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EDITORIAL

Cryospheric ecosystems: a synthesis of snowpack and glacial research

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Abstract

The fourteen letters that contributed to this focus issue on cryospheric ecosystems provide an excellent basis for considering the state of the science following a marked increase in research attention since the new millennium. Research letters from the focus issue provide significant insights into the biogeochemical and biological processes associated with snow, glacier ice and glacial sediments. This has been achieved via a significant, empirical effort that has given particular emphasis to glacier surface habitats. However, far less is known about aerobiology, glacial snow covers, supraglacial lakes and sub-ice sedimentary habitats, whose access for sampling and *in-situ* monitoring remains a great challenge to scientists. Furthermore, the use of models to explore key fluxes, processes and impacts of a changing glacial cryosphere are conspicuous by their absence. As a result, a range of process investigations and modelling studies are required to address the increasing urgency and uncertainty that is associated with understanding the response of cryospheric ecosystems to global change.

Introduction

Since the turn of the last millennium, our perception of glaciers and ice sheets has shifted from one of a lifeless, abiotic realm to a distinct biome with a microbial biomass broadly similar to all of Earth's unfrozen freshwater (Priscu *et al* 2008, Hodson *et al* 2008, Anesio and Laybourn-Parry 2012). This paradigm shift was a long time coming, because the very earliest explorers crossing the Greenland Ice Sheet in the 1890s had already drawn our attention to the discolouring of snow and ice surfaces by microorganisms, and investigations of snow micro-biota were conducted during expeditions to Antarctica in the 1900s by groups under the leadership of Scott, Mawson and others (e.g. McLean 1918). The meiofauna, algae, Protozoa and bacteria were then studied from the 1930s onwards, including during the 1957 International Geophysical Year (Sisler 1961). However, the data were qualitative rather than quantitative. We had an idea of what organisms were present but no information on their role. It was not until the 1960s

that snow algal photosynthesis was quantified (Fogg 1967): a challenging measurement that has been replicated by few studies since (e.g. Mosser *et al* 1977). Investigations of bacterial and viral production only started at the beginning of this century (Laybourn-Parry *et al* 2012). However, in spite of this protracted development history, we are now in a position where a profoundly important role for glaciers and ice sheets in global biogeochemical cycles is being realised (e.g. Wadham *et al* 2013, Hood *et al* 2015;) and demands for a better understanding of the implications of global cryospheric change are being made by many new research groups. This synthesis therefore places the research letters in this Cryospheric Ecosystems Focus Issue in the context of the recent literature and reviews our present understanding of the cascade of biogeochemical and ecological processes through ice-bound and ice-marginal terrestrial habitats. The intention is to identify the multidisciplinary approaches needed to understand global cryospheric change, and to identify where future research effort should be directed.

Snowpacks and snowmelt

Seasonal snow cover exerts a fundamental control upon biological production in underlying habitats: a problem that is best understood in the context of soil and tundra ecology in boreal and Arctic landscapes (e.g. Luus *et al* 2013). Interestingly, in the context of glacial snowpacks, changes in the distribution and persistence of snow cover are reasonably well known through mass balance studies (e.g. Mernild *et al* 2013), yet its influence upon the ecological and biogeochemical processes in underlying glacial habitats remains largely unexplored. However, the importance of glacial snow cover as a control upon subglacial biogeochemical processes is at least established in the literature. For example, several studies have demonstrated how the seasonal recession of glacial snowpacks greatly influences the evolution of subglacial drainage networks: a process that is linked to the aeration of sediments at the glacier bed (and thus the redox environment that characterises their microbial ecology) and also the delivery of nutrients and organic matter by surface melt (Hodson *et al* 2008, Tranter *et al* 2005). As snowlines retreat up-glacier, large fluxes of surface meltwater enter the subglacial environment from the glacier surface, and transform long residence time, poorly oxygenated meltwater flowpaths into well-aerated arteries or conduits at the glacier bed. Sediments in close proximity to these conduits will favour oxic or sub-oxic biogeochemical processes, while those that remain at distance are most likely to remain anoxic, and thus conducive to processes such as sulphate reduction and even methanogenesis, especially beneath ice sheets, where inputs of surface meltwater are negligible (e.g. Wadham *et al* 2012). However, our characterisation of the redox changes that occur beneath melting ice masses has been largely restricted to outflow measurements of stable isotopes and dissolved oxygen at the ice margin (e.g. Wynn *et al* 2006, Irvine-Fynn and Hodson 2010), or *in-situ* measurements via invasive boreholes (e.g. Christner *et al* 2014). Understanding the spatio-temporal variation of redox conditions beneath ice masses will therefore remain a major research priority for the future, because it will reveal new insights into subglacial ecology and show how the redox-sensitive acquisition of certain key nutrients (such as N, Fe and S) by meltwaters will change with increasing melt.

