

***Dynamics of ecological communities following current retreat  
of glaciers***

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## ABSTRACT

Glaciers are retreating globally, and the resulting ice-free areas provide an experimental system for understanding species colonization patterns, community formation and dynamics. The last years have seen crucial advances in our understanding of biotic colonization after glacier retreats, resulting from the integration of methodological innovations and ecological theories. Recent empirical studies demonstrate how multiple factors can speed up or slow down the velocity of colonization, and have helped scientists develop theoretical models that describe spatio-temporal changes in community structure. There is a growing awareness of how different processes (e.g. time since glacier retreat, onset or interruption of surface processes, abiotic factors, dispersal, biotic interactions) interact to shape community formation and, ultimately, their functional structure through succession. Here, we examine how these studies address key theoretical questions about community dynamics, and show how classical approaches are increasingly being combined with environmental DNA metabarcoding and functional trait analysis to document the formation of multitrophic communities, revolutionizing our understanding of the biotic processes that occur following glacier retreat.

**Key-words: climate change; food web; environmental DNA metabarcoding; chronosequence; succession; colonization**

## 1. INTRODUCTION

Glaciers are steadily retreating on all continents, at a rate that has accelerated in recent decades (Hock et al. 2019; Zemp et al. 2019). For instance, in the European Alps, glaciers have lost 25-30% of their surface area over the last 60 years, and the rate of glacier reduction is now 200-300% faster than twenty years ago (Smiraglia & Diolaiuti 2015; Sommer et al. 2020). The retreat of glaciers since the mid-19<sup>th</sup> Century is attributable to a combined effect of natural and anthropogenic causes, but the importance of anthropogenic factors has increased in recent years, and human activities are the main drivers of the retreats observed since 1990 (Marzeion et al. 2014).

The study of environmental changes occurring after the retreat of glaciers provides a great opportunity to understand the formation of communities, and has been a classic approach to understanding the temporal dynamics of ecosystems (Clements 1916; Connell & Slatyer 1977; Matthews 1992). Ice-free areas are rapidly colonized by organisms and, in less than a century, complex ecosystems, including forests, can sometimes develop in areas previously occupied by glaciers. The possibility of having multiple freshly exposed surfaces, the fact that these areas are clearly delimited by the glacier path, and that these dated study sites are in chronological sequence (a chronosequence – Fig. 1), make them ideal for ecological succession studies. When glacier retreat is well described and chronologically constrained, it is possible to provide a maximum date for the ecosystems (the time elapsed since the glacier retreat), and thus to analyze the chronosequences, assuming that time is a major factor in the evolution of ecosystems. The studies of deglaciaded areas carried out since the beginning of the 20<sup>th</sup>

Century were a milestone in the development of ecological succession theory (Box 1), with a strong emphasis on plants and invertebrates.

Although classic studies of ecological succession in deglaciated areas provided critical insight into ecosystem formation, they tended to focus on just one trophic level (often plants). More recent studies have provided crucial advances in our understanding of biotic colonization after glacier retreats, with a growing interest on the overall community and on how it is structured. On the one hand, ecologists are now using community, functional and network theories and tools to go beyond the mere description of biodiversity patterns and to tease apart the role of different processes (i.e., habitat filtering, dispersal and biotic interactions) in the formation of species and functional communities, and in the emergence of functional diversity. On the other hand, recently developed molecular tools have opened a new window on the invisible, providing information on the formation of multitrophic communities, including the microbes that play crucial roles in soil food webs.

