Final Accepted Version of

Miller, H.R. and Lane, S.N., 2019. Biogeomorphic feedbacks and the ecosystem engineering of recently deglaciated terrain. Forthcoming in Progress in Physical Geography, 43, 24-45

Typeset version available at
https://journals.sagepub.com/doi/full/10.1177/0309133318816536

DOI: 10.1177/0309133318816536

Keywords
vegetation, microbes, Alpine, biogeomorphic feedbacks, glacial forefields, succession

I Introduction

Glacier recession since the Little Ice Age has provided ecologists with a means for investigating ecosystem succession, as glacier retreat exposes bare ground, "switching on" the potential for high rates of phototrophic activity (Coaz, 1887; Matthews, 1992). In theory, since the duration of exposure increases in age with distance from the glacier's margin, scientists have commonly used a space-for-time (chronosequence) approach to investigate successional pathways of primary colonizers (Coaz, 1887; Schreckenthal-Schimitschek, 1935). Chronosequence approaches have provided the framework for determining succession with classic work undertaken in Glacier Bay, Alaska (Cooper, 1923, 1931, 1939) and at the Storbreen glacier in Norway (Matthews, 1979a, 1979b; Matthews and Whittaker, 1987). These studies have provided the general classifications in glacial forefields of pioneer species (e.g. *Linaria alpina, Campanula cochlearifolia, Saxifraga aizodes, Salix arctica, Dryas drummondii),* early-successional stage species (e.g. *Anthyllis vulneraria, Poa alpina, Trifolium pallescens, Salix stichensis)*, intermediate successional stage species (e.g. *Salix* spp. and *Salix herbaceae,* and *Dryadeto-firmetum* and *Elynetum* associations*)*, and late-successional tree species (e.g. *Larix decidua*) and shade tolerant plants (e.g. *Pyrola minor*). A major assumption in the chronosequence approach, however, is that factors other than time either do not matter or can be held constant by careful sampling (see also Matthews and Whittaker, 1987; Heckmann et al., 2016). This assumption may not always apply as it is hard to control for all environmental factors in such heterogeneous systems, and such factors may actually be of importance in driving succession (Rydgren et al., 2014).

By combining chronosequence approaches with an understanding of environmental heterogeneity, more nuanced understandings of vegetation succession have been developed for glacial forefields by correlating (both statistically and through simple observation) environmental factors, terrain age, and vegetation patterns. Researchers have done this primarily by collecting detailed environmental data at the sites used in the chronosequence, and then using ordination to determine statistically which factors correlate most strongly with vegetation parameters (e.g. Caccianiga and Andreis, 2001; Matthews and Whittaker, 1987; Raffl et al., 2006; Wietrzyk et al., 2016). As a result, grain size, water content, micro-relief, and micro-climate have all been shown to be important factors in driving vegetation succession (Burga et al., 2010; Rydgren et al., 2014; Wietrzyk et al., 2016). In the Morteratsch glacier forefield in Switzerland, Burga et al. (2010) found that plant succession could take a variety of paths depending on the starting soil material (e.g. clay/silt or coarse gravel) and its moisture retention capacity; and sites that retained soil moisture had much higher rates of plant growth. Garibotti et al. (2011) investigated the impacts of meso-topographic heterogeneity on vegetation development along a chronosequence of eight consecutive moraines in the southern Patagonian Andes. They identified four major successional stages that depended on the specific location on the moraine (and therefore differences in environmental factors such as slope and geomorphic stability).

Different models have been proposed to identify the mechanistic underpinnings of these observed successional patterns. In Matthews' classic text, *Ecology of Recently-Deglaciated Terrain* (1992), he reviews these different models, and then proposes a "geoecological" model for vegetation succession. This model is powerful as it combines time since deglaciation with abiotic drivers (e.g. initial physical conditions, disturbance) and biotic drivers (e.g. soil formation, biological factors) (Fig. 1). Abiotic processes initially dominate but are eventually overtaken by biotic processes as the landscape becomes more stable. The relationship between these two factors depends on environmental stress. In environments with little disturbance, biotic processes become dominant much more quickly, whereas in more regularly disturbed environments abiotic processes may remain dominant indefinitely. This model is useful as the idea of stress gradients can be applied to gradients in latitude, altitude, disturbance, and resource availability (Matthews, 1992) and hence reconcile geographic differences in successional processes between different environments.

[Insert Figure 1 here]

Since Matthews (1992) first proposed this geoecological model, accelerated rates of glacier recession in many Alpine and Polar regions have been reported (Casty et al., 2005; Gabbud et al., 2016; Lynch et al., 2016; Paul et al., 2004; Pellicciotti et al., 2005; Salzmann et al., 2012), notably since the 1980s. Thus, the production of paraglacial terrain has become more rapid, which may influence both abiotic (e.g. Barnett et al., 2005; Casty et al., 2005) and biotic (e.g. Cannone, 2008; Hall and Fagre, 2003) factors, making it important to reconsider their role in ecosystem succession. Two abiotic factors, namely water availability and disturbance potential, have recently gained more attention as they represent dynamic physical factors within glacial forefields that create strong stress gradients, and are therefore important in driving ecosystem succession (Eichel et al., 2013; Gurnell et al., 1999; Levy et al., 2015; Mercier et al., 2009; Stawska, 2017). Our understanding of biotic factors is also evolving rapidly with new research investigating the succession of microbial and vegetation communities, and the important role they can play as ecosystem engineers (Eichel et al., 2016, 2017; Frey et al., 2013; Raab, 2012; Schulz et al., 2013; Viles, 2012). With a better understanding of the interactions between these factors, biogeomorphic feedbacks are starting to be considered an important part of ecosystem succession; however, these feedbacks are not explicitly addressed in Matthews (1992) model. While not specific to proglacial forelands, Corenblit et al. (2007) proposed a four-stage ecosystem successional model also based on the balance between biotic (vegetation dynamics) and abiotic (hydrogeomorphic processes and landforms) that describes the occurrence of biogeomorphic feedbacks (Fig. 2). Initially, abiotic factors dominate over biotic factors. With time, biotic factors gain importance resulting in a transition from a geomorphic phase (abiotic factors completely dominant) to a pioneer phase (biotic factors present but dominated by abiotic factors), to a biogeomorphic phase (abiotic and biotic factors of relatively equal importance) and finally an ecological phase (biotic factors dominant) (Corenblit et al., 2007). Although glacier forefields are considered to be extreme environments where abiotic factors typically dominate, an accumulating volume of research illustrates how biotic factors can play important roles, even rapidly following deglaciation, that could allow for a window of biogeomorphic feedbacks. This was illustrated by Eichel et al. (2013) who applied Corenblit et al.'s (2007) model to sediment-mantled slopes in the Turtmann glacier forefield, Switzerland and identified conditions that allowed for a biogeomorphic phase where *Dryas octopetala* actively stabilized slope processes allowing for continued ecosystem succession by later successional species. This suggests that this model can be relevant for understanding ecosystem succession in proglacial settings.

[Insert Figure 2 here]

This paper investigates wider literature on the interaction between abiotic (water dynamics and disturbance potential) and biotic factors (vegetation and microbes) within glacial forefields to better understand the potential for a window of biogeomorphic feedbacks within these systems. Understanding the role of biogeomorphic feedbacks in extreme environments such as glacial forefields is particularly important as these processes enable succession to proceed to later stages than would typically be possible in such settings. We begin by investigating recent literature looking at how disturbance and water dynamics can drive microbial and vegetation development (the pioneer phase where abiotic factors dominate biotic factors), and how once established vegetation and microbes have the potential to act as ecosystem engineers (the biogeomorphic phase where the importance of abiotic and biotic factors becomes relatively equal). We finish by proposing a model for ecosystem succession that synthesizes both Matthews (1992) and Corenblit et al.'s (2007) models to take into account stress gradients, changing importance of abiotic and biotic factors, and successional time in determining the stage of ecosystem succession within glacier forefields.

II Paraglacial disturbance and water dynamics, and their impact on microbial and vegetation establishment

Following glacier recession, the newly exposed landscape enters a paraglacial period dominated by sediment reworking and hydrological flow, conditioned by the earlier presence of ice (Ballantyne, 2002a, 2002b; Church and Ryder, 1972). These disturbances and water dynamics establish dynamic gradients of physical stress within the landscape that can exert a strong control on ecosystem succession (the pioneer phase described by Corenblit et al. (2009)). In this section, we briefly review disturbance mechanisms and water dynamics within paraglacial systems, and how these factors ultimately drive establishment of microbial and vegetation communities.

1 Disturbance and its ecological impact

Disturbance comes in many forms within glacial forefields (Ballantyne, 2002b; Curry et al., 2006). Paraglacial rock-slope stability is determined by numerous factors including lithology, debuttressing, glacial erosion, and climatic factors (water, permafrost, and weathering) and results in perturbation in the form of rock falls and rock avalanches (Ballantyne, 2002b; Grämiger et al., 2017; McColl, 2012). Sediment mantled slopes such as lateral moraines experience debris flows, slope wash, interrill, and rill erosion that can produce disturbance on a variety of scales such as the formation of gullies, slumps, and slides. All of these processes can be responsible for mobilizing and transporting large amounts of sediment (Curry et al., 2006; Hugenholtz et al., 2008). The less steep forefield area experiences a variety of disturbances including mass movement (e.g. slumps, slides, and solifluction), frost action, fluvial erosion, and aeolian processes (Ballantyne, 2002b). Oliver et al., 1985 found that approximately 63% of the Nooksack Glacier forefield in Washington, USA experienced secondary disturbances following initial glacial retreat (~A.D. 1800), including avalanches, rockslides, intermittent snowfields, creeping snowfields, and glacio-fluvial streams.

These processes tend to limit the establishment of microbes and vegetation by eroding away surfaces where these communities have the potential to develop (Ballantyne, 2002b; Lane et al., 2017; Matthews, 1992; Mercier et al., 2009). Therefore, micro- and meso-topographic factors (as a result of differences in morphology and level of disturbance) have been found to drive successional stages (Caccianiga and Andreis, 2001). This was observed by Eichel et al. (2013) in the Turtmann valley glacial forefield in Valais, Switzerland where successional pathways were found to diverge on older terrain with primary stages found next to late successional stages. As a result, three different successional stages were identified that were independent of time and instead dependent on the level of geomorphic activity occurring on the lateral moraines (Eichel et al., 2013). Stawska (2017) also found disturbance to be the primary driver of vegetation development in the Ebba Glacier forefield on Svalbard where three zones were characterized by different disturbance mechanisms. Disturbance in each zone was found to either prevent primary succession or result in secondary succession if the disturbance was sufficient to impact primary colonizers but not so great that the resources they had created (e.g. soil) were totally removed.

Disturbances can also sometimes have a positive effect by depositing fine material that can promote moisture retention and soil development (Gurnell et al., 1999; Matthews, 1979a; Smith, 1976; Whittaker, 1991). This was also observed by Stawska (2017) who found that within a zone characterized by areas of both sediment erosion and deposition, vegetation development was much greater within the depositional areas as a result of the fine grains retaining moisture (Stawska, 2017). Snow avalanches and debris flows on slopes that have been deglaciated for millennia can also promote ecosystem succession by transporting developed soils, diaspores, and sometimes living plant material into the glacial forefield (Temme and Lange, 2014).

