Patterns of biogeochemical soil evolution in glacier forefields

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Eidesstattliche Erklärung

Hiermit versichere ich, die vorliegende Dissertation selbstständig und ohne unerlaubte Hilfe angefertigt zu haben. Bei der Verfassung der Dissertation wurden keine anderen als die im Text aufgeführten Hilfsmittel und Quellen verwendet. Ein Promotionsverfahren zu einem früheren Zeitpunkt an einer anderen Hochschule oder bei einem anderen Fachbereich wurde nicht beantragt.

Berlin, November 2020

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Robin Wojcik

Declaration of contributions for the authors and co-workers

This thesis is a “cumulative dissertation” and consists of five chapters. Three of these chapters are complete manuscripts either published, in review or submitted to international peer reviewed journals. The following paragraph clarifies the contributions of the PhD candidate and all involved co-authors. The candidate confirms that the work submitted is his own, except where work of jointly-authored publications has been included. The contribution of the candidate and the other authors are explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2 is reproduction of a peer-reviewed publication in *Annals of Glaciology*:

Wojcik, R., Donhauser, J., Frey, B., Holm, S., Holland, A., Anesio, A.M., Pearce, D.A., Malard, L., Wagner, D. and Benning, L.G., 2018. Linkages between geochemistry and microbiology in a proglacial terrain in the High Arctic. *Annals of Glaciology*, *59*(77), pp.95-110. https://doi.org/10.1017/aog.2019.1

The project was designed by Liane G. Benning and Robin Wojcik. The field work was conducted by Robin Wojcik, Johanna Donhauser, Stine Holm, Alexendra Holland, and Lucie Mallard. Sample processing for physical, geochemical and mineralogical analyses was performed by Robin Wojcik, while elemental, mineralogical and C/N contents was analyses by dedicated staff at the GFZ or at the University of Leeds. All data processing and interpretation on solids was carried out by Robin Wojcik and Liane G. Benning. The geochemical analyses on liquids were performed by Alexandra Holland under the guidance of Alex Anesio. The bacterial and fungal communities sequencing and interpretation were performed by Johanna Donhauser and Beat Frey, while the work on archaeal communities was done by Stine Holm. The preparation of the manuscript was primarily conducted by Robin Wojcik and Johanna Donhauser. Liane G. Benning, Beat Frey and Alex Anesio also contributed to the writing of the manuscript.

Chapter 3 is a reproduction of a manuscript published in *Geoderma*:

Wojcik, R., Donhauser, J., Frey, B. and Benning, L.G., 2020. Time since deglaciation and geomorphological disturbances determine the patterns of geochemical, mineralogical and microbial successions in an Icelandic foreland. *Geoderma*, *379*, p.114578. https://doi.org/10.1016/j.geoderma.2020.114578

The idea of the project was designed by Robin Wojcik and Liane G. Benning. The field work was carried out by Wojcik, Donhauser and Benning. Sample processing for physical, geochemical and mineralogical analyses was performed by Robin Wojcik, while elemental, mineralogical and C/N contents was analyses by dedicated staff at the GFZ or at the University of Leeds. All physical, geochemical and mineralogical processing and interpretation on solids was carried out by Robin

Wojcik under the guidance of Liane G. Benning. The bacterial analyses and interpretation was done by Johanna Donhauser and Beat Frey. Robin Wojcik wrote the main part of the manuscript with contribution from Johanna Donhauser, Liane G. Benning and Beat Frey .

Chapter 4 is a chapter that is written as a manuscript in preparation for post PhD defense submission

Wojcik, R., Els, N., Sattler, B., Winkel., M. Trivedi C., Schleicher A. M., and Benning L.G. Influence of aeolian deposition of phosphorus budgets in the forefield of Vernagt glacier (Austrian Alps). (*in prep.*)

Robin Wojcik, Nora Els and Liane G. Benning designed the project and planned the field work. Robin Wojcik with the help of staff from the University of Innsbruck collected the samples. All physical, geochemical and mineralogical sample processing and analyses were performed by / or under the supervision of Robin Wojcik and Liane G. Benning. Anja Schleicher helped with the X-ray diffraction quantification. DNA extraction was performed by Nora Els while PCR amplification and sequencing as well as bioinformatic data processing were performed by Matthias Winkel and Christopher Trivedi. All sequencing was carried out at the Bristol University sequencing facility. The chapter was written by Robin Wojcik.

Chapter 5 is a reproduction of a manuscript. *Under review.*

Wojcik, R., Eichel, J., Bradley, J. and Benning L.G. How allogenic environmental factor affect successions in glacier forefields (*under review*).

The design and writing of the manuscript was done by Robin Wojcik. Jana Eichel, James Bradley and Liane G. Benning each contributed with ideas and suggestions and to the writing of the manuscript.

I list of the publications outside the PhD thesis as well as oral and poster presentations done at scientific conferences over the course of the PhD is presented in the Appendix section.

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English summary

Soil plays a central role in the functioning of terrestrial ecosystems and is essential for the production of food for the world population. Yet, soil is a fragile resource whose health is increasingly endangered by unsustainable land-use practices, growing population and global warming. Acquiring knowledge on the processes controlling the natural formation of soils and their associated ecosystems through studies of primary successions is crucial to develop sustainable land-use strategies and predict the adaptation of soil ecosystems to global warming. Chapter #1 of this thesis discusses these issues.

While most studies on ecological successions focus on relatively well-developed ecosystems, our understanding of initial development of ecosystems, soils in particular, is comparatively scarce. Glacier forefields provide ideal setting to study the earliest stages of soil development and primary successions. Glacier forefield successions are most commonly studied using a chronosequence approach in which distance from the ice front of a retreating glacier ('time since deglaciation') is used as a proxy from 'terrain age'.

The development of pioneer microbial communities in glacier forefields is limited by the scarcity of nutrients. Chemical weathering, which can be enhanced by microbial activity, is often considered to be the dominant mechanism controlling the initial build-up of nutrients in these environments. However, the linkages between microbial communities, nutrient contents and weathering are still poorly understood. A major goal of my thesis was to study the changes in physical, chemical, mineralogical and microbiological parameters and their linkages using a chronosequence approach to gain insights into the processes controlling the initial autogenic development of soil ecosystems in glacier forefields. Interestingly, these tight relationships between chemical weathering and microbial communities indicate that microbial weathering is a strong driver of the build-up of a labile nutrient pool in early successional stages.

The chronosequence approach is based on the two core assumptions that (1) all sites of the succession were characterized by homogeneous initial conditions and (2) all sites followed the same sequence of change after the original disturbance that is glacier erosion. The work presented in this thesis shows that these assumptions about chronosequences are not always valid because abiotic initial environmental conditions and geomorphological disturbances can affect successional behavior in a temporally and spatially heterogeneous manner. The second major goal of my thesis was to investigate how allogenic factors (initial site conditions and geomorphological disturbances) can affect successional patterns in glacier forefields in a heterogeneous .

In Chapters #2 and #3, I present published studies in which I investigated the physical, geochemical and microbial successions leading to soil development in glacier forefields in Svalbard

and in Iceland. With increasing terrain age, my data shows a build-up of nutrient contents, a progression of chemical and physical weathering and an increase in microbial diversity and abundance. My dataset also highlights the strong correlations between nutrient cycling, weathering and microbial community structures. Altogether, these trends evidence an increasing degree of soil ecosystem development along the chronosequence. I emphasize that patterns of successional change related to time since deglaciation are also strongly influenced by geomorphological disturbances and heterogeneous initial environmental conditions. Specifically, in Chapters #2 (Longyearbreen proglacial area, Svalbard) and 3 (Fláajökull glacier forefield, Iceland) I show that areas affected by hillslope and glacio-fluvial erosion disturbances depict considerably delayed succession rates.

In Chapter #4, I investigated how the supply of dry (dust) vs. wet (snow /rain) aeolian deposition has contributed to the build-up of phosphorus in the forefield of Vernagt glacier (Austrian Alps). I assessed if this P supply enhanced the ecosystem succession rates in this glacier forefield. Importantly, I also investigated the effects of seasonal variability on biogeochemical processes in this glacier forefield by monitoring the year-round variability of aeolian phosphorus, as well as soil nutrient contents.

Finally, Chapter #5 is a review, where I present a comprehensive overview of how initial site conditions (substrate characteristics, microclimatic conditions and resources availability) and geomorphological disturbances (hillslope, glacio-fluvial, periglacial and aeolian processes) may affect the rate and/or trajectory in a spatially heterogeneous manner. I end this last chapter with a discussion on the changes in the relative importance of autogenic, allogenic and stochastic processes over the course of successions in glacier forefields.

Zusammenfassung

Der Boden spielt eine zentrale Rolle für das Funktionieren terrestrischer Ökosysteme und ist für die Produktion von Nahrungsmitteln für die Erdfauna von wesentlicher Bedeutung. Der Boden ist jedoch eine fragile Ressource, deren Gesundheit zunehmend durch nicht nachhaltige Landnutzungspraktiken, wachsende Bevölkerung und globale Erwärmung gefährdet wird. Der Erwerb von Wissen über die Prozesse, die die natürliche Bodenbildung und die gemeinsame Entwicklung der damit verbundenen Ökosysteme steuern, durch Studien der Primärfolgen ist entscheidend, um nachhaltige Landnutzungsstrategien zu entwickeln und die Anpassung der Bodenökosysteme an die globale Erwärmung vorherzusagen. Kapitel 1 dieser Arbeit behandelt diese Themen.

Während sich die meisten Studien zu ökologischen Folgen auf relativ gut entwickelte Ökosysteme konzentrieren, ist unser Verständnis der anfänglichen Entwicklung von Ökosystemen und insbesondere von Böden vergleichsweise schlecht entwickelt. Gletscher-Vorfelder bieten ideale Rahmenbedingungen, um die frühesten Stadien der Primärfolgen und der Bodenentwicklung zu untersuchen, die fortschreiten, wenn das Land allmählich freigelegt wird. Solche Gletscher-Vorfeldfolgen werden am häufigsten mit einem Chronosequenz-Ansatz untersucht, bei dem die Entfernung von der Eisfront eines sich zurückziehenden Gletschers ('Zeit seitdem Deglaciation ') wird als Proxy für' Terrain Age 'verwendet.

Die Entwicklung von mikrobiellen Pioniergemeinschaften in solchen Gletschervorfeldern ist durch die Nährstoffknappheit begrenzt. Chemische Verwitterung wird oft als der dominierende Mechanismus angesehen, der den anfänglichen Aufbau von Nährstoffen in diesen Umgebungen steuert, und die jüngsten Arbeiten haben auch gezeigt, dass diese Prozesse häufig durch mikrobielle Aktivität gesteuert werden. Die Zusammenhänge zwischen mikrobiellen Gemeinschaften, Nährstoffgehalt und Verwitterung sind jedoch noch wenig bekannt. Basierend auf dem Chronosequenzansatz bestand ein Hauptziel meiner Arbeit darin, die Änderungen der physikalischen, chemischen, mineralogischen und mikrobiologischen Parameter und ihre Verknüpfungen zu untersuchen, um Einblicke in die Prozesse zu erhalten, die die anfängliche autogene Entwicklung von Bodenökosystemen in Gletschervorfeldern steuern.

Der Chronosequenzansatz basiert auf den beiden Kernannahmen, dass (1) alle Orte der Abfolge durch homogene Anfangsbedingungen gekennzeichnet waren und (2) nach der ursprünglichen Störung, der Gletschererosion, der gleichen Änderungssequenz folgten. Die in dieser Arbeit vorgestellte Arbeit zeigt, dass diese Annahmen über Chronosequenzen nicht immer gültig sind, da abiotische Anfangsumweltbedingungen und geomorphologische Störungen das Sukzessionsverhalten zeitlich und räumlich heterogen beeinflussen können. Ein weiteres

ergänzendes Ziel meiner Arbeit war es zu untersuchen, wie sich Störungen durch geomorphologische Prozesse auf die Sukzessionsmuster des Bodens in Gletschervorfeldern auswirken.

In den Kapiteln 2 und 3 präsentiere ich veröffentlichte Studien, in denen ich die physikalischen, geochemischen und mikrobiellen Folgen untersuchte, die zur Bodenentwicklung in Gletschervorfeldern in Spitzbergen und in Island führen. Mit zunehmendem Alter des Geländes zeigen meine Daten eine Zunahme des Nährstoffgehalts, ein Fortschreiten der chemischen und physikalischen Verwitterung und eine Zunahme der mikrobiellen Vielfalt und Häufigkeit. Mein Datensatz hebt auch die starken Korrelationen zwischen Nährstoffkreislauf, Verwitterung und mikrobiellen Gemeinschaftsstrukturen hervor. Insgesamt zeigen diese Trends einen zunehmenden Grad der Entwicklung des Bodenökosystems entlang der Chronosequenz. Meine Ergebnisse zeigen auch, dass geomorphologische Störungen die Nachfolgemuster stark beeinflussen und nicht übersehen werden sollten. Ich betone, dass Muster der sukzessiven Veränderung in Bezug auf die Zeit seit der Enteisung auch stark von geomorphologischen Störungen und heterogenen anfänglichen Umweltbedingungen beeinflusst werden. Insbesondere in den Kapiteln 2 (Longyearbreen Proglazialgebiet, Spitzbergen) und 3 (Fláajökull-Gletscher-Vorfeld, Island) zeige ich, dass Gebiete, die von Hang- und Gletscher-Erosionsstörungen betroffen sind, erheblich verzögerte Sukzessionsraten aufweisen.

In Kapitel 4 habe ich untersucht, wie die Zufuhr von trockener (Äolischer Staub) und nasser (Schnee / Regen) Ablagerung zum Aufbau von Phosphor im Vorfeld des Vernagt-Gletschers (Österreichische Alpen) beigetragen hat. Ich habe festgestellt, ob dieses P die Ökosystemnachfolge in diesem Gletschervorfeld erhöht. Wichtig ist, dass ich auch die Auswirkungen der saisonalen Variabilität auf biogeochemische Prozesse in diesem Gletscher-Vorfeld untersuchte, indem ich die ganzjährige Variabilität des äolischen Phosphors sowie das Nährstoffpotential in den Böden überwachte. Schließlich ist Kapitel 5 eine Übersicht, in der ich einen umfassenden Überblick darüber gebe, wie sich die anfänglichen Standortbedingungen (Substrateigenschaften, mikroklimatische Bedingungen und Ressourcenverfügbarkeit) und geomorphologische Störungen (Hang-, Gletscher-Fluss-, Periglazial- und Äolische Prozesse) auf die Rate und / oder Prozesse auswirken können oder Flugbahn auf räumlich heterogene Weise. Ich beende dieses letzte Kapitel mit einer Diskussion über die Veränderungen in der relativen Bedeutung autogener, allogener und stochastischer Prozesse im Verlauf von Abfolgen in Gletschervorfeldern.

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Chapter 1: Background and Introduction

1.1. The Little Ice Age and glacier forefields

At around 11,500 BP, the Earth transitioned from the glacial Pleistocene to the warmer Holocene period due to changes in Milankovitch's orbital cycles, causing glaciers to retreat significantly worldwide. At least seven major climate cooling events and concurrent glacier expansion episodes occurred throughout the Holocene (Grove, 2004; Matthews and Briffa, 2005). The term 'Little Ice Age' (LIA) 'glacierization' generally refers to the latest glacier expansion episode of the late Holocene and is dated as the period ca. AD 1300–1850 in the European Alps. The climate cooling during the LIA is commonly explained as the result of a combination of increased volcanic activity and reduced solar activity (Mann, 2002; Wanner et al., 2008). Unlike the LIA 'glacierization', the LIA 'climate' is defined as the period ca. AD 1570–1900 the summer temperatures in the Northern Hemisphere significantly dropped below the AD 1961–1990 mean (Matthews and Briffa, 2005). The LIA glacier expansion of the episode reliant on changes in both summer temperature and winter precipitations (Nesje and Dahl, 2003). Glaciers are globally rapidly decreasing in area and volume since the end of the LIA and are retreating at increasing rates over the last three to four decades as a response to the anthropic global warming (Barry, 2006; IPCC, 2019; Marzeion et al., 2014; Zemp et al., 2015). The rapid global melting of glaciers since the mid-XXth century is illustrated in Fig. 1 that shows the decrease of glacier mass in various glacierized regions around the world. The melting and retreat of glaciers is expected to continue at increasing rates at high latitudes where the near-surface air warms at least twice as fast as the global average (Pithan and Mauritsen, 2014, IPCC 2019).

The retreat of glacier's ice front results in the exposure of large expanses of till material. The area extending between the front of the glacier and the moraine of the latest glacial maximum is called the glacier forefield (also known as glacier foreland or glacier marginal zone; Matthews, 1992; Anderson, 2007). The ground in glacier forefields will eventually transform into soil due to the combined action of physical and chemical weathering as well as microbial and finally plant colonization (Matthews, 1992; Bernasconi et al., 2011). These environments provide a unique field setting to study the initial geochemical, physical and ecological processes leading to the formation of terrestrial soil ecosystems.

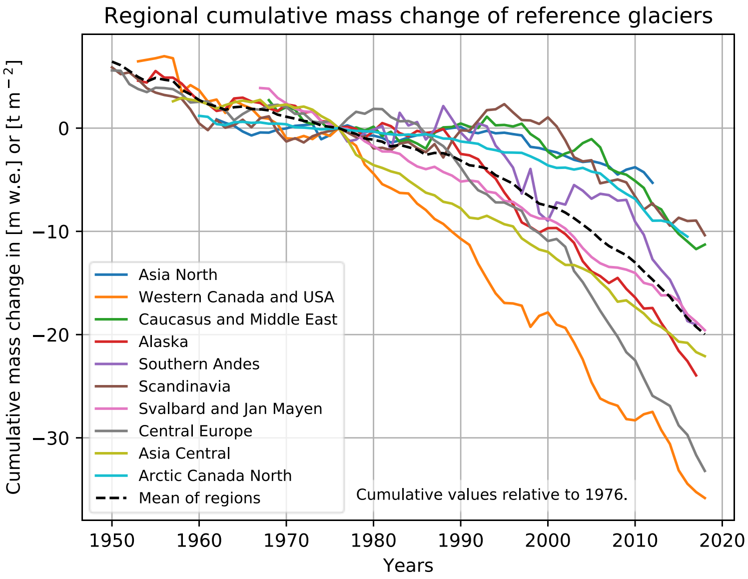

Figure 1: Cumulative mass change relative to 1976 for regional and global means based on data from reference glaciers. Cumulative values are given on the y-axis in the unit meter water equivalent (m w.e.). The mass balance estimates considered here are based on a set of global reference glaciers with more than 30 continued observation years for the time period, which are compiled by the World Glacier Monitoring Service (WGMS). Regional values are calculated as arithmetic averages. Global values are calculated using only one single value (averaged) for each region with glaciers to avoid a bias to well-observed regions. Figure adapted from the WGMS (2017) report.

The onset of the LIA was mostly synchronous around the world (Kreutz et al., 1997) and climatic fluctuations were spatially coherent at a sub-hemispherical scale (Briffa et al., 2002a, b). Regional differences in glacier retreat rate and soil development rates in glacier forefields around the globe are most often explained as the result of regional climatic differences. The latitude, altitude as well as continental and oceanic influences, which in turn naturally also regulate temperature and humidity gradients in these areas are among the most important parameters driving these regional climatic differences. Note that little is known on how these parameters affect ecosystem and soil successional developments altogether or individually.

1.2 Applications of primary succession research in glacier forefields

Soil plays a central role in the functioning of terrestrial ecosystems as it provides a foundation supporting the growth and subsistence of flora and fauna and regulates surface erosion, nutrient availability and water infiltration (NRC, 2010). Worldwide, soils store large amounts of carbon as organic matter and thus soils are an important component of the global climate system (Crowther et al., 2016). Human societies, too, crucially depend on soil health and soil ecosystem services for food and fibre production (MEA, 2005; Jónsson and Davíðsdóttir, 2016). The health or quality of a soil generally characterizes its ability to sustain the productivity and health of flora and fauna and preserves or improves the quality of water (Doran, 1999).

Despite its paramount importance, soil is a fragile and non-renewable resource (regenerating over times scales of decades to centuries) that can readily be threatened by erosion, physical degradation or chemically depletion (Doran, 2002). Over the last century, the widespread implementation of unsustainable industrial agricultural practices has led to a severe degradation of soils and reduction of crop yields worldwide. This is the result of increases soil erosion, depletion of soil organic matter reserves, loss of soil structure and compaction, which all aggravate drought stress (Lal, 2008; 2009; Gomiero, 2016). Other major examples of anthropogenic environmental degradations include: unmanaged urbanization, channelization, industrial land and water pollution, mining, radioactive pollution and acid rains (Mitchell et al., 2006; Walker and del Moral, 2011). Furthermore, it is expected that global warming will drive extensive environmental changes, as it leads to a global latitudinal shift of biomes (Parmesan and Yohe, 2003; Beck et al., 2011), changes in climatic seasonal patterns and intensification of hurricanes and coastal flooding (Pachauri and Reisinger, 2007). The growth of human population and associated anthropogenic driven climatic change are expected to increase soil degradation rates in the future, despite the fact that our dependence on soils for food production will grow to feed the global human population.

In this respect, developing and implementing sustainable land-use strategies is becoming one of the most pressing environmental challenges of the 21st century for the welfare of mankind. Developing a sound scientific understanding on how soil ecosystems form in natural settings and how such soils react to disturbances is important and is the necessary first step in our ability to develop tools for ecosystem protection and restoration (Willig and Walker, 1999; Robinson et al., 2012). Every modern ecosystem, natural or artificial, is the result of a primary succession and the outcome of an evolution that was initiated by a disturbance.

Anthropogenic environmental modifications can be viewed as disturbances that create conditions for primary successions (Walker and del Moral, 2011). Research on primary succession and disturbance ecology has valuable tools to offer to ecosystem restoration as it studies the processes of ecosystem development or recovery after the removal of most legacies of biological activity (Walker and Del Moral, 2003; Hobbs et al., 2007; Walker et al., 2007; Walker and del Moral, 2009). Our ability to understand natural primary succession is also essential for the restoration of damaged land and the protection of natural habitats. This can be done by controlling successional trajectories and avoiding undesirable conditions. Such an approach is also useful for optimizing the production of resources by improving an ecosystem's fertility, productivity and diversity (Walker and del Moral, 2001; Walker and del Moral 2003).

Also, the study of early ecosystem development in glacial forefield can serve as an analogue to inform us about the conditions that make a landscape habitable, and this, in turn, has implications for our understanding of other extreme terrestrial or extra-terrestrial environments where similar oligotrophic and harsh climatic conditions prevail (Czempiński and Dąbski, 2017; Kornei, 2018, Walker and Del Moral, 2003).

The studies of Adolphe Dureau de la Malle (as cited in Drouin, 1994), Ragnar Hult (Hult, 1881) and David Henry Thoreau (Thoreau, 1887) carried out in the second half of the 19th century are recognized as some of the earliest primary succession studies (Egerton, 2015). The term 'succession' as used in this PhD thesis, refers to the set of changes in species composition and ecosystem structure and their physical environment over time following a disturbance (Matthews, 1992; Walker et al., 2010). Complementarily, a 'disturbance' is defined as an event (a temporary change in environmental conditions) relatively discrete in time and space that causes an abrupt alteration of the composition, density, the biomass, or the spatial distribution of biota and/or affects the availability and properties of resources or the physical substrate (Walker and Willig, 1999; Chapin et al., 2011; Walker et al., 2010). Further, primary successions are initiated on newly formed land surfaces after primary disturbances have removed or buried most of the products of ecosystem processes. Secondary successions occur after less severe (secondary) disturbances, where biological legacies remain (Matthews, 1992; Walker et al., 2010; Chapin et al., 2011). After they are initiated, successions enter a 'progressive phase' in which the biomass and nutrient availability increase over time. These changes are accompanied by concomitant changes in the physicochemical composition of the soils. Over time scales of thousands of years, successions can reach a 'maximal phase' and then experience a 'retrogression phase' in which biomass and nutrient availability decline in the absence of rejuvenating disturbances (Peltzer et al., 2010; Walker et al., 2010). Primary succession can be studied in various settings, across a large range of ecosystem evolution time scales (Wardle et al., 2004). These include for example: (i) surfaces of varying ages caused by a glacier retreat (LIA glacier retreat for example; ca. 150 yr succession; Chapin et al., 1994), (ii) islands where major fires happened at varying times (ca. 6000 yr succession; Wardle et al, 2003), (iii) surfaces of varying age caused by the older, (iv) Pleistocene glacier expanse variations (ca. 22 000 - 120 000 yr succession; Wardle and Ghani, 1995; Richardson et al., 2004), (v) terraces of varying ages caused by marine sediments uplift (up to ca. 600 000 succession; Mark et al., 1988) and (vi) sand dunes of varying age caused by aeolian sand deposition (up to ca. 2 000 000 yr succession; Laliberté et al., 2012). Thus, despite being one of the oldest and most elaborated themes of theoretical ecology, primary succession research still develops dynamically and continues to reveal new insights into how ecosystems develop and function (Meiners et al., 2015; Chang and Turner, 2019).

While the greatest research efforts related to primary succession focus on regions that host relatively well-developed ecosystems (e.g., temperate or tropical regions), comparatively little is known on the initial stages on primary successions (Schaaf et al., 2011), and particularly in polar or alpine glacier regions. Forefields of receding glaciers provide the ideal setting to study the development of embryonic ecosystems. In glacier forefields, primary successions are initiated by the primary disturbance that is glacier erosion on a substrate that becomes exposed upon glacier recession. Such newly exposed terrains have not been exposed to aerial conditions for many 10ns to 1000ds of years or longer. In addition to contributing to fundamental primary succession theory, ecological studies in glacier forefields also help to clarify the differences in nature and rate between primary and secondary successions.

Glacier forefields typically host poorly developed ecosystems whose development is slow because they are critically hindered by oligotrophic conditions, harsh climatic conditions with low temperature and water stress as well as widespread and frequent environmental disturbances. (Matthew, 1992). It is commonly considered that the legacy of subglacial microbial ecosystems to glacier forefields does not prevent the use of the term ‘primary succession’ with reference to glacier forefields (Matthews, 1999) and that subglacial effects disappear rapidly upon exposure of the new land post glacier retreat. Glacier forefields most commonly exhibit progressive successions, although examples of retrogressive tendencies in some older stages of glacier forefield development also exist (Matthews, 1999).

Glacier forefield successions are most commonly studied using a chronosequence approach. Using a time for space substitution, the proglacial chronosequence approach is based on the assumption that time is the dominant driver the soil development and uses the distance from the glacier as a proxy for terrain age. It is further assumed that all sites along a chronosequence were subjected to homogeneous initial conditions at the moment of deglaciation and that they later followed the same development trajectory, the same sequence of changes after deglaciation and that they only differ in their time since deglaciation (Johnson and Miyanishi, 2008; Walker et al., 2010). Cooper (1923 a, b) and Croker and Major (1955) provided some of the earliest examples of chronosequence studies in glacier forefield at Glacier Bay, Alaska. The research on glacier forefield grows, as evidenced by the increasing number of publications (Heckmann et al., 2016).

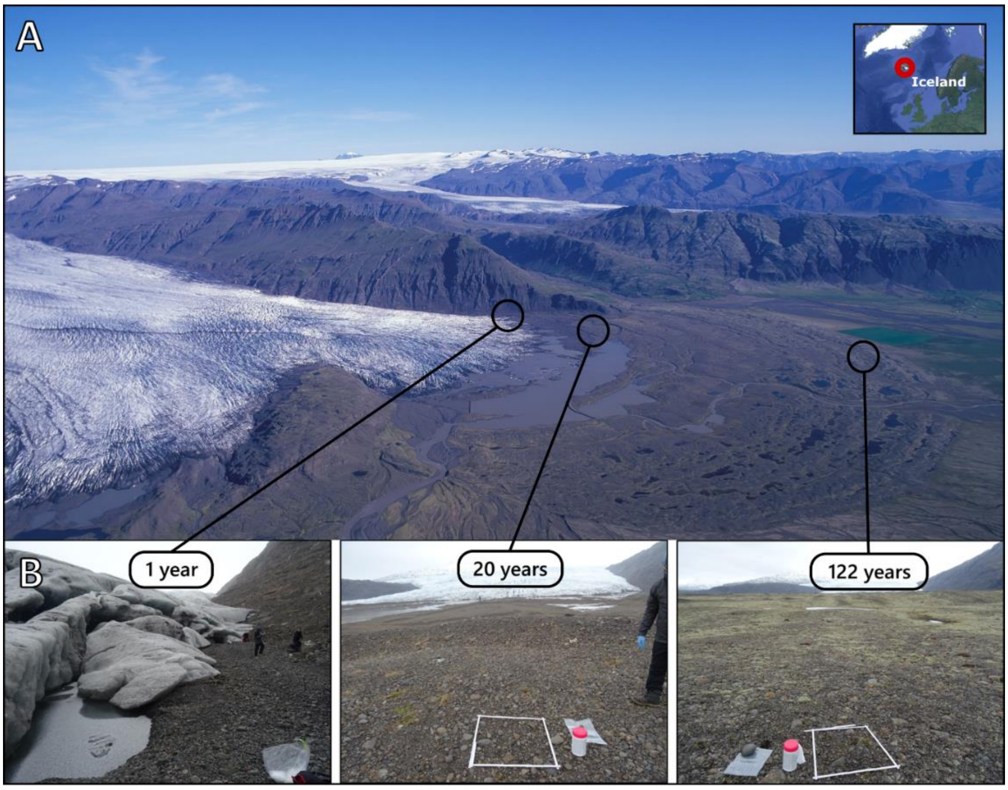

Figure 2: Typical deglaciated forefield (A) aerial photograph of the forefield of Fláajökull glacier in south-eastern Iceland. The ice front retreated by ~ 3km since the end of the LIA, exposing a conspicuous arcuate moraine assemblage along a well-dated 112 yr old chronosequence (see Chapter 3). (B) Photographs of initial (1 year after deglaciation), intermediate (20 year after deglaciation) and advanced (122 year after deglaciation) stages of soil-ecosystem development along the Fláajökull forefield chronosequence.

1.3 Additional applications of research in glacier forefields

1.3.1 The Influence of proglacial terrains on downstream and adjacent environments

The shrinkage of glaciers is going to have increasingly significant consequences on both downstream natural and human environments well beyond glacier forefields. Barry (2006) predicted that the retreat or disappearance of glaciers will affect human societies in various manners including: the rise in sea level, amount and timing of fresh / drinking water availability, socio-economic impacts on for example Alpine tourism, or the opening of new mining opportunities (e.g., Greenland), of new commercial transport pathways on the ocean (e.g., Northern Passage) and on land (European Arctic). Besides changes caused directly by the melting of glacier ice, the retreat of glaciers is the driver numerous paraglacial changes in proglacial environments. The term 'paraglacial geomorphology' can be defined as the set of *"earth-surface processes, sediments, landforms, landsystems and landscapes that are directly conditioned by former glaciation and* *deglaciation*" (Ballantyne, 2002). Paraglacial changes typically include the modification of glacier forefields as well as the intensification of glacio-fluvial sediment transport, the destabilization of rock slopes or sediment mantled slopes, or the formation of debris cones and alluvial fans, permafrost melt as well as lacustrine sedimentation (Ballantyne, 2002). Any such rapid paraglacial topographic modifications and their associated sediment mobilization can potentially cause local geohazards due to rock falls, landslides, lake outbursts, debris flows etc, which can for example dramatically affect populated Alpine areas (Chiarle et al., 2007; Korup and Clague, 2009; Keiler et al., 2010).

The development of glacier forefield ecosystems has ecological implications also at the watershed scale. Glacier forefield ecosystems are tightly connected to neighbouring ecosystems of streams, lakes, or through intertidal and coastal areas (Milner et al., 2007; Anderson et al., 2017; Diaz et al., 2018). These connections occur through glacio-fluvial, hillslope or aeolian geomorphological processes. In particular, glacier forefield ecosystems exert a strong influence on the productivity and biodiversity of these adjacent or downstream ecosystems because they export substantial amounts of sediments (e.g., Geilhausen et al., 2013; Micheletti and Lane, 2016) and nutrients such as dissolved organic carbon (e.g., Chifflard et al., 2018), nitrogen (e.g., McKnight et al., 2004) and /or phosphorus (e.g., Hawkings et al., 2016). Finally, the development of glacier forefield ecosystems can strongly affect downstream hydrological regimes also because they can moderate *peak outflows during extreme precipitation events or ensure a regulated supply of water to downstream areas during droughts* (Xu et al. 2009). Jacobsen et al. (2012) also noted that the increasing proportion of glacier meltwater in downstream rivers could affect the biodiversity in downstream riverine ecosystems as well as ecosystem services to humans for example regarding the planning of water availability for agriculture and hydroelectricity production (Beniston, 2003; Knight and Stephan, 2014; Milner et al., 2017).

1.3.2 The influence of proglacial terrains on major global biogeochemical cycles

1.3.2.1 Biomass build-up and organic carbon sequestration

At the global scale, the sequestration of organic carbon in soils (Smittenberg et al., 2012) and living biomass (e.g. Tscherko et al., 2005; Raffl et al., 2006) that results from the development of glacier forefield ecosystems may influence atmospheric carbon budget and ultimately provide a negative feedback effect on global warming (Anderson, 2007). There currently exists no global estimate of the total storage and regional distribution of organic carbon in glacier forefields ecosystems. Yet, acquiring a global quantitative estimate of sequestration of organic carbon in soils in glacier forefields is crucial.

1.3.2.2 Silicate weathering

On longer time scales, the expansion of the area of glacier forefields may impact the atmospheric carbon budget due to the drawdown of atmospheric CO_2 through silicate weathering (Anderson, 2007). Raymo and Ruddiman (1992) argued that the increasing supply of fresh material exposed by tectonic uplift (or by glacier retreat) will likely increase the chemical weathering rates of rocks by carbon dioxide dissolved in rain and river waters. The resulting carbon sink could drive climate cooling. In particular, the 'transformation' of silicate rocks to carbonate rocks cause the drawdown of atmospheric CO_2 (Eq. 1,2 and 3; Anderson et al., 2000; Kump et al., 2000; Chierici and Fransson, 2009). Equation 1 describes the formation of carbonic acid by dissolving atmospheric carbon dioxide in rainwater. Through weathering, the carbonic acid dissolves silicate rocks releasing calcium (or other alkaline earth metal) and bicarbonate into solution (Eq. 2). The products of such weathering reactions are typically transported in rivers to oceans where they precipitate as carbonate rocks (Eq. 3).

(equation 1) $$CO_{2(g)} + H_2O_{(aq)} \rightarrow H_2CO_{3(aq)}$$

(equation 2) $$2H_2CO_{3(aq)} + CaSiO_{3(s)} \rightarrow Ca^{2+}_{(aq)} + SiO_{2(aq)} + 2HCO^{-}_{3(aq)} + H_2O_{(aq)}$$

(equation 3) $$2Ca^{2+} + 2HCO^{-}_{3(aq)} \rightarrow 2CaCO_{3(s)} + H_2O_{(aq)} + CO_{2(aq)}$$

This same series of chemical reactions yield particularly important weathering fluxes in glacier forefields. There the physical weathering by glacier ice supplies large amounts of fresh and fine-textured materials that are highly reactive and have a great surface area (Anderson, 2007) that will react with atmospheric CO_2 dissolved in waters. On the other hand, the weathering flux of glacier debris tends to be lower than in for example tropical or temperate areas, because of the low temperatures (Anderson, 2007; Egli et al., 2014) and most often dry conditions (Egli et al., 2006). Nevertheless, the chemical weathering fluxes of glacierized catchments are commonly found to be greater than those of non-glacierized catchments (Anderson et al., 2005). This observation has served as a basis for several studies to speculate that the important weathering fluxes originating from products of glacial erosion could provide negative feedback to global warming (e.g. Sharp et al., 1995; Tranter, 1996; Anderson, 2007; Gislason et al., 2009).

1.3.2.3 Aeolian sediments

The retreat of glacier exposes formidable amounts of fine-grained (<100 μm) glacier erosion sediments that are readily susceptible to aeolian transport. The intensity of aeolian erosion (deflation) is primarily controlled by the rate of sediment supplied through glacier retreat, the wind transport capacity, the vegetation cover and soil moisture (Wiggs et al., 2004; Bullard, 2013).

Proglacial areas in general and glacio-fluvial outwash plains, in particular, are major sources of aeolian sediments (Bullard and Austin, 2011). These often silt- or even clay-sized sediments can travel vast distances (e.g. ca. 1800 km; Gassó and Stein, 2007) and can affect global biogeochemical cycles in various ways. Minerals aerosols may affect climate by reflecting or absorbing terrestrial and solar radiations (Yoshioka et al., 2007) and may affect cloud formation and precipitations (Dentener et al., 1996; Rosenfeld et al., 2011). Locally, dust produced in proglacial areas can considerably accelerate the melting of glaciers and ice sheets by lowering their albedo (Bøggild et al., 2010; Wientjes et al., 2011). The deposition of aeolian sediments has also been found to be a rich source of nutrients and thus promote the development of numerous oceanic (Baker et al., 2003; Jickells et al., 2005; Mahowald et al., 2005) and terrestrial ecosystems (Okin et al., 2004; Derry and Chadwick, 2007; McClintock et al., 2015; Aciego et al., 2017; Arvin et al., 2017; Herbert et al., 2018) around the world. In turn, the supply of minerals and nutrients derived from aeolian deposition may contribute to onset and sustain the growth of glacier forefields ecosystems themselves (Hawes, 2008; Šabacká et al., 2012; Diaz et al., 2018; see detailed seasonal study and a review related to this topic the Chapters 4 of this thesis).

