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Lichens as pioneer organisms and their role in primary succession

Lišejníky jako pionýrské organismy a jejich role v primární sukcesi

Bachelor's thesis

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Čestné prohlášení

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce, ani její podstatná část, nebyla předložena k získání jiného, nebo stejného akademického titulu.

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Abstract

Primary succession is the process through which a recently unearthed or newly created substrate becomes habitable for colonising organisms. This typically occurs either after a volcanic eruption or the melting of a glacier, or in extreme cases of fire or soil contamination, and can be differentiated from secondary succession by the lack of a seed bank. Pioneer organisms are those considered to be the first to colonise substrates undergoing succession, enduring long periods with minimal nutrients and soil cover, often with little water or shade as well. Certain species of lichen are capable of surviving such conditions and can therefore be found occupying this role. They are also able to weather the substrate and enrich it with nutrients, setting the scene for further colonisation by less hardy species. This work looks at the traits certain lichens possess that make them well-suited to this role, both in facilitating progress into further stages of succession and in surviving the early stage in which they can first appear. It will also cover the weathering process and how lichen metabolites contribute to it. Additionally, the differences between types of localities (such as variance in substrate or climate) where primary succession is occurring will be explored.

Keywords:

Colonisation, competition, facilitation, glacier forefields, lichen metabolites, lichens, nitrogen fixation, substrate, succession, symbiosis, volcanoes, weathering

Abstrakt

Primární sukcese je proces, ve kterém se recentně obnažený nebo nově vytvořený substrát stává více schopný podporovat organismy, které tento substrát osídlí. K iniciaci tohoto procesu typicky dochází po vulkanické erupci, tání ledovce, nebo v extrémních příkladech požáru nebo poškození substrátu toxickými látkami. Tyto lokality se dají charakterizovat nepřítomností diaspor. Pionýrské organismy jsou tedy první kolonizátoři těchto substrátů. V průběhu tohoto procesu musí tedy přežít dlouhé období s minimálním přísunem živin, pokryvem půdy a často i s malým množstvím stínu a vody. Některé druhy lišejníků jsou schopné tyto podmínky přežít a z tohoto důvodu se tyto druhy často nacházejí v roli pionýrských organismů. Jsou schopny zvětrávat substrát a obohatit ho živinami, které fixují, což umožní následné osídlení druhy, které jsou méně životaschopné v těchto podmínkách. Cílem práce je sledovat vlastnosti určitých lišejníků, které jim umožňují uspět v těchto podmínkách – jak ve facilitaci, tak v přežití raných fází sukcese. Zaměřila jsem se zároveň na vliv lišejníkových metabolitů na zvětrávací proces a na odlišnosti mezi lokalitami procházejícími sukcesi (například rozdíly v substrátu nebo klimatu).

Klíčová slova:

Facilitace, fixace dusíku, kolonizace, kompetice, lišejníkové metabolity, lišejníky, předpolí ledovců, substrát, sukcese, symbióza, vulkány, zvětrávání

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1. INTRODUCTION

Succession is the process of gradual replacement of one species by another in response to ecological changes (Bazzaz, 1979). Primary succession is a process in which either completely new or severely disturbed substrates are colonised and become more habitable over time (Walker & del Moral, 2003). In some cases, however, the substrate undergoing this process is either new and has never been colonised previously or has been so affected by a disturbance such as mining or fire that there is no seed bank present (Keane et al., 2004). So, primary succession is the process in which such substrates are colonised for the first time, and lichens are typically found amongst the first colonists (Shure & Ràgsdale, 1977). These early colonisers are referred to as pioneer organisms (Kelly et al., 2014). Current research that is relevant to this topic can include both studies specifically centring successional localities and the species they contain (Wasowicz et al., 2018), along with other studies that focus on the weathering process and soil formation (Aikio et al., 2000), which is key in widening the window of potential colonising species in later phases of the successional process.

This thesis aims to cover the unique conditions that govern the facilitative stage of succession and to elaborate on its importance; to summarise current research on the presence of lichens in different successional localities; to list some of the species of lichen have been observed in varied successional contexts; and to explain how lichens contribute to substrate weathering in primary succession.

Typically, pioneer organisms include not only lichens but also mosses, bacteria, algae, cyanobacteria, and other microorganisms, often found growing together in biological soil crusts (Yoshitake et al., 2010). These organisms are therefore able to benefit from existing within a space where there is little competition, as they are some of the relative few that are well-adapted to survival there. Their presence then benefits other colonisers, as they play an important role in substrate weathering and establishing nutrient cycling (Glime, 2007), which must take place in order for further colonisation to be possible.

Lichens are the product of symbiosis between a mycobiont and a photobiont. The mycobiont, a fungus, is what each species is classified by taxonomically (Nash, 2008). The photobiont is typically a species of green microalgae, but cyanobacterial photobionts are also possible, allowing the lichen access to atmospheric nitrogen (Büdel et al., 2024). Lichens can also contain more than one photobiont; in such cases, they are considered tripartite (e.g. García-Breijo et al., 2023). While, in some rare occasions, lichens can also have stramenopiles (yellow-green algae) as a photobiont, such cases are extremely infrequent (Nash, 2008). Lichen thalli contain their own microbiome in addition to housing photobionts, which has been shown to play

an important function in lichen fitness (Grube et al., 2015). In many cases, lichens are also affected by parasitic fungi growing atop the thallus (Nash, 2008). Therefore, they can be classified both as complete individuals and as manifestations of the ecological interactions that occur between the symbionts and other potential partners, as they are made up of a complex web of various types of relationships between different organisms.

The unique physiological characteristics created within this symbiosis allow lichens to carry out complex ecological functions. If they contain a cyanobacterial photobiont, they are capable of fixing atmospheric nitrogen (Büdel et al., 2024), which can then be deposited into the substrate. Depending on the species, they can live on various substrates such as soil, trees, and rocks (Nash, 2008). Some species are capable of surviving extreme states of being, such as desiccation, which is relevant in the case of very dry and unshaded successional seres (Kranner et al., 2008; Stretch & Viles, 2002). Some are so sensitive in their response to environmental changes to the point that the state of lichen biota in a given location can be used for biomonitoring (Garibotti & Villalba, 2017), which can be helpful in studying what traits are being selected for in different phases of succession. Their nitrogen-fixing abilities make them effective in the role of pioneer organisms, as substrates tend to be poor in nutrients at the beginning of the successional process (Walker & del Moral, 2003).

2. PRIMARY SUCCESSION

While primary succession is distinguished from secondary succession by the severity of the disturbance and a lack of diaspores, a definitive limit between primary and secondary succession is hard to define, and it can be more accurate to see the two as a continuum (Walker & del Moral, 2003). Substrates that provide the highest degree of primary succession, with no existing seed bank or soil cover, are those that were recently created through volcanic activity. Glacial forefields are also very limited as they have lacked biotic cover for thousands of years due to the substrate being covered by the glacier. Post-mining sites differ from the two previous examples because they usually already have some soil cover, but in cases of extreme devastation, this soil can be near-uninhabitable due to changes such as high levels of soil contamination by heavy metals (Mourinha et al., 2022).

When pioneer organisms colonise a new substrate, it is typical for several species to do so either simultaneously or in close proximity to each other, time-wise. This often happens through the establishment of biological soil crusts, which are especially common in arid and semi-arid environments (Zhuang et al., 2015). Biological crusts are made up of lichens, mosses, algae and cyanobacteria (Nyenda et al., 2019). In some cases, lichens are even the dominant organisms (Lalley & Viles, 2008). Due to the soil crusts' extremely low height and adhesion to the surface on which they grow, they are more able to resist being swept away by strong winds or rainfall, which can be helpful in the early stages of succession where there is little protection from the elements (Lalley & Viles, 2008). They also play a key role in nutrient cycling through their uptake of nitrogen (Fernández-Martínez et al., 2017), which allows them to establish this nutrient cycle where it had not been established before. In cases of succession initiated by mining, these crusts are capable of growing on slag and both mechanically and chemically fixing pollutants and thus decreasing their effect on the surrounding environment (Kuang et al., 2023). One key factor in the success of lichens in early succession, therefore, lies in the fact that they do not act alone.

2.1. STAGES OF PRIMARY SUCCESSION

Primary succession can be broken down into different stages, the broadest of which are facilitation and competition. Some organisms, through functions such as substrate weathering or nitrogen fixation, make their surrounding environment more liveable for different species that have more specific ecological needs (Walker & del Moral, 2003). This is the process of facilitation. As succession indicates the replacement of previous species with different ones (one literally succeeds the other), it is natural to assume that primary succession also involves one

species replacing the other. This is largely encompassed in the competitive phase, which follows facilitation. The competitive phase tends to favour larger organisms such as perennial vascular plants (Felinks & Thorsten, 2008). In this part of succession, further colonisation by species that could not have survived in a given sere in its previous state occurs, and these newcomers then begin to compete with previously established populations, and, as they are optimised for existence within the conditions that have come to exist in the sere, they can outcompete facilitative species (Walker & del Moral, 2003). *Figure 1* shows a successional sere, illustrating how the gradual retreat of a glacier allows for a literal timeline of successional phases to appear.

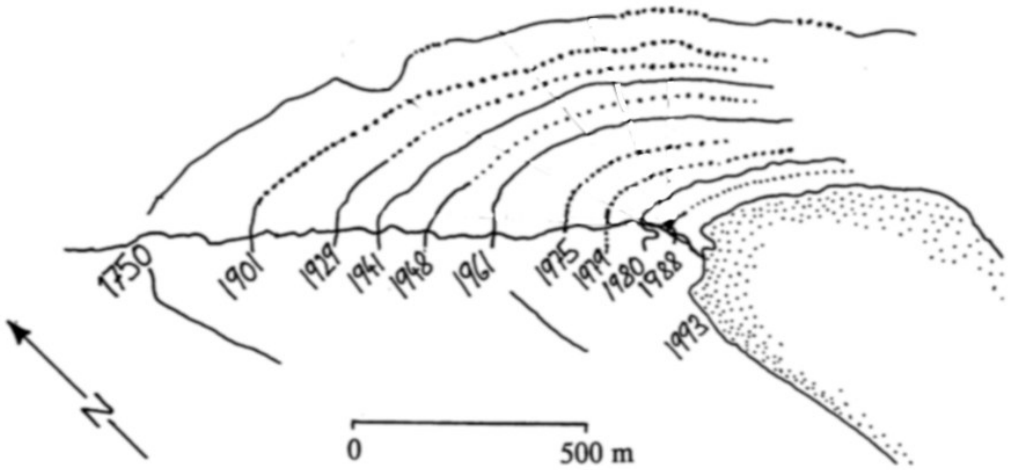

Figure 1: Illustration of the timeline of Hellstugubreen glacier retreat (image source: Hestmark et al., 2007).

