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Remarks and advice to the study of early arthropod succession near melting glaciers

Sigmund Hågvar [a], Barbara Valle [b,c], and Mauro Gobbi [d]

aFaculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; bDepartment of Life Sciences, Università degli Studi di Siena, Siena, Italy; cNBFC, National Biodiversity Future Center, Palermo, Italy; dClimate and Ecology Unit, Research and Museum Collections Office, MUSE-Science Museum, Trento, Italy

ABSTRACT

Melting glaciers give a unique possibility to study how life colonizes newly exposed ground. Research during the last two decades has shown that arthropods play a key role in establishing the first functioning ecosystems. However, there are still gaps in our knowledge about this succession process and a need to identify key research directions. Good case studies are the basis for a general understanding of patterns and driving forces in primary succession. We present remarks and advice on this topic, using examples from European studies. We explore the driving forces supporting the early ecosystem, discuss the ability of certain micro- and macroarthropods to be pioneers, and highlight the autecology of pioneer species and their role in building early trophic networks. Relevant research questions are identified. Different colonization patterns are discussed, and we stress the importance of a geoecological approach to the succession. We discuss relevant methods to collect sufficient material, how to tackle the scale problem and "ecological noise," and the importance of a good taxonomic resolution. The present "package" of updated knowledge, research questions, and advice about fieldwork practice is meant especially for ecologists who are in their early phase of investigating succession in glacier forelands.

Introduction

Within community ecology it is of basic interest to understand species interactions and succession in space and time. How can we explain driving forces, dynamics, and patterns in a succession? What is the relative importance of biotic and abiotic factors? Why is the succession pattern sometimes predictable and sometimes affected by local conditions? Though secondary succession may be studied in many situations—for instance, after clearcutting in forests—options to study primary succession have been limited; for instance, to rare natural disturbances like vulcanism creating lifeless lava fields (e.g., Moral 2009).

Due to recent climate change, glaciers all over the world are now melting and exposing large areas of barren ground (Oerlemans 2005; Jomelli et al. 2011; Malcomb and Wiles 2013). For ecologists, such "natural laboratories" (Figure 1) provide unique possibilities to study the process of primary succession and species interactions (e.g., Kaufmann 2001; Hågvar 2012;

Ficetola et al. 2021; Gaudio and Gobbi 2022). Furthermore, if the foreland of a receding glacier has a number of known earlier positions of the ice border, these points with known age can be used to sample the likely results of successional change instead of waiting for a long time to observe changes in a given point. This "space for time substitution" is widely used, and the time sequence indirectly created in this way is called a chronosequence (Franzén et al. 2019; de Vries et al. 2021). Though botanical succession in glacier forelands has been described rather thoroughly in several studies (e.g. Matthews 1992; Kaufmann and Raffl 2002; Erschbamer and Caccianiga 2016), documentations of zoological succession are fewer.

On the other hand, studies during the two last decades have significantly increased our understanding of the zoological succession near melting glaciers (see Ficetola et al. 2021), and arthropods play an important role during colonization and early succession (Hågvar et al. 2020).

CONTACT Sigmund Hågvar ✉ sigmund.hagvar@nmbu.no 🖃 Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, Ås 1432, Norway.

Figure 1. Foreland of the Forni Glacier, Italy. The length (about 3 km) and the width (see the lateral moraine on the left) of the foreland offers a wide substrate open to the colonization of biocoenosis. Photo: Mauro Gobbi.

The main focus of the present article is on this early phase of succession, mainly before higher plants establish. We find this phase especially interesting because arthropods are important participants and because significant driving forces may have been overlooked. Recent studies have provided ecological surprises (Hågvar and Gobbi 2022); for example, the discovery of very early presence of chlorophyll in biofilm and tiny pioneer mosses, on which pioneer Collembola (springtails) can feed. A deeper understanding of succession in glacier forelands and the role of arthropods in starting and driving the succession may be of general ecological interest.

The present review is based on data from European glacier forelands in Svalbard, Iceland, Norway, Sweden, and the Alps. With similarities in arthropod fauna, often at the genus level, and having forelands at different latitudes and altitudes, European data are suitable for giving remarks and advice about future investigations. In addition, to the best of our knowledge, the only studies focusing on ground-dwelling arthropods in primary succession performed outside Europe are along two Andean glacier forelands (Moret et al. 2020; Rosero et al. 2021). We initially focus on the driving forces that could support the early food web. This implies presentation of the first colonizers, explaining what they are, how they can arrive, and what they can eat. Next, we comment on two central topics in succession studies. The first is related to the succession pattern and how species come and go. The other topic is the "geoecological perspective," which stresses that abiotic factors must be taken into consideration to understand local succession patterns. On this background, we give practical advice for fieldwork, discussing methods and the "ecological noise" in sampling. We highlight the importance of good taxonomic resolution for a full understanding of community structure and the food web. Furthermore, we address

conservation issues related to oversampling of small populations and threats to cold-adapted species due to glacier disappearance.

Never before have scientists had so good opportunities to study primary succession. Having worked with arthropods near melting glaciers for many years, we call for closer studies on the role of this animal group in the succession process. The present article can be regarded as a "package" of updated knowledge, research questions, and advice about fieldwork practice that we hope might inspire young researchers in particular.

