Review Article

How allogenic factors affect succession in glacier forefields

Robin Wojcik [a,b,*], Jana Eichel [c], James A. Bradley [a,d], Liane G. Benning [a,b]

[a] GFZ German Research Centre for Geosciences, Telegrafenberg, 14473 Potsdam, Germany
[b] Department of Earth Sciences, Free University of Berlin, 12248 Berlin, Germany
[c] Department of Physical Geography, Utrecht University, 3584, CB, Utrecht, the Netherlands
[d] School of Geography, Queen Mary University of London, London, UK

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 successional sequences in a spatially and temporally heterogeneous manner. Here, we emphasize that the patterns of glacier forefield successional sequences should be interpreted as the result of (1) autogenic changes (equivalent to time since deglaciation), (2) initial site conditions and (3) geomorphological disturbances. We provide an original and up-to-date synthesis of knowledge from various fields on how initial local conditions (climate, substrate properties and resources availability) and geomorphological (hillslope, 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 successional sequences. Lastly, we summarize how biota may provide biogeomorphological feedbacks to the major types of geomorphological disturbances taking place in glacier forefields.

1. Introduction

1.1. Succession and chronosequence

A succession is the 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 and 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). A sere (or seral community) is an intermediate stage of a succession. Two different types of successional seres can be distinguished: primary and secondary. Primary successional seres are initiated on recently formed or recently denuded land surface after a primary disturbance has led to the removal or burial of most products of a previous ecosystem, while secondary

successional seres occur after a less severe disturbances where biological legacies such as plant debris and soil organic matter 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, and developing sustainable land-use strategies regarding the protection and management of natural ecosystems, the restoration 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).

The term 'glacial forefield' refers to the area extending between the front of a glacier and the moraine deposited through the latest glacier recession (i.e., the LIA; Matthews, 1992; Anderson, 2007). In addition, the LIA moraine is the terminal moraine that formed at the latest advance of glaciers during the Little Ice Age (LIA), a climatic cooling period that lasted between the 14th and ~ the 19th century. Glacier forefield successional sequences are most commonly studied using a post-incisive chronosequence (space-for-time substitution) approach

---

(Vreeken, 1975), which uses time since deglaciation 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 factors and all sites of a succession are assumed to 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). However, other studies such as Walker et al. (2010) highlighted that these assumptions are likely not always valid and that allogenic factors may affect terrain age.

1.2. Features of autogenic development in succession

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 section provides an overview of the major features of autogenic developments in glacier forefield successional sequences.

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 successional sequences, microbial populations comprise primarily autotrophic (Walker and del Moral, 2003; Bardgett and Walker, 2004) and heterotrophic (Bardgett et al., 2007) microbial populations. 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 novo* microbial colonization (see also Stibal et al., 2020). Microbial communities exert a dominant control on chemical 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; Ciccazzo et al., 2016). The abundance, diversity and activity of soil microbes tend to increase over time since deglaciation (Schmidt et al., 2008; Zumsteg et al., 2012). 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 successional sequences (Jones and Henry, 2003; Jones and del Moral, 2005).

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 (Pérez 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 the soils of recently deglaciated moraines. The effect of nutrient scarcity on soil microbial communities was demonstrated by artificial nutrient addition experiments in glacier forefields (Knelman et al., 2014), that showed that added nutrients dramatically accelerated microbial community succession. 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). Darcy et al. (2018) suggested that phosphorus is more likely to be a limiting nutrient at sites that are subjected to particularly cold and dry conditions (e.g., in areas that have continental climate or high-latitude areas) because cold and dry conditions tend to slow chemical weathering rates. Alternatively, the development of glacier forefield ecosystems rather tends to be limited by nitrogen because at sites with temperate climate where weathering rates are higher and phosphorus is more abundant (Darcy et al., 2018).

The progression of chemical weathering is a commonly observed feature of autogenic development along glacier forefield chronosequences (Egli et al., 2011; Blacker, 2018; Wojcik et al., 2020). Rather than examining the progression of chemical weathering by studying changes in the relative abundance of individual elements or minerals, Wojcik et al. (2020) noted that the overall progression of chemical weathering is better quantified using principal component analyses to evaluate shifts in complementary geochemical, mineralogical and microbiological patterns in forefield soils. Studies on chemical weathering in glacier forefield chronosequences are drastically limited by the facts that: (1) the composition of topsoil material often vary significantly along chronosequence due to the heterogeneous nature of glacial debris, (2) ca. 150 years of exposure is a short amount of time to study chemical weathering and (3) chemical weathering rates in glacier forefield are particularly slow due to cold (Anderson, 2007; Egli et al., 2014) and dry (Egli et al., 2006) climatic conditions. As a result of cold and dry climatic conditions, chemical weathering tends to operate over a kinetic-limited regime rather than a supply-limited regime in glacier forefield (Anderson, 2007). The intensity of the chemical weathering fluxes is directly affected by the reactive mineral surface area exposed and, therefore, is controlled by soil texture.

Changes in soil texture in glacier forefields are driven by two major processes: erosion (allogenic factor) and physical weathering (autogenic factor). Erosion (the transport of rock particles) is primarily driven by the action of gravity, water flow and wind while and physical weathering (the mechanical breakdown of rock particles) is driven by, for example, the action of gravity, water flow, winds as well as plant roots, ice wedges and thermal stress. Soils at the earliest stages of glacier forefield 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 terrain age (Egli et al., 2006; Bernasconi et al., 2011; Wojcik et al., 2020), largely attributed to the effect of physical weathering (Frenot et al., 1995; Mavris et al., 2010). The progression of physical weathering has also been studied via the decrease in surface hardness and surface microroughness on rock weathering rinds along chronosequences in glacier forefields using Schmidt hammer tests (Dąbski, 2009; Dąbski, 2014).

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 essentially driven by time and are taking place in the absence of external environmental factors. On the opposite, changes that are caused by factors or environmental forcings other than time are called allogenic factors (Picket and White, 1985; Matthews, 1992). Note that both autogenic and allogenic factors can be either abiotic or biotic. Biotic autogenic factors can include e.g., organic matter accumulation, plants interactions such as competition, facilitation, predation and abiotic autogenic factors can include e.g., chemical weathering reaction driven by non-biological acidic compounds, physical weathering driven by gravity or frost action. Biotic allogenic factors include e.g., pathogens, allogenic species invasion, animal droppings (e.g., Vilmundardóttir et al., 2015). In this study, we primarily focus on the role of abiotic allogenic factors.

Allogenic factors can influence successional change by affecting the rate and/or the trajectory of successional sequences (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 (Picket and White, 1985; Whittaker, 1991; del Moral and Bliss, 1993). In the case of glacier forefields, the actual 'terrain age' or 'seral community' (intermediate succession stage) 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) and may be strongly uncorrelated with 'distance from the ice front'. For example, if a moraine that was deglaciated 100 yr ago (time since deglaciation) underwent an intense erosion event (e.g., fluvial erosion or slope failure) that has removed most living organisms and organic matter 50 yr ago, then the relative terrain age of this ecosystem should be considered to be 50 yr (scenario B in Fig. 1). Alternatively, ecosystems located in concave formation or at the foot of hillslopes on terrains that have been deglaciated 100 yr ago may resemble the ecosystems of 150 yr old moraines if their development had been enhanced by a balanced addition of nutrients, moisture and fine grained-sediments (scenario C in Fig. 1).

Allogenic factors can also force successional sequences 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
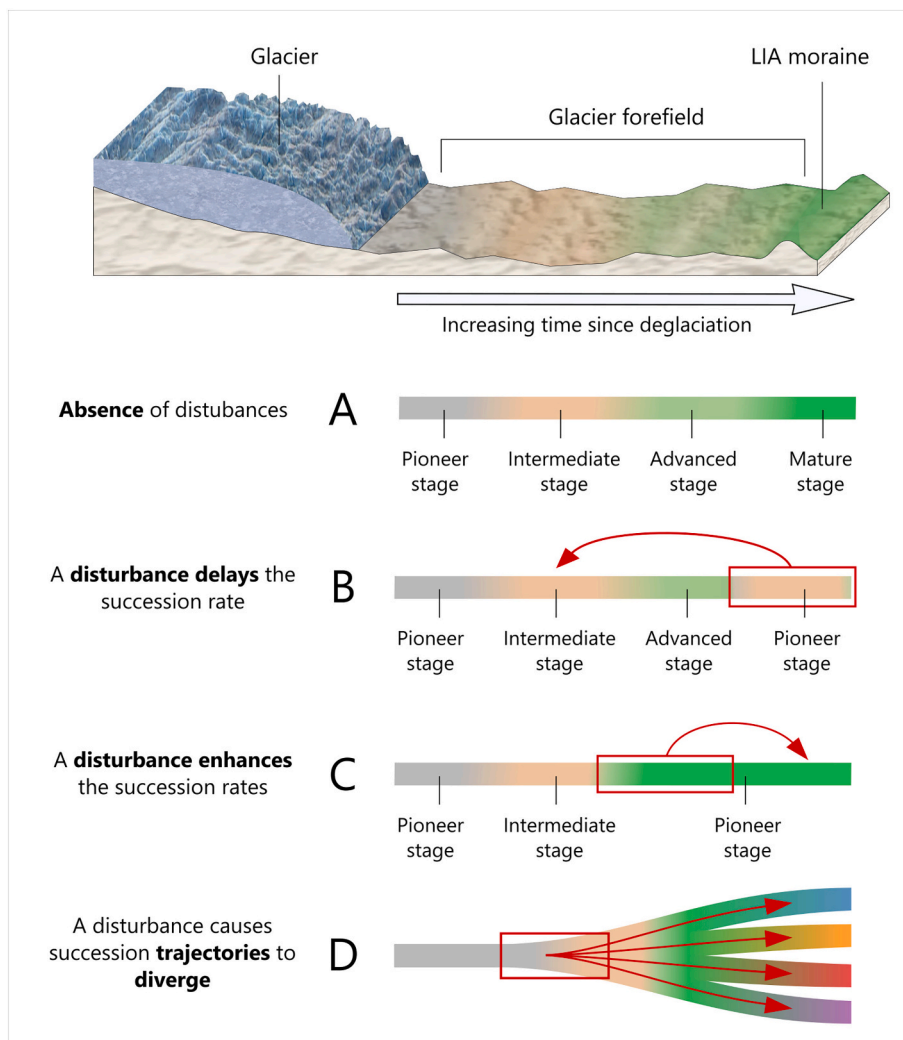
Fig. 1. Schematic representation of how disturbances can affect the rate or trajectory of successional sequences. In scenario A, the succession is solely driven by autogenic change and gradually progresses from pioneer to mature stage without set back, enhancement or trajectory changes. In scenario B, 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 successional sequences, note that initial abiotic site conditions too may create heterogeneity by affecting the rate and trajectory of successional sequences unevenly.

with an 'evolutionary view' of pedogenesis that views soil as an entity that can evolve toward multiple steady states and that is the result of heterogeneous allogenic factors (Huggett, 1998; Phillips, 2017). Disturbances and spatially uneven environmental conditions lead to heterogeneity in successional sequences and can result in the formation of 'mosaic of patches' (Picket and White, 1985; Willig and Walker, 1999; Turner, 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 successional sequences either along divergent or convergent trajectories (Matthews, 1999; del Moral, 2007; del Moral and Titus, 2018). Generalizing on the effect of disturbances on the rate and trajectory of successional sequences 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 successional sequences.