Newly deglaciated areas represent increasingly important components of mountain and high-latitude ecosystems due to climate change, and rates of glacier retreat are predicted to accelerate in the coming decades (Hock et al. 2019). Understanding the consequence of glacier retreat is therefore becoming an increasingly important topic for both ecology and global change studies, with researchers trying to understand the consequence of retreat and to develop scenarios on how mountain environments may change over the next century. In this paper, we review recent studies on the biotic colonization after glacial retreat to provide insight on the formation of complex multitrophic communities and suggest valuable ways forward for future studies. First, we

summarize the observed patterns of community change. Second, we evaluate how major processes (dispersal, biotic and abiotic factors) interact for the development of communities. Third, we show how the recent focus on functional traits and multitrophic studies (Box 2) has broadened our understanding of the processes and the functions that underlie ecosystem changes. Finally, we identify new research avenues that can improve our understanding of succession dynamics, and of how near-glacier ecosystems respond to ongoing climate change.

## **2. PATTERNS OF COMMUNITY CHANGE**

### **2.1 Patterns of colonization rate**

How long does it take for a community to be established? This question remains essential for fundamental and applied ecology, and is particularly important should we want to predict the long-term consequences of global change. The colonization of glacier forelands is assumed to start immediately after the glacier retreat (but see Box 3) with local-scale environmental factors and feedbacks driving community development over time. Thousands of years can be required for the full establishment of mature ecosystems (Delgado-Baquerizo et al. 2019). However, in some cases, colonization can be surprisingly fast, as the rate at which different taxa colonize glacier forelands is not constant, and there are clear differences both between taxonomic groups and regions of the world. Factors triggering differences in the rate of biotic colonization include i) successional stage (e.g. early successional vs mid- and late-successional stage), ii) traits of the surrounding species pool (e.g. dispersal ability, diet) and iii) abiotic factors, such as

climate, geomorphic stability of surfaces, and altitudinal gradients along glacier forelands (Section 3).

*Changes of colonization rate through time.* The rate of colonization is not constant over time, with a rapid development of pioneer communities in the first 20-50 years, followed by a decrease in colonization rate at later successional stages (Kaufmann 2001; Gobbi et al. 2006a; Gobbi et al. 2010; Schlegel & Riesen 2012). The deceleration of colonization rate is consistent with the predictions of the facilitation and inhibition hypotheses (Connell & Slatyer 1977). Indeed, biotic interactions affect colonization rate in multiple ways, with facilitation in the early colonization stages and an increasing importance of competition, parasitism, or predation, decelerating colonization at later stages (section 3.4; Koffel et al. 2018; Benavent-González et al. 2019). This change in the type of biotic interactions can create complex patterns when glacier forelands are wide and include multiple altitudinal zones (e.g. both areas above and below the tree line) (Gobbi et al. 2007; Schlegel & Riesen 2012; Vater & Matthews 2015).

*Differences in colonization rate across taxa.* The rate of colonization strongly varies from one taxonomic group to another, and even between related species. Some taxa (e.g. bacteria, rotifers, bacterivorous nematodes, springtails, ground beetles, spiders) can colonize the sediments immediately after the glacier retreat, whereas the rate of colonization can be much slower for other taxa (Matthews 1992; Gobbi et al. 2006b; Hågvar 2011; Brown & Jumpponen 2014; Lei et al. 2015; Hågvar et al. 2020; Rosero et al. 2021). Differences are determined by the interplay between dispersal ability and tolerance to environmental conditions. Aerial transport by windy tides allows very rapid colonization by pioneer species. Most of microscopic animals (rotifers, nematodes,

tardigrades), and several species of mosses, springtails, mites, spiders and insects, can reach recently ice-free lands as "aeroplankton" (Coulson et al. 2003; Flø & Hågvar 2013; Gobbi et al. 2017; Fontaneto 2019; Hågvar et al. 2020). Aerial transport is an effective dispersal mechanism if the transported species are able to survive and reproduce on the colonized substrate, and is also frequent for many non-flying organisms. These species are capable of rapidly colonizing newly deglaciated terrains and, since they also have specific traits (e.g. ability to perform ballooning, fast growth, short larval stages), they determine the functional differences between early- and late-stage communities (Section 4).