1.3.2.4 Marine sediments

A large fraction of glacial erosion products that are not eroded and transported away by aeolian processes are transported via rivers and streams to the oceans where they accumulate in marine sediments (Anderson, 2007). These glacigenic sediments will affect global biogeochemical cycles by promoting the burial and preservation of organic matter-rich marine sediments (Lopes et al., 2015; Cartapanis et al., 2016). This is especially important in deltas as well as on continental shelves (Blair et al., 2004)where burial rates primarily depend on sediment delivery rates (Blair et al., 2004) and grain size (Hedges and Keil, 1995). Overall, glacierized catchments yield high amounts of fine-grained sediments, which in turn lead to ideal conditions for the burial of organic matter (Anderson, 2007).

1.4 Scope of the thesis and research goals

The overall aim of my PhD thesis is to improve our understanding of the autogenic and allogenic processes controlling the development and successional patterns of glacier forefield ecosystems.

In order to investigate the features of autogenic development in glacier forefield ecosystems, I focus on examining the relationship between microbial communities and their abiotic environment. In glacier forefields, the development of pioneer ecosystems is drastically limited by the scarcity of the available nutrients. Although autochthonous chemical weathering is commonly considered to be the dominant mechanism controlling the release and later build-up of nutrients in proglacial soils, we lack an understanding of the functional linkages between nutrient cycling, weathering progression and microbial community development. To address this gap, the primary goal of the first two chapters of my PhD (Chapters #2 and #3) was to examine the successional patterns of soil nutrient budgets, soil geochemical and mineralogical properties and soil microbial communities in proglacial terrains in Svalbard and Iceland. I use multivariate analyses to quantify the relationship between microbial communities and their geochemical environments. I study the close relationship between carbon and nitrogen build-up, weathering-induced changes in soil geochemical and mineralogical properties and the diversification in the microbial community structures.

Time since deglaciation (equivalent to autogenic development) is often the most important factor explaining the patterns of successional change in glacier forefields. However, successional patterns do not result from time since deglaciation alone. The second major goal of this thesis is to investigate how allogenic factors (initial site conditions and geomorphological disturbances) can affect the rate and trajectory of successions in a heterogeneous manner. In Chapters #2 and #3, I study the effect of hillslope and glacio-fluvial disturbances on the spatial variability of succession rates. Complementarily, in Chapter #4, I examine the contribution of aeolian-derived phosphorus to a glacier forefield in the Austrian Alps. Lastly, in Chapter #5, I summarize and discuss through a thorough literature review how allogenic factors can affect the spatial variability of glacier forefield ecosystems. Specifically, this chapter aims to reviews how variations in initial site conditions (bedrock characteristics, microclimate and resources availability) and geomorphological disturbances (hillslope, glacio-fluvial, periglacial and aeolian processes) can affect the rate and/or trajectory of successions. This chapter also discusses changes in the relative importance of autogenic, allogenic and stochastic factors over the course of successions. As well, I present a brief overview of the main forms of biogeomorphological feedback between biota and geomorphological disturbances in these ecosystems.

The thesis ends with a concluding and summary chapter which reviews the main findings of the different contributions and presents an outlook for future work in this research area.

Chapter 2: Linkages between geochemistry and microbiology in a proglacial terrain in the High Arctic

This chapter is adapted from:

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Abstract

Proglacial environments are ideal for studying the development of soils through the changes of rocks exposed by glacier retreat to weathering and microbial processes. Carbon (C) and nitrogen (N) contents, as well as soil pH and soil elemental compositions, are thought to be dominant factors structuring the bacterial, archaeal and fungal communities in the early stages of soil ecosystem formation. However, the functional linkages between C and N contents, soil composition and microbial community structures remain poorly understood. Here, we describe a multivariate analysis of geochemical properties and associated microbial community structures between a moraine and a glacio-fluvial outwash in the proglacial area of a High-Arctic glacier (Longyearbreen, Svalbard). Our results reveal distinct differences in developmental stages and heterogeneity between the moraine and the glacio-fluvial outwash. We observed significant relationships between C and N contents, $\delta^{13}C_{org}$ and $\delta^{15}N$ isotopic ratios, weathering and microbial abundance and community structures. We suggest that the observed differences in microbial and geochemical parameters between the moraine and the glacio-fluvial outwash are primarily a result of geomorphological variations of the proglacial terrain.

2.1 Introduction

Due to global warming, the rate of glacier recession has increased since the beginning of the 20th century and is expected to increase further in the future (Weller and others, 2005). The retreat of glaciers results in the exposure of large expanses of deglaciated ground that transforms rapidly due to physical and chemical weathering as well as microbial and finally plant colonization (Frey and others, 2010; Zumsteg and others, 2012). Proglacial environments of receding glaciers have received increasing recognition in recent years as they provide a unique field setting to study the geochemical and microbial development of young terrestrial soil ecosystems. Both the initiation of rock weathering and the activity of pioneer microorganisms play important roles in the initial growth and maintenance of soil ecosystems. Initial microbial colonizers fix C and N into bioavailable forms, which in turn promote the development of more complex and efficient microbial communities as well as later plant establishment (Donhauser and Frey, 2018). Such shifts in microbial communities in recently deglaciated terrains have been extensively studied (e.g. Ohtonen and others, 1999; Nemergut and others, 2007; Bajerski & Wagner, 2013; Rime and others, 2015).

The development of microbial communities in recently deglaciated terrain is primarily limited by low C and nutrient contents (Mindl and others, 2007; Göransson and others, 2011), as well as large temperature and moisture fluctuations (Bradley and others, 2014; Mateos-Rivera and others, 2016). Weathering is considered to be one of the dominant processes controlling C and nutrient availability as it exerts a strong control on the development of microbial communities and their ability to generate and recycle organic matter (Bradley and others, 2014). Changes in C and nutrient contents, weathering advancement and microbial community structures are thought to have strong feedbacks with each other. Previous interdisciplinary studies have integrated both comprehensive geochemical data and microbial data (e.g., Bernasconi and others, 2011; Bradley and others, 2016), yet, the correlation between geochemical and microbiological variables remains poorly quantified. Thus, our understanding of the functional linkages between soil weathering, C and nutrients and microbial community structures in recently deglaciated terrain remains limited.

Little is known about the variability of ecosystem development different on the dominant landforms of proglacial terrains. Among these, the differences between ecosystems developing on moraines or in glacio-fluvial outwash area remain poorly understood. To address these gaps, we compared a proglacial moraine and glacio-fluvial outwash in a High-Arctic terrain and examined and quantified the relationships between weathering advancement, C and nutrient contents and the development of microbial community structures.

2.2 Materials and Methods

2.2.1 Study area and sampling method

Soil samples were collected in November 2016 in the proglacial area of Longyearbreen (Spitsbergen, Svalbard (78.19°N, 15.54°E) (Fig. 1). Longyearbreen is a glacier that is flowing within a catchment with a lithology made up of late Tertiary shales, siltstones, and sandstones and coal seams (Major and others, 1972).

The average annual temperature at Longyearbyen airport (5 km away, 28 a.p.s.l) is -5.6°C, ranging between -12.7°C for February (coldest month), 6.7°C for July (warmest month) and -7.5°C for November (sampling period) (Norwegian Meteorological Institute, 2017). The mean annual temperature in 2016 was -0.1°C and the mean temperature in November 2016 was -1°C at Longyearbreen's airport meteorological station (timeanddate.com., 2018). The annual precipitation is typically 213 mm (water equivalent) (Climate-Data.org., 2017).

Longyearbreen is a 4.5 km long, 0.5 km wide glacier that flows into a near V-shaped subglacial valley (Etzelmüller and others, 2000), enclosed within sediment-mantled slopes characterized by steep incision gullies and slope-foot debris cones. Longyearbreen is a cold-based glacier presumably frozen to the bed in most parts, at least in its outer margins, with temperatures at the glacier bed of about -4°C in (March-May 2001, 2002, 2003; Humlum and others, 2005). As a result, basal ice sliding is expected to be limited or even absent, while surface ice flow velocities are <1 ma^{-1} in the lowermost part of its ablation area (Etzelmüller and others, 2000). The ice mass flux is dominated by internal deformation and has little erosion potential. Longyearbreen's ice front is debris-covered and no evidence of surging for Longyearbreen exists (Humlum and others, 2005). Overall, the total glaciated area of Svalbard has decreased by 13.1% since the end of the LIA (Martin-Moreno and others, 2017). However, Longyearbreen has not or only minimally retreated since the end of the LIA, yet it has thinned by 20-30 meter (Humlum and others, 2005) and has thus no LIA moraine. Based on mass balance measurements, Etzelmüller and others (2000) estimated an annual mass loss of -0.5 m (water equivalent) for Longyearbreen during the period 1977 to 1992 (Hagen & Liestol, 1990).

The geomorphology of the proglacial area of Longyearbreen is dominated by two major landforms: an ice-cored moraine and a glacio-fluvial outwash (Fig. 1). The moraine consists of unsorted angular glacigenic deposits containing a random mixture of boulder to gravel-sized rocks within a fine soil matrix that is ice-cored in many places (Etzelmüller and others, 2000). Etzelmüller and others (2000) pointed out that the lower part of Longyearbreen is a mix of ice-cored moraines and debris-covered glacier and further specifically indicated that an ice-cored moraine terminates Longyearbreen's marginal area. The glacio-fluvial outwash is a gently sloping depositional landform that consists of secondary glacigenic or slope deposits that are frequently reworked by fluvial processes. However, estimates of the formation ages for both the moraine and the outwash are lacking.

We collected a set of 9 soil samples at three locations: site 1 was located on the ice-cored moraine (from here onwards called moraine for simplicity) and two sites on the glacio-fluvial outwash plain (sites 2 and 3, from here onwards called outwash) (Fig 1.). At all sites, the ground was covered with between 5-10 cm of fresh snow. At each location, triplicate samples were collected in a ~15 m radius area to assess local soil heterogeneities. The three soil samples at site 1 (Fig 1 and Table 1) were collected on the steep (30°) toe-slope of the moraine, 500 m away from the glacier terminus. In contrast, the six soil samples at sites 2 and 3 were collected in the flat-lying area on the glacio-fluvial outwash on the same terrace. The distance between site 1 and site 2 was 300 m and the distance between site 2 and site 3 was 150 m. Note that reaching the glacier snout was not possible for security reasons due to unstable ice-cored moraines and dark winter conditions.

GPS-coordinates, air and ground temperature, as well as land cover and geomorphological setting were documented in detail (Table 1). Subsequently, soil samples were collected to a maximum depth of ~15 cm into sterile whirl-pack sample bags using a shovel, chisel and hammer. Before each sampling, the sampling equipment was sterilized using ethanol wipes and then was also conditioned in the surrounding soil. Finally, at each site a host rock (free lying ~20 cm diameter rock) was also collected. After sampling, all samples were maintained frozen at -20°C until processed.

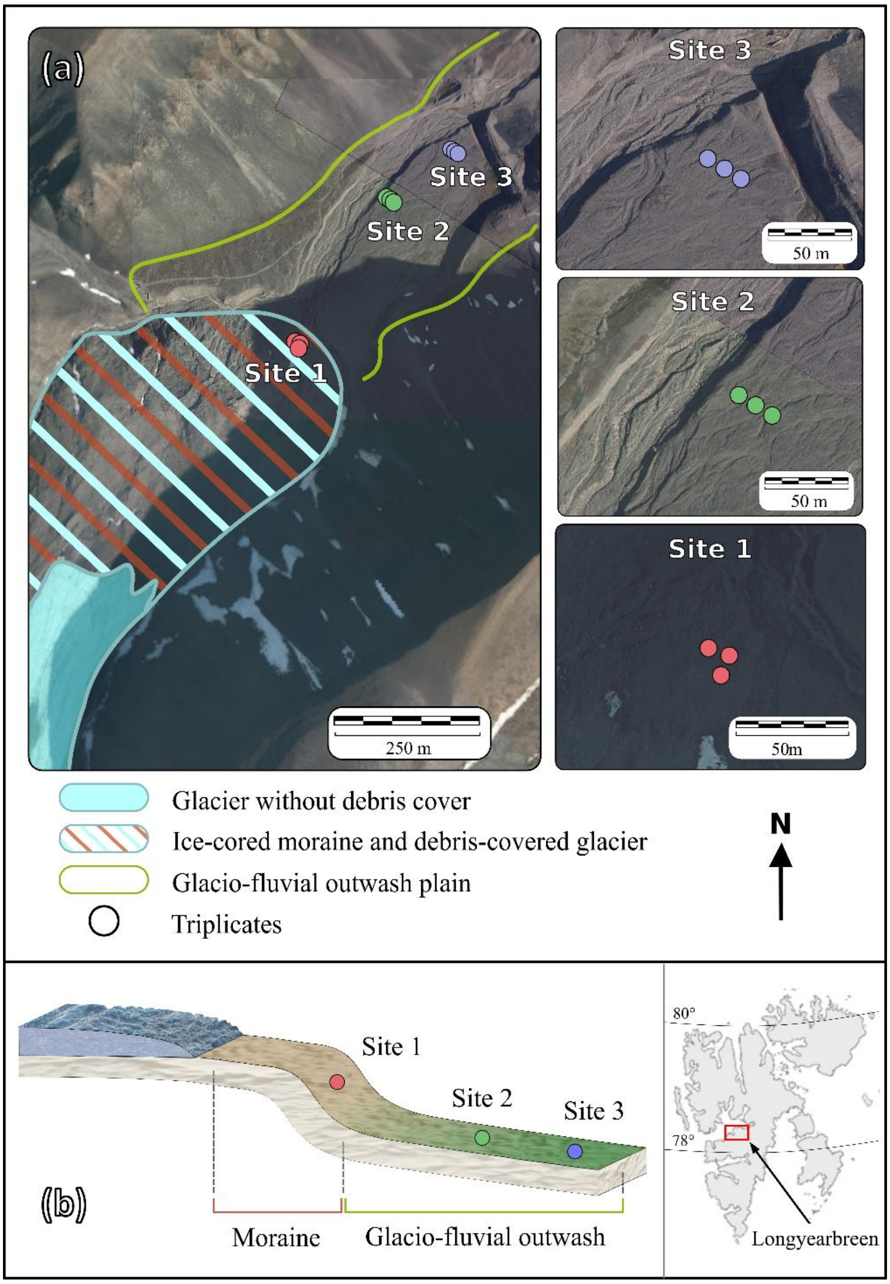


Figure 1: Aerial images, geomorphological setting (A), topographical schematic and location (B) of the proglacial area of Longyearbreen, Svalbard.

2.2.2 Geochemical analyses on liquids

Prior to analyses, samples were thawed and the excess water was separated from the solids through settling and decanting. The pH and conductivity were measured in aliquots of the separated waters using an Orion Star^{TM} pH and conductivity meter, after calibration with NIST standards. The majority of the remaining separated waters were filtered through 0.2 µm polycarbonate filters and particulates on the filters were retained for geochemical analyses of the solids. Aliquots of the separated soil water were filtered through single-use 0.22 µm syringe filters directly into acid-washed 30 ml HDPE Nalgene bottles and into 1.5 ml Dionex vials for nutrients and major ion analyses, respectively. Inorganic nutrient concentrations (PO_4^{3-}, NH_4^+, NO_3^-, NO_2^-) were analyzed using a Gallery Plus Automated Photometric Analyzer (Thermo Fischer Scientific^{TM}), while major ion concentrations (Cl^-, NO_3^-, SO_4^{2-}, PO_4^{3-}, Na^+, NH_4^+, Mg^+, Ca^+, K^+) were analyzed using an ICS-5000 Capillary System (Thermo Fischer Scientific^{TM}).

2.2.3 Geochemical analyses of solids

Upon thawing it became apparent that large proportions of the samples from sites 2 and 3 were vegetation (grasses, mosses). This vegetation was manually separated from the soil as well as possible; weighing before and after revealed that about 13 ± 10% and 5 ± 4% of the sample wet weight in sites 2 and 3, respectively, was vegetation and not soil. This separated vegetation as well as all soil samples were dried at 105 °C for a week. Soils were subsequently size-fractionated by sieving into <2 mm, 2-8 mm, 8-15 mm, 15-50 mm and >50 mm size fractions in order to study the progression of weathering. Note that none of the soil material collected was larger than 100 mm diameter. All soil size fractions, as well as the three-collected host rocks were crushed (<63 μm powder) using a ball mill. Care was taken to avoid particularly carbon cross-contamination between the crushing of samples, and, therefore, in-between each sample, the ball mill was cleaned by milling ashed sand for 10 minutes. Vegetation samples from sites 2 and 3 were also crushed in a separated batch for elemental analyses.

In all separated fractions (including filtered particulates and vegetation samples), total carbon (TC), total organic carbon (TOC), total nitrogen (TN) as well as organic carbon ($\delta^{13}C_{org}$) and nitrogen ($\delta^{15}N$) isotopes were determined using an elemental analyzer (NC2500 Carlo Erba) coupled with an ConFlowIII interface on a DELTAplusXL mass spectrometer (ThermoFischer Scientific). The TOC contents and $\delta^{13}C_{org}$ values were determined on in-situ decalcified samples. Replicate determinations show a standard deviation < 0.2% for TC, TOC and TN and 0.2‰ for $\delta^{13}C_{org}$ and $\delta^{15}N$. The analytical precision was 0.1% for TC, TOC and TN and was 0.2‰ for $\delta^{13}C_{org}$ and $\delta^{15}N$. Replicate determinations show a standard deviation better than 0.2% for C and N and 0.2‰ for $d^{15}N$. The analytical precision was 0.1% for TC, TOC and TN and was 0.2‰ for $\delta^{13}C_{org}$ and $\delta^{15}N$.

The elemental composition of the milled soil fractions was determined through X-ray fluorescence (XRF) analyses of fused glass beads using a PANalytical AXIOS Advanced XRF machine equipped with a rhodium tube. For major elements, we achieved a detection limit of 0,01% and ≤ 10 ppm for minor elements. Further details of the geochemical analyses on solids are found in Supporting Information (Table S3 and S4).

Using the XRF data, we calculated the Chemical Index of Alteration (CIA) to obtain an indicator of weathering progress. Overall, a CIA value of ≤ 50 indicates fresh, un-weathered rocks, whereas CIA values > 50 indicate an increased degree of alteration. The CIA index is primarily applicable for metasediments (thus applicable for the type of rock types in our catchment) and has been widely employed (see review of Bahlburg & Dobrzinski, 2009) since it was first introduced in Nesbitt & Young (1982). Compared to other chemical weathering indices (Meunier and others, 2013), the CIA takes also into account the contributions of potassium and its association with calcium and sodium (Price & Velbel, 2003). The CIA index values were calculated from the molecular proportions of oxides as the ratio of aluminium to the sum of major cations as follows (equation 1):

$$CIA = 100 \times \frac{Al_2O_3}{Al_2O_3 + CaO + Na_2O + K_2O} \qquad (1)$$

Further details on all geochemical analyses of solids are given in Supporting Information.

2.2.4 DNA extraction, PCR amplification and Illumina MiSeq sequencing

Total genomic DNA was extracted from approximately 20 g soil per sample using the Power Soil DNA Isolation Maxikit (Qiagen, Hilden, Germany) according to the manufacturer’s instructions with some modifications: just before loading the extracts on columns, we switched to using the Power Soil DNA Isolation Minikit (Qiagen, Hilden, Germany) in all subsequent steps according to the Minikit protocol to obtain a concentrated DNA eluate. DNA was quantified with PicoGreen (Invitrogen, Carlsbad, CA, USA). The V3-V4 region of the bacterial small-subunit (16S) rRNA and the internal transcribed spacer region 2 (ITS2) of the eukaryotic (fungal and some groups of protists and green algae) ribosomal operon were PCR amplified using primers and conditions previously described in Frey and others (2016) with 5 ng of template DNA. PCRs were run in triplicate and pooled. Bacterial and fungal amplicon pools were sent to the Génome Québec Innovation Center at McGill University (Montréal, Canada) for barcoding using the Fluidigm Access Array technology (Fluidigm) and paired-end sequencing on the Illumina MiSeq v3 platform (Illumina Inc., San Diego, CA, USA). Archaeal 16S rRNA genes were amplified with a nested PCR approach. The first PCR reaction was performed using the primers 20F and 958R (Delong, 1992) with a total of 5 ng template DNA per reaction. The second PCR was performed with the primers Arch349F and Arch806-R (Takai & Horikoshi, 2000) with 3 µL of the first PCR amplicon as template for the second PCR reaction. The PCR products were purified using Agencourt Ampure Xp (Agencourt Bioscience, USA). The pooled amplicons were sent to GATC Biotech (Konstanz, Germany) and sequenced on a Genome Sequencer Illumina platform. (Illumina Inc., San Diego, CA, USA). A detailed description of PCR conditions and sequencing of archaeal amplicons can be found in the supporting information. Raw sequences have been deposited in the European Nucleotide Archive under the accession number PRJEB23649.

2.2.5 Sequence quality control, OTU clustering and taxonomic assignments

Quality filtering, clustering into operational taxonomic units and taxonomic assignment were performed as described previously (Frey and others, 2016). A customized pipeline largely based on UPARSE (Edgar 2013; Edgar and Flyvbjerg 2015) implemented in USEARCH v. 9.2 (Edgar 2010), but with some additional modifications, was used. Briefly, paired-end reads were merged using the USEARCH fastq mergepairs algorithm (Edgar and Flyvbjerg 2015). Substitution errors arising due to phasing events during Illumina sequencing were corrected by applying Bayes Hammer (Nikolenko and others, 2013). PCR primers were removed using Cutadapt (Martin 2011) and reads were quality-filtered using the USEARCH fastq filter function. Subsequently, sequences were dereplicated discarding singletons and clustered into OTUs of 97% identity (Edgar 2013). OTU centroid sequences were checked for the presence of ribosomal signatures with Metaxa2 (Bengtsson-Palme and others, 2015) or ITSx (Bengtsson-Palme and others, 2013). Quality-filtered reads were mapped on the filtered set of centroid sequences and taxonomic classification was conducted querying against customized versions of GREENGENES (De Santis and others, 2006), SILVA (Quast and others, 2013) and UNITE (Nilsson and others, 2015) for bacteria, archaea and fungi, respectively.

2.2.6 Quantitative real-time PCR

In order to obtain an absolute quantification of bacterial and archaeal gene copy numbers, we performed a quantitative PCR using the CFX Connect™ Real-Time PCR Detection System (Bio-Rad Laboratories, Inc., Hercules, USA). Primers (100 µM) Eub341F and Eub534R (Muyzer and others, 1993) were used to amplify bacterial 16S rRNA genes applying KAPA HiFi SYBR Green reagent (KAPA Biosystems). qPCR reactions were run in triplicates. For amplification of the archaeal 16S rRNA, the primers Parch340-F and Arch1000-R were used (Gantner and others, 2011). The specificity of qPCR reactions was verified by melt curve analysis. Genomic standards (Escherichia coli culture for bacteria and Methanosarcina barkeri for archaea) were included in each qPCR run to ensure linearity and expected slope values of the Ct/log curves. PCR efficiency, based on the standard curve, was calculated using the BioRad CFX manager software and varied between 95 and 100%. Bacterial and archaeal 16S rRNA gene copy numbers were calculated per g of sediment (wet weight). A detailed description of qPCR can be found in the supporting information.

2.2.7 Statistical analyses

Arithmetical mean properties and standard deviation of geochemical properties of triplicate samples were calculated for each site and each size fraction. Pearson's linear correlation coefficients were used to examine whether CIA, TC, TOC, $\delta^{13}C_{org}$, TN and $\delta^{15}N$ vary significantly with size fraction. All statistical analyses of the geochemical data were performed using OriginPro 8.5 or Microsoft EXCEL.

For analysis of microbial diversity, indices of alpha-diversity (local diversity; Whittaker 1960), observed richness (Sobs) and Shannon diversity (H), were estimated based on OTU abundance matrices rarefied to the lowest sequence numbers. We assessed differences in alpha-diversity indices as well as bacterial and archaeal gene copy numbers between different sites by performing a one-way analysis of variance (ANOVA) in R v.2.15 (R development Core Team, 2012). Tukey's Honestly Significant Difference (Tukey HSD) post hoc tests were conducted to examine pairwise differences among habitats with the TukeyHSD function (R development Core Team, 2012). Bray–Curtis dissimilarities were calculated based on square-root transformed relative abundances of OTUs. Differences in community structures (beta-diversity) were assessed by conducting a permutational ANOVA (PERMANOVA, number of permutations = 9999) with the function adonis and analysis of similarity (ANOSIM, number of permutations = 9999) implemented in the vegan R package (Oksanen and others, 2012). Principal coordinate analysis (PCoA) ordinations were calculated using the ordinate function implemented in the R package phyloseq (McMurdie and Holmes, 2013). PCoAs on geochemical variables were performed on z-transformed data. All graphs were generated in R with the ggplot2 package (Wickham, 2009) if not specified otherwise. The DistLM procedure (McArdle & Anderson 2001) was performed in Primer6+ (Clarke and Gorley, 2006) to identify geochemical parameters that correlate best with microbial community structures using the adjusted R2 selection criterion with the ‘stepwise’ procedure. Correlation of geochemical variables significantly explaining variance in the microbial data individually and the PCoA ordination scores were subsequently calculated with the envfit function implemented in the R package vegan (Oksanen and others, 2012). Colinearity between geochemical variables was assessed based on a correlation matrix of pairwise Pearson correlations. This matrix was visualized as a heatmap with a dendrogram calculated by hierarchical clustering using the function heatmap.2 implemented in the R package gplots (Team R, 2012; Warnes and others, 2016). We conducted an indicator species analysis to identify OTU-site associations using the multipatt function (number of permutations = 99 999) implemented in the indicspecies R package (De Caceres and others, 2010). Singleton sequences were removed for the analysis. Indicator OTUs with $P<0.05$ were considered significant. Indicator OTUs classified at the genus level were depicted in a taxonomic tree generated in iTOL (Letunic & Bork, 2011) together with the correlation values indicating OTU-site associations. To test the relationship between OTU-site associations and geochemical properties, we also calculated Spearman rank correlation values between the relative abundance of the indicator OTUs and geochemical variables which significantly explained variance in the microbial community structures as determined by the DistLM procedure. To this end, we used the corr.test function implemented in the psych R package (Revelle, 2014). Correlations were depicted as heatmap using the function heatmap.2 implemented in the R package gplots (Team R, 2012, Warnes and others, 2016) together with the taxonomic tree of indicator OTUs.

2.3 Results and Discussion

2.3.1 Geochemical characteristics of liquids

The pH and conductivity were higher in site 1 (moraine) than in sites 2 and 3 (glacio-fluvial outwash) with values of 8.8 and 380 µS.cm^{-1} in samples from site 1 and 7.4 and 86 µS.cm^{-1} in the samples from site 3 (Table 1). The changes in pH and conductivity observed in the present study are likely a consequence of root exudates (e.g., protons and organic acids) released from the vegetation present in samples from sites 2 and 3 and may also be affected by the snow covering the collected soil samples. Overall, no noteworthy variations were measured in aqueous geochemical parameters, except that Na and Cl^- were higher in site 1 than in sites 2 and 3, while K, Mg and Ca and SO_4^{2-} were lower in site 1 than in sites 2 and 3 (Table S2, Supporting Information).

Table 1: Location details, sites description and basic physical and chemical parameters measurements of samples at each site.

Site unit	Major landform unit	GPS location (decimal)	Elevation m.a.p.s.l.	Soil temperature [°C]	Air temperature [°C]	pH *	Conductivity * [µS/cm]
Site 1	Moraine	78.193°N; 15.545°E	227	-1.0	-3.7	8.83	380.5
Site 2	Glacial-fluvial outwash plain	78.195°N; 15.552°E	176	-1.9	-3.9	7.73	153.7
Site 3	Glacial-fluvial outwash plain	78.196°N; 15.557°E	164	-2.1	-4.2	7.40	86.4

* pH and conductivity were measured in an aliquot of the separated waters.

2.3.2 Geochemical and Physical analyses of solids

2.3.2.1 Physical characteristics

Grain size fractionation measurements revealed smaller grain size in the glacio-fluvial outwash than in the moraine (Fig. 2; Table 2). Overall, the <2 mm size fraction was more abundant in the glacio-fluvial outwash (on average 34% for sites 2 and 3) than in the moraine (12% for site 1) whereas >2 mm showed the opposite trend (89% for site 1 and on average 66% for sites 2 and 3). This pattern can likely be explained as the result of physical weathering being more intense in the glacio-fluvial outwash as it undergoes more frequent hydrological disturbances than the moraine.

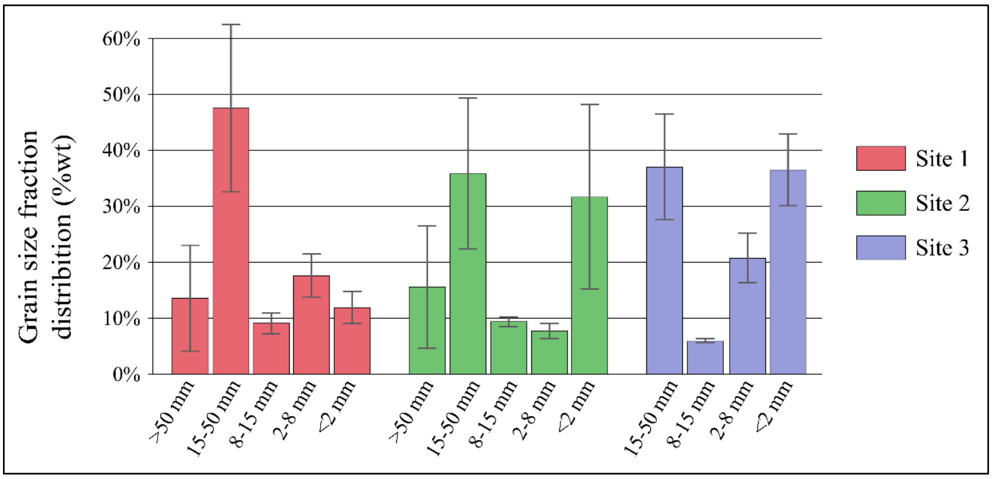


Figure 2: Average grain size distribution per site (mean of triplicate per site). Vertical bars indicate the standard deviation among triplicates.

2.3.2.2 Weathering parameters

The CIA values for the finer fractions (<2 and 2-8 mm) suggest a slightly greater weathering advancement in the glacio-fluvial outwash than in the moraine with CIA values being ~2% lower in site 1 than in sites 2 and 3. Furthermore, the CIA values of the <8 mm and >8 mm size fractions do not display any noticeable difference in site 1 but such differences were clearer in sites 2 and 3. When the data was plotted in a ternary diagram (Fig. 3; Table S3, Supporting Information), the <2 mm and 2-8 mm size fractions showed a clear decreasing relative abundance in Ca and Mg and the relative increase in Na and K. The observed changes in the relative abundance of Ca, Mg, Na and K are typical characteristics indicating feldspar alteration (Price & Velbel, 2003).

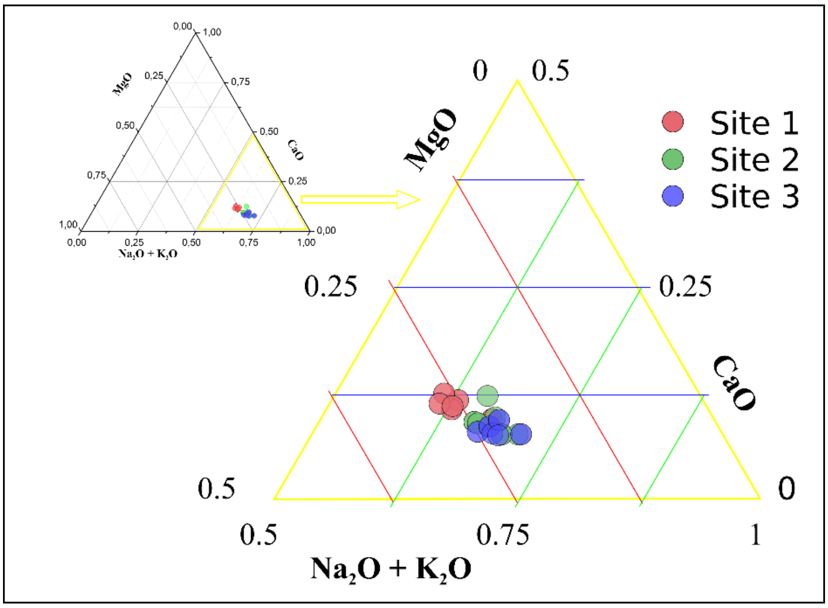


Figure 3: Ternary plot showing the differences in geochemical characteristics of sites 1 to 3 (for simplicity only the values of the <2 mm and 2-8 mm soil fractions are plotted; data set for all other size fractions are available in Table S3, Supporting Information).

The samples from the moraine (site 1) clustered together, and somewhat apart from the samples from the glacio-fluvial outwash (sites 2 and 3). These different patterns are also supported by the aqueous analyses (Table S2, Supporting information). It should however be noted that the comparison between solid and liquid geochemical data is less conclusive due to the variability of both ice content of the soils and snow cover at the sites during collection. In our study, the assertion that weathering is more advanced in the glacio-fluvial outwash than in the moraine is not as straight forward and is in part contradicted by the gradual decrease in CIA for the larger size fractions (15-50 and >50 mm) with CIA values being ~4% lower in site 1 than in sites 2 and 3. Overall, CIA results, therefore, suggest heterogeneous patterns of weathering progression from the moraine to the glacio-fluvial outwash (Table 2). Additionally, the high variability in CIA values between triplicate samples at each site indicates a large degree of compositional heterogeneity (Table 2). Although a weathering progression between soil size fractions is clear, it is possible that mineralogical changes that result from the advancement of weathering from the moraine to the glacio-fluvial outwash might be masked by the inherent heterogeneities on the complex lithologies in the catchment area. Elucidating this variability was however outside of the scope of this study. The 3 host rocks collected as possible representative lithologies at each site (Table 2), had variable CIA values with the host rock sample from the moraine at site 1 being far more weathered (CIA value of 75) than those from the glacio-fluvial outwash at sites 2 and 3 (CIA values of 56 and 65).

This likely indicates that the single rocks collected randomly in the dark under snow cover cannot be considered representative of the lithology at the same sites.

Table 2: Chemical index of alteration (CIA) and carbon and nitrogen data for the various soil size fractions. Values indicate averages and standard deviation on triplicate samples.

		CIA	TC	TOC	δ13Corg	TN	δ15N	Weight of dry size fractions
		-	%	%	‰	%	‰	%
Site 1	Particulates	n.a.	2 ± 0.2	1.8 ± 0.2	-26.2 ± 0	0.11 ± 0.01	3.1 ± 0	
	<2mm	76.9 ± 1.0	1.8 ± 0.1	1.4 ± 0.4	-26.1 ± 0	0.09 ± 0	3.2 ± 0.2	12 ± 6
	2-8mm	75.6 ± 2.3	1.7 ± 0.5	1.4 ± 0.6	-26 ± 0.2	0.09 ± 0.01	3.2 ± 0.2	18 ± 8
	8-15mm	76.9 ± 1.2	1 ± 0.2	0.9 ± 0.2	-26 ± 0.2	0.07 ± 0.01	3.8 ± 0.2	9 ± 4
	15-50 mm	75.6 ± 0.2	0.9 ± 0.3	0.7 ± 0.3	-26 ± 0.2	0.05 ± 0.02	3.2 ± 0.1	48 ± 30
	>50mm	74.3 *	0.3 *	0.1 *	-27.1 *	0.01 *	n.a.	14 ± 19
	host rock	74.9 *	0.3 *	0.1 *	-26 *	0.02 *	n.a.	n.a.
Site 2	Particulates	n.a.	5.4 ± 1.5	5.1 ± 1.5	-26.5 ± 0.2	0.27 ± 0.06	1.6 ± 0.2	
	<2mm	77.9 ± 0.6	4.1 ± 1.3	4.1 ± 1.3	-26.6 ± 0.2	0.17 ± 0.03	2.3 ± 0.4	32 ± 33
	2-8mm	76.0 ± 0.7	4.8 ± 4.9	2.8 ± 2.2	-26.2 ± 0.3	0.17 ± 0.13	1.7 ± 0.5	8 ± 3
	8-15mm	75.1 ± 1.9	0.6 ± 0.1	0.4 ± 0.1	-25.6 ± 0.2	0.03 ± 0.01	2.6 ± 0	9 ± 2
	15-50 mm	73.1 ± 3.1	0.4 ± 0.2	0.4 ± 0.2	-25.7 ± 0.1	0.03 ± 0.01	2.6 ± 0	36 ± 27
	>50mm	66.2	0.3 ± 0	0.3 ± 0	-24.4 ± 0	0.03 ± 0	n.a.	16 ± 22
	host rock	56. 0 *	0.7 *	0.2 *	-24.8 *	0.02 *	n.a.	n.a.
	Plants	n.a.	12.6 ± 1.8	10.6 ± 0.8	-27.4 ± 0.5	0.4 ± 0.03	0.5 ± 1.1	n.a.
Site 3	Particulates	n.a.	3.3 ± 0.7	3.5 ± 1	-26.2 ± 0.1	0.17 ± 0.04	1.9 ± 0.6	
	<2mm	78.0 ± 1.2	3.6 ± 1.7	3.8 ± 1.9	-26.1 ± 0.2	0.15 ± 0.05	2.9 ± 0.4	36 ± 13
	2-8mm	77.0 ± 0.7	1.8 ± 0.4	1.8 ± 0.3	-25.9 ± 0.1	0.08 ± 0.01	1.4 ± 0	21 ± 9
	8-15mm	72.4 ± 2.9	0.4 ± 0.1	0.4 ± 0.1	-25.2 ± 0.1	0.03 ± 0.01	n.a.	6 ± 1
	15-50 mm	71.8 ± 1.8	0.4 ± 0.1	0.3 ± 0.1	-25.2 ± 0.2	0.02 ± 0.01	n.a.	37 ± 19
	>50mm	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	host rock	65.0	0.2 *	0.1 *	-24.8 *	0.01 *	n.a.	n.a.
	Plants	n.a.	17 *	15.3 *	-27.5 *	0.44 *	-0.3 *	n.a.