Other models have attempted to define stages by the species that dominate at each level. *Figure 2* portrays such shifts in dominance through the example of a successional sere in Puerto Rico. Depending on the locality, these stages can be characterised by the appearance of the substrate's cover (Archer et al., 2017). This is especially relevant to characterising lichen growths as some species, especially those of crustose growth forms, can be difficult to differentiate from the rock surface; effects of biotic weathering can also change the appearance of substrata, which allows changes to be seen as indirect indicators of succession occurring, such as in the case of the surface of sandstones undergoing weathering by endolithic lichens becoming more orange (Jie & Blume, 2002). However, most studies that make use of this method of describing successional stages tend to focus on colonisation by vascular plants, and so, the presence of lichen species is not specified or is only given cursory attention. There are, however, studies that aim to rectify this, such as Fryday and Dillman's (2022) study on the lichen biota at various glacier forefields in different stages of succession, which allowed them to

describe what species were most common in different timespans after the initiation of succession.

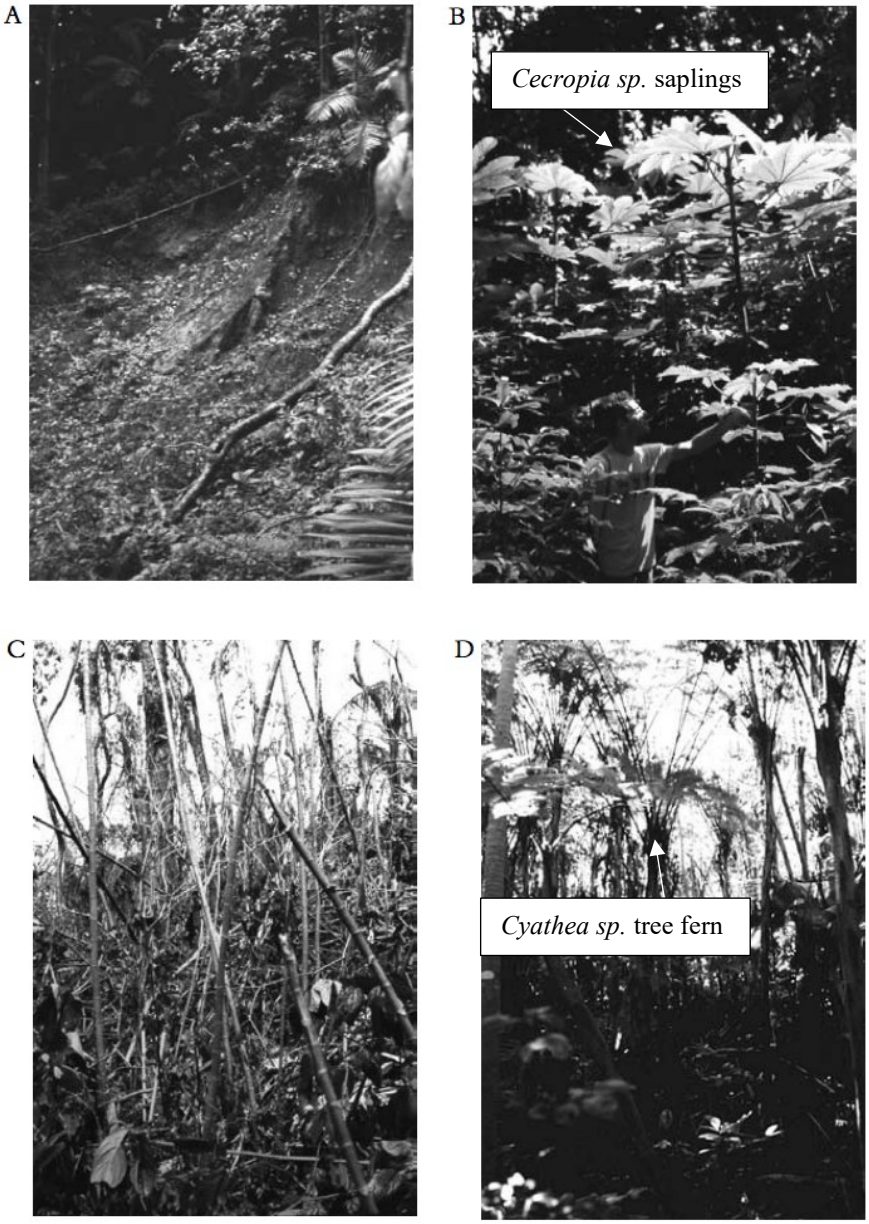

Figure 2: Trajectory of a successional locality, with succession being initiated by a landslide, Puerto Rico; A – initial seedling invasion; B – sapling growth; C – destruction of saplings following a hurricane (disturbance); D – dominance of tall tree ferns (image source: Walker & del Moral, 2003).

2.2. KEY FACTORS IN PRIMARY SUCCESSION

The most impactful factor on successional trajectories has been shown to be the distribution of early colonists, which enter the system mostly by chance, although naturally, the chances of colonisation are improved by closeness to the mainland (in the case of islands) and

favourable air currents that can carry spores or vegetatively reproducing organisms; since it is easier for colonisation by species living closer to the sere to occur than by faraway species, this can slow the successional process, as key species may be prevented from colonising a given sere (Walker & del Moral, 2003). Additionally, challenges that arise from living within environments that are generally considered less hospitable (such as tundras, arctic regions, high elevation, or deserts), compounded with the difficulties that come with living in a successional environment, may slow the pace of the process overall. Since each successional sere is unique, however, and many of the ones that are in more advanced stages today have been undergoing succession for as much as one hundred years or more (Buma et al., 2019; Hestmark et al., 2007; Llambí et al., 2021), it is difficult to disentangle the web of factors that affect each locality and point to one specific factor as the cause of a given condition.

Geomorphological factors already present at the onset of primary succession can also have an effect on the speed of the process. For example factors such as the cardinal direction a sere is facing have been found to affect succession according to McCarthy (1997). Interestingly, cardinal direction can also affect the speed of deglaciation, which has been found to be slowest in glaciers facing north (Rode et al., 2020). This could then affect the time at which primary succession begins to occur in a glacier forefield in comparison to others facing different directions. However, the fact that south-facing seres have been observed to house higher-quality, healthier lichen cover (McCarthy, 1997) could mean that this difference would balance out over time. Elevation could also have an effect. In the case of the Mauna Loa volcano, nitrogen fixation by *Stereocaulon vulcani* was found to be more nutrient limited in higher elevation, due to the comparative lack of nutrients in that area compared to lower elevations in older parts of the sere, where presumably, some nutrient leaching had already occurred and so less was available overall, making nutrients more of a limiting factor than in lower-elevation sites (Kurina & Vitousek, 1999).

The timeline of succession is also affected by the local disturbance regime, especially the extent to which the locality undergoing succession is prone to large-scale disruptions, which can alter or delay the course of succession (Walker & del Moral, 2003). One predictor of an ongoing pattern of disturbance can be volcanic activity, as this typically occurs in places that are geologically unstable in the long term, leading to a higher incidence of earthquakes and further eruptions (Namiki et al., 2019). Since newly formed volcanic substrates are common sites for primary succession, this could indicate that there is a higher chance of repeated disturbances that could affect the outcome of succession. However, any successional locality can be prone to disturbance depending on its geomorphology or even its inhabitants. For example, a steep

mountainside sere might be more prone to disturbance by rockfalls, as steepness has been found to be a contributing factor (Blahůt et al., 2013). Smaller-scale disturbances caused by grazers or trampling from larger animals can also slow the progress of succession due to causing compaction, which, while important in the pedogenetic process, can also make the establishment of seedlings more difficult (Walker & del Moral, 2003).

Climate, especially rainfall, is also an important factor. For example, biological soil crusts, which, as mentioned previously, play a key role at the onset of primary succession, have been found to be less active in polar conditions in comparison to alpine ones, in large part because arctic conditions are very dry in comparison to the Alps, which experience much more fog and, in addition to that, rainfall and dew as well (Colesie et al., 2016). Colesie et al.'s (2016) study found that the only time that Antarctic biological crusts were productive in the summer was during periods following the melting of ice, which resulted in the availability of water. As climate is partially affected by the local topography, it can also be seen as a partial reflection of the geomorphology of a given area (French & Burningham, 2013).

It is important to note that in studies focused on changes over time in one locality, the compounding variables of small differences in conditions at the onset of primary succession are very difficult to accommodate for as such variables cannot be controlled (Wojcik et al. 2021). For example, even highly similar localities, such as two volcanic islands, could have vastly different timing of early colonisation due to dispersal limitations (Makoto & Wilson, 2019). Additionally, it can be difficult to determine the extent to which certain changes brought about in succession – such as the mechanical weathering of rocks – are caused by the passage of time (and the subsequent abiotic weathering that occurs during that timespan) or the biotic activity of the substrate's colonisers, although some studies focus on this as well (Brady et al., 1999).