Driving forces in the early ecosystem

This section deals with the first trophic resources available along a primary succession and the very pioneer organisms that are able to use these trophic sources.

Early access to chlorophyll

Primary producers containing chlorophyll molecules form the basis of any independent ecosystem through the conversion of sunlight to biomass. The primary succession was firstly assumed to start as a heterotrophic community without chlorophyll (e.g., algae and plants), fed by airborne prey like flies and midges, according to Hodkinson, Webb, and Coulson (2002), because only predators were easily observed or collected. More recently we learned that springtails can colonize before those predators, eating chlorophyll-based food in cryptic biofilm with diatom algae, cyanobacteria, or tiny pioneer mosses (Birkemoe and Liengen 2000; Hågvar and Pedersen 2015). Thus, it is possible to substitute the "predator-first paradox" with "the springtail-first principle," named after the earliest documented arthropods to colonize (Hågvar and Gobbi 2022). Establishment of reproducing populations of springtails could facilitate the colonization of predators like carabid

beetles, spiders, or harvestmen, which typically appear soon after the springtails.

Specifically, springtails are true pioneer organisms in cold habitats: on Svalbard, two species were recorded the same year as the ice melted, at the very border of the ice (Gwiazdowicz et al. 2020), and four species were found after two years, compared to three spider species (Hodkinson, Coulson, and Webb 2004). In the Alps, springtails colonize not only the early successional stages but they dominate, in terms of biomass, the supraglacial habitat on debris-covered glaciers (Fjellberg 2010; Valle et al. 2022a, 2022b).

Research question: Is the sequence biofilm–springtails–predators a general pattern for early succession in glacier forelands?

Ancient and bioavailable carbon

Another early energy source could be bioavailable in the form of ancient carbon released by the glacier. In some cases, it is possible to find an old deposit of organic carbon just beneath the ice when a glacier retreats (Indren glacier, European Alps; Freppaz et al. 2021). Bardgett et al. (2007) demonstrated that along a glacier foreland in the European Alps (Ödenwinkelkees, Austrian Alps), pioneer heterotrophic microbial communities fed on ancient carbon coming from the glacier. Only after 50 years of succession was the microbial community supported primarily by modern carbon. The Norwegian glacier Hardangerjøkulen has been shown to release bioavailable ancient carbon (Hågvar and Ohlson 2013). This carbon accumulated in the bottom of young ponds during their formation. Pond-living larvae of Chironomidae (nonbiting midges) assimilated ancient carbon and the adult midges achieved a "false" radiocarbon age of 1,040 years. Predators among carabid beetles, wolf spiders, and harvestmen, feeding on these midges on 6-year-old ground, achieved false radiocarbon ages between 340 and 1,100 years, proving that the ancient carbon had been transported from aquatic to terrestrial communities (Hågvar and Ohlson 2013; Hågvar, Ohlson, and Brittain 2016).

Ancient carbon was also documented in silt sampled near the ice border, as well as in front of another retreating Norwegian glacier, Hellstugubreen (Hågvar, Ohlson, and Brittain 2016). It was assumed that the source of ancient carbon was easily dispersible aerosol particles, resulting from the incomplete combustion of fossil fuels like coal and oil (e.g., Kastovska et al. 2006; Stubbins et al. 2012).

More data are needed to infer the origin of carbon and of biofilm in recently deglaciated terrains. Algae or cyanobacteria may have been carried to the pioneer ground by wind. In addition, a growing amount of literature demonstrates how the glacier surface (both ice-clean glaciers and debris-covered glaciers) may host an exclusive biodiversity of bacteria, yeasts, algae, plants, nematodes, rotifers, tardigrades, springtails, insects, and spiders (Branda et al. 2010; Zawierucha et al. 2017; Gobbi et al. 2021; Valle et al. 2022a). We have evidence from isotope analysis that springtails living on supraglacial habitat on the alpine Forni glacier (Central Italian Alps) feed on biofilm (Jaroměřská et al. 2023). It is possible that this is true also at the ice front, to which this biofilm can be transported by the melting ice. In fact, but still to be demonstrated, on recently deglaciated terrains, melting glaciers may deposit a large amount of organisms and organic matter able to originate biofilm layers and consequently trigger a primary succession. The organic matter deposited on the ice surface could originate from wind transport (Cook et al. 2016).

Research question: Is release of ancient carbon from the glacier a widely distributed, but overlooked, source of carbon for early ecosystems?

The ability of microarthropods to be pioneers

Microarthropods is a common term for springtails and mites (Acari). Though springtails seem to be generally the first colonizers near receding glaciers, mites can also be present very early (Hågvar, Solhøy, and Mong 2009; Hågvar et al. 2020). The general ability for springtails and mites to be pioneers may be due to a combination of several factors.

