849 radiation for hole development, with Phillip (1912) suggesting direct transmission through hole walls to
850 be the dominant control, whereas Brandt (1931) and Wagner (1938) thought diffuse radiation was more
851 important. Sharp (1947) made early suggestions of lateral expansion of cryoconite holes, presaging Cook
852 et al. (2010) by 63 years, proposing convection currents in cryoconite hole water as a primary driver.
853 Gajda (1958) later summarised cryoconite hole formation (Table 5) that was heavily reliant upon the
854 work of early polar scientists and, although efforts have been made to describe the system numerically
855 and some further insights made since (e.g. Gribbon, 1979; McIntyre, 1984; Cook et al. 2010) remains
856 relevant today.

857 Observations of cryoconite hole dimensions and frequency distribution have been made regularly
858 between Nordenskiöld (1875) and the present day, and in fact earlier reports were occasionally provided
859 by scientists such as Agassiz (1947). Early data was predominantly gathered in Greenland (e.g.
860 Nordenskiöld, 1875; Nansen, 1906; von Drygalski, 1897; Hobbs, 1910; Steinbock, 1936). Extensive
861 empirical observations in the 'cryoconite zone' (between the ice margin and 700m elevation) in Thule
862 (Greenland) were provided by Gajda (1958), who found spatial variations in cryoconite hole sizes
863 between the ice margin and snow line. Similar measurements have been made recently, with Stibal et al.
864 (2012b), Yallop et al. (2012) and Cook et al. (2012) examining elevational gradients of cryoconite
865 dimensions in South-West Greenland. The suggestion that cryoconite hole morphology could provide an
866 indicator of synoptic meteorology was proposed by Steinbock (1936) and reiterated by Gajda (1958),
867 Gerdel and Drouet (1960), Brochu (1975) and Gribbon (1979). Recently, cryoconite holes have begun to
868 be recognised as components of the hydrologically active porous 1-2 m of surface ice on glaciers known
869 as the "weathering crust" (Muller and Keeler, 1969; Irvine-Fynn et al. 2012; Irvine-Fynn and Edwards,
870 2014); however Gribbon (1979) referenced unpublished work by Thurmann that showed the frequency
871 distribution of cryoconite holes to be dependent primarily upon supply of sediment transported through

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3 872 the weathering crust and temporarily stored in interstitial pores. Gerdel and Drouet (1960) also
4 873 highlighted weathering crust decay as a key control on hole development, reinforcing work by Drygalski
5 874 (1897).

6 875 Upon examining individual granules of cryoconite, Nordenskiöld and other nineteenth century scientists
7 876 quickly realised they comprised both mineral and biological components. Nordenskiöld showed
8 877 cryoconite to form “small, round balls of loose consistency” composed mainly of quartz, feldspar, augite
9 878 and OM as well as mysterious magnetic particles. Nordenskiöld’s botanist revealed the OM to be largely
10 879 composed of brown-coloured polycellular algae. Around the same time, Swedish explorer N.O. Holst made
11 880 similar observations, describing cryoconite as “little balls as big as beans” (Lindahl, 1888). On the origin
12 881 of cryoconite, however, these scientists disagreed. To Nordenskiöld, cryoconite mineralogy indicated
13 882 wind deposited terrestrial dust from distant sources, supplemented by a cosmic component. Holst,
14 883 amongst others (including von Lasaulle, Zirkel and Swedmark) argued that cryoconite contained “nothing
15 884 but the ordinary components of primitive rock” (Lindahl, 1888). Petrographic analyses by Bayley (1891)
16 885 identified feldspar, quartz, mica and hornblende as dominant constituents, with minor contributions from
17 886 garnet, zircon, magnetite, augite and sillimanite, all thought to have been deposited by wind from a region
18 887 of crystalline schist’s, although Bayley (1891) also suggested commonalities with deep-sea sediments
19 888 supporting cosmic contributions. Later analyses by Drygalski (1897) and observations of non-uniform
20 889 cryoconite distribution (Nansen, 1882) largely discredited cosmic origins (Garret and Verzella, 2008). It
21 890 is possible that some of the particles that Nordenskiöld (1875) identified as cosmic were derived from
22 891 anthropogenic activity. The industrial revolution was underway but he likely considered Greenland too
23 892 remote to receive contaminants. It is now known that these pollutants provide bio-available C and N to
24 893 polar glaciers and darken ice (e.g. Kozak et al. 2013; Hodson, 2014). Later, researchers such as Kornerup
25 894 and de Quervain suggested cryoconite to be formed from clays or even decomposition products of
26 895 ptarmigan guano. Guano has been recognised recently as a potentially important N source on some
27 896 mountain glaciers (Zarsky et al. 2013) and near penguin colonies in Antarctica (Hodson 2006). As
28 897 research continued, a consensus that cryoconite comprises terrestrial materials emerged, although
29 898 sources vary between glaciers (Kayser, 1928). Gajda (1958) and Gerdel and Drouet (1960) highlighted
30 899 wind deposition from local deglaciated land as a primary source of cryoconite minerals, corroborated by
31 900 a negative correlation between granule size and distance from the ice margin, supporting Nansen (1906).
32 901 Although a contemporary debate continues regarding the details of sediment delivery to glaciers (e.g.
33 902 Bullard et al. 2013; Tedesco et al. 2013; Zarsky et al. 2013; Langford et al. 2014), the early twentieth
34 903 century consensus that minerals are deposited by wind from local and distant sources, supplemented by
35 904 inputs from adjacent exposed rock faces and subglacial pressure faulting, persists.

36 905 OM in cryoconite holes has been studied intensely during the nineteenth, twentieth and twenty-first
37 906 centuries. Nordenskiöld and Berggreen had already identified cyanobacteria as the dominant species
38 907 inhabiting Greenland cryoconite when Whittock (1885) observed algae and, later, Drygalski (1897)
39 908 reported cyanobacteria, chlorophytes and desmids in nearby samples. Furthermore, Nordenskiöld (1870)
40 909 identified a near-ubiquitous dust covering the ice between cryoconite holes and identified it as brown
41 910 coloured polycellular alga that was also present in cryoconite sediment. The same algae interested
42 911 Nansen (1906), who described ice surfaces as “dirty, grayish, or even brownish” due to “dust” containing
43 912 sixteen diatomaceous taxa of algae, thought to be deposited from the atmosphere (Nordenskiöld, 1870;
44 913 Nansen, 1906). Nansen (1906) identified the same algae on sea ice and in cryoconite holes (Garrett and
45 914 Verzella, 2008). Nansen (1906) reported “big basilums of a simple rod-like appearance, rapidly oscillating
46 915 and often forming long chains” on ice surfaces. Such filamentous bacteria were later recognised as crucial
47 916 for cryoconite aggregation (Langford et al. 2014) and providing particulate OC for cryoconite ecosystems
48 917 (Hodson et al. 2008).

49 918 Steinbock (1936) provided the only major study of supraglacial biota undertaken during the first half of
50 919 the twentieth century, reporting cyanobacteria, various algae, protozoa, ciliates and other
51 920 microorganisms in cryoconite on Disko Island (Greenland). He expressed the opinion that cryoconite
52 921 holes represent well-established and well-organised habitats for diverse organisms, and possibly
53 922 facilitated the *in situ* survival of microbes throughout past ice ages, presaging Wharton et al. (1985) by
54 923 almost fifty years. The longevity of cryoconite holes was questioned again much later by Hodson et al.
55 924 (2007) and Anesio et al. (2009) amongst others who confirmed multi-year and possibly multi-decadal
56 925 residence on glaciers. Apart from Odell (1949), who reported ice worms in Alaskan cryoconite, it was
57 926 over two decades before further investigations into cryoconite biota were published, when Charlesworth
58 927 (1957) observed algae, rotifers, pollen, and even insects and small dead birds. Gerdel and Drouet (1960)

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3 928 found 13.2 – 20.1% of Greenland cryoconite to be composed of OM including cyanobacteria, unicellular
4 929 desmids, rotifers, fungi, and diatoms. Gerdel and Drouet (1960) noted that organisms in cryoconite holes
5 930 primarily utilise radiation in the same waveband that is most effectively transmitted through ice and
6 931 referred to measurements by Thacker and Babcock (1957) showing ~10% of full sunlight is optimal for
7 932 algal photosynthesis, implying that cryoconite holes might provide optimal light conditions for
8 933 autochthonous C fixation. This concept was revisited by Cook et al. (2010) half a century later. Therefore,
9 934 despite only recently becoming widely recognised, the concept of biotic-abiotic equilibration in
10 935 cryoconite hole systems has been present in the literature for over half a century.