3. LICHENS AS PIONEER ORGANISMS

Numerous species of lichen are able to survive the harsh conditions that characterise the outset of primary succession, which has led to them being found in the roles of pioneer organisms. However, the makeup of lichen communities also changes with time as species succeed each other (Fryday & Dillman, 2022). This could indicate that while lichens do tend to thrive more in the facilitative phase than in the competitive phase, some species are adapted to survive in the competitive phase as well. Additionally, it could be due to the opening of other ecological niches than those that were available previously. In other chronosequences, certain lichen guilds have managed to remain successful (Hestmark et al., 2007). *Figure 3* shows a glacial forefield in which changes in the local community occurred over time (Fryday & Dillman, 2022).

While the main participants in lichen symbiosis are the photobiont and the mycobiont, various bacteria, parasitic fungi, and secondary photobionts also play an important role in the organism's physiology and overall functioning (Nash, 2008). There are varying interpretations of lichen symbiosis. For example, some posit the role of the mycobiont as the metaphorical farmer of the photobiont (Büdel et al., 2024). This position is strengthened by the fact that while the mycobiont is incapable of surviving without the photobiont, the photobiont can survive on its own (Nash, 2008) – and often does, though not always in the same environmental conditions.

The sexual reproduction of lichens – in other words, the sexual reproduction of the fungal partner in lichen symbiosis – necessitates that the mycobiont acquire a photobiont shortly after establishing itself in order to survive (Nash, 2008). This means that, for sexually reproducing fungi, it is necessary for there to already be an established population of potential photobionts in a given area, and so, colonisation of a successional sere by sexually reproducing lichens necessitates previous or at least simultaneous colonisation by algae or cyanobacteria. However, this is only relevant in the case of sexually reproducing fungi, and so it is not universally applicable to all lichen colonisation processes. For asexually reproducing lichens, soredia have been found to be most effective at long-distance dispersal in Arctic contexts and without correlation to wind speed, temperature or humidity (Marshall, 1996).

Whether or not cyanobacteria or algae are more readily available could also be relevant. Cyanobacteria have been described as being some of the original pioneer organisms of this planet (Zanchett & Oliveira-Filho, 2013), meaning that they are also found in the role of pioneer organisms and in some ways served in that role even during the slow process of initial land colonisation, where they grew in conjunction with other microorganisms on rocks in intertidal zones and formed stromatolites (Petránek et al., 2016). As cyanobacteria are the chief movers in

nitrogen fixation processes in lichen, their presence and incorporation into a colonising lichen could alter the course of succession by speeding up the establishment of nutrient cycling. Therefore, high abundance of cyanobacteria in a given environment could allow for high rates of nitrogen fixation not only from the cyanobacteria themselves but also from lichens in which they have been recruited as photobionts. Higher exposure to light has been found to be effective in increasing nitrogen fixation in some cases (Kurina & Vitousek 1999; Kurina & Vitousek, 2001). Additionally, the photobionts utilised by lichenised fungi in symbiosis could change within a given chronosequence, as the available microorganisms can change over the course of a sere as well (Fernández-Martinez, 2017).

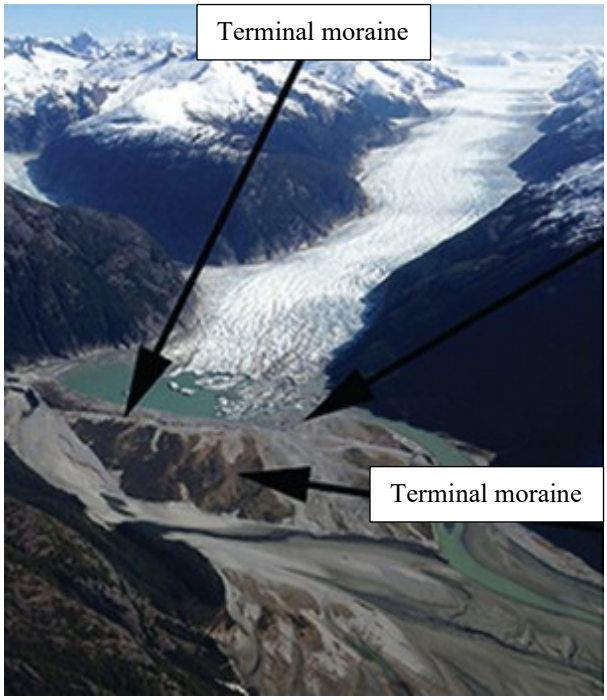

Figure 3: Baird glacier, with arrows pointing towards terminal moraine (image source: Fryday & Dillman, 2022).

3.1. KEY LICHEN SPECIES IN PRIMARY SUCCESSION

Table 1: Key lichen species in primary succession from varied localities

Lichen species	Substrate	Additional information	Source
Placopsis antarctica	Glacial forefields, Antarctica	Transitions between photobiont species over time; the current photobiont is *Stichococcus antarcticus*	Beck et al., 2019
Placopsis contertuplicata	Glacial forefields, Antarctica	Transitions between photobiont species over time; the current photobiont is *Stichococcus allas*	Beck et al., 2019
Stereocaulon alpinum	Glacier forefield in West Greenland	Appeared at the site only 10 years after deglaciation	Beschel & Weidick, 1973
Micarea incrassata	Baird glacier terminal moraine, Alaska	One of the most commonly found species in this location	Fryday & Dillman, 2022
Protopannaria pezizoides	Baird glacier terminal moraine, Alaska	One of most commonly found species in given location	Fryday & Dillman, 2022
Peltigera extenuata	Baird glacier terminal moraine, Alaska	Generally, a rare species outside of this locality	Fryday & Dillman, 2022
Placopsis fustiduloides	Baird glacier terminal moraine, Alaska	Generally, a rare species outside of this locality	Fryday & Dillman, 2022
Protothelenella sphinctrinoidella	Baird glacier terminal moraine, Alaska	Generally, a rare species outside of this locality	Fryday & Dillman, 2022
Placopsis sp.	Baird glacier terminal moraine in pioneer stage, Alaska	Three previously undescribed species; one only found in this locality	Fryday & Dillman, 2022
Umbilicaria sp.	Norwegian glacier forefield, roughly 245 years since deglaciation	Recently deglaciated sections contained only *Umbilicaria hyperborea*, *Umbilicaria cylindrica*	Hestmark et al., 2007
Placopsis gelida	Surtsey Island, volcanic rock; formed November 1963-June 1967	Found present every year for duration of the study (1970-2008)	Kristinsson & Heiðmarsson, 2009
Stereocaulon vesuvianum	Surtsey Island, volcanic rock; formed November 1963-June 1967	Found present every year for duration of the study (1970-2008)	Kristinsson & Heiðmarsson, 2009
Trapelia coarctata	Surtsey Island, volcanic rock; formed November 1963-June 1967	Found present every year for duration of the study (save for 1984) before any other species	Kristinsson & Heiðmarsson, 2009
Stereocaulon vulcani	Mauna Loa volcano in Hawaii; substrate age differs between flows being studied	Higher rates of nitrogen fixation in well-lit areas, with cyanobacteria as secondary photobiont	Kurina & Vitousek, 1999
Stereocaulon vulcani	Réunion island basaltic lava flows; 24 years old since substrate formation	Lichen contains high amounts of Fe and Si	Meunier et al., 2014
Stereocaulon vesuvianum	Volcanic rock in Lanzarote, substrate age: 289 years	Fruticose lichen showing changes in substrate underneath	Stretch & Viles, 2002
Lecanora sp.	Volcanic rock in Lanzarote, substrate age: 289 years	Crustose mosaic co-occuring alongside *Rhizocarpon sp.*	Stretch & Viles, 2002
Rhizocarpon sp.	Volcanic rock in Lanzarote, substrate age: 289 years	Crustose mosaic co-occuring alongside *Lecanora sp.*	Stretch & Viles, 2002
Stereocaulon exutum	Silicate slag at abandoned mine site in Okayama, Japan	Reduces heavy metal pollution in post-mining sites; captures heavy metal fragments in thalli	Sueoka et al., 2015

The genus *Placopsis* has been found in successional contexts on multiple occasions and changes in its photobiont have been correlated with deglaciation time. In *Figure 4*, it can be seen photographed in a successional context at a glacier forefield. As stated in *Table 1*, *Placopsis* lichens have been found to change photobionts in successional localities. Neither *Stichococcus allas* or *Stichococcus antarcticus* occur regularly in the role of photobionts, but despite this, they were found performing that role by Beck et al.'s (2019) study. This could be due to the limitations of the locality during its development, as, at the time the photobionts were incorporated into the symbiosis, there may not have been many alternate options for the role, as common photobionts of the *Placopsis* genus have yet to be found in the Arctic (Beck et al., 2019). Nevertheless, the changes in photobiont over time that *Placopsis antarctica* and *Placopsis contertuplicata* in this locality display imply that the current state is some sort of adapted equilibrium and not simply a product of a scarce potential photobiont pool. The presence of *Placopsis fustiloides* on an Alaskan glacier forefield found by Fryday and Dillman (2022), is also unusual, as this species is generally very rare.

The findings of yet another member of the genus *Placopsis*, namely *Placopsis gelida*, on Surtsey, further illustrate its success in successional contexts (Kristinsson & Heiðmarsson, 2009). Here, these pioneer species were typically found growing inside of air bubble cavities formed during the escape of gases as lava cooled, which would have shielded them from wind due to the concave shape of these cavities (Kristinsson & Heiðmarsson, 2009). Similarly to the studies centring the genus *Placopsis*, *Umbilicaria sp. w*ere also found together with other members of the same genus as mentioned in *Table 1*, with *Umbilicaria cylindrica* being the most common overall in the entire locality, and *Umbilicaria cylindrica* and *Umbilicaria hyperborea*, the third most common overall, being the initial colonising lichens, meaning that they were able to continue to proliferate and increase in ground cover after initial phases of colonisation (Hestmark et al., 2007). *Stereocaulon vesuvianum* and *Placopsis gelida* also went on to be the most widely proliferated of the initial lichen colonisers on Surtsey, along with *Stereocaulon capitellatum*, although that species appeared in 1971, a year after the other two (Kristinsson & Heiðmarsson, 2009).