Our understanding of the snowpack as an ecosystem in its own right (rather than as a mere mediator of the abiotic conditions that lie beneath it) is also beginning to improve, but again, this focus is not sufficiently directed towards glacial snow covers. For example, Larose *et al* (2013) show how microbial community structure and nitrogen cycling within coastal tundra snows may be identified using molecular techniques during spring melt and in spite of the low temperatures that limit water availability for metabolic processes. This work follows a number of other important

studies of 'dry snow' biology and biogeochemistry, some of which have emphasised the role of clay particles or dust in biogeochemical transformation of nitrogen (Amoroso *et al* 2009). These reduce the likelihood of its photolytic loss to the atmosphere (e.g. Beine *et al* 2003, Björkman *et al* 2014), and therefore enhance the opportunities for assimilation into cryospheric ecosystems. The nitrogen cycle therefore remains one of the best examples of how closely the biological, chemical and physical processes can be integrated in cryospheric ecosystems. In spite of this, there still persists a tendency for studies to depend heavily upon just one technique or approach.

Takeuchi *et al* (2013) compared the microbial dynamics in seasonal (ablation area) and perennial (accumulation area) glacial snowpacks, revealing distinct differences in their algal taxa (e.g. *Cd. Nivalis* on snow and *A. nordenskiöldii*, *M. berggrenii* and the Oscillatoracea on the ice). The duration and intensity of algal 'blooms' within these different habitats is an important research problem, because they can increase surface melting by reducing the snow/ice reflectance (albedo). This particular issue is attracting most research attention on the Greenland Ice Sheet, because there are strong reasons to expect autotrophic processes to expand rapidly across the low gradient upper ablation area of this ice sheet in future (e.g. Uetake *et al* 2010, Wientjes *et al* 2010, Yallop *et al* 2012), Cook *et al* 2012, Lutz *et al* 2014.

Ice surface habitats

Glacier surfaces are characterised by inorganic and organic debris layers that support significant rates of biological activity when liquid water becomes available. The bioflocculation of dust and other impurities such as black carbon upon this layer produce aggregate particles called cryoconite (e.g. Takeuchi *et al* 2010, Hodson 2014). The structure and persistence of cryoconite is becoming increasingly well researched, with conceptual models of cell-mineral attachment akin to those employed in biofilm research being used to explain the role of exudates in the cementation of the aggregate (Hodson *et al* 2010, Takeuchi *et al* 2010). Zarsky *et al* (2013) and Langford *et al* (2011) studied perhaps the largest aggregate clasts yet described in the literature, whose formation was enhanced by ammonium deposition from nearby sea birds, and reactive clay particles from cliffs overlooking the Aldegondabreen glacier (Svalbard). Interestingly, the size of these aggregates and the presence of labile carbon enabled low redox environments to develop, and thus form anoxia in an environment that is otherwise conducive to oxygenation (Hodson *et al* 2008). The proximity of Aldegondabreen to local sources of guano and fine sediment supply also gave the large aggregates studied by Zarsky *et al* (2013) the capacity to support ammonia-oxidising archaea. Local environmental factors therefore influence the functional activity of

