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NEWS AND VIEWS

PERSPECTIVE

Microbial dynamics in glacier forefield soils show succession is not just skin deep

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All over the world, glaciers are receding. One key consequence of glacier area loss is the creation of new terrestrial habitats. This presents an experimental opportunity to study both community formation and the implications of glacier loss for terrestrial ecosystems. In this issue of *Molecular Ecology*, Rime *et al.* (2015) describe how microbial communities are structured according to soil depth and development in the forefield of Damma glacier in Switzerland. The study provides insights into the contrasting structures of microbial communities at different stages of soil development. An important strength of the study is the integration of soil depth into the paradigm of primary succession, a feature which has rarely been considered by other studies. These findings underscore the importance of studying the interactions between microbial communities and glaciers at a time when Earth's glacial systems are experiencing profound change.

Keywords: community development, forefield, glacier pyrosequencing, succession

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In volumetric terms, Earth's glacial systems are its largest freshwater ecosystems; however, global glacial ice surface area has declined from ~30% to ~11% since the last glacial maximum (Edwards *et al.* 2014). Moreover, contemporary climate change is rapidly affecting glacial systems, with mountain glaciers proving especially sensitive to atmospheric warming (Fig. 1). Therefore, while the multifarious glaciological, climatological and hydrological implications of glacier loss are highly evident, ecological interactions with glacial systems are less well studied but no less important for downstream terrestrial and coastal environments (Wilhelm *et al.* 2013).

Indeed, the liberation of land in glacier forefields as glaciers recede has presented a paradigm for primary succession and soil development along chronosequences. The development of plant communities has been studied most intensively; however, the advent of high-throughput sequencing has permitted insights into the interlinked development of soils with microbial and plant communities in glacier forefields (Schmidt *et al.* 2014). In this regard, studies of note include those which have revealed plant associations with fungal and bacterial community assembly (Brown & Jumpponen 2014); gradients in bacterial diversity (Schutte *et al.* 2010) and root-associated fungal biodiversity (Blaalid *et al.* 2012). However, few studies have considered Alpine glaciers or the effects of soil depth.

Consequently, Rime *et al.* (2015) coupled measurements of environmental properties with amplicon pyrosequencing of bacterial (16S rRNA genes) and fungal (ITS2) marker loci present in community genomic DNA to infer the bacterial and fungal community diversity and structure across the 110-year chronosequence of soil development in the Damma glacier forefield. Rime *et al.* (2015)'s research questions aimed to address three specific lacunae in our knowledge of glacier forefield ecology. First, the effect of soil depth on microbial community development is poorly detailed as most studies examine topsoils, and thus, the potential for interactions between soil depth and development in shaping microbial communities was unknown. Second, associations between specific microbial taxa and soil depth and development had not been determined; therefore, the potential for microbial taxa to be indicators of soil formation was unclear. Finally, while Brown & Jumpponen (2014) examined the fungal and bacterial communities of Lyman glacier forefield (Washington, USA), the drivers of fungal and bacterial community structure across soil development and depth gradients of Damma glacier remained to be elucidated.

Resolving these questions has shown that soil depth interacts with the development of soils in shaping the diversity and structure of both bacterial and fungal communities in the Damma glacier forefield (Fig. 2). In particular, depth most strongly affected the communities of soils at early stages of development with limited or no vegetation. This stage revealed microclimatic variation, soil moisture and hence changes in water regime as the predominant drivers of community structure. Later stages harboured a proliferation of root-associated ectomycorrhizal fungi and other taxa capable of degrading complex organic carbon sources (e.g. candidatus *Solibacter* or lignocellulolytic ascomycetes). Therefore, while the translocation of carbon via rhizodeposition may influence the microbial communities of older soils, it appears that the promotion of habitat stability and buffering against fluctuating environmental conditions afforded by increased vegetation cover is important for the maturation of soil microbial communities.