* The standard deviation was not calculated if less than three samples were collected.
n.a. no data available.

2.3.2.3 Carbon and nitrogen

On average for all sites, our data revealed that TC (R^2 = 98%), TOC (R^2 = 79%) and TN (R^2 = 99%) were negatively correlated with size fractions (Fig. 4; Table 2), whereas $\delta^{13}C_{org}$ (R^2 = 92%) showed a positive correlation with size fraction ($p < 0.05$). Carbon and nitrogen analyses revealed clear differences between the moraine and the glacio-fluvial outwash with TC, TOC and TN being two to three-fold higher in sites 2 and 3 than in site 1 for the particulates, <2 mm and 2-8 mm fractions. For example, the TOC of the <2 mm fraction samples from site 1 (1.4 ± 0.4%) were almost 3 times lower than in samples from site 3 (4.0 ± 1.6%) and little to no variations in carbon or nitrogen values were evident between samples from sites 2 and 3 (Fig. 4 and Table 2). Similar TOC and TN values were reported in the moraine (1.6 and 0.02%, respectively) (Nakatsubo and others, 2005) and glacio-fluvial outwash (2.8 and 0.2%, respectively) (Wojcik and others, 2017) of another glacier in Svalbard (Austre Brøggerbreen). Furthermore, the measured differences in TOC and TN values between the moraine samples and the glacio-fluvial outwash samples in this current study are consistent with estimates reported from various other recently deglaciated areas e.g. Puca glacier, Peru (Nemergut and others, 2007), the Damma glacier, Switzerland (Bernasconi and others, 2011), Dongkemadi glacier, China (Liu and others, 2012), Larsemann Hills glaciers, Antarctica (Bajerski & Wagner, 2013) or Robson glacier, Canada (Hahn and Quideau, 2013). Neither $\delta^{13}C_{org}$ nor $\delta^{15}N$ values varied significantly between sites. Not surprisingly, the vegetation separated from the soils in the samples from sites 2 and 3 had substantially higher TOC and TN values and the $\delta^{13}C_{org}$ and $\delta^{15}N$ values indicated higher plant signatures (-27.4 and -0.1). The slight decrease in $\delta^{13}C_{org}$ with decreasing grain size likely only indicates a shift from C derived from microbes to C derived more from plant organic material. It should be noted that several coal seams from the Lower Tertiary sequence are present in the Longyear catchment (Yde and others, 2008). Besides affecting acidity, the presence of coal and dispersed organic matter in sedimentary and metasedimentary rocks and soils may result in the supply of nitrogen to the biota via the degradation of nitrogen-bearing minerals (Holloway & Dahlgren, 2002; Yde and others, 2008).

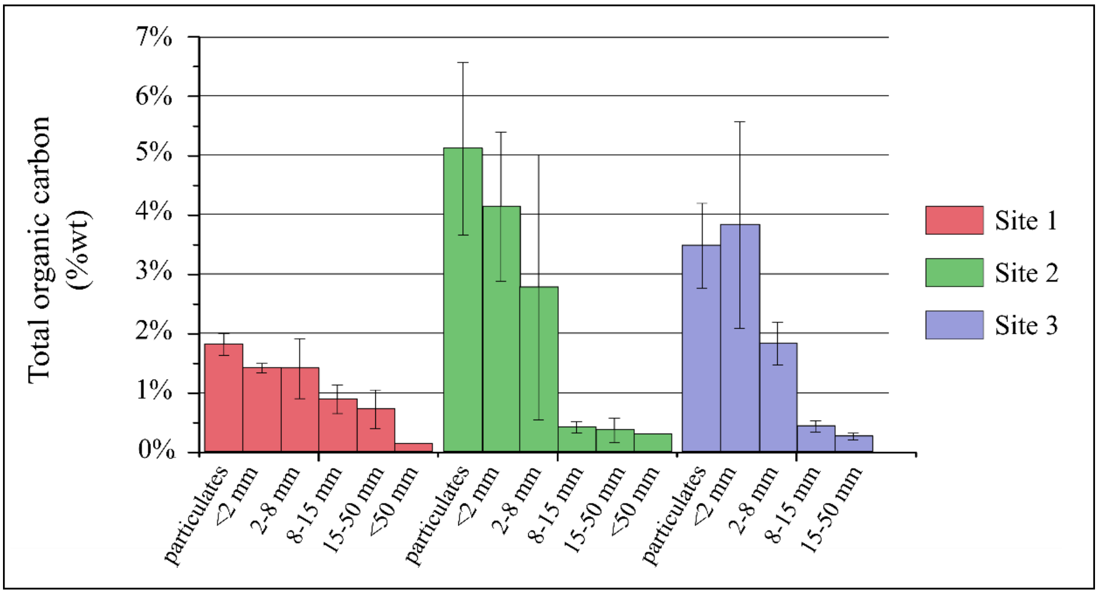


Figure 4: Variation in TOC contents in the different size fractions at the three sites with error bars representing the standard deviations of replicates. Different colours indicate different sites. Similar trends were observed for TC and TN (see Table 2).

Overall, the shift in C and N isotopic ratios, the increase in C and N contents as well as the observed progression of chemical and physical weathering indicate a higher degree of soil ecosystem development in the glacio-fluvial outwash (sites 2 and 3) than in the moraine (site 1).

2.3.3 Microbial Community structures

2.3.3.1 Microbial community compositions

We retrieved 116013 (12890 ± 2238 per sample) bacterial 16S rRNA gene, 322649 (35850 ± 59571) archaeal 16S rRNA gene and 413374 (45930 ± 11782 per sample) fungal ITS2 high-quality sequences, which were clustered into 1638 (850 ± 58 per sample) bacterial, 24 (3 ± 2.6 per sample) archaeal and 1157 (390 ± 123 per sample) fungal OTUs, respectively. Bacterial communities were dominated by Proteobacteria (31.4% of all sequences), followed by Bacteroidetes (27.1%), Verrucomicrobia (11.7%), Acidobacteria (7.7%) while 0.4% of the sequences remained unclassified at the phylum level. Thaumarchaeota constituted the majority of archaeal communities (62.4% of all sequences) followed by Euryarchaeota (31.3%), Bathyarchaeota (3.9%), Woesearchaeota (2.1%) and Lokiarchaeota (0.35%). Fungal communities consisted mainly of Ascomycota (78.3%) followed by Basidiomycota (3.63%), Zygomycota (0.180%) and Chytridiomycota (0.0382%), while 17.9% of the fungal sequences remained unclassified at the phylum level.

2.3.3.2 Microbial gene copy numbers and alpha-diversity

Bacterial 16S rRNA gene copy numbers were highest in samples from site 2 and lowest in samples from site 1 (1.72 x 10^7± 3.62 x 10^6 and 5.17 x 10^4± 8.29 x 10^4 per g soil, respectively) with significant differences ($P < 0.05$) between site 2 versus site 1 and 3 (Table 3). Archaeal gene copy numbers ranged from 1.73 x 10^2 ± 2.83 x 10^2 in site 1 to 2.01 x 10^5 ± 2.62 x 10^5 per g soil in site 2. Archaeal gene copy numbers, followed a similar pattern among sites as bacterial gene copies, however, differences between the sites ($P < 0.05$) were not significant.

Table 3: Bacterial and archaeal 16S rRNA gene copy numbers and bacterial, archaeal and fungal alpha-diversity.

	Bacteria	Archaea	Bacteria		Archaea		Fungi	
	16S rRNA copies / g soil	16S rRNA copies / g soil	S_{obs}	H	S_{obs}	H	S_{obs}	H
Site 1	5.17 x 10^4 ± 8.29 x 10^4 **A**	1.73 x 10^2 ± 2.83 x 10^2	691 ± 12.10	5.42 ± 0.01	8.00 ± 3.46	1.50 ± 0.44	237.33 ± 64.29	2.95 ± 0.26
Site 2	1.72 x 10^7 ± 3.62 x 10^6 **B**	2.01 x 10^5 ± 2.29 x 10^5	755 ± 65.60	5.50 ± 0.24	4.33 ± 3.51	0.93 ± 0.84	369.33 ± 119.08	3.95 ± 0.57
Site 3	4.21 x 10^6 ± 3.56 x 10^6 **A**	1.39 x 10^4 ± 6.75 x 10^3	779 ± 20.07	5.35 ± 0.07	3.33 ± 2.52	0.34 ± 0.30	397.33 ± 60.86	3.97 ± 0.36
p-value	0.00092^{***}	$0.197^{n.s}$	$0.0856^{n.s}$	$0.471^{n.s}$	$0.249^{n.s}$	$0.123^{n.s}$	$0.126^{n.s}$	0.0403^{*}

Values represent means ± standard deviations (n = 3). Different letters indicate significant ($P < 0.05$) differences between individual means. P-values were obtained by one-way analysis of variance (ANOVA) followed by Tukey's HSD post-hoc testing, ∗∗∗$P < 0.001$, ∗∗$P < 0.01$, ∗$P < 0.05$, n.s. = not significant.

Bacterial observed richness (S_{obs}) was higher in the glacio-fluvial outwash sites 2 (755 ± 65.60) and 3 (779 ± 20.07) than in the moraine site 1 (691 ± 12.10) while Shannon diversity (H) was highest in the samples from site 2 (5.50 ± 0.24) and lowest in samples from site 3 (5.35 ± 0.07, Table 3). However, neither S_{obs} nor H indicated significant differences between the sites for bacteria ($P <0.05$). For fungal communities, both S_{obs} and H were higher in sites 2 (237.33 ± 64.29 and 2.95 ± 0.26, respectively) and 3 (397.33 ± 60.86 and 3.97 ± 0.36, respectively) than in site 1 (237.33 ± 64.29 and 2.95 ± 0.26, respectively), but only differences in H were significant. On the contrary, archaeal S_{obs} and H were higher in site 1(8 ± 3.46 and 1.50 ± 0.44, respectively) than in sites 2 (4.33

± 3.51 and 0.93 ± 0.84, respectively) and 3 (3.33 ± 2.52 and 0.34 ± 0.30, respectively), however not significantly.

Collectively, for both gene copy numbers and alpha-diversity indices, a contrasting picture between the outwash plain sites 2 and 3 versus the moraine site 1 is apparent with higher gene copies and higher diversity in the former two. Higher gene copy numbers and diversity indices indicate richer, more complex microbial communities. Taken together with the observed increase in C, N content and the progression of weathering, these patterns point towards alleviation of severe, restrictive environmental conditions such as the paucity of C and nutrients in sites 2 and 3 compared to site 1, creating an increase in available niches. Likewise, several authors found increasing bacterial (Rime and others, 2015, Bajerski and others, 2013; Frey and others, 2013; Kandeler and others, 2006), fungal (Rime and others, 2015) and archaeal (Mateos-Rivera and others, 2016) gene copy numbers with increasing soil development along forefields of receding glaciers. Also, microbial diversity was found to increase with increasing distance from the glacier and thus increasing ecosystem development in other studies (Brown & Jumpponen, 2014; Nemergut and others, 2007; Rime and others, 2015).

2.3.3.3 Microbial beta-diversity

Principal coordinate analyses showed distinct bacterial, fungal and archaeal community structures among the three sites with a high percentage of total variation explained by the first two axes (in total 72.2% for bacteria, 57.1% and fungi and 72.1% for archaea, respectively, Fig. 5A, B, C). Bacterial and fungal communities in samples from the two glacio-fluvial outwash sites 2 and 3 were similar to each other but they both strongly differed from the samples from the moraine site 1. Archaeal communities showed a similar trend, but the separation of site 1 from the other two sites was less pronounced. Interestingly, the bacterial community structures from sites 2 and 3 exhibited a much higher within-site variability compared to samples from site 1, while for fungi and archaea a larger variability was only observed in samples from site 2. Significant differences of microbial community structures between the sites were confirmed by PERMANOVA ($P = 0.0061$, 0.016 and 0.0111 for bacteria, archaea and fungi, respectively) and supported by ANOSIM statistics ($P = 0.0104$, 0.0227 and 0.0069 for bacteria, archaea and fungi, respectively). These results are congruent with other studies that report pronounced changes of microbial community structures from recently deglaciated sites to sites at intermediate distance from the glacier front with the convergence of the community in more distant sites which was associated with increasing vegetation cover stabilizing microbial communities (e.g. Kazemi and others, 2016, Rime and others, 2015, Brown & Jumpponen, 2014). Plant establishment likely also contributes to driving differences of microbial community structures between the vegetated sites 2 and 3 and the unvegetated site 1.

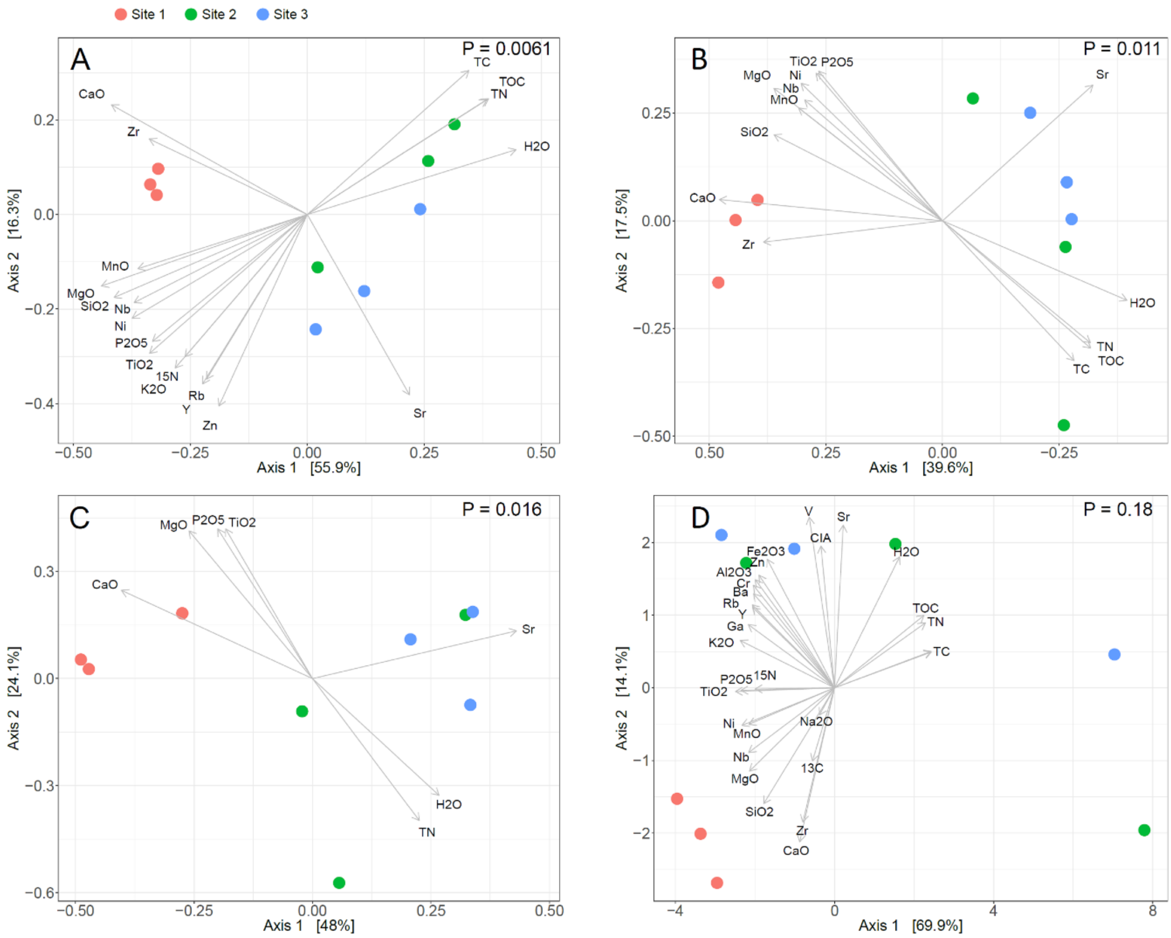


Figure 5: PCoA of geochemical variables at the three sites geochemical parameters with bacterial (A), fungal (B) and archaeal (C) community structures and geochemical parameters alone (D). Ordination of microbial community structures was based on Bray–Curtis dissimilarities. The variance explained by each PCoA axis is given in parentheses. Vectors represent correlations of geochemical parameters with the PCoA ordination scores. P-values indicate significance of the differences between sites based on permutational analysis of variance (PERMANOVA).

Furthermore, for archaea, on the moraine site 1, we detected Lokiarchaeota, Bathyarchaeota and Woesearchaeota, which were not present in any of the samples from sites 2 and 3 (see also Fig. S1, Supporting information). In contrast, site 3 was dominated by Thaumarchaeota with only a few Euryarchaeota sequences (Fig. S1, Supporting information). In the light of geochemical soil properties indicating an increase of soil development in the two glacial outwash sites compared to the moraine sites, this shift from Euryarchaeota to Thaumarchaeota is in line with previous studies

(Zumsteg et al, 2012; Mateos-Rivera., et al, 2016), where Euryarchaeota were found to colonize the bare soil and Thaumarchaeota were suggested to colonize more developed soils. In addition, Thaumarchaeota include members of the Nitrososphaerales, which are able to oxidize ammonia to nitrite and to fix CO_2 (Mateos-Rivera et al 2016; Schleper et al, 2005; Spang et al, 2010), and might thus importantly contribute to the C and N-cycle (Nicol et al, 2008; Spang et al, 2010).

It should be noted that our sampling campaign took place in winter. Seasonality has been shown to exert an impact on microbial communities in arctic and alpine environments (Schmidt & Lipson, 2004; Lazzaro and others, 2012; Schostag and others, 2015). Seasonal variations are associated with low temperature and frozen ground as well as low UV radiations (Lazzaro and others, 2012; Bradley and others, 2014). Moreover, climatic variations and snow cover across different seasons affect C and nutrient fluxes which additionally influence microbial communities (Hodkinson and others, 2003; Schmidt and others, 2008; Lazzaro and others, 2010). Therefore, seasonal effects should be studied more intensively to enhance our understanding of biogeochemical cycles in proglacial ecosystems.

In order to link changes in the overall community structure to certain taxa at the OTU level and to assess, whether these taxa were associated with a certain site or distributed evenly across sites, we performed an indicator species analysis. We found 83 bacterial (5.2% of all OTUs; Fig. 6A) and 30 fungal indicator OTUs (2.6% of all OTUs; Fig. 6B) that were significantly associated with one or several sites ($P<0.05$) and could be classified at the genus level. Archaea displayed very little diversity and hardly classified at genus level, therefore indicator analysis did not reveal meaningful patterns for archaea and was not included. For both bacteria and fungi most OTUs were associated with site 1. The abundance of bacterial and fungal indicator OTUs ranged from 0.004% to 1.37% and 0.0012% to 2.07%, respectively.

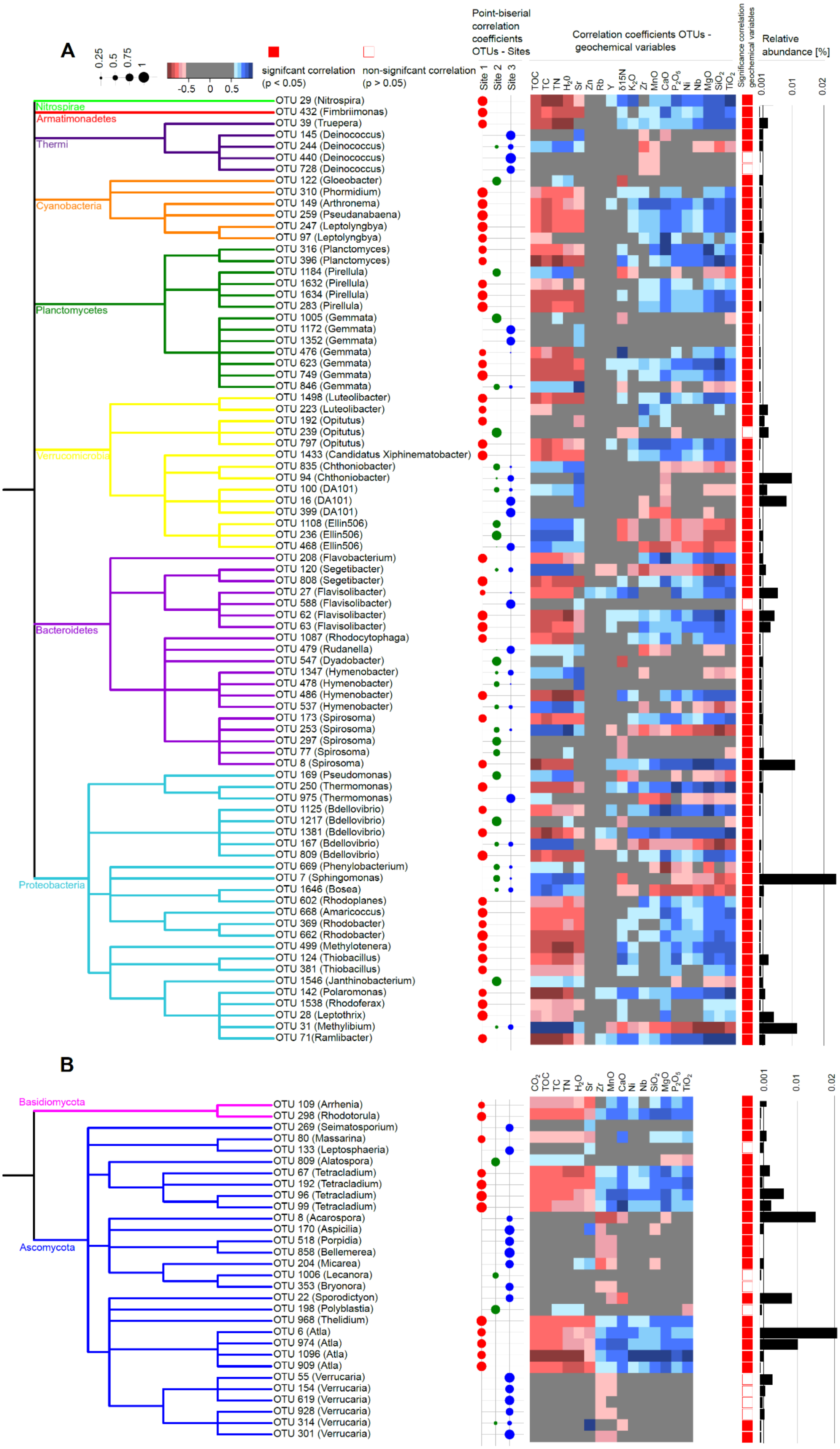

A
0.25
0.5
0.75
1
-0.5
0
0.5
signifcant correlation
(p < 0.05)
non-signifcant correlation
(p > 0.05)
Point-biserial correlation coefficients OTUs - Sites
Site 1
Site 2
Site 3
Correlation coefficients OTUs - geochemical variables
TOC
TC
TN
H_20
Sr
Zn
Rb
Y
δ15N
K_2O
Zr
MnO
CaO
P_2O_5
Ni
Nb
MgO
SiO_2
TiO_2
Significance correlation geochemical variables
Relative abundance [%]
0.001
0.01
0.02
Nitrospirae
Armatimonadetes
Thermi
Cyanobacteria
Planctomycetes
Verrucomicrobia
Bacteroidetes
Proteobacteria
OTU 29 (Nitrospira)
OTU 432 (Fimbriimonas)
OTU 39 (Truepera)
OTU 145 (Deinococcus)
OTU 244 (Deinococcus)
OTU 440 (Deinococcus)
OTU 728 (Deinococcus)
OTU 122 (Gloeobacter)
OTU 310 (Phormidium)
OTU 149 (Arthronema)
OTU 259 (Pseudanabaena)
OTU 247 (Leptolyngbya)
OTU 97 (Leptolyngbya)
OTU 316 (Planctomyces)
OTU 396 (Planctomyces)
OTU 1184 (Pirellula)
OTU 1632 (Pirellula)
OTU 1634 (Pirellula)
OTU 283 (Pirellula)
OTU 1005 (Gemmata)
OTU 1172 (Gemmata)
OTU 1352 (Gemmata)
OTU 476 (Gemmata)
OTU 623 (Gemmata)
OTU 749 (Gemmata)
OTU 846 (Gemmata)
OTU 1498 (Luteolibacter)
OTU 223 (Luteolibacter)
OTU 192 (Opitutus)
OTU 239 (Opitutus)
OTU 797 (Opitutus)
OTU 1433 (Candidatus Xiphinematobacter)
OTU 835 (Chthoniobacter)
OTU 94 (Chthoniobacter)
OTU 100 (DA101)
OTU 16 (DA101)
OTU 399 (DA101)
OTU 1108 (Ellin506)
OTU 236 (Ellin506)
OTU 468 (Ellin506)
OTU 208 (Flavobacterium)
OTU 120 (Segetibacter)
OTU 808 (Segetibacter)
OTU 27 (Flavisolibacter)
OTU 588 (Flavisolibacter)
OTU 62 (Flavisolibacter)
OTU 63 (Flavisolibacter)
OTU 1087 (Rhodocytophaga)
OTU 479 (Rudanella)
OTU 547 (Dyadobacter)
OTU 1347 (Hymenobacter)
OTU 478 (Hymenobacter)
OTU 486 (Hymenobacter)
OTU 537 (Hymenobacter)
OTU 173 (Spirosoma)
OTU 253 (Spirosoma)
OTU 297 (Spirosoma)
OTU 77 (Spirosoma)
OTU 8 (Spirosoma)
OTU 169 (Pseudomonas)
OTU 250 (Thermomonas)
OTU 975 (Thermomonas)
OTU 1125 (Bdellovibrio)
OTU 1217 (Bdellovibrio)
OTU 1381 (Bdellovibrio)
OTU 167 (Bdellovibrio)
OTU 809 (Bdellovibrio)
OTU 669 (Phenylobacterium)
OTU 7 (Sphingomonas)
OTU 1646 (Bosea)
OTU 602 (Rhodoplanes)
OTU 668 (Amaricoccus)
OTU 369 (Rhodobacter)
OTU 662 (Rhodobacter)
OTU 499 (Methylotenera)
OTU 124 (Thiobacillus)
OTU 381 (Thiobacillus)
OTU 1546 (Janthinobacterium)
OTU 142 (Polaromonas)
OTU 1538 (Rhodoferax)
OTU 28 (Leptothrix)
OTU 31 (Methylibium)
OTU 71(Ramlibacter)
B
CO_2
TOC
TC
TN
H_2O
Sr
Zr
MnO
CaO
Ni
Nb
SiO_2
MgO
P_2O_5
TiO_2
0.001
0.01
0.02
Basidiomycota
Ascomycota
OTU 109 (Arrhenia)
OTU 298 (Rhodotorula)
OTU 269 (Seimatosporium)
OTU 80 (Massarina)
OTU 133 (Leptosphaeria)
OTU 809 (Alatospora)
OTU 67 (Tetracladium)
OTU 192 (Tetracladium)
OTU 96 (Tetracladium)
OTU 99 (Tetracladium)
OTU 8 (Acarospora)
OTU 170 (Aspicilia)
OTU 518 (Porpidia)
OTU 858 (Bellemerea)
OTU 204 (Micarea)
OTU 1006 (Lecanora)
OTU 353 (Bryonora)
OTU 22 (Sporodictyon)
OTU 198 (Polyblastia)
OTU 968 (Thelidium)
OTU 6 (Atla)
OTU 974 (Atla)
OTU 1096 (Atla)
OTU 909 (Atla)
OTU 55 (Verrucaria)
OTU 154 (Verrucaria)
OTU 619 (Verrucaria)
OTU 928 (Verrucaria)
OTU 314 (Verrucaria)
OTU 301 (Verrucaria)

Figure 6: Bacterial and fungal indicator species and their correlations with geochemical variables. Bacterial (A) and fungal (B) indicator OTUs that correlated significantly ($P<0.05$ with one or several sites) and could be classified at the genus level are depicted in a taxonomic tree, respectively. The shape plot represents the point-biserial correlation coefficients between OTUs and sites. Geochemical variables significantly ($P<0.05$) explaining variance in the bacterial and fungal community structures as determined by the distLM procedure were correlated with the relative abundance of the indicator OTUs using Spearman rank correlations, represented in a heatmap. Closed and open symbols indicate if these correlations were significant ($P<0.05$) or not, respectively. Bar plots indicate the relative abundance of the OTUs in the whole dataset.

For bacteria, association with a certain site was mostly not consistent throughout taxonomic groups with a few exceptions: For instance, indicators within the genus *Deinococcus* were associated with site 3. Cyanobacterial genera with the exception of *Gloeobacter* were associated with site 1. Cyanobacteria are autotrophic organisms with the ability to fix N_2. They can also withstand strong UV radiation, fluctuating temperature and moisture conditions (Janatkova and others, 2013). Thus, these organisms might contribute to the build-up of the carbon and nitrogen pool in the plant free moraine site. Cyanobacteria such as *Phormidium* or *Leptolyngya* have been isolated previously in Arctic environments such as Svalbard (Matula and others, 2007; Pessi and others, 2018) and have also been found to increase with altitude and thus decreasing stage of soil development in the Himalaya (Janatkova and others, 2013; Capkova and others, 2016). *Phormidium* was also found to be associated with the surface of barren soils at the Damma glacier in the Swiss Alps (Frey et and others, 2013; Rime and others, 2015). Moreover, we found several genera among α- and β-Proteobacteria associated with site 1 which are known for a versatile metabolism involving photoorganoheterotrophy, photolithoautotrophy and chemoheterotrophy under both aerobic and anaerobic conditions, such as *Rhodobacter* and *Rhodoplanes* (Imhoff and others, 1984, Hiraishi & Ueda, 1994, Pujalte and others, 2014). Furthermore, the chemolithotrophic sulfur oxidizer *Thiobacillus* was associated with site 1 and might contribute to mobilizing nutrients from the bedrock by weathering (Garrity and others, 2005, Borin and others, 2010; Dold and others, 2013). Likewise, *Polaromonas*, commonly retrieved from cold environments (Darcy and others, 2011, Hell and others, 2013, Larose and others, 2013) and known to contribute to granite weathering in alpine environments (Frey and others, 2010), was associated with site 1. Conversely, the predominantly plant-associated genera *Pseudomonas*, *Sphingomonas* and *Bosea* were associated with the vegetated sites 2 and 3 (Vorholt and others, 2012, Marcondes de Souza and others, 2012).

For fungi, we found two indicator OTUs within the phylum Basidiomycota which were associated with site 1. On the one hand, we found the yeast-like genus *Rhodotorula,* which is known for a versatile lifestyle, global distribution and has been found previously in cold environments such as glacial ice and barren rocks (Buzzini and others,2017) and permafrost soils (Frey and others, 2016). On the other hand, we found an OTU affiliated with *Arrhenia* which has been recovered previously from cold environments (Ohenoja and others, 2010). Within the phylum Ascomycota we mostly found lichenized fungi which are associated with nutrient-poor environments, moisture and temperature fluctuations and being involved in obtaining nutrients by weathering from the bedrock material (Nash, 2008; Brunner and others, 2011). The genus *Verrucaria* was associated with site 3 and encompasses mostly sub-aquatic representatives such as *V. margacea* to which 3 of our 6 indicator OTUs affiliated with *Verrucaria* belong. Thus, temporarily submerged conditions at the floodplain site 3 might favour the presence of OTUs affiliated with *Verrucaria.* This genus displays a global distribution and is not restricted to cold environments (Galloway, 2008). Members of the class Lecanoromycetes, of which indicator OTUs were also mostly associated with site 3, on the other hand, comprise mostly terrestrial species, although a few sub-aquatic representatives exist and grow predominantly on tree bark and rocks (Gueidan and others, 2015). As for *Verrucaria,* indicator OTUs belonging to Lecanoromycetes mostly include cosmopolitan species although for some genera members have been associated also with e.g. a bipolar distribution (*Bryonora*) or even semiarid environments *(Aspicilia)* (Galloway, 2008). The genus *Atla,* which was consistently associated with site 1, including *A. alpina* to which all the indicator OTUs identified here has been described rather recently (Savic and Tibell, 2008) and has been reported to grow on soil and calcareous rocks in Scandinavia, Spitsbergen and the Alps and thus seems to prefer temperate to cold environments. Moreover, we found OTUs affiliated with the genus *Tetracladium* to be associated with site 1 which was found to be associated with sparsely vegetated soils in the forefield of the Damma glacier by Rime and others (2015).

2.3.4 Relationships between geochemical and microbial variables

A major goal of this study was to quantify the correlation between weathering advancement, C and nutrients contents and microbial community structures. Principal coordinate analysis of the geochemical parameters (Fig. 5D; Fig. S2, Supporting Information) revealed similar clustering of the sites compared to the patterns of microbial community structures (Fig. 5A, B, C). Samples from site 1 formed a distinct group that was well separated from samples from sites 2 and 3, which were more closely related to each other but which also displayed a higher within-site variability. However, the three sites were not significantly distinct based on PERMANOVA. The similarities of patterns between the sites for geochemistry and microbial community structures suggest strong relationships between the two. We also employed DistLM to estimate to what extent geochemical variables correlate with changes in microbial community structures (Table 4; Table S5, Supporting Information). Investigated separately, 21 of 29 geochemical variables significantly (P = 0.05) correlated with the bacterial data, whereas only 15 and 7 variables significantly correlated with the fungal and archaeal data, respectively. For bacteria CaO (48.6% of variance), H_2O (48.4%), MgO (47.9%), SiO_2 (44.4%) and TOC (44.1%) were revealed as the best predictors of community structures. For fungi CaO (37.1%), MgO (31.6%), H_2O (30.4%), Sr (28.2%), and SiO_2 (27.4%) and for archaea CaO (40.2%), Sr (39.9%), MgO (33.3%), P_2O_5 (28.6%) and TN (27.2%) explained most variance, respectively. These results highlight the tight relationship between microbial community structures development and nutrient build-up (increasing TOC and TN abundance) together with the progression of weathering (decreasing CaO, MgO and SiO_2 abundances).

Table 4: Variance of prokaryotic and fungal community structure constrained by geochemical variables.

Bacteria			**Archaea**			**Fungi**		
Variable	P	Variance explained	Variable	P	Variance explained	Variable	P	Variance explained
CaO	0,0026	49%	CaO	0,005∗∗	40%	CaO	0,0015∗∗	37%
H_2O	0,0014∗∗	48%	Sr	0,003∗∗	40%	MgO	0,0013∗∗	32%
MgO	0,0003∗∗∗	48%	MgO	0,010∗	33%	H2O	0,0125∗	30%
SiO_2	0,0053∗∗	44%	P_2O_5	0,022∗	29%	Sr	0,0151∗	28%
TOC	0,0047∗∗	44%	TN	0,039∗	28%	SiO2	0,0144∗	27%
TN	0,0036∗∗	43%	H2O	0,0412∗	28%	TN%	0,013∗	27%
TC	0,0093∗∗	42%	TiO_2	0,0497∗	26%	TOC	0,0151∗	27%
CO_2	0,0111∗	41%	TOC	0,0593 n.s.	26%	Ni	0,0232∗	27%
Ni	0,0092∗∗	41%	V	0,0615 n.s.	26%	TN	0,0203∗	27%

Variance in the microbial data explained by each variable individually was assessed based on the marginal test of the DistLM procedure; P values are obtained from a permutational test implemented in DistLM; ∗∗∗P < 0.001, ∗∗P < 0.01, ∗P < 0.05, n.s. = not significant; The first ten variables explaining most variance in the bacterial, archaeal and fungal data are shown, respectively, the full table can be found in the supporting information material. b.d. below detection limit.