microorganisms on glacier surfaces. However, while the influence of bird colonies is now established (Mindl *et al* 2007, Grzesiak *et al* 2015), other environmental factors and gradients are less understood (e.g. Stibal *et al* 2011). Recent insights have been provided by diatom biogeography in cryoconite-filled surface melt pools ('cryoconite holes') of the arid McMurdo Dry Valleys, Antarctica (Stanish *et al* 2013), which showed a clear increase in diatom species richness with distance from the coast, further influence by nearby ephemeral streams and/or perennial (ice covered) lakes, and a sediment size effect. The sediment size effect suggests that a greater understanding of sediment provenance and transport history should be sought. For example, Nagatsuka *et al* (2014) showed how the long-range transport of fine aeolian particles may be established using their rare earth element composition and then used to understand bioflocculation into Asian cryoconite. Future work should therefore integrate the techniques described above to understand better the linkages between sediment provenance and microbial diversity. Studies of the long-term changes in the storage of dust and associated microorganisms in large ice sheets should also be included, because ice core analyses from the Greenland Ice Sheet have revealed clear evidence for longer-term changes forced by dust deposition over glacial cycles (Miteva *et al* 2009).

The above synthesis shows that there exists a clear bias towards cryoconite research within the literature which needs to be addressed before we understand the cascade of nutrients, energy and life that is initiated by seasonal melting on glacier surfaces. However, the use of cryoconite as a model ecosystem for the exploration of tight linkages between physical, chemical and biological drivers should not be overlooked. For example, Bellas *et al* (2013) show that since there is a food web within cryoconite dominated by microorganisms, viruses can play an important role in bacterial mortality and the subsequent release of nutrients and organic carbon for recycling. The same processes are invoked in streams upon McMurdo Dry Valley glaciers by Foreman *et al* (2013). Quantifying this biological driver of DOC cycling and considering it alongside climate forcing is a research priority for the future, because it is increasingly clear that glacial meltwaters are distinctive on account of the high proportion of labile, proteinaceous organic matter within their DOC pool (e.g. Spencer *et al* 2014). Modern molecular techniques should also be employed to pinpoint the precise microorganisms and compounds involved, because much of the recent evidence seems to suggest that the labile DOC is produced *in-situ* (Barker *et al* 2006).

Despite conceptual advances in our understanding of snow and ice surface microbial communities and their potential feedbacks to melting and runoff nutrient transfer, the direction and magnitude of net ecosystem exchange (NEE) of CO₂ with the atmosphere

remains unclear. Great emphasis is currently placed upon the importance of autotrophic processes on account of their albedo-reducing potential (e.g. Yallop *et al* 2012) and likely importance for the generation of labile DOC. However, Edwards *et al* (2013a) used molecular techniques to reveal how the phylogenetic composition of microbial communities in cryoconite debris can be dominated by heterotrophic bacteria in the cryoconite of a north-facing Alpine glacier. This work also showed how functional genes were most likely adapted to the exploitation of allochthonous C, N and P. Similarly, subsidy of allochthonous organic matter and a likely net heterotrophic ecosystem have been emphasised in the study of Svalbard glaciers (Stibal *et al* 2008). Furthermore, debris-covered glaciers, where the thickness of surficial debris is sufficient to suppress ablation (rather than promote it) are even more likely to promote heterotrophic processes (e.g. Franzetti *et al* 2013). However, although these glacier types have been subject to limited investigation, recent CO₂ flux measurements have revealed that the debris layer can in fact be a significant sink of CO₂, perhaps due to weathering processes (Wang *et al* 2014).

The most recent NEE model that included both heterotrophic and autotrophic production on the Greenland Ice Sheet indicated a net autotrophic system dominated by micro-algae rather than cryoconite (Cook *et al* 2012). Therefore we must challenge the view that biological production on glacier surfaces is dominated by cryoconite before we can deduce whether glaciers are net sources or sinks of atmospheric CO₂. The causes and likely distribution of net heterotrophy also deserves equal attention. One of the greater uncertainties in this context is the so-called bacterial growth efficiency, which Foreman *et al* (2013) suggest is likely to be as low as 1–2% in a range of ice surface habitats and thus capable of explaining a large proportion of the CO₂ transfer to the atmosphere that is inferred from incubation studies (e.g. Telling *et al* 2012). However, the empirical approaches used to calculate this crucial parameter might not be appropriate for supraglacial ecosystems.