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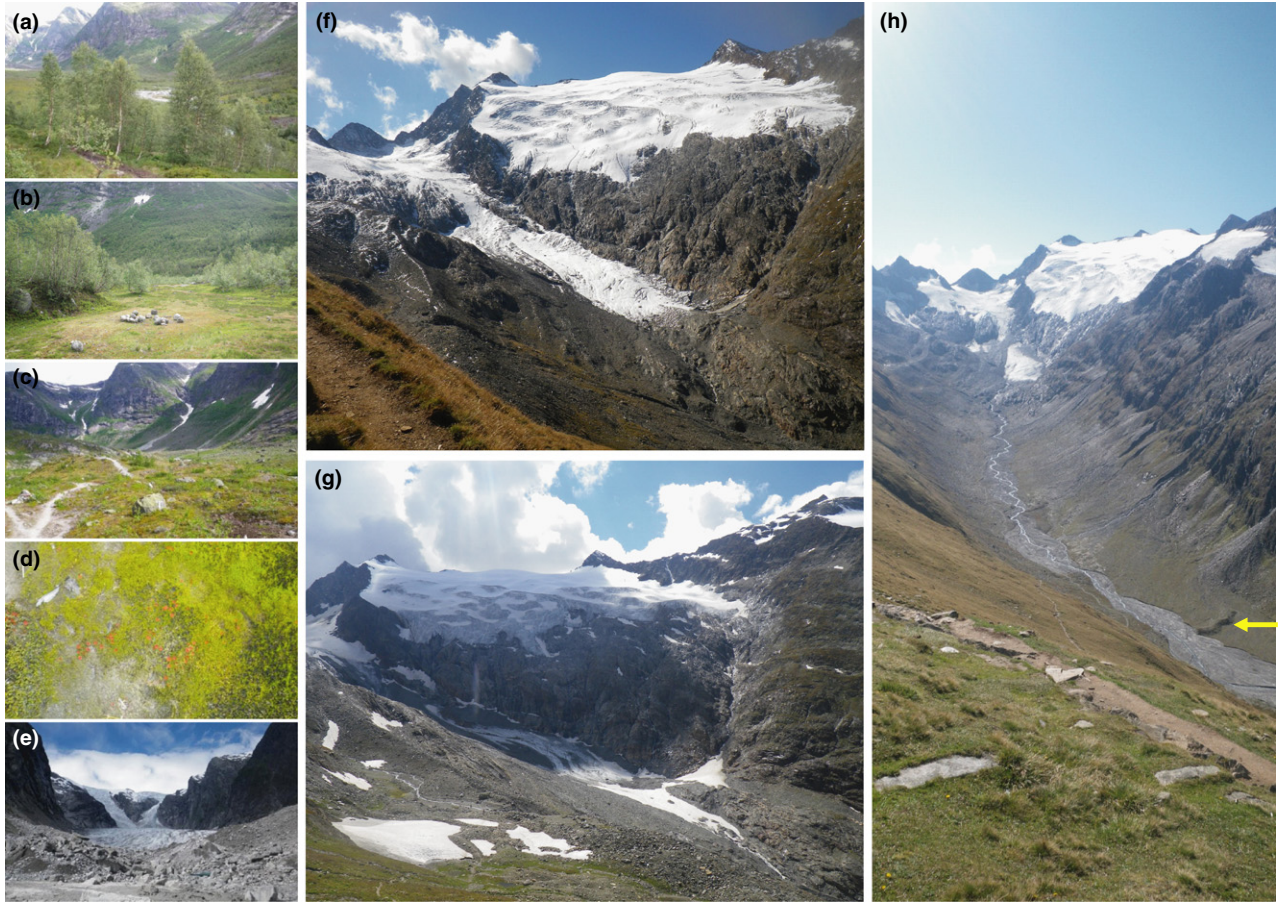


Fig. 1 The loss of glaciers creates new habitats. (a–e) shows the 280 years. Chronosequence of Austerdalsbreen, Norway, with out-wash plain woodland (a; 10 000 years old), terminal moraine (b; 280 years old), sparse forefield vegetation (c; 100 years old), pioneering moss and cup fungi (d; 50 years old) and the glacier front (e; <10 years old). (f–g) In Alpine regions, glacier loss is dramatic, for example Rotmoosferner in Tyrol (f; September 2010, g; September 2014), creating opportunities to study the succession of microbes in relation to soil development (h; Rotmoosferner forefield, with Little Ice Age maximum moraine arrowed). All images from the collection of A. Edwards.

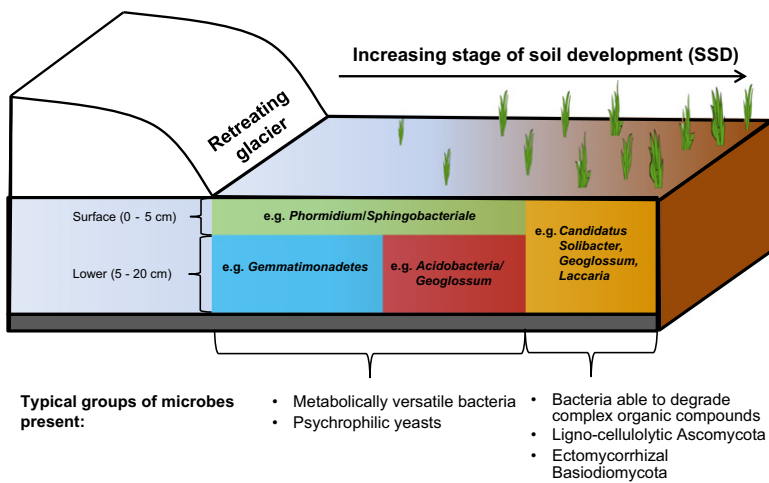


Fig. 2 Conceptual block diagram illustrating the findings of Rime *et al.* (2015), with distinct communities identified according to soil stage development and depth.

