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Environmental factors influencing diatom communities in Antarctic cryoconite holes

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Abstract

Cryoconite holes are ice-bound habitats that can act as refuges for aquatic and terrestrial microorganisms on glacier surfaces. In the McMurdo Dry Valleys of Antarctica, these holes are often capped by an ice lid that prevents the exchange of material and gases with the surrounding atmosphere and aquatic environment. Diatoms have been documented in cryoconite holes, and recent findings suggest that these habitats may harbour a distinctive diatom flora compared to the surrounding aquatic environments. In this study, we examined diatom community composition in cryoconite holes and environmental correlates across three glaciers in Taylor Valley, Antarctica. The diatom communities were dominated by two genera, *Muelleria* and *Diadesmis*, both of which had high viability and could have been seeded from the surrounding ephemeral streams. The location of the cryoconite hole within the valley was a key determinant of community composition. A diatom species richness gradient was observed that corresponded to distance inland from the coast and co-varied with species richness in streams within the same lake basin. Cryoconite holes that were adjacent to streams with higher diversity displayed greater species richness. However, physical factors, such as the ability to withstand freeze–thaw conditions and to colonize coarse sediments, acted as additional selective filters and influenced diatom diversity, viability and community composition.

Keywords: diatoms, cryoconite holes, dry valley glaciers

1. Introduction

Cryoconite holes are small, transient habitats that exist for days to decades on the surface of glaciers worldwide (Hodson *et al* 2008). They are formed when wind-blown debris that has been deposited on glacier surfaces melts into the ice, forming a small, water-filled depression (Wharton *et al* 1985). In addition to sediment, the debris typically includes fragments of algal mat, microorganisms and organic material from the surrounding environment (Christner *et al* 2003, Takeuchi *et al* 2005, Langford *et al* 2010), and active

microbial communities can develop (Hodson *et al* 2008, Telling *et al* 2012). Cryoconite holes that form in cold ice regions, such as Antarctica, are unique compared to those elsewhere because many retain an ice lid throughout the summer months, thereby isolating them from the atmosphere for multiple melt seasons (Fountain *et al* 2004). This isolation promotes the development of extreme geochemical conditions (Tranter *et al* 2004), since biogeochemical activity in a closed system results in an accumulation of organic matter and supersaturation of oxygen (Bagshaw *et al* 2011). The existence of diatoms in cryoconite holes has been documented (Mueller *et al* 2001, Yallop and Anesio 2010, Cameron *et al* 2012a), and recent findings suggest that these habitats support a distinctive diatom flora compared to the surrounding lake and stream habitats (Van de Vijver *et al* 2010).

The landscape of Taylor Valley in the McMurdo Dry Valleys of Antarctica is comprised of a mosaic of perennially ice-covered lakes, ephemeral streams, polar alpine glaciers and poorly developed soils (Priscu 1999). A climatic gradient exists along the valley axis, from the eastern end at the coast to the western end 29 km inland: the climate warms, precipitation decreases and wind speed increases (Fountain *et al* 1999, Doran *et al* 2002), governed by the influence of onshore breezes from the Ross Sea to the east and katabatic winds descending from the Antarctic ice sheet to the west (Nylen *et al* 2004). The eastern Lake Fryxell basin is relatively wide and shallow in gradient and is characterized by higher soil moisture (Barrett *et al* 2006) and greater snow accumulation (Fountain *et al* 2010). This lake basin hence has a greater extent of suitable stream habitats for algal mats (McKnight *et al* 1998) and greater biomass in the local streams. The diatom communities of the stream and lake habitats have been well characterized, and are dominated by benthic, pennate diatoms of aerophilic genera (Konfirst *et al* 2011, Stanish *et al* 2011). While eukaryote diversity in the Dry Valleys is low compared to similar temperate ecosystems, the relative diversity of freshwater diatoms is high, with 46 species from 17 genera currently described, many of which have not been found outside of the Antarctic (Esposito *et al* 2008). Algal mats within the streams and lakes which harbour diatoms can be redistributed by winds (Nkem *et al* 2006) and may be an important source of biomass to cryoconite holes (Christner *et al* 2003).