Time since deglaciation (autogenic development) is almost always found to be the dominant parameter explaining patterns observed in glacier forefield successional sequences (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 successional sequences report evidence indicating that typical allogenic factors (i.e., uneven environmental conditions and geomorphological disturbances) affect the rate and trajectory of plant successional sequences (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. 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 for example in Svalbard (e.g., Zwoliński et al., 2013; Miccadei et al., 2016), in Iceland (Jónsson et al., 2016) or in 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 (equivalent to time since deglaciation), as well as variations in (2) initial site conditions and (3) geomorphological disturbances (see Fig. 2).

Similarly, Matthews (1992) highlighted that glacier forefield ecosystems are the result of interactions between multiple biotic and abiotic factors and emphasizes the spatially heterogeneous nature of these ecosystems. Allogenic factors exert a continual influence on the rate and trajectory of glacier forefields successional sequences. 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 succession and the associated soil evolution in glacier forefields. We also discuss how the relative importance of these factors may change over the course of succession.

2. Initial site conditions

As mentioned above, the classical chronosequence approach relies

Glacier forefield succession patterns should be interpreted as the result of variations in:
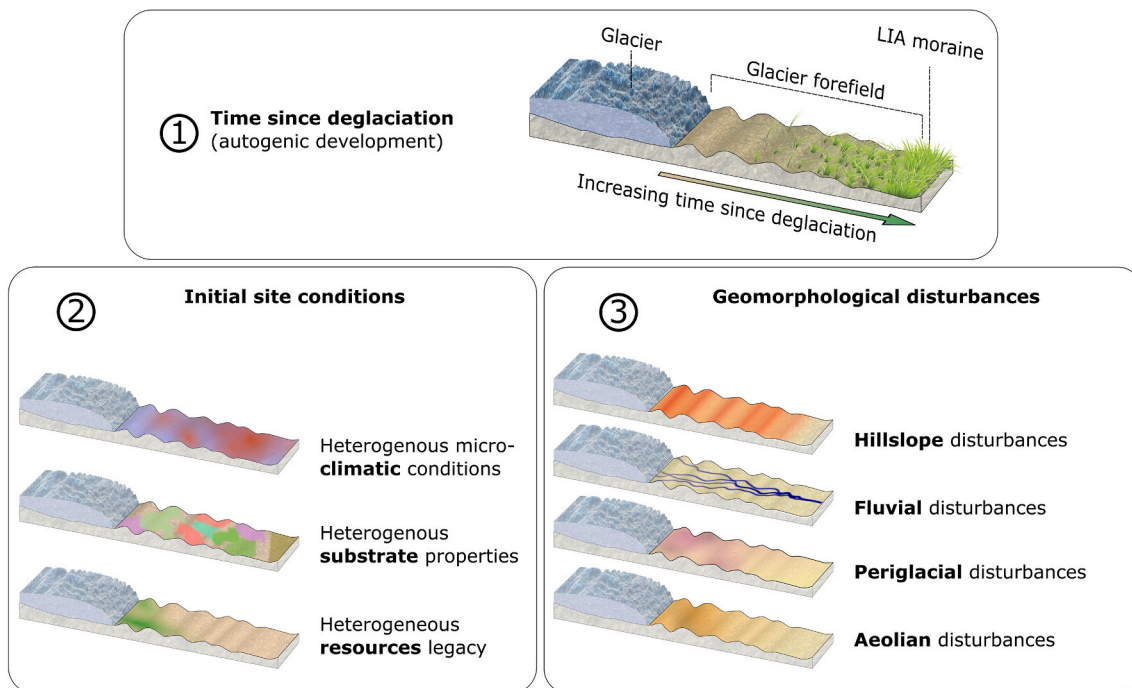

Fig. 2. Schematic representation of the major factors determining ecosystem succession patterns: time since deglaciation, initial site conditions and geomorphological disturbances.

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 these terrains are affected by 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. 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 successional sequences.

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 Fig. 3. In view of the potential differences between 'time since deglaciation' and actual 'terrain age' at sites affected by disturbances, we use the term 'terrain age' to refer to the actual age of the ecosystem since that last major disturbance. Note, however, that parameters such as microclimatic variations are primarily determined by 'distance from the glacier' (katabatic winds) and these are mostly unaffected by geomorphological disturbances.

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 this 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 5.5 °C per 1000 m 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 successional sequences proceeded from pioneer vegetation to birch woodland in a timeframe of 70 years at altitudes below 1000 m, while glacier forefields at 1100 to 1600 m 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 1600 m, 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 angle, aspect 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), because solar radiation directly enhances photosynthetic production, increases temperatures and thus enhances weathering rates, and thus enhances nutrient
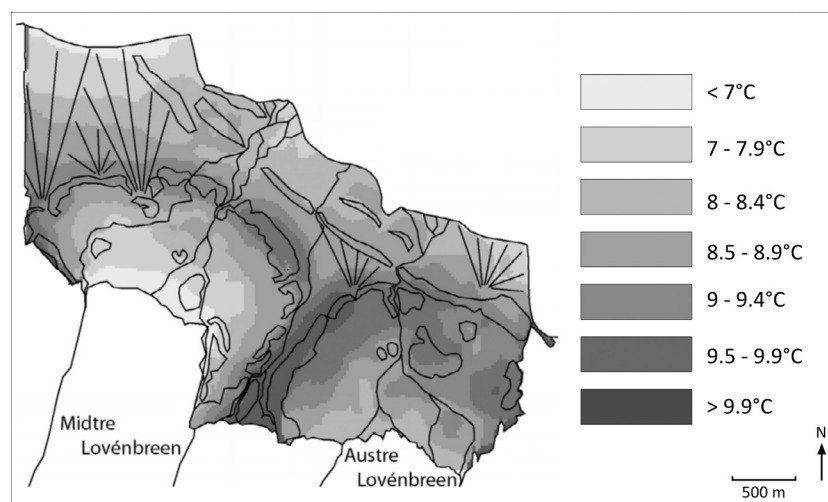

	< 7°C
	7 - 7.9°C
	8 - 8.4°C
	8.5 - 8.9°C
	9 - 9.4°C
	9.5 - 9.9°C
	> 9.9°C

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

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; Tonin et al., 2019) 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 successional sequences (ca. 150 years in the European Alps; Kreutz et al., 1997; Matthews and Briffa, 2005), 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 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).

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 'delivery' 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). Fig. 4 illustrates how differences in the geochemical composition of the substrate can cause sharp differences in biota development in glacier forefields.

Fig. 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 Borin et al. (2010).

The physical properties of the substrate exert also a strong control on ecosystem development. Rates of soil evolution and plant development are typically lower on bedrock outcrops than on unconsolidated sediments (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. Indeed, 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 successional seres 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 Cross, 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).

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).

2.3. Resource availability

Glacier forefield successional sequences are generally considered as primary successional seres (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 (Kabala and Zapart, 2012; Górniak et al., 2017). Subglacial microbial communities are equally abundant and diverse as in many other many permafrost terrains (Skidmore et al., 2000; Foght et al., 2004). Regarding pioneer colonization, Rime et al. (2016) 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 and Hodson, 2007; Lawson et al., 2014a), phosphorus (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. Importantly, subglacial environments may supply large amounts of sediments of various grain sizes to glacier forefields. Note that the regional and interannual variability in catchment scale subglacial sediment discharge rates depend are mainly controlled by variations in water discharge and changes in the morphology of the subglacial environment, which condition the access to subglacial sediments by meltwater (Delaney et al., 2018a, 2018b).

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 glacier forefields 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), it is important to note that it is 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 because 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 and may promote the local development of glacier forefield 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 successional sequences.

3. Geomorphological disturbances

The primary glacigenic deposits exposed by glacier retreat are reworked or 'disturbed' by various 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, 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). 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 disturbances with a specific focus on hillslope, 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.

3.1. Hillslope disturbances

Hillslope disturbances in glacier forefields include mass movement (e.g., slumps, slides, debris flows, Blair Jr, 1994; Emmer et al., 2020) and water-related transport 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) and Eichel (2016) showed a clear impact of hillslope disturbances 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; Eichel, 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 landslides 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). 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 enhance ecosystem succession rates in glacier forefields. In the Rotmoos glacier forefield (Austria), Erschbamer et al. (2001) and Raffl et al. (2006) observed that plant material and earth lumps transported into the forefield by snow avalanches contributed to facilitate 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 often 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 on steep terrains or terrains with pronounced convexity are frequently subjected to erosion and, as a result, tend to be underdeveloped. Alternatively, ecosystems located on terrains that have a concave topography 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 disturbances is illustrated in Fig. 5 which shows that vegetation is more more developed at sites with concave topography rather than at sites with convex topography.

The often-greater soil organic matter content at sites that have a concave topography 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 Cross, 2001) and promotes soil water-retention capacity (Tavenas et al., 1983) at sites that have a concave topography. Sites that have a concave topographyecosystems 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 sites that have a concave topography 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 sites with
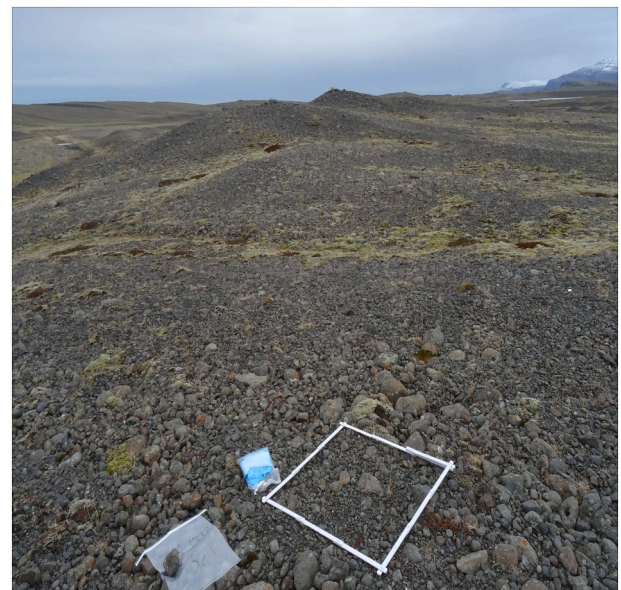

Fig. 5. Photograph of recessional moraines in the forefield of Fláajökull glacier, south-eastern Iceland. The accumulation of nutrients, moisture and fine-grained material enhance the succession rate of ecosystems at sites that have a concave topography. On the contrary, the succession rate of ecosystems on terrains with convex topography (e.g., moraine ridges) and steep terrains is delayed by erosion. © Picture taken by Robin Wojcik in 2017.

concave topography (i.e., footslopes) than at sites with convex topography (i.e., 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. The weight mean method is an interesting approach to acquire data that are representative of the average characteristics of moraines (see also Garibotti et al., 2011a).