Dispersal by land tends to be a slower process than by air, although some ground dwelling arthropods can colonize new areas rapidly (Lei et al. 2015; Hågvar et al. 2020). Capture-recapture data on ground beetles (Nebrinae) suggest they only move few meters per day (Kaufmann & Gobbi Unpublished; Hågvar et al. 2020), possibly because they have to walk between stones and across the three-dimensional space (Tenan et al. 2016). Consequently, for some taxa there is a lag between the availability of suitable habitats and colonization (Brambilla & Gobbi 2014). Sites where suitable habitats are already available, but which have been ice-free for limited periods (e.g. <100 years), are mainly occupied by species with high dispersal abilities (e.g. winged carabid beetles and ballooning spiders; Gobbi et al. 2017), while slow dispersers may take more than 100 years to colonize suitable habitats. Large animals such as birds and mammals can quickly disperse to the ice-free areas for foraging, but the establishment of self-sustaining populations is generally delayed by the need of stable and abundant food resources that can require several decades (Rosvold 2016; Williams et al. 2019). Overall, the rate of



dispersal of different taxa is determined by the combined effects of environmental constraints, species characteristics and interspecific interactions. All these factors need to be integrated for an effective understanding of the processes involved. Finally, this also depends on the available species pool nearby the glacier, as species-poor areas of the world will likely be colonized more slowly and will form less complex communities than more biodiverse regions.

## **2.2 Patterns of community dynamics: additions, replacements, and tipping points.**

Early models of community succession after glacier retreat (Box 1) focused on **replacement** change, i.e. the sequential colonization of communities with high compositional turnover. These models proposed that assemblages of pioneer species colonize recently deglaciated grounds and are then replaced by significantly different communities. Replacement has long been demonstrated for plants, for instance in the intermediate and late successional stages, when early colonizers are substituted by more competitive, slow-growing species and tolerant species (Connell & Slatyer 1977; Chapin et al. 1994). Community replacement, with little overlap between early and late successional stages, has also been observed for some invertebrates (Kaufmann 2001; Gobbi et al. 2007), and the advent of high throughput sequencing has shown replacement also for some microbial communities (Davey et al. 2015; Edwards & Cook 2015; Rime et al. 2015). However, observations on invertebrate successions suggested an alternative model, with the **addition** and persistence of taxa (Vater & Matthews 2013; Tampucci et al. 2015; Moret et al. 2020). For instance, in Norwegian forelands, arthropod richness increases along chronosequences, the number of first appearances is higher than the

number of last appearances, and the majority of taxa detected in younger terrains are also found in older zones, with patterns that differ considerably from those of plant communities (Vater & Matthews 2013, 2015). Although originally applied mostly to invertebrates, the addition model is gaining support from a broad range of taxa, from fungi to lichens (Dong et al. 2016; Nascimbene et al. 2017), and even for plants in resource-poor environments (Matthews et al. 2018).

Distinguishing between these models can help identify the drivers of community change for the different components of biodiversity (Fig. 3). Communities of plants often follow the replacement model, suggesting a major role of competition (Connell & Slatyer 1977; Chapin et al. 1994). The observation of the replacement model for some invertebrates suggested that biotic relations such as plant-animal interactions are major drivers of community turnover (Kaufmann & Raffl 2002; Davey et al. 2015). Conversely, the observation that invertebrate colonization more often follows an addition pattern suggests that differences in colonization or tolerance play a larger role than competition in determining community turnover for these groups (Gobbi et al. 2017). Although these are sometimes described as "alternative" models (Vater 2012), their distinction is not always clear-cut. In the real world, replacements and additions may jointly concur to community changes over time, and their relative importance can be assessed by partitioning beta-diversity into its dissimilarity and nestedness components for different taxa or trophic groups (Dong et al. 2016; Ohlmann et al. 2019). The few studies assessing the components of community changes suggest that, in the same chronosequence, both nestedness and turnover can play a significant role (Nascimbene et al. 2017), but so far

data are scarce and more analyses are required to quantitatively measure the importance of these processes and test whether they vary between taxa and trophic levels.