First: Wide distribution, high abundance, and species richness

Springtails and mites dominate arthropod communities of soils (Badejo 1982; Hopkin 1997; Gibert and Culver 2009). Their abundance and species richness increase the chance for suitable candidates to colonize a given foreland. Both groups are well represented even in rather harsh, cold, and open environments, as in high-altitude habitats, on Svalbard, and in Antarctica (e.g., Haybach 1972; Fjellberg 2010; Beet et al. 2022). The springtail *Agrenia bidenticulata* (Tullberg, 1877) is a cold-adapted pioneer species near glaciers both on Svalbard and in Norway. This species also dominates "glacier mice" (moss balls) directly growing on the ice surface (Coulson and Midgley 2012). Many springtail species are positively related to cold biomes (Potapov

et al. 2022) or have the ability to adapt physiologically to the cold (e.g., Bahrndorff et al. 2009), and some are strictly cryophilic (Eisenbeis and Meyer 1999; Fjellberg 2010; Valle et al. 2022a). In the European Alps, which were not completely covered by ice during the Last Glacial Maximum and have a springtail fauna different from that of Northern Europe, species belonging to the genera *Desoria* and *Vertagopus* (Figure 2) are the only known terrestrial arthropods able to live permanently and exclusively above the bare ice (Haybach 1980; Eisenbeis and Meyer 1999; Valle et al. 2021). In general, the supraglacial community of springtails is consistent and could actively contribute to the first stages of glacier foreland succession (Haybach 1972; Valle et al. 2022a, 2022b). Foreland studies on Svalbard, Norway, and in Iceland have documented Oribatida, Prostigmata (Actinedida), and Gamasida on young ground (Skubala and Gulvik 2005; Hågvar, Solhøy, and Mong 2009). In a Svalbard foreland, predacious Gamasida mites and an Oribatida species (*Camisia anomia* Colloff, 1993) were recorded on two-year-old ground (Hodkinson, Coulson, and Webb 2004). In an Austrian glacier foreland (Rotmoos), mites seemed to have a higher total biomass than springtails in early succession (Kaufmann, Fuchs, and Gosterxeier 2002).

Second: Ecological flexibility

Springtails can be very flexible in habitat and food choice (e.g., Bödvarsson 1961; Hågvar and Kjøndal 1981; Hågvar 1982). Petersen (1971) concluded from a literature review that variations in gut contents of springtails can be explained if we assume that each species constantly selects the best food items from what is available. In the foreland of the Norwegian glacier Hardangerjøkulen, *Isotoma viridis* Bourlet, 1839 grazed on biofilm with diatom algae close to the glacier

Figure 2. The cold-adapted springtail *Vertagopus* sp. from Forni glacier, Italy. Photo: Barbara Valle.

edge but gradually shifted to more fungal hyphae as the ground became older (Hågvar and Pedersen 2015). Food flexibility is also demonstrated by keeping springtails in cultures, fed with brewer's yeast and fungi (Scheu and Simmerling 2004; Menta et al. 2019). Pioneer mites may cover different roles in the trophic web, covering a wide spectrum of the trophic web. For instance, oribatid mites are typically decomposers, and mesostigmatid mites can prey on springtails, other mites, or nematodes (Hågvar, Solhøy, and Mong 2009).

Third: Dispersal ability

Springtails, and probably also mites, have a high dispersal ability. Although they cannot fly, surface-active microarthropods seem to be dispersed by wind. This has been illustrated by sticky traps and pan traps in a Norwegian glacier foreland (Flø and Hågvar 2013), by pitfall water trap in Svalbard (Grewling et al. 2023), by colonizing nunataks in Iceland (Ingimarsdóttir et al. 2012), and for springtails by water traps in the Antarctic peninsula (Hawes et al. 2007). Aerial springtail dispersal is also true near alpine glaciers at middle and low latitudes, as suggested by some observations on sticky traps located on the Miage Glacier (European Graian Alps; Gobbi, Isaia, and De Bernardi 2011). On the other hand, in the Alps, the great variability of cryophilic springtail species indicates a great isolation even among close glaciers, which does not fit with the hypothesis of long-distance wind dispersion (B. Valle, unpublished data). However, even by use of their furca, springtails can make jumps and perhaps move several meters per day in this way (Zhang et al. 2017), sufficient to chase the retreating ice edge. Long-distance migration of a springtail on snow has been documented in high-altitude spruce forest in southern Norway (Hågvar 1995, 2000). The actual species, *Hypogastrura socialis* (Uzel, 1891), was able to jump 200 to 300 m per day on the snow surface. Field experiments indicated that the animals navigated using the position of the sun (Hågvar 2000). For mites, aerial transport has been documented, indirectly and directly. In Iceland, mites have been shown to colonize isolated nunataks (Ingimarsdóttir et al. 2012), and wind transport seems to be the explanation. In a Norwegian foreland, sticky traps and fallout traps illustrated aerial transport of Oribatida and Prostigmata on a five- to six-year-old moraine (Flø and Hågvar 2013). A deeper understanding of dispersal ability of springtails and mites in high-altitude glacial ecosystem is still lacking.

Research questions: 1. Are springtails always the first arthropods to colonize, even at high altitudes or latitudes? In that case, why? 2. What is the dispersal ability

of springtails and mites into newly deglaciated ground in mountain glaciers?