3.2. Fluvial disturbances

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). Fluvial disturbance refers to the effects of flowing water on or under glacier forefields.

In a fashion similar to the effects of hillslope disturbances described above, the effects that 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., Gurnell et al., 2000; Osterkamp et al., 2012). Ecosystems and soils on 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 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, 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 melt (Comiti et al., 2019) and snowmelt (Hock, 2005), changes in the magnitude of precipitation events (Haas et al., 2012) or outburst floods (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 topography of

proglacial (i.e., located close to the ice front) (Marren and Toomath, 2014) and subglacial environments (Delaney et al., 2018a, 2018b). In view of the dynamic nature of ecosystems in 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 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). Terrains that are more frequently disturbed (e.g., intermittent river bed) tend to depict lower degrees of development than terrains that are rarely disturbed (e. g., inactive river bed).

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., 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 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 (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

Fig. 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.
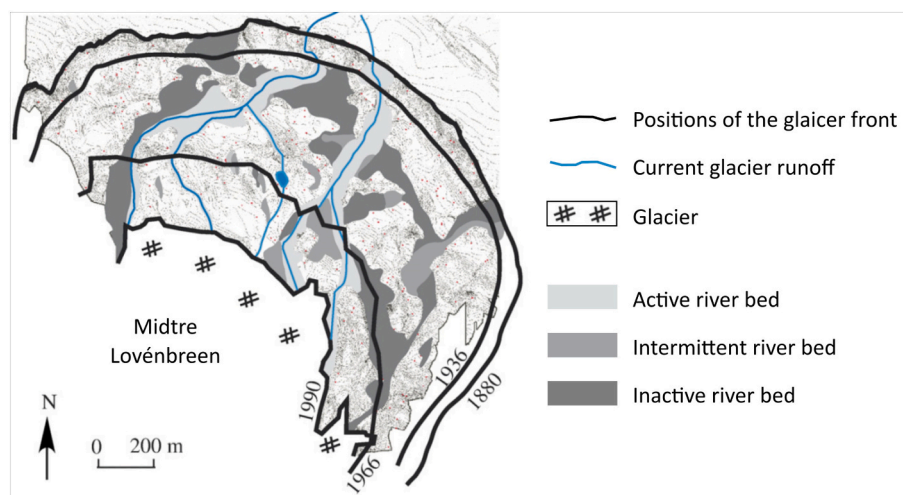

Fig. 6. Map of the forefield of Midtre Lovénbreen glacier (Svalbard). Gray colors represent fluvial landforms with different disturbance frequencies. Figure adapted from Moreau et al. (2008).

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). As well, Haugland and Haugland (2008) described decreasing soil horizon development with increasing frost activity disturbance from undisturbed ground from a polygon border to a polygon center.

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 fluvial processes and thus on the position of streams (Vandenberghe and 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., 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; Wojcik et al., 2020). On solifluction lobes in the Turtmann glacier forefield (Switzerland), Eichel et al. (2017) and Eichel (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. Solifluction disturbances can create fine-scale succession mosaics in glacier forefields, similar to succession mosaics observed at patterned ground.

3.4. Aeolian disturbances

Aeolian processes can also exert a great influence on the rate of succession and its spatial variability in glacier forefields (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 succession. 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, 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

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

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, exposed slopes, moraine crests and other sites that have a convex topography are the most exposed to winds and have higher aeolian erosion rates (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 and Seppälä, 2004), a process that has been extensively described (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 Vater, 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 (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; Müller et al., 2016). Aeolian material preferentially accumulates on the lee side of topographic barriers and vegetation patches (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 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 fluvial areas (Seppala and Seppälä, 2004; Lawrence and Neff, 2009). 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).

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; 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; 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 about 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; Aciego et al., 2017; Diaz et al., 2018), nitrogen (Witherow et al., 2006; Hodson et al., 2010) and other minor and trace elements (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.g., 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 (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; Šantl-Temkiv et al., 2018). However, 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 sub-glacial 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.

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

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 successional change 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 succession in glacier forefields.

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 and Tanner (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 succession 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 succession 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 terrains with convex topography (i.e., moraine crests) and terrains with concave topography (i.e., moraine footslopes) tended to increase with increasing time since deglaciation. However, in some cases, the impact of geomorphological disturbances 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 et al., 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 slope angle of moraine was a strong predictor of the variability of vegetation abundance and diversity, especially in the older parts of glacier forefields.

Fluvial erosion disturbances are generally most intense near the glacier ice front and thereafter decreases downstream direction as successional change 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 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, that 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 of plants (Schulz et al., 2013).

The magnitude of periglacial disturbances tends to be the greatest near the glacier ice front 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 succession 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 near the margins 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 (Djikmans 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).

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 unfavorable 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). Similarly, 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 succession 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 succession. 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 successional sequences 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. 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 successional sequences shifts from being governed by abiotic factors toward being dominated by biotic factors is also supported in Raab et al. (2012). Note, however, that it is possible that rare but high-magnitude events such as glacial lake outburst flood or slope failure erode intensively the valley bottom in a stochastic manner, even at advanced stages of succession.

Here we present a new conceptual model that integrates these various findings and views the evolution of primary successional seres 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. Our conceptual model presented in Fig. 9 shows changes in the relative importance of stochastic, allogenic and autogenic processes over the course of glacier forefield successional sequences. By integrating initial stochastic processes (Mong and Vetaas, 2006; del Moral, 2009; Matthews, 1992; Marteinsdóttir et al., 2010; Dini-Andreote et al., 2015), the changing dominance from allogenic to autogenic factors (Matthews, 1992; Raab et al., 2012) and biogeomorphic feedbacks that influence this transition between the allogenic and autogenic phase (Corenblit et al., 2007; Eichel et al., 2013; Miller and Lane, 2019), our model unifies these different theories (stochasticity/determinism vs. allogenic/autogenic vs. biogeomorphology) into a single synthesis model for the first time.

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. The 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
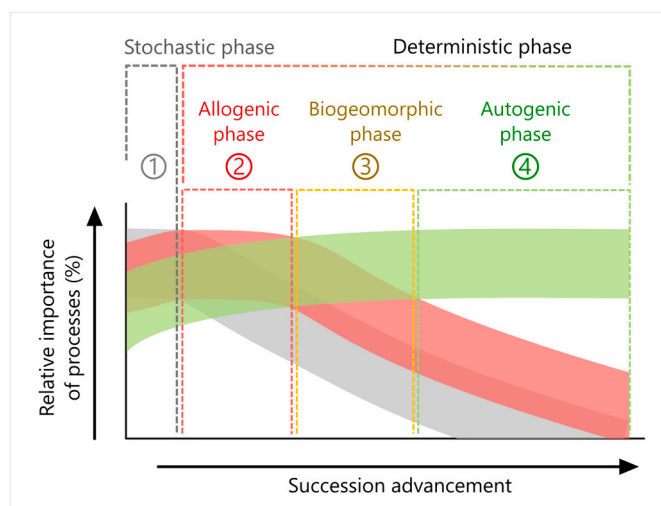
different settings. For example, it is possible that allogenic processes dominate over stochastic processes in the early steps of succession.

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 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 (Eichel, 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). At intermediate succession stages, the increase in moisture and nutrient content from microbial communities combined with with the gradual stabilization of slopes due to decreasing geomorphological activity, promote the development of plant communities, which further contribute to terrain stabilization (Breen and Levesque, 2006; Eichel, 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, 2016; Eichel et al., 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, 2016; 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 et al., 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).

6. Future outlooks

Here we emphasize that typical chronosequence studies in glacier forefield should also consistently take into account the variations in initial site conditions and geomorphological disturbances for the study design, sampling strategy and the analysis and interpretation of data. Overall, we recommend that future research should be mindful of the representativeness of samples in the wider context of the environment being studied, especially considering the heterogeneity of present and past environments and processes. Specifically, we recommend that future research should focus on the following key topics:

(1) Investigating how the variability in the type and intensity of geomorphological disturbances affects glacier forefield ecosystems, and vice versa.
(2) Investigating how the variability of substrate types affects glacier forefield ecosystems.
(3) Investigating how the variability of microclimates affect glacier forefield ecosystems.
(4) Investigating how the legacy of nutrients from subglacial environments affect glacier forefield ecosystems.

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

Furthermore, an aspect that needs attention are studies carried out at smaller spatial scales (i.e., 1 to 100 m), to enable determination of how allogenic factors affect ecosystems of the same age yet that are made up of different substrates, are characterized by different microclimates, are supplied by different resources, or are exposed to different types of geomorphological disturbances. For example, one can gain insights on the variability that is induced by geomorphological disturbances by studying the variability of ecosystems properties across an area affected by disturbances using a transect-based sampling approach (e.g., top-osequence in Wojcik et al., 2020; Garibotti et al., 2011a, 2011b) or even a trench-based sampling approach (e.g., Horwath et al., 2008). Working in interdisciplinary teams and collaborating with geomorphologists working in glacier forelands will help to better map and understand geomorphic disturbances and their effects. One can evaluate in a more quantitative manner the effects of allogenic factors for example by artificially modifying the natural environments and following the change over time. For example, artificial fertilization of soil via the addition of N or P (as in Knelman et al., 2014) can simulate the supply of nutrients from subglacial microbial communities. Furthermore, a better understanding of the effect of climate on ecosystems by artificially modifying climatic condition is needed. Although some studies have addressed these aspects, a compresnesive understanding is still lacking. Better quantitifcation of heterogeneities at the scale of typical glacier forefields (> 1 km) are needed, for example, by using a GIS-based approach to quantify the correlations between the spatial variability of plant communities and various allogenic abiotic environmental parameters, and combining this with detailed ground based monitoring. Finally, remote sensing techniques can also be used to complement chronosequence approaches and assess temporal vegetation changes over larger areas than typicaly possible with ground-based studies (e.g., Klaar et al., 2015; Fischer et al., 2019). Remote sensing studies could also be potentially related to geomorphic disturbances in time and space.

7. Conclusion

The evolution of glacier forefields should be interpreted as the result of (1) time since deglaciation and associated autogenic change, (2) initial site conditions and (3) geomorphological disturbances. 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 succession may also change over the course of succession as a result of disturbances driven by geomorphological (hillslope, fluvial, periglacial and aeolian) processes. We provide a comprehensive summary of how these allogenic factors can affect the rates and trajectories of glacier forefield successional sequences in a spatially and temporally heterogeneous manner. Additionally, we present a new conceptual model describing the relative importance of stochastic, autogenic and allogenic factors, and how allogenic factors tends to decline over the course of successional sequences, also due to biogeomorphic 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.

Declaration of Competing Interest

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

References

Aciego, S.M., Riebe, C., Hart, S., et al., 2017. Dust outpaces bedrock in nutrient supply to montane forest ecosystems. Nat. Commun. 8, 1–10.

Anderson, S.P., 2007. Biogeochemistry of glacial landscape systems. Annu. Rev. Earth Planet. Sci. 35, 375–399.