2 Water dynamics and their controls on microbe and vegetation communities

Water can enter a glacial forefield either through surface sources (e.g. precipitation, snowmelt, and glacier melt) or subsurface sources (e.g. groundwater seeps and moraine ice core melt out); and then flows through the forefield (Malard, 1999; Tockner et al., 2000; Ward et al., 2002). The role of water within paraglacial systems is complex as it can act both destructively and as a resource depending on the source, path, and intensity of the hydrological flow (Crossman et al., 2011; Egli, 2006; Marteinsdóttir et al., 2010, 2013; Raffl et al., 2006; Rydgren et al., 2014; Schumann et al., 2016).

Due to the well-drained nature of glacially-derived sediments, glacial forefields often involve water-limited geo-ecological processes (Burga et al., 2010; Cooper, 1923; Matthews, 1992; Viles, 2012). Thus the presence of water, and notably zones of preferential water retention, may provide an important stimulus for microbial and vegetation development (Marteinsdóttir et al., 2010, 2013; Raffl et al., 2006; Rydgren et al., 2014; Schumann et al., 2016). Preliminary observations suggest that groundwater upwelling has a positive impact on ecosystem development. Groundwater fed lakes and seeps in the Skeiôarársandur glacier forefield were identified as important environments for promoting the growth of microbial mats (Robinson et al., 2008) and vegetation (Levy et al., 2015). This may be the result of groundwater upwelling providing a moisture source that has more constant temperatures, lower turbidity, and higher nutrient concentrations compared to meltwater channels (Brown et al., 2007; Crossman et al., 2011). Hydrological flow and conductivity are also essential for the supply, modification and dispersal of microbes (Hotaling, Hood, et al., 2017) as these communities are primarily sourced from sub-, supraglacial sediments, and meltwater streams (Rime et al., 2015). The presence of water can also act as a stimulus for weathering and soil development. Work by Egli (2006) showed that north facing slopes in the Morteratsch Glacier, Switzerland have greater snow pack and therefore higher water content, and result in faster weathering rates and soil development that can help stimulate ecosystem succession (Egli, 2006; Egli et al., 2006).

When the flow speed becomes too great, hydrologic flow can switch from being a resource to being destructive by eroding the embryonic soil-vegetation complex (Gurnell et al., 1999). Generally, water acts destructively within glacial forefields when flowing through active channels such as laterally incising braided river networks (Church and Ryder, 1972; Gurnell et al., 1999; Moreau et al., 2008; Tockner et al., 2000). Moisture within the surface layer of sediments can also promote debris flows and other mass movement processes such as solifluction, which have found to be greatest near glacier margins where the soil moisture content is higher (Ballantyne, 2002b). When moisture within soils freezes, it can be responsible for initiating frost action processes that results in the sorting of sediments (Ballantyne, 2002b). These disruptive activities by water can erode away areas where microbes and vegetation may become established thereby limiting development.

Gradients of water stress can drive stages of ecosystem development and be observed within the landscape. In the forefield of Lovénbreen glacier on Svalbard, Moreau et al. (2008) found that vegetation increased in abundance and diversity with decreasing channel activity as a result of decreasing disturbance. Where water acted most erosively, pioneer successional pathways were maintained and superimposed on the larger-scale vegetation patterns driven by time since deglaciation (Moreau et al., 2008). Another example of this may also be found in the forefield of the glacier d'Otemma in Val de Bagnes, Switzerland where vegetation zonation was observed along an intermittent meltwater channel within the floodplain (Fig. 3a). This area was exposed in the late 1980s, but vegetation didn't start developing until after 2010 when downcutting of the main central channel resulted in terrace formation and less erosion potential. The current zonation appears to now reflect distance above the water table and distance away from the active channel. A comparison of vegetation cover with stream power and wetness potential show that vegetation is most abundant at intermediate values of these factors (Fig. 3b). At high values of stream power and wetness, vegetation cannot establish and/or is eroded away. At low values of stream power there is less erosion, however, vegetation cannot establish due to limitations in water availability. This illustrates how gradients in disturbance and water can drive vegetation development in ways that are visible within the landscape. Water table dynamics and their ecological significance in glacial forelands, however, are still poorly understood making future research on this topic important (Kollmann et al., 1999; Levy et al., 2015).

[Insert Figure 3 here]

III Ecosystem engineering of microbes and vegetation

While microbes and vegetation are both initially driven by the abiotic factors of disturbance and water dynamics within glacial forefields, once they become established these communities can initiate feedbacks in the system (biogeomorphic phase described by Corenblit et al., 2009). In the following sections we investigate the ecosystem engineering role of microbes and vegetation within glacial forefields. While we have generally considered microbes and vegetation separately for simplicity in understanding certain ecosystem engineering mechanisms, it is important to note that they also influence each other and the resulting impact on ecosystem succession.

1 Microbes

During the early stages following glacial retreat, the abiotic processes of disturbance and water dynamics are not acting alone. Microbial communities, which can be present even prior to the retreat of a glacier (Mader et al., 2006; Sharp et al., 1999; Skidmore et al., 2000), are an integral part of early paraglacial environments helping convert barren substrate into a habitat that can support ecosystem succession (Raab, 2012). Adapted to extreme environments, microbes are able to overcome resource limitations in a variety of ways (Anesio et al., 2017; Frey et al., 2013; Schulz et al., 2013). Microbes overcome water limitations by establishing in moist areas and developing biofilms that help retain water during dry periods (Borin et al., 2010; Frey et al., 2013; Schulz et al., 2013). They overcome limited pools of carbon by sourcing carbon from the deposition of allochthonous organic matter (OM), close-by cyanobacterial and algal communities, or from ancient carbon pools (Bradley et al., 2014; Frey et al., 2013; Schulz et al., 2013). And finally, they can source nitrogen (N) from remineralization of OM and via N-fixation to deal with limited nutrient availability (Bardgett et al., 2007; Bradley et al., 2014; Frey et al., 2013; Kaštovská et al., 2005; Schmidt et al., 2008; Schulz et al., 2013; Töwe et al., 2010).

Work over the last three decades has developed this field of “microbial geomorphology” illustrating how microbes provide the first and perhaps most fundamental engineering of deglaciated terrain (Viles, 2012). The influence of microbial communities occurs on the scale of the individual cell to the scale of the extracellular polymeric substances (EPS; e.g. crust, biofilm). Jones et al. (1994) defined ecosystem engineers as organisms that either through their physical presence or work done provide: 1) resources; 2) changes to the environment; or 3) changes to abiotic factors influencing the environment. In glacial forefields, studies have illustrated how microbes can act as an ecosystem engineer at all three levels by supplying nutrients and carbon (resources), initiating soil development (changes to environment), and impacting rates of stabilization (changes to abiotic factors) (Table 1).

[Insert Table 1 here]

Cyanobacteria and algae, dominant primary colonizers of barren deglaciated terrain (Wynn-Williams, 1988), provide an excellent example of ecosystem engineering resource provision, as they play a critical role in making carbon and nutrients available. Schmidt et al. (2008) and Frey et al. (2013) both report rapid colonization of cyanobacteria in the Peruvian Alps and the Swiss Alps, respectively, following glacial retreat. These communities subsequently augment the surrounding sediment organic matter content, providing a source of carbon for higher orders of life. High rates of remineralization have been measured within glacial forefields with 33gCm^{-2} released via respiration during three summer months within the Damma glacier forefield, Switzerland (Schulz et al., 2013). This high rate of organic matter breakdown subsequently releases nutrients into the system such as nitrogen.

Diazotrophic (nitrogen fixing) cyanobacterial groups such as *Nostocales* have also been shown to play an important role in supplying nitrogen within glacial forefields (Kaštovská et al., 2005). The type of nitrogen turnover occurring within glacial forefields can vary along a chronosequence. In the Damma Glacier forefield, Brankatschk (2011) found that in embryonic soils (<10 years old), mineralization through the decomposition of organic matter was the main driver of nitrogen turnover, whilst soils between 50 and 70 years old were characterized by nitrogen fixing organisms. In the oldest soils (>120 years old), nitrification and denitrification were found to be occurring at significant rates (Brankatschk et al., 2011; Schulz et al., 2013). This dominance of nitrogen mineralization indicates that initial ecosystem development in glacier forefields is subject to the release of large amounts of organic compounds that then prepares the ground for higher plant colonization (Brankatschk et al., 2011; Raab, 2012). Although mineralization may dominate within young soils, N-fixation within these young sediments can be important for plant growth. Using soils from the Damma Glacier, Töwe et al., (2010) found that high rates of nitrogen fixation by microbial communities within young (~10 years) soils resulted in greater concentrations of nitrogen (and lower C/N) within the *L. alpina* plant after 7 and 13 weeks of growth, suggesting that N-fixation following glacial retreat is important for early vegetation development. When cyanobacteria and algae are able to form biofilms by excreting EPSs, they can become even more efficient at performing photosynthesis and/or fixing N. N-fixation by biofilms has been shown to be active at just 3°C, which is much colder than when such activity typically starts for plants (Dickson, 2000). Additionally, EPSs excreted by certain cyanobacteria typically become coated with clay creating a negatively charged surface that positively charged nutrients can hold onto, preventing leaching and increasing nutrient content (Belnap et al., 2001; Schulz et al., 2013). Microbes can also play important roles in the release of other elements such as phosphorous (P) and sulfur (S) by increasing rates of weathering of bedrock that contain these elements (Bradley et al., 2014; Schulz et al., 2013). This release of nutrients and carbon by microbial activity illustrates the ecosystem engineering role microbes play by supplying resources to glacial forefields that can then be used by higher orders of life such as heterotrophic bacteria and plants (Kaštovská et al., 2005).

The gradual buildup of organic matter and release of nutrients by microbial activity also impacts the environment by initiating and sustaining soil development. Soil development is marked by the accumulation of organic matter and nitrogen and a decrease in pH often associated with increasing time since deglaciation (Bernasconi et al., 2011; Zumsteg et al., 2012). Microbial succession along a chronosequence at the Damma Glacier, Switzerland, was shown to influence soil pH, carbon content, and nitrogen content illustrating a microbial influence on soil development (Zumsteg et al., 2012). Biofilms and microbial crusts formed by conglomerated cyanobacteria, green algae, and lichens have been shown to be especially efficient at weathering and nutrient turnover, helping accelerate soil development (Schulz et al., 2013). Symbiotic algae living within fungi can also play an important role in weathering and early soil development. Frey et al., (2013) completed one of the first assessments of green algae community assemblages in an Alpine glacier environment at the Damma glacier in Switzerland and found that the most common photobiont genera were *Trebouxia* and *Asterochloris,* two species known to substantially contribute to carbon production and initial soil formation. Microbially-mediated soil formation can then support further ecosystem development, such as the establishment of vegetation (Borin et al., 2010).