The ability of certain macroarthropod predators to be early colonizers

Soon after the presence of springtails, certain typical macroarthropod predators are usually present. In Europe, carabid beetles of the genus *Nebria* (Figure 3), wolf spiders of the genus *Pardosa* (Figure 4), Linyphiidae spiders of the genus *Mughiphantes*, and harvestmen (Opiliones) of the genus *Mitopus* (Figure 5) include cold-adapted species able to live and reproduce in front of the glaciers and even on debris-covered glaciers (Martens 1978; Gobbi et al. 2006; Bernasconi et al. 2019; Valle et al. 2020). In forelands of the High Arctic, as in Svalbard, Carabid beetles and harvestmen are lacking, and mainly small Linyphiidae spiders represent the predators. In Iceland, only one

Figure 3. *Nebria soror tresignore* (K. Daniel, 1903), a stenoendemic and cold-adapted carabid species of the Orobian glaciers (Central Italian Alps). Photo: Mauro Gobbi.

Figure 4. The wolf spider *Pardosa cavannae* Simon, 1881, from the Calderone glacier foreland, Italy (Valle et al. 2022a). Photo: Barbara Valle.

Figure 5. The cold-adapted, generalist predator *Mitopus glacialis* (Heer, 1845) (Opiliones) from the pioneer stages of the Forni glacier foreland (Central Italian Alps). Photo: Mauro Gobbi.

carabid species, *Amara quenseli* (Schönherr, 1806), is found in forelands, but *Pardosa* and *Mitopus* occur. Northern Europe and the Alps have several genera of macroarthropod predators in common (Hågvar et al. 2020).

At high altitudes or latitudes, carabid beetles, spiders, and opilionids are often the only predatory ground-dwelling macroarthropods. Analyzing eight forelands younger than twenty years in Jostedalen and Jotunheimen (Norway), Vater (2006) demonstrated that these sites had a rather predictable predator community. All mentioned groups are generalist predators, taking "everything" from springtails to Diptera, and even other predators (König, Kaufmann, and Scheu 2011; Raso et al. 2014; Sint et al. 2019). Macroarthropod predators should not have problems following a retreating ice edge, even if Gobbi et al. (2006) and Brambilla and Gobbi (2014) pointed out how some alpine spiders and carabid beetles could have different times of response to climate change (e.g., time lag) due to their different dispersal ability or propensity to quickly colonize new habitats. These predators are able to use microtopography for concealment and shelter, even vertical "labyrinths" (Tenan et al. 2016).

Some species prefer open ground; for instance, the carabid beetle *Bembidion hastii* C. R. Sahlberg, 1827, which disappears when vegetation closes (Bråten et al. 2012). A vegetation-poor soil is perhaps a good hunting ground for predators, allowing them to move easily without resistance by vegetation. Pitfall catches have shown that springtails (as a possible prey) are fully active on open ground (Hågvar 2010). Sheet weaver spiders (Linyphiidae) may disperse by air, hanging in their silk thread (Hodkinson et al. 2001; Hodkinson, Webb, and Coulson 2002; Coulson, Hodkinson, and Webb 2003).

On the other hand, we are not sure that all sheet weavers colonize recently deglaciated terrain only by wind. The early colonizers could in certain cases be individuals coming from the glacier surface or mountain slopes surrounding the glacier. However, currently there is no evidence about their ability to reproduce in those sites.

Research question: What is the role of macropredators in early food webs under different climatic and geographical situations?

The autecology of pioneer species

According to Hågvar et al. (2020), a pioneer species must pass through four "ecological filters" to establish. It must disperse, it must survive after arrival, it must find food, and, finally, a true pioneer species should also be able to reproduce. Newly deglaciated ground is both a young ecosystem and an ecological sink for those organisms that cannot survive. A sample of arthropods from a newly revealed site only tells us one thing: these species have arrived to this place. But are they all "pioneer species"? In this article, we define a pioneer species rather restrictively, thinking that only reproducing species are active participants in the young ecosystem. We may, however, miss relevant information if we are uninterested in the sink category; for instance, in-blown aphids lacking their host plant or the adult stage of some aquatic insects that have developed elsewhere (e.g., chironomids). Such nonsurviving arthropods may have a function as food for early predators or they may end up as fertilizer for the young soil. We should also be aware that even species that seem to have a stable population on young ground may belong to the sink category. This can be due to a constant colonization; for instance, by ballooning sheet weavers flying by their silk threads. This is probably the case with the spider *Agyneta rurestris* (Koch 1836), a common species from the sea coast up to mountain regions (Nentwig et al. 2023), which "balloons" up to high altitudes. The species is commonly sampled on debris-covered glaciers and on recently deglaciated terrain of the European Alps (Gobbi et al. 2017; Bernasconi et al. 2019; Valle et al. 2022a).

One might expect that species having passed through the same four ecological filters would show strong similarities in their ecology. As shown by Cauvy-Fraunié and Dangles (2019), early arthropod communities are neither a collection of specialists nor generalists but contain both categories. Furthermore, a species can be both generalist and specialist; for instance, a predator generalist that is also a cold-adapted specialist (e.g., the spider *Mughiphantes brunnerii* (Thaler 1984) on the European Alps). With

high tolerances to habitat, climate, and food choice, the harvestman *Mitopus morio* (Fabricius, 1799) was considered a "super generalist" (Hågvar and Flø 2015).