Anderson, D.G., Bliss, L., 1998. Association of plant distribution patterns and microenvironments on patterned ground in a polar desert, Devon Island, NWT, Canada. Arct. Alp. Res. 30, 97–107.

Anderson, S.P., Drever, J.I., Frost, C.D., et al., 2000. Chemical weathering in the forefield of a retreating glacier. Geochim. Cosmochim. Acta 64, 1173–1189.

Anderson, N.J., Saros, J.E., Bullard, J.E., et al., 2017. The Arctic in the twenty-first century: changing biogeochemical linkages across a paraglacial landscape of Greenland. BioScience 67, 118–133.

Andreis, C., Caccianiga, M., Cerabolini, B., 2001. Vegetation and environmental factors during primary succession on glacier forefields: some outlines from the Italian Alps. In: Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology, 135, pp. 295–310.

Angiel, P., 2006. Variability of textural characteristics of Sandur deposits of Fláajökull and Falljökull (SE Iceland). Miscellanea Geographica 12, 111–117.

Antony, R., Willoughby, A.S., Grannas, A.M., et al., 2017. Molecular insights on dissolved organic matter transformation by supraglacial microbial communities. Environ. Sci. Technol. 51, 4328–4337.

Applegarth, M.T., Dahms, D.E., 2004. Aeolian modification of moraine soils, Whiskey Basin, Wyoming, USA. In: Earth Surface Processes and Landforms: The Journal of the British Geomorphological Research Group, 29, pp. 579–585.

Arce, M.I., Mendoza-Lera, C., Almagro, M., et al., 2019. A conceptual framework for understanding the biogeochemistry of dry riverbeds through the lens of soil science. Earth Sci. Rev. 188, 441–453.

Archer, A., Simpson, M.J.A., Macmillan, B., 1973. Soils and vegetation of the lateral moraine at Malte Brun, Mount Cook region, New Zealand. N. Z. J. Bot. 11, 23–48.

Augusto, L., Achat, D.L., Jonard, M., et al., 2017. Soil parent material—a major driver of plant nutrient limitations in terrestrial ecosystems. Glob. Chang. Biol. 23, 3808–3824.

Bagshaw, E.A., Tranter, M., Fountain, A.G., et al., 2013. Do cryoconite holes have the potential to be significant sources of C, N, and P to downstream depauperate ecosystems of Taylor Valley, Antarctica? Arct. Antarct. Alp. Res. 45, 440–454.

Ballantyne, C.K., 2002. Paraglacial geomorphology. Quat. Sci. Rev. 21, 1935–2017.

Ballantyne, C.K., Matthews, J.A., 1983. Desiccation cracking and sorted polygon development, Jotunheimen, Norway. Arct. Alp. Res. 15, 339–349.

Bardgett, R.D., Walker, L.R., 2004. Impact of coloniser plant species on the development of decomposer microbial communities following deglaciation. Soil Biol. Biochem. 36, 555–559.

Bardgett, R.D., Richter, A., Bol, R., et al., 2007. Heterotrophic microbial communities use ancient carbon following glacial retreat. Biol. Lett. 3, 487–490.

Barry, R., 2008. Geographical controls of mountain meteorological elements. In: Mountain Weather and Climate, pp. 24–108.

Benn, D., Evans, D., 1998. 1998: Glaciers and Glaciation. Arnold, London.

Bennett, M.M., Glasser, N.F., 2011. Glacial geology: ice sheets and landforms. John Wiley and Sons.

Berhe, A.A., Harden, J.W., Torn, M.S., et al., 2008. Linking soil organic matter dynamics and erosion-induced terrestrial carbon sequestration at different landform positions. J. Geophys. Res. Biogeosci. 113.

Bernasconi, S.M., Bauder, A., Bourdon, B., et al., 2011. Chemical and biological gradients along the Damma glacier soil chronosequence, Switzerland. Vadose Zone J. 10, 867–883.

Berthling, I., Etzelmüller, B., Larsen, C.K., et al., 2002. Sediment fluxes from creep processes at Jomfrunut, southern Norway. Norsk Geografisk Tidsskrift-Norwegian J. Geogr. 56, 67–73.

Betz, S., Croce, V., Becht, M., 2019. Investigating morphodynamics on Little Ice Age lateral moraines in the Italian Alps using archival aerial photogrammetry and airborne LiDAR data. Z. Geomorphol. 62, 231–247.

Birkeland, P., Burke, R., 1988. Soil catena chronosequences on eastern Sierra Nevada moraines, California, USA. Arct. Alp. Res. 20, 473–484.

Birkeland, P.W., Berry, M.E., Swanson, D.K., 1991. Use of soil catena field data for estimating relative ages of moraines. Geology 19, 281–283.

Blacker, J.J., 2018. Chemical Weathering Processes Leading to Soil Development in Arctic Glacial Forefields. University of Leeds.

Blair Jr., R., 1994. Moraine and valley wall collapse due to rapid deglaciation in Mount Cook National Park, New Zealand. Mt. Res. Dev. 347–358.

Bockheim, J.G., 2007. Importance of cryoturbation in redistributing organic carbon in permafrost-affected soils. Soil Sci. Soc. Am. J. 71, 1335–1342.

Borin, S., Ventura, S., Tambone, F., et al., 2010. Rock weathering creates oases of life in a High Arctic desert. Environ. Microbiol. 12, 293–303.

Boulton, G.S., Dent, D., 1974. The nature and rates of post-depositional changes in recently deposited till from south-East Iceland. Geografiska Annaler: Seri. A, Phys. Geogr. 56, 121–134.

Boy, J., Godoy, R., Shibistova, O., et al., 2016. Successional patterns along soil development gradients formed by glacier retreat in the Maritime Antarctic, King George Island. Rev. Chil. Hist. Nat. 89, 6.

Bradley, J.A., Singarayer, J.S., Anesio, A.M., 2014. Microbial community dynamics in the forefield of glaciers. Proc. R. Soc. B Biol. Sci. 281, 20140882.

Bradley, J.A., Anesio, A.M., Arndt, S., 2017. Microbial and biogeochemical dynamics in glacier forefields are sensitive to century-scale climate and anthropogenic change. Front. Earth Sci. 5, 26.

Brankatschk, R., Töwe, S., Kleineidam, K., et al., 2011. Abundances and potential activities of nitrogen cycling microbial communities along a chronosequence of a glacier forefield. ISME J. 5, 1025–1037.

Breen, K., Levesque, E., 2006. Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the High Arctic. Botany 84, 1714–1731.

Brockmann-Jerosch, H., 1925. Die Vegetation der Schweiz: Rascher.

Brookfield, M.E., 2011. Aeolian processes and features in cool climates. Geol. Soc. Lond., Spec. Publ. 354, 241–258.

Brunner, I., Plötze, M., Rieder, S., et al., 2011. Pioneering fungi from the Damma glacier forefield in the Swiss Alps can promote granite weathering. Geobiology 9, 266–279.

Burga, C.A., Krüsi, B., Egli, M., et al., 2010. Plant succession and soil development on the forefield of the Morteratsch glacier (Pontresina, Switzerland): straight forward or chaotic?. In: Flora-Morphology, Distribution, Functional Ecology of Plants, 205, pp. 561–576.

Caccianiga, M., Andreis, C., Diolaiuti, G., et al., 2011. Alpine debris-covered glaciers as a habitat for plant life. The Holocene 21, 1011–1020.

Cannone, N., Guglielmin, M., Gerdol, R., 2004. Relationships between vegetation patterns and periglacial landforms in northwestern Svalbard. Polar Biol. 27, 562–571.

Cannone, N., Diolaiuti, G., Guglielmin, M., et al., 2008. Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. Ecol. Appl. 18, 637–648.

Carson, J.K., Rooney, D., Gleeson, D.B., et al., 2007. Altering the mineral composition of soil causes a shift in microbial community structure. FEMS Microbiol. Ecol. 61, 414–423.

Castle, S.C., Sullivan, B.W., Knelman, J., et al., 2017. Nutrient limitation of soil microbial activity during the earliest stages of ecosystem development. Oecologia 185, 513–524.

Cauvy-Frauníe, S., Dangles, O., 2019. A global synthesis of biodiversity responses to glacier retreat. Nat. Ecol. Evol. 3, 1675–1685.

Chapin, F.S., Matson, P.A., Vitousek, P., 2011. Principles of terrestrial ecosystem ecology. Springer Science and Business Media.

Chase, J.M., Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosoph. Transac. Royal Soc. B: Biol. Sci. 366, 2351–2363.

Chesworth, W., 1973. The parent rock effect in the genesis of soil. Geoderma 10, 215–225.

Chesworth, W., 1976. Conceptual models in pedogenesis: a rejoinder. Geoderma 16, 257–260.

Choler, P., 2005. Consistent shifts in alpine plant traits along a mesotopographical gradient. Arct. Antarct. Alp. Res. 37, 444–453.

Ciccazzo, S., Esposito, A., Borruso, et al., 2016. Microbial communities and primary succession in high altitude mountain environments. Ann. Microbiol. 66, 43–60.

Comiti, F., Mao, L., Penna, D., et al., 2019. Glacier melt runoff controls bedload transport in Alpine catchments. Earth Planet. Sci. Lett. 520, 77–86.

Corenblit, D., Tabacchi, E., Steiger, J., et al., 2007. Reciprocal interactions and adjustments between fluvial landforms and vegetation dynamics in river corridors: a review of complementary approaches. Earth Sci. Rev. 84, 56–86.

Crossman, J., Bradley, C., Boomer, I., et al., 2011. Water flow dynamics of groundwater-fed streams and their ecological significance in a glacierized catchment. Arct. Antarct. Alp. Res. 43, 364–379.

Curry, A., Cleasby, V., Zukowskyj, P., 2006. Paraglacial response of steep, sediment-mantled slopes to post-'Little Ice Age' glacier recession in the central Swiss Alps. J. Quat. Sci.: Published Quat. Res. Assoc. 21, 211–225.

Cutler, N., Belyea, L., Dugmore, A., 2008. The spatiotemporal dynamics of a primary succession. J. Ecol. 96, 231–246.

Dabski, M., 2005. Small-scale sorted nets on glacial till, Fláajökull (Southeast Iceland) and Elisbreen (Northwest Spitsbergen). Permafr. Periglac. Process. 16, 305–310.

Dąbski, M., 2009. Early stages of weathering of glacially-abraded limestone surfaces as determined by various Schmidt hammer tests: Biferten glacier forefield, Glarner Alps (Switzerland). Landform Anal. 11, 11–15.

Dąbski, M., 2014. Rock surface micro– roughness, Schmidt hammer rebound and weathering rind thickness within LIA Skálafellsjökull forefield, SE Iceland. Polish Polar Res. 99–114.

D'Amico, M.E., Freppaz, M., Leonelli, G., et al., 2015. Early stages of soil development on serpentinite: the proglacial area of the Verra Grande Glacier, Western Italian Alps. J. Soils Sediments 15, 1292–1310.