Variables that significantly (P < 0.05) explained variance in the microbial data were subsequently correlated with PCoA ordination scores of the microbial community data. For all three domains, CaO, Sr and Zr were correlated with the differences between site 1 vs. sites 2 and 3, although Zr was not found as a significant predictor of archaeal community structure. All other variables were either correlated with the high within-site variations within sites 2 and 3 or showed no clear pattern. Both DistLM and correlation of the geochemical parameters with the PCoA ordinations scores indicated a high colinearity between geochemical variables. A strong correlation was found between TC, CO_2, TN, TOC, and H_2O (Fig. S3, Supporting Information). This cluster was strongly negatively correlated with SiO_2, MgO, TiO_2, K_2O, Ni, and Nb. Sr, $\delta^{13}C_{org}$, Na_2O, CIA, V, Zr and CaO did not exhibit any strong positive or negative correlation, whereas Fe_2O_3, Rb, Zn, Al_2O_3, Cr, Ba, Ga and Y formed another cluster.

Changes in Ca and Mg could be linked to changes in pH (Chigira and Oyama, 2000), which in other proglacial ecosystems studies has been inferred to be strongly correlated to microbial community structures in previous studies (Zumsteg and others, 2012, Rime and others, 2015). In addition, TOC and TN contents were closely linked with bacterial and fungal communities and to a smaller extent with archaeal community structures. This is consistent with the results of previous studies that revealed that soil C and N contents were tightly associated with the microbial community structure (Zumsteg and others, 2012, Rime and others, 2015) and enzymatic activity in soil (Tscherko and others, 2003). Our results also indicated a strong correlation between soil geochemical elemental composition and microbial community structures. Soil elemental composition has previously been found to exert a major influence on microbial community structures in oligotrophic environments (e.g. Carson and others, 2007) and this relationship was reported in previous studies on recently deglaciated terrains (Bernasconi and others, 2011), highlighting the feedbacks between soil geochemistry and ecosystem development and their interconnectivity with each other. Biological weathering performed by pioneer microorganisms, in particular, has previously been reported to play a central role in the initial build-up of a labile nutrient pool in recently deglaciated terrain (Schmidt and others, 2008; Frey and others, 2010; Schulz and others, 2013). Also, it should be noted that we also found strong correlations among the geochemical variables themselves (Fig S3, Supporting information). With the available data we are not able to further elucidate causal associations between geochemical variables and microbial community structures.

In order to elucidate the relationship of OTU-site associations with geochemical variables, we correlated our indicator species with the set of variables significantly explaining variance in the bacterial and fungal community data, respectively (Fig. 6). For both bacteria and fungi, indicators associated with site 1 were negatively correlated with TOC, TC and TN and positively correlated with most of the mineral oxides, of which CaO, P_2O_5, MgO, SiO_2, TiO_2 displayed the strongest correlations. OTUs associated with sites 2 and 3 consistently showed the reverse trend. Fungal indicator OTUs generally displayed weaker correlations with geochemical variables than bacterial indicator OTUs, especially those associated with site 2 or site 3. Also for bacteria, correlations of indicators associated with site 2 or 3 with geochemical variables were weaker than those of indicators associated with site 1.

The consistent relationship between indicator OTUs for a certain site and geochemical variables suggests that the latter are crucial drivers of OTU-site associations. The positive correlation of site 1 associated indicators with minerals and negative correlation with soil C and N is in agreement with the ecological role of the respective indicators discussed above: For instance, among bacterial indicators associated with site 1, we found versatile autotrophs capable of C- and N-fixation as well as of obtaining nutrients from rocks by weathering such as Cyanobacteria, *Thiobacillus* and *Polaromonas* (Garrity and others, 2005, Frey and others, 2010, Janatkova and others, 2013). Fungal indicators associated with site 1 include for example the highly versatile yeast-like genus *Rhodotorula* (Buzzini and others, 2017). The predominant occurrence of these taxa in the C and nutrient-poor site one in our study confirms that they possess a highly specialized lifestyle allowing them to thrive under oligotrophic conditions allocating carbon and nutrients from external sources. Conversely, in the more developed glacial outwash sites 2 and 3 such specialized oligotrophs are likely outcompeted by organisms that degrade more complex, plant-derived organic matter present in the soil, such as *Sphingomonas* and *Pseudomonas* (Goldfarb and others, 2011). In accordance with this interpretation, Rime and others (2015) found oligotrophic, versatile taxa such as *Geobacter* in a barren soil while taxa able to degrade complex organic compounds were associated with developed soils in the proglacial area of Damma glacier, Switzerland. Here, we corroborate such associations of indicator OTUs with barren, plant-free soils versus more developed, vegetated soils. Also, for the first time, we support an indicator analysis with a comprehensive geochemical characterization thus substantiating the linkage between OTU-site associations with soil C- and N-content as well as elemental composition. Collectively, linking the results of indicator analysis with geochemical soil properties confirms the contrast of both geochemistry and microbial communities in the glacio-fluvial outwash sites 2 and 3 versus site 1 and highlight the importance of TOC, TC and TN versus mineral oxides structuring microbial communities between these contrasting sites.

2.3.5 Comparison of the moraine and the glacio-fluvial outwash

The shift in C and N isotopic ratios, the increase in C and N contents, the observed weathering progression, and microbial abundance, species richness and community composition together point towards a higher degree of soil ecosystem development in the glacio-fluvial outwash (sites 2 and 3) than in the moraine (site 1). In addition, the microbiological and geochemical characteristics of sites 2 and 3 can also be distinguished from those of the samples from site 1 due to their higher within-site variability as is highlighted by our principal coordinate ordinations (Fig. 5). We suggest that the contrasting ecosystem development pattern between site 1 *vs.* sites 2 and 3 can largely be explained by geomorphological differences (Fig. 1). The glacio-fluvial outwash is more heterogeneous and dynamic than the moraine. Hydrological dynamics lead to the formation of dynamic braided drainage pattern in the glacio-fluvial floodplain, which likely explains the larger within-site variability in the two glacio-fluvial outwash sites 2 and 3. All sites, in particular on the glacio-fluvial outwash (sites 2 and 3), have been subjected to deposition of new material, erosion, and they have likely undergone drastic geomorphological and hydrological disturbances since deglaciation. Thus, it is important to note that the age of the soil ecosystem sampled in this study could potentially differ markedly from the age of the terrain since deglaciation. We suggest that the different patterns observed at our sites can be explained as the result of both the geomorphological setting and terrain age since deglaciation. However, our dataset does not allow us to elucidate the relative contribution of these factors.

2.4 Conclusions

In conclusion, our complementary and interdisciplinary dataset allowed us to develop a generic framework for how changes in microbial communities and geochemical variables linked to weathering lead to soil development in a High-Arctic proglacial terrain. Our data overall indicated a more developed and heterogeneous soil ecosystem in the glacio-fluvial outwash plain than in the moraine. Specifically, we found more abundant and diversified microbial community structures, greater C and N contents as well as more advanced physical and chemical weathering (via the depletion of Ca and Mg) in the glacio-fluvial outwash plain than in the moraine. Our dataset highlights the close relationship between C and N, weathering-induced geochemical changes and microbial community structures. Our results suggest functional linkages between geochemical and microbial assemblages but also reveals that such linkages must be investigated with greater care in future studies to deepen our understanding of the habitability of recently deglaciated environments. Finally, we suggest that the effect of variations in geomorphological features on ecosystem development in proglacial environments should be studied in greater depth in the future.

2.5 Supplementary Methods and Material

Carbon and nitrogen content and isotopes measurements

The isotopic composition is given in delta notation relative to a standard: d (‰) = [(R_{sample} – $R_{standard}$)/$R_{standard}$)] x 1000. The ratio (R) and standard for carbon is $^{13}C/^{12}C$ and VPDB (Vienna PeeDee Belemnite) and for nitrogen $^{15}N/^{14}N$ and air. The TOC contents and $d^{13}C_{org}$ values were determined on in-situ decalcified samples. Around 3 mg of sample material was weighted in Ag-capsules, dropped first with 3% and second with 20% HCl, heated for 3 h at 75°C, and finally wrapped into Ag-capsules and measured as described above. The calibration was performed using elemental (Urea) and certified isotope standards (USGS24, CH-7) and proofed with an internal soil reference sample (Boden3, HEKATECH). The reproducibility for replicate analyses is 0.2 % for TOC and 0.2‰ for $d^{13}C_{org}$. For total C, N and $d^{15}N$ determination, around 25 mg of sample material were loaded in tin capsules and burned in the elemental analyzer. TOC and TN were calibrated against Acetanilide whereas for the nitrogen isotopic composition two ammonium sulfate standards (e.g. IAEA N-1 and N-2) were used. The analytical precision was 0.1% for TC, TOC and TN and was 0.2‰ for δ13Corg and $\delta^{15}N$.

X-ray fluorescence measurements

All soil size fractions (excluding particulates) and boulder samples were melted into glass tablet for X-ray fluorescence (XRF) measurements using 1 g of grounded sample, 6 g of di-Lithiumtetraborate (FX-X65-2) and 0.5 g of ammonium nitrate. XRF measurements were performed on a 'PANalytical AXIOS Advanced' equipped with a rhodium tube. The measurements were calibrated using 130 standards made of different material, including basalts, granites and soil sediments (e.g. JSO-1, JSO-2 GXR-2-GXR-5, GXR-5, GXR-6). The detection limit is 0,01 % for major elements (SiO2, TiO2, Al2O3, Fe2O3, MnO, MgO, CaO, Na2O, K2O, P2O5, CO2 and H2O) is ≤ 10 ppm for minor elements (Ba, Cr, Ga, Nb, Ni, Rb, Sr, Y, Zn, Zr).

PCR amplification of archaeal 16S rRNA genes

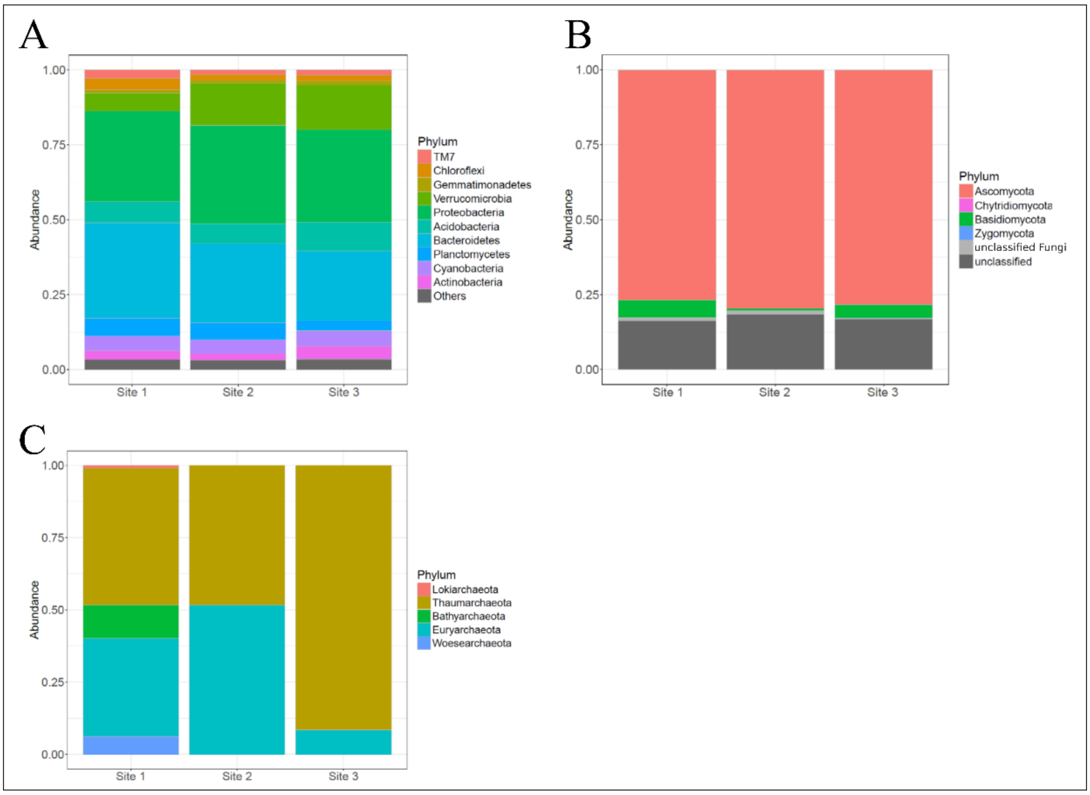
The archaeal 16S rRNA gene was amplified using the primers 20F and 958R (100µM) 0.5µM, dNTP MiX (5mM), 0.2mM, and mgCl$_2$ (25mM) using (0.5mM). The polymerase Optitaq (Roboklon, Germany) in a concentration of 1.25U was used. A template concentration of 5ng and a total of 25 µL reaction volume was used. PCR conditions were as follows: initial denaturation at 95°C for 5 min, followed by 40 cycles of denaturation (95°C for 30 s), annealing (55°C for 30 s) and elongation (72°C for 1 min), and a final extension step of 72°C for 7 min. The second PCR was performed with the primers Arch349R (10 µM) and Arch806-R (10 µM). As a template, 3 µL of

PCR reaction one was used. A total of 50 µL reaction volume was amplified by 95°C for 5 min, followed by 35 cycles of denaturation (95°C for 30 s), annealing (55°C for 30 s) and elongation (72°C for 1 min), and a final extension step of 72°C for 7 min. The PCR amplification was carried out with a T100™ Thermal Cycler (Bio-Rad Laboratories, CA, USA) comprising different combinations of barcodes. The PCR products were purified using Agencourt Ampure Xp (Agencourt Bioscience, USA), using 50 µL PCR product and 180uL magnetic bead solution.

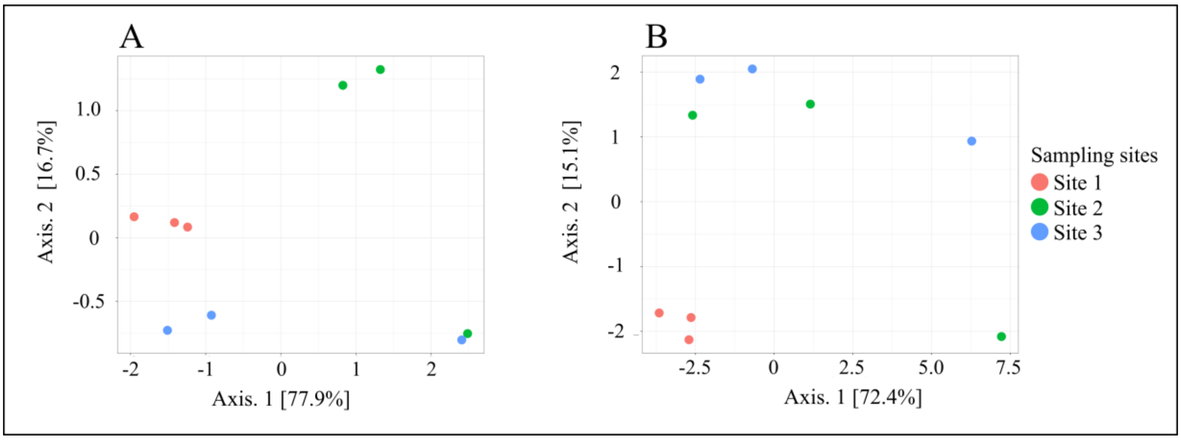
Quantitative real-time PCR

Each reaction (20 µL) contained 2× concentrate of KAPA HiFi SYBR Green (KAPA Biosystems), 100 µM of the forward (0.04 µL), and reverse primer (0.04 µL), sterile water, and 5 µL of DNA template. The environmental DNA samples were diluted 10-fold and run in three technical replicates. The PCR reactions comprised an initial denaturation (3 min at 95°C), followed by 35 cycles of 0.03min at 95°C, 0.20 min an annealing temperature of 60°C, 0.30min at 72°C, and a plate read step at 80°C for 0.03 min, as positive control E.coli was used for Archaea 45 cycles was used and an annealing temperature of 57°C. As a positive control SMA-21, *Methanosarcina solegilidi* was used, furthermore, a bacterial positive control, E.coli, was included to assess potential bacterial 16S rRNA targeting. Melt curve analysis from 65 to 95°C with 0.5°C temperature increment per 0.5 s cycle was conducted at the end of each run to identify nonspecific amplification of DNA. All cycle data were collected using the single threshold Cq determination mode.

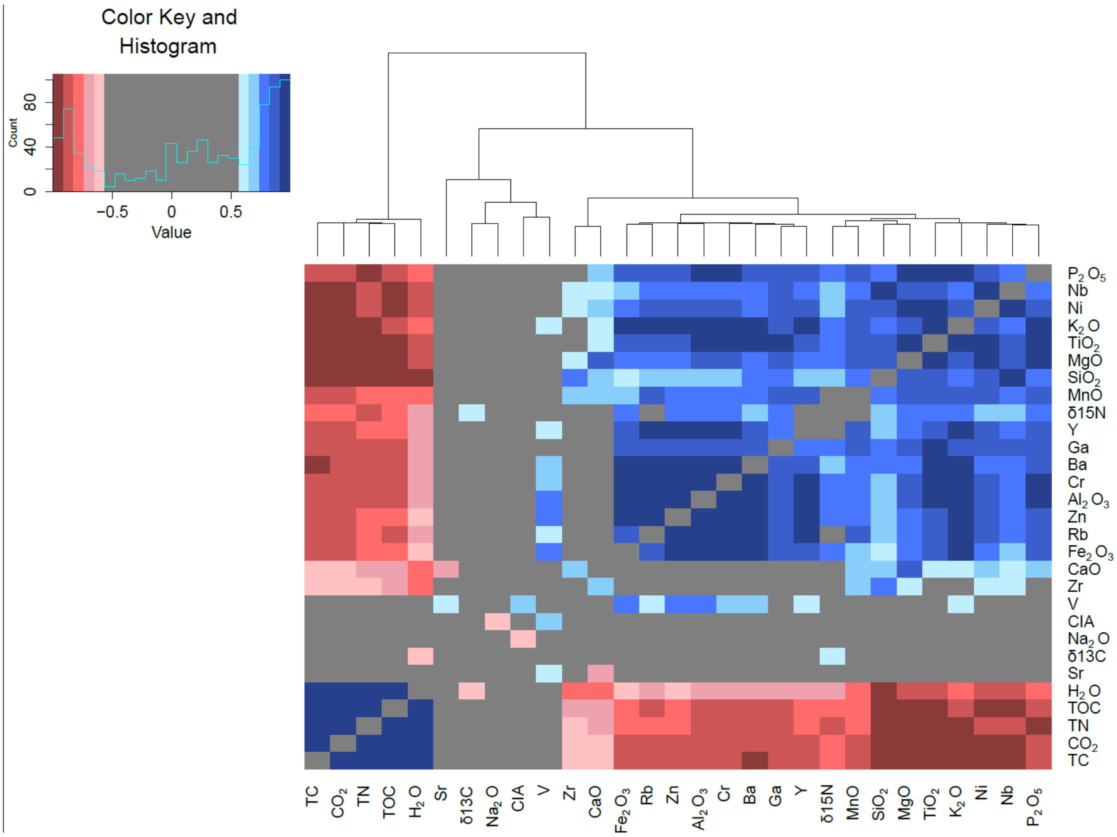
Supplementary Information Figure S1: Bacterial (A), fungal (B) and archaeal (C) relative abundances (mean per site) at the phylum level.



Supplementary Information Figure S2: PCoA on (A) TOC, TN, δ13C, δ15N and (B) major and minor oxides.



Supplementary Information Figure S3: Heatmap showing pairwise Pearson correlations of geochemical variables. Variables are grouped according to the degree of correlation.



Supplementary Information Table S1: Primers for archaea

Sample name	Gene	Forward barcode	Forward primer (including Linker)	Reverse barcode	Reverse primer (including linker)
Site 1.1	16S rRNA Archaea	TACACGTGAT	gYg CAS CAg KCg MgA AW	CGACGTGACT	GGACTACVSGGGTATCTAAT
Site 1.2	16S rRNA Archaea	TACAGATCGT	gYg CAS CAg KCg MgA AW	TACACACACT	GGACTACVSGGGTATCTAAT
Site 1.3	16S rRNA Archaea	TACGCTGTCT	gYg CAS CAg KCg MgA AW	TACACGTGAT	GGACTACVSGGGTATCTAAT
Site 2.1	16S rRNA Archaea	TAGTGTAGAT	gYg CAS CAg KCg MgA AW	TACAGATCGT	GGACTACVSGGGTATCTAAT
Site 2.2	16S rRNA Archaea	TCGATCACGT	gYg CAS CAg KCg MgA AW	TACGCTGTCT	GGACTACVSGGGTATCTAAT
Site 2.3	16S rRNA Archaea	TCTAGCGACT	gYg CAS CAg KCg MgA AW	TAGTGTAGAT	GGACTACVSGGGTATCTAAT
Site 3.1	16S rRNA Archaea	TCTATACTAT	gYg CAS CAg KCg MgA AW	TCTAGCGACT	GGACTACVSGGGTATCTAAT
Site 3.2	16S rRNA Archaea	TGTGAGTAGT	gYg CAS CAg KCg MgA AW	TCTATACTAT	GGACTACVSGGGTATCTAAT
Site 3.3	16S rRNA Archaea	ACGCGATCGA	gYg CAS CAg KCg MgA AW	TGACGTATGT	GGACTACVSGGGTATCTAAT

Supplementary Information Table S2: Major ions in soil water

	Chloride (µmol/L)	Nitrate (µmol/L)	Sulfate (µmol/L)	Sodium (µmol/L)	Ammonium (µmol/L)	Potassium (µmol/L)	Magnesium (µmol/L)	Calcium (µmol/L)
Site 1	13.73	1.13	7.69	14.47	b.d	7.05	44.43	48.83
Site 2	13.09	0.46	3.36	21.17	b.d	1.92	7.11	8.99
Site 3	20.63	b.d	2.64	27.39	5.37	1.17	2.43	3.34

b.d. below detection limit

Supplementary Information Table S3: Descriptive analyses for soil major oxides group (oxides presented as percentage by weight). Values are shown as the average (± standard deviation) of the triplicate soil samples or average of all sites.

		SiO_2 (%)	TiO_2 (%)	Al_2O_3 (%)	Fe_2O_3 (%)	MnO (%)	MgO (%)	CaO (%)	Na_2O (%)	K_2O (%)	P_2O_5 (%)	H_2O (%)	CO_2 (%)
Site 1	<2mm	62.53 ± 0.77	0.71 ± 0.01	13.17 ± 0.31	5.61 ± 0.03	0.06 ± 0	1.41 ± 0	0.6 ± 0.04	0.86 ± 0.16	2.49 ± 0.07	0.2 ± 0.01	5.35 ± 0.16	6.46 ± 0.37
Site 1	2-8mm	61.93 ± 2.66	0.73 ± 0.01	13.53 ± 0.61	5.59 ± 0.47	0.06 ± 0	1.46 ± 0.1	0.64 ± 0.05	1.22 ± 0.6	2.57 ± 0.16	0.21 ± 0.01	5.42 ± 0.49	6.12 ± 1.78
Site 1	8-15mm	66.6 ± 3.3	0.68 ± 0.02	12.97 ± 1	5.23 ± 0.53	0.05 ± 0.01	1.39 ± 0.13	0.55 ± 0.08	0.88 ± 0.15	2.47 ± 0.18	0.19 ± 0.02	4.44 ± 0.56	3.7 ± 0.9
Site 1	15-50 mm	70.77 ± 3.14	0.7 ± 0.08	11.53 ± 0.6	4.47 ± 0.32	0.04 ± 0	1.24 ± 0.05	0.7 ± 0	0.84 ± 0.07	2.19 ± 0.14	0.2 ± 0.05	3.64 ± 0.61	3.28 ± 1.24
Site 1	>50mm	79.3 *	0.49 *	9.3 *	3.07 *	0.04 *	0.92 *	0.63 *	1.02 *	1.57 *	0.09 *	2.27 *	1.02 *
Site 1	host rock	75.9 *	0.64 *	10.9 *	3.79 *	0.06 *	1.09 *	0.79 *	0.86 *	2 *	0.13 *	2.67 *	0.99 *
Site 2	<2mm	55.27 ± 2.55	0.62 ± 0.06	11.9 ± 1.67	5.14 ± 0.86	0.05 ± 0.01	1.08 ± 0.17	0.41 ± 0.04	0.76 ± 0.07	2.19 ± 0.27	0.16 ± 0.03	7.68 ± 0.69	14.29 ± 4.36
Site 2	2-8mm	55.7 ± 11.2	0.57 ± 0.16	11.03 ± 3.29	5.34 ± 1.82	0.07 ± 0.02	0.99 ± 0.28	0.38 ± 0.04	0.96 ± 0.28	2.12 ± 0.66	0.15 ± 0.05	7.42 ± 3.28	14.96 ± 14.44
Site 2	8-15mm	68.27 ± 3.17	0.69 ± 0.05	12.47 ± 0.45	5.16 ± 1.05	0.06 ± 0.03	1.17 ± 0.09	0.57 ± 0.11	1.11 ± 0.18	2.46 ± 0.12	0.16 ± 0.01	3.45 ± 0.33	4.14 ± 3.34
Site 2	15-50 mm	73.9 ± 7.16	0.59 ± 0.12	10.23 ± 2.07	4.03 ± 0.28	0.03 ± 0.01	0.88 ± 0.3	0.37 ± 0.07	1.02 ± 0.12	2.28 ± 0.17	0.13 ± 0.02	2.72 ± 0.83	3.53 ± 3.77
Site 2	>50mm	72.4 *	0.52 *	11 *	5.36 *	0.01 *	0.63 *	0.4 *	2.06 *	3.16 *	0.14 *	2.69 *	1.12 *
Site 2	host rock	76.5 *	0.45 *	8.5 *	3.26 *	0.16 *	0.41 *	2.35 *	1.77 *	2.57 *	0.1 *	1.37 *	2.29 *
Site 3	<2mm	55.73 ± 4.92	0.64 ± 0.06	12.63 ± 1.41	5.49 ± 0.73	0.05 ± 0.01	1.11 ± 0.12	0.39 ± 0.01	0.86 ± 0.04	2.29 ± 0.22	0.17 ± 0.02	7.42 ± 1.21	12.74 ± 6.11
Site 3	2-8mm	63.23 ± 1.19	0.67 ± 0.04	13.23 ± 0.98	6.3 ± 0.13	0.07 ± 0	1.16 ± 0.12	0.41 ± 0.03	1.01 ± 0.09	2.52 ± 0.14	0.19 ± 0.01	5.44 ± 0.45	5.37 ± 0.71
Site 3	8-15mm	69.37 ± 6.19	0.55 ± 0.07	10.67 ± 0.95	4.31 ± 0.5	0.03 ± 0.01	0.82 ± 0.13	0.44 ± 0.1	1.32 ± 0.25	2.28 ± 0.06	0.13 ± 0.02	5.55 ± 3.53	4.27 ± 3.98
Site 3	15-50 mm	75.77 ± 2.25	0.59 ± 0.09	9.97 ± 1.05	4.4 ± 0.46	0.05 ± 0.02	0.87 ± 0.08	0.54 ± 0.09	1.42 ± 0.23	2 ± 0.43	0.14 ± 0.03	2.56 ± 0.12	1.38 ± 0.26
Site 3	>50mm	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Site 3	host rock	74 *	0.44 *	9.8 *	6.69 *	0.03 *	0.61 *	0.46 *	1.81 *	3.01 *	0.17 *	2.07 *	0.56 *

* The standard deviation was not calculated if less than three samples were available. n.a. No data available.

Supplementary Information Table S4: Descriptive analyses for soil minor oxides group (oxides presented as percentage by weight). Values are shown as the average (± standard deviation) of the triplicate soil samples or average of all sites.

		Ba (ppm)	**Cr (ppm)**	**Ga (ppm)**	**Nb (ppm)**	**Ni (ppm)**	**Rb (ppm)**	**Sr (ppm)**	**V (ppm)**	**Y (ppm)**	**Zn (ppm)**	**Zr (ppm)**
Site 1	<2mm	451 ± 13.93	85.33 ± 1.25	17.33 ± 0.94	13.33 ± 0.47	35.67 ± 1.25	102 ± 2.83	99.67 ± 2.62	112.67 ± 0.94	25.33 ± 0.47	79.67 ± 0.47	217.33 ± 8.34
Site 1	2-8mm	485 ± 68.07	85.33 ± 5.79	16.33 ± 0.47	14.67 ± 0.94	34 ± 1.41	102.67 ± 7.32	101.33 ± 2.05	115.33 ± 7.72	24.67 ± 1.25	77.67 ± 3.4	210.33 ± 18.12
Site 1	8-15mm	456.67 ± 17.13	82.33 ± 3.3	16.33 ± 2.05	12 ± 0.82	29.67 ± 1.89	99.67 ± 8.38	95 ± 6.68	117 ± 15.3	25.67 ± 1.25	74 ± 6.38	224.67 ± 67.36
Site 1	15-50 mm	425 ± 21.12	75.67 ± 7.72	15 ± 0.82	13 ± 1.63	31.33 ± 1.7	92 ± 1.41	101.33 ± 10.62	84.33 ± 20.15	26.67 ± 2.36	75.67 ± 13.82	273.67 ± 2.87
Site 1	>50mm	323 *	72 *	11 *	10 *	22 *	65 *	78 *	44 *	16 *	43 *	191 *
Site 1	host rock	409 *	65 *	14 *	11 *	27 *	79 *	84 *	56 *	22 *	52 *	367 *
Site 2	<2mm	415.67 ± 36.94	76.67 ± 10.66	15.67 ± 1.89	12 ± 0.82	30.67 ± 3.68	92 ± 19.65	120.67 ± 10.62	118 ± 27.65	23.33 ± 3.68	72.67 ± 10.34	193.33 ± 23.61
Site 2	2-8mm	420.67 ± 125.02	67.33 ± 17.21	17 ± 1	13 ± 1	27.67 ± 7.72	81.33 ± 28.66	99.67 ± 24.23	97.33 ± 36.38	21.67 ± 4.71	64.33 ± 20.07	187.33 ± 41.33
Site 2	8-15mm	551 ± 9.8	71.67 ± 5.44	16.67 ± 0.94	13 ± 0.82	29.67 ± 1.25	95.67 ± 5.31	104.67 ± 17.25	81 ± 12.08	25.67 ± 1.89	65.67 ± 4.92	324.33 ± 52.82
Site 2	15-50 mm	529 ± 16.08	70.33 ± 8.96	15 ± 3	12.5 ± 1.5	22.33 ± 5.79	83.33 ± 13.6	104.33 ± 9.46	92 ± 23.37	20.67 ± 4.5	58 ± 10.2	344.67 ± 81.18
Site 2	>50mm	801 *	69 *	13 *	14 *	10 *	102 *	205 *	199 *	19 *	36 *	295 *
Site 2	host rock	678 *	63 *	10 *	**	13 *	75 *	442 *	93 *	23 *	40 *	285 *
Site 3	<2mm	437.33 ± 44.9	81.67 ± 10.08	15.67 ± 1.89	11.67 ± 1.25	30.33 ± 3.68	92.67 ± 12.5	123.33 ± 4.19	139 ± 16.67	23.67 ± 2.05	77.67 ± 6.94	171 ± 11.43
Site 3	2-8mm	480.67 ± 11.09	83.67 ± 5.56	17 ± 1.63	11.67 ± 0.47	33 ± 2.94	98 ± 7.26	119.67 ± 5.25	135.33 ± 4.92	24.67 ± 0.94	78 ± 4.24	206 ± 13.59

Site 3	8-15mm	666.33 ± 205.69	64 ± 5.1	13.33 ± 1.25	12.5 ± 1.5	21.67 ± 6.13	89.67 ± 11.81	137 ± 17.38	103.67 ± 20.07	21 ± 3.74	50.33 ± 10.34	285.33 ± 42.32
Site 3	15-50 mm	538.67 ± 214.45	65 ± 8.04	11.67 ± 0.94	12 ± 0	25.33 ± 5.73	73.67 ± 11.79	114 ± 39.3	85.33 ± 25.77	21.67 ± 1.7	56 ± 8.83	283 ± 86.74
Site 3	>50mm	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Site 3	host rock	801 *	73 *	13 *	13 *	14 *	85 *	197 *	197 *	23 *	55 *	318 *

* The standard deviation was not calculated if less than three samples were available. n.a. No data available.

Supplementary Information Table S5: Variance of prokaryotic and fungal community structure constrained by geochemical variables.

Bacteria			**Archaea**			**Fungi**		
Variable	P	Variance explained	Variable	P	Variance explained	Variable	P	Variance explained
CaO	0.0026^{**}	49%	CaO	0.005^{**}	40%	CaO	0.0015^{**}	37%
H_2O	0.0014^{**}	48%	Sr	0.003^{**}	40%	MgO	0.0013^{**}	32%
MgO	0.0003^{***}	48%	MgO	0.010^{*}	33%	H2O	0.0125^{*}	30%
SiO_2	0.0053^{**}	44%	P_2O_5	0.022^{*}	29%	Sr	0.0151^{*}	28%
TOC	0.0047^{**}	44%	TN	0.039^{*}	28%	SiO_2	0.0144^{*}	27%
TN	0.0036^{**}	43%	H2O	0.0412^{*}	28%	TN	0.013^{*}	27%
TC	0.0093^{**}	42%	TiO_2	0.0497^{*}	26%	TOC	0.0151^{*}	27%
CO_2	0.0111^{*}	41%	TOC	$0.0593^{\text{n.s.}}$	26%	Ni	0.0232^{*}	27%
Ni	0.0092^{**}	41%	V	$0.0615^{\text{n.s.}}$	26%	TN	0.0203^{*}	27%
TiO_2	0.005^{**}	40%	Ni	$0.0786^{\text{n.s.}}$	25%	Zr	0.0293^{*}	26%
Nb	0.0091^{**}	38%	SiO_2	$0.066^{\text{n.s.}}$	25%	TiO_2	0.0228^{*}	25%
P_2O_5	0.0063^{**}	37%	TC	$0.0688^{\text{n.s.}}$	24%	MnO	0.0383^{*}	25%
K_2O	0.016^{*}	34%	K_2O	$0.0554^{\text{n.s.}}$	24%	CO_2	0.0179^{*}	25%
MnO	0.0192^{*}	34%	CO_2	$0.0674^{\text{n.s.}}$	24%	Nb	0.0245^{*}	25%
Zr	0.0416^{*}	32%	MnO	$0.0988^{\text{n.s.}}$	23%	P_2O_5	0.03^{*}	25%
Sr	0.0456^{*}	31%	Nb	$0.0859^{\text{n.s.}}$	23%	K_2O	$0.0513^{\text{n.s.}}$	22%
$\delta^{15}N$	0.0444^{*}	30%	Zn	$0.1^{\text{n.s.}}$	22%	Y	$0.0731^{\text{n.s.}}$	21%
Y	0.0378^{*}	30%	$\delta^{15}N$	$0.1197^{\text{n.s.}}$	21%	Rb	$0.1107^{\text{n.s.}}$	19%
Rb	0.0499^{*}	28%	Al_2O_3	$0.1158^{\text{n.s.}}$	21%	Zn	$0.0885^{\text{n.s.}}$	19%
Cr	$0.0578^{\text{n.s.}}$	28%	Cr	$0.1271^{\text{n.s.}}$	21%	Cr	$0.107^{\text{n.s.}}$	19%
Zn	$0.0444^{\text{n.s.}}$	28%	Ga	$0.1332^{\text{n.s.}}$	21%	$\delta^{15}N$	$0.1191^{\text{n.s.}}$	19%
Al_2O_3	$0.0581^{\text{n.s.}}$	27%	Fe_2O_3	$0.1327^{\text{n.s.}}$	20%	Al_2O_3	$0.1034^{\text{n.s.}}$	18%
Ba	$0.0694^{\text{n.s.}}$	26%	Zr	$0.1353^{\text{n.s.}}$	20%	Ga	$0.1322^{\text{n.s.}}$	18%
Ga	$0.0825^{\text{n.s.}}$	26%	Y	$0.1692^{\text{n.s.}}$	19%	V	$0.133^{\text{n.s.}}$	17%
Fe_2O_3	$0.13^{\text{n.s.}}$	21%	Rb	$0.1943^{\text{n.s.}}$	18%	Ba	$0.1914^{\text{n.s.}}$	16%
$\delta^{13}C_{org}$	$0.1427^{\text{n.s.}}$	21%	Ba	$0.1908^{\text{n.s.}}$	18%	Fe_2O_3	$0.1791^{\text{n.s.}}$	16%
V	$0.322^{\text{n.s.}}$	13%	CIA	$0.2746^{\text{n.s.}}$	16%	CIA	$0.3007^{\text{n.s.}}$	14%
CIA	$0.507^{\text{n.s.}}$	10%	Na_2O	$0.6399^{\text{n.s.}}$	9%	$\delta^{13}C_{org}$	$0.3163^{\text{n.s.}}$	14%
Na_2O	$0.6445^{\text{n.s.}}$	9%	$\delta^{13}C_{org}$	$0.6224^{\text{n.s.}}$	9%	Na_2O	$0.8143^{\text{n.s.}}$	9%

Variance in the microbial data explained by each variable individually was assessed based on the marginal test of the DistLM procedure. P values are obtained from a permutational tests implemented in DistLM; ∗∗∗P < 0.001, ∗∗P < 0.01, ∗P < 0.05, n.s. = not significant.