Finally, the idea that communities steadily change only through replacement or addition following glacier retreat is probably an oversimplification. Besides changes in the rate of colonization, priority effects, thresholds and tipping points are likely to occur. For instance, it is possible that additions dominate at the earliest phases while, beyond a given level of complexity, space or some resources become limited and competitive interactions become more frequent, increasing the number of replacements (or vice versa; Perez et al. 2013), or that some taxa are only able to colonize after a certain stage (Brambilla & Gobbi 2014), but the frequency of thresholds and tipping points along colonization is yet to be established.

### **3. THE PROCESSES DETERMINING COLONIZATION**

Early studies on the colonization of deglaciated terrains assumed that the time after glacier retreat is the main factor in colonization (Johnson & Miyanishi 2008). Chronosequences are imperfect space-for-time substitutions and may not always be able to cleanly capture effects of time on colonization, given many factors (e.g. differences in site characteristics, altitude, differences between species...) can have profound consequences on communities (Johnson & Miyanishi 2008). We now know that time is only one driver, with colonization rates influenced by multiple stochastic and environmental factors, such as the availability of potential propagules, the surrounding species pool, microclimate, topography, solar radiation, bedrock type and (proto-)soil properties (Rydgren et al. 2014; Tampucci et al. 2015; Vater & Matthews 2015; Makoto

& Wilson 2016). What is the relative importance of time, abiotic features/processes, biotic interactions and dispersal limitations? Understanding how environmental factors shape community changes and functions is pivotal to predict impacts of ongoing environmental changes (Johnson & Miyanishi 2008; Bjorkman et al. 2018).

### **3.1 Abiotic factors and processes: time, soil and disturbance**

Traditionally, time since glacier retreat (age) was considered as a major predictor of succession along glacier forelands, based on the assumption that sites along the sequence share the same biotic and abiotic history and differ only in age (space-for-time substitution; Johnson & Miyanishi 2008). Dating of deglaciation steps is readily available for hundreds of glaciers around the world (Leclercq & Oerlemans 2012), and can be a good indicator of many key environmental properties. Nevertheless, it is essential to distinguish between the direct effects of time on successional processes (e.g. some species take some time to colonize; Brambilla & Gobbi 2014), its indirect effects on environmental properties that can affect community assembly, and factors that are simply collinear to age (e.g. within a foreland older terrain often are at the lowest elevations; Fig. 1).

Most abiotic features change rapidly over time, influencing biogeochemical cycles, the rate of colonization, and the identity of colonizers (Chapin et al. 1994; Raffl et al. 2006; Mori et al. 2017). Increasing age is related to higher surface stability and related soil development (Erhart 1951; Raffl et al. 2006; Erschbamer et al. 2008), including accumulation of organic matter, due to positive feedback loops between sediments/soils, vegetation and fauna (Chapin et al. 1994; Eichel et al. 2016; Whitesides

253 & Butler 2016; Mori et al. 2017; Vega et al. 2020; Khedim et al. 2021; see Section 4.1  
254 for multi-trophic feedbacks). At the same time, soil pH and nutrient content can change  
255 with age (Rydgren et al. 2014; Tampucci et al. 2015; Khedim et al. 2021), soil texture  
256 becomes finer, and organic debris form organic topsoil horizons (Schumann et al. 2016).  
257 In addition, geological, geomorphological and climatic differences between regions  
258 influence the kind and rate of rock weathering and thus the resulting physical and  
259 chemical properties of soils (Jenny 1994; Walker et al. 2010; Khedim et al. 2021),  
260 determining divergent trajectories of soil development.

261 In turn, variable soil characteristics due to time can impact all components of  
262 communities, with multiple feedbacks. For instance, soil stability favors plant  
263 germination and invertebrate establishment (Erschbamer et al. 2008; Cauvy-Fraunié &  
264 Dangles 2019), while increased nitrogen availability in older soils facilitates plant  
265 growth (Chapin et al. 1994) and soil development influences the structure of both  
266 bacterial and fungal communities (Dong et al. 2016; Gorniak et al. 2017; Kim et al.  
267 2017). Direct relationships between animal communities and soil characteristics are  
268 more difficult to identify, given their frequent association with plant communities. Still,  
269 fine-scale analyses revealed that grain size, micro-topographic position, litter and  
270 edaphic characteristics create multiple microhabitats that drive the distribution of  
271 arthropods (Schlegel & Riesen 2012; Hågvar et al. 2020).