Darcy, J.L., Schmidt, S.K., Knelman, J.E., et al., 2018. Phosphorus, not nitrogen, limits plants and microbial primary producers following glacial retreat. Sci. Adv. 4 eaaq0942.

del Moral, R., 2007. Limits to convergence of vegetation during early primary succession. J. Veg. Sci. 18, 479–488.

del Moral, R., 2009. Increasing deterministic control of primary succession on Mount St. Helens, Washington. J. Veg. Sci. 20, 1145–1154.

del Moral, R., Bliss, L.C., 1993. Mechanisms of primary succession: insights resulting from the eruption of Mount St Helens. Adv. Ecol. Res. 1–66. Elsevier.

del Moral, R., Titus, J.H., 2018. Primary succession on Mount St. Helens: rates, determinism, and alternative states. In: Ecological Responses at Mount St. Helens: Revisited 35 Years After the 1980 Eruption. Springer, New York, NY.

Delaney, I., Bauder, A., Werder, M.A., et al., 2018a. Regional and annual variability in subglacial sediment transport by water for two glaciers in the Swiss Alps. Front. Earth Sci. 6, 175.

Delaney, I., Bauder, A., Huss, M., et al., 2018b. Proglacial erosion rates and processes in a glacierized catchment in the Swiss Alps. Earth Surf. Process. Landf. 43, 765–778.

Derbyshire, E., Owen, L., 2018. Glacioaeolian processes, sediments, and landforms. Past Glacial Environ. 273–308. Elsevier.

Deuerling, K., Lyons, W., Welch, S., et al., 2014. The characterization and role of aeolian deposition on water quality, McMurdo Dry Valleys, Antarctica. Aeolian Res. 13, 7–17.

Diaz, M.A., Adams, B.J., Welch, K.A., et al., 2018. Aeolian material transport and its role in landscape connectivity in the McMurdo Dry Valleys, Antarctica. J. Geophys. Res. Earth Surf. 123, 3323–3337.

Dini-Andreote, F., Stegen, J.C., van Elsas, J.D., et al., 2015. Disentangling mechanisms that mediate the balance between stochastic and deterministic processes in microbial succession. Proc. Natl. Acad. Sci. 112, E1326–E1332.

Djikmans, J.A., Törnqvist, T.E., 1991. Modern periglacial eolian deposits and landforms in the Søndre Strømfjord area, West Greenland and their palaeoenvironmental implications. Meddelelser om Grønland. Geosci. 25, 3–39.

Dolezal, J., Homma, K., Takahashi, K., et al., 2008. Primary succession following deglaciation at Koryto Glacier valley, Kamchatka. Arct. Antarct. Alp. Res. 40, 309–322.

Donhauser, J., Frey, B., 2018. Alpine soil microbial ecology in a changing world. In: FEMS Microbiology Ecology, 94 fiy099.

Draebing, D., Eichel, J., 2017. Spatial controls of turf-banked solifluction lobes and their role for paraglacial adjustment in glacier forefields. Permafr. Periglac. Process. 28, 446–459.

Draebing, D., Eichel, J., 2018. Divergence, convergence, and path dependency of paraglacial adjustment of alpine lateral moraine slopes. Land Degrad. Dev. 29, 1979–1990.

Du, Z., Xiao, C., Ding, M., et al., 2018. Identification of multiple natural and anthropogenic sources of dust in snow from Zhongshan Station to Dome A, East Antarctica. J. Glaciol. 64, 855–865.

Dubnick, A., Wadham, J., Tranter, M., et al., 2017. Trickle or treat: the dynamics of nutrient export from polar glaciers. Hydrol. Process. 31, 1776–1789.

Dusik, J.-M., Leopold, M., Haas, F., 2019. Periglacial morphodynamics in the upper Kauneral. In: Geomorphology of Proglacial Systems. Springer, pp. 99–116.

Egli, M., Wernli, M., Kneisel, C., et al., 2006. Melting glaciers and soil development in the proglacial area Morteratsch (Swiss Alps): I. Soil type chronosequence. Arct. Antarct. Alp. Res. 38, 499–509.

Egli, M., Wernli, M., Burga, C., et al., 2011. Fast but spatially scattered smectite-formation in the proglacial area Morteratsch: an evaluation using GIS. Geoderma 164, 11–21.

Egli, M., Dahms, D., Norton, K., 2014. Soil formation rates on silicate parent material in alpine environments: different approaches–different results? Geoderma 213, 320–333.

Eichel, J., 2016. Biogeomorphic Dynamics in the Turtmann Glacier Forefield. Universitäts-und Landesbibliothek Bonn, Switzerland.

Eichel, J., 2019. Vegetation succession and biogeomorphic interactions in glacier forefields. In: Geomorphology of Proglacial Systems. Springer, pp. 327–349.

Eichel, J., Krautblatter, M., Schmidtlein, S., et al., 2013. Biogeomorphic interactions in the Turtmann glacier forefield, Switzerland. Geomorphology 201, 98–110.

Eichel, J., Draebing, D., Klingbeil, L., et al., 2017. Solifluction meets vegetation: the role of biogeomorphic feedbacks for turf-banked solifluction lobe development. Earth Surf. Process. Landf. 42, 1623–1635.

Eichel, J., Draebing, D., Meyer, N., 2018. From active to stable: Paraglacial transition of Alpine lateral moraine slopes. Land Degrad. Dev. 29, 4158–4172.

Emmer, A., Klimeš, J., Hölbling, D., et al., 2020. Distinct types of landslides in moraines associated with the post-LIA glacier thinning: observations from the Kinzl Glacier, Huascarán, Peru. Sci. Total Environ. 139997.

Eneroth, K., Kjellström, E., Holmén, K., 2003. A trajectory climatology for Svalbard; investigating how atmospheric flow patterns influence observed tracer concentrations. Phys. Chem. Earth, Parts A/B/C 28, 1191–1203.

Erel, Y., Dayan, U., Rabi, R., et al., 2006. Trans boundary transport of pollutants by atmospheric mineral dust. Environ. Sci. Technol. 40, 2996–3005.

Erschbamer, B., Kneringer, E., Schlag, R.N., 2001. Seed rain, soil seed bank, seedling recruitment, and survival of seedlings on a glacier forefield in the Central Alps. Flora 196, 304–312.

Fahnestock, J., Povirk, K., Welker, J., 2000. Ecological significance of litter redistribution by wind and snow in arctic landscapes. Ecography 23, 623–631.

Ferguson, R., 1987. Hydraulic and sedimentary controls of channel pattern. In: River channels: Environments and Processes, pp. 129–158.

Feuillet, T., Mercier, D., 2012. Post-Little Ice Age patterned ground development on two Pyrenean proglacial areas: from deglaciation to periglaciation. Geografiska Annaler: Seri. A, Phys. Geogr. 94, 363–376.

Fischer, A., Fickert, T., Schwaizer, G., et al., 2019. Vegetation dynamics in Alpine glacier forelands tackled from space. Sci. Rep. 9, 1–13.

Foght, J., Aislabie, J., Turner, S., et al., 2004. Culturable bacteria in subglacial sediments and ice from two southern hemisphere glaciers. Microb. Ecol. 47, 329–340.

Fortner, S.K., Lyons, W.B., Olesik, J.W., 2011. Eolian deposition of trace elements onto Taylor Valley Antarctic glaciers. Appl. Geochem. 26, 1897–1904.

Fountain, A.G., Lyons, W.B., Burkins, M.B., et al., 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. BioScience 49, 961–971.

French, H.M., 2013. The periglacial environment. John Wiley & Sons.

French, H.M., 2017. The Periglacial Environment. John Wiley and Sons.

French, H., Thorn, C.E., 2006. The changing nature of periglacial geomorphology. Géomorphologie: Relief, Processus, Environ. 12.

Frenot, Y., Van Vliet-Lanoë, B., Gloaguen, J.-C., 1995. Particle translocation and initial soil development on a glacier forefield, Kerguelen Islands, Subantarctic. Arct. Alp. Res. 27, 107–115.

Frey, B., Rieder, S.R., Brunner, I., et al., 2010. Weathering-associated bacteria from the Damma glacier forefield: physiological capabilities and impact on granite dissolution. Appl. Environ. Microbiol. 76, 4788–4796.

Garbarino, M., Lingua, E., Nagel, T.A., et al., 2010. Patterns of larch establishment following deglaciation of Ventina glacier, central Italian Alps. For. Ecol. Manag. 259, 583–590.

Garibotti, I.A., Pissolito, C.I., Villalba, R., 2011a. Spatiotemporal pattern of primary succession in relation to meso-topographic gradients on recently deglaciated terrains in the Patagonian Andes. Arct. Antarct. Alp. Res. 43, 555–567.

Garibotti, I.A., Pissolito, C.I., Villalba, R., 2011b. Vegetation development on deglaciated rock outcrops from Glaciar Frías, Argentina. Arct. Antarct. Alp. Res. 43, 35–45.

Garrido-Benavent, I., Pérez-Ortega, S., Durán, J., et al., 2020. Differential Colonization and Succession of Microbial Communities in Rock and Soil Substrates on a Maritime Antarctic Glacier Forefield. Front. Microbiol. 11, 126.

Geiger, R., Aron, R.H., Todhunter, P., 2009. The Climate Near the Ground. Rowman and Littlefield.

Gellatly, A.F., 1982. Holocene glacial activity in Mt Cook National Park New Zealand: the use of multi-parameter dating techniques to define glacial moraine chronologies.

Glasser, N.F., Hambrey, M.J., 2002. Sedimentary facies and landform genesis at a temperate outlet glacier: Soler Glacier, North Patagonian Icefield. Sedimentology 49, 43–64.

Glausen, T.G., Tanner, L.H., 2019. Successional trends and processes on a glacial forefield in Southern Iceland studied by repeated species counts. Ecol. Process. 8, 11.

Göransson, H., Edwards, P.J., Perreijn, K., et al., 2014. Rocks create nitrogen hotspots and N: P heterogeneity by funnelling rain. Biogeochemistry 121, 329–338.

Göransson, H., Welc, M., Bünemann, E.K., et al., 2016. Nitrogen and phosphorus availability at early stages of soil development in the Damma glacier forefield, Switzerland; implications for establishment of N 2-fixing plants. Plant Soil 404, 251–261.

Górniak, D., Marszałek, H., Kwaśniak-Kominek, M., et al., 2017. Soil formation and initial microbiological activity on a forefield of an Arctic glacier (SW Svalbard). Appl. Soil Ecol. 114, 34–44.

Graly, J.A., Humphrey, N.F., Licht, K.J., 2018. Two metrics describing the causes of seasonal and spatial changes in subglacial aqueous chemistry. Front. Earth Sci. 6, 195.

Grousset, F.E., Ginoux, P., Bory, A., et al., 2003. Case study of a Chinese dust plume reaching the French Alps. Geophys. Res. Lett. 30.

Gruber, S., Hoelzle, M., Haeberli, W., 2004. Permafrost thaw and destabilization of Alpine rock walls in the hot summer of 2003. Geophys. Res. Lett. 31.