Microbes have also been shown to exert a strong control on abiotic factors within glacial systems mainly through mediation of weathering rates and stabilization processes (Viles, 2012). Matthews and Owen (2008) found that the endolithic lichen *Lecidea auriculata* enhanced weathering rates on Little Ice Age moraines in the Storbreen glacier forefields in southern Norway. On lichen-colonized boulders, Schmidt hammer R-values (proxy for hardness) were found to decrease by at least 20 units (from mean values of 61.0+- 0.3) over 30-40 years. Such a reduction in hardness values would usually take about 10ka on boulders not colonized by lichens (Matthews and Owen, 2008). They argued that this biological weathering by endolithic lichens can be 200-300 times faster than rates of physico-chemical weathering alone and plays an important role in paraglacial sediment pulses (Matthews and Owen, 2008; Viles, 2012). The formation of biofilms can also increase weathering rates as these biofilms are highly efficient at dissolving underlying bedrock by exuding organic acids (Schulz et al., 2013).

In addition to enhancing weathering, biofilms can also have a stabilizing effect by acting as an interface between air and ground, causing deposition of fine sediment, and by helping to bind sediment particles together (Schmidt et al., 2008; Viles, 2012). EPS filaments formed by *Oscillatoriales* (cyanobateria unable to fix nitrogen) were found to help stabilize the sediment substrate in glacial forefields within Switzerland (Frey et al., 2013) and on Svalbard (Kaštovská et al., 2005). In the Peruvian alps, Schmidt et al., (2008) found that as cyanobacterial biofilm diversity increased along a chronosequence, soil stability also increased with soil shear strength nearly doubling in their oldest soils (~79 years) as a result of cyanobacteria producing exopolysaccharides that stick to the sediments holding the soils together.

The forefield of the Glacier d'Otemma may offer an example of the ecosystem engineering role of biofilms by altering water table dynamics and creating habitat for further ecosystem succession (Fig. 4). A sediment pit profile dug to a depth of 72cm and located only 50cm from an actively flowing side channel within the forefield shows no sign of groundwater presence. This suggests that the finer sediments and biofilm colony within the side channel hold water at the surface that would otherwise drain out of the system. By keeping water at the surface, a more favorable habitat is created for vegetation establishment, which is observed by the preferential vegetation colonization occurring along the river channel bank where there is greater moisture availability.

[Insert Figure 4 here]

Studies have shown that current climate amelioration and subsequent glacial retreat may be influencing microbial diversity by increasing within-stream microbial diversity (alpha diversity) moving away from the glacier snout, but reducing among-stream diversity (beta diversity) with glacial retreat and increasing temperature (Wilhelm et al., 2014). This suggests that continued climate change and more rapid glacial recession could cause a homogenization of microbial communities (Hotaling, Finn, et al., 2017; Wilhelm et al., 2013, 2014). How microbes will respond to climate change is further complicated by their ability to adapt to environmental conditions via plasticity (the ability to alter the nature of their genomes and to exchange DNA between microorganisms). In three Swiss Alpine glaciers, Freimann et al., (2013) found that heterotrophic bacteria in groundwater fed streams were able to withstand changes in environmental conditions by adapting their single-cell metabolism. Interestingly, bacteria within the glacial-meltwater fed streams handled rapid environmental changes by having a community composition dominated by specialists that could perform specific enzyme functions under a variety of conditions. This suggests that communities will either show functional shifts or community turnover with climate amelioration, with potential implications for their ecosystem engineering role.

2 Vegetation

Whilst vegetation is known to act as an important ecosystem engineer in temperate ecosystems and floodplains (Bätz et al., 2015; Corenblit et al., 2009; Gurnell, 2014; Gurnell et al., 2001; Polvi and Sarneel, 2017), much less research has been done looking at their potential ecosystem engineering within paraglacial systems. For vegetation succession to begin on glacial forefields, migration of seeds must occur followed by ecesis (germination and survival) (reviewed in Matthews 1992). Seed migration is limited by the available seed pool around the glacial forefield, in addition to the dispersal ability of the seed (e.g. shape and weight). Ecesis is subsequently limited by environmental conditions, such as aspect, slope, soil development, disturbance, water availability, and nutrient pools (Jumpponen et al., 1999; Marteinsdóttir et al., 2010, 2013). These factors, in addition to time since deglaciation, then go on to drive successional stages of ecosystem development. Climate change, however, is resulting in changes to the distribution and successional stages of vegetation making understanding the engineering role of these plants more important (Cannone, 2008; Fickert et al., 2017). In the following section, we review the limited research that currently exists investigating the ecosystem engineering role of vegetation within paraglacial glacier forefield systems. We consider 1) vegetation's ability to supply resources through N-fixation, 2) vegetation's impact on the surrounding environment through soil development, modification of microbial community structure, and creation of seed banks, and 3) vegetation's impact on the abiotic factors of water and disturbance dynamics (Table 1).

Vegetation associated with diazotrophic bacteria can provide resources to the local environment by acting as a source of nitrogen. Kohls (1994, 2003) illustrated how growth of N-fixing plants during primary succession of glacial forefields can provide a source of N which can then be used by non-N-fixing plants. He found this effect was most dominant 40 years following deglaciation, and that the transfer of N from N-fixing plants to non-N-fixing plants occurred via the decomposition of actinorhizal litter by microbes which then made the fixed N available for uptake by non-N-fixing species (Kohls et al., 2003). N-fixation in bryophyte-cyanobacteria associations has also been shown to impact vegetation succession. Within the forefield of the Tierra del Fuego glacier in southern Chile, Arróniz-Crespo et al, (2014) compared two chronosequences with different levels of N-fixation and found that the chronosequence with higher rates of N-fixation by cyanobacteria resulted in a more rapid vegetation succession. However, the exact mechanism by which the bryophyte-cyanobacteria system makes N available to vascular plants is still unclear (Arróniz-Crespo et al., 2014).

Vegetation can help to initiate and to sustain soil development by providing OM inputs via the exudation of carbon-rich substances from their roots and from litter from above-ground biomass (Boy et al., 2016; D'Amico et al., 2014; Duc et al., 2009; Grayston et al., 1996). This was observed at the Val Roseg glacial floodplain, Switzerland where allochthonous organic matter inputs increased downstream with increasing vegetation cover (Zah and Uehlinger, 2001). D'Amico et al. (2014) also described a similar process at the Lys glacier forefield in the north-western Italian Alps where weathering processes, the loss of soluble compounds, decrease in pH, and primary mineral weathering all increased after the establishment of continuous vegetation cover (D'Amico et al., 2014). This was the attributed to organic matter accumulation caused by litter inputs and root decomposition below the soil surface.

Whilst microbes help prepare soil for vegetation development, once vegetation becomes established it can also influence the microbial community (which can also subsequently influence continued soil development). Along a 110-year chronosequence in the Damma glacier forefield, Rime (2015) found that vegetation development drove microbial processes along a temporal gradient (time since deglaciation), but not a vertical gradient (soil depth). Newly exposed barren soils were characterized by metabolically versatile bacteria and yeasts, while vegetated soils with higher carbon, nitrogen and biomass had bacteria able to degrade more complex organic compounds. Community structure varied little with soil depth, except in barren soils where higher silt and moisture content made surfaces more habitable (Rime et al., 2015). On a smaller scale, Miniaci (2007) investigated the potential impact of the pioneer *Leucanthemopsis alpina* on biological and chemical-physical parameters near plants in the Damma glacier in Switzerland. They found that *Leucanthemopsis alpina* influenced bacterial cell numbers and activities up to 20cm away from the plant with microbial cell count, active cells, and saccharase glucosidase, and acid phosphatase activities all increasing with greater proximity to the plant (Miniaci et al., 2007). It is important to note that the relationship between vegetation and microbes is not always symbiotic with microbes being generally more competitive for resources over short timescales as a result of higher volume-surface ratios, and vegetation being more competitive over a long time period as a result of a longer lifespan and ability to retain assimilated nutrients (Hodge et al., 2000; Schulz et al., 2013).

Once established, vegetation can create a seed bank, which becomes important during secondary succession. The effect of this was observed by Moreau et al. (2008) who found that secondary succession of vegetation occurred either more rapidly or slowly than the initial primary succession depending on the proximity of the seed bank, in addition to modification of the sediment substrate. *Deschampsia alpina, Saxifraga cespitosa* and *Minuartia rubella* were found to take longer to colonize during a secondary succession, whereas species such as *Cerastium arcticum, Draba* species and *Sagina nivalis* were found to establish themselves more quickly (Moreau et al., 2008).

Vegetation has also been shown to exert a control on abiotic factors within glacial forefields. Recent work has shown that biogeomorphic feedbacks can impact rates of disturbance and in turn succession. Graf et al. (2009) used soils from a moraine in the subalpine landslide area “Schwandrübi in Central Switzerland to test the impact of vegetation development on soil stabilization. They found that soils with planted alder (*Alnus incana*) had an angle of internal friction about 5° greater than pure soils with no vegetation present as a result of the roots stabilizing the substrate (Graf et al., 2009). Eichel et al., (2016) illustrated in the Turtmann valley, Valais, Switzerland how the establishment of *Dryas octopetala* on Little Ice Age lateral moraines permanently decreased geomorphic activity once *D. octopetala* reached about 35% cover. Eichel et al. (2017) also showed that as a result of various plant traits, *D. octopetala* can contribute to the development of turf-banked solifluction lobes by, for example, adapting its root growth through phenotypic plasticity to soil movement making it able to colonize areas that are still undergoing solifluction. Eventually material accumulates behind the growing mat of *D. octopetala* forming the initial structure of the solifluction lobe, which as it continues to stabilize becomes inhabited by tree and grassland species. In this way, *D. octopetala* acts as an ecosystem engineer both helping the formation of the turf-banked solifluction lobe, and the ability for other species to colonize the area (Eichel et al., 2017). Eichel et al. (2018) also illustrated how once mature vegetation and soil horizons are able to develop on lateral moraine complexes in the Turtmann glacier forefield, geomorphic processes halt allowing for stabilization of the paraglacial region. This stabilizing effect of vegetation illustrated by the work of Eichel et al. (2013, 2016, 2017, 2018) is important to consider when constructing models of sediment exhaustion within glacial forefields (Klaar et al., 2015).