Also, the observed correlation of photobiont change to deglaciation time is another example of how lichens can be used as bioindicators. Beschel and Weidick (1973) were able to extrapolate deglaciation time from lichen growth rates. Therefore, lichens can be used as bioindicators not only of anthropogenic disturbance (Sueoka et al., 2015) or environmental changes (Malaspina et al., 2014), but also for measuring the passage of time from the rate of their growth. The presence of species that are generally considered rare in other contexts, such

as *Peltigera extenuata*, *Placopsis fustiloides*, and *Protothelenella sphinctrinoidella*, as observed by Fryday and Dillman (2022), could be used to show how the specific ecological constraints of a glacier forefield allow more specialised species to thrive, though they may not in other contexts. The initial findings of *Trapelia coarcata* occurred on the wall of the Surtungur crater, which allowed the site to be consistently warm and often also well-hydrated, which also made the site of their colonisation relatively unique (Kristinsson & Heiðmarsson, 2009).

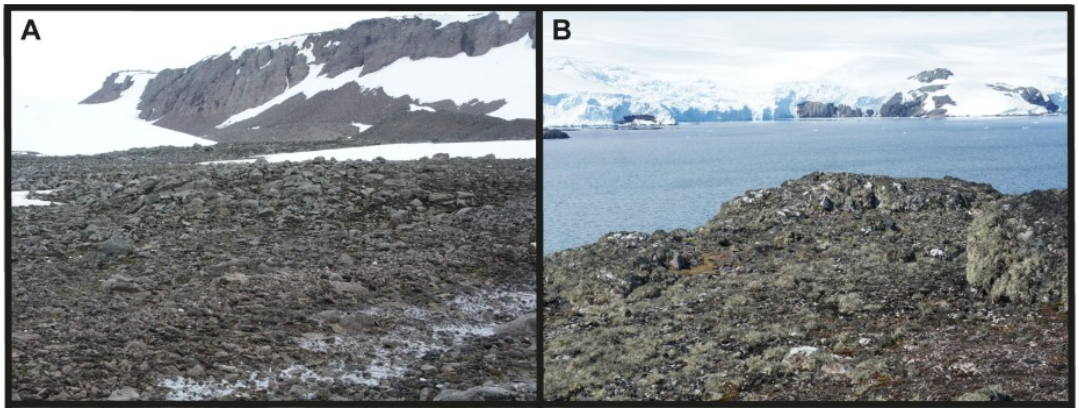

Figure 4: A – pioneer community on King George Island; B – growing Placopsis sp. population (image source: Beck et al., 2019).

Members of the genus *Stereocaulon* were found in volcanic, glacial, and post-mining contexts. As outlined in *Table 1*, *Stereocaulon exutum* was found to contain fragments of post-mining slag substrate that showed signs of weathering, such as being coated in extracellular polymers and secondary minerals (Sueoka et al., 2015). As biological soil crusts often form in these contexts, it is possible that ameliorating effects from this lichen are helped by other pioneer organisms as well, especially in highly acidic contexts (Kuang et al., 2023). Additionally, the species *Stereocaulon alpinum* has been found in post-glacial successional contexts almost immediately after deglaciation. In a glacier foreland in West Greenland, it was found in the earliest possible stages of succession as a pioneer organism, approximately 10 years post-deglaciation (Beschel & Weidick, 1973). The fact that *Stereocaulon vulcani* was found on Réunion Island only 24 years after substrate formation could be used to illustrate how at least some members of this genus are capable of success as pioneer organisms (Meunier et al., 2014).

The lava flows of Lanzarote have been found to be abundant in two fruticose lichens, *Stereocaulon vesuvianum* and *Ramalina bourgeana*, and a mosaic of crustose lichens from the genera *Lecanora* and *Rhizocarpon* (Stretch & Viles, 2002). There is a possibility that the species of *Stereocaulon* found on Lanzarote could actually be *Stereocaulon canariense*, according to Vančurová et al. (2021). The precise nature of the taxonomy of this population of

Stereocaulon remains under study. The island of Lanzarote, which was deeply affected by volcanic activity starting in 1730 and ending in 1736, is a part of the Canary Islands, which experience sub-Saharan climates, with higher magnitudes of evaporation than rainfall (Stretch & Viles, 2002). Interestingly, *Stereocaulon vesuvianum* has also been found on Surtsey Island, despite the very different climates of these two localities (Kristinsson & Heiðmarsson, 2009). The crustose lichens *Lecanora* and *Rhizocarpon* may be at an advantage in this locality over other growth forms, as they retain more water (Inoue et al., 2017), which can be helpful in primary succession in dry locales. However, one important aspect of crustose lichen colonisation is that they often lack vegetative propagules and therefore must rely on sexual reproduction. This could cause issues as it lowers the means through which a given crustose species is able to establish itself by and colonise a successional substrate (Ramkaer, 1978).

Fruticose lichens such as *Stereocaulon* are able to reproduce both sexually and vegetatively (Marshall, 1996), and from these findings, it is clear that species of the genus *Stereocaulon* are abundant in successional contexts. *Stereocaulon vulcani* is capable of fixing atmospheric nitrogen using secondary cyanobacterial photobionts (Kurina & Vitousek 1997; Kurina & Vitousek 1999). In fact, as much as 40% of its nitrogen content has been found to originate from nitrogen fixation (Kurina & Vitousek, 2001). *Stereocaulon vulcani* is also capable of fixing silicon, which was found in the same volume in *Stereocaulon vulcani* growing on 24-year-old lava flows as in a well-established forest above the aforementioned lava flows (Meunier et al., 2014). It is possible to see the dynamic of facilitation play out in its decline on the Mauna Loa volcano in Hawaii, which occurred together with the proliferation of vascular plants (Kurina & Vitousek, 1997). In terms of functioning in a post-mining site, as outlined in *Table 1*, *Stereocaulon exutum* was found to contain fragments of post-mining slag substrate that showed signs of weathering, such as being coated in extracellular polymers and secondary minerals (Sueoka et al., 2015).

4. SUBSTRATE WEATHERING

Weathering is a process in which a rock's surface is broken down, typically through a combination of biotic and abiotic as well as chemical and mechanical processes (Petránek et al., 2016). In the context of succession, this process of breaking down is helpful in soil formation and the establishment of various forms of nutrient cycling (Song et al., 2019), which subsequently enables wider colonisation. The contribution of biotic factors in this process can be substantial; in one described case, biotic weathering processes were found to occur as much as 16 times faster than abiotic ones (Stretch & Viles, 2002). However, in the very beginning stages of succession, there is a much smaller pool of potential sources of biotic weathering, which could make the biotic activity of pioneer organisms all the more impactful.

4.1. CHEMICAL WEATHERING

The close contact of crustose lichens with the substrate surface ensures a high degree of proximity to the object of weathering (Stretch & Viles, 2002), which may allow for more contact with secondary metabolites. However, numerous metabolites are found in all growth forms. They often include compounds such as oxalic acids, oxidoreductases, and cellulases (Beckett et al., 2013; Song et al., 2019). Due to the morphology of lichen thalli, it can be difficult to determine which metabolites are secreted by the photobiont and which originate from the mycobiont (Nash, 2008). There is some evidence that lichen photobionts produce different secondary metabolites than free-living ones, which could allow for colonising lichens in the early stages of succession to contribute metabolites that were previously unavailable in a given locality upon colonisation (Calcott et al., 2018).

Cellulases and oxidoreductases can break down soil organic matter (Beckett et al., 2013; Song et al., 2019), although this process cannot be expected to be as impactful in early phases of succession, in which there are generally not as many sources of organic material as in an ecosystem closer to climax due to low rates of colonisation (Walker & del Moral, 2003). Water melting off glaciers, however, could be a potential source of organic matter that was previously frozen (Stevens et al., 2022), which could be relevant in the case of succession in glacier forefields. As the successional process progresses, the postmortem and excretory processes of other colonisers would allow for the introduction of higher amounts of soil organic matter (Walker & del Moral, 2003), which could help with forming an organic layer in newly formed soil and with enriching this soil with nutrients.

Another key process in lichen weathering is solubilisation, which includes processes such as acidolysis, complexolysis, and alkanolysis, which result in the formation of many

different types of compounds (Berthelin & Munier-Lamy, 1983). The dissolution of carbon dioxide in water into carbonic acid can also contribute to the process, as carbonic, oxalic, and potentially other organic acids contained in lichens cause the dissolution of rock surfaces using hydrogen ions and cation complexation (Jie & Blume, 2002). This is in many cases due to the position of their polar groups, such as OH, CHO, and COOH (Syers & Iskandar, 1973).

Visually, solubilisation can be seen to occur in several steps, illustrated here through the way this process occurs on sandstones. Weed and Norton (1991) describe the process as follows: First, elements of the substrate are mobilised and translocated, which causes changes in the substrate's appearance, which is followed by the formation of a thin silicate crust, which precedes silicification, in which the visual patterns caused by the element migration are preserved in rock due to its hardening. This can allow for these effects to be witnessed in the fossil record (Weed & Norton, 1991). However, organic acids can weather non-sedimentary rock as well (Song et al., 2019), though lichens may not always have as strong of an impact on other kinds of rock, such as in the case of granite (Silva et al., 1999).

4.2. MECHANICAL WEATHERING

The process of mechanical weathering centres around disturbing the cohesion of the rock substrate, which leads to the formation of lesions that increase the surface on which further chemical and mechanical weathering can occur. It can also include erosion. Biotic sources of mechanical weathering include cracking due to the growth of roots into the rock substrate and compaction from the ambulatory movement of large animals, although large animals are not typically present in the earliest phases of succession (Walker & del Moral, 2003). In early successional communities, the lack of meaningful soil cover heightens the degree of contact with bedrock, compounding the effect of the weathering agent. The degree of a lichen's contact with the substrate's surface are highest in crustose species, with foliose lichens coming in second and fruticose having the lowest degree as they grow outwards into bush-like configurations (Nash, 2008), and, as demonstrated by the species present in *Table 1* in Chapter Two, crustose and foliose lichens tend to be more common in successional contexts in comparison to their fruticose counterparts. The proliferation of these growth forms can have an impact on both the chemical and mechanical weathering processes.