Analysis of microbial communities in cryoconite holes has previously shown that they contain a diverse range of bacteria, eukarya and archaea (Cameron *et al* 2012a, 2012b) and they are likely seeded from the surrounding aquatic and terrestrial landscape via aerial deposition (Wharton *et al* 1981, Porazinska *et al* 2004, Edwards *et al* 2010), but there is still a lack of understanding of the distribution of and factors affecting microbial communities in Antarctic cryoconite holes. Diatoms are responsive to their physical and chemical environments and may therefore act as useful indicators of habitat conditions in cryoconite holes. Diatom taxa are also morphologically distinct and are large enough to allow for direct microscopic quantification, which is advantageous given the lack of genetic information available to identify diatoms using molecular methods. The unique geochemical conditions within cryoconite holes, including periodic freeze–thaw cycles and oxygen supersaturation (Bagshaw *et al* 2011), may select for distinct subsets of microbiota from the surrounding habitats. Certain taxa may even be specially adapted to life within the glaciers, as for example the diatom *Muelleria cryoconicola*, which thus far has only been found in cryoconite holes in Taylor Valley (Van de Vijver *et al* 2010). In the Arctic, where the holes are frequently hydrologically connected and lack an ice lid, the community function and composition appears to be influenced by surface hydrology (Edwards *et al* 2010, Irvine-Fynn *et al* 2011). However, Dry Valley cryoconite holes are often isolated from the atmosphere and surrounding supraglacial hydrological system, thus they are influenced by different physico-chemical and biological processes. In this study,

we describe the diatom communities in cryoconite holes on three glaciers in Taylor Valley, Antarctica, with the goal of identifying the factors that drive community composition and viability.

2. Field site and methodology

Samples were collected from Taylor Valley at two valley glaciers (Canada and Commonwealth) and one outlet glacier of the East Antarctic Ice Sheet (Taylor Glacier) (figure 1). These glaciers are characterized by low annual accumulation (<10 cm water equivalent per year), high sublimation (which constitutes 80% of annual ablation), annual ice temperatures of $-18\,°C$ and limited summer melting (Fountain *et al* 2006). Melt is confined to the top 1 m of ice, flowing through a network of open-topped supraglacial streams and subsurface passages that connect supraglacial cryolakes and, occasionally, cryoconite holes (Fountain *et al* 2004, Fortner *et al* 2005, Hoffman *et al* 2008). These cryoconite holes contain water for 4–8 weeks each year, before refreezing for winter, and the majority remain ice lidded year-round. Some cryoconite holes may develop a subsurface hydrological connection with the surrounding drainage system beneath the ice lid, via cracks and veins in the ice matrix. In a typical summer, approximately 50% become hydrologically connected (Fountain *et al* 2008), whilst the remainder are hydrologically isolated for multiple melt seasons. Solute and organic material, which accumulate in the cryoconite holes over time, can provide bioavailable nutrients to the ephemeral streams and ice-covered lakes (Foreman *et al* 2004, Bagshaw *et al* 2013), and propagules from cryoconite holes may re-seed downstream microbial communities (Schutte *et al* 2009, Yallop and Anesio 2010).