The biogeomorphic impact of vegetation on surface water flow has been studied extensively in non-Alpine environments with strong evidence that above ground biomass and below ground root systems help stabilize and retain sediments along river banks (e.g. Bennett et al., 2002; Corenblit et al., 2009; Gurnell, 2014; Gurnell and Grabowski, 2016; Liu et al., 2010). This type of research, however, is very limited for sparsely vegetated paraglacial settings. Gurnell (1999) proposed a conceptual model of Alpine proglacial river channel evolution which considers the balance between sediment regime-controlled versus riparian vegetation-controlled dynamics depending on altitude, proximity to the tree line, and glacial retreat or advance. In this model, there are three zones within the proglacial river channel: a braided section dominated by the sediment regime, a transitional zone influenced by both sediment regime and riparian vegetation, and a more stable single- or multi-thread zone influenced primarily by riparian vegetation (Gurnell et al., 1999). They hypothesize that the size and importance of each of these zones depends on both altitude and glacier dynamics. A retreating glacier at lower altitudes would be more transitional with both the sediment regime and riparian vegetation having an important influence. Alternatively, a rapidly retreating glacier in high altitudes (or in areas with sparser vegetation cover) would be dominated by the sediment regime of the proglacial river, with vegetation playing less of an important role. This model was supported by Ielpi (2017)'s work in the sparsely vegetated Fossalar River in southern Iceland which showed that variations in river sinuosity and vegetation cover were not significantly correlated, whereas discharge regime more accurately predicted fluvial planform (stable discharge led to accretion, while floods led to erosion). While it seems likely that the forefields of high altitude, Alpine glaciers would be sediment regime dominated, no study to date has specifically investigated this question in these environments. Based on the impact that vegetation has been shown to have on disturbance mechanisms on moraines and solifluction lobes within high altitude paraglacial systems (e.g. Eichel et al., 2017, 2016, 2013), it seems reasonable that the same stabilizing mechanisms could also influence surface water flow in glacial meltwater channels. Further research is needed to elucidate the relationship between vegetation and water flow, and the potential for biogeomorphic feedbacks in paraglacial environments. As early successional stages shift as the result of climate change (e.g. Cannone, 2008) the associated biogeomorphic feedbacks may also evolve making it important to understand their role in these ecosystems.

IV Synthesis: Biogeomorphic feedbacks between water, disturbance, microbes, and vegetation

This review addresses the linkages between abiotic factors, notably water availability and disturbance, and biotic factors, notably microbes and vegetation and how they interact as mechanistic drivers of primary succession in glacial forefields. In this section, we consider these biogeomorphic feedbacks and how their interactions are key to developing an accurate mechanistic model of succession in deglaciated terrains.

Microbes are tightly coupled with water availability and disturbance within glacial ecosystems through biogeomorphic feedbacks. Water flow and hydrological connections are what initially bring microbes into glacial forefields (Dubnick et al., 2017; Hotaling, Hood, et al., 2017; Rime et al., 2016), and moisture availability is essential for their successful establishment and growth (Lazzaro et al., 2009, 2012; Zumsteg et al., 2012). The EPS of biofilms can then feedback into water availability within the forefield by helping retain moisture in the surrounding sediments, which can ultimately result in a higher water table and greater water holding capacity (Borin et al., 2010; Frey et al., 2013). This can then impact water-influenced disturbance processes (e.g. debris flows and frost sorting), as well as support future water-dependent ecosystem succession. High rates of disturbance can limit microbial establishment by, for example, inhibiting the formation of biofilms (Schulz et al., 2013); but disturbance can also promote establishment by depositing fine sediments that reduce surface drainage rates and transporting preexisting microbial communities to potentially more favorable sites (Meola et al., 2014). Disturbance can also be important in maintaining diversity within microbial communities, with fluctuating environments such as glacier-fed streams producing seasonal and diurnal changes to water chemistry and temperature that result in different microbes activating under the changing conditions (Wilhelm et al., 2014). Microbes can also influence disturbance processes by mediating rates of weathering and stabilization within glacial forefields (Sigler et al., 2002; Viles, 2012).

Vegetation is also tightly coupled with water availability and disturbance. Moisture provides a key ingredient for plant germination and survival. However, it can also cause erosion thereby preventing vegetation establishment or leading to vegetation removal. Vegetation in turn has the potential to influence surface water flow patterns and help retain moisture below ground. However, this interaction between vegetation and moisture is not well understood in glacial forefields. Disturbances drive vegetation by limiting growth as the result of erosion, but also by enhancing plant establishment via the deposition of fine sediment material. Vegetation in turn plays an important role in stabilizing paraglacial systems, which subsequently promotes continued ecosystem succession (Eichel et al., 2017).

Microbial colonization and vegetation succession are also strongly linked and ultimately cannot be considered as separate within glacial forefields. Microbial provision of nutrients, development of soil, and impact on weathering and stabilization rates helps prepare the substrate for vegetation establishment (Schulz et al., 2013; Töwe et al., 2010). Subsequently, vegetation succession modifies the microbial environment through continued soil development and the provision and/or competition for resources (Arróniz-Crespo et al., 2014; Miniaci et al., 2007; Rime et al., 2016).

From the above review, it is clear that even in “extreme” environments such as glacier forefields, biotic factors can have a great enough influence where biogeomorphic feedbacks occur ultimately influencing the continued succession of the ecosystem. Based on this, we propose an updated successional model that synthesizes both Matthews' (1992) geoecological model and Corenblit et al.'s (2007) model by using stress gradients and successional time to predict the balance between abiotic and biotic factors, which ultimately determines the successional state of the system (and subsequently the potential for biogeomorphic feedbacks; Fig. 5a). In high stress environments where abiotic factors dominate biotic factors throughout successional time, there is no biogeomorphic stage and the system will likely never reach a mature successional state (Fig. 5b). In intermediately stressful environments, biotic factors eventually come to balance abiotic factors allowing for a phase of biogeomorphic feedbacks (Fig. 5b). This system, however may never reach an ecological phase as disturbances may continue resetting the system to earlier successional stages. In low stress environments, biotic factors start playing an important role much earlier on allowing for a biogeomorphic phase that can then help the system reach a mature successional stage not achieved in the higher stress environments (Fig. 5d). Therefore, depending on the environmental stress and successional time at any given point within a glacial forefield, a certain balance of abiotic and biotic factors will exist that determines the successional state of the system. Generally, stress decreases and successional time increases moving away from the glacier margin, active streams, and active slope processes resulting in a trend toward a greater dominance in biotic factors and greater potential for biogeomorphic feedbacks.

Several sites within the glacier d'Otemma forefield offer potential examples of different successional stages within this model. The geomorphic phase is illustrated by the active braided channels and active slope processes near the retreating glacial margin (Fig. 5e, "Geomorphic phase"). The pioneer phase is illustrated by active single-thread channels and slopes further downstream where bacteria and vegetation are starting to establish in isolated patches (Fig. 5e, "Pioneer phase"). The biogeomorphic phase is illustrated by communities of biofilms and vegetation establishing further downstream in intermediate and inactive channels (Fig. 5e, "Biogeomorphic phase"), although the potential ecosystem engineering effect of these communities has yet to be investigated in this forefield. Future work is needed to quantify this model and so to constrain the balance between abiotic and biotic controls and the potential for ecosystem engineering within high altitude glacial forefield environments to help determine at which point biogeomorphic feedbacks take effect during ecosystem succession in both space and in time.

[Insert Figure 5 here]

V Conclusions

New understandings of abiotic and biotic drivers within glacial forefields suggest that biogeomorphic feedbacks must be seen as an important step in ecosystem succession. Disturbance and water dynamics drive initial establishment of microbes and vegetation creating visible patterns within the landscape. Once established, microbes and vegetation can act as ecosystem engineers setting up biogeomorphic feedbacks that influence the continued ecosystem successional patterns. The forefield of Glacier d'Otemma offers examples of the driving forces of disturbance and water dynamics, in addition to geomorphic, pioneering, and biogeomorphic stages of ecosystem succession. With continued climate amelioration, the impact of biogeomorphic feedbacks may change making it important to develop better understandings of their current role in high altitude glacial forefields.

Conflict of Interest

The authors declare there are no conflicts of interest.

References

Anesio AM, Lutz S, Chrismas NAM, et al. (2017) The microbiome of glaciers and ice sheets. *npj Biofilms and Microbiomes* 3(1): 10. DOI: 10.1038/s41522-017-0019-0.

Arróniz-Crespo M, Pérez-Ortega S, Ríos AD los, et al. (2014) Bryophyte-Cyanobacteria Associations during Primary Succession in Recently Deglaciated Areas of Tierra del Fuego (Chile). *PLOS ONE* 9(5): e96081. DOI: 10.1371/journal.pone.0096081.

Ballantyne CK (2002a) A general model of paraglacial landscape response. *The Holocene* 12(3): 371–376.

Ballantyne CK (2002b) Paraglacial geomorphology. *Quaternary Science Reviews* 21(18): 1935–2017. DOI: 10.1016/S0277-3791(02)00005-7.

Bardgett R, Richter A, Bol R, et al. (2007) Heterotrophic microbial communities use ancient carbon following glacial retreat. *Biology Letters* 3: 487–490.

Barnett TP, Adam JC and Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature* 438(7066): 303–309. DOI: 10.1038/nature04141.

Bätz N, Verrecchia EP and Lane SN (2015) The role of soil in vegetated gravelly river braid plains: more than just a passive response?: SOIL IN VEGETATED GRAVELLY RIVER BRAID PLAINS: A REVIEW. *Earth Surface Processes and Landforms* 40(2): 143–156. DOI: 10.1002/esp.3631.

Belnap J, Büdel B and Lange OL (2001) Biological Soil Crusts: Characteristics and Distribution. In: *Biological Soil Crusts: Structure, Function, and Management*. Ecological Studies. Springer, Berlin, Heidelberg, pp. 3–30. DOI: 10.1007/978-3-642-56475-8_1.

Bennett SJ, Pirim T and Barkdoll BD (2002) Using simulated emergent vegetation to alter stream flow direction within a straight experimental channel. *Geomorphology* 44(1): 115–126.

Bernasconi SM, Bauder A, Bourdon B, et al. (2011) Chemical and Biological Gradients along the Damma Glacier Soil Chronosequence, SwitzerlandAll rights reserved. No part of this periodical may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. *Vadose Zone Journal* 10(3): 867–883. DOI: 10.2136/vzj2010.0129.

Borin S, Ventura S, Tambone F, et al. (2010) Rock weathering creates oases of life in a High Arctic desert. *Environmental Microbiology* 12(2): 293–303. DOI: 10.1111/j.1462-2920.2009.02059.x.

Boy J, Godoy R, Shibistova O, et al. (2016) Successional patterns along soil development gradients formed by glacier retreat in the Maritime Antarctic, King George Island. *Revista Chilena de Historia Natural* 89(1). DOI: 10.1186/s40693-016-0056-8.

Bradley JA, Singarayer JS and Anesio AM (2014) Microbial community dynamics in the forefield of glaciers. *Proc. R. Soc. B* 281(1795): 20140882. DOI: 10.1098/rspb.2014.0882.

Brankatschk R, Töwe S, Kleineidam K, et al. (2011) Abundances and potential activities of nitrogen cycling microbial communities along a chronosequence of a glacier forefield. *The ISME Journal* 5(6): 1025–1037. DOI: 10.1038/ismej.2010.184.

Brown LE, Milner AM and Hannah DM (2007) Groundwater influence on alpine stream ecosystems. *Freshwater Biology* 52(5): 878–890. DOI: 10.1111/j.1365-2427.2007.01739.x.

Burga CA, Krüsi B, Egli M, et al. (2010) Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): Straight forward or chaotic? *Flora - Morphology, Distribution, Functional Ecology of Plants* 205(9): 561–576. DOI: 10.1016/j.flora.2009.10.001.

Caccianiga M and Andreis C (2001) Vegetation and environmental factors during primary succession on glacier forelands: some outlines from the Italian Alps. *Plant Biosystems* 135(3): 295–310.

Cannone N (2008) Accelerating Climate Change Impacts on Alpine Glacier Forefield Ecosystems in the European Alps. *Ecological Applications* 18(3): 637–648.