Different growth forms can have an effect on the weathering process in different ways. For example, in foliose lichens, the presence of rhizines is most abundant, which allows for the mechanical breakup of rock surfaces (Syers & Iskandar, 1973). Through this, they break up the homogeneity of the rock surface, which allows for the formation of cracks, thus increasing the

weathering surface. Crevices in the substrate can house endolithic lichens, which also interact with the rock surface. While they grow most commonly in sandstones, they have been found in other substrates as well (Archer et al., 2017).

Endolithic (cryptoendolithic, chasmoendolithic, and eudendolithic) lichens play an important role in rock weathering. Cryptoendolithic lichens grow in rock cavities, chasmoendolithic in fissures, and eudendolithic lichens attach to the rock substrate by directly growing into it and because of this, euendolithic lichens can cause a larger mechanical disturbance than the other two types (Jie & Blume, 2002). However, not all successional seres are going to contain the necessary substrates for their growth (which are typically sandstones and other sedimentary rocks) to such a degree that these lichens are able to proliferate enough to have a large impact (Syers & Iskandar, 1973). Additionally, it is possible for lichens to denude a substrate by incorporating its shards into their thalli, as shown in *Figure 5*.

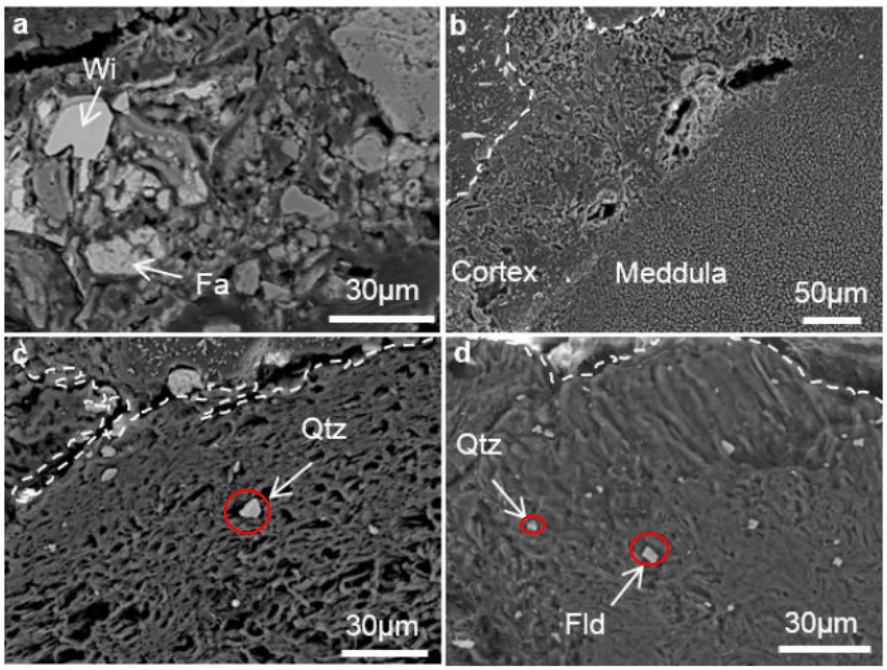

Figure 5: Slag fragments in lichen thalli; red circles used to highlight smaller shards that may otherwise be harder to locate (image source: Sueoka et al., 2015).

The chemical makeup of a substrate is also dependent on nutrient fixation, and lichens' ability to deposit valuable nutrients into their substrate (Kurina & Vitousek, 1997) is a key part of what makes them effective in successional contexts. As mentioned previously, biological soil crusts also take part in this process, such as through the establishment of carbon cycling, although the effectiveness of this can be negatively impacted by increases in temperature outside of the norm and by changes in moisture outside of the optimum (Yoshitake et al., 2010). Additionally, while the ability of nitrogen fixers and other organisms that play pivotal roles in

nutrient cycling may astound in comparison to other species that do not take part in these processes, the nutrients made bioavailable by the contribution of these organisms have to come from somewhere, such as the substrate being weathered. One interesting aspect of the methods used by lichens to assimilate nutrients is that they may not utilise just atmospheric nitrogen, but uptake minerals from their substrate as well, which can be exemplified from the trend towards higher rates of atmospheric rather than substrate-based assimilation was found on Mauna Loa lava flows (Kurina & Vitousek, 1997). Presumably, this is due to the substrate becoming poorer in nutrients over time and atmospheric fixation therefore becoming more profitable.

4.3. FACTORS AFFECTING THE WEATHERING PROCESS

One factor that could change the way weathering affects the substrate is moisture. This includes not only mechanical weathering such as erosion due to streaming water (Petránek et al., 2016), but also more indirect correlations, such as the amount of moisture afforded to colonisers. A successional sere in Svalbard was found to contain high amounts of moisture in young soils (with the youngest being deglaciated for approximately 5 years), but with a lower level of moisture content availability (Cimpoiasu et al., 2024). Certain lichens, especially those with higher-than-average desiccation tolerance, can survive very dry conditions, though they may not be able to be as biologically active during drier periods (Colesie et al., 2016). This can be seen in the way that the deposition rate of organic carbon remains slow even in the presence of biological soil crusts in glacial areas (Stevens et al., 2022), as much of the water in those localities is stored in solid form. Therefore, it can be extrapolated that the speed at which soil cover forms is much slower in cold, dry areas than in more temperate zones, as organic matter is a key component of soil (Voltr et al., 2021). The presence of plant litter, which contributes to soil organic matter, can even be beneficial due to its being a source of phosphorus (Chapin et al., 1994).

Of course, water oversaturation can also affect the direction this process takes. For example, high amounts of water in an ecosystem can cause gleiation (Likhanova et al., 2021). The process of weathering can also be affected by the presence of water, as high precipitation has been shown to quicken the process (Antić et al., 2023). Humidity can increase the speed at which subcritical cracking occurs, which can lead to the formation of larger cracks, which would contribute to mechanical weathering (Eppes & Keanini, 2017). Lichen in combination with water could also increase the weathering rate. While Brady et al. (1999) found abiotic weathering to be proportional to the amount of rainfall, patches of olivine and plagioclase under lichen cover were found to be much more sensitive to weathering from rainfall.

The characteristics of the substrate being weathered heavily affect the process as well. Different factors also impact different substrates in various ways. For example, clay-cemented sandstones are most affected by mineral composition, while pore structure is more important in silicate-cemented sandstones (Labus & Bochen, 2012). However, higher porosity enables faster weathering in general, as it heightens the area of the surface on which weathering is occurring (Oguchi, 2004). The conditions under which a substrate exists also determine the impact of factors such as weather. While rainfall was found to be the leading cause of weathering in silicate substrates, it had an even stronger effect on patches of rock that had been colonised by lichens (Brady et al., 1999). Therefore, the combination of different factors at play in each locality can lead to varying outcomes. Climactic factors can also affect a substrate over time, resulting in cracking (such as when repeated freezing over of water inside the substrate results in changes in the amount of space it takes up, which then over time weakens the rock), and even low-level stressors such as subcritical cracking can culminate in change over time (Eppes & Keanini, 2017).

There has also been some degree of disagreement on the level of importance of lichens as a factor in weathering. In some cases, they can serve as both defences against this process and its enactors, even in localities that have undergone succession for a relatively short period of time, such as Mt. Etna in Sicily and Mt. Vesuvius in Campania (Vingiani et al., 2013). They typically protect primarily against mechanical weathering, such as in the case of lichen cover ameliorating the effects of salt-based erosion on coastal sandstones in the Hilbre Islands (Mikuláš, 1999). In a case of granitic rock weathering, lichen was found to impact the mobility of various elements, although the overall impact of chemical weathering was very similar in lichen-covered and uncovered rocks (Silva et al., 1999). Therefore, while the contributions of lichens to both chemical and mechanical weathering are a recorded phenomenon, they also have their limits, and may be highly situational, as weathering is a dynamic process affected by a large combination of factors.

5. FACILITATION: ENABLING OF COLONISATION BY OTHER ORGANISMS

The processes described in previous chapters are essential to the role lichens play in facilitating primary succession. For example, cracks created in the substrate as a part of mechanical weathering processes can allow other organisms to reside there (Archer et al., 2017), and a lichen's ability to fix nutrients into the substrate can increase their bioavailability to other organisms. This includes not only the photobiont's potential nitrogen fixing ability but also the activities of the lichen's microbiome (Grube et al., 2015). They are also capable of ameliorating the effects of even extreme degrees of pollution, such as those found at abandoned mining sites (Sueoka et al., 2015), which could be helpful in ameliorating the effects of extreme disturbances originating in anthropogenic activities.

Over time, the compounding effects of these improvements allow for colonisation by other organisms, which, compounded with the effects of the previous colonisers, leads to an increase in weathering because more weathering agents are present (Walker & del Moral, 2003). Additionally, over the course of succession, the substrate comes to contain higher amounts of soil organic matter (Shure & Ràgsdale, 1977), which then contributes nutrients to the newly forming substrate. Therefore, lichens are not the only organisms that participate in this process. Some studies conducted on this topic include mosses (Caruso & Rudolphi, 2009) or other parts of biological soil crusts in order to account for the fact that weathering activities and fixation abilities are not limited to one type of organism. Since succession lies in the ecology of a given locality, it is important to acknowledge the contributions of other organisms, at least in passing, to the process as well in order to understand the extent to which lichens contribute and to see how these different organisms interact and potentially even work together in facilitation.

Different levels of population density can affect facilitation. Population density of biological soil crusts was found to increase with time on abandoned gold mine tailings, and biological soil crusts were also found to correlate with higher species richness and vegetation cover overall (Nyenda et al., 2019). However, Nyenda et al. (2019) found that different soil crust classes were associated with different surrounding vegetation, implying that not only is the population density of pioneer organisms important, but the community species makeup is, too; algae and cyanobacteria were found to decrease, while lichens and mosses increased in number in older sampling sites. This could be a move from facilitation to competition at work. Additionally, biological soil crusts can fulfil much of the same role as lichens in post-mining sites, as they can also physically absorb small fragments of the substrate, much like the fragments of substrate in *Figure 3.* Therefore, their contributions in post-mining sites include

both mechanical weathering and facilitative effects, largely stemming from the fixation of nitrogen and other nutrients.