272 Finally, glacier forelands are often subject to important disturbances such as  
273 flooding, geomorphological instability, cryoturbation and grazing (Kaufmann 2002;  
274 Garibotti et al. 2011; Chapin et al. 2016; Schumann et al. 2016), all of which may alter,  
275 slow down or even stop succession, resulting in non-linear trajectories of community

development (Walker et al. 2010). Geomorphic instability (e.g. debris flow, erosion) is particularly frequent and strongly limits the development of vegetation but, also in this case, feedbacks are frequent, as some pioneer plants greatly increase the stability of slopes, promoting the development of soil and of plant communities (Eichel et al. 2016).

It is difficult to measure the relative importance of time since glacier retreat vs. abiotic factors, as the effects can be highly scale- and context-dependent. In some cases, abiotic factors may have a comparable, and sometimes stronger effect than that of time (Raffl et al. 2006; Garibotti et al. 2011), particularly at fine (microhabitat) scale (Burga et al. 2010). For instance, recently deglaciated but wet microhabitats can reach high plant diversity 20 years earlier than sunny areas of the same foreland (Raffl et al. 2006), and the effects of soil characteristics may outweigh those of time at later (century) stages of succession (Rydgren et al. 2014). Nevertheless, generalizations remain difficult, with other researchers observing a limited impact of local abiotic conditions, and suggesting that time since deglaciation remains the best driver of community richness and structure, especially over large spatial scales (Burga et al. 2010; Nascimbene et al. 2017).

### **3.2 Abiotic factors and processes: the role of climate**

Micro- and macro-climatic characteristics are major drivers of biodiversity patterns (Ficetola et al. 2018; Thuiller et al. 2020; Zellweger et al. 2020) and play also a key role in the colonization of deglaciated terrains. Mountain environments have complex topographies. Along a single chronosequence, interactions between topography (mainly slope and aspect) and local climate, altitude and solar irradiance generate different

micrometeorological conditions determining differences in species distributions and colonization rates (Garibotti et al. 2011; Schumann et al. 2016; Feldmeier et al. 2020). Some studies suggested that warm climatic conditions accelerate colonization (Vater & Matthews 2015; Fridley & Wright 2018). For instance, in the Alps, a 0.6°C increase in summer temperatures can double the colonization rate of early successional stages by invertebrates (Kaufmann 2002). It has therefore been proposed that the current colonization by plants is significantly faster than a century ago, due to the acceleration of climate change (Fickert et al. 2017). Faster development under warmer climates has been proposed for other features of succession in glacier forelands (e.g. accumulation of soil organic matter; Khedim et al. 2021), probably because of increased primary productivity of autotrophs and/or faster metabolism of heterotrophs.

Temperature is not the only important climatic factor. Precipitation regimes and climate continentality affect the water balance and may consequently alter the successional trajectories (Vater & Matthews 2015). Additionally, season length and solar irradiance vary with latitude and altitude, conditioning the time and energy available for life processes (Körner 2000). Finally, climate interacts with other abiotic features. Insolation and temperature influence snow cover persistence, melting-water discharge and the length of growing season (Tampucci et al. 2015). This, in turn, may have additional effects on decomposition rate, C and N mineralization, CO<sub>2</sub> and NO<sub>2</sub> fluxes and net nitrification (Williams et al. 1998; Khedim et al. 2021). Microclimate, soil texture and aspect also influence soil moisture, affecting the development of plant communities and nitrogen mineralization (Raffl et al. 2006; Rydgren et al. 2014; Schumann et al. 2016).