Casty C, Wanner H, Luterbacher J, et al. (2005) Temperature and precipitation variability in the European Alps since 1500. *International Journal of Climatology* 25(14): 1855–1880. DOI: 10.1002/joc.1216.

Church M and Ryder JM (1972) Paraglacial Sedimentation: A Consideration of Fluvial Processes Conditioned by Glaciation. *Geological Society of America Bulletin* 83(10): 3059.

Coaz J (1887) Erste ansiedlung phanerogame pflanzen auf vom gletscher verlassenen boden. Mitteilungen der Natur. Available at: https://scholar.google.ch/scholar?hl=en&as_sdt=0,5&q=Coaz,+J.,+1887%3A+Erste+ansiedlung+phanerogame+pflanzen+auf+vom+gletscher+verlassenen+boden.+Mitteilungen+der+Natur-+forschenden+Gesellschaft+in+Bern,+1886%3A+3-12. (accessed 19 February 2018).

Cooper (1923) The Recent Ecological History of Glacier Bay Alaska: II. The Present Vegetation Cycle. *Ecology* 3(4): 223–246.

Cooper WS (1931) A Third Expedtion to Glacier Bay, Alaska. *Ecology* 12(1): 61–95.

Cooper WS (1939) A Fourth Expedition to Glacier Bay, Alaska. *Ecology* 20(2): 130–155.

Corenblit D, Tabacchi E, Steiger J, et al. (2007) Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: A review of complementary approaches. *Earth-Science Reviews* 84(1): 56–86. DOI: 10.1016/j.earscirev.2007.05.004.

Corenblit D, Steiger J, Gurnell AM, et al. (2009) Control of sediment dynamics by vegetation as a key function driving biogeomorphic succession within fluvial corridors. *Earth Surface Processes and Landforms* 34(13): 1790–1810. DOI: 10.1002/esp.1876.

Crossman J, Bradley C, Boomer I, et al. (2011) Water Flow Dynamics of Groundwater-Fed Streams and Their Ecological Significance in a Glacierized Catchment. *Arctic, Antarctic, and Alpine Research* 43(3): 364–379. DOI: 10.1657/1938-4246-43.3.364.

Curry AM, Cleasby V and Zukowskyj P (2006) Paraglacial response of steep, sediment-mantled slopes to post-‘Little Ice Age’ glacier recession in the central Swiss Alps. *Journal of Quaternary Science* 21(3): 211–225. DOI: 10.1002/jqs.954.

D’Amico ME, Freppaz M, Filippa G, et al. (2014) Vegetation influence on soil formation rate in a proglacial chronosequence (Lys Glacier, NW Italian Alps). *CATENA* 113: 122–137. DOI: 10.1016/j.catena.2013.10.001.

Dickson LG (2000) Constraints to Nitrogen Fixation by Cryptogamic Crusts in a Polar Desert Ecosystem, Devon Island, N.W.T., Canada. *Arctic, Antarctic, and Alpine Research* 32(1): 40–45. DOI: 10.2307/1552408.

Dubnick A, Kazemi S, Sharp M, et al. (2017) Hydrological controls on glacially exported microbial assemblages. *Journal of Geophysical Research: Biogeosciences* 122(5): 2016JG003685. DOI: 10.1002/2016JG003685.

Duc L, Noll M, Meier BE, et al. (2009) High Diversity of Diazotrophs in the Forefield of a Receding Alpine Glacier. *Microbial Ecology* 57(1): 179–190. DOI: 10.1007/s00248-008-9408-5.

Egli M (2006) Melting Glaciers and Soil Development in the Proglacial Area Morteratsch (Swiss Alps): I. Soil Type Chronosequence. *Arctic, Antarctic, and Alpine Research* 38(4): 499–509.

Egli M, Wernli M, Kneisel C, et al. (2006) Melting Glaciers and Soil Development in the Proglacial Area Morteratsch (Swiss Alps): II. Modeling the Present and Future Soil State. *Arctic, Antarctic, and Alpine Research* 38(4): 510–521. DOI: 10.1657/1523-0430(2006)38[510:MGASDI]2.0.CO;2.

Eichel J, Krautblatter M, Schmidtlein S, et al. (2013) Biogeomorphic interactions in the Turtmann glacier forefield, Switzerland. *Geomorphology* 201: 98–110. DOI: 10.1016/j.geomorph.2013.06.012.

Eichel J, Corenblit D and Dikau R (2016) Conditions for feedbacks between geomorphic and vegetation dynamics on lateral moraine slopes: a biogeomorphic feedback window. *Earth Surface Processes and Landforms* 41(3): 406–419. DOI: 10.1002/esp.3859.

Eichel J, Draebing D, Klingbeil L, et al. (2017) Solifluction meets vegetation: the role of biogeomorphic feedbacks for turf-banked solifluction lobe development. *Earth Surface Processes and Landforms* 42(11): 1623–1635. DOI: 10.1002/esp.4102.

Eichel J, Draebing D and Meyer N (2018) From active to stable: Paraglacial transition of Alpine lateral moraine slopes. *Land Degradation & Development* 0(0): 1–15. DOI: 10.1002/ldr.3140.

Fickert T, Grüninger F and Damm B (2017) Klebelsberg revisited: did primary succession of plants in glacier forelands a century ago differ from today? *Alpine Botany* 127(1): 17–29. DOI: 10.1007/s00035-016-0179-1.

Freimann R, Bürgmann H, Findlay SE, et al. (2013) Bacterial structures and ecosystem functions in glaciated floodplains: contemporary states and potential future shifts. *The ISME Journal* 7(12): 2361–2373. DOI: 10.1038/ismej.2013.114.

Frey B, Bühler L, Schmutz S, et al. (2013) Molecular characterization of phototrophic microorganisms in the forefield of a receding glacier in the Swiss Alps. *Environmental*

Research Letters 8. Available at: http://iopscience.iop.org/article/10.1088/1748-9326/8/1/015033/pdf (accessed 8 February 2018).

Gabbud C, Micheletti N and Lane SN (2016) RESPONSE OF A TEMPERATE ALPINE VALLEY GLACIER TO CLIMATE CHANGE AT THE DECADAL SCALE: RESPONSE OF A TEMPERATE ALPINE VALLEY GLACIER TO CLIMATE CHANGE AT THE DECADAL SCALE. *Geografiska Annaler: Series A, Physical Geography* 98(1): 81–95. DOI: 10.1111/geoa.12124.

Graf F, Frei M and Böll A (2009) Effects of vegetation on the angle of internal friction of a moraine. *For. Snow Landsc. Res.*: 17.

Grämiger LM, Moore JR, Gischig VS, et al. (2017) Beyond debuttressing: Mechanics of paraglacial rock slope damage during repeat glacial cycles. *Journal of Geophysical Research: Earth Surface* 122(4): 1004–1036. DOI: 10.1002/2016JF003967.

Grayston SJ, Vaughan D and Jones D (1996) Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. *Applied Soil Ecology* 5: 29–56.

Gurnell A (2014) Plants as river system engineers. *Earth Surface Processes and Landforms* 39(1): 4–25. DOI: 10.1002/esp.3397.

Gurnell AM and Grabowski RC (2016) Vegetation-Hydrogeomorphology Interactions in a Low-Energy, Human-Impacted River: Vegetation-Hydrogeomorphology Interactions. *River Research and Applications* 32(2): 202–215. DOI: 10.1002/rra.2922.

Gurnell AM, Edwards PJ, Petts GE, et al. (1999) A conceptual model for alpine proglacial river channel evolution under changing climatic conditions. *CATENA* 38(3): 223–242. DOI: 10.1016/S0341-8162(99)00069-7.

Gurnell AM, Petts GE, Hannah DM, et al. (2001) Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms* 26(1): 31–62. DOI: 10.1002/1096-9837(200101)26:1<31::AID-ESP155>3.0.CO;2-Y.

Hall M and Fagre D (2003) Modeled Climate-Induced Glacier Change in Glacier National Park, 1850-2100. *BioScience* 53(2): 131–140.

Heckmann T, McColl S and Morche D (2016) Retreating ice: research in pro-glacial areas matters. *Earth Surface Processes and Landforms* 41(2): 271–276. DOI: 10.1002/esp.3858.

Hodge A, Robinson D and Fitter A (2000) Are microorganisms more effective than plants at competing for nitrogen? *Trends in Plant Science* 5(7): 304–308. DOI: 10.1016/S1360-1385(00)01656-3.

Hotaling S, Finn DS, Joseph Giersch J, et al. (2017) Climate change and alpine stream biology: progress, challenges, and opportunities for the future. *Biological Reviews* 92(4): 2024–2045. DOI: 10.1111/brv.12319.

Hotaling S, Hood E and Hamilton TL (2017) Microbial ecology of mountain glacier ecosystems: biodiversity, ecological connections and implications of a warming climate. *Environmental Microbiology* 19(8): 2935–2948. DOI: 10.1111/1462-2920.13766.

Hugenholtz CH, Moorman BJ, Barlow J, et al. (2008) Large-scale moraine deformation at the Athabasca Glacier, Jasper National Park, Alberta, Canada. *Landslides* 5(3): 251–260. DOI: 10.1007/s10346-008-0116-5.

Ielpi A (2017) Controls on sinuosity in the sparsely vegetated Fossálar River, southern Iceland. *Geomorphology* 286: 93–109.

Jones C, Lawton J and Shachak M (1994) Organisms as Ecosystem Engineers. *Oikos* 69(3): 373–386.

Jumpponen A, Väre H, Mattson KG, et al. (1999) Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology* 87(1): 98–105. DOI: 10.1046/j.1365-2745.1999.00328.x.

Kaštovská K, Elster J, Stibal M, et al. (2005) Microbial Assemblages in Soil Microbial Succession After Glacial Retreat in Svalbard (High Arctic). *Microbial Ecology* 50(3): 396. DOI: 10.1007/s00248-005-0246-4.

Klaar MJ, Kidd C, Malone E, et al. (2015) Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. *Earth Surface Processes and Landforms* 40(8): 1088–1100. DOI: 10.1002/esp.3691.

Kohls SJ, Baker DD, van Kessel C, et al. (2003) An assessment of soil enrichment by actinorhizal N2 fixation using δ15N values in a chronosequence of deglaciation at Glacier Bay, Alaska. *Plant and Soil* 254: 11–17.

Kollmann J, Vieli M, Edwards P j., et al. (1999) Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science* 2(1): 25–36. DOI: 10.2307/1478878.

Lane SN, Bakker M, Gabbud C, et al. (2017) Sediment export, transient landscape response and catchment-scale connectivity following rapid climate warming and Alpine glacier recession. *Geomorphology* 277(Supplement C). Connectivity in Geomorphology from Binghamton 2016: 210–227. DOI: 10.1016/j.geomorph.2016.02.015.

Lazzaro A, Abegg C and Zeyer J (2009) Bacterial community structure of glacier forefields on siliceous and calcareous bedrock. *European Journal of Soil Science* 60(6): 860–870. DOI: 10.1111/j.1365-2389.2009.01182.x.