11 936 The early polar explorers did not overlook the impact of microbes, including those in cryoconite, as
12 937 glacier melt catalysts. Nordenskiöld described them as ice's "greatest enemy" and implicated cryoconite
13 938 in the waxing and waning of earth's ice over geologic time. He explained that dark algae on ice both
14 939 "accelerates melting" and "drills holes all over the ice" (Leslie, 1879). This was frequently corroborated in
15 940 the twentieth century, notably by Gajda (1958) who examined cryoconite scattered on ice surfaces in
16 941 ubiquitous layers of varying thickness and concentrated 'stripes' ~10 cm in width. In both, granules
17 942 varied from fine to coarse and were reddish-brown in colour (probably due to the presence of
18 943 filamentous algae and photo-protective pigmentation, although this was not explicitly identified). An
19 944 important observation was the influence of sediment layer thickness on ablation rate, where uniformly
20 945 distributed, thin layers of cryoconite had greatest melt impact. This was later revisited by Cook et al.
21 946 (2010) and Telling et al. (2012a) who recognised the significance of sediment arrangement for NEP.
22 947 Cryoconite, according to Gajda (1958), "undoubtedly has an effect on the melting of glaciers, ice and snow
23 948 surfaces of land, rivers, lakes and seas". Current efforts to understand the regional and global impacts of
24 949 cryoconite phenomena are therefore grounded in over a century of scientific thought.

25 950 Therefore, by the end of the nineteenth century, ice surface microbiota was already known to be
26 951 widespread, diverse, concentrated into cryoconite holes and responsible for accelerating glacier wastage.
27 952 The arrangement of sediment within cryoconite holes was known to be a crucial determinant of albedo
28 953 and radiation absorption was identified as a control upon biotic activity. Cryoconite holes were known to
29 954 contain complex ecosystems to which minerals and inoculants were delivered largely by wind from
30 955 various sources, supplemented by debris falls from valley sides and extrusion of material from the basal
31 956 bedrock. There has long been an appreciation that cryoconite mass loading varies geographically and
32 957 over time, yet we still lack understanding of spatiotemporal variations in spatial distribution of
33 958 cryoconite. Crude linear upscaling of mass loading from the plot scale to the regional, ice sheet or even
34 959 global scale by Anesio et al. (2009), Hodson et al. (2010a) and Cook et al. (2012) were foreshadowed by
35 960 similar work in the late 1800s (Bayley, 1891), implying that our understanding of cryoconite as a global
36 961 phenomenon has advanced little over the past century. Similarly, although a numerical basis for
37 962 cryoconite hole formation has had attention our understanding of hole morphology has not progressed
38 963 far beyond that of the early twentieth century. Cryoconite holes had been established as energy balance
39 964 phenomena by the turn of the twentieth century, with researchers such as Nansen (1906) even
40 965 recognising biological darkening of minerals contributing to melt differentials. What were major
41 966 uncertainties a century ago remain so today, even at the broadest scale. This includes regional and global
42 967 scale impacts of cryoconite phenomena, supraglacial biotic-abiotic feedbacks, relationship with climate
43 968 change and the role of microbial processes in glacier scale melt dynamics. Linking microbial and glacier
44 969 scale processes remains a major challenge for twenty-first century scientists. Crucially though, the
45 970 twenty-first century has seen growing appreciation of cryoconite as a component of a wide and complex
46 971 supraglacial ecosystem.

47 972 **VIII Where should cryoconite science go from here?**

48 973 *1 Directing future research*

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51 974 Glaciology has progressed from an abiotic to a biotic paradigm; however much of the modern literature
52 975 assumes the supraglacial biome to be simple, quasi-static and exclusively comprising organisms
53 976 contained in discrete cryoconite holes and algal blooms. Regarding cryoconite, there remains a tendency
54 977 to ignore the diversity of hole shapes and sizes present on natural ice surfaces and instead discuss (and
55 978 sample) symmetrical, cylindrical holes with flat floors and even sediment arrangements. Since hole
56 979 morphology impacts the photic conditions at the hole floor (Cook et al. 2010) and cryoconite microbes
57 980 are sensitive to changes in their environments (Edwards et al. 2014b) it follows that hole morphology
58 981 probably influences cryoconite microbial ecology and therefore deserves research attention.

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3 982 Furthermore, if cryoconite holes undergo morphological evolution and migration then their contribution
4 983 to supraglacial melt might be continuous. It has also recently been recognised that cryoconite holes are
5 984 not spatially isolated entities occasionally interlinked by ephemeral, discrete hydrological flowpaths, but
6 985 rather represent dynamic sites of organic and inorganic matter storage and high microbial activity
7 986 punctuating a spatially expansive aquatic ecosystem within the porous near-surface ice layer known as
8 987 the weathering crust (Muller and Keeler, 1969; Irvine-Fynn et al. 2012). This weathering crust ecosystem
9 988 is then widely connected to other glacial and extraglacial environments (Fig. 7). Since the top of the
10 989 weathering crust represents the interface between ice and atmosphere and is exposed to incoming solar
11 990 radiation, it is the primary site of radiative and sensible heat exchange and its properties therefore
12 991 strongly influence supraglacial melt rates. Key variables in the surface energy balance include surface
13 992 roughness and albedo, both of which are influenced by microbial activity, yet biology has not been
14 993 incorporated into any predictive models of glacier melt. To do so will require better knowledge of the
15 994 interactions between microbes and the ice matrix they inhabit. To improve our understanding of ice-
16 995 microbe interactions, microbial ecology and biogeochemistry in the supraglacial zone, cryoconite and
17 996 other microbial habitats must be studied in concert with the evolution of ice surface roughness,
18 997 topography and hydrology. We propose a framework for integrating these biological and glaciological
19 998 processes and introduce the term 'biocryomorphology' in reference to ice-microbe interactions.