Species may have quite different "reasons" for being a pioneer species. Future research would profit from detailed ecological studies of pioneer arthropods. An adequate large-scale analysis of the functional profile of biological communities along the glacier foreland could help us in understanding the ecology of these species but is still lacking.

Figure 6 illustrates a hypothetical food web in a pioneer community, less than ten years old. The illustration shows how arthropods contribute as primary consumers, detritivores, and predators. Many organisms can be airborne, including suitable prey (here exemplified by aphids). Organisms can also be transported to pioneer ground via running water or landslides from side valleys, from the glacier surface by meltwater, or even from the underside of the glacier. Certain organisms, like harvestmen, spiders, and carabid beetles, are more or less able to follow the retreating ice edge by foot.

Research questions: 1. To what degree is competition (i.e., some species are more or less mutually exclusive) or facilitation (i.e., some species facilitate the co-occurrence of others) a regulating factor? 2. What is the functional profile of very pioneer organisms?

To what degree do species persist during the succession: Different succession models

Is succession simply an addition of species until a certain number is reached, or is there a constant turnover of species, or perhaps something between? This question has to do with the way a new ecosystem develops and challenges our ecological understanding. During pitfall-based studies of arthropod succession in Norwegian glacier forelands, Vater (2012) and Vater and Matthews (2013) noted that when a species colonized, it almost always remained during the further succession process. Due to the very small turnover of species, they theorized the "addition and persistence" model. In a later publication, however, Vater and Matthews (2015) modified the principle, noting that at lower altitudes, the element of replacement change increased. A deviation from the addition and persistence model was also documented along a Norwegian alpine glacier foreland, showing that some species were restricted to a certain phase of the succession (Hågvar, Ohlson, and Flø 2017). Leaving species may be cold-adapted and need the closeness to the ice, for example, or they may demand non-closed vegetation (Bråten et al. 2012).
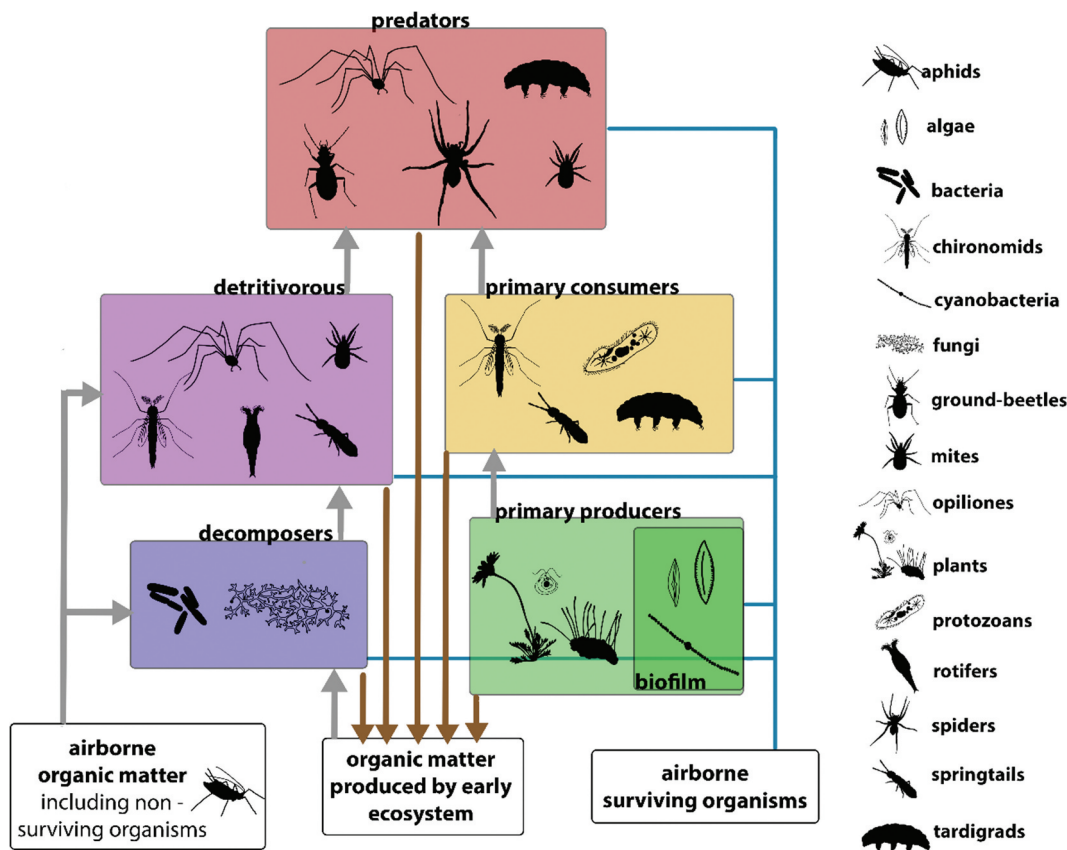
Figure 6. Typical pioneer organisms and a hypothesized early food web, less than ten years old, close to a melting glacier. Energy flow is shown by arrows. Intraguild predation among predators occur but is not shown in the diagram. In the figure, arthropods are represented by the following groups: carabid beetles, spiders, harvestmen, mites, aphids, chironomid midges, and springtails. Illustration by Barbara Valle.