Lazzaro A, Brankatschk R and Zeyer J (2012) Seasonal dynamics of nutrients and bacterial communities in unvegetated alpine glacier forefields. *Applied Soil Ecology* 53(Supplement C): 10–22. DOI: 10.1016/j.apsoil.2011.10.013.

Levy A, Robinson Z, Krause S, et al. (2015) Long-term variability of proglacial groundwater-fed hydrological systems in an area of glacier retreat, Skeiðarársandur, Iceland. *Earth Surface Processes and Landforms* 40(7): 981–994. DOI: 10.1002/esp.3696.

Liu D, Diplas P, Hodges CC, et al. (2010) Hydrodynamics of flow through double layer rigid vegetation. *Geomorphology* 116(3–4): 286–296. DOI: 10.1016/j.geomorph.2009.11.024.

Lynch CM, Barr ID, Mullan D, et al. (2016) Rapid glacial retreat on the Kamchatka Peninsula during the early 21st century. *The Cryosphere* 10(4): 1809–1821. DOI: 10.5194/tc-10-1809-2016.

Mader HM, Pettitt ME, Wadham JL, et al. (2006) Subsurface ice as a microbial habitat. *Geology* 34(3): 169–172. DOI: 10.1130/G22096.1.

Malard F (1999) Shifting Dominance of Subcatchment Water Sources and Flow Paths in a Glacial Floodplain, Val Roseg, Switzerland. *Arctic, Antarctic, and Alpine Research* 31(2): 135–150.

Marteinsdóttir B, Svavarsdóttir K and Thórhallsdóttir TE (2010) Development of vegetation patterns in early primary succession. *Journal of Vegetation Science* 21(3): 531–540. DOI: 10.1111/j.1654-1103.2009.01161.x.

Marteinsdóttir B, Thórhallsdóttir TE and Svavarsdóttir K (2013) An experimental test of the relationship between small scale topography and seedling establishment in primary succession. *Plant Ecology* 214(8): 1007–1015. DOI: 10.1007/s11258-013-0226-6.

Matthews J (1992) *The Ecology of Recently-Deglaciated Terrain*.

Matthews JA (1979a) The Vegetation of the Storbreen Gletschervorfeld, Jotunheimen, Norway. I. Introduction and Approaches Involving Classification. *Journal of Biogeography* 6(1): 17. DOI: 10.2307/3038150.

Matthews JA (1979b) The Vegetation of the Storbreen Gletschervorfeld, Jotunheimen, Norway. II. Approaches Involving Ordination and General Conclusions. *Journal of Biogeography* 6(2): 133. DOI: 10.2307/3038049.

Matthews JA and Owen G (2008) Endolithic Lichens, Rapid Biological Weathering and Schmidt Hammer R-Values on Recently Exposed Rock Surfaces: Storbreen Glacier Foreland, Jotunheimen, Norway. *Geografiska Annaler: Series A, Physical Geography* 90(4): 287–297. DOI: 10.1111/j.1468-0459.2008.00346.x.

Matthews JA and Whittaker RJ (1987) Vegetation Succession on the Storbreen Glacier Foreland, Jotunheimen, Norway: A Review. *Arctic, Antarctic, and Alpine Research* 19(4): 385–395.

McColl ST (2012) Paraglacial rock-slope stability. *Geomorphology* 153–154: 1–16. DOI: 10.1016/j.geomorph.2012.02.015.

Meola M, Lazzaro A and Zeyer J (2014) Diversity, resistance and resilience of the bacterial communities at two alpine glacier forefields after a reciprocal soil transplantation. *Environmental Microbiology* 16(6): 1918–1934. DOI: 10.1111/1462-2920.12435.

Mercier D, Étienne S, Sellier D, et al. (2009) Paraglacial gullying of sediment-mantled slopes: a case study of Colletthøgda, Kongsfjorden area, West Spitsbergen (Svalbard). *Earth Surface Processes and Landforms* 34(13): 1772–1789. DOI: 10.1002/esp.1862.

Miniaci C, Bunge M, Duc L, et al. (2007) Effects of pioneering plants on microbial structures and functions in a glacier forefield. *Biology and Fertility of Soils* 44(2): 289–297. DOI: 10.1007/s00374-007-0203-0.

Moreau M, Mercier D, Laffly D, et al. (2008) Impacts of recent paraglacial dynamics on plant colonization: A case study on Midtre Lovénbreen foreland, Spitsbergen (79°N). *Geomorphology* 95(1). Paraglacial Geomorphology: Processes and Paraglacial Context: 48–60. DOI: 10.1016/j.geomorph.2006.07.031.

Oliver CD, Adams AB and Zasoski RJ (1985) Disturbance patterns and forest development in a recently deglaciated valley in the northwestern Cascade Range of Washington, U.S.A. *Canadian Journal of Forest Research* 15(1): 221–232. DOI: 10.1139/x85-040.

Paul F, Huggel C and Kääb A (2004) Combining satellite multispectral image data and a digital elevation model for mapping debris-covered glaciers. *Remote Sensing of Environment* 89(4): 510–518. DOI: 10.1016/j.rse.2003.11.007.

Pellicciotti F, Brock B, Strasser U, et al. (2005) An enhanced temperature-index glacier melt model including the shortwave radiation balance: development and testing for Haut Glacier d'Arolla, Switzerland. *Journal of Glaciology* 51(175): 573–587.

Polvi LE and Sarneel JM (2017) Ecosystem engineers in rivers: An introduction to how and where organisms create positive biogeomorphic feedbacks. *Wiley Interdisciplinary Reviews: Water* 5(2). DOI: 10.1002/wat2.1271.

Raab T (2012) Initial Ecosystem Processes as Key Factors of Landscape Development - A Review. *Physical Geography* 33(4): 305–343.

Raffl C, Mallaun M, Mayer R, et al. (2006) Vegetation Succession Pattern and Diversity Changes in a Glacier Valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research* 38(3): 421–428. DOI: 10.1657/1523-0430(2006)38[421:VSPADC]2.0.CO;2.

Rime T, Hartmann M, Brunner I, et al. (2015) Vertical distribution of the soil microbiota along a successional gradient in a glacier forefield. *Molecular Ecology* 24(5): 1091–1108. DOI: 10.1111/mec.13051.

Rime T, Hartmann M and Frey B (2016) Potential sources of microbial colonizers in an initial soil ecosystem after retreat of an alpine glacier. *The ISME Journal* 10(7): 1625–1641. DOI: 10.1038/ismej.2015.238.

Robinson ZP, Fairchild IJ and Russell AJ (2008) Hydrogeological implications of glacial landscape evolution at Skeiðarársandur, SE Iceland. *Geomorphology* 97(1). Glacial Landscape Evolution - Implications for Glacial Processes, Patterns and Reconstructions: 218–236. DOI: 10.1016/j.geomorph.2007.02.044.

Rydgren K, Halvorsen R, Töpper JP, et al. (2014) Glacier foreland succession and the fading effect of terrain age. *Journal of Vegetation Science* 25(6): 1367–1380. DOI: 10.1111/jvs.12184.

Salzmann N, Machguth H and Linsbauer A (2012) The Swiss Alpine glaciers' response to the global '2 °C air temperature target'. *Environmental Research Letters* 7(4): 044001. DOI: 10.1088/1748-9326/7/4/044001.

Schmidt SK, Reed SC, Nemergut DR, et al. (2008) The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. *Proc. R. Soc. B* 275: 2793–2802.

Schreckenthal-Schimitschek G (1935) Der Einflu\s s des Bodens auf die Vegetation im Moränengelände des Mittelbergferners (Pitztal, Tirol). *Zeitschrift für Gletscherkunde und Glazialgeologie* 23(1/3): 57–66.

Schulz S, Brankatschk R, Dümig A, et al. (2013) The role of microorganisms at different stages of ecosystem development for soil formation. *Biogeosciences* 10: 3983–3996.

Schumann K, Gewolf S and Tackenberg O (2016) Factors affecting primary succession of glacier foreland vegetation in the European Alps. *Alpine Botany* 126(2): 105–117. DOI: 10.1007/s00035-016-0166-6.

Sharp M, Parkes J, Cragg B, et al. (1999) Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling. *Geology* 27(2): 107–110. DOI: 10.1130/0091-7613(1999)027<0107:WBPAGB>2.3.CO;2.

Sigler WV, Crivii S and Zeyer J (2002) Bacterial Succession in Glacial Forefield Soils Characterized by Community Structure, Activity and Opportunistic Growth Dynamics. *Microbial Ecology* 44: 306–316.

Skidmore ML, Foght JM and Sharp MJ (2000) Microbial Life beneath a High Arctic Glacier. *Applied and Environmental Microbiology* 66(8): 3214–3220. DOI: 10.1128/AEM.66.8.3214-3220.2000.

Smith DG (1976) Effect of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. *Geological Society of America Bulletin* 87: 857–860.

Stawska M (2017) Impacts of Geomorphic Disturbances on Plant Colonization in Ebba Valley, Central Spitsbergen, Svalbard. *Quaestiones Geographicae* 36(1): 51–64.

Temme AJAM and Lange K (2014) Pro-glacial soil variability and geomorphic activity – the case of three Swiss valleys. *Earth Surface Processes and Landforms* 39(11): 1492–1499. DOI: 10.1002/esp.3553.

Tockner K, Malard F and Ward JV (2000) An extension of the flood pulse concept. *Hydrological Processes* 14(16–17): 2861–2883. DOI: 10.1002/1099-1085(200011/12)14:16/17<2861::AID-HYP124>3.0.CO;2-F.

Töwe S, Albert A, Kleineidam K, et al. (2010) Abundance of Microbes Involved in Nitrogen Transformation in the Rhizosphere of <Emphasis Type="Italic">Leucanthemopsis alpina</Emphasis> (L.) Heywood Grown in Soils from Different Sites of the Damma Glacier Forefield. *Microbial Ecology* 60(4): 762–770. DOI: 10.1007/s00248-010-9695-5.

Viles HA (2012) Microbial geomorphology: A neglected link between life and landscape. *Geomorphology* 157–158. Special Issue Zoogeomorphology and Ecosystem Engineering Proceedings of the 42nd Binghamton Symposium in Geomorphology, held 21-23 October 2011: 6–16. DOI: 10.1016/j.geomorph.2011.03.021.

Ward JV, Tockner K, Arscott DB, et al. (2002) Riverine landscape diversity. *Freshwater Biology* 47(4): 517–539. DOI: 10.1046/j.1365-2427.2002.00893.x.

Whittaker RJ (1991) The Vegetation of the Storbreen Gletschervorfeld, Jotunheimen, Norway. IV. Short-Term Vegetation Change. *Journal of Biogeography* 18(1): 41–52. DOI: 10.2307/2845243.

Wietrzyk P, Wegrzyn M and Lisowska M (2016) Vegetation diversity and selected abiotic factors influencing the primary succession process on the foreland of Gasbreen, Svalbard. *Polish Polar Research* 37(4): 493–509.