Cryoconite holes were sampled along transects across the three glaciers (figure 1) in the Austral summer of 2005/6. A core was collected from the centre of the hole using a SIPRE corer. If the cryoconite hole was completely frozen at the time of sampling, drilling continued until clean ice below the basal debris layer was encountered to ensure that the entire sediment layer was collected for analysis. Cores were removed and stored in Ziploc bags that had been triple-rinsed with deionized water. If any meltwater was present at the time of sampling, the ice lid was removed with the SIPRE corer, and then a water sample was pumped out using a hand powered vacuum pump. A sample of sediment was scooped out using disposable nitrile gloves and stored in a triple-rinsed Ziploc bag. Ice cores were stored frozen until processing up to 30 days later. Samples were eventually allowed to melt out in the collection bags and water samples were drawn off using syringes, whilst leaving the sediment behind. Electrical conductivity and pH of the water were measured in the field laboratory, and the remaining sample was filtered and transported to McMurdo Station for major ion and dissolved organic carbon analysis within 30 days. Full details of analyses and errors can be found in Bagshaw *et al* (2007) and Welch *et al* (1996). The length of time since the cryoconite hole was hydrologically connected was determined using the Cl^- age method (Fountain *et al* 2004, Tranter *et al* 2004, Bagshaw *et al* 2007).
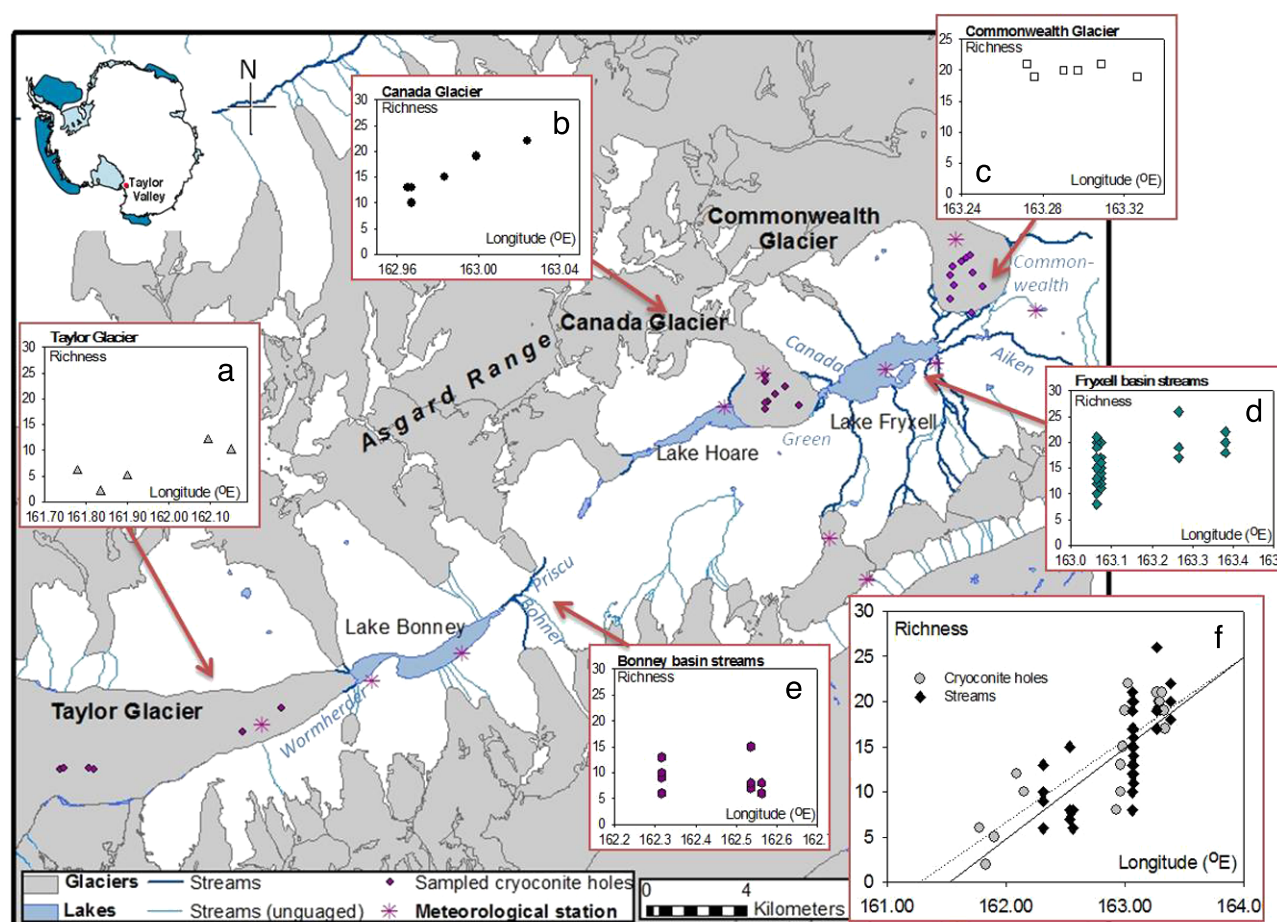
Figure 1. The location of sampled cryoconite holes on glaciers in Taylor Valley, Antarctica, with adjacent streams and lakes. The inset plots show variation in diatom species richness with longitude (distance inland) on Taylor, Canada and Commonwealth Glaciers ((a)–(c)), and in streams in the Lake Fryxell ((d); Commonwealth, Canada, Aiken and Green Creeks) and Lake Bonney ((e); Bohner, Priscu, Wormherder Creek) basins. (f) shows the regression plot of diatom species richness versus longitude for all the cryoconite hole (grey line) and stream (black line) samples.