5.1. BIOLOGICAL SOIL CRUSTS AND MICROBES

The presence of biological soil crusts, in which lichens often proliferate, can affect the surrounding vegetation. While this is already implied by their participation in nutrient cycling (Aikio et al., 2000), the changes occurring can be seen directly in some of the plants themselves. Biological soil crusts can aid in the release of carbon on glaciers, which are currently melting (Stevens et al., 2022). They also aid in photosynthesis, which also contributes to the carbon cycle, and were found to have more of an impact than vascular plants, at least in a glacial context (Yoshitake et al., 2010). It may be possible that different results would be obtained in localities where vascular plants are able to photosynthesise more effectively.

Interactions between vascular plants and the local microbial community can also take on an interesting dimension. A study of a glacier forefield correlated changes in vegetation type with changes in microbial communities (potentially due to soil acidification, litter, and root exudates), and changes in microbial communities were found to correlate with changes in nitrogen fixation (Knelman et al., 2012). The diversity of cyanobacterial communities has also been found to change in response to moisture, organic matter, and total nitrogen in karst regions undergoing desertification (Chen et al., 2023), which share similarities with some successional seres in their dryness. Additionally, biological soil crusts have been found to have an effect on vascular plant characteristics such as leaf area or the amount of chlorophyll they contain, as well as on the biochemical makeup of the plants (Zhuang et al., 2015).

One locality in Iceland was colonised by a microbial community several months after substrate formation (Kelly et al., 2014). While this locality shows little diversity, potential new species were found, much like in Fryday and Dillman's study (2022), in which three novel members of the *Placopsis* genus were found, as outlined in *Table 1.* Additionally, this locality showed signs of sulphur fixation by the present bacteria, likely due to the release of sulphuric gases during the eruption (Kelly et al., 2014). The fixation activities of pioneer organisms are therefore often dependent on what is available in a locality. In fact, biological soil crusts have been found to immobilise toxic waste from acid mine drainage (Kuang et al., 2023).

5.2. OTHER ORGANISMS: VASCULAR PLANTS AND INVERTEBRATES

After the retreat of the Werenskiold Glacier in the Svalbard area, noticeable amounts of biotic cover became apparent in the 5th and 6th year post-deglaciation, consisting mainly of

lichens and *Saxifraga sp*, which occurredat a time where soil formation was already underway, with both organic matter accumulation and nitrogen fixation occurring, and chemical changes in the substrate indicated pH lowering (Kabala & Zapart, 2012). This could be seen as the product of the facilitative process, as Kabala and Zapart (2012) had found other, newer colonisers had been found, such as *Saxifraga sp.* Vascular plants may also serve as facilitators, especially in later phases of succession, such as in the case of *Silene acaulis* as observed in southern Norway (Kjær et al., 2018).

One pivotal locality in the study of primary succession is Surtsey Island, which can be seen pictured in *Figure 6*, due to the close monitoring of its successional process. This island was formed during an eruption, as *Figure 6* indicates due to the presence of volcanic craters, which occurred from November 1963 to June 1967, and it has been closely monitored ever since in studies such as the one conducted by Wasowicz et al., (2018), in which the vascular plant life of the island was monitored, or Kristinsson & Heiðmarsson's study (2009), which focused on lichens and bryophytes. Due to sea currents, plant material started to appear on the island even as the eruption was occurring, and over time, as the successional process advanced, it became increasingly difficult to map all newly appearing vascular plants and the species *Hockenya peploides* had proliferated so widely by 1980 that its distribution was no longer recorded using individual points on maps (Wasowicz et al., 2018). Some of the island's initial colonisers were bryophytes, which were found at the same time as lichens (Kristinsson & Heiðmarsson, 2009).

Figure 6: Aerial photograph of Surtsey (image source: Kristinsson & Heiðmarsson, 2009).

Changes that occur in succession can allow colonisation by invertebrates. Here, the interactions between lichens and invertebrates may be particularly relevant, as one species of invertebrate, the gastropod *Arion fuscus*, has been found to prefer cyanolichens over lichens with primarily algal photobionts (Asplund & Gauslaa, 2010). This is particularly relevant due to the fact that cyanolichens are crucial in nitrogen fixation, as the mycobiont of the lichen symbiosis cannot be effective in nitrogen fixation without a cyanobacterial photobiont (Seneviratne & Indrasena, 2006). Additionally, lichens can serve as food for both invertebrate and vertebrate animals (Asplund & Wardle, 2017).

6. DISCUSSION

In this thesis, I have discussed the strategies used by lichens and other pioneer organisms in order to facilitate primary succession, with a focus on weathering and nutrient cycling. I have also listed important species found in successional seres and elaborated on their importance. Finally, I mentioned other organisms involved in the successional process, such as those found in biological soil crusts, vascular plants, and invertebrates, in order to better put the facilitative process into context.

Current existing literature on this topic sometimes encompasses lichens specifically in the role of pioneer organisms, such as Fryday and Dillman's 2022 study, and in other times, or pioneer organisms as an entire category, with a study then including lichens that were found along with other, non-lichen organisms, such as in Timoshok et al.'s (2020) study. Some studies, of course, do not focus on lichens, but still prove to be useful in understanding the involvement of lichens in the successional process in some way, such as Eppes and Keanini's 2017 study. Some studies focused on the weathering effects of lichens can be relevant even when performed outside of the context of primary succession, as the weathering process is very similar as long as the substrate being weathered has not undergone such changes previously, although there are studies that focus on the substrate in successional contexts specifically (Klaar et al., 2015). Studies on the reproductive methods of lichens even outside of pioneer substrates could be relevant as well, as those may affect the methods and levels of success of colonisation by a given species (Marshall, 1996).

The study of primary succession and the organisms involved in it is quite vast in its literature, though not without issue. In the study of lichens, there is also the issue of the pace at which changes occur. While it is possible to see some changes in a relatively short span of time (Matthews & Owen, 2008), the complexities of successional dynamics may not show to the full extent, as this process can last hundreds of years to even begin reaching climax (Timoshok et al., 2020). Another challenge in the study of lichens can be the difficulty that lies in isolating their metabolites, which could, in this context, cause issues in studying their weathering effects (Jie & Blume, 2002). Finally, it can be argued that the uniqueness of each successional sere makes it impossible to truly compare the processes of each locality, as no two seres are the same (Wojcik et al., 2021).

Some of these issues could, to some capacity, be fixed with changes in methodology (such as extending studies of various seres into longer timespans), but implementing these changes would likely be costly, which would cause new issues altogether. Additionally, some of these problems simply cannot be changed; the fact that each sere is unique and in some ways

incomparable to even nearby localities is simply due to the fact that the conditions at the start of each successional process are unique. Therefore, these issues are likely to persist in the future as well.

A potential space for further research could lie in the photobionts of lichens. While some studies (Beck et al., 2019) touch on this topic, most do not, and I believe it would be interesting to study this area due to the potential for correlating (or contrasting) the results with the species found in biological soil crusts. This would allow for further study of how, exactly, the first lichens colonise a given substrate. Additionally, different studies could look into the microbiome of a lichen living on a successional sere to see the extent to which the pioneer microbes in a given locality also colonise lichen thalli. The fact that discovery of new species has occurred repeatedly in successional contexts (Fryday & Dillman, 2022; Kelly et al., 2014), could also indicate that further study of this topic may continue to yield similarly novel results.

7. REFERENCES

Aikio, S., Väre, H., & Strömmer, R. (2000). Soil microbial activity and biomass in the primary succession of a dry heath forest. *Soil Biology and Biochemistry*, *32*(8–9). https://doi.org/10.1016/S0038-0717(00)00019-5

Antić, N., Kašanin-Grubin, M., Štrbac, S., Xie, C., Mijatović, N., Tosti, T., & Jovančićević, B. (2023). Type of precipitation and durations of sediment exposure as important weathering factors. *Catena*, *228*. https://doi.org/10.1016/j.catena.2023.107192

Archer, S. D. J., de los Ríos, A., Lee, K. C., Niederberger, T. S., Cary, S. C., Coyne, K. J., Douglas, S., Lacap-Bugler, D. C., & Pointing, S. B. (2017). Endolithic microbial diversity in sandstone and granite from the McMurdo Dry Valleys, Antarctica. *Polar Biology*, *40*(5). https://doi.org/10.1007/s00300-016-2024-9

Asplund, J., & Gauslaa, Y. (2010). The gastropod *Arion fuscus* prefers cyanobacterial to green algal parts of the tripartite lichen *Nephroma arcticum* due to low chemical defence. *Lichenologist*, *42*(1). https://doi.org/10.1017/S0024282909990284

Asplund, J., & Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, *92*(3). https://doi.org/10.1111/brv.12305

Bazzaz, F. A. (1979). The Physiological Ecology of Plant Succession. *Annual Review of Ecology and Systematics*, *10*(1). https://doi.org/10.1146/annurev.es.10.110179.002031

Beck, A., Bechteler, J., Casanova-Katny, A., & Dzhilyanova, I. (2019). The pioneer lichen *Placopsis* in maritime Antarctica: Genetic diversity of their mycobionts and green algal symbionts, and their correlation with deglaciation time. *Symbiosis*, *79*(1), 1–24. https://doi.org/10.1007/s13199-019-00624-4

Beckett, R. P., Zavarzina, A. G., & Liers, C. (2013). Oxidoreductases and cellulases in lichens: Possible roles in lichen biology and soil organic matter turnover. *Fungal Biology*, *117*(6), 431–438. https://doi.org/10.1016/j.funbio.2013.04.007

Berthelin, J., & Munier-Lamy, C. (1983). Microbial mobilization and preconcentration of uranium from various rock materials by fungi. *Ecological Bulletin*

Beschel, R. E., & Weidick, A. (1973). Geobotanical and Geomorphological Reconnaissance in West Greenland, 1961. *Arctic and Alpine Research*, *5*(4). https://doi.org/10.2307/1550123

Blahůt, J., Klimeš, J., & Vařilová, Z. (2013). Quantitative rockfall hazard and risk analysis in selected municipalities of the České Švýcarsko National Park, northwestern Czechia. *Geografie-Sbornik CGS*, *118*(3). https://doi.org/10.37040/geografie2013118030205

Brady, P. v., Dorn, R. I., Brazel, A. J., Clark, J., Moore, R. B., & Glidewell, T. (1999). Direct measurement of the combined effects of lichen, rainfall, and temperature on silicate weathering. *Geochimica et Cosmochimica Acta*, *63*(19–20). https://doi.org/10.1016/S0016-7037(99)00251-3

Büdel, B., Friedl, T., & Beyschlag, W. (2024). *Biology of Algae, Lichens and Bryophytes* (1st ed.). Springer.