Guerrido, C.M., Villalba, R., Amoroso, M.M., et al., 2020. Patterns of tree Establishment following Glacier-Induced Floods in Southern Patagonia. Latin Am. Dendroecol. 225–246. Springer.

Gurnell, A.M., Edwards, P.J., Petts, G.E., et al., 2000. A conceptual model for alpine proglacial river channel evolution under changing climatic conditions. Catena 38, 223–242.

Haas, F., Heckmann, T., Hilger, L., et al., 2012. Quantification and modelling of debris flows in the proglacial area of the Gepatschferner/Austria using ground-based LiDAR.

Haeberli, W., Gruber, S., 2009. Global warming and mountain permafrost. Permafrost Soils 205–218. Springer.

Hancock, G., Murphy, D., Evans, K., 2010. Hillslope and catchment scale soil organic carbon concentration: an assessment of the role of geomorphology and soil erosion in an undisturbed environment. Geoderma 155, 36–45.

Haugland, J.E., 2004. Formation of patterned ground and fine-scale soil development within two late Holocene glacial chronosequences: Jotunheimen, Norway. Geomorphology 61, 287–301.

Haugland, J.E., Beatty, S.W., 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forefields within patterned ground chronosequences. J. Biogeogr. 32, 145–153.

Haugland, J.E., Haugland, B.S.O., 2008. Cryogenic disturbance and pedogenic lag effects as determined by the profile developmental index: the styggedalsbreen glacier chronosequence, Norway. Geomorphology 96, 212–220.

Hawkings, J., Wadham, J.C., Tranter, M., et al., 2016. The Greenland Ice Sheet as a hot spot of phosphorus weathering and export in the Arctic. Glob. Biogeochem. Cycles 30, 191–210.

Heckmann, T., McColl, S., Morche, D., 2016. Retreating ice: research in pro-glacial areas matters. Earth Surf. Process. Landf. 41, 271–276.

Heindel, R.C., Culler, L.E., Virginia, R.A., 2017. Rates and processes of aeolian soil erosion in West Greenland. The Holocene 27, 1281–1290.

Hell, K., Edwards, A., Zarsky, J., et al., 2013. The dynamic bacterial communities of a melting High Arctic glacier snowpack. ISME J. 7, 1814–1826.

Hock, R., 2005. Glacier melt: a review of processes and their modelling. Prog. Phys. Geogr. 29, 362–391.

Hodson, A., Mumford, P., Kohler, J., et al., 2005. The High Arctic glacial ecosystem: new insights from nutrient budgets. Biogeochemistry 72, 233–256.

Hodson, A., Roberts, T.J., Engvall, A.-C., et al., 2010. Glacier ecosystem response to episodic nitrogen enrichment in Svalbard, European High Arctic. Biogeochemistry 98, 171–184.

Horwath, J.L., Sletten, R.S., Hagedorn, B., et al., 2008. Spatial and temporal distribution of soil organic carbon in nonsorted striped patterned ground of the High Arctic. J. Geophys. Res. Biogeosci. 113.

Huggett, R.J., 1998. Soil chronosequences, soil development, and soil evolution: a critical review. Catena 32, 155–172.

Inauen, N., Körner, C., Hiltbrunner, E., 2012. No growth stimulation by CO 2 enrichment in alpine glacier forefield plants. Glob. Chang. Biol. 18, 985–999.

Jäger, D., Winkler, S., 2012. Paraglacial processes on the glacier forefield of Vernagtferner (Ötztal Alps, Austria). In: Zeitschrift für Geomorphologie, Supplementary Issues, 56, pp. 95–113.

Jenny, H., 1941. Factors of soil formation. McGraw-Hill, New York. In: Factors of Soil Formation. McGraw-Hill, New York.

Jerin, T., Phillips, J., 2020. Biogeomorphic keystones and equivalents: examples from a bedrock stream. Earth Surf. Process. Landf. 45 (830), 1877–1894.

Jiang, Y., Lei, Y., Qin, W., et al., 2019. Revealing microbial processes and nutrient limitation in soil through ecoenzymatic stoichiometry and glomalin-related soil proteins in a retreating glacier forefield. Geoderma 338, 313–324.

Johnson, E.A., Miyanishi, K., 2008. Testing the assumptions of chronosequences in succession. Ecol. Lett. 11, 419–431.

Joly, D., Brossard, T., 2007. Contribution of environmental factors to temperature distribution at different resolution levels on the forefield of the Loven Glaciers, Svalbard. Polar Record 43, 353–359.

Jones, C.C., del Moral, R., 2005. Patterns of primary succession on the forefield of Coleman Glacier, Washington, USA. Plant Ecol. 180, 105–116.

Jones, G.A., Henry, G.H., 2003. Primary plant succession on recently deglaciated terrain in the Canadian High Arctic. J. Biogeogr. 30, 277–296.

Jónsson, S.A., Benediktsson, Í.Ö., Ingólfsson, Ó., et al., 2016. Submarginal drumlin formation and late Holocene history of Fláajökull, Southeast Iceland. Ann. Glaciol. 57, 128–141.

Jumpponen, A., Väre, H., Mattson, K.G., et al., 1999. Characterization of 'safe sites' for pioneers in primary succession on recently deglaciated terrain. J. Ecol. 87, 98–105.

Kääb, A., Kneisel, C., 2006. Permafrost creep within a recently deglaciated glacier forefield: Muragl, Swiss Alps. Permafr. Periglac. Process. 17, 79–85.

Kabala, C., Zapart, J., 2009. Recent, relic and buried soils in the forefield of Werenskiold Glacier, SW Spitsbergen. Polish Polar Res. 30, 161–178.

Kabala, C., Zapart, J., 2012. Initial soil development and carbon accumulation on moraines of the rapidly retreating Werenskiold Glacier, SW Spitsbergen, Svalbard archipelago. Geoderma 175, 9–20.

Klaar, M.J., Kidd, C., Malone, E., et al., 2015. Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability. Earth Surf. Process. Landf. 40, 1088–1100.

Knelman, J.E., Schmidt, S.K., Lynch, R.C., et al., 2014. Nutrient addition dramatically accelerates microbial community succession. PLoS One 9, e102609.

Kobierska, F., Jonas, T., Griessinger, N., et al., 2015. A multi-method field experiment to determine local groundwater flow in a glacier forefield. Hydrol. Process. 29, 817–827.

Kociuba, W., Janicki, G., Dyer, J.L., 2019. Contemporary changes of the channel pattern and braided gravel-bed floodplain under rapid small valley glacier recession (Scott River catchment, Spitsbergen). Geomorphology 328, 79–92.

Konhauser, K., 2007. Introduction to geomicrobiology, microbial weathering (pp. 192–235). Blackwell Publishing, UK.

Körner, C., 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems. Springer, Berlin, Germany.

Kreutz, K.J., Mayewski, P.A., Meeker, L.D., et al., 1997. Bipolar changes in atmospheric circulation during the Little Ice Age. Science 277, 1294–1296.

Kroonenberg, S., Hoorn, M., Moura, M., et al., 1990. Variability in bulk geochemistry of fluvial terrace sands: consequences for the study of weathering chronosequences. Pédologie 40, 19–31.

Krüger, J., 1994. Sorted polygons on recently deglaciated terrain in the Highland of Mælifellssandur, South Iceland. Geografiska Annaler: Seri. A, Phys. Geogr. 76, 49–55.

Lambers, H., Raven, J.A., Shaver, G.R., et al., 2008. Plant nutrient-acquisition strategies change with soil age. Trends Ecol. Evol. 23, 95–103.

Lambert, C.B., Resler, L.M., Shao, Y., et al., 2020. Vegetation change as related to terrain factors at two glacier forefronts, glacier National Park, Montana, USA. J. Mt. Sci. 17, 1–15.

Langston, A.L., Tucker, G.E., Anderson, R.S., et al., 2015. Evidence for climatic and hillslope-aspect controls on vadose zone hydrology and implications for saprolite weathering. Earth Surf. Process. Landf. 40, 1254–1269.

Lawrence, C.R., Neff, J.C., 2009. The contemporary physical and chemical flux of aeolian dust: a synthesis of direct measurements of dust deposition. Chem. Geol. 267, 46–63.

Lawson, D.E., 1979. Semdimentological Analysis of the Western Terminus Region of the Matanuska Glacier, Alaska (Cold regions research and engineering lab hanover nh).

Lawson, E.C., Bhatia, M.P., Wadham, J.L., et al., 2014a. Continuous summer export of nitrogen-rich organic matter from the Greenland Ice Sheet inferred by ultrahigh resolution mass spectrometry. Environ. Sci. Technol. 48, 14248–14257.

Lawson, E.C., Wadham, J.L., Tranter, M., et al., 2014b. Greenland Ice Sheet exports labile organic carbon to the Arctic oceans. Biogeosciences 11.

Lazzaro, A., Hilfiker, D., Zeyer, J., 2015. Structures of microbial communities in alpine soils: seasonal and elevational effects. Front. Microbiol. 6, 1330.

Leopold, M., Dusik, J., Stocker-Waldhuber, M., et al., 2015. Permafrost Aggradation in Recently Deglaciated Alpine Environments (EGU General Assembly Conference Abstracts).

Lepš, J., Rejmánek, M., 1991. Convergence or divergence: what should we expect from vegetation succession? Oikos 261–264.

Li, X., Yi, C., Chen, F., et al., 2006. Formation of proglacial dunes in front of the Puruogangri Icefield in the Central Qinghai–Tibet Plateau: Implications for reconstructing paleoenvironmental changes since the Lateglacial. Quat. Int. 154, 122–127.

Lugon, R., Delaloye, R., Serrano, E., et al., 2004. Permafrost and little ice age glacier relationships, Posets Massif, Central Pyrenees, Spain. Permafr. Periglac. Process. 15, 207–220.

Magnusson, J., Kobierska, F., Huxol, S., et al., 2014. Melt water driven stream and groundwater stage fluctuations on a glacier forefield (Dammagletscher, Switzerland). Hydrol. Process. 28, 823–836.

Mahowald, N.M., Artaxo, P., Baker, A.R., et al., 2005. Impacts of biomass burning emissions and land use change on Amazonian atmospheric phosphorus cycling and deposition. Glob. Biogeochem. Cycles 19.

Maizels, J., 1973. Le glacier des Bossons. Quelques aspects caracteristiques de l'environnement proglaciaire. In: Revue de Geographie Alpine, 61, pp. 427–447.

Marcante, S., Sierra-Almeida, A., Spindelböck, J.P., et al., 2012. Frost as a limiting factor for recruitment and establishment of early development stages in an alpine glacier forefield? J. Veg. Sci. 23, 858–868.

Marren, P.M., 2005. Magnitude and frequency in proglacial rivers: a geomorphological and sedimentological perspective. Earth Sci. Rev. 70, 203–251.

Marren, P.M., Toomath, S.C., 2014. Channel pattern of proglacial rivers: topographic forcing due to glacier retreat. Earth Surf. Process. Landf. 39, 943–951.

Marteinsdóttir, B., Svavarsdóttir, K., Thórhallsdóttir, T.E., 2010. Development of vegetation patterns in early primary succession. J. Veg. Sci. 21, 531–540.