20 999 1.1 Biocryomorphology

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22 1000 A systems-based strategy for studying cryoconite holes has been suggested before (MacDonnell and
23 1001 Fitzsimons, 2008; Stibal et al. 2012); however a robust framework for implementing such a strategy is
24 1002 lacking. To address this issue, we suggest integrating biological and glaciological processes, in particular
25 1003 ice surface roughness, near surface hydrology and microbial ecology under the term 'biocryomorphology'.
26 1004 The overall aim is to develop a holistic, process-based understanding of ice-microbe interactions for
27 1005 integrating microbial processes into glaciological, biogeochemical and climate models. Cryoconite
28 1006 provides a crucial starting point for biocryomorphic investigations, since there are reciprocal
29 1007 relationships between microbial activity, hole morphology and surface energy balance that are yet to be
30 1008 constrained. Gribbon (1979) and Cook et al. (2010) imply that stable hole morphology is only likely in
31 1009 conditions of constant, even irradiance where there is no addition or growth of cryoconite granules and
32 1010 granules are evenly distributed over hole floors. This combination of conditions is unlikely, suggesting
33 1011 that holes often exist out of equilibrium and adapt their shapes and sizes in response to changing
34 1012 environmental conditions. The well-studied cylindrical holes probably represent a point along a
35 1013 morphological continuum that includes dispersed cryoconite, shallow and irregular holes, cryoconite
36 1014 alluvium, colluvium and stream-bound debris. This growth and movement of cryoconite holes indicates
37 1015 potential significance as catalysts of supraglacial melt and highlights their role in shaping ice surfaces.
38 1016 Furthermore, since microbial community structure-function relationships are known to be sensitive to
39 1017 environmental conditions, there may be concomitant changes in cryoconite microbial ecology. Irvine-
40 1018 Fynn et al. (2012) demonstrated transport of microbes through the top 1-2m of porous ice on Arctic
41 1019 glaciers, indicating that models of cryoconite hole biogeochemistry should incorporate delivery and efflux
42 1020 of cells and nutrients via hydrologic flow through the weathering crust. Some measurements of nutrient
43 1021 delivery and export have been made in Antarctic cryoconite systems, notably by Tranter et al. (2004),
44 1022 Fountain et al. (2008), Bagshaw et al. (2013) and Telling et al. (2014). Interactions with other glacial
45 1023 (including seasonal and perennial snow, impermeable ice beneath the weathering crust and subglacial
46 1024 ice) and extraglacial (including atmospheric exchanges, moraines, rivers, lakes, oceans and glacier
47 1025 forefields) environments are certain to occur but are currently weakly addressed (Fig 7). Biocryomorphic
48 1026 investigations should take these connections into account. A holistic understanding of ice surfaces must
49 1027 incorporate cross-scale linkages from molecular-level processes to the dynamics of entire glaciers and ice
50 1028 sheets. The subsections below introduce specific research questions at a range of scales that provide
51 1029 crucial starting points for developing an integrated, biocryomorphic understanding of ice surfaces.

52 1030 1.2 Molecular Scale

53 1031 Concomitant with the recognition of glacial surfaces as loci of biological activity, the molecular microbial
54 1032 ecologist's toolbox has expanded rapidly. High throughput DNA sequencing of marker gene amplicons
55 1033 (for example 16S/18S ribosomal RNA genes), metagenomes, metatranscriptomes and microbial genomes
56 1034 promises a sequence-centred, systems orientated understanding of cryoconite ecosystems. However, the
57 1035 application of high throughput sequencing to cryoconite ecosystems is in its infancy. At the time of
58 1036 writing, only nine glaciers and the margin of the Greenland Ice Sheet (Edwards 2014b; Zarsky et al. 2013;

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3 1037 Hamilton et al. 2013; Segawa et al. 2014; Stibal et al. 2014) have any peer-reviewed published cryoconite
4 1038 16S bacterial amplicon sequencing datasets and only the margin of the Greenland Ice Sheet has been
5 1039 studied over a melt season (Stibal et al. 2014); one metagenome is reported (Edwards et al. 2013b). To
6 1040 our knowledge, only one glacier has published eukaryotic marker gene amplicon data (Hamilton et al.
7 1041 2013) and there are no published metatranscriptomes. Evidently sequence space in the cryoconite
8 1042 ecosystem has been poorly explored, but it is also clear that sequencing for its own sake could not be
9 1043 justified. Therefore, we propose that molecular tools be applied within a systems-orientated framework,
10 1044 which integrates across both the suite of 'omics approaches (i.e. meta- genomics, transcriptomics,
11 1045 proteomics, metabolomics) and tools and approaches from biogeochemistry and glaciology. Such a
12 1046 framework could encompass mapping cryoconite ecosystems at spatial and temporal scales ranging from
13 1047 individual metabolic reactions to cell-mineral interactions to microbial dynamics within single granules,
14 1048 and reach beyond the scale of the parent ice mass. An integrated framework such as this would firstly
15 1049 serve to map cryoconite ecosystems across scales of space and time spanning several orders of
16 1050 magnitude, secondly understand the mechanisms of cryoconite ecosystem structure, stability and
17 1051 function, and thirdly, when integrated with climate and ice mass models, underpin a predictive
18 1052 understanding of cryoconite ecosystem dynamics in the context of contemporary climate change. At a
19 1053 time when projects with the objective of mapping Earth's microbiome and its metabolic potential (Gilbert
20 1054 et al. 2014) are being realised, it is vital that ecosystems with the potential to sense and amplify the
21 1055 profound changes occurring in the cryosphere are not left out in the cold

22 1056 *1.3 Microhabitat Scale*

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24 1057 Cryoconite granules provide microhabitats for autotrophic and heterotrophic microbes. Having relatively
25 1058 few trophic interactions and abiotic influences, cryoconite granules might provide excellent model
26 1059 systems for microbial ecology in other environments. Their high density allows them to settle on ice
27 1060 surfaces their albedo is lowered by biological activity, making them the primary agents of biocryomorphic
28 1061 evolution. However, our understanding of granule formation and stabilisation remains basic and there
29 1062 are currently only a few studies (e.g. Takeuchi et al. 2010; Langford et al. 2010) explicitly examining
30 1063 granule initiation, growth and erosion. Key gaps in our understanding of cryoconite microhabitats include
31 1064 the origin of cryoconite materials, the mechanisms by which those materials are assimilated into
32 1065 granules, their longevity and stability, granule morphodynamics and granule-scale microbial ecology.
33 1066 Links between atmospheric processes, including wet and dry deposition of minerals, biota and
34 1067 anthropogenic compounds onto ice and snow, post-depositional transformation, redistribution and
35 1068 interaction with cryoconite granules are unknown. Biogeochemical transformation and storage within
36 1069 cryoconite granules, which may govern the export of organic and inorganic compounds to other
37 1070 environments is poorly understood. These processes determine the properties of granules which
38 1071 collectively determine hole morphology and therefore influence patterns of albedo and melt rate that
39 1072 shape the wider ice surface, thereby connecting molecular and cellular level processes with those
40 1073 operating at the habitat scale and beyond.

41 1074 *1.4 Habitat Scale*

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43 1075 Diverse hole shapes and sizes on ice surfaces imply evolution and even migration of cryoconite holes in
44 1076 response to changing surface energy balance and sediment dynamics. The mechanisms by which this
45 1077 occurs are currently unknown but likely depend upon microbially-mediated growth and stabilisation of
46 1078 cryoconite granules and heterogeneous melt rates across hole floors, which are in turn driven by granule
47 1079 distribution and patterns of light and shade. Ice surface topography may therefore control hole
48 1080 morphology by determining patterns of hole-floor shading, and is also reciprocally influenced by
49 1081 cryoconite-induced changes in surface energy balance. Lateral equilibration (Cook et al. 2010) should also
50 1082 be integrated into a biocryomorphic understanding of cryoconite evolution since variable granule
51 1083 distributions may drive asymmetric hole expansion, providing a mechanism of migration.