Another factor influencing succession pattern is temperature variations between years. A repeated survey along the subalpine Norwegian glacier Austerdalsbreen fifteen years after an initial assessment in 2004 indicated faster colonization of both vegetation and invertebrates due to climate warming (Klopsch et al. 2023). That study showed a high degree of taxonomic replacement in early succession, and cold-adapted species were assumed to be more isolated in a narrow zone close to the ice edge.

As discussed in Ficetola et al. (2021), species turnover (i.e., species substitution along the chronosequence of glacier retreat) is more common in climates with warmer conditions during the growing season, as in the Mediterranean forelands (Valle et al. 2022b) and along forelands in the Inner Alps characterized by a continental climate with warm summer, and in some cases crossing the treeline. The addition and persistence model is much more relevant in areas characterized by colder conditions during the growing season (e.g., in Scandinavia and the Andes; Vater and Matthews 2013; Moret et al. 2020; Ficetola et al. 2021) and along glacier forelands in oceanic climates located in peripheral mountain ranges, due to the long-lasting duration of snow cover (e.g., Orobian Alps, Italy; Tampucci et al. 2015). It is easy to understand that cold-adapted species have to follow the retreating ice edge but also that species preferring open soil disappear or decline when vegetation closes in. In both cases, knowledge of the species' ecology is the key.

It is also of considerable interest to describe how the relative numbers of different species vary throughout succession, not only their presence or absence. A species that remains for a long time may have periods with high populations and large ecological influence but other periods with very low numbers and insignificant ecological contribution (e.g., Bråten et al. 2012). Species turnover should be studied closer, including cases at different altitudes and latitudes, by identifying more completely the species diversity, population size, and traits like preferences for temperature, moisture, or diet.

Research question: Are successional models similar when species distribution and trait distribution along the glacier forelands are compared?

A geoecological perspective

Connell and Slatyer (1977) introduced the concepts of facilitation, inhibition, and tolerance to illustrate how species favored or inhibited each other during the succession process. Such a view on the driving forces of succession was purely biotic. Later, a more fruitful "geoecological" perspective was introduced, taking abiotic factors into consideration (Matthews 1992). The geoecological concept has proved very useful. It is relevant both in the above discussion about why species come and go and in describing effects of local geology, topography, or climate on succession pattern. For example, studies performed in Scandinavia (Matthews and Vater 2015) and in the European Alps (Kaufmann 2001; Tampucci et al. 2015) have clearly shown how local physical and chemical environmental changes, soil properties (e.g., pH, organic matter content), and local spatial heterogeneity influenced arthropod colonization and succession patterns. The importance of local climatic conditions was documented by Marta et al. (2022). In the Alps, some glaciers are covered by supraglacial debris, creating complex, cold microhabitats even on the glacier surface (Figure 7). Furthermore, wind can be an important abiotic factor. It acts both as a direct climatic factor and as a transport mechanism for colonizing animals, including airborne prey items, as well as for organic matter (Ingimarsdóttir et al. 2012, 2013a, 2013b, 2014; Flø and Hågvar 2013; Sint et al. 2019).

Inclusion of abiotic factors in our thinking about succession and in understanding species assemblage distribution in lithosols and glacial landforms (see Gobbi et al. 2021) is clearly a valuable improvement compared to the older, purely biological view. However, in arthropod succession, properties of the species themselves must not be underestimated. The turnover of species can only be understood by thorough knowledge of the ecology of each participating species. Moreover, every local arthropod succession is started and driven by species recruited from the nearest species pool.

It is important to consider the current global warming, even at a local scale (Marta et al. 2022). This phenomenon is accelerating succession processes and potentially increase competition stress for cold-adapted pioneer species (Bosson et al. 2023; Klopsch et al. 2023), with risks for local extinction of these species (Gobbi et al. 2021). Even a higher frequency of extreme climatic events may affect succession patterns.

Research question: Is the increase in extreme climatic events (e.g., heavy storms, slope instability due to permafrost melting) affecting spatiotemporal arthropod colonization?

Figure 7. Ice front melting with deposition of supraglacial debris along young glacier foreland. Agola glacier, Dolomites (TN, Italy). Photo: Barbara Valle.

Advice about the collection of field data

Use a relevant method and get sufficient material

Different sampling methods can be used to investigate the spatial distribution of the arthropods colonizing a glacier foreland. A certain standardization of sampling will make comparison between case studies easier. The use of quantitative or semiquantitative methods is recommended to obtain more robust data and to infer information about the populations size in space and time. Various sampling methods for studying arthropods in glacier forelands are summarized in Table 1.

Pitfall trapping is the most commonly used method to collect surface-active arthropods like beetles and spiders (Eymann et al. 2010). However, the results regarding species richness and assemblage composition can be biased by the trap type (Brown and Matthews 2016; Knapp et al. 2020). Furthermore, the catches reflect surface activity and not the density of the animals. The method is still not properly standardized. For instance, some research groups used ethylene glycol as a conservation liquid (Bråten et al. 2012), and others

Table 1. Field methods for sampling arthropods in glacier forelands.