2.1. Diatom preparation and analysis

After meltwater samples were removed for chemical analyses, sediment samples for diatom analysis were scooped into triple-rinsed, combusted glass bottles, and were preserved in 5% formalin. Samples were kept chilled ($<4\,^{\circ}$C) during storage and transport to the United States up to 4 months after sample collection. A subsample of the preserved sediments was prepared for diatom community analysis by digestion with heat and H_2O_2 and then by several rinses with distilled water (Blanco *et al* 2008). The inorganic remains were collected on a nucleopore filter (1.0 mm pore size, Whatman, USA) to remove fine particulates and resuspended in distilled water to remove clumps prior to counting. A subset of this homogenate was dried onto cover slips and permanently mounted on glass microscope slides with the mounting medium Zrax (W P Dailey, Philadelphia, USA). Relative abundances of diatom species were determined using an Olympus Vanox light microscope (Japan) at 1250× magnification, with ≥250 valves enumerated per slide. Diatoms were very rare in some samples, and in these instances the entire slide was counted. Relative abundance data were not analysed for samples with fewer than 250

valves counted, although these data were included in richness analyses. In total, 16 samples were used for community analyses, with an additional 4 samples from Taylor Glacier analysed for richness estimates. Taxonomic identifications were done according to the descriptions of Sabbe *et al* (2003), Van de Vijver *et al* (2004), Van de Vijver and Mataloni (2008), Esposito *et al* (2008), and the Antarctic freshwater diatoms database (http://huey.colorado.edu/diatoms).

The proportion of viable cells was assessed for selected samples ($n = 4$) by determining the per cent of cells with viable chloroplasts in wet mounts of preserved samples. Chloroplast viability was determined based on light microscopy and chloroplast autofluorescence in at least 100 intact cells. When possible, cells were taxonomically identified to the genus level.

2.2. Diatom community analysis

Diatom community composition was analysed using non-metric multidimensional scaling (NMDS), which is an ordination method that reduces the complexity of community data into fewer dimensions, and can use any distance matrix (Shepard 1962). NMDS was performed using a similar approach to that employed by Stanish *et al* (2011).

Table 1. Species richness and geochemical characteristics of sampled cryoconite holes. Cl^- age represents the length of time that the cryoconite hole has remained hydrologically isolated (Bagshaw *et al* 2007).

Glacier	Richness	pH	DOC (mg l^{-1})	Total cations (μ eq l^{-1})	Sediment thickness (cm)	Cl^- age (yr)
Commonwealth						
Mean	20.0	7.02	0.88	418	2.75	0.52
St. Dev.	1.40	1.06	0.63	204	3.20	1.24
n	7.00	10.0	10.0	9.00	10.0	9.00
Canada						
Mean	13.7	6.89	1.14	225	4.50	0.25
St. Dev.	4.70	1.30	0.53	147	3.43	0.46
n	8.00	8.00	4.00	8.00	8.00	8.00
Taylor						
Mean	7.00	6.17	0.24	319	2.69	11.0
St. Dev.	4.00	0.64	0.05	291	1.10	7.79
n	5.00	8.00	5.00	8.00	8.00	7.00

Briefly, after removing rare species (<1.0% abundance), a Bray–Curtis dissimilarity matrix of diatom community data was made, and the NMDS analysis was run in R's vegan package (R Development Core Team 2009). A three-dimensional model produced a goodness-of-fit value of 0.11 using Kruskal's stress formula, indicating that the ordination reasonably approximates the among-sample relationships (Clarke 1993). A Shepard plot of calculated versus raw dissimilarities showed strong nonmetric ($R^2 = 0.987$) and linear ($R^2 = 0.924$) fits.