52 1084 The storage of cryoconite, the photic conditions on hole floors and the continuous flow of meltwater
53 1085 through the weathering crust make cryoconite holes analogous to continuous flow immobilised biomass
54 1086 bioreactors, which are commonly utilised in industry to optimise synthesis of various biomolecules.
55 1087 Based upon cyanobacteria research in other environments, potentially valuable biomolecules synthesised
56 1088 in cryoconite holes likely include UV-screening pigments such as scytonemin and mycosporine-like amino
57 1089 acids (Garcia-Pichel and Castenholz, 1991; Quesada and Vincent, 1993; Cockell and Knowland),
58 1090 photosynthetic pigments such as phycoerythrin or phycocyanin (Squier et al. 2002; Hodgson et al. 2004)

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3 1091 and complex carbohydrates that can be used as industrial thickeners, gellifiers and stabilisers in the paint,
4 1092 cosmetic, pharmaceutical and food industries as well as having potentially useful antiviral properties
5 1093 (Colica and Philippis, 2014). These same molecules might also represent useful biomarkers in the
6 1094 supraglacial environment (Langford et al. 2014). There is also great potential for microbial communities
7 1095 in cryoconite holes to provide novel antibiotic compounds, antifreeze proteins and cold-active enzymes
8 1096 (Singh et al. 2014a,b). Future research could therefore fruitfully examine the potential of cryoconite as
9 1097 natural biofactories on ice surfaces, simultaneously improving our understanding of ice-microbe
10 1098 interactions and offering opportunities for novel research in biotechnology and bioprospecting. A holistic
11 1099 understanding of ice-microbe interactions must also take into account other microbial habitats, including
12 1100 surface-dwelling algae and cryoconite outside of cryoconite holes. Rates of C cycling in cryoconite
13 1101 dispersed on ice surfaces have been estimated several times (e.g. Hodson et al. 2007; Chandler et al.
14 1102 2015) and the importance of algal blooms for supraglacial albedo and biogeochemistry have been
15 1103 investigated by Yallop et al. (2012) and Cook et al. (2012); however, spatiotemporal changes and
16 1104 interactions between these environments remain unknown. Analogising cryoconite holes as bioreactors,
17 1105 examining their morphological evolution and incorporating additional microbial habitats will yield
18 1106 important insights into habitat-scale biogeochemistry and microbiology and facilitate the integration of
19 1107 molecular, microhabitat, habitat and glacier scale processes.

20 1108 *1.5 Glacier Scale*

21 1109 Recent work by Irvine-Fynn et al. (2012) suggests the entire weathering crust (porous ice in the top 1-2m
22 1110 of the supraglacial zone) represents a dynamic ecosystem through which cells are continuously
23 1111 transferred by meltwater. Due to both light intensity and ice permeability attenuating with depth in the
24 1112 weathering crust, there may be a depth dependent down-glacier transfer of cells (Irvine-Fynn and
25 1113 Edwards, 2014). As well as a medium for hydrologic and biologic transport, the weathering crust
26 1114 provides the substrate for cryoconite hole formation, and the role of cryoconite as a component of the
27 1115 weathering crust is uncertain. Cook et al (2015) recently demonstrated the utility of cryoconite holes as
28 1116 natural piezometers penetrating the weathering crust. Entrainment of microbes by cryoconite might
29 1117 punctuate the down-glacier transfer of cells and prolong their exposure to favourable light and nutrient
30 1118 conditions. Transformation of OC and modification of community structures in cryoconite holes might
31 1119 define to some extent the composition of OM exported to other environments and also influence glacier
32 1120 ablation. Cell fluxes, storage and growth within supraglacial ice were shown to be potentially important
33 1121 for glacier albedo feedbacks and seeding of downstream ecosystems by Irvine-Fynn et al. (2012), while
34 1122 weathering crust evolution might release and activate dormant microbes interred in near-surface ice
35 1123 (Dancer et al. 1997). Further research is required to advance understanding of microbial processes
36 1124 throughout the weathering crust, and this may help us to relate processes at the microbial scale to those
37 1125 operating within cryoconite holes, and then at the regional scale and beyond. This will be essential for
38 1126 developing predictive models microbially-mediated glacier melt.

39 1127 *1.6 Landscape Scale*

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41 1128 Figure 7 illustrates connections between the supraglacial zone and other glacial and extraglacial
42 1129 environments. This includes inputs from moraine slumps, snow melt and atmospheric deposition,
43 1130 transport of cells and nutrients through the weathering crust, storage and biogeochemical
44 1131 transformations in cryoconite holes and ultimately export of nutrients, biomolecules and biomass to
45 1132 rivers, lakes, oceans and forefields. These wide interconnections urgently require research attention
46 1133 because landscape-scale processes respond to, and establish the initial conditions for smaller scale
47 1134 biocryomorphology. An integrated biocryomorphic understanding of supraglacial ice-microbe
48 1135 interactions will therefore necessarily include landscape-scale processes.

49 1136 **IX Conclusions**

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51 1137 This paper reviewed cryoconite literature from the earliest reports to the present day. Early polar
52 1138 explorers were shown to be remarkably prescient in establishing fundamental knowledge that continues
53 1139 to underpin cryoconite science today. We now have ample evidence to support early claims that
54 1140 cryoconite holes are biologically distinct from other habitats and we have begun to recognise specific
55 1141 community structures and functions defined by specific environmental niches. Evidence is also
56 1142 accumulating to support nineteenth century suggestions that cryoconite and other supraglacial microbes
57 1143 darken ice surfaces and contribute to glacier wastage. However, we also recognise that several
58 1144 assumptions that originated with the nineteenth century polar scientists are now outdated. This includes
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3 1145 the traditional view of cryoconite holes as discrete, biologically isolated entities. Instead, they should be
4 1146 considered hotspots of biodiversity and biogeochemistry within a dynamic and continuous glacier-wide
5 1147 ecosystem with connections to extraglacial environments. The analogy of cryoconite holes as natural
6 1148 continuous flow immobilised biomass bioreactors may prove useful in understanding the productivity of
7 1149 these ecosystems despite multi-dimensional stresses. The community should also trend away from the
8 1150 assumption that cryoconite holes have simple and stable morphologies, since cryoconite can clearly be
9 1151 identified in a wide range of environments on glacier surfaces, and there are likely feedbacks between
10 1152 hole shape and microbial ecology. Adopting a “systems” approach that focusses upon relationships and
11 1153 feedbacks in and between the various glacial and extraglacial zones will allow us to better understand
12 1154 cryoconite as a bioglaciological entity. Attention should be placed upon linking processes at the scale of
13 1155 individual microbes, cryoconite granules, cryoconite holes, plots, catchments, glaciers and landscapes.
14 1156 This should ultimately integrate bio-glaciological, hydrological, meteorological, climatological and
15 1157 geological processes. To this end, we identified several specific areas of interest for future studies,
16 1158 particularly building upon recent work framing cryoconite holes as components of a dynamic weathering
17 1159 crust ecosystem and employing molecular analyses, and suggested a ‘biocryomorph’ framework for
18 1160 achieving an integrated understanding of the role of cryoconite in the cryosphere.