Buma, B., Bisbing, S. M., Wiles, G., & Bidlack, A. L. (2019). 100 yr of primary succession highlights stochasticity and competition driving community establishment and stability. *Ecology*, *100*(12). https://doi.org/10.1002/ecy.2885

Calcott, M. J., Ackerley, D. F., Knight, A., Keyzers, R. A., & Owen, J. G. (2018). Secondary metabolism in the lichen symbiosis. In *Chemical Society Reviews* (Vol. 47, Issue 5). https://doi.org/10.1039/c7cs00431a

Caruso, A., & Rudolphi, J. (2009). Influence of substrate age and quality on species diversity of lichens and bryophytes on Stumps. *Bryologist*, *112*(3). https://doi.org/10.1639/0007-2745-112.3.520

Chapin, F. S., Walker, L. R., Fastie, C. L., & Sharman, L. C. (1994). Mechanisms of primary succession following deglaciation at Glacier bay, Alaska. *Ecological Monographs*, *64*(2). https://doi.org/10.2307/2937039

Chen, Q., Yan, N., Xiong, K., & Zhao, J. (2023). Cyanobacterial diversity of biological soil crusts and soil properties in karst desertification area. *Frontiers in Microbiology*, *14*. https://doi.org/10.3389/fmicb.2023.1113707

Cimpoiasu, M. O., Kuras, O., Harrison, H., Wilkinson, P. B., Meldrum, P., Chambers, J. E., Liljestrand, D., Oroza, C., Schmidt, S. K., Sommers, P., Irons, T. P., & Bradley, J. A. (2024). Characterization of a Deglaciated Sediment Chronosequence in the High Arctic Using Near-Surface Geoelectrical Monitoring Methods. *Permafrost and Periglacial Processes*, *35*(2). https://doi.org/10.1002/ppp.2220

Colesie, C., Green, T. G. A., Raggio, J., & Büdel, B. (2016). Summer activity patterns of antarctic and high alpine lichen-dominated biological soil crusts-similar but different? *Arctic, Antarctic, and Alpine Research*, *48*(3), 449–460. https://doi.org/10.1657/AAAR0015-047

Eppes, M. C., & Keanini, R. (2017). Mechanical weathering and rock erosion by climate-dependent subcritical cracking. *Reviews of Geophysics*, *55*(2). https://doi.org/10.1002/2017RG000557

Felinks, B., & Wiegand, T. (2008). Exploring spatiotemporal patterns in early stages of primary succession on former lignite mining sites. *Journal of Vegetation Science*, *19*(2). https://doi.org/10.3170/2008-8-18369

Fernández-Martínez, M. A., Pérez-Ortega, S., Pointing, S. B., Allan Green, T. G., Pintado, A., Rozzi, R., Sancho, L. G., & de los Ríos, A. (2017). Microbial succession dynamics along glacier forefield chronosequences in Tierra del Fuego (Chile). *Polar Biology*, *40*(10). https://doi.org/10.1007/s00300-017-2110-7

French, J. R., & Burningham, H. (2013). Coasts and climate: Insights from geomorphology. *Progress in Physical Geography*, *37*(4). https://doi.org/10.1177/0309133313494962

Fryday, A. M., & Dillman, K. L. (2022). A preliminary investigation of the lichen biota associated with recently deglaciated terrain in southeastern Alaska. *Botany*, *100*(3), 313–328. https://doi.org/10.1139/cjb-2021-0087

García-Breijo, F. J., Molins, A., Reig-Armiñana, J., & Barreno, E. (2023). The Tripartite Lichen *Ricasolia virens*: Involvement of Cyanobacteria and Bacteria in Its Morphogenesis. *Microorganisms*, *11*(6). https://doi.org/10.3390/microorganisms11061517

Garibotti, I. A., & Villalba, R. (2017). Colonization of mid- and late-Holocene moraines by lichens and trees in the Magellanic sub-Antarctic province. *Polar Biology*, *40*(9), 1739–1753. https://doi.org/10.1007/s00300-017-2096-1

Glime, J. M. (2007). Chapter 8-8: Nutrient relationships: Cycling. *Bryophyte Ecology*, *1*(July).

Grube, M., Cernava, T., Soh, J., Fuchs, S., Aschenbrenner, I., Lassek, C., Wegner, U., Becher, D., Riedel, K., Sensen, C. W., & Berg, G. (2015). Exploring functional contexts of symbiotic sustain within lichen-associated bacteria by comparative omics. *ISME Journal*, *9*(2), 412–424. https://doi.org/10.1038/ismej.2014.138

Hestmark, G., Skogesal, O., & Skullerud, Ø. (2007). Early Recruitment Equals Long-Term Relative Abundance in an Alpine Saxicolous Lichen. *Mycologia, 99*(2).

Inoue, T., Kudoh, S., Uchida, M., Tanabe, Y., Inoue, M., & Kanda, H. (2017). Factors affecting water availability for high Arctic lichens. *Polar Biology*, *40*(4). https://doi.org/10.1007/s00300-016-2010-2

Jie, C., & Blume, H.-P. (2002). Rock-weathering by lichens in Antarctic: patterns and mechanisms. *Journal of Geographical Sciences*, *12*(4). https://doi.org/10.1007/bf02844595

Kabala, C., & Zapart, J. (2012). Initial soil development and carbon accumulation on moraines of the rapidly retreating Werenskiold Glacier, SW Spitsbergen, Svalbard archipelago. *Geoderma*, *175–176*. https://doi.org/10.1016/j.geoderma.2012.01.025

Keane, R. E., Cary, G. J., Davies, I. D., Flannigan, M. D., Gardner, R. H., Lavorel, S., Lenihan, J. M., Li, C., & Rupp, T. S. (2004). A classification of landscape fire succession models: Spatial simulations of fire and vegetation dynamics. *Ecological Modelling*, *179*(1–2), 3–27. https://doi.org/10.1016/j.ecolmodel.2004.03.015

Kelly, L. C., Cockell, C. S., Thorsteinsson, T., Marteinsson, V., & Stevenson, J. (2014). Pioneer Microbial Communities of the Fimmvörðuháls Lava Flow, Eyjafjallajökull, Iceland. *Microbial Ecology*, *68*(3). https://doi.org/10.1007/s00248-014-0432-3

Kjær, U., Olsen, S. L., & Klanderud, K. (2018). Shift from facilitative to neutral interactions by the cushion plant *Silene acaulis* along a primary succession gradient. *Journal of Vegetation Science*, *29*(1). https://doi.org/10.1111/jvs.12584

Klaar, M. J., Kidd, C., Malone, E., Bartlett, R., Pinay, G., Chapin, F. S., & Milner, A. (2015). Vegetation succession in deglaciated landscapes: Implications for sediment and landscape stability. *Earth Surface Processes and Landforms*, *40*(8). https://doi.org/10.1002/esp.3691

Knelman, J. E., Legg, T. M., O'Neill, S. P., Washenberger, C. L., González, A., Cleveland, C. C., & Nemergut, D. R. (2012). Bacterial community structure and function change in association with colonizer plants during early primary succession in a glacier forefield. *Soil Biology and Biochemistry*, *46*. https://doi.org/10.1016/j.soilbio.2011.12.001

Kranner, I., Beckett, R., Hochman, A., & Nash, T. H. (2008). Desiccation-tolerance in lichens: A review. In *Bryologist* (Vol. 111, Issue 4, pp. 576–593). https://doi.org/10.1639/0007-2745-111.4.576

Kristinsson, H., & Heiðmarsson, S. (2009). Colonization of lichens on Surtsey 1970–2006. *Surtsey Research*, *12*. https://doi.org/10.33112/surtsey.12.9

Kuang, X., Peng, L., Chen, S., Peng, C., & Song, H. (2023). Immobilization of metal(loid)s from acid mine drainage by biological soil crusts through biomineralization. *Journal of Hazardous Materials*, *443*. https://doi.org/10.1016/j.jhazmat.2022.130314

Kurina, L. M., & Vitousek, P. M. (1997). Controls over the accumulation and decline of *Stereocaulon vulcani*, a nitrogen-fixing lichen colonist of young Hawaiian lava flows [abs.]. *Geological Society of America Abstracts with Programs*, *v. 29*(5).