Supraglacial streams and lakes

Supraglacial streams are crucial vectors in glacial ecosystems, yet their role in moderating (rather than merely advecting) the flux of nutrients, organic matter and cells downstream during the melt season remains unclear. A study on Mendenhall Glacier in Alaska was perhaps the first to directly assess nutrient conservation in these streams by using a tracer addition approach, finding evidence for DOC retention and NO₃ production (Scott *et al* 2010). Work by Foreman *et al* (2013) considered the ecology and biogeochemistry of supraglacial streams of Antarctica, and emphasised how they are subject to high UV irradiance levels that are harmful for aquatic life. In many aquatic ecosystems, humic substances play an important role

in the absorption of UV radiation. However, intense photo-degradation, low rates of production and flushing by meltwater contributed to their absence in the streams of Foreman *et al*'s study. As a result, Foreman *et al* (2013) describe how other adaptations, including pigmentation and ice nucleation, were important for success, and enabled an autotrophic community to support a heterotrophic bacterial community through the production of young, labile (proteinaceous) DOM. By contrast, Cawley *et al* (2013) found that stable hypersaline coastal ponds in Antarctica develop humic substances to a far greater degree than freshwater supraglacial lakes and streams described above. This occurs without any plant cover within the watershed and enabled the researchers to describe a much-needed reference microbial fulvic acid from this environment. The results therefore suggest that photo-degradation is not the most important factor governing the lack of humic substances upon glaciers, because the process also occurs on ice shelf and coastal ponds where humic substances accumulate. Ice shelf ponds perhaps make better cases for comparison to glacier surface lakes than coastal ponds, although their abiotic conditions can be surprisingly different. For example, Sorrel *et al* (2013) showed that primary production was greatest in basal brines of the stratified ponds: conditions that are clearly unlikely on glacier surfaces. They also found N limitation and a tight coupling of primary and secondary production there, with the former dominating by far. Surprisingly, the N limitation existed in spite of a large and potentially available organic C and N pool. The recalcitrance of the older organic nutrients accumulating in the ice shelf lakes clearly deserves further attention, because it is at odds with the emerging paradigm of labile autochthonous DOM production in ice surface ecosystems.

The excess of primary production over bacterial production in some icy habitats and the reverse situation (net heterotrophy) in others suggest that the lability and composition of DOM exported by meltwaters might vary according to ambient light conditions and nutrient availability. Therefore, unless viral lysis is a dominant control upon DOM acquisition by meltwater, there should be detectable temporal and spatial changes in the lability of DOM draining glaciers and ice sheets. To date, however, there are an insufficient number of studies with which to assess this. Furthermore, any changes in DOM characteristics due to variations in *in-situ* production and processing need to be isolated from a strong signal associated with DOM elution throughout snow cover depletion (Meyer and Wania 2011) and seasonal inputs from ice-marginal ecosystems (Spencer *et al* 2014). Until experimental work has isolated these various controls, the impact of labile DOM export from glaciers and ice sheets will remain unclear. Further, the fluorometric techniques that dominate the study of DOM composition need to

augmented with other techniques, because not all DOM is detectable by fluorescence, and the molecular composition of the DOM needs to be better understood (Singer *et al* 2012). Recent research suggests Fourier Transform Ion Cyclotron Resonance Mass Spectrometry (Singer *et al* 2012) and Nuclear Magnetic Resonance (Paulter *et al* 2012) show promise.