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3 Figure 1:
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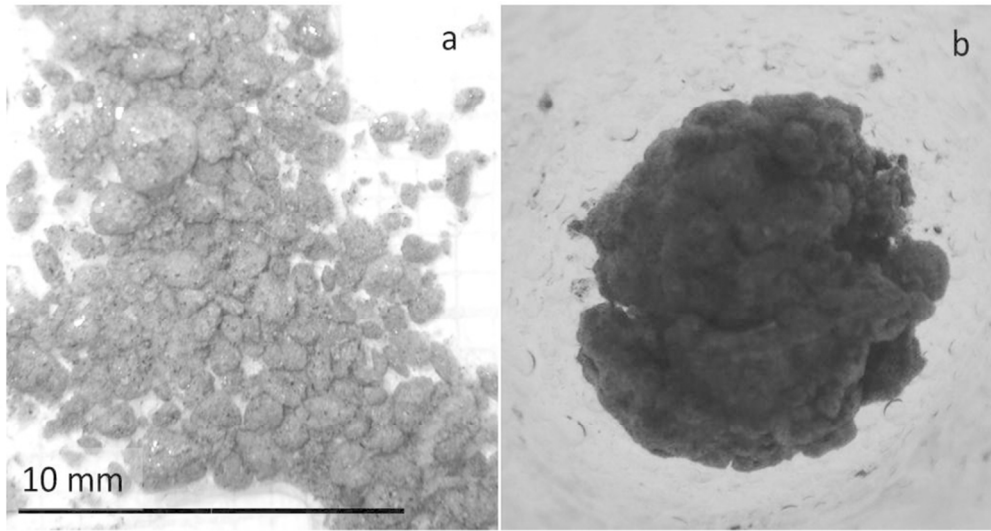
6 Figure 1 a) Discrete quasi-spherical cryoconite granules of 1-2.5 mm diameter sampled ~2km
7 inland of the ice margin on the Greenland ice sheet near Kangerlussuaq; b) a complex of
8 cryoconite granules ca. 10mm diameter, sampled ~34km inland of the ice margin on the
9 Greenland ice sheet near Kangerlussuaq. Scale bar applies to both images.
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12 Figure 2:
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15 Figure 2 Cryoconite granule structures: a = simple concentric ring structure; b = granule
16 containing a dark humic ring; c = granule containing subgranules, each with individual
17 concentric ring structures; d = granule with a large central mineral grain; e is an example of a
18 granule with no specific internal structure. Reprinted from Takeuchi et al. (2010), *Annals of
19 Glaciology* with permission from the International Glaciology Society). 86x93mm (300 x 300
20 DPI)
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24 Figure 7:
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27 Figure 7: Three diagrams that show carbon fluxes through supraglacial systems. Black arrows
28 denote flux of C. A) Carbon cycling within an individual cryoconite hole; B) Connectivity
29 between cryoconite holes and other glacial and extraglacial environments; C)
30 Interconnectivity between cryoconite holes via hydrologic fluxes through the weathering
31 crust. We gratefully acknowledge Antony Smith (DGES, Aberystwyth University) for his
32 assistance with this figure. 152x83mm (300 x 300 DPI)
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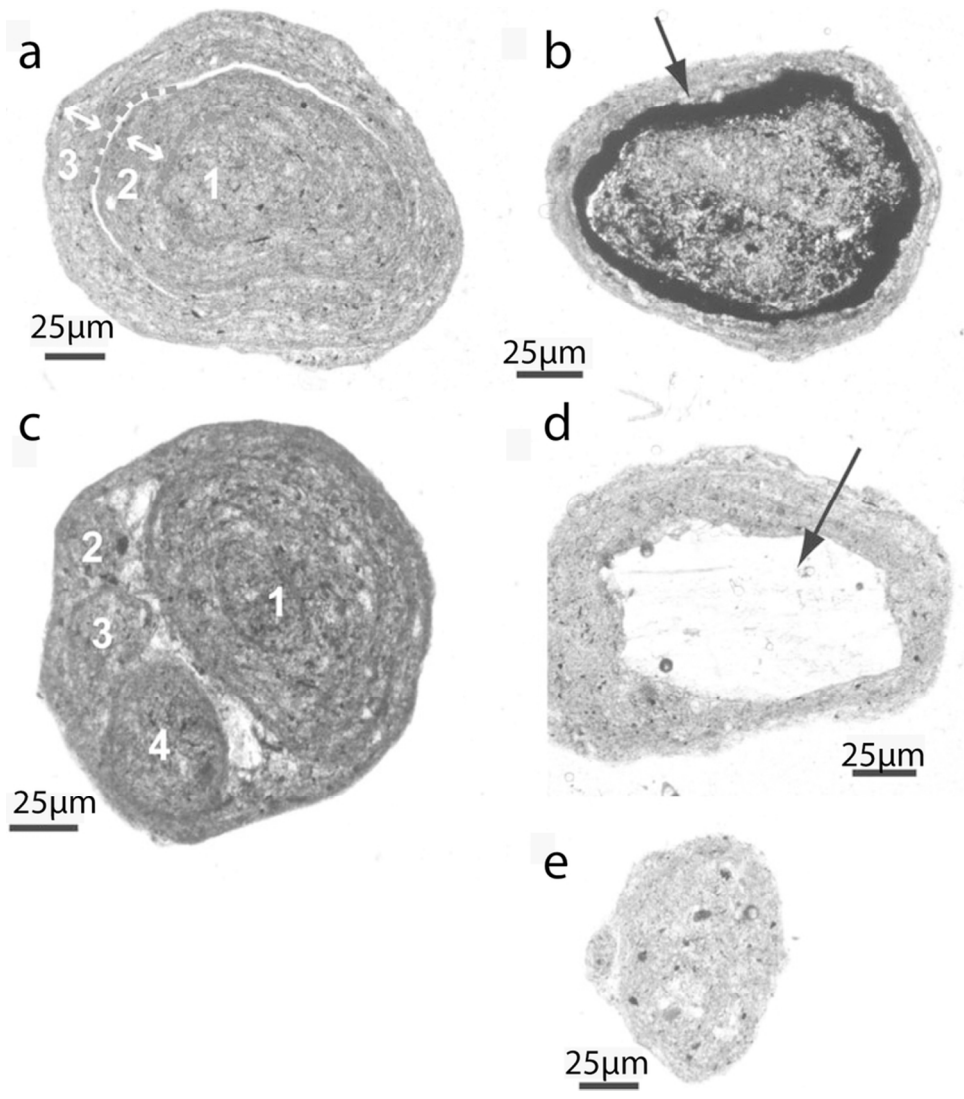


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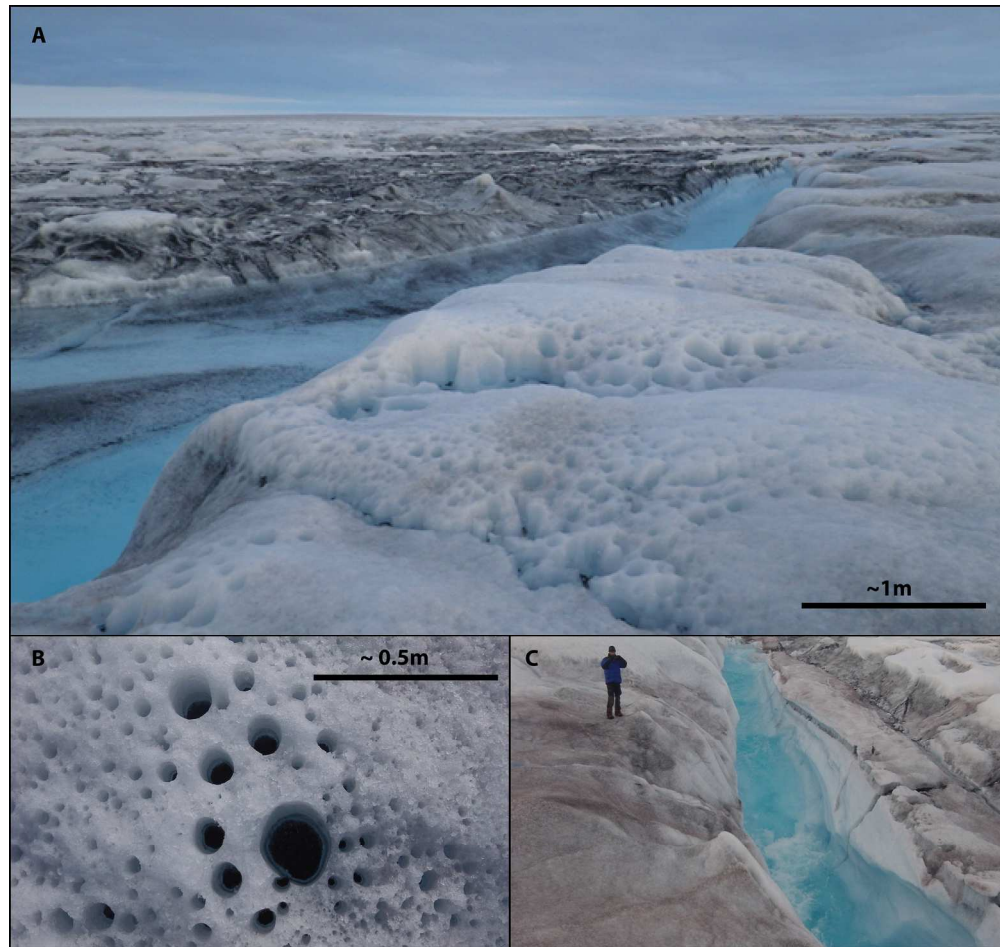