Matsuoka, N., 2001. Solifluction rates, processes and landforms: a global review. Earth Sci. Rev. 55, 107–134.

Matthews, J.A., 1978. Plant colonisation patterns on a gletschervorfeld, southern Norway: a meso-scale geographical approach to vegetation change and phytometric dating. Boreas 7, 155–178.

Matthews, J.A., 1987. Regional variation in the composition of Neoglacial end moraines, Jotunheimen, Norway: an altitudinal gradient in clast roundness and its possible palaeoclimatic significance. Boreas 16, 173–188.

Matthews, J.A., 1992. The ecology of recently-deglaciated terrain: a geoecological approach to glacier forefields. Cambridge University Press.

Matthews, J.A., 1999. Disturbance regimes and ecosystem response on recently-deglaciated substrates. Ecosyst. World 17–38.

Matthews, J.A., Briffa, K.R., 2005. The 'Little Ice Age': re-evaluation of an evolving concept. Geografiska Annaler: Seri. A, Phys. Geogr. 87, 17–36.

Matthews, J.A., Vater, A.E., 2015. Pioneer zone geo-ecological change: Observations from a chronosequence on the Storbreen glacier forefield, Jotunheimen, southern Norway. Catena 135, 219–230.

Matthews, J.A., Harris, C., Ballantyne, C.K., 1986. Studies on a gelifluction lobe, Jotunheimen, Norway: 14C chronology, stratigraphy, sedimentology and palaeoenvironment. Geografiska Annaler: Seri. A, Phys. Geogr. 68, 345–360.

Matthews, J.A., Shakesby, R.A., Berrisford, M.S., et al., 1998. Periglacial patterned ground on the Styggedalsbreen glacier forefield, Jotunheimen, southern Norway: micro-topographic, paraglacial and geoecological controls. Permafr. Periglac. Process. 9, 147–166.

Mavris, C., Egli, M., Plötze, M., et al., 2010. Initial stages of weathering and soil formation in the Morteratsch proglacial area (Upper Engadine, Switzerland). Geoderma 155, 359–371.

McCarroll, D., 1991. Relative-age dating of inorganic deposits: the need for a more critical approach. The Holocene 1, 174–180.

McColl, S.T., Draebing, D., 2019. Rock slope instability in the proglacial zone: state of the Art. Geomorphol. Progl. Syst. 119–141. Springer.

McConnell, J.R., Edwards, R., Kok, G.L., et al., 2007. 20th-century industrial black carbon emissions altered arctic climate forcing. Science 317, 1381–1384.

McCutcheon, J., Lutz, S., Williamson, C., et al., 2020. Mineral phosphorous drives glacier algal blooms on the Greenland Ice Sheet. Nat. Commun. 12, 1–11.

Meier, L.A., Krauze, P., Prater, I., et al., 2019. Pedogenic and microbial interrelation in initial soils under semiarid climate on James Ross Island, Antarctic Peninsula region. Biogeosciences 16, 2481–2499.

Mercier, D., 2001. Le ruissellement au Spitsberg. Presses Univ Blaise Pascal.

Miccadei, E., Piacentini, T., Berti, C., 2016. Geomorphological features of the Kongsfjorden area: Ny-Ålesund, Blomstrandøya (NW Svalbard, Norway). Rendiconti Lincei 27, 217–228.

Miller, H.R., Lane, S.N., 2019. Biogeomorphic feedbacks and the ecosystem engineering of recently deglaciated terrain. Progr. Phys. Geogr.: Earth. Environ. 43, 24–45.

Mindl, B., Anesio, A.M., Meirer, K., et al., 2007. Factors influencing bacterial dynamics along a transect from supraglacial runoff to proglacial lakes of a high Arctic glacieri. FEMS Microbiol. Ecol. 59, 307–317.

Mitchell, R.B., Clark, W.C., Cash, D.W., et al., 2006. Global environmental assessments: information and influence. MIT Press.

Mong, C.E., Vetaas, O.R., 2006. Establishment of Pinus wallichiana on a Himalayan glacier forefield: stochastic distribution or safe sites? Arct. Antarct. Alp. Res. 38, 584–592.

Morche, D., Schuchardt, A., Dubberke, K., et al., 2015. Channel morphodynamics on a small proglacial braid plain (Fagge River, Gepatschferner, Austria). Proce. Int. Assoc. Hydrol. Sci. 367, 109.

Moreau, M., Mercier, D., Laffly, D., 2004. Un siècle de dynamiques paraglaciaires et végétales Sur les marges du Midre Lovénbreen, Spitsberg Nord-occidental/a century of paraglacial and plant dynamics in the Midre Lovénbreen forefield (northwestern Spitsbergen). Géomorphologie: Relief, Processus, Environ. 10, 157–168.

Moreau, M., Mercier, D., Laffly, D., et al., 2008. Impacts of recent paraglacial dynamics on plant colonization: a case study on Midtre Lovénbreen forefield, Spitsbergen (79 N). Geomorphology 95, 48–60.

Mori, A.S., Osono, T., Uchida, M., et al., 2008. Changes in the structure and heterogeneity of vegetation and microsite environments with the chronosequence of primary succession on a glacier forefield in Ellesmere Island, high arctic Canada. Ecol. Res. 23, 363–370.

Mori, A.S., Uchida, M., Kanda, H., 2013. Non-stochastic colonization by pioneer plants after deglaciation in a polar oasis of the Canadian High Arctic. Polar Sci. 7, 278–287.

Müller, M., Thiel, C., Kühn, P., 2016. Holocene palaeosols and aeolian activities in the Umimmalissuaq valley, West Greenland. The Holocene 26, 1149–1161.

Nakatsubo, T., Bekku, Y.S., Uchida, M., et al., 2005. Ecosystem development and carbon cycle on a glacier forefield in the High Arctic, Ny-Ålesund, Svalbard. J. Plant Res. 118, 173–179.

Okin, G.S., Mahowald, N., Chadwick, O.A., et al., 2004. Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Glob. Biogeochem. Cycles 18.

Oliver, C.D., Adams, A., Zasoski, R.J., 1985. Disturbance patterns and forest development in a recently deglaciated valley in the northwestern Cascade Range of Washington, USA. Can. J. For. Res. 15, 221–232.

Osterkamp, W., Hupp, C.R., Stoffel, M., 2012. The interactions between vegetation and erosion: new directions for research at the interface of ecology and geomorphology. Earth Surf. Process. Landf. 37, 23–36.

Palmtag, J., Cable, S., Christiansen, H.H., et al., 2018. Landform partitioning and estimates of deep storage of soil organic matter in Zackenberg, Greenland. Cryosphere 12, 1735–1744.

Pearce, D.A., Alekhina, I.A., Terauds, A., et al., 2016. Aerobiology over Antarctica–a new initiative for atmospheric ecology. Front. Microbiol. 7, 16.

Pech, P., Arques, S., Jomelli, V., et al., 2007. Spatial and temporal biodiversity variations in a high mountain environment: the case of the proglacial margin of the Evettes, Natura 2000 area (Savoie, French Alps). Cybergeo. Eur. J. Geogr. 374, 23.

Pérez, C.A., Aravena, J.C., Silva, W.A., et al., 2014. Ecosystem development in short-term postglacial chronosequences: N and P limitation in glacier forefields from Santa Inés Island, Magellan Strait. Austral Ecol. 39, 288–303.

Phillips, J.D., 2017. Soil complexity and pedogenesis. Soil Sci. 182, 117–127.

Picket, S.T., White, P., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic, Orlando (FL).

Pickett, S.T.A., Wu, J., Cadenasso, M., 1999. Patch dynamics and the ecology of disturbed ground: a framework for synthesis. Ecosyst. World 707–722.

Pithan, F., Mauritsen, T., 2014. Arctic amplification dominated by temperature feedbacks in contemporary climate models. Nat. Geosci. 7, 181–184.

Pörtner, H.-O., Roberts, D.C., Masson-Delmotte, V., et al., 2019. IPCC Special Report on the Ocean and Cryosphere in a Changing Climate.

Pourrier, J., Jourde, H., Kinnard, C., et al., 2014. Glacier meltwater flow paths and storage in a geomorphologically complex glacial forefield: the case of the Tapado glacier, dry Andes of Chile (30 S). J. Hydrol. 519, 1068–1083.

Pye, K., 2015. Aeolian dust and dust deposits. Elsevier.

Raab, T., Krümmelbein, J., Schneider, A., et al., 2012. Initial ecosystem processes as key factors of landscape development—a review. Phys. Geogr. 33, 305–343.

Raffl, C., Mallaun, M., Mayer, R., et al., 2006. Vegetation succession pattern and diversity changes in a glacier valley, Central Alps, Austria. Arct. Antarct. Alp. Res. 38, 421–428.

Rasmussen, C., Heckman, K., Wieder, W.R., et al., 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry 137, 297–306.

Ravi, S., Breshears, D.D., Huxman, T.E., et al., 2010. Land degradation in drylands: Interactions among hydrologic–aeolian erosion and vegetation dynamics. Geomorphology 116, 236–245.

Rech, J.A., Reeves, R.W., Hendricks, D.M., 2001. The influence of slope aspect on soil weathering processes in the Springerville volcanic field, Arizona. Catena 43, 49–62.

Rehberger, S., 2002. Vegetationsdynamik auf Moränendauerflächen des Grossen Aletschgletschers im Wallis: erste Ergebnisse aus den Neuaufnahmen der 54-jährigen Flächen van Lüdi. Geographica Helvetica 57, 184–193.

Ren, Z., Martyniuk, N., Oleksy, I.A., et al., 2019. Ecological stoichiometry of the mountain cryosphere. Front. Ecol. Evol. 7, 360.

Riezebos, P., Boulton, G., Van Der Meer, J., et al., 1986. Products and effects of modern eolian activity on a nineteenth-century glacier-pushed ridge in West Spitsbergen, Svalbard. Arct. Alp. Res. 18, 389–396.

Rime, T., Hartmann, M., Frey, B., 2016. Potential sources of microbial colonizers in an initial soil ecosystem after retreat of an alpine glacier. ISME J. 10, 1625–1641.

Robbins, J.A., Matthews, J.A., 2009. Pioneer vegetation on glacier forefields in southern Norway: emerging communities? J. Veg. Sci. 20, 889–902.

Robbins, J.A., Matthews, J.A., 2010. Regional variation in successional trajectories and rates of vegetation change on glacier forefields in south-Central Norway. Arct. Antarct. Alp. Res. 42, 351–361.

Rydgren, K., Halvorsen, R., Töpper, J.P., et al., 2014. Glacier forefield succession and the fading effect of terrain age. J. Veg. Sci. 25, 1367–1380.

Šabacká, M., Priscu, J.C., Basagic, H.J., et al., 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. Geomorphology 155, 102–111.

Šantl-Temkiv, T., Gosewinkel, U., Starnawski, P., et al., 2018. Aeolian dispersal of bacteria in Southwest Greenland: their sources, abundance, diversity and physiological states. FEMS Microbiol. Ecol. 94 fiy031.