Chapter 3: Time since deglaciation and geomorphological disturbances determine the patterns of geochemical, mineralogical and microbial successions in an Icelandic forefield

This chapter is adapted from:

Wojcik, R., Donhauser, J., Frey, B. and Benning, L.G., 2020. Time since deglaciation and geomorphological disturbances determine the patterns of geochemical, mineralogical and microbial successions in an Icelandic forefield. Geoderma, 379, p.114578.

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Abstract

Glacier forefields are an ideal natural laboratory to study the initial stages of pedogenesis. Here, we document a build-up in organic carbon (C), nitrogen (N) and phosphorous (P), an increase in bacterial communities as well as a progression of physical and chemical weathering along a ~ 2 km long and 122 yr old chronosequence in the glacier forefield of Fláajökull in south-eastern Iceland. We complemented this chronosequence dataset with an assessment of the variability in soils that were affected by geomorphological disturbances along a 175-m long toposequence transect. While soils at the crest of the toposequence moraines were anomalously under-developed due to frequent erosion, the soils at the footslopes were characterized by a more advanced successional stage in that they benefited from an ample supply of nutrients, fine and more weathered materials as well as higher moisture. The large variability in soil properties across the toposequence demonstrates that, even across short distances, disturbances driven by hillslope and glacio-fluvial processes can lead to substantial heterogeneities in soil development in glacier forefields. We emphasize that the geochemical and biological features of soil development and patterns of succession in glacier forefields should be interpreted as the result of both changes in time since deglaciation and geomorphological disturbances.

Chapter 4: Influence of aeolian deposition of phosphorus budgets in the forefield of Vernagt glacier (Austrian Alps).

Abstract

Glacier forefields are an ideal setting to study the earliest stages of succession. Recent studies suggested that glacier forefield may be P-limited. Althoμgh it is commonly considered that weathering of local bedrock is the dominant control of P supply to ecosystems, the contributions from aeolian deposition to the total P budgets and fluxes have so far been little studied. In order to fill this gap, we quantified total aeolian dust and P deposition rates and their seasonal variability over a year using a combination of passive aerosol and soil samples and sampling every two months. The yearly total aeolian dust deposition rate was 2.25 $g.m^{-2}.yr^{-1}$ and this aeolian dust had an average P concentration of 0.98 ± 0.70 $mg.g^{-1}$. The largest part (92%) of the aeolian P supply was delivered by dry aeolian dust deposition, while wet deposition (rain and snow) contributed to the minor part (8%). On average, P in the dry-deposited aeolian dust was composed of 52 ± 10% organic P, 47 ± 10% inorganic P and 1 ± 0% loosely bound P. As much as 85% of the yearly aeolian P deposition occurred between March and September and the P deposition rate was correlated with sunshine duration temperature variations throμghout the year. We estimate that the seasonal variations in aeolian dust deposition rates are primarily controlled by variations in snow cover in the surrounding landscape. This estimate is consistent with HYSPLIT back trajectory models, which show that aeolian material primarily originated from regional (<250 km) sources. Regarding the phosphorus budgets, we estimate that the deposition of aeolian P may contribute to promote the development of glacier forefield ecosystems where (1) these ecosystems are P-limited due to the lack of phosphorous in the local bedrock and their slow weathering rates due to cold and dry conditions and (2) where aeolian delivered P rates are high and the deposited aeolian material is rich in organic phosphorus.

4.1 Introduction

Glaciers in the European Alps are receding at increasing rates since the end of the Little Ice Age (LIA) (Paul et al., 2004). The terrains exposed by the retreat of glacier's ice fronts (glacier forefields) are disturbed by the action of glacial erosion which exposes primary glacigenic deposits that are ideal grounds for soil ecosystem primary successions (Matthews, 1992). Physical and chemical weathering as well as microbiological and finally plant colonization are the processes driving the gradual transformation of recently exposed glacigenic deposits into soils and ecosystems (Bernasconi et al., 2011). In alpine settings, the increasing abundance and diversity of pioneer microbial communities rapidly promotes the establishment of plant communities soon after deglaciation (Schulz et al. 2013). These features of autogenic ecosystem development are commonly studied using a chronosequence approach, where the distance from the current ice front is used as a proxy for terrain-age.

The colonization and development of both microbial and plant communities in such environments is primarily limited by oligotrophic conditions as well as harsh climatic conditions because of large meteorological variations (Bradley et al., 2014). Changes in organic carbon (OC), nitrogen (N) and phosphorus (P) contents in the developing soils usually exert the dominant control on the variability of the developing ecosystem diversity, abundance and composition (Göransson et al., 2011; Schmidt et al., 2016; Castle et al., 2017). Specifically, it is commonly thoμght that ecosystems tend to be primarily N limited in early stages of development and P limited in later stages (Chapin et al., 1994; Wardle et al., 2004; Lambers et al., 2008; Peltzer et al., 2010; Jiang et al., 2019). This long-held paradigm is being challenged by recent studies that have demonstrated that P-limitation is also widespread at the earliest stages of successions in glacier forefields (Zhou et al., 2013; Darcy et al., 2018) a phenomenon that is well documented in various other ecosystems globally (e.g. Elser et al., 2007; Harpole et al., 2011; Bracken et al., 2015). For all living organisms, phosphorous is an essential macronutrient in the synthesis of ATP as energy storage within cells and in the formation of nucleic acids (White et al., 2008). Thus, under P limited conditions, ecosystem development can be dramatically slowed down or hampered in its development.

N limitation at early stage succession is controlled by the supply of bioavailable nitrogen from the fixation of atmospheric nitrogen by cyanobacteria and root-associated microbial groups (Brankatschk et al., 2011; Aμgusto et al., 2017). In contrast, the chemical weathering of local parent material is commonly considered to be the major process controlling the supply of P (Aμgusto et al., 2017) and other critical nutrients such as: Na, K, Mg (e.g. Wojcik et al., 2019; Wojcik et al., 2020). In glacier forefields, the supply of weathering-derived P is slow because weathering generally operates under a kinetic-limited regime due to the usually cold and dry climatic conditions

(Anderson, 2007; Egli et al., 2014). Besides weathering as a prime source of P, increasingly various studies have pointed out that aeolian material deposition may also be a substantial source of P into certain P-limited terrestrial ecosystems (e.g., Okin et al., 2004; Šabacká et al., 2012; Aciego et al., 2017; Herbert et al., 2018; Diaz et al., 2018). Particularly prominent examples of this phenomenon are the strong dependence of Hawaiian (Chadwick et al., 1999) and Amazonian (Swap et al., 1992) forest ecosystems on aeolian-derived P inputs from distant source regions to maintain their productivity. Similarly, other studies have pointed out that the deposition of aeolian material may be a critical source of other nutrients to glacier forefields and other polar ecosystems (Hawes, 2008; Šabacká et al., 2012; Bradley et al., 2015; Rime et al., 2016; Anderson et al., 2017; Diaz et al., 2018).

Despite the growing recognition of the importance of aeolian depositional processes on nutrient budgets and cycling in glacier forefield ecosystems, quantitative estimates of the supply of P derived from aeolian deposition remain scarce. Furthermore, most often alpine or polar studies on glacier forefields are usually carried out in summer during the warm period. The seasonal variability of aeolian-derived P supply and the relative contribution of phosphorous throμgh wet *vs.* dry deposition are largely unexplored. To address these gaps, our major objective here was to quantitatively estimate the total supply and seasonal variability of P inputs derived throμgh aeolian deposition to an Alpine glacier forefield (Vernagt glacier in the Austrian Alps. As well, we aim to examine the features of nutrient build-up, chemical and physical weathering progression along a soil chronosequence in the Vernagt glacier forefield.

4.2 Study Area

The studied area is located within the Ötztal-Stubai massif (Tyrol, Austria) and is part of Vernagt glacier forefield catchment. The sampled area extends from the eastern-most tongue of the glacier 'Taschachtongue' (46.8717°N; 10.8226°E) down to the weather station 'Pegelstation Vernagtbach' (46.8567°N; 10.8287°E) (Fig. 1A). The catchment drained by the station 'Pegelstation Vernagtbach' has an area of 11.44 km² (Reinwarth and Young, 1993) and has an altitudinal range from 2635 m to 3633 m.a.p.s.l.

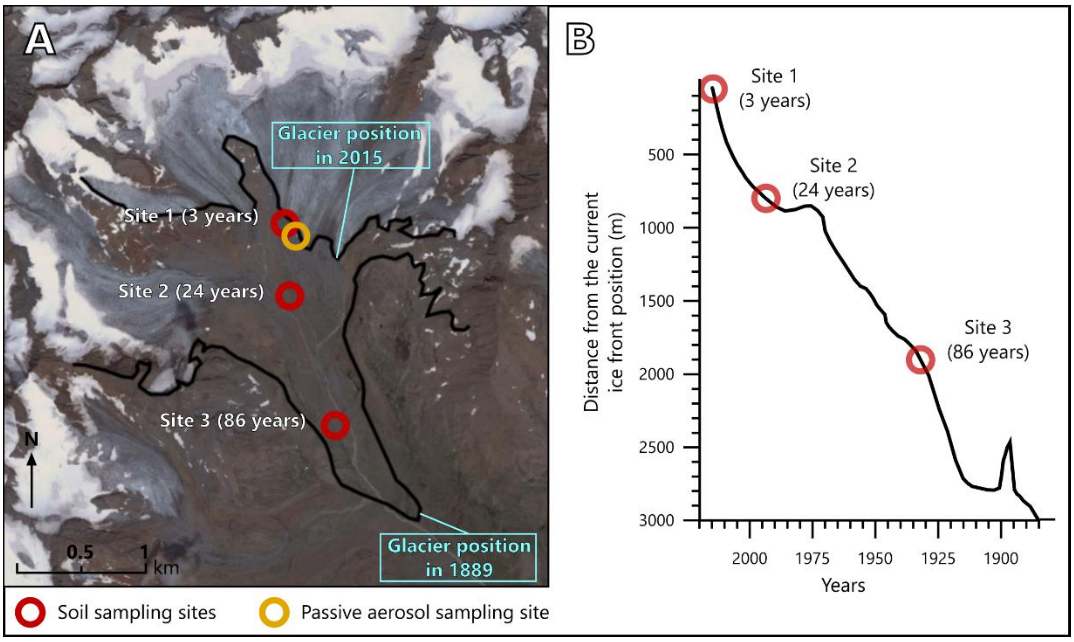

Figure 1: A: Location (red circles) and age since deglaciation of the sampling sites along the chronosequence in the glacier forefield of Vernagt glacier, Austria Alps. Annotated on a Google Earth image (17/10/2017). Site 1 is also the site where the seasonal aeolian samples were collected. B: Historical variation in the position of the ice front of Vernagt glacier.

The ice front of Vernagt glacier is retreating gradually since the end of the Little Ice Age in ca. 1850 (Nicolussi, 2013; Fig. 1B) and has retreated at increasing rates in the last decades (Haeberli et al., 2007). The exception was a short-lived glacier re-advance in 1902 (Jäger and Winkler, 2012). The position of the ice front has retreated by ~ 2.5 km between 1902 (2550 m.a.p.s.l.) and 2018 (‘Taschachtongue’; 2970 m.a.p.s.l.) (Finsterwalder, 1897; Jäger and Winkler, 2012). As of 2018 (year of sample collection), 62% of the catchment area was glacierized while in 1964 still 85% was glaciarized (Braun et al., 2007).

At the weather station ‘Pegelstation Vernagtbach’, the mean annual temperature between 1988 and 2018 was -3.6°C and the mean annual precipitation was 1650 mm. Over the same period, the coldest month was February, with a mean temperature -11.3°C and the warmest month was Aµgust, with a mean temperature of 5.2°C (MeteoBlue data, 2018). Between 2002 and 2012, the yearly average water runoff at the was 0.84 m^3.s^{-1}, which is about four times lower than the mean runoff of July and Aµgust (Escher-Vetter et al., 2014).

The bedrock lithology of the Vernagt glacier forefield is dominated by paragneisses, intersected with quartzites, amphibolites and mica schists (Jäger and Winkler, 2012; Tappeiner et al., 2013). The weathering rates of mica schist-associated mineral phases are typically much greater than the weathering rates of the paragneiss and quartzite-associated minerals.

The area in the Vernagt glacier forefield studied (between Taschachtongue and Pegelstation Vernagtbach) has an average slope angle of 16%, and has prominent lateral moraines with sediment-covered bedrock structures and cone-shaped colluvial cone debris at their base. The lateral moraines have deep gullies and gully-like channels (Jäger and Winkler, 2012). Furthermore, the dominant glaciofluvial landforms are perennial channels as well as several smaller episodic channels whose position vary in response to the retreat of the glacier's ice front.

The recently exposed forefield is unvegetated. After ca. 10 years of exposure lichens (e.g., *Solorina spongiosa*) and mosses (e.g., *Racomitrium canescens subsp. Canescent*) colonize the exposed morainic debris. After ca. 40 years of exposure, plants such as *Saxifraga aizoides* and *Saxifraga oppositifolia* colonized the terrain (Beschel, 1973; Tappeiner et al., 2013).

4.3 Methods

4.3.1 Sample collection

Seven sample collection campaigns were carried out at two-monthly intervals (between 31/10/2017 and 08/11/2018). At each sampling campaign, both soil samples and aerosol samples were collected. At the beginning of the sampling campaign, we deployed a passive aeolian (PA) sampler unit at the site closest to the glacier (Fig. 1, Fig. 2, Table 1) and left it there until the next sampling campaign. Subsequently, at each sampling event, any accumulated aerosol samples were collected and thus each aeolian sample represents the accumulation of aeolian material over a ~2-month period.

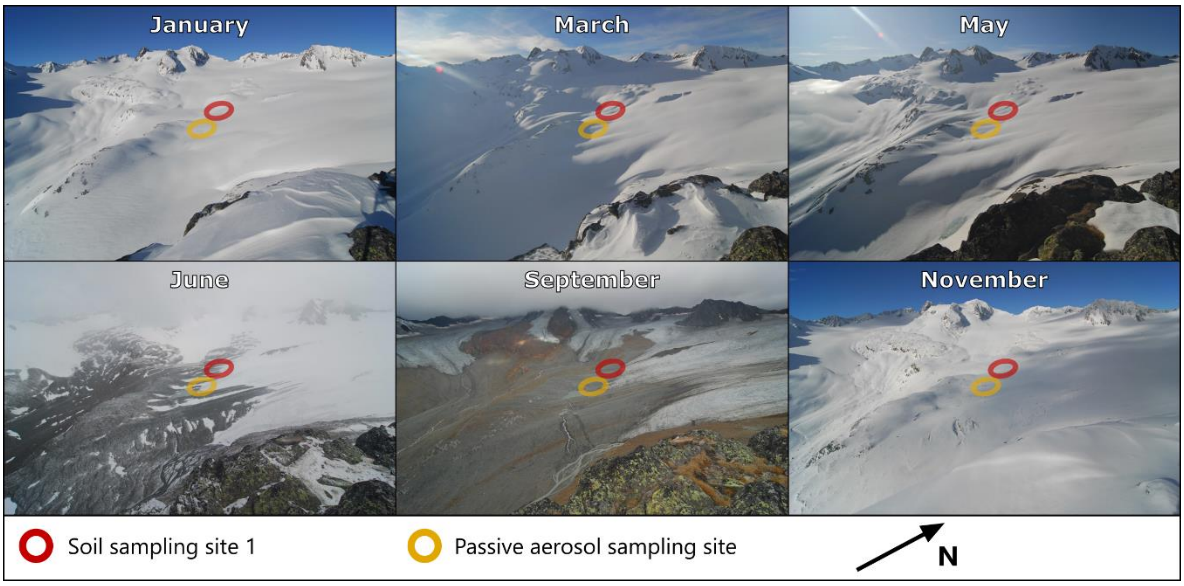

Figure 2: Photographs of the youngest part of the Vernagt glacier forefield at the dates of sampling campaigns in 2018. Photographs by the Bayerische Akademie der Wissenschaften (2018). The photographs were taken from the point with the GPS coordinate [46.8688°N; 10.8312°E].

Soil samples were collected also at each sampling campaign at three different sites (sites 1, 2 and 3, Fig. 1 and Table 1), along a chronosequence that contains soils exposed since 1932 (site 3) and 2015 (site 1). At each site, triplicate soil samples were collected from the top 10 cm and within a 5 m radius of each other. This way we could assess the local spatial variability in the physical and chemical properties of the collected soils. The recession history of Vernagt glacier's ice front (and thus the soil exposure dates) was determined after the data presented in Nicolussi (2013).

A PA sampler (Fig. 3) was deployed near the ice front in order to quantify the total annual input and seasonal variation of aeolian inputs to the forefield of Vernagt glacier (Fig. 1, Fig. 2 and Table 1). The PA sampler was set-up on a flat-lying open area ca. 30 m away from the glacier's ice front and was mounted onto a 1.5 m high tripod to avoid collecting particles saltating off the ground surface. The upper part of the PA sampler consisted of a 32 cm diameter teflon-coated pan. Glass marbles, held by a teflon-coated mesh were placed into the pan to prevent the remobilization of aeolian dust material by winds after their deposition (Lancaster, 2002). The design of our PA sampler was a somewhat modified version of similar samplers deployed elsewhere (e.g., Goossens and Offer, 1994; Reheis and Kihl, 1995; Šabacká et al. 2012; Aciego et al. 2017). However, we also added single-use sterile filtering units (0.2 µm PES, 90mm diameter) underneath the pan to allow the collection/retention of any rain or snow precipitation separately from the aeolian dust collected in the pan. This unit contained a 47 mm filter unit top with a 0.2µm filter. In this contribution, we refer to the solid aeolian samples as ‘PA dust samples’ and to liquid aeolian samples as ‘PA wet samples’.

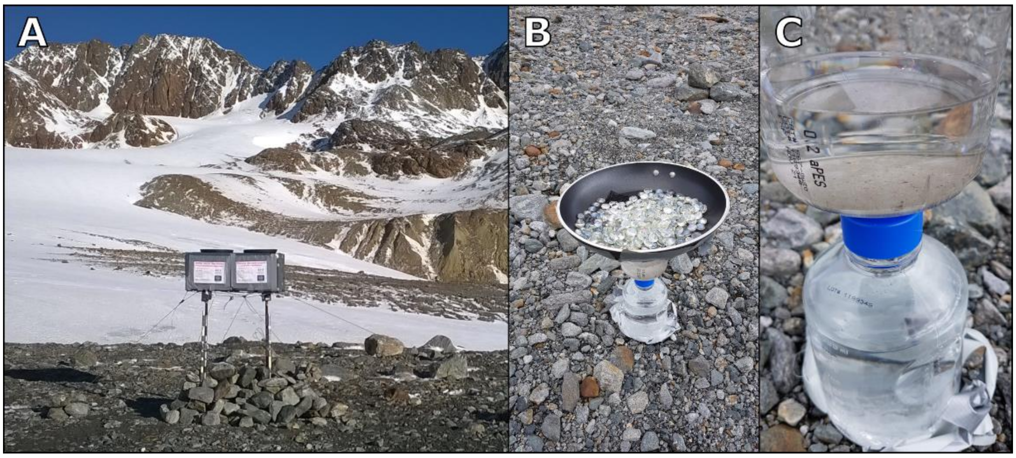

Figure 3: A: Photograph of the tripod holding the two passive aerosol samplers at 1.5 m from the ground. B: Photograph of a single passive aerosol sampler: a pan filled with a teflon-coated mesh and marbles fixed on top of a single-use sterile filtering unit. C: Close view photograph of aeolian dust deposits that have accumulated in a sterile filtering unit

At each sampling campaign, the PA samplers were disassembled and the pan was transferred into a sterile bag, while the wet sampling units were capped with a sterile cap and both returned to the laboratory. Before each deployment, the Teflon-coated pan, the glass marbles and the Teflon mesh were cleaned and sterilized. First, they were rinsed with a 2 M HCl solution, washed with Milli-O water, rinsed with a 3 M HNO_3 solution followed by a final Milli-Q water rinse (following Aciego et al. 2017). The so prepared PA sampler were placed inside large sterile bags for transport to the field site where they were assembled and deployed. After the return of the samples to the laboratory, the aeolian dust collected in the PA sampler (PA dust samples) was retrieved by rinsing and sonicating the pan, mesh, glass marbles and the filter of the disposable filtering unit for 3 times 3 minutes, separated by 1 min break. The aeolian dust collected in the PA samplers was then pooled and filtered throµgh a 0.2 µm polycarbonate filter, which was then dried (35°C for 48h) and weighted. The handling of all PA samples was performed in a sterile laminar flow chamber.

Table 1: Location details and age of each sampling site.

Sites (informal)	GPS coordinates [decimal]	Altitude [m.a.p.s.l]	Age since deglaciation (in 2018) [years]	Year of deglaciation [date]
Site 1	[46.8722°N; 10.8217°E]	2960	3	2015
Site 2	[46.8658°N; 10.8224°E]	2770	24	1994
Site 3	[46.8568°N; 10.8277°E]	2650	86	1932

Soil samples were collected at sites 1, 2 and 3. PA dust and PA wet samples were collected in site 1.

4.3.2 Analytical measurements

All soil samples for geochemical analyses were dried at 55 °C for a week and the visible below and above ground vegetation was manually separated from the soil fractions where there was any. The resulting soils were sieved into <2 mm, 2-8 mm, 8-16 mm and 16-50 mm size fractions and these were crushed (<0.62 µm powder) using a ball mill. The separated plant materials were milled using a mixer mill MM 200 (Retsch).

The total carbon (TC), total organic carbon (TOC) and total nitrogen (TN) contents as well as carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) of the <2 mm size fraction of all soil samples were determined using an elemental analyzer (NC2500 Carlo Erba) coupled with an ConFlowIII interface on a DELTAplusXL mass spectrometer (ThermoFischer Scientific).

Phosphorus sequential extraction analyses were performed on the <2 mm size fraction of soil samples collected in March and September 2018 as well as on the PA dust samples (aeolian dust) and PA wet samples (aeolian wet precipitation). The analyses were performed at the University of Leeds following the steps I, IV and V of the SEDEX procedure presented in Ruttenberg (1992). In step I, the concentration in loosely-sorbed P was determined by performing a reaction with $MgCl_2$ (pH 8). Next, the samples were reacted with a 1M HCl solution to extract the inorganic P (step IV). Finally, the samples were ashed at 550 °C and were reacted with a 1M HCl solution to extract the organic P (step V). We measured the loosely-sorbed P, inorganic P and organic P for the soil samples and the PA dust samples but only the total phosphorus for the PA wet samples.

4.3.3 Aeolian-derived P flux calculations

The total P deposition rate was calculated as the sum of the ‘$\mathrm{dry\ P\ deposition\ rate}$’ and the ‘$\mathrm{wet\ P\ deposition\ rate}$’ (equation 1). In equation 1, ‘$\mathrm{dry\ P\ deposition\ rate}$’ corresponds to the flux of P derived from the deposition of solid aeolian material (dust) that have been collected on the filter of our PA sampler. On the contrary, ‘$\mathrm{wet\ P\ deposition\ rate}$’ corresponds to the flux of P dissolved in wet precipitations (rain and melted snow).

(eq. 1) $$\mathrm{Total\ P\ deposition\ rate} = \mathrm{dry\ P\ deposition\ rate} + \mathrm{wet\ P\ deposition\ rate}$$

The $\mathrm{dry\ P\ deposition\ rate}$ (expressed as $\mathrm{g.m^{-2}.day^{-1}}$) was calculated using equation 2:

(eq. 2) $$d\mathrm{ry\ P\ deposition\ rate} = \frac{\mathrm{M[P]} \times \mathrm{MolarMassP} \times \mathrm{Vsubsample}}{\mathrm{Area} \times \mathrm{nDay}}$$

where ‘$\mathrm{M[P]}$’ is the original P concentration (μmol.L^{-1}),‘$\mathrm{MolarMassP}$’ is the molar mass of P (30,973 g.mol^{-1}), ‘$\mathrm{Vsubsample}$’ is the volume of the subsample used for the P sequential extraction (L) and ‘Area’ is the surface area of the 14 cm radius PA collecting pan (0.615 m^{2}). Finally, ‘nDay’ is the number of days in each sampling period considered. Lawrence and Neff (2009) and Aciego et al. (2017) have performed similar calculations to estimate aeolian derived element flux rates based on both aeolian deposition rates and average chemical composition of aeolian materials.

Complementing the dry P deposition rate, we also calculated the ‘$\mathrm{wet\ P\ deposition\ rate}$’ ($\mu$mol.L^{-1}) using equation 3:

(eq. 3) $$\mathrm{wet\ P\ deposition\ rate} = \frac{\mathrm{M[P]} \times \mathrm{MolarMassP} \times \mathrm{Vprecipitation}}{\mathrm{Area} \times \mathrm{nDay}}$$

where ‘$\mathrm{Vprecipitation}$’ is the total volume of liquid (rain and/or melted snow) collected during the sampling period. All other terms are similar to those of equation 2. Note that the ‘$\mathrm{wet\ P\ deposition\ rate}$’ accounts for the amount of P dissolved in the rain and snow collected in the unit below the PA collecting pan (Fig. 3).

4.3.4 Statistical analyses and aeolian back trajectory estimates

Arithmetical mean properties and standard deviations and Pearson's linear correlation coefficients were calculated to assess linkages between the seasonal variation in aeolian P deposition rate and various meteorological parameters (temperature, precipitations, snowfall, sunshine duration, wind speed, wind direction, cloud cover retrieved from MeteoBlue, 2018). It was considered significant if $p < 0.05$. Student's t-test was used to assess for differences between groups of PA dust samples and soil samples. All statistical analyses were performed using Microsoft Excel. We used the HYSPLIT back trajectory model (Stein et al., 2015) to estimate the source area of the aeolian materials deposited on the Vernagt glacier forefield.

4.4 Results and Discussion

4.4.1 Aeolian dust and aeolian P deposition rates

Over the sampling period, the dust deposition rate was 2.25 g.m^{-2}.yr^{-1}. This derived value is consistent other rates calculated for example by Deangelis and Gaudichet (1991) who reported deposition rates of 2.10 g.m^{-2}.yr^{-1} in the neighboring French Alps as well as many other dust deposition rate estimates across the globe (Lawrence and Neff, 2009). In our study, the PA dust had an average P concentration of 0.98 ± 0.70 mg.g^{-1} (minimum: 0.04 mg.g^{-1}, maximum: 1.98 mg.g^{-1}). Lawrence and Neff (2009) estimated that aeolian deposits have an average P concentration of 1.086 mg.g^{-1} based on numerous studies carried out around the globe. More recently, Aciego et al. (2017) and Zhang et al. (2018) have reported P concentration in aeolian dust ranging from 0.2 to 3 mg.g^{-1} and from 0.6 to 0.8 mg.g^{-1} in the Sierra Nevada and in the Rocky Mountains of Colorado (USA).

Over the entire year studied, the average daily P deposition rate from aeolian dry dust deposition was 7.86 ± 6.15 µg P.m^{-2}.day^{-1} whereas the average P deposition rate from aeolian wet precipitations was 0.67 ± 0.44 µg P.m^{-2}.day^{-1}. The daily P deposition rate (PA dry dust and PA wet dust) was 8.53 ± 6.39 µg P.m^{-2}.day^{-1}. This estimate is consistent with the P deposition rate predicted by Šabacká (2012) for the Taylor Valley, Antarctica (0.3 to 14 µg P.m^{-2}.day^{-1}) but is lower than the estimates of Aciego et al. (2017) in the Sierra Nevada (28.6 µg P.m^{-2}.day^{-1}) or by Tipping et al. (2014) for the European region (90.4 µg P.m^{-2}.day^{-1}).

4.4.1.1 Seasonal variability of deposition rates

The supply of aeolian-derived P is not evenly distributed throughout the year. We find that as much as 70% of the aeolian dust and 85% of the total aeolian-derived P supply occurred between March and September. The daily average aeolian-derived P flux was 13.25 µg P.m^{-2}.day^{-1} for the period March-September and 2.86 µg P.m^{-2}.day^{-1} for the period September-March (Table 4; Fig. 5). Sun et al. (2003) and Morales-Baquero et al. (2006) reported similar seasonal variation patterns in dust and total P deposition rates over the Loess Plateau (China) and the Mediterranean region, respectively, with the highest values in spring and early summer and the lowest rates in the winter season, over the Loess Plateau (China) and the Mediterranean region, respectively.

Table 4: Seasonal variation of P flux from dry and wet aeolian deposition.

Sampling period	Weight PA dust	P concentration in PA dust	Number of days of the sampling period	P deposition rate from PA dust	P deposition rate from PA wet	Total P deposition rate (PA dust and PA wet)
(informal)	[g PA dust.m^{-2}.day^{-1}]	[mg.g^{-1}]	[n days]	[µg P.m^{-2}.day^{-1}]	[µg P.m^{-2}.day^{-1}]	[µg P.m^{-2}.day^{-1}]
Nov 2017 / Jan 2018	0.002	0.15	76	0.26	0.47	0.72
Jan 2018 / Mar 2018	0.002	0.04	53	0.07	0.71	0.78
Mar 2018 / May 2018	0.011	1.39	51	14.58	0.84	15.42
May 2018 / Jul 2018	0.008	1.98	61	15.55	1.56	17.11
Jul 2018 / Sep 2018	0.007	1.39	87	9.13	0.14	9.28
Sep 2018 / Nov 2018	0.012	0.81	37	9.67	0.58	10.25

Results from Pearson's linear correlation revealed that the seasonal variation in aeolian P deposition rate was significantly correlated with sunshine duration (p = 0.01, R2 = 0.85) and had a strong correlation with temperature (p = 0.06, R2 = 0.62) throµghout the year (Table 5). Pearson's linear correlation also showed good correlations between the aeolian P deposition rate and cloud cover (p = 0.17, R2 = 0.41) and wind direction (p = 0.18, R2 = 0.4) but no correlation with wind speed, snow fall and precipitation.

Table 5: Meteorological parameters and statistical summary of correlation tests.

Sampling period (informal)	Average sunshine Duration [min]	Average temperature [°C]	Average cloud Cover [%]	Average wind Direction [Â°]	Average wind Speed [km/h]	Total snowfall [cm]	Total precipitation [mm]
Yearly averages and totals	314.65	-3.52	58.26	224.38	18.38	784.98	1674.00
* Pearson's correlation	p = 0.01 R2 = 0.85	p = 0.06 R2 = 0.62	p = 0.17 R2 = 0.41	p = 0.18 R2 = 0.4	p = 0.45 R2 = 0.15	p = 0.69 R2 = 0.04	p = 0.93 R2 = 0

* Pearson's linear correlation coefficients to assess the correlation between the seasonal variation in the weight of PA dust deposits (Table 4) and various meteorological parameters (MeteoBlue, 2018). Significant correlation if $p < 0.05$.

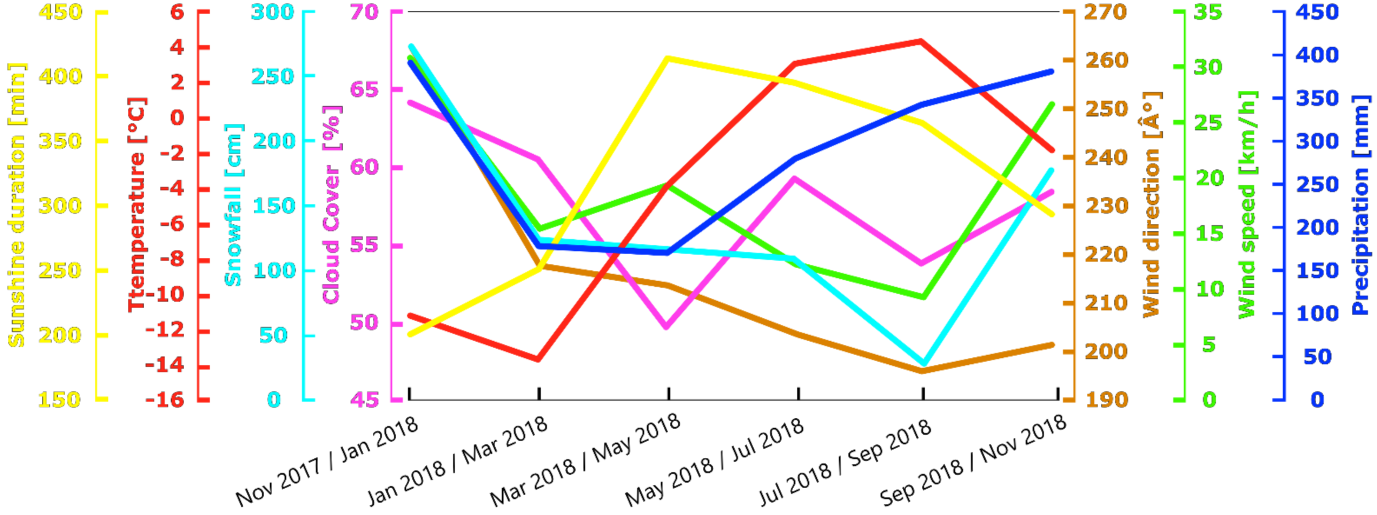

Figure 4: Seasonal variability of meteorological variables at the Pegelstation Vernagtbach weather station, retrieved from MeteoBlue (2018).

4.4.1.2 Dry P and Wet P

Of the total yearly aeolian-derived P flux, 92% occurred via dry deposition (dust) whereas only 8% occurs as wet precipitations (rain and/or snow) (Table 4). Both P fluxes follow the same seasonal pattern with the major part of the P flux being during the summer season (Fig. 5). Morales-Baquero et al. (2006) reported that in the Sierra Nevada (Spain), aeolian P deposition rates were primarily associated with dry rather than wet deposits. Similarly, they reported that dry deposits contributed to two to three times more P than wet deposits on average over a year. Interestingly, they also showed that nitrogen deposition was primarily associated with wet delivery rather than dry dust delivery. In this same location, Ponette-González et al. (2018) and Rodriguez-Navarro et al. (2018) further highlighted that infrequent but intense 'dust in rain' events could contribute a major part of the annual cumulative aeolian budget of key nutrients such as phosphorus.

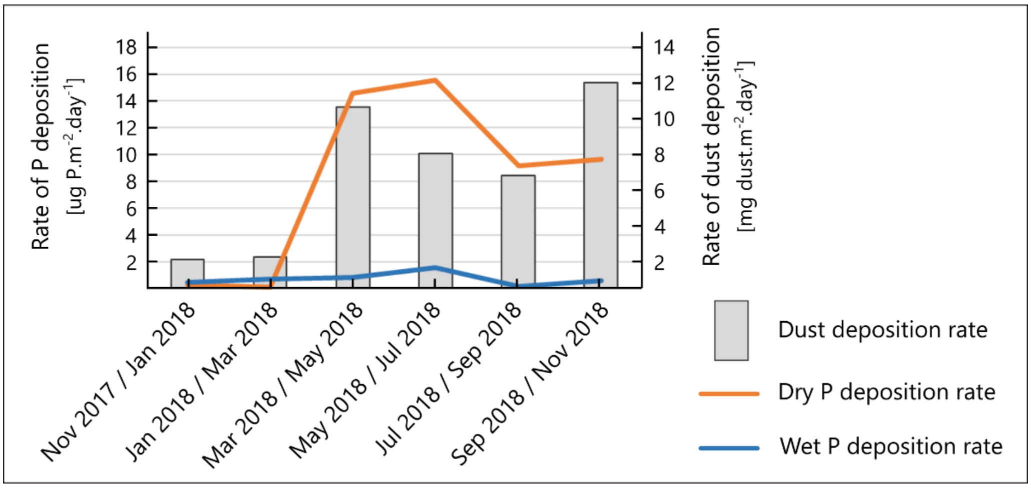

Figure 5: Seasonal variation of P flux from dry and wet aeolian precipitations.

4.4.4.3 P speciation

The speciation of P in the PA dust samples was on average distributed as follows: 52 ± 10% was organic P, 47 ± 10% inorganic P and 1 ± 0% was loosely bound P (Fig. 6). Our data indicates that in the Vernagt catchment, variations in the proportions of each P speciaties deposited in the PA dust samples over the year were not linked to seasonal variations. This is in contrary to the values by Chen et al. (2006) for Taiwan, who reported that aeolian-derived P tends to be more associated with organic particles in the spring and summer seasons.

Our estimates show a relatively high proportion of organic P in comparison with measurements reported in Zhang et al. (2018) for dust samples collected in the Rocky Mountains of Colorado, USA (~80% inorganic P; ~16% organic P; ~4% loosely bound P) and in Chen et al. (2006) based on samples collected in Taiwan (79% inorganic P; 21% organic P). At the global scale, Mahowald et al. (2008) estimated that aeolian delivered P is composed on average of 82% mineral (inorganic) aerosols, 12% biogenic (organic) particles and 5% combustion sources. Our P species distribution differs from this trend in the collected dust samples yet our values in the soils (specifically in sites 1 and 2) showed a distribution closer to the world average.