Figure 3. A range of cryoconite habitats. A = wide shot of ice surface at "S6", 38km inland of the ice margin, Greenland ice sheet. Cryoconite holes are visible in the foreground, stream cryoconite and cryoconite mantle is visible in the midground. B = Aerial view of cryoconite holes at the same location. C = Loose cryoconite granules, fine dusts and algae dispersed upon the ice surface (T. Irvine-Fynn for scale).
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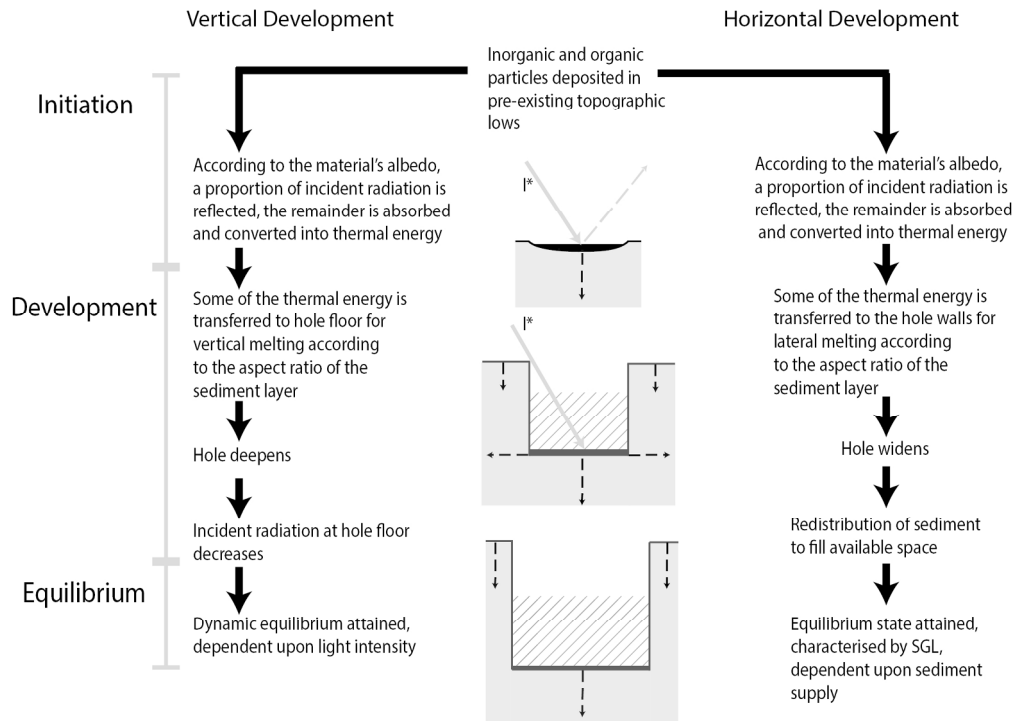


Figure 4: Flow diagram depicting the vertical and horizontal development of cryoconite holes. The term ' I^* ' refers to solar radiation and 'SGL' stands for Single Grain Layer. Ice is depicted using light grey shading and water is depicted using diagonal hatching.
184x132mm (300 x 300 DPI)

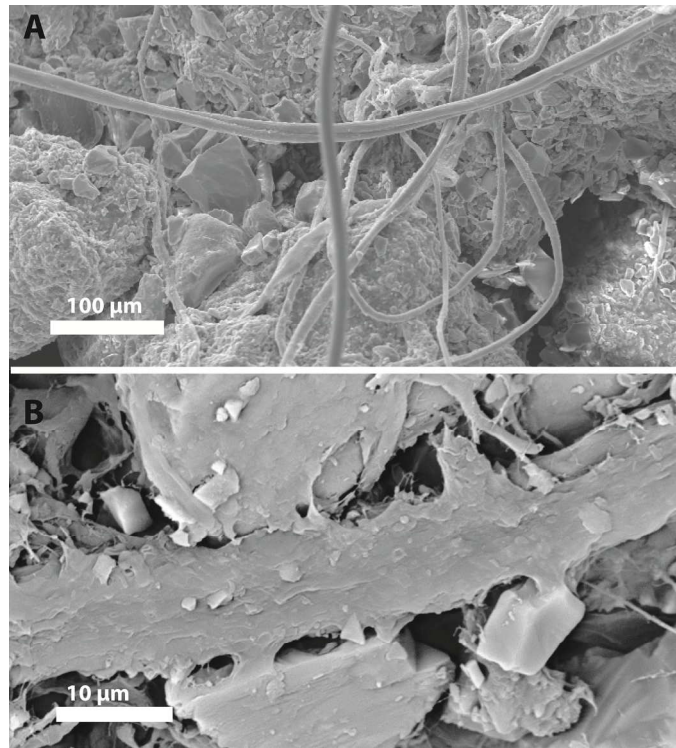


Figure 5: Scanning electron microscope images of cryoconite from 38 km inland on the Greenland Ice Sheet (near Kangerlussuaq) showing A) a 'net' of cyanobacterial filaments binding mineral fragments; B) EPS-mineral interactions along the sheath of a cyanobacterial filament.
96x71mm (600 x 600 DPI)

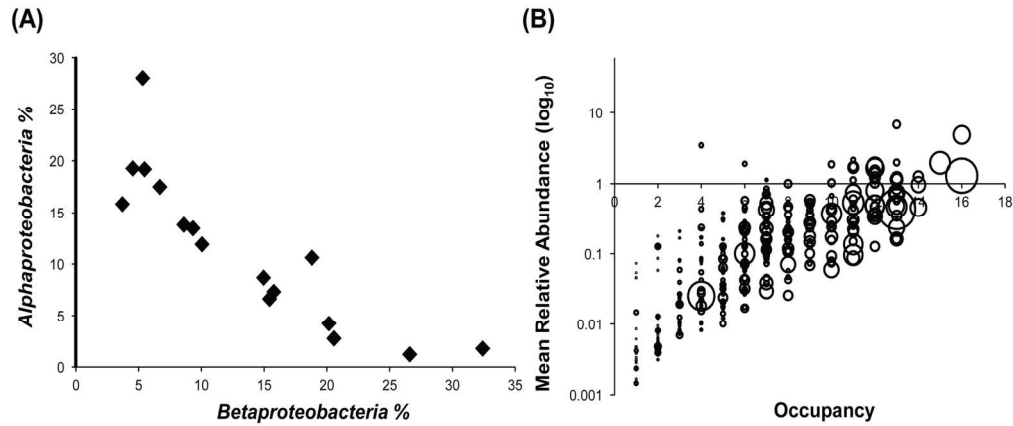
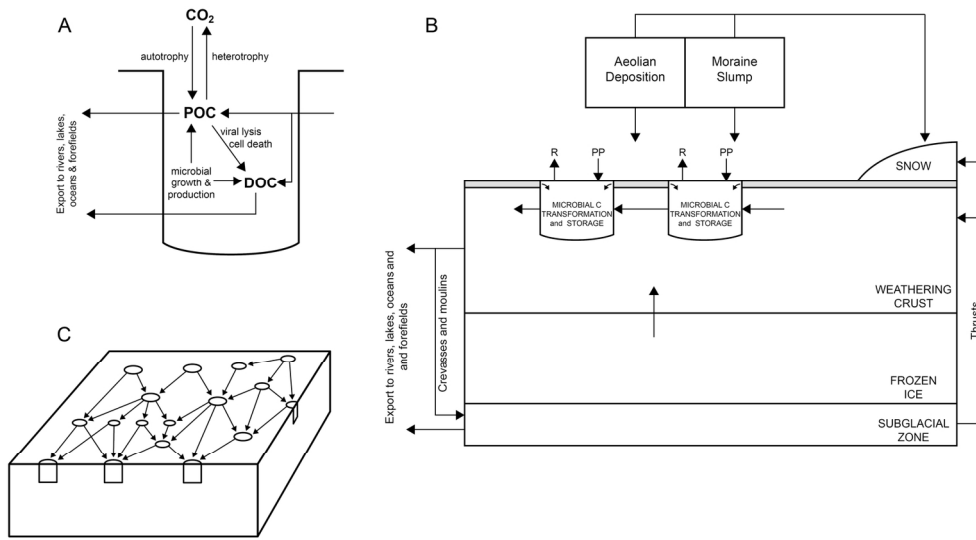