Organism and purpose	Sampling technique	Remarks	Reference
Microarthropods (springtails and mites)	Pitfall traps	Detect surface activity density of ground-dwelling organisms	Bråten et al. (2012), Valle et al. (2023)
	Flotation	Detects density also of less mobile soil organisms (e.g., juveniles) in mineral soils (e.g., supraglacial debris, young glacier foreland)	Marshall et al. (1994), Valle et al. (2022a, 2023)
	Extraction of soil samples	Detects density of active soil organisms in different soils	Hågvar, Solhøy, and Mong (2009), Valle et al. (2023)
Ground-dwelling macroarthropods (beetles, spiders, harvestmen)	Pitfall traps	Detect surface activity density of ground-dwelling organisms	Bråten et al. (2012), Gobbi (2020)
	Sampling by hand	Recommended if the aim is to obtain an inventory of species diversity	Andersen and Arneberg (2016), Gobbi et al. (2018)
Active or passive aerial transport of arthropods and organic matter into the study site	Sticky traps	Can be placed on poles at different heights and in different directions. Collect both flying and windblown arthropods as well as organic matter	Gobbi, Isaia, and De Bernardi (2011), Flø and Hågvar (2013)
	Fallout traps	Placed on the ground. Collects fallout of windborne animals and organic matter. Avoids arthropods climbing into them by a high rim	Flø and Hågvar (2013)
	Pitfall traps	Collect both flying and windblown arthropods, as well as organic matter, but catches are random	Gobbi, Isaia, and De Bernardi (2011), Bråten et al. (2012), Flø and Hågvar (2013)
	Malaise traps	Collect flying arthropods	Hodkinson et al. (2001)

used a solution of wine vinegar and salt (Gobbi 2020). Because arthropods may theoretically be attracted or repelled by the smell from the trap, such differences can make data comparison difficult. A comparative study on the attractiveness of different preservative liquids is still lacking. One should also be aware that pitfall traps may contain airborne arthropods, as well as in-blown organic matter, in addition to resident arthropods. Common weaknesses in sample practice are too few traps and sampling during a too-restricted period. Carabid beetles, for instance, may have their main activity period during and just after the snowmelt in early spring; thus, sampling during the entire snow-free period is highly recommended.

Another method that could be used for sampling arthropod is by hand searching. Andersen and Arneberg (2016) demonstrated that this method for collecting carabid beetles reduces the bias due to body mass that affects collection with pitfall traps. In general, this method is recommended if the aim is to obtain an inventory of species diversity (Gobbi et al. 2018). However, on some substrates (e.g., highly vegetated areas) it could be time-consuming and not sufficiently satisfying.

Soil cores for microarthropod sampling—that is, for Tullgren funnels or for flotation methods (Marshall et al. 1994)—are commonly used. However, large springtail species easily jump away when we try to take soil samples, so pitfall traps should be used in addition even if your purpose is only springtail sampling. To study springtails in incoherent lithosol, in addition to pitfall traps, it is necessary to use flotation methods instead of a Tullgren funnel, which is more efficient in stable soils (Marshall et al. 1994; Valle et al. 2022a, 2022b, 2023).

Aerial dispersal of arthropods can be studied using sticky traps and fallout traps. Sticky traps can be fastened to poles, at different heights and directions. Fallout traps should have high enough walls to avoid arthropods crawling into them (Flø and Hågvar 2013).

All types of traps or soil samples present a common problem: how many traps or samples are sufficient? A recommended study design is the use of at least three pitfall traps for each plot (i.e., dated site along the chronosequence of glacier retreat). To cover the microscale environmental heterogeneity we suggest selecting at least two plots for each dated site. The optimal solution, if you have time for it, is to use one season for pilot studies. If you can take a relatively high number of samples or operate a high number of pitfall traps, you can analyze the relationship between increasing trap numbers (or samples) and cumulative species number. Try to find at what trap (or sample) number the cumulative species number levels off. An example illustrating cumulative number of mite taxa related to number of soil cores was given by Hågvar, Ohlson, and Flø (2017). It is, however, important to remember that too-heavy trapping could reduce the local population too much. If studying rare species, we must be aware of the impact of the sampling design and technique in maintaining viable populations (Lencioni and Gobbi 2021).

Another question that should be evaluated is whether one should take many small soil samples or fewer, larger ones covering the same surface area. Especially in a locality that obviously contains variations in habitats, several small samples from various microhabitats would probably reveal the highest number of taxa.

In search of food choice among carabid beetles, Austrian researchers used a nondestructive method (Raso et al. 2014; Sint et al. 2019). Individuals caught alive by empty pitfall traps were allowed to regurgitate their gut content, which was then analyzed for prey items by DNA. The living animals were then released at the site where they were captured. The results of these studies contributed significantly to describing the food web of an early arthropod community.