3. Results

There was a clear relationship between longitude and diatom species richness ($R^2 = 0.70$, figure 1(f)). This trend was particularly prevalent on Canada Glacier (mean 13.8, standard deviation (sd) 4.7, range 11–29), in which longitude explained almost all of the variation in richness (figure 1(b), $R^2 = 0.92$). At the eastern and western ends of Taylor Valley (respectively), richness was greatest on Commonwealth Glacier (mean 19.6, sd 1.4), and lowest on Taylor Glacier (mean 7.0, sd 4.0). The same longitudinal trend, although less pronounced, was displayed when species counts only included samples which contributed >1% of the total diatom abundance, where Commonwealth Glacier had a greater number of species (mean 13), compared with an average of 10 and 8 species on Canada and Taylor Glaciers, respectively. Geochemical and physical factors of the parent cryoconite hole, such as sediment thickness, DOC, pH, and total cations (table 1), had little control on species richness, with no significant correlation found. The length of time that the hole had remained hydrologically isolated (Bagshaw *et al* 2007) also showed little correlation with richness, with the exception of Taylor Glacier, where the small sample size prevented a significant result (Cl^- age, table 1).

Diatom species richness in the streams of Taylor Valley also varied with longitude (figures 1(d)–(f), $R^2 = 0.50$ for all stream samples), with a mean of 23.0 species (sd 4.1) in streams in the coastal Fryxell basin, and 12.4 in the furthest inland Bonney basin streams (sd 3.2). Whilst streams in the Fryxell basin (Canada, Green, Commonwealth and Aiken Creek) had greater species richness than those in Bonney, richness in the Bonney basin (Bohner, Priscu and Wormherder Creek) varied more widely, possibly due to large, basin-wide differences in stream geomorphology and hydrology (Stanish *et al* 2012). The relationship between richness and longitude was nevertheless similar on the glaciers and in the streams (figure 1(f)), with similar regression slopes of 9.2 and 10.0, respectively.

The diatom taxa inhabiting cryoconite holes represented a subset of the taxa found in stream habitats, with 29 of the 46 stream taxa also present in cryoconite holes (stream $n = 39$, cryo-holes $n = 16$). The taxonomic distribution of these species, however, was strikingly different, with an absence of *Hantzschia* species that are abundant in stream algal mats (figure 2). Species of the genus *Luticola* were also differentially distributed in stream algal mats and cryoconite holes, in particular with higher abundances of the cosmopolitan species *L. gaussii* in cryoconite holes (*t*-test $p = 0.001$), and reductions in the abundances of other taxa, such as *L. austroatlantica* and *L. muticopsis*. The two dominant cryoconite hole genera, *Diadesmis* and *Muelleria*, had significantly lower abundances in stream habitats.

As a result of these genus-level differences, cryoconite hole diatom communities also differed significantly from stream algal mat diatom communities (PERMANOVA results, $F = 16.48, p = 0.001$). After controlling for the effect of habitat, diatom communities also differed by lake basin (PERMANOVA, $F = 7.61, p = 0.001$). Visualization of diatom communities across samples showed an overall clustering of samples by habitat along NMDS axis 1, with axis 2 separating samples from different locations (figure 3).