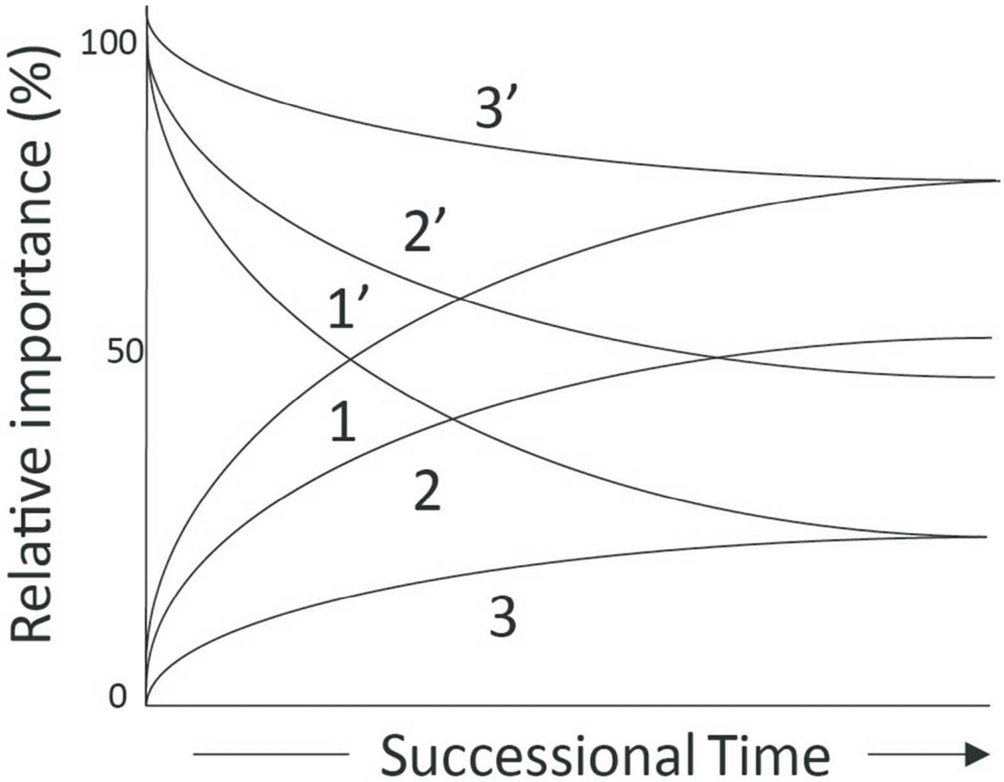
Wilhelm L, Singer GA, Fasching C, et al. (2013) Microbial biodiversity in glacier-fed streams. *The ISME Journal* 7(8): 1651–1660. DOI: 10.1038/ismej.2013.44.

Wilhelm L, Besemer K, Fasching C, et al. (2014) Rare but active taxa contribute to community dynamics of benthic biofilms in glacier-fed streams. *Environmental Microbiology* 16(8): 2514–2524. DOI: 10.1111/1462-2920.12392.

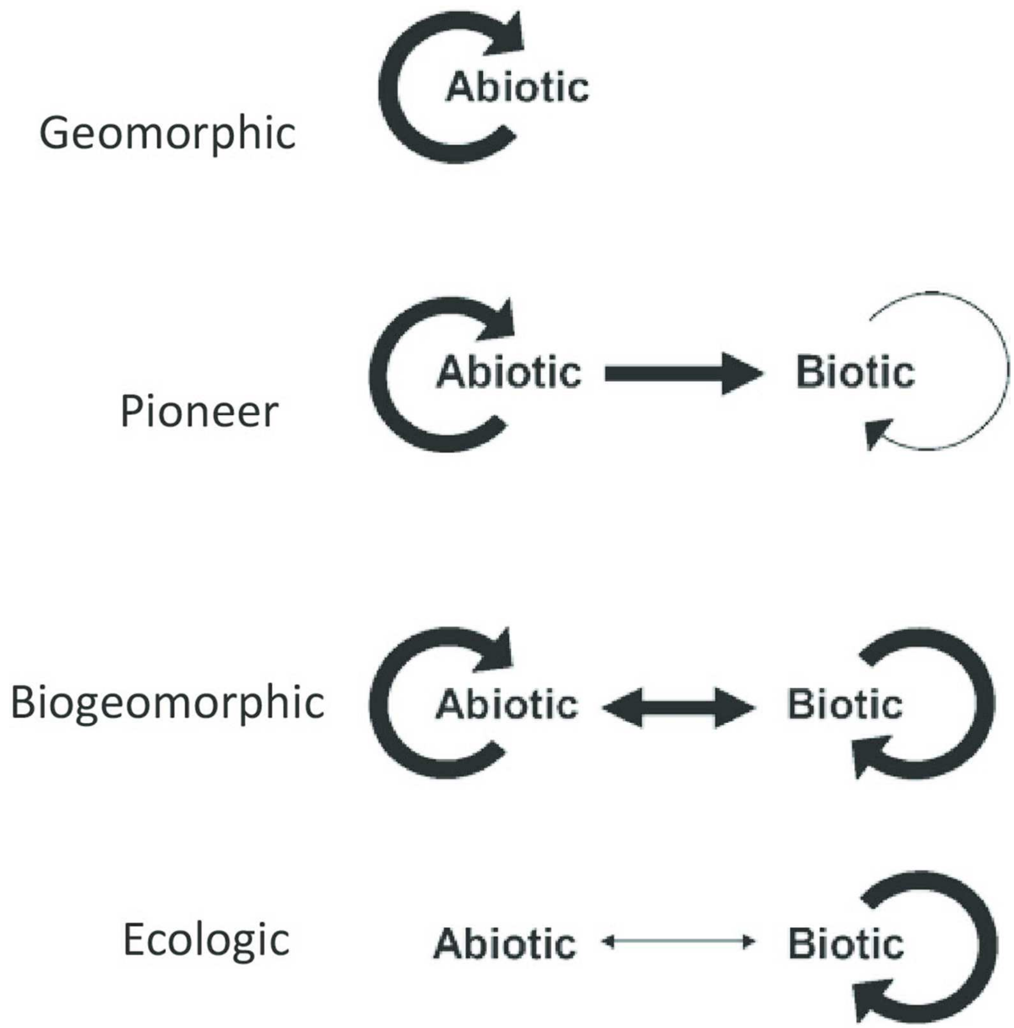
Wynn-Williams DD (1988) Television Image Analysis of Microbial Communities in Antarctic Fellfields. *Polarforschung* 58(213): 239–249.

Zah R and Uehlinger U (2001) Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps. *Freshwater Biology* 46(12): 1597–1608. DOI: 10.1046/j.1365-2427.2001.00847.x.

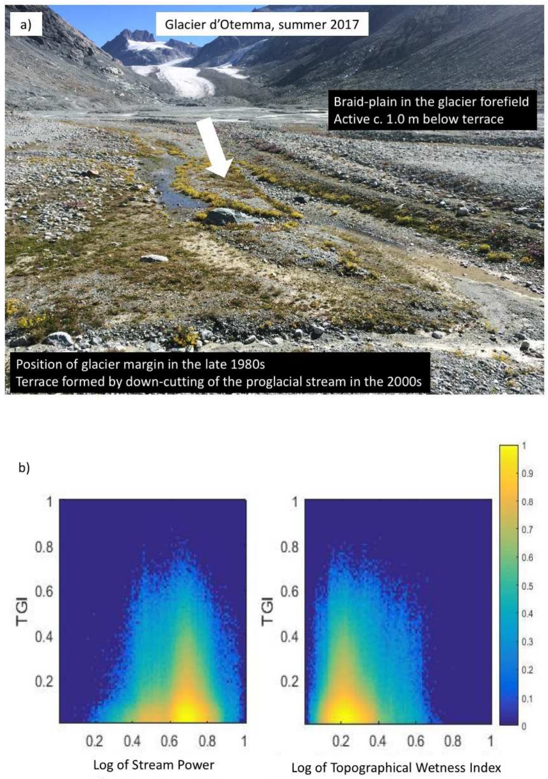
Zumsteg A, Luster J, Göransson H, et al. (2012) Bacterial, Archaeal and Fungal Succession in the Forefield of a Receding Glacier. *Microbial Ecology* 63(3): 552–564. DOI: 10.1007/s00248-011-9991-8.



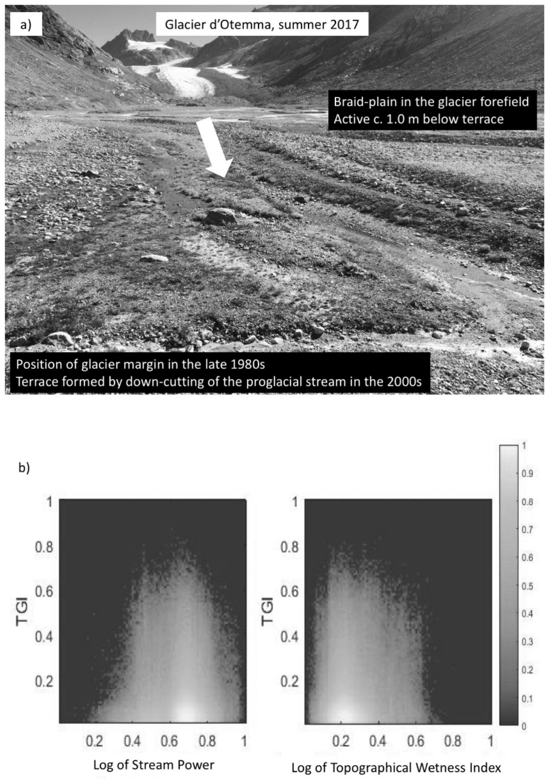
84x66mm (300 x 300 DPI)



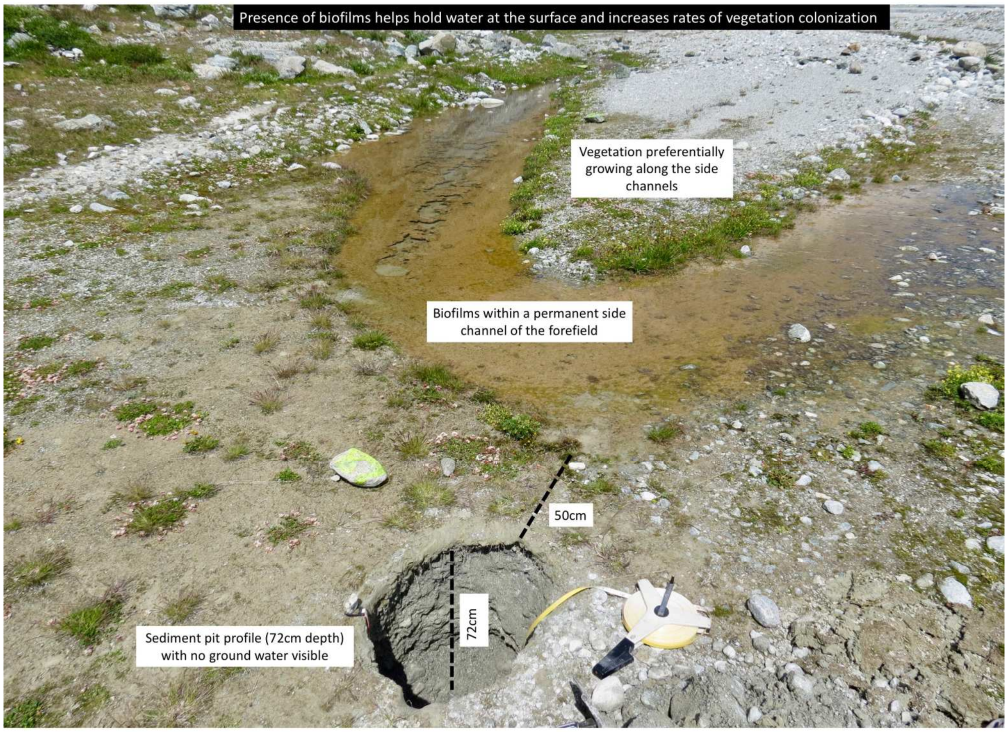
97x99mm (300 x 300 DPI)