Consider the scale problem and "ecological noise"

Ecological studies often contain much "noise": variation in habitat quality between replicates, samples taken at different seasons, too few data, or varying weather conditions that affect sample efficiency. Say we want to describe the succession of the surface-active beetle fauna in a glacier foreland with known positions of the glacier front during the last hundred years. Due to topography, sites of the same age vary in dryness, exposition, plant cover, and vegetation type. To reduce ecological noise, one researcher might decide to sample only on dry ridges with a characteristic vegetation, whereas another researcher might choose the moist patches throughout the foreland. A third person might want to sample the full variation of beetle species at each age of the ground and place traps in many different habitats. Who is doing the best job? It depends on the purpose of the study. If the aim is to study environmental microheterogeneity, the best solution would be to study microarthropods that are more habitat sensitive or may have limited dispersal ability (Rusek 2001; Valle et al. 2022a). The microarthropod specialist will perhaps crawl around, exploring every possible microhabitat that could harbor specialist species: in the lichen vegetation on top of boulders, in moist moss along a brook, under stones, or in patches of organic accumulation between stones. If the aim is to follow general ecological trends along the glacier foreland, maybe of surface-active macroarthropods, which are more mobile and less linked to microheterogeneity, randomly placed pitfall traps may be the best choice. A researcher studying the ability of cold-adapted species to survive may be interested in cool subsurface labyrinths between large blocks and needs to investigate the "third" dimension under the ground (e.g., Edwards 1975). In practice, many different succession patterns occur in parallel within the same glacier foreland; for instance, both a dry ridge succession and a moist depression succession (Hågvar, Ohlson, and Flø 2017). We can think of the foreland as a mosaic made up of many simultaneous succession processes and different spatial dimensions in different layers of the terrain.

Ecological noise may also be due to unpredictable disturbances like organic matter coming during heavy rainfalls from the mountain slopes around the foreland, as well as individuals moving from the slopes or the glacier surface to the forefield. A glacier foreland should be considered an "open system" that interacts with the neighboring habitats and landforms. The result after, for example a hundred years, may be an ecological mosaic that has a greater biodiversity than if the succession pattern had been similar on every square meter.

Good taxonomic resolution is gold

To describe a succession process or a food web, collected arthropods should, as far as possible, be identified to species level. A hypothesis to be to tested might be whether taxonomically related species (e.g., species belonging to the same genus or subgenus) have different ecologies and play quite different roles in the succession (e.g., Gereben 1995; Kaufmann and Juen 2001; Gereben-Krenn, Krenn, and Strodl 2011; Tenan et al. 2016). Species-rich groups like springtails, mites, or some beetle families can be difficult to identify, and undescribed species may appear as well. Despite the general presence of springtails in glacial habitats, their taxonomy is still not well known at the global scale, and new species of cryophilic springtails probably need to be described for European mountain chains (Valle et al. 2021). The presence of species highly adapted to cold and wet conditions makes these organisms particularly sensitive to glacier retreat, and their ecology and possible conservation are urgent topics. Cooperation with taxonomic specialists is often necessary. Education in taxonomy is mandatory for taxonomists to be able to identify the "glacial biodiversity." With time, DNA techniques may take over much of the species identification, but we will still need reference DNA for each species, based on morphological characters. For this reason, the use of integrative taxonomy is currently incentivized (Potapov et al. 2020). Promising studies from a glacier foreland are those of Raso et al. (2014) and Sint et al. (2019), who described prey items eaten by macroarthropod predators based on DNA studies of gut contents.

Epilogue

The current global warming scenario is of conservation interest because some endemics—especially on mountain glaciers at low latitudes—are threatened by climate change and disappear during succession. While Northern Europe was covered by ice during the last glaciation and today's fauna in that area is a result of later colonization, the Alps were only partly ice covered.

Animal and plant life survived on more or less isolated mountains and in many cases developed endemism (Medail and Quezel 1999; Schmitt 2009; Branda et al. 2010). The threat for these species can be due to biotic factors, such as a gradually closed vegetation or direct competition with other arthropods, or to abiotic factors; for instance, a gradual change in soil substrate or a need for cold-adapted species to stay close to the ice.

Though most studies are performed on plots of different ages to simulate the succession process (Ficetola et al. 2021), we have too few studies that really follow, via temporal replicates, the actual succession pattern on a specific site through several years. During the early succession phase, say up to five to ten years after deglaciation, both colonization rate and species turnover could change over time due to the increasing number of climate extreme events (Harvey et al. 2022). That could affect the colonization speed in different years (Kaufmann 2002). We must always be aware that sampling data represent snapshots in a dynamic process, and comparisons between forelands must take that into consideration.

We hope that this overview might inspire young people to study how virgin ground near melting glaciers gradually develops into functioning ecosystems. Further scientific progress depends on good case studies under different climatic and geographical conditions; thus, additional studies are mandatory. A better understanding of driving forces and principles in primary succession is of basic ecological interest, and glacier forelands have a potential to give us such insight.

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ORCID

Sigmund Hågvar 🄳 http://orcid.org/0000-0002-9020-9005
Barbara Valle 🄳 http://orcid.org/0000-0003-4829-4776
Mauro Gobbi 🄳 http://orcid.org/0000-0002-1704-4857

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