Cell viability counts showed that *Muelleria* spp. and *Diadesmis* spp. had the highest viability in the cryoconite holes, with up to 85% of the cells in a sample showing viable chloroplasts (table 2). Viability increased for both genera after the cryoconite holes melted later in the season ($p < 0.05$ for both genera), indicating biological activity within the holes after melting.
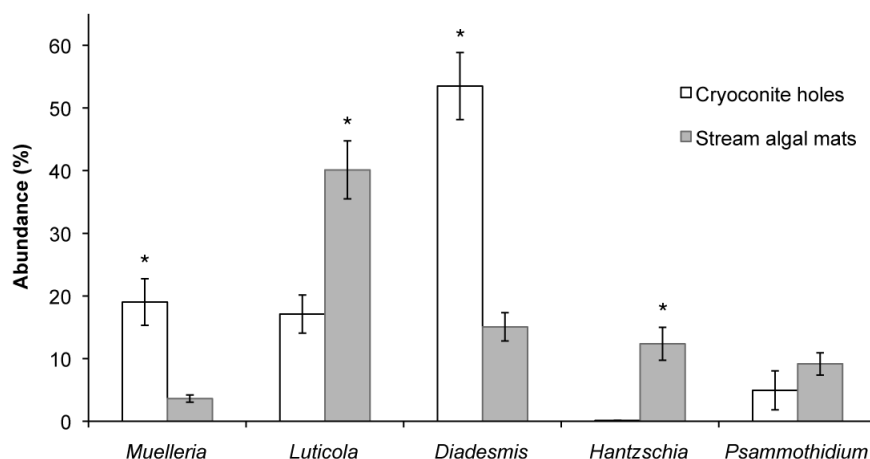
Figure 2. Mean relative abundances (±SE) of the most abundant diatom genera in cryoconite holes and stream algal mats. Genera that are significantly more abundant in one habitat than another are noted by an asterisk ($p < 0.001$).
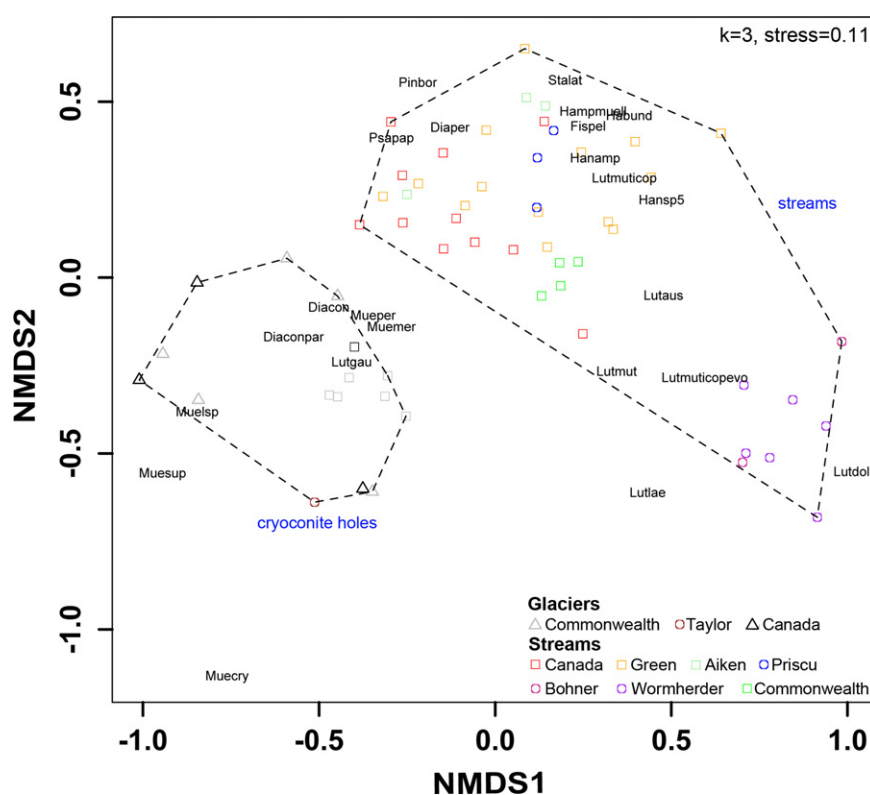

Figure 3. Nonmetric multidimensional scaling of diatom communities from cryoconite holes and surrounding streams: *K* refers to the number of dimensions of the ordination model, and stress measures the fit of the modeled ordination distances to the Bray–Curtis distances. Hulls are drawn around samples derived from cryoconite holes and streams. Diatoms with relative abundances greater than 10% are plotted. Species abbreviations: Pinbor—*Pinnularia borealis*, Stalat—*Stauroneis latistauros*, Hampmuell—*Hantzschia amphioxys* f. *muelleri*, Habund—*Hantzschia abundans*, Fispel—*Fistulifera pelliculosa*, Diaper—*Diadesmis perpusilla*, Psapap—*Psammothidium papilio*, Hanamp—*Hantzschia amphioxys*, Lutmuticop—*Luticola muticopsis*, Hansp5—*Hantzschia* species #5, Lutaus—*Luticola austroatlantica*, Diacon—*Diadesmis contenta*, Mueper—*Muelleria peraustralis*, Muemer—*Muelleria meridionalis*, Diaconpar—*Diadesmis contenta* var. *parallela*, Lutgau—*Luticola gaussii*, Lutmut—*Luticola mutica*, Lutmuticopevo—*Luticola muticopsis* var *evoluta*, Lutlae—*Luticola laeta*, Lutdol—*Luticola dolia*, Muelsp—*Muelleria* sp., Muesup—*Muelleria supra*, Muecry—*Muelleria cryoconicola*.