Beyond the ice limit

The use of space-time substitution in the study of glacier forefields has made them valuable observatories for studying ecosystem succession. This research has begun to give increasing emphasis to the role of microbial processes in biogeochemical cycles and soil development (Schütte *et al* 2009, Zumsteg *et al* 2012, Bernasconi *et al* 2011, Bradley *et al* 2014), and therefore complements the studies of higher trophic levels that have dominated in the past (e.g. Chappin *et al* 1994). For example, Brunner *et al* (2014) examined pioneering fungi in the Damma Glacier forefield—and showed that a heterogeneous range of carbohydrates typified early ecosystem development and influenced which particular organic acids are used to mine nutrients like phosphorus from glacial till. The efficacy of these processes, along with inorganic acid production by other heterotrophs and the extended opportunities for rock-water interaction that young glacial till affords (Engstrom *et al* 2000), are most likely the key reasons why nitrogen and carbon are usually reported as the limiting nutrient following deglaciation (Bernasconi *et al* 2011). The immediate question to arise from this work is how influential fungi and yeasts are in the other habitats where debris is present, such as in cryoconite and subglacial till (e.g. Butinar *et al* 2007, Turchetti *et al* 2008, Edwards *et al* 2013b). Frey *et al* (2013) gave emphasis to the microbial autotrophic community in the Damma Glacier forefield and also found that heterogeneity within different successional stages was greater than expected. In this case it was shown how cyanobacteria and green algae communities along the successional gradient clearly shifted and that each soil environment selected for its own photoautotrophic community. These studies therefore show how autotrophic and heterotrophic microbial communities deserve more research attention before the links between ecological succession and soil development can be fully understood. Further, they are important for developing a better understanding of how expanding glacier forefields influence aquatic biogeochemistry (Engstrom *et al* 2000, Milner and Robertson 2010) and the composition of nutrients exported to downstream ecosystems (e.g. Nowak *et al* 2014).

Conclusions and recommendations for future research

Over the last few decades, the traditional view that glaciers and ice sheets are passive, abiotic cryospheric environments has been justifiably overturned in favour of a paradigm that treats them as one of Earth's most vulnerable biomes. It is now very clear that cryospheric environments support relatively simple yet important ecosystems, whose tight integration between physical, chemical and biological processes offer ideal opportunities for conducting research with a broad appeal to ecologists. This research is now being given a sense of great urgency on account of the vulnerability of icy habitats to climate change (Hood et al 2014, Yde et al 2011) and the compelling cases being made for developing a better understanding of the consequences of nutrient and organic matter losses from ice to downstream ecosystems. The following future research priorities deserve attention in these contexts:

- We must continue working across the 'ice divide' and integrate expertise from glacial and non-glacial research. It is very clear that the wider importance of glaciers in global biogeochemical cycles needs transdisciplinary interaction among researchers at dedicated conferences and workshops, because there is still too much fragmentation to address the key uncertainties.
- Quantitative, not qualitative, insights into the sensitivity of cryospheric ecosystems to climate change must be sought. Particular attention needs to be given to how small temperature increases might give rise to very significant changes in the biological production upon the flatter parts of polar ice sheets and ice shelves, where the expanse of water-soaked snow could increase markedly in the near future.
- The representation of the above processes in conceptual or physically-based models must improve as we move away from empirical understanding and adopt a more mechanistic approach. For example, models of carbon, water and nutrient fluxes are urgently needed to improve understanding of how polar ice sheets fertilise adjacent seas. Critical feedbacks such as the influence of biological production upon ice albedo and thus melting also require modelling. At present, models remain conspicuous by their absence in glacial cryospheric ecology, yet there are several being used to explore sea ice biogeochemistry and biological production from which we can draw inspiration (e.g. Pogson et al 2011).
- Particular emphasis has been given to the surface processes in this synthesis. This was no coincidence:

surface meltwater is the key vector for understanding how the transfer of nutrients, cells and organic matter will respond to climate change. However, atmospheric scientists and aerobiologists must help us understand the inoculation of such habitats. Further, subglacial environments will also play a crucial role in regulating surface-derived meltwater outputs. The community therefore needs to continue to address the great technological challenges associated with sampling and monitoring the environments above and below the ice surface.

With these research drivers it is hoped that we can begin to understand the biogeochemical and ecological consequences of global mass balance decline in the cryosphere.

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