Figure 6: Population trends in Arctic and alpine cryoconite bacterial communities revealed by 16S rRNA gene amplicon pyrosequencing (Edwards et al. 2014b) (A) a negative correlation between the relative abundance of 97% id OTUs assigned by ribosomal database project taxonomy to Alphaproteobacteria and Betaproteobacteria classes is clearly apparent (Pearson's $r=-0.88$, $p<0.0001$). (B) dominance of "generalist" OTUs sensu Barberan et al. (2012). Bubble size is proportional to cumulative relative abundance of each Operational Taxonomic Unit. Raw data are available at EBI-SRA (PRJEB5067-ERP004426).
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Table 1: Percentage fractions of organic matter (OM) in cryoconite samples (error is 1σ)

Location	Latitude ($^{\circ}$ N or S)	OM (%)	Reference
Tyndall Glacier, Patagonia	40 $^{\circ}$ S	1.8 \pm 0.4	Takeuchi et al. (2001c)
Rhikha Samba Glacier, Nepal	29 $^{\circ}$ N	5.8 \pm 0.9	Takeuchi et al. (2009)
AX010 Glacier, Nepal	28 $^{\circ}$ N	2.0 \pm 0.8	Takeuchi, unpublished
Yala Glacier, Nepal	28 $^{\circ}$ N	7.8 \pm 0.4	Takeuchi et al. (2001a)
Meikuang, Tibet	35 $^{\circ}$ N	5.5	Takeuchi et al. (2002a)
Gohza, Tibet	35 $^{\circ}$ N	5	Takeuchi et al. (2002a)
Xiao Dongkemadi, Tibet	33 $^{\circ}$ N	13.2	Takeuchi et al. (2002a)
Urumqi No.1, China	43 $^{\circ}$ N	9.7 \pm 1.6	Takeuchi and Li (2008)
Qiyi Glacier, China	39 $^{\circ}$ N	8.6 \pm 1.9	Takeuchi et al. (2005)
Akkem Glacier, Russia	49 $^{\circ}$ N	4.8 \pm 0.7	Takeuchi et al. (2006)
Gulkana Glacier, Alaska	63 $^{\circ}$ N	8.2 \pm 1.3	Takeuchi (2002b)
Worthington Glacier, Alaska	61 $^{\circ}$ N	6.2 \pm 0.6	Takeuchi et al. (2003)
Devon and Penny Ice Caps, Canadian Arctic	76 $^{\circ}$ N (Devon) 67 $^{\circ}$ N (Penny)	8.5 \pm 6.7	Takeuchi et al. (2001b)
Qaanaaq Ice Cap, Greenland	77 $^{\circ}$ N	5.1 \pm 1.6	Takeuchi et al. (2014)
Nuna Ice Ramp, Greenland	76 $^{\circ}$ N	13.9 \pm 1.1	Gerdel and Drouet (1960)
Thule Ice Ramp, Greenland	76 $^{\circ}$ N	18.3 \pm 2.3	Gerdel and Drouet (1960)
Kronprinz Christian's Land, Greenland	80 $^{\circ}$ N	5	Bøggild et al. 2010
Blue ice near Kangerlussuaq, Greenland	67 $^{\circ}$ N	7.1 \pm 3.3	Hodson et al. (2010a)
Marginal ice near Kangerlussuaq, Greenland	67 $^{\circ}$ N	1.9 \pm 0.8	Hodson et al. (2010a)
Hansbreen, Werenskioldbreen, Nannbreen, and Austre Torellbreen, Svalbard	77 $^{\circ}$ N	8.4 \pm 5.0	Stibal et al. (2006)
Austre Brøggerbreen	79 $^{\circ}$ N	9.7	Takeuchi (2002)
Taylor Valley, Antarctica	77 $^{\circ}$ S	3	Foreman et al. 2007

Table 2: Cryoconite granule sizes for a range of glaciers.

Location	Latitude	Granule Size (mm)	Reference
Yala Glacier, Nepal	28° N	0.39 ± 0.15	Takeuchi et al. (2002a)
AX010, Nepal	28° N	0.29 ± 0.12	Takeuchi et al. (2002a)
Rihka Samba, Nepal	29° N	0.54 ± 0.20	Takeuchi et al. (2002a)
Meikuang, Tibet	35° N	0.55 ± 0.26	Takeuchi et al. (2002a)
Gohza, Tibet	35° N	0.55 ± 0.28	Takeuchi et al. (2002a)
Xiao Dongkemadi, Tibet	33° N	0.80 ± 0.35	Takeuchi et al. (2002a)
Urumqi No.1, China	43° N	1.10 ± 0.39	Takeuchi et al. (2010)
Austre Brøggerbreen, Svalbard	79° N	0.49 ± 0.29	Takeuchi et al. (2002a)
Penny Ice Cap, Canada	67° N	0.33 ± 0.11	Takeuchi et al. (2002a)
Devon Ice Cap, Canada	76° N	0.33 ± 0.13	Takeuchi et al. (2002a)
Longyearbreen, Svalbard	78° N	8.92 ± 6.93	Hodson et al. (2010)
Longyearbreen, Svalbard	78° N	8.59 ± 6.67	Irvine-Fynn et al. (2010)
Aldegondabreen, Svalbard	79° N	110 ± 35	Zarsky et al. (2013)
79 km transect along Leverett Glacier, Greenland	67° N	2.59 ± 1.54	Cook (2012)

Table 3: Equations relating to the thermodynamics of cryoconite hole evolution

	Equation	Definitions	Reference
Equation 1	$(1-\alpha) * S e^{-kz} + fGa + M = 0$	α = albedo; S = incident radiation; k = extinction coefficient for sunlight; z = depth; M = downward melt; Ga = undefined heat flux	Gribbon (1979)
Equation 2	$\rho_i Lv = Q_1 - Q_c$	ρ_i = ice density; L = latent heat of fusion for water; v = absolute sediment velocity; Q1 = shortwave energy absorbed by the sediment; Qc = defined in Equation 3	Jepsen et al. (2010)
Equation 3	$Q_c = -K \lambda T_{ice}(z,t)$	K = thermal conduction coefficient; λ = thermal conductivity of ice	Jepsen et al. (2010)
Equation 4	$Q_1 = T (1-R) (1+S) I_o(t) \exp(-kz)$	T = fraction of downwelling shortwave radiation transmitted into the ice through a semi-opaque surface layer; R = all-wave albedo of the sediment; S = ratio of upwelling to downwelling shortwave flux at the sediment; $I_o(t)$ = downwelling shortwave flux above the ice surface; k = all-wave absorption coefficient for ice.	Jepsen et al. (2010)
Equation 5	$Q_v = aT (1-R) (1+S) I_o(t) \exp(-kz)$	Q_v = thermal energy directed to the hole floor	Cook (2012)
Equation 6	$Q_L = (1-a) T (1-R) (1+S) I_o(t) \exp(-kz)$	Q_L = thermal energy directed to the hole walls	Cook (2012)

Table 4: Previously reported rates of PP, R and NEP in debris in natural cryoconite holes. The methods used to derive these data are shown: DO_2 refers to changes in dissolved oxygen concentration, ^{14}C refers to incorporation of traceable radioisotopes of C and $\Delta TDIC$ refers to changes in dissolved inorganic C concentration. 'n.d.' refers to values that were not reported. A and H refer to net autotrophy and net heterotrophy respectively.