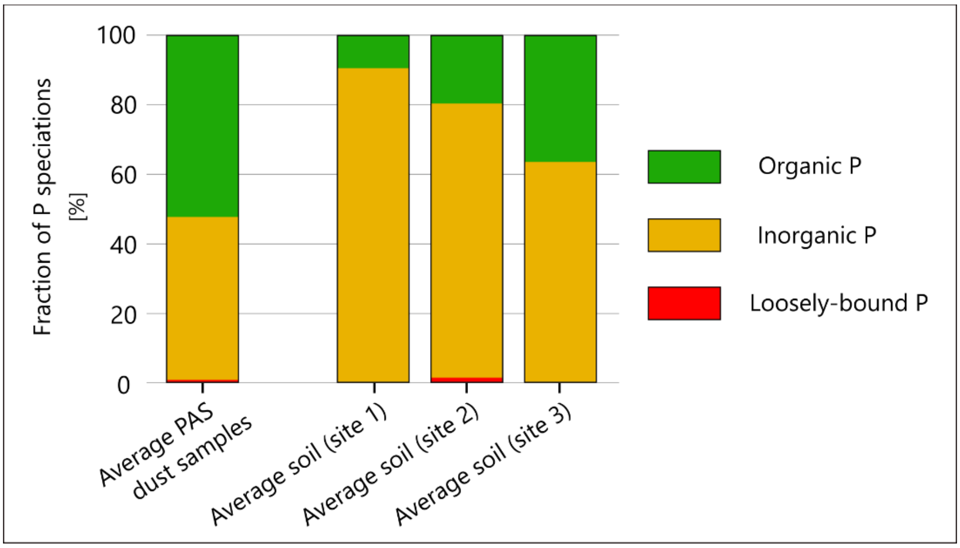

Figure 6: Proportion of organic, inorganic and loosely bound P species among the PA dust samples and the soils samples.

4.4.4.3 P speciation

4.4.2 Origin of aeolian deposits

Pearson's linear correlation tests revealed a strong correlation between the seasonal variability in the dust deposition rates, temperature and sunshine duration. We hypothesize that this correlation points to the fact that the aeolian P deposition rates were largely controlled by snow cover, which determines the exposure of soils in the landscape and thus controls its potential availability for aeolian transport. As a result, we hypothesize that a large part of the aeolian dust present in our traps likely originate from neighboring valleys at a lower altitude. At local scales, Figgis et al. (2018) found that wind speed was a dominant parameter controlling the aeolian dust deposition rate.

We suggest that the relatively high proportion of organic P in our aeolian samples is likely the result of the presence of aeolian biogenic particles such as pollen, spores and microbial cells (see also Graham et al., 2003). Festi et al. (2017) also observed an important presence of pollen in snow samples with a clear increasing abundance of pollen in spring and summer season at a nearby site at the Alto dell'Ortles glacier (South Tyrol, Italy). Another potential cause for the enrichment of aeolian dust in organic matter may be the input of biomass combustion (Barkley et al., 2019; Meng et al., 2020).

The hypothesis that aeolian dust primarily originates from local sources is consistent with the result of the back-trajectory calculation done with the HYSPLIT model (Fig. 7). The HYSPLIT model sµggests that on average, over 90% of the aeolian material comes from less than 250 km away from the sampling site (Austria, eastern Switzerland, northern Italy). Results of the HYSPLIT model show no clear patterns in aeolian material source change as a function of seasons. Based on observations compiled from numerous studies, Lawrence and Neff (2009) sµggested that aeolian deposits that originate from local sources (< 10 km from source) generally consist of 20% clay, 50% silt and 30% sand while deposits that originate from regional sources (10-1000 km from source) generally consist of 25% clay, 60% silt and 15% sand.

The HYSPLIT model also shows that a small fraction of the aeolian material may have been delivered by long-range transport from dust sources such as northern Africa. This information is consistent with the results of previous studies that suggested that much of aeolian material deposit in the Alps originates from the classic dust bowls of the Sahara (Baumann-Stanzer et al., 2018; Greilinger et al., 2018).

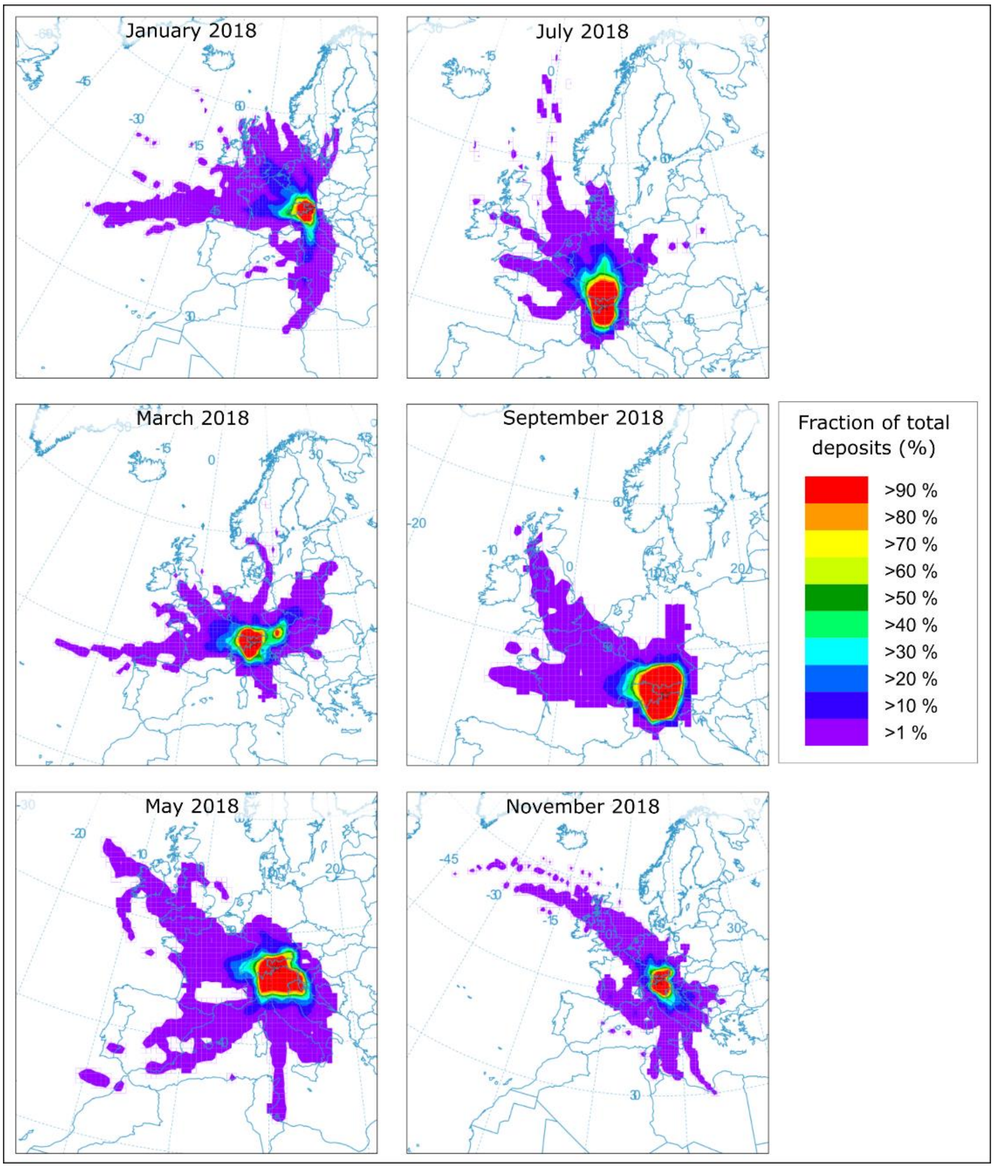

Figure 7: Source areas of aeolian material deposited on the Vernagt glacier forefield. HYSPLIT back trajectory model results for six different periods over a year. Back trajectory locations tracks (different colors) are initiated 30 days prior the date on each panel.

4.4.3 Soil nutrient contents

From site 1 to site 3, soil total carbon (TC) increased from 0.014 ± 0.001 to 0.165 ± 0.157 $mg.g^{-1}$, organic carbon (TOC) increased from 0.013 ± 0.001 to 0.155 ± 0.145 $mg.g^{-1}$ and nitrogen (TN) increased from 0.002 ± 0 to 0.011 ± 0.009 $mg.g^{-1}$ (Table 2). These values are consistent with Wojcik et al. (2020) who reported TC values ranging from 0.7 to 1.5 $mg.g^{-1}$ TOC values ranging from 0.2

to 1.5 mg.g^{-1} and TN values ranging from 0.1 to 0.2 mg.g^{-1} and across a 122 yr old glacier forefield in south-eastern Iceland. The TOC and TN concentration found in our study are also similar to those reported by Bernasconi et al., (2011) and Smittenberg et al. (2012) in the forefield of the Damma glacier in the Swiss Alps. Neither TC, TOC or TN show significant patterns of variation throμghout the year related to seasonal meteorological changes.

Table 2: Total carbon (TC), total organic carbon (TOC) and total nitrogen (TN) concentration for the soil samples.

Sampling period (informal)	TC [mg.g^{-1}]			TOC [mg.g^{-1}]			TN [mg.g^{-1}]		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
NOV17	0.014	0.017	0.075	0.013	0.016	0.071	0.002	0.002	0.005
JAN18	0.014	0.067	0.129	0.014	0.065	0.124	0.002	0.004	0.009
MAR18	0.015	0.109	0.311	0.014	0.104	0.301	0.001	0.006	0.020
MAY18	0.014	0.083	0.087	0.013	0.077	0.083	0.001	0.005	0.005
JUL18	0.013	0.022	0.029	0.013	0.020	0.027	0.002	0.002	0.003
SEP18	0.013	0.023	0.040	0.012	0.021	0.036	0.002	0.002	0.003
NOV18	0.017	0.146	0.483	0.014	0.137	0.442	0.002	0.009	0.029
Average	0.014 ± 0.001	0.067 ± 0.046	0.165 ± 0.157	0.013 ± 0.001	0.063 ± 0.043	0.155 ± 0.145	0.002 ± 0	0.004 ± 0.002	0.011 ± 0.009

Soil total phosphorus concentration (TP) did not change significantly from site 1 (0.70 mg.g^{-1}) to site 3 (0.73 mg.g^{-1})(Table 3). This value is lower than the soil phosphorus content value (~ 1.2 mg.g^{-1}) reported in Wojcik et al. (2020). Interestingly, however, the concentration of organic P increased from 0.07 to 0.27 while the concentration of inorganic P decreased from 0.63 to 0.46 from site 1 to site 3 (Table 3; Fig. 6). This can be explained by the increase of microbial and plant biomass with increasing time since deglaciation. Zhou et al. (2013) similarly estimated that organic P made up ~30% of the total P content in the soils of the Hailuogou Glacier forefield, China.

Table 3: Phosphorus speciations and total phosphorus concentration for the soil samples.

Sampling period (informal)	Loosely bound P [mg.g^{-1}]			Organic P [mg.g^{-1}]			Inorganic P [mg.g^{-1}]			Total P [mg.g^{-1}]		
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
MAR18	0.001 + 0	0.001 + 0	0.002 + 0.001	0.07 + 0.02	0.21 + 0.08	0.28 + 0.05	0.62 + 0.05	0.8 + 0.21	0.55 + 0	0.69 + 0.02	1 + 0.1	0.83 + 0.02
SEP18	0.002 + 0	0.025 + 0.031	0.003 + 0.001	0.07 + 0.01	0.12 + 0.04	0.26 + 0.2	0.64 + 0.01	0.53 + 0.09	0.37 + 0.16	0.71 + 0.01	0.68 + 0.05	0.63 + 0.12
Average	0.001 + 0	0.013 + 0.016	0.003 + 0.001	0.068 + 0.011	0.165 + 0.059	0.267 + 0.126	0.632 + 0.033	0.664 + 0.152	0.461 + 0.083	0.7 + 0.01	0.84 + 0.08	0.73 + 0.07

4.4.4 Implications of aeolian deposition on nutrient budgets glacier forefield ecosystems

The data we collected does not enable us to carry out quantitative estimation of the bedrock weathering-derived P. As a result, we cannot directly quantitatively compare the supply of aeolian-derived P with regards to the supply of bedrock weathering-derived P in the forefield of Vernagt glacier.

The fact that the surface area of primary glacigenic debris exposed far exceeds the surface area of aeolian dust deposits leads us to hypothesize that the yearly total aeolian-derived P flux is negligible in comparison to the weathering-derived P flux. However, the soil P weathering flux is not supply-limited because newly deglaciated primary glacigenic deposits have not been exposed to extensive weathering and therefore are not P-depleted in the Vernagt glacier forefield as well as in most glacier forefields. Instead, soil P weathering flux at most glacier forefield is limited by slow weathering rate kinetics, which are slow due to cold and dry environmental conditions (Anderson, 2007). Our aeolian dust samples had a greater total P concentration (0.98 ± 0.70 $mg.g^{-1}$) than our soil samples at all sites in the Vernagt glacier forefield (0.76 ± 0.05 $mg.g^{-1}$ in average) and at other glacier forefields (e.g. ~2 $\mu g\ P.g^{-1}$ in Nemergut et al., 2007; Sattin et al., 2009).

Addition to considering phosphorus supply in quantitative terms, one should take into account the bioavailability of phosphorus, which is determined by its speciation. Soluble P lost via leaching may either be directly be assimilated by microorganisms and plants and transformed to organic P or it may become absorbed on mineral surfaces to form Fe and Al oxides, or as Ca, Mg, Fe and Al phosphate (Walker and Syers, 1976). Organic P and loosely bound P are the most bioavailable P species, Ca- and Mg-bound P species are less bioavailable and Fe and Al-bound P are the least bioavailable P species (Gu et al., 2019). In our case, organic P made up a greater proportion of total P in our aeolian dust samples (52 ± 10%) in comparison to our soil samples (22 ± 11%). The greater total P concentration and the greater proportion of organic P in our aeolian dust samples compared to our soil samples can be explained by the facts that (1) aeolian dust tends to be composed of fine-grained materials (25% clay, 60% silt and 15% sand; Lawrence and Neff, 2009). These high surface area minerals in the clay fraction promote the adsorption of phosphate, nitrate, ammonium and other nutrients (Okin et al., 2006) and (2) aeolian material may be enriched in nutrients due to inputs of biogenic particles and biomass burning residuals. Previous studies have demonstrated that even the addition of labile sources of P and N triggered a rapid acceleration of microbial community succession rates (Göransson et al., 2011; Knelman et al. 2014).

In view of the data and ideas presented above, we estimate that aeolian-derived P may contribute to the onset and to sustain the development of microbial and plant communities in the forefield of Vernagt glacier. This is in agreement with previous studies that found that aeolian deposition may be an important pathway of nutrient supply (Bradley et al., 2015). This may also aid in microbial colonization (Rime et al. 2016) and arthropod (Hawes, 2008) immigration to in glacier forefields. Note that besides supplying minerals and organic matter from distant sources, aeolian processes can affect the spatial patterns of glacier forefield ecosystem development by re-distributing materials locally, thus creating connectivity among landscape units (Šabacká et al., 2012; Anderson et al., 2017; Diaz et al., 2018).

Based on a compilation of global datasets, Arvin et al. (2017) and Mahowald et al. (2008) challenge traditional views that tend to undermine the role of aeolian processes in P cycling by showing that aeolian-derived P inputs can be a large fraction of the total inputs of P for many ecosystems around the world. The supply of nutrients by aeolian deposits is considered to be an important factor determining the fertility of ecosystems of semi-arid and arid regions in particular (e.g., Reynolds et al., 2001; Reynolds et al., 2006; Ponette-González et al., 2018). Aciego et al. (2017) suggested that aeolian deposition was a more important pathway of P input than weathering of local bedrock to montane ecosystems of the Sierra Nevada (USA). However, this latter estimate was challenged by Uhlig et al. (2017), who suggested that Aciego et al. (2017) underestimated the supply of P derived from local weathering. Augusto et al. (2017) found that bedrock composition was the primary factor explaining global patterns of nutrient limitations to ecosystems, while aeolian P deposition only played a minor role in average. Augusto et al. (2017) however emphasized that the relative importance of aeolian deposition and local weathering was contrasted around the globe and that the aeolian P deposition may be an important parameter controlling P limitation to ecosystems where aeolian material deposition rates are particularly important.

4.5 Conclusions

Recently exposed glacier forefield provide the ideal setting to study the earliest stages of primary succession. Recent studies have suggested the early development of glacier forefield ecosystems may be limited by the availability of P. Bedrock weathering is considered the most important mechanism controlling P availability but the contribution of aeolian material deposition to P budgets in glacier forefield is unclear. In order to investigate the contribution of aeolian dust to P budgets, we monitored the seasonal variability of aeolian dust and P deposition rates. Our result show that the largest part of aeolian P deposition occurs via dust deposition and was mostly composed of organic P. Most aeolian dust deposition occurred during the spring-summer period and originated primarily from regional sources with some input through long-range delivery. We estimated that aeolian deposition may contribute to addressing the typical P-limitation of glacier forefield ecosystems in cases like ours where aeolian material is rich in organic P and when deposition rates are important. This is particularly relevant in settings where bedrock weathering is slow due to cold and dry conditions. We suggest the future work should focus on providing a direct comparative quantitative estimate of the relative contribution of local bedrock weathering and aeolian deposition to P budgets in glacier forefield ecosystems.

Chapter 5: How allogenic environmental factor affect successions in glacier forefields

This chapter is adapted from:

Wojcik, R., Eichel, J., Bradley, J., and Benning, L.G. How allogenic environmental factor affect successions in glacier forefields. Under revision in Progress in Physical Geography.

Abstract

In glacier forefields, the chronosequence approach is used to investigate ecological, biogeochemical and physical features of autogenic successional change as a function of time. Chronosequences rely on the central assumptions that all sites were subjected to the same initial environmental conditions and have undergone the same sequence of change, and thus sites only differ by their age. In many cases, these two assumptions can be challenged by the fact that allogenic factors (initial environmental conditions and geomorphological disturbances) may affect the rates and/or trajectories of successions in a spatially and temporally heterogeneous manner. Here, we review the patterns of glacier forefield successions and emphasize that they should be interpreted as the result of (1) time since deglaciation and associated autogenic changes, (2) initial site conditions (inactive allogenic factors) and (3) geomorphological disturbances (active allogenic factors). To encourage future studies to adopt such a holistic view of successions, we review the diverse ways in which initial local conditions (climate, substrate properties and resources availability) and geomorphological (hillslope, glacio-fluvial, periglacial and aeolian) disturbances may affect the evolution of glacier forefield ecosystems. Further, we present a conceptual model for glacier forefield ecosystem development whereby stochastic and allogenic factors are important in early successional stages but gradually decline thereafter, while the relative importance of autogenic processes increases over the course of successions. Lastly, we summarize how biota may provide biogeomorphological feedbacks to the major types of geomorphological disturbances taking place in glacier forefields.

5.1 Introduction

5.1.1 Succession and chronosequence

A succession is the combined set of changes in species composition and ecosystem structure and their physical environment occurring over time, following an initial disturbance (Matthews, 1992; Walker et al., 2010). A disturbance is a temporary change in environmental conditions that is relatively discrete in time and space that causes abrupt alterations in the density, biomass and spatial distribution of biota and/or that affects the availability of resources or physical substrate (Walker and Willig, 1999; Chapin et al., 2011; Walker et al., 2010). Two different types of successions can be distinguished: primary and secondary. Primary successions are initiated on a newly formed land surface after a primary disturbance has led to the removal or burial of most products of a previous ecosystem (e.g., glacier retreat), while secondary successions occur after a less severe (secondary) disturbances where biological legacies remain (e.g., forest fire; Matthews, 1992; Walker et al., 2010; Chapin et al., 2011). Knowledge of successional change is key to understanding the evolution of landscapes, developing sustainable land-use strategies regarding the protection and management of natural ecosystems, the restauration of damaged ecosystems as well as to improve our ability to predict how ecosystems are affected by changing environmental conditions (Walker and Del Moral, 2003; Mitchell et al., 2006; Walker and del Moral, 2009).

Glacial recession exposes new terrains on which successions are initiated. Glacier forefield successions are most commonly studied using a post-incisive chronosequence (space-for-time substitution) approach (Vreeken, 1975), which uses terrain age as a proxy for time to study ecological development (Walker et al., 2010). Following the classical conceptual model proposed by Jenny (1941), the development of geo-ecosystems is controlled by five major soil-forming factors: climate, biota (autogenic change), parent material, topography and time. A chronosequence is ideally implemented where the variation in the effects of all factors other than time is negligible. As a result, the chronosequence approach rests upon two intrinsic assumptions. First, all study sites of a chronosequence were subjected to the same initial environmental conditions. Second, successional change is primarily driven by autogenic change and thus all sites of a succession have undergone the same sequence of changes after the initial disturbance, thus mainly differing by the time since the initiating disturbance (Johnson and Miyanishi, 2008; Walker et al., 2010).

5.1.2 Features of autogenic development in successions

Glacier forefield chronosequence studies commonly focus on autogenic development – that is, the development of ecosystems as a function of time. Note that here, we use the term ecosystem to refer to a unit that includes both biotic and abiotic components and their interactions (following Walker 1999). Microbial and plant colonization, chemical weathering and physical weathering are the major processes driving autogenic successional development and these processes are strongly linked. This paragraph provides an overview of the major features of autogenic developments in glacier forefield successions. With increasing age, the main autogenic features of biota development are increasing species diversity and abundance, and thus increasing biodiversity (Cauvy-Fraunié and Dangles, 2019). Microbes are the pioneer colonizers in recently deglaciated terrains. In the earliest stages of glacier forefield successions, microbial populations comprise primarily autotrophic (Walker and del Moral, 2003; Bardgett and Walker, 2004) and heterotrophic microbial populations (Bardgett et al., 2007). Rime et al., (2016) found that microbial communities on recently deglaciated moraines of the Damma glacier (Swiss Alps) mostly originated from endogenous subglacial or supraglacial habitats, rather than from exogenous atmospheric depositions and that thus they reflect more the loss of ice habitats due to glacier retreat and less so a de nuovo microbial colonization (see also Stibal et al, 2020). Microbial communities exert a dominant control on weathering progression in glacier forefields by producing organic acids that contribute to the enhancement of mineral dissolution (Skidmore et al., 2005; Borin et al., 2010; Frey et al., 2010; Brunner et al., 2011). Once plants establish, organic acids produced within plant rhizosphere networks further lower soil pH and accelerate chemical weathering (Drever and Stillings, 1997; Jones, 1998). The abundance, diversity and activity of soil microbes tend to increase with increasing time since deglaciation (Bradley et al, 2014; Schmidt et al., 2008; Zumsteg et al., 2012; Donhauser and Frey, 2018). Photosynthetic microorganisms including Diazotrophs, Firmicutes and Cyanobacteria play a central role in the initiation and maintenance of ecosystem development by fixing C and N from the atmosphere into bioavailable forms that promote the development of more complex microbial communities and eventually allow the establishment of plants (Tscherko et al., 2003). Similarly, plant primary succession studies generally show that both plant abundance and diversity tend to increase over the course of successions (Chapin et al., 1994; Burga, 1999; Hodkinson et al., 2003; Jones and Henry, 2003; Jones and Del Moral, 2005). Nitrogen fixation and organic carbon sequestration performed by the first plant colonizers leads to an abrupt increase in readily available nutrients and organic matter (D’Amico et al., 2014), enabling the establishment of further biota in later successional stages (Chapin et al., 1994) and the formation of well-defined soil horizons (Schulz et al. 2013; Wietrzyk et al., 2018). The accumulation of organic matter in developing soils typically causes the soil bulk density to decrease with increasing distance front the ice front (Vilmundardóttir et al., 2014; Vilmundardóttir et al., 2015). The availability of macronutrients, including organic carbon (Nakatsubo et al., 2005; Smittenberg et al., 2012), dissolved nitrogen (Göransson et al., 2016; Castle et al., 2017; Turpin-Jelfs et al., 2018) and phosphorus (Perez et al., 2014; Schmidt, et al., 2016; Darcy et al., 2018) is the dominant parameter limiting the development of microbial and plant communities. Based on a compilation of data from 20 independent glacier forefield studies, Bradley et al. (2014) reported the typical concentrations of organic carbon (0.1 to 40 mg g-1), nitrogen (0.1 to 2 mg g-1) and phosphorus (2 to 8 mg g-1) in recently deglaciated soils and moraines. These soils generally exhibited increasing concentration in these compounds with increasing age. The effect of nutrient scarcity on soil microbial communities was demonstrated by artificial nutrient addition experiments forefields (Knelman et al., 2014), that showed that added nutrients dramatically accelerated microbial community succession. Organic matter accretion rates are commonly found to be the greatest in recently exposed soils (Amundson, 2001), during the phase in which soils are colonized by pioneer plants. Some studies have indicated that carbon and nitrogen are predominantly limiting nutrients during the early successional stages and phosphorus is limiting in later stages (Lambers et al., 2008; Diaz et al., 2018; Jiang et al., 2019), whereas other studies have documented phosphorus as the major limiting nutrient also during the earliest stages of succession (Anderson et al., 2000; Konhauser, 2007; Augusto, et al. 2017; Darcy et al., 2018). While phosphorus supply is primarily driven by weathering kinetics of local glacigenic phosphate-bearing minerals, the supply of bioavailable nitrogen is controlled by fixation rates of atmospheric nitrogen gas by cyanobacteria and other root-associated microbes (Brankatschk et al., 2011; Augusto et al., 2017). Note that weathering tends to operate over a kinetic-limited regime rather than a supply-limited regime and is hindered by both low temperatures (Anderson, 2007; Egli et al., 2014) and dry conditions (Egli et al., 2006). The intensity of the chemical weathering fluxes is directly affected by the reactive mineral surface area exposed and, therefore, is controlled by soil texture. Initially deglaciated soils usually contain a high fraction of very fine materials (often clays) as a legacy of glacial erosion, but these fine deposits are rapidly eroded in less than a decade (Boulton and Dent, 1974; Temme et al., 2016). After decades of exposure, there is typically a decrease in soil grain size and an increase in the clay and silt fraction with distance from the ice front (Egli et al., 2006; Bernasconi et al., 2011; Wojcik et al., 2020), largely attributed to the effect of physical weathering (Frenot et al., 1995; Marvis et al., 2010). In particular, Frenot et al. (1995) highlighted the action mechanical weathering via periglacial frost heaving and particle translocation. The progression of physical weathering has also been studied via the decrease in surface hardness and surface micro-roughness on rock weathering rinds along chronosequences in glacier forefields using Schmidt hammer tests (Dąbski, 2009; Dąbski, 2014). Changes in bulk soil geochemical and mineralogical soil composition induced by chemical weathering generally tend to become more conspicuous over the course of successions (Egli et al., 2011; Zhou et al. 2016; Blacker, 2018; Wojcik et al., 2020).

5.1.3 Allogenic factors and synthesis

The autogenic processes described above are a major driver of successional change in the forefields of retreating glaciers. Yet, successional patterns do not result from autogenic processes and time alone (Matthews, 1992). The evolution of glacier forefield ecosystems is subject to both autogenic and allogenic processes, as well as the interplay between them (Matthews, 1992). In ecological succession theory, autogenic changes are controlled by biological processes (e.g., competition, facilitation and predation) whereas allogenic changes are driven by allogenic factors, also called external environmental factors (Matthews, 1992) or abiotic environmental forcings (White and Picket, 1985). In the context of successions, allogenic factors can be classified into two major categories: disturbances (active allogenic factors) and initial environmental conditions (inactive allogenic factors). Note that here we will discuss and review primarily the role of abiotic allogenic factors, but biotic allogenic factors also exist (e.g., pathogens, allogenic species invasion).

Allogenic factors can influence successional change by affecting the rate and/or the trajectory of successions (Matthews, 1999 and Fig 1). Where allogenic factors only affect the rate of succession, they can 'delay' (e.g., via erosion) or 'enhance' (e.g., via nutrient supply) the rate of succession without influencing its deterministic endpoint (White and Pickett, 1985; Whittaker, 1991; del Moral and Bliss, 1993). In the case of glacier forefields, the 'succession stage' or 'relative terrain age' of a seral community (the intermediate stage of a succession) affected by disturbances must be considered as potentially drastically different from its absolute 'time since deglaciation' (McCarroll, 1991; Huggett, 1998). Allogenic factors can also force successions along different directional trajectories, which can converge, diverge but also evolve in parallel, diverted or network-like trajectories (Walker et al., 2010). Convergence and divergence respectively refer to the average decrease or increase in variability, irregularity, differentiation and diversity of different seral communities as a succession proceeds from early to late stages over time (Lepš and Rejmánek, 1991; Phillips, 2017). Research on successional trajectories has traditionally been more focused on vegetation studies rather than soil studies. More recent studies aimed to update the classical linear soil development models with an 'evolutionary view' of pedogenesis that views soils as an entity that can evolve toward multiple steady states and that is the result of heterogeneous environmental conditions (Huggett, 1998; Phillips, 2017). Disturbances and spatially uneven environmental conditions lead to heterogeneity in successions and this can result in the formation of 'mosaic of patches' (White, 1985; Willig and Walker, 1999; Turner et al., 2010). Yet, the idea that divergence tends to be associated with strong disturbance regimes, while convergence occurs where autogenic change is dominant, typically in later successional stages, is not always true (Matthews, 1992). Allogenic factors (and autogenic processes too; Robbins and Matthews, 2010; Walker and del Moral, 2011), can force successions either along divergent or convergent trajectories (Matthews, 1999; del Moral, 2007). Generalizing on the effect of disturbances on the rate and trajectory of successions is difficult, considering the large variability in the type, intensity and frequency of disturbances as well as the variability of the spatial and temporal scale at which they operate (Matthews, 1992; Matthews, 1999; Willig and Walker, 1999; Mori et al., 2008). Fig. 1 illustrates how disturbances can affect the rate and/or trajectory of glacier forefield successions.

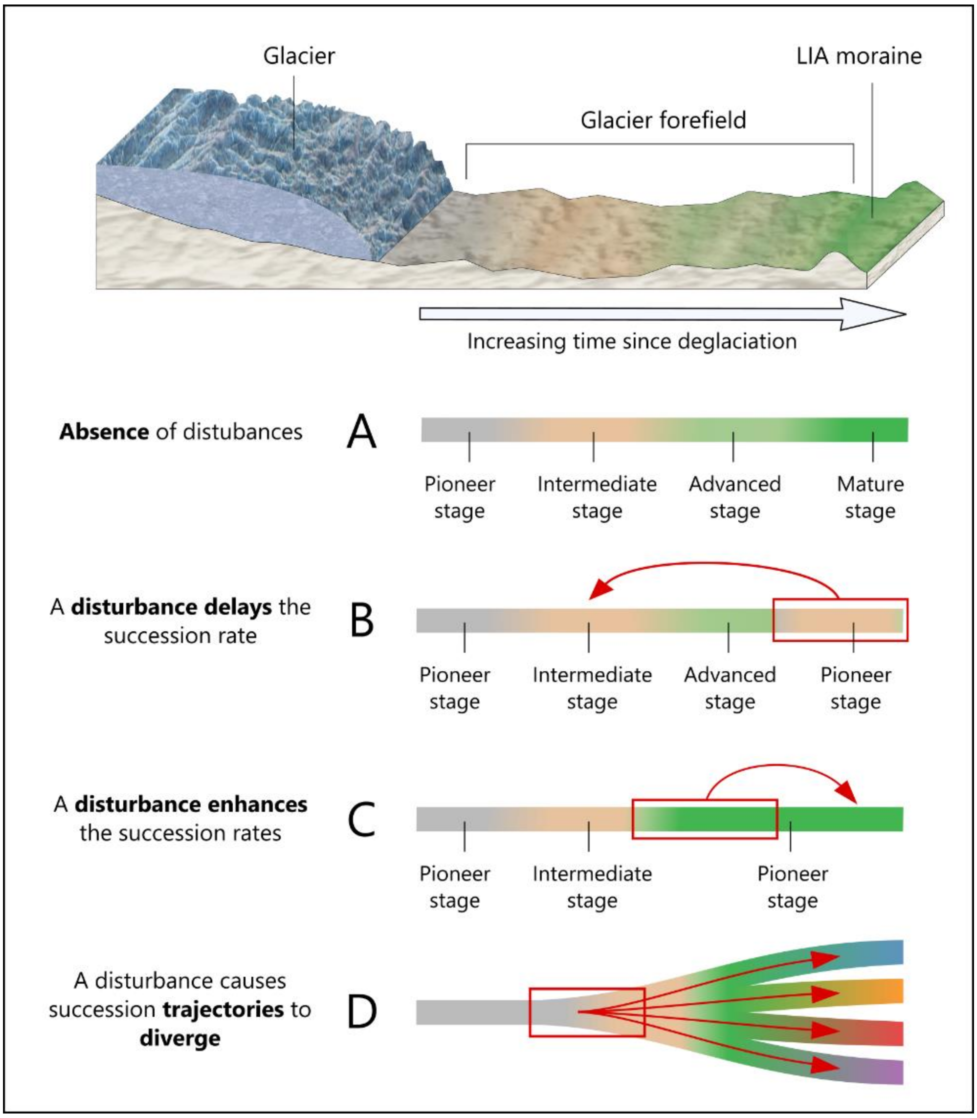

Figure 1: Schematic representation of how disturbances can affect the rate or trajectory of successions. In scenario A, the succession is solely driven by autogenic change and gradually progresses from pioneer to mature stage without set back, enhancement or trajectory changes. In scenario B, a disturbance sets back the succession to a prior successional stage (e.g., plant damage or organic matter removal due to erosion). In scenario C, a disturbance enhances the succession rate to a more advanced stage (e.g., via the addition of nutrients, moisture or fine materials). Finally, scenario D depicts the case of a succession trajectory divergence where seral communities (intermediate successional stages) evolve toward different mature stages in equilibrium with prevailing local allogenic conditions determined by e.g., geomorphological disturbances. Although this figure focuses on how disturbances may change successional behavior over the course of successions, note that initial abiotic site conditions too may create heterogeneity by affecting the rate and trajectory of successions unevenly.

Time since deglaciation (autogenic development) is almost always found to be the dominant parameter explaining patterns observed in glacier forefield successions (e.g., Andreis et al., 2001; Raffl et al., 2006; Temme et al., 2016). However, in some cases, variations in allogenic factors are important enough so that time since deglaciation is not the dominant control of successional change and in some cases even explains less than half of the successional patterns (e.g., Temme and Lange, 2014; Rydgren et al., 2014; Stawska, 2017). Many studies on glacier forefield successions report evidence indicating that typical allogenic factors (i.e., uneven environmental conditions and geomorphological disturbances) affect the rate and trajectory of plant successions (e.g., Andreis et al., 2001; Raffl et al., 2006; Pech et al., 2007; Moreau et al., 2008; Garibotti et al., 2011a) and soil evolution (Matthews, 1999; Haugland and Haugland, 2008; Temme and Lange, 2014; Heckmann et al., 2016; Wojcik et al., 2020) in glacier forefields. Although time since deglaciation is most often the dominant factor explaining generic succession patterns at large spatial scales, heterogeneous small-scale successional patterns can in part be explained by local variations in allogenic factors (Gurnell et al., 2000; Burga et al., 2010). This is not surprising, considering that in glacier forefields, geomorphological disturbances are ubiquitous, and their occurrences are spatially and temporally heterogeneous. For example, Lawson (1979) estimated that as much as 95% of the primary till deposits in the forefield of Manatuska glacier (Alaska) were affected by geomorphological disturbances. Similarly, Oliver et al. (1985) reported that 63% of the primary deposits in the Nooksack Glacier forefield (USA) were affected by geomorphological disturbances. The geomorphological diversity of glacier forefields have also been described for sites in Svalbard (e.g., Zwoliński et al., 2013; Miccadei et al., 2016), Iceland (Jónsson et al., 2016) or the European Alps (Eichel et al., 2013).

These observations demonstrate that acquiring a holistic understanding of how allogenic factors affect ecosystems is critical to develop an accurate interpretation of the features of successional change. We suggest that one has to evaluate the spatial patterns of glacier forefield ecosystems evolution as being determined by (1) autogenic processes occurring over time (since deglaciation), as well as variations in (2) initial site conditions (inactive abiotic allogenic factors) and (3) geomorphological disturbances (active abiotic allogenic factors) (see Fig. 2).