The identification of operational taxonomic units (OTUs) affiliated to *Phormidium* sp., as oscillatorean cyanobacteria typical of microbial mats, metabolically plastic *Geobacter* sp.

and psychrophilic basidiomycete yeast (e.g. *Mrakia* sp.) as indicators of unvegetated soils is consistent with the interpretation of environmental fluctuations as drivers of early

stage soil microbial communities. Moreover, these taxa are found in a diverse range of habitats associated with glacial systems and are presumed to be cosmopolitan, for example (Edwards *et al.* 2011, 2013). It is likely that priority effects (Brown & Jumpponen 2014) support microbial community assembly in early stages of soil development, with potential inoculation from glacial ecosystems. Finally, the role of microbes as agents of biogeomorphology (Viles 2012) in glacier forefields (Anderson 2007; Edwards *et al.* 2014) should be considered, as autotrophic mat-forming consortia such as those supported by *Phormidium* sp. can play important roles in stabilizing the proglacial landscape, as reported by Frey *et al.* (2013) for Damma glacier.

The reader may be left pondering the significance of observations constrained to a single glacier. There are an estimated 198 000 glaciers (Pfeffer *et al.* 2014) and three ice sheets. Damma glacier is but one of those glaciers, and comparative studies of glacial ecosystems are limited. Presently, less than 0.05% of all glaciers have any published high-throughput sequence data. While it is clear that we must be circumspect in extrapolating from one glacier forefield to others which will necessarily differ in environmental conditions, intensive studies of key locations have considerable value. Indeed, the integrated study of ecology, glaciology, hydrology and pedogenesis over many annual cycles necessary to provide a holistic overview of glacial system change is best facilitated by the establishment of field sites intensively studied by multidisciplinary teams. The Damma glacier catchment is an outstanding example in this respect. It could be regarded as the *Escherichia coli* K12 of the glacier world. Coordinated multidisciplinary studies have been in place in the Damma catchment for nearly a decade, building on prior observations to monitor changes and investigate their mechanisms in detail, as summarized recently (Bernasconi 2014). It is clear that to understand the consequences of glacier wastage, complementing both intensive catchment-centred studies and comparative approaches is required. In this regard, the high-throughput sequencing analyses and rich environmental context provided by Rime *et al.* (2015) add to the detailed narrative of the Damma glacier project.

Although they do not compromise the clear insights provided by Rime *et al.* (2015), there are two apparent limitations to the investigation offering future directions of study. In common with many surveys of glacier-associated microbial diversity, these are limited temporal coverage and the inherent difficulties in interpreting DNA-based analyses.

While a particular strength of the methodology is that independent replicates are collected in transects co-aligned with the well-characterized BigLink project (Bernasconi 2014) to provide robust spatial coverage, the study is limited to a single time point. This is suitable for the study's objectives of describing microbial community development in three dimensions in forefield chronosequences, but shorter-term changes in the fourth dimension are unmapped. As recently outlined our understanding of seasonality in glacier forefields is limited (Bradley *et al.* 2014).

As climatic changes affect seasonality, perturbed environmental conditions may impact upon the stability of forefield community structure and function, and prolonged or warmer growing seasons may affect carbon cycling (Bradley *et al.* 2014). To our knowledge, how microbial communities change in forefields in response to dynamic snow cover, hydrology, temperature and incident radiation and other seasonally variable factors at intra-annual time-scales is entirely unknown.

The abundance of OTUs affiliated to sporogenic and anaerobic taxa (e.g. *Clostridium*, *Sporotalea* or *Anaeromyxobacter*) in the early stages of soil development illustrate the potential for a conditionally active seed bank within the glacier forefield. On the basis of marker gene or metagenomic analyses, it is difficult to infer whether such taxa are active or dormant with the potential to contribute to ecosystem function under different conditions. Likewise, nonviable cells will be detected by DNA-based analyses but assume the function of necromass, vital in such carbon-limited habitats, rather than contributing to functional potential. In contrast, low-abundance OTUs within marker gene data sets may be highly abundant in co-extracted rRNA-based amplicon data sets, as illustrated recently in Alpine glacial streams (Wilhelm *et al.* 2014), implying that taxa within the long-tailed phylotype distribution typical of microbial communities may be disproportionately active in proglacial environs. Unfortunately, the most popular strategies to resolve the active phylogeny, the use of rRNA amplicons or metatranscriptomics, both present significant challenges (Blazewicz *et al.* 2013; Moran *et al.* 2013). It is hoped that future studies offering a nuanced interpretation of integrated amplicon and multi-omic data will be rewarded with rich insights into the complex relationships between community structure, activity and function.

In conclusion, Rime *et al.* (2015) provides a novel three-dimensional insight into the properties of soil microbiota along a glacier forefield and highlights potential directions for future studies. These could consider seasonal dynamics and integrating amplicon with multi-omic data. Such approaches will help us understand microbial interactions which assume ever greater significance as glaciers recede in our warming climate.

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