Understanding how colonization is influenced by climate is particularly important in the context of ongoing climate change, as this would complicate the extrapolation of current observations to the future. Despite substantial efforts to understand the drivers of colonization, most studies focused on a single, or a limited number of chronosequences without assessing the effect of climatic and environmental differences between areas (Cauvy-Fraunié & Dangles 2019). However, even limited variation across areas can lead to drastic divergence in the trajectories of ecological communities (Vater & Matthews 2015; Chapin et al. 2016), thus more data are needed to understand the dependence of colonization on climate, with comparisons of several glacier forelands through meta-analytic approaches (Cauvy-Fraunié & Dangles 2019), or with new broad-scale studies.

### **3.3 The role of dispersal, spatial proximity, and landscape context**

Dispersal and connectivity are major determinants of species distributions, leading to similar communities in nearby habitats. The role of spatial connections is particularly important for glacier forelands. These ecosystems are often adjacent to glaciers, grasslands or mature forests, which act as the sources of colonizers (Cauvy-Fraunié & Dangles 2019; Stibal et al. 2020; Rosero et al. 2021) for many species with severe dispersal limitations (Brambilla & Gobbi 2014; Makoto & Wilson 2019). Consequently, communities in glacier forelands often show strong spatial autocorrelation. For instance, spatial analyses of Alpine arthropods revealed that nearby patches host similar communities, while distant patches in the meta-community were rather different (Gobbi & Brambilla 2016). This suggests that dispersal limitations play a major role in



determining the distribution of spiders and insects, with isolation preventing the colonization of several potentially suitable sites.

While many studies have shown that, within regional meta-communities, nearby sites have communities more similar than expected by chance (Brown & Jumpponen 2014; Rime et al. 2015; Gobbi & Brambilla 2016; Wietrzyk et al. 2018), the actual importance of dispersal remains controversial (Makoto & Wilson 2019). Spatial autocorrelation can arise both because of connectivity/ dispersal limitation (intrinsic autocorrelation), and because species are constrained by environmental features (e.g. soil, temperature...) that, in turn, are spatially autocorrelated (extrinsic autocorrelation) (Beale et al. 2010). Glacier forelands often include sequences of habitats where adjacent sites share similar age and altitude (Fig. 1). In addition, glaciers influence the microclimate of nearby areas and determine gradients of wind, moisture and temperature with spatially autocorrelated structure (Matthews 1992; Gentili et al. 2015). As a consequence, separating the role of environmental modifications vs. dispersal is challenging.

Available evidence suggests that dispersal is particularly important at early stages of successions, but data remain scanty and heavily biased, with almost no information for tropical areas (Makoto & Wilson 2019). At early stages, the impact of dispersal can be assessed through experimental analyses, or by evaluating the abundance of species with particular traits (Hodkinson et al. 2004; Erschbamer et al. 2008; Brambilla & Gobbi 2014; Erschbamer & Caccianiga 2016). Documenting the importance of dispersal in later stages is more complex, but at least two approaches exist. First, spatially-explicit analytical frameworks can be integrated with ecological theory and a-priori hypotheses to tease apart the role of environmental and spatial factors (McIntire & Fajardo 2009;

Monteiro et al. 2017). This approach can be particularly useful for analyses based on metabarcoding, which produce an extremely rich (and complex) picture of communities (Box 4). Second, multiscale chronosequence comparisons evaluate the importance of dispersal using natural gradients of dispersal limitation, by comparing chronosequences with different spatial scales and/or different distance from sources of propagules, but similar temporal extent (e.g. kilometric glacier forelands vs. sorted circles spanning a few meters) (Makoto & Wilson 2016, 2019). Both these approaches are promising, even though they have been rarely used for the communities of deglaciaded terrains (Gobbi & Brambilla 2016; Makoto & Wilson 2016).

### **3.4 Biotic drivers of colonization: facilitation and competition**

Biotic interactions have always been considered important for the evolution of communities colonizing deglaciaded terrains, because certain taxa can both facilitate and hamper colonization by other functional components (Box 1).