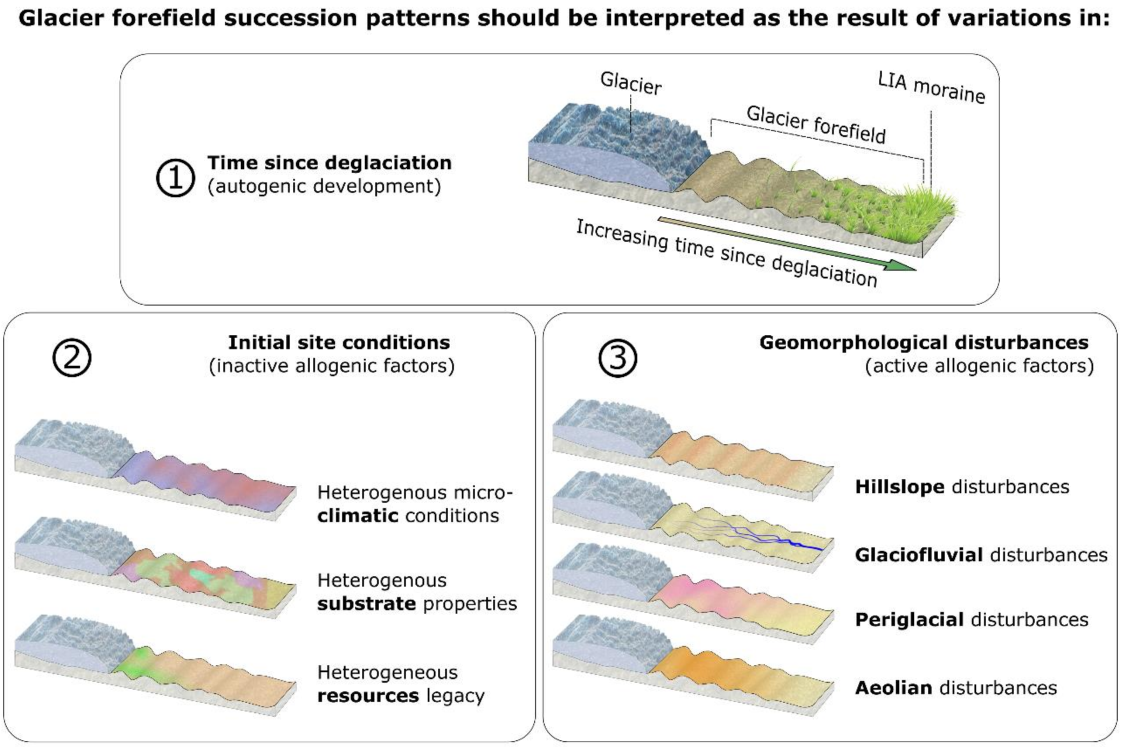

Figure 2: Schematic representation of the major factors determining ecosystem succession patterns: time since deglaciation, initial site conditions and geomorphological disturbances.

This idea is consistent with the geoecological approach presented in Matthews (1992), who highlights that glacier forefield ecosystems are the result of interactions between multiple biotic and abiotic factors and emphasizes the spatially heterogeneous nature of these ecosystems. As such, allogenic factors exert a continual influence on the rate and trajectory of ecological successions and soil evolution in glacier forefields. Therefore, it is of great importance to consider both autogenic and allogenic factors at all stages of an investigation, including study design, site selection, data analysis, and hypothesis testing. To address these various steps, we provide a comprehensive inventory of the many ways in which heterogeneous initial site conditions and geomorphological disturbances can affect microbial and plant successions and the associated soil evolution in glacier forefields. We also discuss how the relative importance of these factors may change over the course of successions.

5.2 Initial site conditions

As mentioned above, the classical chronosequence approach relies on the assumption that sites of a succession were subjected to the same initial environmental conditions. Nevertheless, glacier retreat may expose terrains that depict spatially uneven environmental conditions for primary succession, even before such terrains are affected by paraglacial geomorphological disturbances. Initial environmental conditions refer to the set of abiotic conditions that make up the original template on which early successional stages evolve on. Initial environmental conditions can be considered as 'inactive' allogenic factors (Matthews, 1992; Willig and Walker, 1999), as opposed to disturbances, which are considered 'active' allogenic factors. Below we discuss how the composition and texture of the substrate, topography of the terrain, climatic and resources legacy can all, individually and together, create spatially heterogeneous site conditions for glacier forefield successions.

5.2.1 Climate and microclimate

Climatic parameters such as mean annual temperature and annual precipitation- are generally considered to be dominant parameters explaining the differences in ecosystem development rates between glacier forefields around the world. At the global or regional scale, climate differences in mountainous regions are primarily controlled by latitude, altitude and continentality (Donhauser and Frey, 2018). Regions located at higher latitudes are subjected to colder climates than temperate and equatorial latitudes due to the lesser amount of incoming solar radiations (Barry, 2008). With increasing altitude, temperature decrease, UV radiation increases and precipitation increases (Barry, 2008; Schulz et al., 2013). Furthermore, proximity to the ocean, prevailing wind direction, and wind speed are important factors in determining regional climatic conditions. As opposed to oceanic climates, continental climates tend to be characterized by lower precipitation and higher daily and annual temperature variations. Glaciers generally occur at increasing altitudes with greater continentality (i.e. distance from the coastline), due to the decrease of precipitation in inland regions (Matthews, 1999). Based on a comparison of 39 glacier forefields in south-central Norway, Robbins and Matthews (2010) found that altitude and continentality were dominant parameters explaining the differences in succession rates and trajectories between glacier forefields.

At the scale of individual glacier forefields, climatic conditions are rarely homogeneous. Within a glacier forefield, microclimatic heterogeneities can occur due to variations in distance from the glacier front, altitude, aspect, solar radiation and snow distribution. For example, microclimatic conditions at younger moraines recently exposed by glacier retreat tend to be colder because they are more often affected by colder air from supraglacial katabatic winds. With increasing distance from the glacier, the influence of katabatic winds weakens and microclimate is increasingly influenced by the larger-scale regional climate (Maizels, 1973; Matthews, 1992). Variations in microclimatic conditions that result from distance from the glacier are well illustrated in Figure 3.

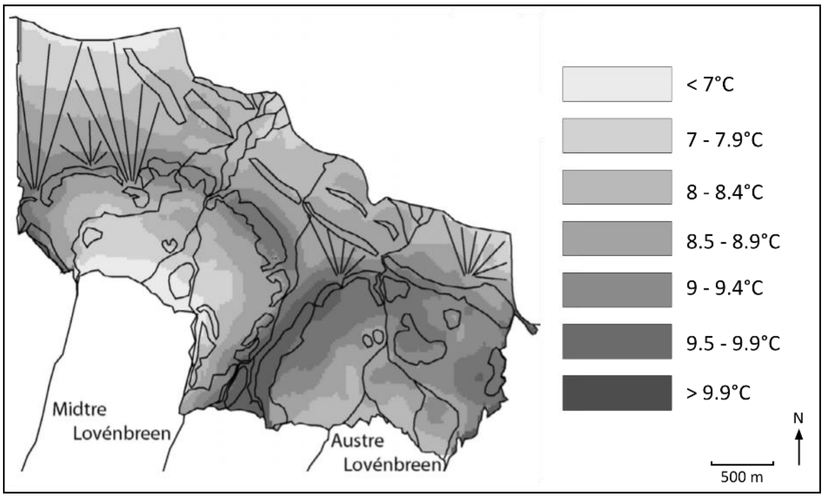

Figure 3: Spatial variation in temperature in the forefields of Midtre Lovénbreen and Austre Lovénbreen glaciers (Svalbard) in July (measurements were taken at a 20-meter resolution, figure adapted from Joly and Brossard 2007).

Additionally, important microclimatic heterogeneities can occur as the result of variations in topographic setting (i.e., variations in altitude, aspect, solar radiation and snow distribution). For example. in mountainous regions (e.g., alpine valleys), altitude may vary up to several hundred meters between different parts of a glacier forefield and such change creates sharp altitude-controlled climatic variations at small spatial scales (Haeberli and Gruber 2009). Older moraines that are located at lower altitudes may be subjected to significantly warmer microclimates than young moraines located at a greater altitude. For example, Matthews (1987) documented a temperature drop of 5.45°C per 1000m of altitude gain in the forefield of Jotunheimen glacier in Central Norway. As a result, glacier forefields located at lower altitudes are often characterized by more rapid succession rates than glacier forefields at higher altitudes (Robbins and Matthews, 2010). Further, Robbins and Matthews (2010) found that glacier forefield successions proceeded from pioneer vegetation to birch woodland in a timeframe of 70 years at altitudes below 1000m, while glacier forefields at 1100 to 1600m of altitude in south-central Norway took 250 years for glacier forefield ecosystems to reach the dwarf-shrub vegetation stage. They also documented that no successional change occurred above an altitude of 1600m, where pioneer vegetation persisted in older soils and did not develop any further complexity. Similarly, Garbarino et al. (2010) found that altitude was a dominant parameter influencing tree stand density in the forefield of the Ventina glacier (Italy), while Lazzaro et al. (2015) suggested that altitude was significantly linked to changes in soil properties.

In addition to altitude variations, Joly and Brossard (2007) determined that temperature variations in forefields of the Midtre and Austre Lovénbreen glaciers (Svalbard) were strongly driven by changes in incoming solar radiation. These variations arise due to changes in slope angles, aspects and the angular position of the sun in the sky. As a result, ecosystems on the sunward side of slopes tend to be more developed than ecosystems on shaded slopes (Barry, 2008), since solar radiation directly enhances photosynthetic production, increases temperatures and thus enhances weathering rates, and thus enhances nutrient availability and the rate of soil formation (Rech et al., 2001). On the shaded side of slopes, ecosystem development may further be delayed by periglacial disturbances, which are enhanced by cold conditions (e.g., Gruber et al., 2004). For example, Matthews (1978) concluded that altitude and aspect were among the dominant parameters explaining the spatial variability of plant community composition in the forefield of Storbreen glacier in central Norway. Similarly, Lambert et al., (2020) reported that changes in vegetation cover were strongly correlated with changes in solar radiation in the forefield of Grinnell Glacier (USA). In the forefield of the Rotmoosferner (Austria), Raffl et al. (2006) observed that vegetation succession followed divergent trajectories on opposite valley sides due to differences in solar radiation (sunward *vs.* shaded side), as well as other geomorphic and lithological differences.

Topography is another important factor that affects the variability already imposed by changes in altitude and solar radiation. Topography controls microclimate variations by, for example, affecting the exposure of ecosystems to wind and precipitation. Parts of glacier forefields exposed to strong winds are generally characterized by colder microclimates (Körner, 2003) and can be subjected to greater aeolian erosion (deflation). Contrarily, microtopographic features, such as small-scale concave surfaces or areas in the vicinity of large boulders, can provide shelter against wind erosion and drought and thus offer favorable sites for the development of microbial ecosystems and pioneer plants (Jumpponen et al., 1999; Mori et al., 2013). The action of wind on topography can also lead to the uneven distribution of snow, which insulates the ground and thus prevents damages due to low temperature in the winter season (Geiger et al., 2009). Finally, spatial and temporal variations in snow distributions have also been suggested to be crucial factors controlling the composition of plant (Choler, 2005) and microbial communities (Zinger et al., 2009) in similar Alpine and Arctic environments, with snow distribution being controlled to a large extent by topography.

Over the timescale of glacier forefield successions (ca. 150 years in most cases), temporal variations in climatic conditions caused by modern global warming should also be taken into account (Pörtner et al., 2019). For example, Cannone et al. (2008) suggested that a recent increase in vegetation succession rates were most likely related to an increase in summer temperature and decrease in snow season duration caused by modern global warming in the forefield of the Sforzellina Glacier (Italy). Similarly, Smittenberg et al. (2012) found that changes in ecosystem carbon balance were directly linked to climate variations over time with a recent increase in primary productivity being linked to increasing temperatures in the forefield of the Damma glacier (Switzerland). At a site near the Furka Pass, also in the Swiss Alps, Inauen et al., (2012) determined that the total plant biomass was not stimulated by rising atmospheric CO_2 concentration. Their results were based on an experiment that tested the reaction of plants to artificial exposure to elevated CO_2 concentrations. They documented that elevated CO_2 exposition indeed leads to a relative increased belowground and decreased aboveground biomass partitioning. These examples all show that overall, climatic changes are particularly important to take into account in regions that warm significantly faster than the global average, (e.g., at high latitudes; Pithan and Mauritsen, 2014).

5.2.2 Substrate characteristics

The geochemical and mineralogical composition and physical properties of the substrate are dominant factors controlling the fertility of terrestrial ecosystems (Walker and Wardle, 2014). Parent material composition and thus the potential 'deliver' of nutrients through the weathering-induced dissolution of minerals strongly influences the structure of microbial communities in glacier forefields (Carson et al., 2007; D'Amico et al., 2015). In particular, rock weathering is a major mechanism controlling the supply of nutrients such as phosphorus (Schmidt, et al., 2016; Darcy et al., 2018), or iron (Hawkings et al., 2014; Hawkings et al., 2018). Figure 4 illustrates how differences in the geochemical composition of the substrate can cause sharp differences in biota development in glacier forefields.

The physical properties of the substrate exert also a strong control on ecosystem development. Rates of soil development and plant successions are typically lower on bedrock outcrops than on unconsolidated sediments (Matthews, 1992; Jumpponen et al., 1999; Garibotti et al., 2011b). For example, Garrido-Benavent et al. (2020) observed that unconsolidated debris hosted more diverse bacterial, fungal and algal communities than bedrock outcrops in a glacier forefield in Antarctica. This is because substrates with coarse textures (e.g., glacial debris) tend to promote microbial mobility, as well as gas and ion exchange capacity, and soil water retention capacity and these all favor successful plant germination (Jumpponen et al., 1999; Schulz et al., 2013). However, coarse substrate textures can also delay succession rate and force successions to follow different trajectories (Gellatly, 1982; Wardle, 1980). For example, in subalpine glacier forefields in Westland, New Zealand, Wardle (1980) found that blocky surfaces were very slowly colonized by shrubby vegetation and that finer material was colonized by more herbaceous vegetation. Conversely, in the forefield of Koryto Glacier (Kamchatka, Russia) Dolezal et al. (2008) found that communities with high species richness developed on fine-grained substrates, while communities with low species richness developed on coarse-grained substrates. Fine-grained materials are known to play an important role in soil formation as they promote the coherence and stability of soil organic matter aggregates (Yariv and Harold, 2001; Rasmussen et al., 2018) and they can also be a strong predictor of vegetation distribution and abundance, especially in the older parts of glacier forefields (Schumann et al., 2016; Wietrzyk et al., 2016).

Figure 4: Photograph of a rusty leaching stripe departing from a stone on the moraine of Midtre Lovénbreen (Svalbard). White arrows indicate areas with denser vegetation cover. Figure adapted from Joly and Borin et al. (2010).

The geochemical or physical properties of primary glacigenic sediments cannot be considered homogeneous at the scale of glacier forefields because they may compose various glacial and subglacial landforms (e.g., moraines, eskers, drumlins, kames, kettles, glacial grooves and roche moutonée; Bennett and Glasser, 2011). The substrates composing different glacial and subglacial landforms often have distinct structural, physical and geochemical properties because of the different processes causing their formation and because sediments in different landforms may originate from different locations within a catchment. As a result, chronosequence studies looking at changes in bulk geochemical and mineralogical compositions induced by chemical weathering are often hindered by the often significant spatial heterogeneity in till deposits (Bernasconi et al., 2011; Egli et al., 2011; Blacker, 2018; Wojcik et al., 2020). In some cases, the spatial heterogeneity of the parent materials can also drive successional trajectories along divergent pathways (Raffl et al., 2006).

5.2.3 Resource availability

Glacier forefield successions are generally considered as primary successions (i.e., beginning in an almost lifeless area; Matthews, 1999). However, in recent years, several studies have documented that the development of pioneer microbial ecosystems on recently deglaciated terrains can largely benefit from the export of microbial organic matter and microbial communities from subglacial and supraglacial environments (Bardgett et al., 2007; Kabala and Zapart, 2012; Górniak et al., 2017). Subglacial microbial communities are equally abundant and diverse as in other many permafrost terrains (Skidmore et al., 2000; Foght et al., 2004). Regarding pioneer colonization, Rime et al.

(2016) recently determined that the pioneer bacterial communities found in a glacier forefield in the Swiss Alps most likely originated from the subglacial environment rather than more distant allochthonous sources. Furthermore, subglacial environments can supply a significant amount of essential nutrients to downstream glacier forefields via both microbial biomass (Sharp et al., 1999; Skidmore et al., 2005) and the products of abiotic weathering reactions (Tranter et al., 2002; Graly et al., 2018). In particular, subglacial streams can export significant amounts of nitrogen (Wynn et al., 2007; Lawson et al., 2014a), phosphorus (Hawkings et al., 2015; Hawkings et al., 2016) and organic carbon (Lawson et al., 2014b), which all are essential for the development of new microbial communities in glacier forefield soils.

Similarly, supraglacial environments can be an important source of carbon, nitrogen and phosphorus compounds delivered to glacier forefields through runoff (e.g., Bagshaw et al., 2013; Antony et al., 2017; Ren et al., 2019). In Polar regions, the development of supraglacial ecosystems in snow, glacier ice, cryoconite holes, cryolakes, and supraglacial streams is primarily sustained by the supply of aeolian-derived mineral and organic matter (Dubnick et al., 2017). Additionally, vegetation colonizing supraglacial debris can be an important source of nutrients when the glaciers melt and these are deposited on glacier forefields (Caccianiga et al., 2011).

The hydrological and biogeochemical connectivity of glacier forefields to adjacent environments are strongly seasonally dependent and spatially heterogeneous. For example, the contribution of carbon and nutrients from supraglacial to proglacial environments is greatest during periods of snowmelt and glacier surface melting (Hodson et al, 2005; Mindl et al, 2007). Whilst allochthonous deposition and input of carbon and nutrients from adjacent habitats, including glaciers, has been shown to contribute to biological productivity on some glacier forefields including in the Andes, Svalbard, and elsewhere (Schmidt et al, 2008; Schulz et al, 2013; Bradley et al, 2016), it is important to note that this not the dominant process everywhere (e.g., Anderson et al., 2017).

Besides nutrients and organic carbon, variations in soil moisture content may enhance or delay microbial and plant succession and soil evolution rates in a spatially heterogeneous manner (Miller and Lane, 2019; Wojcik et al., 2020). Note that modern views of disturbances include spatially discrete events (e.g., landslides) as well as environmental fluctuations such as water stress that have diffuse boundaries (Pickett et al., 1999; Willig and Walker, 1999). Plant (Schulz et al., 2013) and microbial communities (Burga et al., 2010) in glacier forefields are commonly subjected to drought stress due to the poor water retention capacity of the often coarse-textured glacigenic deposits, even in regions that may receive relatively high amounts of precipitation. Soil moisture exerts a strong control on the spatial variability, diversity and abundance of plant (Raffl et al. 2006; Burga et al., 2010; Rydgren et al., 2014; Schumann et al., 2016) and microbial communities

(Zumsteg et al., 2013) as well as soil geochemical properties (Szymański et al., 2019). Interestingly, Szymański et al. (2019) found that the greatest soil nitrogen and carbon stocks occur at sites with moderate soil moisture since permanently waterlogged soil may develop anaerobic conditions which can delay or prohibit the establishment of plants. Besides surface runoff, groundwater upwelling (Kobierska et al., 2015) may also be a significant pathway of moisture and nutrient supply and redistribution. In turn, this may promote the local flourishment of proglacial soil ecosystems (Ward et al., 1999; Crossman et al., 2011). Terrains close to the ice front benefit from constant groundwater recharge due to the melting of glacier snow and ice (Matthews, 1999). However, groundwater upwelling is heterogeneous due to the high soil texture variability of glacigenic deposits (Magnusson et al., 2014; Pourrier et al., 2014).

In summary, heterogeneous environmental conditions due to variable microclimatic substrate properties and initial resources availability can each exert a strong control on ecological succession, by providing different initial conditions and therefore introducing heterogeneity in glacier forefield successions.

5.3 Geomorphological disturbances

The primary sediments exposed by glacier retreat are reworked or ‘disturbed’ by various paraglacial geomorphic processes during the transition from glacial to non-glacial conditions (Ballantyne, 2002). The assumption that, once exposed, all sites of a succession are subjected to the same sequence of change and that they only differ by their time since deglaciation is one pillar of the chronosequence approach. Nevertheless, glacier forefields are subject to constant change according to conditions determined by prevailing geomorphological processes, which are heterogeneous in space and time. Hillslope, glacio-fluvial, periglacial and aeolian processes are among the most important geomorphological processes taking place in glacier forefields (Matthews, 1992; Ballantyne 2002). These geomorphological disturbances affect glacier forefield ecosystems either by disturbing the plants themselves or by modifying substrate and changing the chemical, physical and biological makeup of soils through erosion, deposition or mixing (Matthews, 1999; Eichel, 2019). Such disturbances can also affect the availability of resources such as nutrients, water and the distribution and dispersal of plant diaspores (Matthews, 1992). Below we discuss the main geomorphological processes linked to such disturbances with a specific focus on hillslope, glacio-fluvial, periglacial and aeolian processes, and their effect on biota, substrate, and resources within glacier forefield ecosystems. We conclude by evaluating how these processes impact the rate of successional development.

5.3.1 Hillslope disturbances

Hillslope disturbances in glacier forefields include mass movement (e.g., slumps, slides, debris flows, Blair, 1994; Emmer et al., 2020) and soil erosional processes (e.g., wash, inter-rill and rill erosion, Eichel et al., 2018; Jäger and Winkler, 2012), as well as gullying as a combination of both (e.g., Curry et al., 2006). Together, hillslope and periglacial processes (discussed in the next section) (e.g., solifluction, Draebing and Eichel, 2017) disturb ecological succession on inclined slopes, such as annual, terminal and lateral moraine slopes. In addition, episodic events such as cliff slope failure, rock falls can occur on steep glacier forefield terrains or in their vicinity (Ballantyne, 2002; McColl and Draebing, 2019). Finally, glacier forefields are also disturbed by snow avalanches from adjacent slopes (Raffl et al., 2006). Chronosequence studies on flat, stable terrain are thus subject to fewer and less intensive hillslope disturbances.

Eichel et al. (2013, 2016) showed a clear impact of paraglacial hillslope processes on vegetation succession in the Turtmann glacier forefield (Switzerland). They found that vegetation successional stages are strongly related to geomorphic disturbance intensity. High-magnitude or high-frequency processes, such as debris flows and gullying can prevent vegetation colonization (Curry et al., 2006) or restrict it to pioneer stages (Eichel et al., 2013, 2016). Similarly, debris flows can prevent or reset soil development by providing fresh material to the forefield (Temme and Lange, 2014). Different types of high magnitude landsliding disturbances were found to have different effects in the Kinzl glacier forefield (Peru) (Emmer et al., 2020). High magnitude disintegrating landsliding of lateral moraines destroyed vegetation cover, while vegetation was completely undamaged by sliding of intact blocks. In the Aletsch glacier forefield (Switzerland) local, lower magnitude sliding changed species composition and reduced species cover, but did not completely destroy vegetation cover (Rehberger, 2002). Lower magnitude, but higher frequency soil erosional processes can restrict vegetation colonization to pioneer stages (Eichel et al., 2013). However, once magnitude or frequency further decreased, a change to intermediate successional dwarf shrub stages was found in the Turtmann glacier forefield (Switzerland). Similarly, (Moreau et al., 2004) found that vegetation started to colonize terminal moraine slopes when hillslope processes only occurred locally and intermittently. Likewise, shrubs and tree seedlings colonized the moraine slopes once geomorphic activity decreased in the Langtauferer glacier forefield (Italy), (Betz et al., 2019). A clear relationship between erosion intensity and soil development was also described at the Gepatsch glacier forefield (Austria), with more developed soils (lower pH value, higher organic matter content) in areas that have been subjected to less erosion (Temme et al., 2016).

Hillslope disturbances can also facilitate glacier forefield colonization and soil development. In the Rotmoos glacier forefield (Austria) (Erschbamer et al., 2001; Raffl et al., 2006) observed that plant material and earth lumps transported into the forefield by snow avalanches contributed to vegetation colonization. Similarly, erosion and downslope transport of fully-grown plants or plant parts from upper slopes can also promote midslope colonization (Brockmann-Jerosch, 1925). Finally, geomorphic disturbances also create opportunities for less competitive species to survive in glacier forefields. For example, in the Morteratsch glacier forefield (Switzerland), the light-demanding larch (Larix decidua) only manages to become established in sites disturbed by geomorphic processes and is otherwise outcompeted by the stone pine (Pinus cembra) (Burga et al., 2010).

Slope angle and position are commonly found to be strongly correlated with the variability of plant community composition in glacier forefields (e.g., Andreis et al., 2001; Rydgren et al., 2014). Ecosystems located at different positions across a slope are differently affected by downhill disturbances. Ecosystems and soils on hill (e.g., moraine) crests, shoulders and backslopes are frequently subjected to erosion and, as a result, tend to be underdeveloped. Alternatively, soils and ecosystems at footslopes are typically more developed because they benefit from the supply of organic matter, moisture and fine-grained sediments (e.g., Wojcik et al., 2020). The spatial heterogeneity in ecosystem succession rate than can occur as the result of hillslope is illustrated in Figure 5.

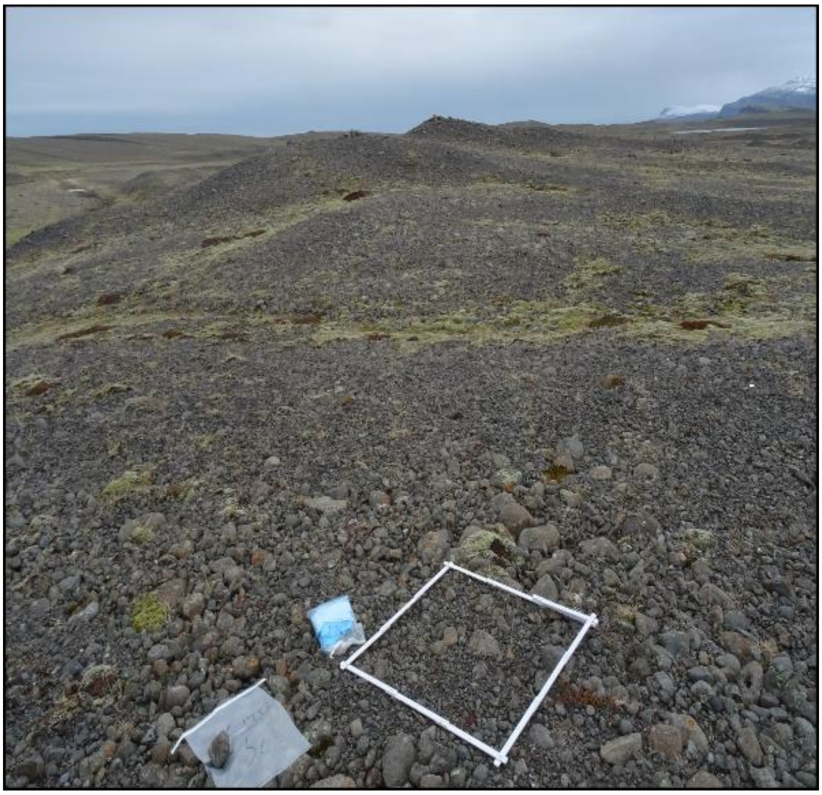

Figure 5: Photograph of recessional moraines in the forefield of Fláajökull glacier, south-eastern Iceland. The accumulation of nutrients, moisture and fine-grained material enhance the succession rate of ecosystems at footslopes. On the contrary,

the succession rate of ecosystems on moraine ridges and backslopes is delayed by erosion. © Picture taken by Robin Wojcik in 2017.

The often-greater soil organic matter content at footslopes can be explained by the combined effect of greater organic matter deposition rates from upslope and wetter conditions, which promote the preservation of buried soil horizons (Yoo et al., 2006; Berhe et al., 2008; Hancock et al., 2010; Palmtag et al., 2018). Additionally, the accumulation of fine soil (i.e., clay and silt) fractions promotes organic matter aggregation and leads to its stabilization (Yariv and Harold, 2001) and promotes soil water-retention capacity (Tavenas et al., 1983) at footslopes. Footslope ecosystems may further benefit from the supply of nutrients derived from weathering products from uphill terrains (Yoo et al., 2007; Langston et al., 2015). The deposition of fine soil grain sizes, chemical weathering products and organic matter at footslopes leads to the thickening of soil horizons toward the lower part of hillslopes (Birkeland and Burke, 1988). Variations of soil evolution along hill profiles are also mirrored in the development and changes in plant communities. For example, Garibotti et al. (2011a) found that plant species diversity was on average higher at footslopes than on moraine crests in glacier forefields in the Patagonian Andes. Considering the important variability of soil and ecosystem properties across hill profiles, Birkeland et al. (1991) proposed to characterize individual moraines using a ‘weighted mean catena profile development index’, which evens out observed variability in soil properties in hill profiles into a single value. This is an interesting approach to acquire data that are representative of the average characteristics of moraines (see also Garibotti et al., 2011a).

5.3.2 Glacio-fluvial and water-related disturbances

Glacio-fluvial disturbances often create most of the spatial heterogeneity in ecosystem and soil evolution in glacier forefields (e.g., Mercier, 2001; Moreau et al., 2008; Delaney et al., 2018; Miller and Lane, 2019). Glacio-fluvial disturbance refers to the effects of flowing water on, in or under glacierized and proglacial areas.

In a similar fashion to the effects of hillslope processes described above, the effects that glacio-fluvial disturbances have on the rate of plant succession and soil evolution depend considerably on the variations in their intensity and frequency (Marren, 2005). Where water flow is intense enough to erode surfaces, it removes fine materials as well as plants and soil organic matter, and this can delay or reset ecosystem development (e.g., Helm and Allen, 1995; Ward, 1998; Osterkamp et al., 2012). Ecosystems and soils on glacio-fluvial deposits tend to be more spatially heterogeneous than on undisturbed primary glacigenic deposits (e.g., Wojcik et al., 2018). This heterogeneity results from the temporally and spatially variable formation of braided channel networks but also because glacio-fluvial substrates tend to have more heterogeneous textures (Angiel, 2006) and geochemical compositions (Kroonenberg et al., 1990) than primary glacigenic deposits. At the scale of a glacier forefield, frequent changes in the position of channel networks (Morche et al., 2015; Kociuba et al., 2019) may be the result of seasonal variations in runoff intensity caused by glacial ice and snowmelt (Hock, 2005), or changes in the magnitude of precipitation events (Haas et al., 2012) or outburst floods (Marren, 2005; Guerrido et al., 2020). Changes in the location and morphology of river channels can also occur as a result of variations in the ice front position or changes in the terrain topography (Marren and Toomath, 2014). In view of the dynamic nature of ecosystems in glacio-fluvial channels, Moreau et al. (2008) and Arce et al. (2019) emphasized the importance of considering the frequency at which intermittent rivers and ephemeral streams are disturbed by runoff. Moreau et al. (2008) document a striking example of how glacio-fluvial disturbances can result in the formation of a mosaic composed of ecosystems exhibiting different development stages that co-exist near each other on moraine of similar ages on the forefield of Midtre Lovénbreen, Svalbard (see Fig. 6).

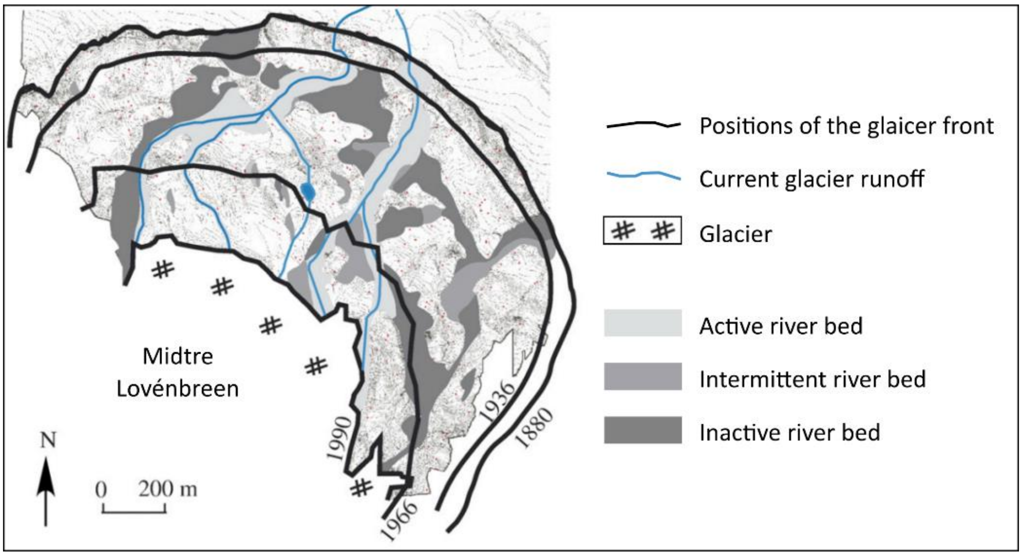

Figure 6: Map of the forefield of Midtre Lovénbreen glacier (Svalbard). Gray colors represent glacio-fluvial landforms with different disturbance frequencies. Figure adapted from Moreau et al. (2008).

5.3.3 Periglacial disturbances

Periglacial processes encompass the set of processes dominated by frost action and/or permafrost (French and Thorn, 2006). Permafrost, defined as ground that has a negative temperature for at least two consecutive years, is present in most subglacial environments and can persist in glacier forefields of both Alpine and Polar regions once the ice has retreated (e.g., Kneisel, 2003; Reynard et al., 2003; Kneisel, 2004; Lugon et al., 2004; Leopold et al., 2015; Dusik et al., 2019). 'Frost action' may occur with or without permafrost and refers to both frost-heave of the soil by ice during freezing and thaw-weakening when frozen ground thaws (French, 2017). The main periglacial processes affecting glacier forefield soils are frost-heaving and frost sorting, resulting in the formation of patterned ground, as well as solifluction landforms (needle ice creep, frost creep, gelifluction, plug-like flow) on inclined slopes (Matsuoka, 2001; Matthews et al., 1998).

While numerous studies investigate the spatial distribution of permafrost and periglacial landforms, the effects of periglacial disturbances on plant succession and soil evolution have been less often considered (e.g., Cannone et al., 2004). Nevertheless, some studies have suggested that periglacial landforms are relevant units to investigate the spatial variability of plant communities and soil properties in glacier forefields (Wietrzyk et al., 2016; Wojcik et al., 2019). Periglacial processes are generally less effective in transporting sediments in comparison to, for example, the glacio-fluvial processes described above (Slaymaker, 2009). However, solifluction processes (the gradual movement of wet material down a slope) can be a significant sediment transport mechanism (Berthling et al., 2002). Instead, the action of successive freeze-thaw cycles is an effective physical weathering agent and may lead to creeping or structural sorting of soil material (French, 2013). The magnitude of periglacial processes on recently exposed terrain is controlled by various factors including: soil water content, soil texture, the amplitude of diurnal and seasonal temperature variations and terrain slope (French, 2013).

On flat terrain, freeze-thaw cycles can create sorted or patterned-ground landforms by differential heaving and thawing of fine and coarser particles (French, 2013). Sorted-ground periglacial landforms such as sorted circles (Ballantyne and Matthews, 1982; Cook-Talbot, 1991; Dabski, 2005) and sorted polygons (Ballantyne and Matthews, 1983; Krüger, 1994) are commonly observed in glacier forefields. On gentle slopes, patterned ground may take the form of stripes (Horwath et al., 2008). The magnitude of ground-sorting disturbances is primarily controlled by soil moisture abundance (Matthews et al., 1998; Feuillet and Mercier, 2012). In glacier forefields in the Jotunheimen area (Norway), Haugland and Beatty (2005) found that frost disturbances in patterned ground generally tended to delay the rate of plant succession and soil evolution in Norwegian glacier forefields. At a smaller scale, the different positions of patterned-ground landforms (e.g., sorted circles; see Fig. 7) are characterized by distinct physical (soil texture, microstructure, pore spacing) and geochemical (nutrients and water content) properties (Meier et al., 2019) and, as a result, form a mosaic of unique microhabitats that host specifically-adapted plant communities (Anderson and Bliss, 1998; Cannone et al., 2004). The development of plant communities tends to be delayed at the center of sorted circles due to frequent ground-material movement and dry conditions. Conversely, plant communities are more developed at the edges of sorted circles with less ground material movement (Haugland, 2004; Haugland and Beatty, 2005). Confirming this observation, Haugland and Haugland (2008) also described decreasing soil horizon development with increasing frost activity disturbance from undisturbed ground from a polygon border to a polygon center.

Figure 7: Photograph of sorted circle landforms on Brøgger Peninsula (Svalbard). Plant communities are more developed at the outer edge of sorted circles, which are less affected by ground material movement. © Picture taken by Hannes Grobe in October 2007.

Even in the absence of surface periglacial landforms, frost-driven migration and sorting of soil particles can bury pockets of organic-matter via cryoturbation (Bockheim, 2007), a feature that is common in glacier forefields (e.g., Kabala and Zapart, 2009; 2012). Importantly, disturbances caused by cryoturbation can in certain cases be a dominant parameter explaining spatial patterns of plant (Whittaker, 1989; Boy et al., 2016) and bacterial communities distribution and abundance (Zdanowski et al., 2013) in glacier forefields. More indirectly, the presence of frozen ground may have an important influence on the erosion and deposition of sediments by glacio-fluvial processes and thus on the position of streams (Vandenberghe and Ming-ko Woo, 2002).

On steeper terrains (> 3° to about 35 °), freeze-thaw cycles lead to solifluction, the slow downslope movement of material by needle ice creep, frost creep, gelifluction and plug-like flow (Matsuoka, 2001; Eichel et al., 2017). These processes produce lobate and terrace-like solifluction landforms commonly observed in glacier forefield (e.g., Watanabe, 1989; Matthews et al., 1986; Kääb and Kneisel, 2006). Similar to other disturbances, solifluction can either promote or delay ecosystem development. For example, at solifluction terraces on lateral moraines of the Tasman glacier (New Zealand), (Archer et al., 1973) found that vegetation and soil development has been retarded by cryoturbation. In contrast, other studies found well-developed ecosystems on depositional hillslope landforms because of the burial and conservation of organic matter (Shelef et al., 2017; Stawska et al., 2017; Wojcik et al., 2019). On solifluction lobes in the Turtmann glacier forefield (Switzerland), Draebing and Eichel (2017) and Eichel et al. (2016) found distinct relationships between plant communities, lobe topography and activity. While lobe ridges rich in fine-material frequently disturbed by frost action were colonized by frost-adapted pioneer species, moving lobe treads were covered by dwarf shrub species and shrub species colonized the most stable lobe borders. This suggests that solifluction disturbances can create fine-scale succession mosaics in glacier forefields, similar to succession mosaics observed at patterned ground.