* Stibal et al. (2012b) reported values for NEP, PP and R at nine sites along a 79km transect. The averages of all sites is presented here; however, there was significant spatial variability and the reader is directed to the original study.

** Bagshaw et al (2011) showed some temporal variability in PP and R values in Antarctic cryoconite – results here are representative of rates following a period of stabilisation in full sunlight.

Location	Lat.	NEP	PP	R	Bacterial Production	Unit	A or H	Method	Source
Midtre Lovenbréen, Svalbard	79° N	n.d.	0.63 ± 0.03 (26 July) 24.6 ± 0.75 (5 Aug) 31.2 ± 2.10 (11 Aug) 157 ± 4 (22 Aug)	n.d.	n.d.	$\mu\text{g C L}^{-1} \text{h}^{-1}$	n.d.	^{14}C	Säwstrom et al. (2002)
Werenskioldbreen, Svalbard	79° N	n.d.	3.4 ± 2.2	0.44 ± 0.17	n.d.	$\mu\text{g L}^{-1} \text{h}^{-1}$	n.d.	$\Delta TDIC$	Stibal and Tranter (2007)
Midtre Lovenbréen, Svalbard	79° N	n.d.	n.d.	1.17 ± 0.18	0.04 ± 0.02	$\mu\text{g C g}^{-1} \text{h}^{-1}$	A	DO_2	Hodson et al. (2007)
Werenskioldbreen (Svalbard)	79° N	n.d.	4.3	n.d.	n.d.	$\mu\text{g C L}^{-1} \text{yr}^{-1}$	n.d.	^{14}C	Stibal et al. (2008a)
Midtre Lovenbréen (Svalbard)	79° N	n.d.	353 ± 248	28.2 ± 4.37	39.7 ± 17.9	$\mu\text{g C g}^{-1} \text{d}^{-1}$ (ng C $\text{g}^{-1} \text{h}^{-1}$ for bacterial prod.)	A	^{14}C (3H Leucine for bacterial prod.)	Anesio et al. (2009) (Anesio et al. (2010) for bacterial prod.)
Austre Brøggerbreen (Svalbard)	79° N	14.6	48.0 ± 35.9	15.3 ± 5.02	8.62 ± 6.41	$\mu\text{g C g}^{-1} \text{d}^{-1}$ (ng C $\text{g}^{-1} \text{h}^{-1}$ for bacterial prod.)	A	^{14}C (3H Leucine for bacterial prod.)	Anesio et al. (2009) (Anesio et al. (2010) for bacterial prod.)
Vestre Brøggerbreen (Svalbard)	79° N	n.d.	208 +/- 106	34.3 ± 2.18	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	A	^{14}C	Anesio et al. (2009) (Anesio et al. (2010) for bacterial prod.)
Stubacher Sonnblickees (Austria)	47° N	n.d.	147 ± 78.3	42.1 ± 7.91	0.13 ± 0.14	$\mu\text{g C g}^{-1} \text{d}^{-1}$ (ng C $\text{g}^{-1} \text{h}^{-1}$ for bacterial prod.)	A	^{14}C (3H Leucine for bacterial prod.)	Anesio et al. (2009) (Anesio et al. (2010) for bacterial prod.)
Froya Glacier (Svalbard)	74° N	n.d.	115 ± 56.3	n.d.	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$ (ng C	n.d.	^{14}C	Anesio et al. (2009)

						$\text{g}^{-1} \text{h}^{-1}$ for bacterial prod.)			(Anesio et al. (2010) for bacterial prod.)
Patriot Hills (Antarctica)	80° S	n.d.	n.d.	n.d.	11.2 ± 4.11	$\text{ng C g}^{-1} \text{h}^{-1}$	n.d.	³ H Leucine	
McMurdo Dry Valleys (Antarctica)	77° S	n.d.	n.d.	n.d.	23.4 ± 11.8	$\text{ng C g}^{-1} \text{h}^{-1}$	n.d.	³ H Leucine	
Longyearbreen (Svalbard)	78° N	-2.03 ± 6.41	17.2 ± 9.7	19.2 ± 5.5	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	H	ΔTDIC	Hodson et al. (2010b)
Vestfold Hills (Antarctica)	67° S	n.d.	2.1 ± 1.5	1.86 ± 1.51	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	A	ΔTDIC	Hodson et al. (2010b)
Greenland Ice Sheet (near Kangerlussuaq)	67° N	n.d.	18.7 ± 10.1	20.9 ± 8.2	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	H	ΔTDIC	Hodson et al. (2010b)
Greenland ice sheet (nr Kangerlussuaq)	67° N	-0.14 (average blue ice areas) 0.01 ± 0.01 (at ice margin)	1.56 (average blue ice areas) 0.01 (at ice margin)	1.74 (average blue ice areas) 0.01 ± 0.01 (at ice margin)	n.d.	$\mu\text{M C g}^{-1} \text{d}^{-1}$	A (blue ice areas) H (at ice margin)	ΔTDIC	Hodson et al. (2010a)
Canada Glacier, Antarctica	77° S	n.d.	~ 1.4 **	~ 2.2 **	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	H	DO ₂	Bagshaw et al. (2011)
Austre Brøggerbreen, Vestre Brøggerbreen, Midtre Lovenbréen, Svalbard	79° N	-0.12 ± 4.1	18.7 ± 10.3	18.7 ± 9.1	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	H	ΔTDIC	Telling et al. (2012a)
Greenland ice sheet (nr Kangerlussuaq)*	67° N	6.11	24.5	18.4	n.d.	$\mu\text{g C g}^{-1} \text{d}^{-1}$	A	ΔTDIC	Stibal et al. (2012b)
Antarctic Blue Ice (mean values from 11 sites)	68° S	0.23	2.22	1.99	5.73 ± 6.00	$\mu\text{g C g}^{-1} \text{d}^{-1}$ ($\text{ng C g}^{-1} \text{d}^{-1}$ for bacterial prod)	A	ΔTDIC	Hodson et al. (2013)
Rotmoosferner (Austria)	46° N	n.d.	3.71	86.6	n.d.	$\mu\text{g C g}^{-1} \text{h}^{-1}$	H	¹⁴ C	Edwards et al. (2013c)
Canada Glacier (Antarctica)	77° S	15.3 ± 11.7	n.d.	n.d.	2.4 ± 1.6	$\text{ng C g}^{-1} \text{h}^{-1}$		³ H Leucine (bact. Prod) ¹⁴ C (PP)	Telling et al. (2014)
Greenland Ice Sheet (nr Kangerlussuaq) Cryoconite in holes	67° N	1.0 ± 0.33	0.76 ± 0.47	0.24 ± 0.11	n.d.	$\text{mg C L}^{-1} \text{d}^{-1}$		DO ₂	Chandler et al. (2015)
Greenland Ice Sheet (nr Kangerlussuaq) Dispersed Cryoconite	67° N	0.64 ± 0.31	0.24 ± 0.17	0.4 ± 0.2	n.d.	$\text{mg C L}^{-1} \text{d}^{-1}$		DO ₂	Chandler et al. (2015)