4. Discussion

Taylor Valley is an ideal location to assess the ecology of cryoconite hole diatoms because strong gradients in physical and environmental factors exist, and the effects of such drivers on community composition can be tested. Furthermore, the surrounding habitats have been well characterized, allowing for improved interpretation of the connections between cryoconite holes and other habitats. Previous studies have hypothesized that cryoconite holes are predominantly seeded

Table 2. Cell viability in the genera *Muelleria* and *Diadesmis* in cryoconite holes that were frozen at the time of sampling (frozen) and those that had thawed (melted).

	Viability (%)	
Sample	*Muelleria*	*Diadesmis*
Commonwealth Glacier (frozen)	21.4	10.0
Canada Glacier (frozen)	62.5	34.7
Commonwealth Glacier (melted)	51.5	16.7
Canada Glacier (melted)	85.7	43.7
Standard deviation (frozen)	29.0	17.5
Standard deviation (melted)	24.2	19.1
P-value (frozen versus melted)	0.041	0.046

by aeolian transport from surrounding aquatic environments (Christner *et al* 2003, Cowan and Tow 2004, Budgeon *et al* 2012), and this trend is also reflected in the diatom communities in cryoconite sediment from Taylor Valley. Diatom diversity was also linked to the position of the parent glacier within the Taylor Valley landscape. The cryoconite holes on Commonwealth Glacier, which is in the most productive hydrological basin (Virginia and Wall 1999, Barrett *et al* 2006) and is closest to the Ross Sea, had the highest diatom richness. This relationship is strongly displayed in the cryoconite across Canada Glacier, where a clear east–west gradient of richness exists (figure 1(f)), with highest richness in holes closest to the coast.

A number of physical differences exist between cryoconite holes on the three glaciers. Geochemical indicators of biological activity, such as pH, bacterial carbon production, and the concentration and phase association of nutrients, show that cryoconite holes at the western end of Taylor Valley (Taylor Glacier) have less active biological communities than those closer to the coast (Commonwealth Glacier) (Foreman *et al* 2007, Bagshaw *et al* 2013). Cryoconite holes on Taylor Glacier are larger and deeper, and remain hydrologically isolated for longer periods (Bagshaw *et al* 2007, table 1). They have predominantly coarser sediment, with a median grain size of 170 μm, compared with 150 and 130 μm on Canada and Commonwealth glaciers, respectively (Bagshaw *et al* 2013). These physical differences may impact the success of colonizing species. The lower species richness on Taylor Glacier, for example, may result from coarser cryoconite sediment providing less favourable habitat than the diatom source in the stream beds, or because the stronger winds that transport these larger grains damage cells during transport (Nkem *et al* 2006).

The glaciers at the coastal end of the valley are adjacent to more productive soils, which have higher soil moisture, organic carbon content and lower salinity than those at the western end (Barrett *et al* 2004). A denser network of ephemeral streams surrounds Lake Fryxell (figure 1), and it is likely that dehydrated algal mats in the stream beds are a significant source of biological material to the glacier surfaces (Lancaster 2002). Indeed, flakes of cyanobacterial mat were a common sight on the surface of Commonwealth Glacier, but were much less common on the western flanks of Canada Glacier and were virtually absent from Taylor Glacier.

The majority of aeolian material is transported during severe drainage winds (Sabacka *et al* 2012), which blow from the west (Doran *et al* 2002, Nylen *et al* 2004, Speirs *et al* 2010). However, lighter algal fragments and microorganisms could be transported via the prevailing easterly sea breezes that can reach speeds of 20 m s^{-1} at 3 m above the ground during the winter months (Doran *et al* 2002). These wind speeds are above the 5 m s^{-1} threshold for particle saltation observed 0.4 m above the ground in the neighbouring Victoria Valley (Speirs *et al* 2008). Turbulent eddies that develop during drainage wind storms can also redistribute algal material in an easterly direction (Speirs *et al* 2008), and result in deposition relatively close to the source area. This means that the glaciers at the coastal end of the valley that receive aeolian inputs from the local area are more likely to collect biological material, including diatoms, from stream beds and exposed lake shores.