5.3.4 Aeolian disturbances

Aeolian processes can also exert a great influence on the rate of successions and its spatial variability in glacier forefields (Matthews, 1992; Ballantyne, 2002; Anderson et al., 2017). The action of aeolian erosion tends to delay ecosystem succession whereas aeolian deposition may, on the contrary, accelerate ecosystem successions. In both cases, aeolian disturbances affect glacier forefield ecosystems in a spatially heterogeneous manner. Note that neither of the two types of aeolian disturbances create mosaics with sharp boundaries (unlike most hillslope, glacio-fluvial and periglacial disturbances).

Aeolian erosion is defined as the removal of ground material by wind forcing. The spatial variability of aeolian erosion is determined by changes in local meteorology, sediment properties, topography, vegetation and hydrological properties of the forefield (Derbyshire and Owen, 2018). In glacier forefields, aeolian erosion is primarily driven by katabatic winds that blow toward the outlet of glaciers and ice sheets (e.g., Fig. 8). Winds that are fast enough to transport of soil particles by saltation or suspension occur most frequently during the winter season (Fountain et al. 1999; Derbyshire and Owen, 2018). Aeolian erosion primarily removes fine-grained or loose material although some studies have also documented transport of sediment particles up to granule grain size (Glasser and Hambrey, 2002).

Aeolian erosion of cemented bedrock outcrops is far less effective. Rock surfaces that have reached a more advanced stage of chemical weathering will be more susceptible to aeolian abrasion and erosion compared to less-altered rock (Derbyshire and Owen, 2018). In contrast, unconsolidated fine-grained sediments from glaciers, rivers and lakes tend to be more susceptible to aeolian erosion (Glasser and Hambrey, 2002). Among primary glacigenic landforms, moraine crests and exposed slopes are the most exposed to winds and have higher aeolian erosion rates (Riezebos et al., 1986; Fahnestock et al., 2000; Derbyshire and Owen, 2018). The winnowing of loose fine-grained particles by intense and frequent winds commonly results in the formation of 'stone-pavement' landforms in glacier forefields (Ballantyne, 2002; Seppala, 2004), a process that has been extensively described (Carter, 1976; Pye, 2015). After only a few years of exposure, the erosion of fine particles results in the thickening and increasing surface area of surface stone layers (Boulton and Dent, 1974; Matthews and Amber, 2015). Aeolian erosion may have a spatially heterogeneous, and discontinuous effect, leading to the formation of deflation patches in areas exposed to strong winds (Glasser and Hambrey, 2002; Heindel et al., 2017). The presence of a vegetation cover as well as abundant soil moisture diminishes aeolian erosion (Matthews, 1992). In turn, the formation of stone pavement landforms due to intense aeolian erosion will affect surface water runoff patterns by reducing water infiltration in soil (Zender et al., 2003; Ravi et al., 2010). Finally, frequent winds may enhance water stress conditions (e.g., Glasser and Hambrey, 2002).

In contrast to erosion, aeolian depositional processes can accelerate the succession rates of forefield ecosystems by supplying nutrients, fine grained-sediments and water. The deposition of aeolian material can result in the formation of various landforms depending on the source area, the availability of the source material, wind speed as well as terrain obstacles and topography (Müller et al., 2016). Blown sheets are among the most common aeolian depositional landforms in glacier forefields (Willemse et al., 2003; Müller et al., 2016; Anderson et al., 2017; Stawska, 2017). These blown sheet landforms typically consist of larges patches of thin drapes of silt and fine sand (Glasser and Hambrey, 2002) and they primarily result from the deposition of aeolian material onto wetted or vegetated surfaces or snowbanks (Riezebos et al., 1986; Matthews, 1992; Müller et al., 2016). Aeolian material preferentially accumulates on the lee side of topographic barriers and vegetation patches (Brookfield, 2011; Müller et al., 2016; Derbyshire and Owen, 2018), leading to the uneven distribution of precipitations and aeolian fallouts. Göransson et al. (2014) found that terrains directly surrounding large emerging rocks tend to be enriched in nitrogen and moisture because rocks are diverting nutrient rich precipitations, thus creating nutritional niches for plants and microbes. Given appropriate wind patterns, ground obstacles can lead to the local material accumulation and the development of dune landforms. Dunes are commonly observed in proglacial terrains and may display various types of structure such as: parabolic dunes (Derbyshire and Owen, 2018), blow-out dunes (Anderson et al., 2017), climbing dunes (Willemse et al., 2003) as well as transverse, dome-shaped and barchan-like dunes (Li, Xiaoze, et al., 2006; Müller et al., 2016). In glacier forefields, such visually conspicuous aeolian depositional landforms primarily consist of material that originate from local sources such as neighboring glacio-fluvial areas (Seppala, 2004; Lawrence and Neff, 2009; Zhang et al., 2015). Aeolian deposits that originate from local sources primarily consist of sand-sized material. In contrast, the proportion of sand decreases while the proportion of silt and clay-sized material increases with increasing distance between the source and deposition area (Lawrence and Neff, 2009).

Figure 8: Photograph of Aeolian activity in the proglacial area of Russell Glacier (Sandflugtdalen, Greenland). © Picture taken by John Anderson.

As described above, aeolian deposition may strongly influence glacier forefield ecosystems by delivering nutrients, microorganisms, seeds and plant debris, and fine sediments - even where deposition rates are not sufficiently high to accumulate thick layers of deposited material and form visually conspicuous landforms. The deposition of aeolian material may either occur via dry precipitations (e.g., Shahgedanova et al., 2013), or wet precipitation (rain or snow e.g., Temkiv et al., 2012; Hodson et al., 2010; Hell et al., 2013). Without consideration of its biogeochemical composition, the deposition of fine aeolian material tends to enhance ecosystem succession rates (Applegarth and Dahms, 2004) as it promotes both soil water-retention and the formation of organic matter aggregates (Rasmussen et al., 2018). Studies increasingly highlight that nutrients in aeolian deposits sustain the productivity of glacier forefield ecosystems (Šabacká et al., 2012; Bradley et al, 2016; Rime et al., 2016; Anderson et al., 2017; Diaz et al., 2018). In addition to fertilizing soils, aeolian deposits can be a significant source of nutrients to river and lake ecosystems within glacier forefields (Deuerling et al., 2014; Diaz et al., 2018). Despite the central importance of nutrient limitations for ecosystems in glacier forefields, little is known on the relative nutrient contribution from aeolian deposition compared to local weathering in these environments. In particular, aeolian deposition can be a significant source of phosphorus (Okin et al., 2004; Šabacká et al., 2012; Aciego et al., 2017; Herbert et al., 2018; Diaz et al., 2018), nitrogen (Witherow et al., 2006; Hodson et al., 2010; Larose et al., 2013) and other minor and trace elements (Witherow et al., 2006; Fortner et al., 2011) in Polar environments. For example, Aciego et al. (2017) suggested that aeolian dust deposition was the dominant processes controlling phosphorus supply over local weathering, in a mountainous environment in the Sierra Nevada (California). Note however that Uhlig et al. (2017) later suggested that Aciego et al. (2017) may have underestimated the contribution of weathering to phosphorus budgets. The deposition of aeolian material may either occur via dry precipitations (e.g., Shahgedanova et al., 2013), wet precipitation (e.g., Temkiv et al., 2012) or snow deposition (Hodson et al., 2010; Hell et al., 2013). Nitrogen is mainly delivered dissolved via rain and snow events, whereas phosphorus adsorbs to aeolian particles (Anderson et al., 2017) or is present and phosphorus-containing mineral (e.gf., hydroxyapatite, see for example McCutcheon et al 2020). Glacier forefield ecosystems may be influenced by the input of exogeneous aeolian materials that originate up to tens of thousands of kilometers away from the deposition site (Grousset et al., 2003; Stres et al., 2013). Aeolian deposits found in recently deglaciated terrains most commonly are from natural origin (e.g., Xiaodong et al., 2004) but may also be mixed with particles from anthropogenic industrial and volcanic emission (Erel et al., 2006; McConnell et al., 2007; Du et al., 2018). Anthropogenic emissions typically tend to enrich the overall organic (Mahowald et al., 2005; Hodson et al., 2010) and trace metal content (Erel et al., 2006) of aeolian material. Nitrogen deposition in the Arctic regions has been enhanced by the airborne transport of pollutants from Europe and Russia (Eneroth et al., 2003). Future reactive nitrogen deposition may impact ecological succession and biogeochemical cycling in glacier forefields (Bradley et al, 2017). Even without material input from distant sources, aeolian transport processes can create spatial heterogeneity in ecosystem development by re-distributing organic matter within a proglacial area (Fahnestock et al., 2000). Besides its influence on nutrient budgets, aeolian transport is receiving increasing attention because it is regarded to be a major pathway for the dispersal of plants and microbial communities in diverse Polar and Alpine environments (e.g., Pearce et al., 2016; Cuthbertson et al., 2017; Šantl-Temkiv et al., 2018; King-Miaow et al., 2019). On this topic, Rime et al. (2016) elucidated that aeolian deposition is likely not a colonization pathway for pioneer bacteria on young moraines (which rather resemble bacterial communities of subglacial and supraglacial habitats) but is, however, a central source of carbon and nutrients to ecosystems on the forefield of the Damma glacier, in the Swiss Alps.

5.4 The relative importance of autogenic and allogenic processes at different stages of succession

Successional changes in glacier forefields must not only be interpreted as a result of time since deglaciation but also as the result of variations in initial site conditions and disturbances. Allogenic factors and their relative importance at different stages in a succession must form an integral part of our understanding of glacier forefield ecosystems. Below, we synthesize the existing knowledge on how the relative importance of different allogenic factors (i.e., initial site conditions and geomorphological disturbances) varies over the course of successions in glacier forefields. We conclude with an assessment of how the relative importance of allogenic factors may change with regard to stochastic factors and autogenic factors over the course of successions in glacier forefields.

5.4.1 Changing importance of allogenic processes

It is generally acknowledged that the importance of initial site conditions, such as parent material composition and topography (e.g. slope angles and microsites), is greatest for young ecosystems and tends to decline as vegetation becomes more abundant and more mature successional stages are established (Matthews, 1992; Raab et al., 2012). Chesworth (1973, 1976) further suggested that the influence of the composition of parent material on soil properties tend to be the greatest in dry regions. Glausen et al., (2019) predicted that the influence of terrain aspect on ecosystems is the greatest on recently deglaciated terrains and tends to decrease with increasing distance from the glacier margin. Similarly, Raffl et al. (2006) noted that the differences in solar irradiation (shaded or sunny side) that result from topographic heterogeneities have greater effects on young moraine ecosystems than on well-developed ecosystems. With increasing distance from the glacier front, the microclimate of glacier forefields shifts from being controlled by glacial katabatic winds in young moraines to being controlled by regional climatic conditions in older moraines. At a larger scale, regional climatic controls on glacier forefield ecosystems, related to altitude and continentality, were found to increase as succession proceeds (Matthews, 1992; Robbins and Matthews, 2010).

Hillslope disturbances are most intense at early stages of successions near the ice front where the slopes are the steepest and ground saturation is higher due to meltwater from glacier and snowmelt (Matthews, 1992). The intensity and frequency of paraglacial geomorphic processes often decreases with time since deglaciation (Ballantyne, 2002), as high magnitude processes, such as debris flows and gullying are replaced by lower magnitude soil erosional, but also periglacial processes when slopes start to stabilize (Draebing and Eichel, 2018; Eichel et al., 2018). Welch (1970) showed that the maximum slope angles of moraines tend to rapidly decrease from 75 ° to 30° in the first 15 years of soil exposition after glacier retreat whereas no noticeable changes were observed between the 15 year and the 100-year-old moraines. Additionally, the relative warming of microclimate that occurs with increasing distance from the glacier front may also indirectly affect plant and soil successions through the melting of ground ice which promotes the destabilization of hillslopes (Ballantyne, 2002; Matthews, 1992). Garibotti et al. (2011a) found that the differences in plant species diversity between moraine crests and moraine footslopes tended to increase with increasing time since deglaciation. However, in some cases, paraglacial impacts on ecological succession can persist much longer. In the Turtmann glacier forefield, high magnitude processes still occurred on slopes deglaciated for more than 80 years and created a distinct mosaic of different successional stages (Eichel, 2017; Eichel et al., 2013), with late-successional vegetation and pronounced soil development only occurring on stable slope parts (Eichel et al., 2018). Wietrzyk et al. (2016) found that the steepness of moraine hills was a strong predictor of the variability of vegetation abundance and diversity, especially in the older parts of glacier forefields.

Glacio-fluvial erosion disturbances are generally most intense near the glacier ice front and thereafter decreases downstream direction as successions proceed (Matthews, 1992; Matthews, 1999). Downstream changes in the pattern of river channels are controlled by numerous parameters including: water discharge, terrain slope, sediment load, bedrock material and riparian vegetation (Ferguson, 1987). Increasing plant cover stabilizes channel banks and thus lessens the impact of glacio-fluvial processes in re-working of glacigenic sediments (Miller and Lane, 2019). Gurnell et al. (2000) suggested that rivers close to the glacier tend to exhibit 'bar braided patterns' with numerous channel threads, due to the sediment yield and an active floodplain that occupy a large part of the glacier forefield cross-profile. In downstream areas, the development of vegetation stabilizes banks and lead to the progressive gathering of river channels into a single thread. As a result, the active floodplain decreases in width but increases in depth. With increasing distance from the glacier, the decreasing width of the active floodplain caused by the progressive gathering of river channels results in a decline of water supply and thus drought stress in parts of forefield that are not near streams (Whittaker, 1991). Note however the ecosystems on young moraines may also be subjected to drought stress due to the well-drained nature of coarse glacigenic deposits making up initial young moraines, especially before the establishment (Schulz et al., 2013).

The magnitude of periglacial disturbances tends to be the greatest near the glacier snout where temperatures are the lowest (due to the proximity of ice and higher altitude) and where soil moisture is high (Ballantyne, 2002; Haugland and Beatty, 2005). For example, patterned-ground landforms can develop within 10 years following deglaciation (Feuillet and Mercier, 2012). Haugland and Beatty (2005) studied the effect of patterned-ground disturbances on plant successions across chronosequences in several Norwegian glacier forefields and found that plant community microscale heterogeneity was the most conspicuous on intermediate moraines (~70-year-old). Older moraines are less subject katabatic winds and do not exhibit such cold microclimates compared to the moraines close to the glacier (Matthews, 1992). As a result, the declining magnitude of frost action allows the center positions of patterned-ground landforms to become colonized by plants, thus decreasing the microscale heterogeneity (Haugland, 2004; Haugland and Beatty, 2005). Matthews et al. (1998) observed that the intensity of solifluction processes was most intense in the first 30 years following deglaciation and then slowly declined in the forefield of Jotunheimen glacier in Norway. Areas of glacier forefield characterized by permafrost, on the contrary, are intensely impacted by periglacial processes over multi-decadal timescales (Ballantyne, 2002). As well, Marcante et al. (2012) documented that seedlings of pioneer species were significantly more vulnerable to frost damages than species of intermediate and late succession stage in the forefield of Rotmoos glacier (Austria).

Aeolian erosion typically is most prevalent at the edges of glaciers, where katabatic winds are the strongest (Benn and Evans, 1998; Brookfield, 2011; French, 2017), and decreases with increasing distance from the glacier margin (Dijkmans and Törnqvist, 1991; Müller et al., 2016). For example, Riezebos et al. (1986) found the intensity of aeolian deflation rapidly decreased after the formation of a surface lag deposit on young moraines. Furthermore, aeolian erosion is most effective on unvegetated sediments, typically on young moraines (Ballantyne, 2002). Conversely, the magnitude of aeolian deposition is the greatest on terrains that have ground obstacles such as plant cover or boulder and therefore is likely to affect more intensely on ecosystems of older moraines with advanced stages of succession (Müller et al., 2016). Other factors that favor aeolian deposition are: rough topography and wet surfaces and these are most common on young moraines (Ballantyne, 2002; Derbyshire and Owen, 2018).

5.4.2 Phases of succession in deglaciated forefields

Understanding the processes controlling the initial ecosystem development is crucial to making a holistic interpretation of the evolution of ecosystems over the course of glacier forefield succession (Raab et al., 2012). As detailed above, successional change can be driven by various processes whose nature can either be stochastic or deterministic (Chase and Myers, 2011). For deterministic processes, the spatial distribution and relative abundance of species directly results from favorable (e.g., safe sites) or disadvantageous abiotic and biotic environmental conditions. In contrast, stochastic ecological processes create random patterns of species dispersal and changes in the composition and relative abundance of species that are not determined by environmental conditions, also called “niche-based mechanisms” (Vellend, 2010; Chase and Myers, 2011). For example, stochastic views often highlight the role of random chance in ecological processes such as random colonization and extinction as well as ecological drift (Chase and Myers, 2011).

It is generally acknowledged that stochastic processes are more important during the initial stages of primary succession, and decline in importance in the later stages. Conversely, deterministic processes become more dominant with ecosystem development (Cutler et al., 2008). Compatible to this notion, Dini-Andreote et al. (2015) observed a shift from stochasticity-dominated microbial communities in the initial stages of succession toward deterministic-dominated (determined by local abiotic and biotic conditions) changes in microbial communities as succession proceeded. Concerning plant communities, Del Moral (2009) similarly found that the colonization of pioneer plants was stochastic and that the establishment of plant communities in more advanced successional stages was increasingly linked to safe sites, which provide more favorable environmental conditions. Similarly, studies on plant successions in glacier forefields in the Himalayas (Mong and Vetaas, 2006) and in Iceland (Marteinsdóttir et al., 2010) reported that the colonization of pioneer plants was stochastic and was neither related to the distribution of ‘safe’ (undisturbed) sites nor topographic heterogeneity. However, based on a compilation of studies in 43 glacier forefields in western Norway, Robbins and Matthews (2009) suggested that the colonization of pioneer vegetation was not entirely stochastic, but that it was characterized by a low level of determinism, which tended to increase over the course of successions. Nevertheless, other studies showed that the initial patterns of plant and microbe colonization in glacier forefields are linked to the distribution of undisturbed sites which offer favorable geochemical conditions and protect organisms against harsh conditions climatic conditions (e.g., Jumpponen et al., 1999; Andreis et al., 2001; Haugland and Beatty, 2005; Burga et al., 2010; Mori et al., 2013).

Overall, it is assumed that following an initial stochastic phase of primary succession, successional changes become increasingly determined by local abiotic and biotic conditions. Matthews (1992) suggests that ecosystem changes during glacier forefield successions are first dominated by allogenic processes (initial environmental conditions and geomorphological disturbances), with their relative importance declining in relation to biotic processes (i.e. autogenesis) in more developed stages of succession. This is because the magnitude of most geomorphological disturbances decreases with increasing distance from the glacier, while biotic processes become more prevalent and influential. In agreement with this view, Miller and Lane’s (2019) successional model, who transferred the fluvial biogeomorphic succession model by (Corenblit et al., 2007) to glacier forefields, identified four distinct biogeomorphological succession stages. During the initial ‘geomorphic phase’, ecosystem changes would be completely dominated by allogenic processes. Next, abiotic factors determine microbe and plant colonization during the ‘pioneer phase’. Then, abiotic and biotic factors would be of equal importance and would interact during the ‘biogeomorphic phase’ and finally, biotic factors becoming dominant over abiotic factors in the ‘ecological phase’. These stages were also documented on lateral moraines in the Turtmann glacier forefield (Eichel et al. 2013). The idea that successions shifts from being governed by abiotic factors towards being dominated by biotic factors is also supported in Raab et al. (2012).

Here we present a new conceptual model that integrates these various findings and views the evolution of primary successions as segmented into four successive phases: (1) the initial stochastic phase, (2) the allogenic (abiotic) phase, (3) the biogeomorphic phase and finally (4) the autogenic phase. This conceptual view is summarized in Fig. 9 that shows changes in the relative importance of stochastic, allogenic and autogenic processes over the course of successions in glacier forefields. During the initial Stochastic phase (1), stochastic processes are important and may be dominant over allogenic processes. Meanwhile, biotic processes are initiated, but with somewhat marginal importance. This initial stochastic phase is rapidly followed by the Allogenic phase (2) in which spatial patterns of ecosystem structure and evolution are primarily determined by allogenic processes (i.e., initial environmental conditions and geomorphological disturbances).

During the Allogenic phase, the relative importance of biotic processes increases and the relative importance of stochastic processes declines. Allogenic and autogenic processes are equally important and interact during the Biogeomorphic phase. Lastly, in the Biotic phase (4), biotic factors become (e.g., species interactions) become dominant while the relative importance of allogenic factors declines and stochastic processes have a marginal role. Note that the important width of the lines means to account for the fact that the relative importance of stochastic, allogenic and autogenic processes may vary significantly between sites that have different settings.

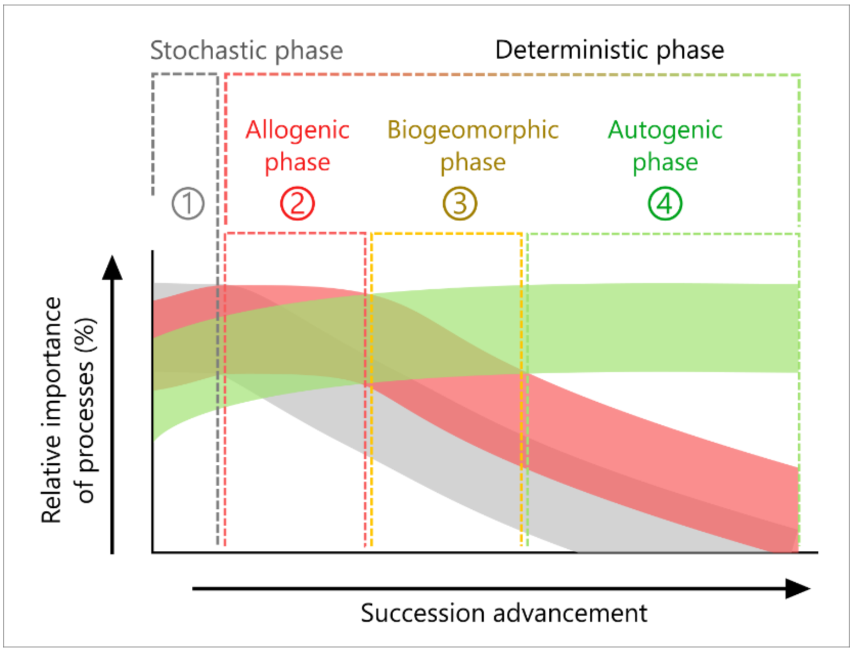

Figure 9: Changes in the relative importance of allogenic, autogenic and stochastic factors over the course of glacier forefield successions. The design of this figure is inspired by Fig. 6.20 in Matthews (1992) as well as Fig. 5 in Miller and Lane (2019).

5.5 Feedbacks between abiotic and biotic processes during ecological succession

Recent research in glacier forefields has demonstrated that the influence of initial site conditions and geomorphological disturbances on soil development and ecological succession is not unidirectional, but that ecological succession changes site conditions and decreases the intensity of geomorphological disturbances (Eichel, 2019; Miller and Lane, 2019). The feedbacks between abiotic and biotic processes dominate in the biogeomorphic phase (Fig. 9), and are an important cause of landscape stabilization in glacier forefields and ecosystem engineering (Gurnell et al., 2000; Eichel et al., 2018).

Ecosystem engineering by microbes and plants in glacier forefields not only promotes soil development and ecological succession but, by creating niches and habitats, it also stabilizes geomorphologically disturbed sites (Haugland and Beatty, 2005; Eichel et al., 2019; Miller and

Lane, 2019). Stabilizing effects by microbial soil crusts, related to increased sediment depositing and binding, have been reported in many forefields (see Miller and Lane 2019 for a complete summary). Initial stabilization, but also increases in moisture and nutrient supply and decreases in paraglacial geomorphic disturbance intensity, can promote colonization by plants, which further contribute to ecosystem engineering and stabilization (Breen and Levesque 2006, Eichel et al. 2016). On lateral moraine slopes in Switzerland, the prostrate, mat-forming shrub *Dryas octopetala L.* was identified as a highly effective ecosystem engineering plant (Eichel et al., 2016; 2017). Through a combination of adapted root and above-ground biomass traits, it mechanically, hydrologically and thermally stabilizes moving slopes. The envelope of conditions under which abiotic-biotic feedbacks dominate depends on process magnitude and plant traits, often termed the "biogeomorphic feedback window" (Eichel et al., 2016; Hortobagyi et al., 2017; Jerin and Phillips, 2020). Biogeomorphic feedbacks can create major alterations to the landscape stability of forefield floodplains and moraine slopes (Eichel, 2019). In floodplains, vegetation colonization stabilizes channel banks and bars, and can, within decades, lead to a shift from braided channel patterns to single thread channel patterns in proglacial runoff (Gurnell, 2000; Moreau et al., 2008). On moraine slopes, colonization by ecosystem engineer species can decrease soil erosional processes and promote periglacial processes, which then cease with increasing colonization of later successional species (Eichel et al. 2018).

5.6 Conclusion

Here we review glacier forefields successions and emphasize that their evolution should be interpreted as the result of (1) time since deglaciation and associated autogenic change, (2) initial site conditions (inactive allogenic factors) and (3) geomorphological disturbances (active allogenic factors). Where abiotic initial site conditions (e.g., microclimate, substrate characteristics and resources availability) are heterogeneous within a glacier forefield, they will differently affect (i.e. by delaying or enhancing) the rate of successional seres toward the same mature stage by providing either favorable or unfavorable conditions, or may even set successional pathways on different trajectories toward different mature stages. The rate and trajectory of successions may also change over the course of successions as a result of disturbances driven by geomorphological (hillslope, glacio-fluvial, periglacial and aeolian) processes. We provide a comprehensive summary of how these allogenic factors can affect the rates and trajectories of glacier forefield successions in a spatially and temporally heterogeneous manner. Additionally, we present a new conceptual model describing the relative importance of autogenic and allogenic factors, and how allogenic factors tends to decline over the course of successions, also due to feedbacks between abiotic and biotic processes.

We emphasize that improving our understanding of the influences of allogenic factors on ecosystems is necessary to develop a correct and holistic understanding of successional changes. Future research efforts must consider not only autogenic processes but also variations in initial site conditions and geomorphological disturbances for any given study design, sampling site selection as well as data analysis and interpretation. Furthermore, we suggest that additional experimental research on laboratory analogues as well as in controlled field settings should be carried out to investigate the effects of variations in allogenic factors on succession behavior in greater details.

Chapter 6: Conclusions

The original work presented in this thesis allows to deepen our understanding of the biogeochemical, physical and microbial features of glacier forefield successions and the processes determining their spatial heterogeneity. This was achieved using an interdisciplinary approach based on empirical work in glacier forefields in Arctic (Svalbard and Iceland) and Alpine (Austrian Alps) environments as well as a literature review.

The first major aim of this thesis was to develop our knowledge of the features of autogenic development in glacier forefields. In succession theory, autogenic development describes the ideal scenario where time since deglaciation is the only variable that explains variation in ecosystem properties. The earliest stages of autogenic development are notoriously studied in glacier forefields with the use of a chronosequence approach, which assumes that distance from the glacier ice front can be used as a proxy for terrain age. In order to investigate the features of the earliest stages of autogenic development, I conducted empirical studies in glacier forefields in Svalbard, Iceland and in the Austrian Alps. In consistence with results of previous studies, I found that the most conspicuous features of autogenic development in glacier forefield include: an increase of nutrient contents, a progression of chemical and physical weathering and increasing abundance and diversity of microbial communities. I consistently found that organic carbon, total nitrogen and total phosphorus contents increased with increasing time since deglaciation in the forefield of Longyearbreen, Fláajökull and Vernagt glaciers. I observed a decrease of soil grain size with increasing terrain age as the result of physical weathering in the forefields of Longyearbreen and Fláajökull glaciers. In the Fláajökull chronosequence, the relative proportion of the <2mm soil size fraction increased along the chronosequence with respect to the >2mm grain size fractions. I documented an increase of clay-sized and silt-sized fraction with increasing time since deglaciation. In the proglacial area of Longyearbreen glacier (shales, siltstones, and sandstones bedrock), I quantified the progression that chemical weathering by documenting an increase of the CIA and a depletion of Ca and Mg in the soil fine-fractions. Similarly, I quantified a progression of chemical weathering in the forefield of Fláajökull glacier (basalt bedrock) via a loss of silica and a decreasing relative abundance in Sr content in the soil fine-fractions. Concurrently, I documented changes in the composition of microbial community structures over the course of successions and observed an overall increase of microbial abundance and diversity with increasing terrain age in the forefield of Longyearbreen and Fláajökull. Finally, I used multivariate statistics to reveal significant correlations between changes in microbial community structures, the build-up of nutrients and the progression of chemical and physical weathering. For example, at the Longyearbreen site, I observed the differences in bacteria, archaea and fungi community structure at the different sites were best explained by variables showing the progression of weathering (Ca, Mg and SiO_2) and nutrient build-up (TOC and TN). At the Fláajökull site, multivariate statistics revealed similar correlations between bacterial community structures and variables showing nutrient build-up (TOC and P), chemical weathering (SiO_2, Sr as well as K_2O, Mg and Ca) and physical weathering (silt, sand and clay). Overall, our complementary and interdisciplinary dataset allowed us to acquire original insights on how changes in microbial communities and geochemical variables linked to weathering lead to the initial formation of soils. I suggest that the functional linkages between geochemical and microbial assemblages must be investigated with greater care in future studies to deepen our understanding of the habitability of recently deglaciated environments.

The second major goal of this thesis was to investigate how factors other than time since deglaciation (allogenic factors) may affect the patterns of glacier forefield successions. In Chapter #5, I build-up a literature review that emphasizes that the features of glacier forefield successions should generically be interpreted as the result of three major factors: (1) time since deglaciation (autogenic development), (2) initial site conditions (inactive allogenic factors) and (3) geomorphological disturbances (active allogenic factors). Specifically, this contribution focuses on how variations in initial site conditions (microclimate, substrate properties and resources availability) and geomorphological disturbances (hillslope, glacio-fluvial, periglacial and aeolian processes) can affect the rate and/or the trajectory of glacier forefield successions in a spatially and temporally heterogeneous manner. The substrate recently exposed by glacier recession may have heterogeneous geochemical and physical characteristics because of different glacigenic depositional processes. Our work done in the forefield of Longyearbreen and Fláajökull glaciers illustrate that the heterogeneity of substrate composition is a major limiting factor to the study of chemical weathering along chronosequences. Additional variability is introduced by heterogeneous microclimatic conditions at the scale of glacier forefields. Microclimatic conditions near the glacier ice front are generally colder because they are determined by katabatic winds that blow down the glacier surface while terrains that are further away from the glacier have a climate that is determined by regional parameters (latitude, altitude, continentality). As well, ecosystems at different positions on a topographic formation may develop differently because they do not have the same level of exposure to winds, precipitations and solar radiations. The development of ecosystems on young moraines may be enhanced by the supply of nutrients in the form of microbial or vegetal organic matter or products of abiotic weathering from subglacial, supraglacial or adjacent ecosystems. Over the course of succession, the evolution of glacier forefield ecosystems may be changed by geomorphological disturbances, which can either directly affect the biota, the substrate (erosion, deposition, mixing) or resources availability (e.g., nutrients and water). Ecosystems at the bottom of hillslopes tend to benefit from the deposition of nutrient, water and fine-grained material whereas ecosystems at the edge of topographic formations (e.g., moraines) or steep slope are underdeveloped as the result of erosion. Similarly, glacio-fluvial and aeolian deposition processes can accelerate ecosystem succession rates by supplying nutrient, water and fine-grained material whereas erosion tends to delay succession rates. At broad spatial scale, the occurrence of periglacial activity tends to delay ecosystem succession rate because of the mixing of ground material. Locally, ecosystems at certain positions of periglacial landforms (e.g. at the edge of sorted circles or at the footslopes of gelifluction landforms) may benefit from the deposition and burial of organic matter. The allogenic processes discussed in chapter 5 are supported by our empirical evidences which emphasize the importance of hillslope (chapter 3), glacio-fluvial (chapters 2 and 3) and aeolian disturbances (chapter 4) on glacier forefield ecosystems. Lastly, in chapter 5, I suggest that the allogenic and stochastic factors are more important at the earliest stages of succession and later tend to decline over the course of succession while autogenic processes become more important.

The findings presented in this thesis emphasize that regular chronosequence studies in glacier forefield should consistently consider the importance of variations in initial site conditions and geomorphological disturbances for the study design, sampling strategy and result analysis and interpretation. Overall, I encourage future research to make efforts to be thoughtful of sample representativity in view of the important heterogeneity of glacier forefield environments. More specifically, I suggest that future research should carry out empirical work to investigate in greater depth how variations in initial site conditions and geomorphological disturbances may affect the ecosystems of glacier forefields at different spatial scales. At small spatial scales (10 to 100 meters), this can be achieved by using a sampling strategy that purposely targets to compare ecosystems of moraines of same ages that have different substrates types, microclimates and resources available or that are exposed to different types of geomorphological disturbances. One can also collect samples along a transect or a trench across an area affect by geomorphological disturbances to examine the variability of ecosystem properties that results from varying degrees of geomorphological disturbances (similar to toposequence in Chapter 3). At the scale of glacier forefields, one would gain insights on the heterogeneity of glacier forefields by using a GIS-based approach to quantitatively characterize the linkages between the spatial variability of plant communities and various abiotic environmental parameters such as microclimatic conditions, substrate properties, terrain slope, aspect and the type and intensity of geomorphological disturbances.

On a related note, little is known on the variability of glacier forefield ecosystems at the global scale and how they may affect the global carbon cycle. I suggest that future research should investigate the parameters controlling the variability of glacier forefield ecosystem's properties (e.g., species composition, biomass, soil carbon storage, succession rates) at the global scale. As well, there currently exists no quantitative estimate of the feedback that biomass build-up and abiotic weathering in glacier forefield may have on the global carbon and nutrient cycles worldwide. Such knowledge would enhance our understanding of the role glacier forefields in global climatic changes and global biogeochemical cycles.

Appendix

List of publications outside the PhD thesis

- Wojcik, Robin, et al. "Land cover and landform-based upscaling of soil organic carbon stocks on the Brøgger Peninsula, Svalbard." Arctic, Antarctic, and Alpine Research 51.1 (2019): 40-57.
- Weiss, N., Faucherre, S., Lampiris, N. and Wojcik, R. (2017). Elevation-based upscaling of organic carbon stocks in High-Arctic permafrost terrain: a storage and distribution assessment for Spitsbergen, Svalbard. Polar Research, 36(1), p.1400363.
- Fláajökull microbiology (Johanna Donhauser)

List of oral presentations

- Wojcik, R., Donhauser, J., Frey, B., Schleicher, A.M. and Benning L.G. Age and geomorphological controls on geo-bio successions in a sub-Arctic glacial forefield. Oral presentation at the EGU2019 Conference in the session 'Biogeochemical cycling in boreal to Polar Regions'. 2019 Apr 7-12; Vienna, Austria.
- Wojcik, R., Donhauser, J., Holm, S., Malard, L., Holland, A., Frey, B., Wagner, D., Pearce, P., Anesio, A. and Benning, L.G. Geochemical and microbiological co-succession in an Arctic glacier forefield. Oral presentation at the POLAR2018 Conference in the session 'Functional ecology of polar microbial communities in a changing world'. 2018 Jun 19-26; Davos, Switzerland.

List of poster presentations

- Wojcik, R., Donhauser, J., Holm, S., Malard, L., Holland, A., Frey, B., Wagner, D., Pearce, P., Anesio, A., Hövelmann, J. and Benning, L.G.B. Geochemical and microbiological gradients in a High-Arctic glacier forefield. Poster presentation at the Arctic Terrestrial Modelling Workshop. 2017 Sep 14-15; Oxford, United Kingdom.
- Wojcik, R., Donhauser, J., Holm, S., Malard, L., Holland, A., Frey, B., Wagner, D., Pearce, P., Anesio, A., Hövelmann, J. and Benning, L.G.B. Geochemical and microbiological gradients in a High-Arctic glacier forefield. Poster presentation at the International Sub-Surface Microbiology conference. 2017 Nov 6-10; Rotorua, New Zealand.
- Wojcik, R., Donhauser, J., Holm, S., Malard, L., Holland, A., Frey, B., Wagner, D., Pearce, P., Anesio, A., Hövelmann, J. and Benning, L.G.B. Geochemical and microbiological gradients in a High-Arctic glacier forefield. Poster presentation at the Goldschmidt Conference. 2017 Aug 13-18; Paris, France.

- Wojcik, R., Palmtag, J. Hugelius, G., Weiss, N. and Kuhry, P. Land cover and landform-based upscaling of soil organic carbon stocks on the Brøgger Peninsula, Svalbard. International Conference on Permafrost (ICOP 2016), Potsdam, Germany, 2016.

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