Schmidt, S., Reed, S.C., Nemergut, D.R., et al., 2008. The earliest stages of ecosystem succession in high-elevation (5000 metres above sea level), recently deglaciated soils. Proc. R. Soc. B Biol. Sci. 275, 2793–2802.

Schmidt, S., Porazinska, D., Concienne, B.-L., et al., 2016. Biogeochemical stoichiometry reveals P and N limitation across the post-glacial landscape of Denali National Park, Alaska. Ecosystems 19, 1164–1177.

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

Schumann, K., Gewolf, S., Tackenberg, O., 2016. Factors affecting primary succession of glacier forefield vegetation in the European Alps. Alp. Bot. 126, 105–117.

Seppala, M., Seppälä, M., 2004. Wind as a geomorphic agent in cold climates. Cambridge University Press.

Shahgedanova, M., Kutuzov, S., White, K.H., et al., 2013. Using the significant dust deposition event on the glaciers of Mt. Elbrus, Caucasus Mountains, Russia on 5 May 2009 to develop a method for dating and" provenancing" of desert dust events recorded in snow pack. Atmos. Chem. Phys. 13, 1797–1808.

Sharp, M., Parkes, J., Cragg, B., et al., 1999. Widespread bacterial populations at glacier beds and their relationship to rock weathering and carbon cycling. Geology 27, 107–110.

Shelef, E., Rowland, J.C., Wilson, C.J., et al., 2017. Large uncertainty in permafrost carbon stocks due to hillslope soil deposits. Geophys. Res. Lett. 44, 6134–6144.

Skidmore, M.L., Foght, J.M., Sharp, M.J., 2000. Microbial life beneath a high Arctic glacier. Appl. Environ. Microbiol. 66, 3214–3220.

Skidmore, M., Anderson, S.P., Sharp, M., et al., 2005. Comparison of microbial community compositions of two subglacial environments reveals a possible role for microbes in chemical weathering processes. Appl. Environ. Microbiol. 71, 6986–6997.

Slaymaker, O., 2009. Proglacial, periglacial or paraglacial? Geol. Soc. Lond., Spec. Publ. 320, 71–84.

Smittenberg, R.H., Gierga, M., Göransson, H., et al., 2012. Climate-sensitive ecosystem carbon dynamics along the soil chronosequence of the D amma glacier forefield, S witzerland. Glob. Chang. Biol. 18, 1941–1955.

Stawska, M., 2017. Impacts of geomorphic disturbances on plant colonization in Ebba Valley, Central Spitsbergen, Svalbard. Quaestiones Geographicae 36, 51–64.

Stibal, M., Bradley, J.A., Edwards, A., et al., 2020. Glacial ecosystems are essential to understanding biodiversity responses to glacier retreat. Nat. Ecol. Evol. 4, 686–687.

Stres, B., Sul, W.J., Murovec, B., et al., 2013. Recently deglaciated high-altitude soils of the Himalaya: diverse environments, heterogenous bacterial communities and long-range dust inputs from the upper troposphere. PLoS One 8.

Szymański, W., Maciejowski, W., Ostafin, K., et al., 2019. Impact of parent material, vegetation cover, and site wetness on variability of soil properties in proglacial areas of small glaciers along the northeastern coast of Sørkappland (SE Spitsbergen). Catena 183, 104209.

Tavenas, F., Jean, P., Leblond, P., et al., 1983. The permeability of natural soft clays. Part II: Permeability characteristics. Can. Geotech. J. 20, 645–660.

Temkiv, T.Š., Finster, K., Hansen, B.M., et al., 2012. The microbial diversity of a storm cloud as assessed by hailstones. FEMS Microbiol. Ecol. 81, 684–695.

Temme, A.J., Lange, K., 2014. Pro-glacial soil variability and geomorphic activity - the case of three Swiss valleys. Earth Surf. Process. Landf. 39, 1492–1499.

Temme, A.J., Heckmann, T., Harlaar, P., 2016. Silent play in a loud theatre—Dominantly time-dependent soil development in the geomorphically active proglacial area of the Gepatsch glacier, Austria. Catena 147, 40–50.

Tonin, R., Gerdol, R., Tomaselli, M., et al., 2019. Intraspecific functional trait response to advanced snowmelt suggests increase of growth potential but decrease of seed production in snowbed plant species. Front. Plant Sci. 10, 289.

Tranter, M., Sharp, M., Lamb, H., et al., 2002. Geochemical weathering at the bed of Haut Glacier d'Arolla, Switzerland—a new model. Hydrol. Process. 16, 959–993.

Tscherko, D., Rustemeier, J., Richter, A., et al., 2003. Functional diversity of the soil microflora in primary succession across two glacier forefields in the Central Alps. Eur. J. Soil Sci. 54, 685–696.

Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849.

Turpin-Jelfs, T., Michaelides, K., Blacker, J.J., et al., 2018. Distribution of soil nitrogen and nitrogenase activity in the forefield of a High Arctic receding glacier. Ann. Glaciol. 59, 87–94.

Uhlig, D., Schuessler, J.A., Bouchez, J., et al., 2017. Quantifying nutrient uptake as driver of rock weathering in forest ecosystems by magnesium stable isotopes. Biogeosciences 14, 3111–3128.

Vandenberghe, J., Woo, M.-k., 2002. Modern and ancient periglacial river types. Prog. Phys. Geogr. 26, 479–506.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q. Rev. Biol. 85, 183–206.

Vilmundardóttir, O.K., Gísladóttir, G., Lal, R., 2014. Early stage development of selected soil properties along the proglacial moraines of Skaftafellsjökull glacier, SE-Iceland. Catena 121, 142–150.

Vilmundardóttir, O., Gísladóttir, G., Lal, R., 2015. Between ice and ocean; soil development along an age chronosequence formed by the retreating Breiðamerkurjökull glacier, SE-Iceland. Geoderma 259, 310–320.

Vreeken, W.J.V., 1975. Principal kinds of chronosequences and their significance in soil history. J. Soil Sci. 26, 378–394.

Walker, L.R., 1999. Ecosystems of disturbed ground. Elsevier.

Walker, L.R., del Moral, R., 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press.

Walker, L.R., del Moral, R., 2009. Lessons from primary succession for restoration of severely damaged habitats. Appl. Veg. Sci. 12, 55–67.

Walker, L.R., del Moral, R., 2011. Primary Succession. eLS. John Wiley and Sons, Ltd, Chichester.

Walker, L.R., Wardle, D.A., 2014. Plant succession as an integrator of contrasting ecological time scales. Trends Ecol. Evol. 29, 504–510.

Walker, L.R., Willig, M.R., 1999. An introduction to terrestrial disturbances. Ecosyst. World 1–16.

Walker, L.R., Wardle, D.A., Bardgett, R.D., et al., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.

Ward, J.V., Malard, F., Tockner, K., et al., 1999. Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. Hydrol. Process. 13, 277–293.

Wardle, P., 1980. Primary succession in Westland national park and its vicinity, New Zealand. N. Z. J. Bot. 18, 221–232.

Welch, D., 1970. Substitution of space for time in a study of slope development. J. Geol. 78, 234–239.

Whittaker, R.J., 1989. The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. III. Vegetation-environment relationships. J. Biogeogr. 413–433.

Whittaker, R.J., 1991. The vegetation of the Storbreen gletschervorfeld, Jotunheimen, Norway. IV. Short-term vegetation change. J. Biogeogr. 41–52.

Wietrzyk, P., Węgrzyn, M., Lisowska, M., 2016. Vegetation diversity and selected abiotic factors influencing the primary succession process on the forefield of Gåsbreen, Svalbard. Polish Polar Res. 493–509.

Willemse, N.W., Koster, E.A., Hoogakker, B., et al., 2003. A continuous record of Holocene eolian activity in West Greenland. Quat. Res. 59, 322–334.

Willig, M.R., Walker, L.R., 1999. Disturbance in terrestrial ecosystems: salient themes, synthesis, and future directions. Ecosyst. World 747–768.

Witherow, R.A., Lyons, W.B., Bertler, N.A., et al., 2006. The aeolian flux of calcium, chloride and nitrate to the McMurdo Dry Valleys landscape: evidence from snow pit analysis. Antarct. Sci. 18, 497–505.

Wojcik, R., Donhauser, J., Frey, B., et al., 2018. Linkages between geochemistry and microbiology in a proglacial terrain in the High Arctic. Ann. Glaciol. 59, 95–110.

Wojcik, R., Palmtag, J., Hugelius, G., et al., 2019. Land cover and landform-based upscaling of soil organic carbon stocks on the Brøgger Peninsula, Svalbard. Arct. Antarct. Alp. Res. 51, 40–57.

Wojcik, R., Donhauser, J., Frey, B., et al., 2020. Time since deglaciation and geomorphological disturbances determine the patterns of geochemical, mineralogical and microbial successions in an Icelandic foreland. Geoderma 379, 114578.

Wynn, P., Hodson, A., 2007. Nitrate production beneath a High Arctic glacier, Svalbard. Chem. Geol. 244, 88–102.

Xiaodong, L., Liguang, S., Xuebin, Y., 2004. Textural and geochemical characteristics of proglacial sediments: a case study in the forefield of the Nelson Ice Cap, Antarctica. Acta Geol. Sinica-English Ed. 78, 970–981.

Yariv, S., Cross, H., 2001. Organo-clay complexes and interactions. CRC Press.

Yoo, K., Amundson, R., Heimsath, A.M., et al., 2006. Spatial patterns of soil organic carbon on hillslopes: Integrating geomorphic processes and the biological C cycle. Geoderma 130, 47–65.

Yoo, K., Amundson, R., Heimsath, A.M., et al., 2007. Integration of geochemical mass balance with sediment transport to calculate rates of soil chemical weathering and transport on hillslopes. J. Geophys. Res. Earth Surf. 112.

Zdanowski, M.K., Żmuda-Baranowska, M.J., Borsuk, P., et al., 2013. Culturable bacteria community development in postglacial soils of Ecology Glacier, King George Island, Antarctica. Polar Biol. 36, 511–527.

Zender, C.S., Newman, D., Torres, O., 2003. Spatial heterogeneity in aeolian erodibility: Uniform, topographic, geomorphic, and hydrologic hypotheses. J. Geophys. Res.-Atmos. 108.

Zinger, L., Shahnavaz, B., Baptist, F., et al., 2009. Microbial diversity in alpine tundra soils correlates with snow cover dynamics. ISME J. 3, 850–859.

Zumsteg, A., Luster, J., Göransson, H., et al., 2012. Bacterial, archaeal and fungal succession in the forefield of a receding glacier. Microb. Ecol. 63, 552–564.

Zumsteg, A., Bååth, E., Stierli, B., et al., 2013. Bacterial and fungal community responses to reciprocal soil transfer along a temperature and soil moisture gradient in a glacier forefield. Soil Biol. Biochem. 61, 121–132.

Zwoliński, Z., Giżejewski, J., Karczewski, A., et al., 2013. Geomorphological settings of polish research areas on Spitsbergen. Landform Anal. 22.