However, whilst our results suggest that the holes are probably seeded by surrounding environments, the diatom species composition is not directly representative of either the ephemeral streams (figure 3) or the ice-covered lakes (Spaulding *et al* 1997, Konfirst *et al* 2011). The cryoconite holes have distinctive diatom communities that are dominated by a subset of the regional diatom community (figure 3) and are enriched in diatoms that are uncommon or rare in streams. Indeed, cryoconite holes are home to a unique diatom, *M. cryoconicola* (Van de Vijver *et al* 2010). Interestingly, the inland decrease in diatom species richness does not seem to be constrained by aeolian transport across lake basins, as the diatom species on Taylor Glacier are more commonly found in the Fryxell basin. The clustering of Priscu Stream diatom communities with other Fryxell basin streams, to the exclusion of other Bonney basin streams, further supports this assertion (figure 3). These findings suggest that, while the suite of organisms available to colonize Taylor Valley glaciers does not vary greatly longitudinally, the mass of biological material varies based on local productivity, which in turn alters the probability of viable propagules seeding the local glacial habitats. Second, the physical stresses of aeolian transport and cryoconite hole environmental extremes select for a subset of the diatom metacommunity that is uniquely suited to glacial life.

Habitat variation is a likely explanation for this finding. The cryoconite hole habitat is markedly different than the stream habitat. Within streams, previous findings suggest that species composition is controlled by habitat variation (Stanish *et al* 2011), and our results support this finding. For example, as previously mentioned, samples from Priscu Stream do not cluster with the other Bonney basin streams, but instead cluster with samples from the Fryxell basin (figure 3). Priscu Stream has a markedly different bed type, with a shallow gradient and sandy bottom that is more similar to other streams in the Fryxell basin than the adjacent, steep gradient and stony-bottomed Bohner Stream. Therefore, while the streams provide a major source of propagules to cryoconite holes, the species that are more resistant to environmental conditions in the cryoconite holes may be superior colonizers: *Muelleria* and *Diadesmis* appear to have an advantage in this habitat compared to other stream diatoms.

Diadesmis and *Muelleria* were the most abundant diatom genera in the cryoconite holes, and both have also been identified in cryoconite holes on Cirque Glacier, Greenland (Yallop and Anesio 2010). These two groups appear to have a survival advantage, either during aeolian transport, or within the hole itself. Our viability counts (table 2) suggest that these taxa can survive the winter months in the frozen cryoconite hole. A similar result of higher viability of *Muelleria* species was reported by Mueller *et al* (2001). The increased percentage of viable cells after thawing also suggests that the diatoms became metabolically active and divided when liquid water was available. Because many of the holes retain an ice lid after thawing, it seems likely that the changes in metabolic activity within the holes resulted from the resident community rather than from recent external aeolian inputs. We propose that the thicker frustules found in *Muelleria* and *Diadesmis* species increase survivability when subjected to frequent freeze–thaw events, and possibly increase their tolerance to other extremes that can occur in cryoconite holes, such as pH (Tranter *et al* 2004). Alternatively, it is possible that these genera have higher survivability from collisions during aeolian transport. Different species traits, such as the ability to colonize new substrates, may also explain our results. Additional studies on the physiology of Dry Valley diatoms and their survivability under different conditions are needed to identify the mechanism.

5. Conclusions

Diatom communities in cryoconite holes on glaciers in Taylor Valley are probably seeded by the surrounding aquatic environments. Cryoconite holes on glaciers that are closer to more productive stream and lake ecosystems are richer in diatom taxa, suggesting strong linkages between glaciers and the local basin characteristics. However, the proximity to seeding communities is not the only control on diversity; the cryoconite habitat also selects for particular suites of diatoms. Species that can survive freeze–thaw cycling and can colonize coarse substrates appear to have the highest viability and relative abundances. The unique selective pressures of cryoconite holes suggest that these habitats may promote speciation. Finally, the occurrence of diatoms in cryoconite holes across the globe (Yallop and Anesio 2010) support the idea that these icy habitats may act as refugia during extreme cold periods in polar environments.

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