Kurina, L. M., & Vitousek, P. M. (1999). Controls over the accumulation and decline of a nitrogen-fixing lichen, *Stereocaulon vulcani*, on young Hawaiian lava flows. *Journal of Ecology*, *87*(5). https://doi.org/10.1046/j.1365-2745.1999.00394.x

Kurina, L. M., & Vitousek, P. M. (2001). Nitrogen fixation rates of *Stereocaulon vulcani* on young Hawaiian lava flows. *Biogeochemistry*, *55*(2). https://doi.org/10.1023/A:1010662900513

Labus, M., & Bochen, J. (2012). Sandstone degradation: An experimental study of accelerated weathering. *Environmental Earth Sciences*, *67*(7). https://doi.org/10.1007/s12665-012-1642-y

Lalley, J. S., & Viles, H. A. (2008). Recovery of lichen-dominated soil crusts in a hyper-arid desert. *Biodiversity and Conservation*, *17*(1). https://doi.org/10.1007/s10531-007-9153-y

Likhanova, I. A., Pystina, T. N., Shushpannikova, G. S., & Zheleznova, G. v. (2021). Reforestation of lichen pine forests at the open pits in the middle taiga of the North-East of European part of Russia. *Theoretical and Applied Ecology*, *2021*(2). https://doi.org/10.25750/1995-4301-2021-2-196-201

Llambí, L. D., Melfo, A., Gámez, L. E., Pelayo, R. C., Cárdenas, M., Rojas, C., Torres, J. E., Ramírez, N., Huber, B., & Hernández, J. (2021). Vegetation Assembly, Adaptive Strategies and Positive Interactions During Primary Succession in the Forefield of the Last Venezuelan Glacier. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.657755

Vančurová, L., Malíček, J., Steinová, J., & Škaloud, P. (2021). Choosing the Right Life Partner: Ecological Drivers of Lichen Symbiosis. *Frontiers in Microbiology*, *12*. https://doi.org/10.3389/fmicb.2021.769304

Makoto, K., & Wilson, S. D. (2019). When and where does dispersal limitation matter in primary succession? *Journal of Ecology, 107*(2). https://doi.org/10.1111/1365-2745.12988

Malaspina, P., Giordani, P., Faimali, M., Garaventa, F., & Modenesi, P. (2014). Assessing photosynthetic biomarkers in lichen transplants exposed under different light regimes. *Ecological Indicators*, *43*. https://doi.org/10.1016/j.ecolind.2014.02.034

Marshall, W. A. (1996). Aerial dispersal of lichen soredia in the maritime Antarctic. *New Phytologist*, *134*(3). https://doi.org/10.1111/j.1469-8137.1996.tb04370.x

Matthews, J. A., & Owen, G. (2008). Endolithic lichens, rapid biological weathering and schmidt hammer r-values on recently exposed rock surfaces: Storbreen glacier foreland,

jotunheimen, Norway. *Geografiska Annaler, Series A: Physical Geography*, *90*(4). https://doi.org/10.1111/j.1468-0459.2008.00346.x

McCarthy, D. P. (1997). Habitat selection and ecology of *Xanthoria elegans* (Link) Th. Fr. in glacier forefields: Implications for lichenometry. *Journal of Biogeography*, *24*(3). https://doi.org/10.1046/j.1365-2699.1997.00134.x

Meunier, J. D., Kirman, S., Strasberg, D., Grauby, O., & Dussouillez, P. (2014). Incipient weathering by *Stereocaulon vulcani* at Réunion volcanic island. *Chemical Geology*, *382*. https://doi.org/10.1016/j.chemgeo.2014.05.033

Mikuláš, R. (1999). The protective effect of lichens and the origin of modern bulge-like traces on weakly lithified sandstones (Hilbre Islands, Wirral Peninsula, Great Britain). *Ichnos*, *6*(4). https://doi.org/10.1080/10420949909386457

Mourinha, C., Palma, P., Alexandre, C., Cruz, N., Rodrigues, S. M., & Alvarenga, P. (2022). Potentially Toxic Elements' Contamination of Soils Affected by Mining Activities in the Portuguese Sector of the Iberian Pyrite Belt and Optional Remediation Actions: A Review. *Environments – MDPI, 9*(1). https://doi.org/10.3390/environments9010011

Namiki, A., Rivalta, E., Woith, H., Willey, T., Parolai, S., & Walter, T. R. (2019). Volcanic activities triggered or inhibited by resonance of volcanic edifices to large earthquakes. *Geology*, *47*(1), 67–70. https://doi.org/10.1130/G45323.1

Nash, T. H. (2008). *Lichen biology* (2nd ed.). Cambridge University Press.

Nyenda, T., Gwenzi, W., Piyo, T. T., & Jacobs, S. M. (2019). Occurrence of biological crusts and their relationship with vegetation on a chronosequence of abandoned gold mine tailings. *Ecological Engineering*, *139*. https://doi.org/10.1016/j.ecoleng.2019.07.029

Oguchi, C. T. (2004). A porosity-related diffusion model of weathering-rind development. *Catena*, *58*(1). https://doi.org/10.1016/j.catena.2003.12.002

Petránek, J., Březina, J., Břízová, E., Cháb, J., Loun, J., & Zelenka, P. (2016). *Encyklopedie geologie*. Česká geologická služba.

Ramkaer, K. (1978). The influence of salinity on the establishment phase of rocky shore lichens. *Botanisk Tidsskrift*, *72*(2–3).

Rode, M., Sass, O., Kellerer-Pirklbauer, A., Schnepfleitner, H., & Gitschthaler, C. (2020). Permafrost distribution and conditions at the headwalls of two receding glaciers (Schladming and Hallstatt glaciers) in the Dachstein Massif, Northern Calcareous Alps, Austria. *Cryosphere*, *14*(4), 1173–1186. https://doi.org/10.5194/tc-14-1173-2020

Seneviratne, G., & Indrasena, I. K. (2006). Nitrogen fixation in lichens is important for improved rock weathering. *Journal of Biosciences*, *31*(5). https://doi.org/10.1007/BF02708416

Shure, D. J., & Ràgsdale, H. L. (1977). Patterns of primary succession on granite outcrop surfaces. *Ecology*, *58*(5). https://doi.org/10.2307/1936920

Silva, B., Rivas, T., & Prieto, B. (1999). Effects of lichens on the geochemical weathering of granitic rocks. *Chemosphere*, *39*(2). https://doi.org/10.1016/S0045-6535(99)00116-2

Song, J. F., Ru, J. X., Liu, X. P., & Cui, X. Y. (2019). Oxalic Acid and Succinic Acid Mediate the Weathering Process of Granite in the Cold-Temperate Forest Regions of Northeast China. *Eurasian Soil Science*, *52*(8), 903–915. https://doi.org/10.1134/S1064229319080131

Stevens, I. T., Irvine-Fynn, T. D. L., Edwards, A., Mitchell, A. C., Cook, J. M., Porter, P. R., Holt, T. O., Huss, M., Fettweis, X., Moorman, B. J., Sattler, B., & Hodson, A. J. (2022). Spatially consistent microbial biomass and future cellular carbon release from melting Northern Hemisphere glacier surfaces. *Communications Earth and Environment*, *3*(1). https://doi.org/10.1038/s43247-022-00609-0

Stretch, R. C., & Viles, H. A. (2002). The nature and rate of weathering by lichens on lava flows on Lanzarote. *Geomorphology*, *47*(1). https://doi.org/10.1016/S0169-555X(02)00143-5

Sueoka, Y., Sakakibara, M., & Sera, K. (2015). Heavy metal behavior in lichen-mine waste interactions at an abandoned mine site in Southwest Japan. *Metals*, *5*(3), 1591–1608. https://doi.org/10.3390/met5031591

Syers, J. K., & Iskandar, I. K. (1973). Pedogenetic significance of lichens. In V. Ahmadjian & M. E. Hale (Eds.), *The Lichens*, pp. 225–248. Academic Press. https://doi.org/10.1016/B978-0-12-044950-7.50012-X

Timoshok, E. E., Timoshok, E. N., Gureyeva, I. I., & Skorokhodov, S. N. (2020). Primary Successions of Vegetation on the Young Moraines in the Severo-Chuiskiy Center of Glaciation (Central Altai). *Contemporary Problems of Ecology*, *13*(1), 36–47. https://doi.org/10.1134/S1995425520010114

Vingiani, S., Terribile, F., & Adamo, P. (2013). Weathering and particle entrapment at the rock-lichen interface in Italian volcanic environments. *Geoderma*, *207–208*(1). https://doi.org/10.1016/j.geoderma.2013.05.015

Voltr, V., Menšík, L., Hlisnikovský, L., Hruška, M., Pokorný, E., & Pospíšilová, L. (2021). The soil organic matter in connection with soil properties and soil inputs. *Agronomy*, *11*(4). https://doi.org/10.3390/agronomy11040779

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

Wasowicz, P., Thorsteinsson, S., Magnússon, B., Einarsson, E., Bjarnason, V., Bjarnason, Á. H., Guomundsson, J., Richter, S. H., Jónasson, R., Sveinbjörnsson, B., & Magnússon, S. P. (2018). Vascular plant colonisation of Surtsey Island (1965-1990) - A dataset. *Biodiversity Data Journal*, *8*. https://doi.org/10.3897/BDJ.8.e54812

Weed, R., & Norton, S. A. (1991). Siliceous Crusts, Quartz Rinds and Biotic Weathering of Sandstones in the Cold Desert of Antarctica. *Developments in Geochemistry, 6*(C). https://doi.org/10.1016/B978-0-444-88900-3.50036-9

Wojcik, R., Eichel, J., Bradley, J. A., & Benning, L. G. (2021). How allogenic factors affect succession in glacier forefields. *Earth-Science Reviews, 218.* https://doi.org/10.1016/j.earscirev.2021.103642

Yoshitake, S., Uchida, M., Koizumi, H., Kanda, H., & Nakatsubo, T. (2010). Production of biological soil crusts in the early stage of primary succession on a High Arctic glacier foreland. *New Phytologist*, *186*(2), 451–460. https://doi.org/10.1111/j.1469-8137.2010.03180.x

Zanchett, G., & Oliveira-Filho, E. C. (2013). Cyanobacteria and cyanotoxins: From impacts on aquatic ecosystems and human health to anticarcinogenic effects. *Toxins, 5*(10). https://doi.org/10.3390/toxins5101896

Zhuang, W. W., Serpe, M., & Zhang, Y. M. (2015). The effect of lichen-dominated biological soil crusts on growth and physiological characteristics of three plant species in a temperate desert of northwest China. *Plant Biology*, *17*(6), 1165–1175. https://doi.org/10.1111/plb.12359