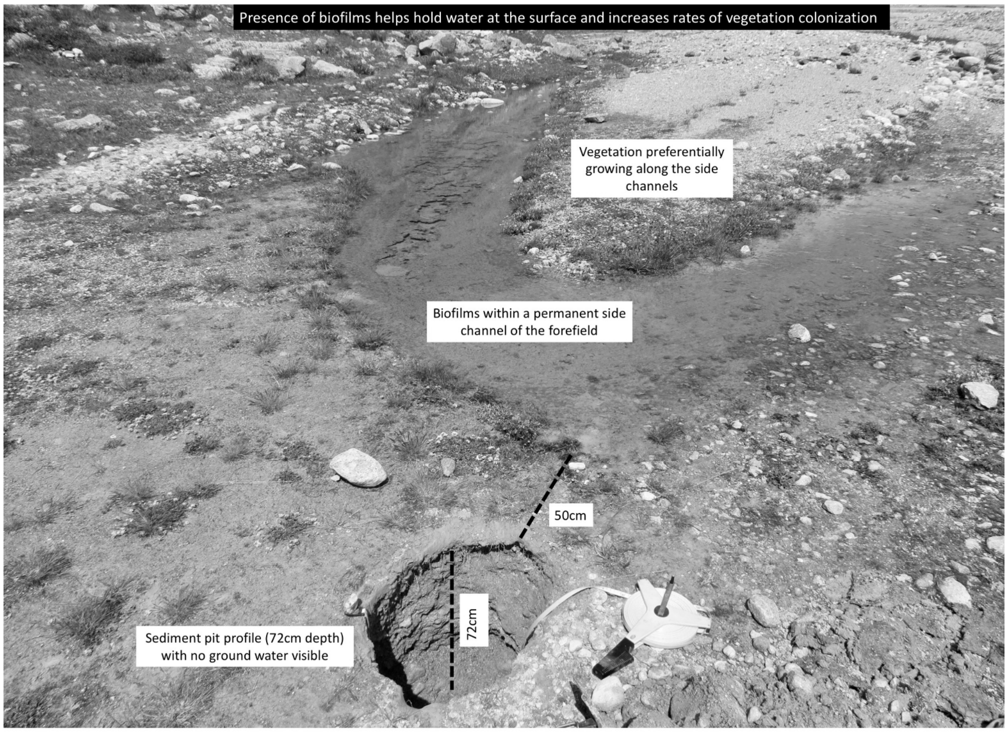
440x356mm (144 x 144 DPI)



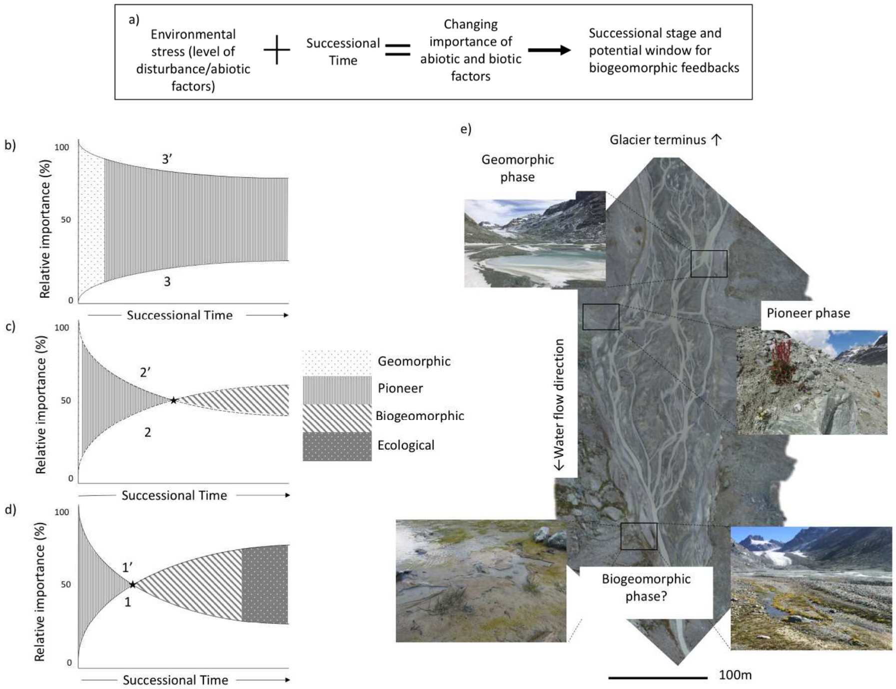
440x356mm (144 x 144 DPI)



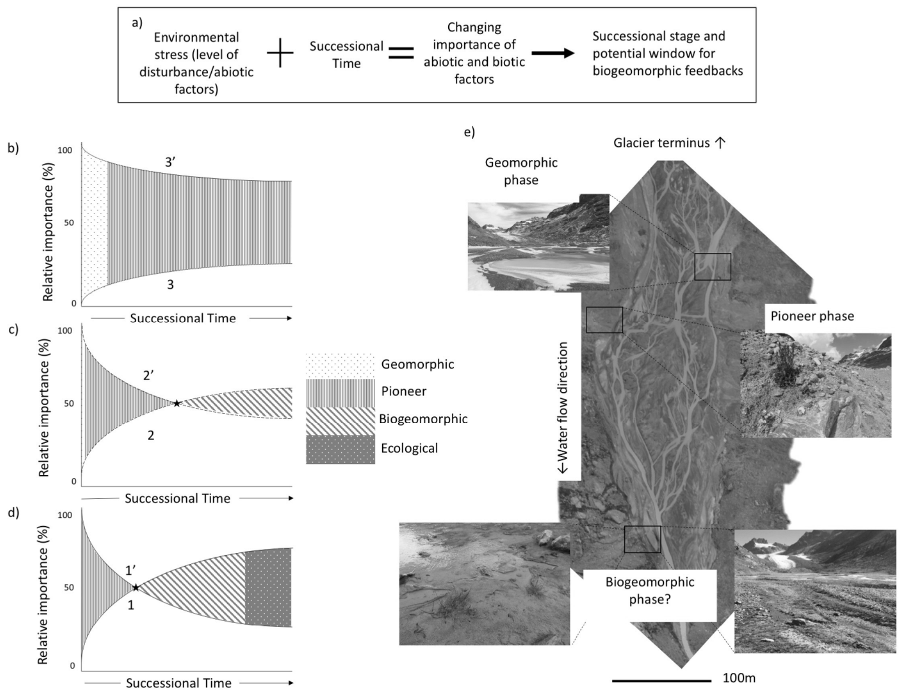
440x356mm (144 x 144 DPI)



440x356mm (144 x 144 DPI)



440x356mm (144 x 144 DPI)



440x356mm (144 x 144 DPI)

Ecosystem Engineering Role	Process	Key Papers
Supplying Resource		
	Microbial C and N remineralization	Bradley et al., (2014), Brankatschk et al., (2011), Schmidt et al., (2008), Schulz et al., (2013), Shulz et al. (2013)
	Microbial N-Fixation	Bradley et al., (2014), Schmidt et al., (2008), Schmidt et al., (2016), Schulz et al., (2013), Töwe et al., (2010)
	Vegetation N-Fixation	Arróniz-Crespo et al. (2014), Brankatschk et al., (2011), Kohls et al., (1994), Kohls et al., (2003), Kaštovská et al., (2005), Töwe et al. (2010)
Modifying Environment		
	Microbial-mediated soil development	Bradley et al., (2014), Borin et al., (2010), Frey et al., (2013), Schmidt et al., (2008), Schulz et al., (2013),
	Vegetation-mediated soil development	Duc et al., (2009), Grayston et al., (1996), Miniaci et al., (2007), Rime et al., (2015), Zah and Uehlinger, (2001)
	Vegetation impact on microbial community	Miniaci (2007), Rime (2015)
	Vegetation impact on seed bank	Moreau et al. (2008) (Wietrzyk et al., 2016)
Modifying abiotic factors		
	Microbial impact on weathering rates	Matthews and Owen, (2008), Schulz et al., (2013)
	Microbial impact on stabilization	Borin et al., (2010), Matthews and Owen, (2008), Schulz et al., (2013), Viles, (2012)
	Microbial impact on water availability	Borin et al., 2010; Frey et al., 2013
	Vegetation impact on stability	Eichel et al., (2013), Eichel et al., (2016), Eichel et al., (2017), Klaar et al., (2015), Moreau et al., 2008), Smith, (1976)
	Vegetation impact on water availability	Gurnell (1999),), Ielpi, (2017), Moreau et al., (2008), Smith (1976)

203x279mm (90 x 90 DPI)

Figure Captions

Figure 1: Schematic representation of the effect of increasing environmental severity (solid, broken, and dotted curves, respectively) on the relative importance of biotic (1, 2, 3) and abiotic (1', 2', 3') processes during succession. Redrawn from Matthews' 1999.

Figure 2: Simplified schematic representing the different stages of Corenblit et al.'s (2007) biogeomorphic phases model.

Figure 3: a) Image of Glacier d'Otemma showing vegetation growth and zonation along the meltwater channel (area indicated by white arrow), which appears to be driven by gradients in disturbance and water availability. b) Probability plots showing the Triangular Green Index (TGI; proxy for vegetation) plotted against stream power (proxy for erosion potential), and a wetness index for this area within the forefield within the vegetated channel area. Vegetation is most abundant at intermediate values of disturbance and wetness showing how these factors act as constraints to growth.

Table 1. The different ecosystem engineering roles of microbes and vegetation based on Jones et al., 1994 description of how organisms can exert changes on resources, the environment, and abiotic factors influencing the environment. Key papers illustrating these ecosystem engineering roles are included for reference.

Figure 4: An image of the potential ecosystem engineering role of biofilms within the Otemma forefield, Val de Bagnes, Switzerland. Fine sediments and biofilm colonies within the side channel help retain water at the surface that then creates a more suitable habitat for vegetation colonization.

Figure 5: Synthesized ecosystem successional model for alpine proglacial forefields illustrating the different successional stages that occur based on the balance of abiotic (1', 2', 3') and biotic (1, 2, 3) factors at a) high environmental stress, b) intermediate environmental stress, and c) low environmental stress. d) Drone image of the forefield of Glacier d'Otemma with sites corresponding to the three different successional stages illustrated in b). e) Schematic representation of synthesized model showing how environmental stress in addition to successional time are what drive the importance of abiotic and biotic factors and subsequently determine the succession stage and potential for biogeomorphic feedbacks.