The *facilitation model* has successfully described many patterns of early community development, particularly for plants (Connell & Slatyer 1977; Koffel et al. 2018). In the early stages of succession, for example, nitrogen-fixing organisms (e.g. actinorhizal plants) dominate due to the initial lack of available nitrogen (N) (Walker & del Moral 2003; Koffel et al. 2018). Fixed N accumulates in the soil through biomass turnover and recycling, becoming available to other organisms and promoting their colonization (Chapin et al. 1994; Walker & del Moral 2003; Koffel et al. 2018; Benavent-González et al. 2019). The presence of taxa with efficient N-fixation can lead to very rapid successions. For instance, herbaceous plants in the foreland of the Pia

Glacier (Chile) have some of the highest nitrogenase activities reported to date and allow extremely rapid development of forests, which are in place only 34 years after the glacier retreat (Benavent-González et al. 2019). In turn, N-fixation is generally associated with symbiosis between plants and microorganisms (mycorrhizal fungi, cyanobacteria...) (Benavent-González et al. 2019; Tedersoo et al. 2020). Mycorrhizae play a key role in plant communities, accelerating successions at both early and late stages, and can affect communities in many ways, including increasing diversity, growth and productivity (Benavent-González et al. 2019; Koziol & Bever 2019; Tedersoo et al. 2020). A comprehensive analysis of the relationships between plants and soil microorganisms is beyond the scope of this review (see Tedersoo et al. 2020), but their importance underlines the centrality of interspecific interactions.

*Competition* can become more important than facilitation at later successional stages. Community assembly models suggest that facilitation-driven successions occur when soil N-availability is low, but increase in available N and decrease in available P over time can lead to a shift from facilitation- to competition-driven systems (Koffel et al. 2018). At later stages, competition also increases for other resources, such as space and light availability (Erschbamer & Caccianiga 2016), and this probably determines the slowdown in colonization rates that is often observed at these stages. Nevertheless, competition and facilitation can interact with complex pathways. For instance, alders are N-fixing shrubs that facilitate the growth and survival of spruces in the very early colonization stages, but decades later alders inhibit spruce growth, for example because their canopy reduces light availability (Chapin et al. 2016).

## **4. MULTITROPHIC LINKAGES AND FUNCTIONAL DIVERSITY**

### **4.1 Reconstructing the dynamics of multitrophic linkages**

The recent broadening of taxonomic focus has revealed the importance of multitrophic interactions to community assembly. Although plant colonization is considered a major precondition for the arrival of other organisms (Gobbi et al. 2006b; Vater 2012; Schmidt et al. 2014), not all animals need an established plant community to colonize (Hågvar 2011; Vater 2012; Hågvar et al. 2020). In many cases spiders, predatory insects, bacterivorous nematodes and detritivores colonize deglaciated terrains well before plants (Hågvar & Ohlson 2013; Lei et al. 2015; Sint et al. 2019; Hågvar et al. 2020). The paradox of many different predators inhabiting areas without primary producers and herbivores was initially explained by the input of allochthonous material blown by wind, but analyses of species traits and food webs revealed more complex mechanisms (Raso et al. 2014).

Strong abiotic filters promote the early establishment of a relatively simple functional pool dominated by heterotrophic organisms (Hodkinson et al. 2002; Raso et al. 2014; Mori et al. 2017; Hågvar et al. 2020). So far, little is known about how these simple food webs develop into complex networks during succession (König et al. 2011; Raso et al. 2014), but the recent increase in multitrophic studies and the application of molecular tools allow unprecedented reconstructions of how the functioning of these communities change. The communities establishing immediately after the retreat of glaciers seem to mostly feed on indigenous materials produced locally by microorganisms, or on old organic matter released by glaciers. Intraguild predation can be frequent; wind inputs apparently have a limited importance even though uncertainties

exist on the role of allochthonous detritus (Hågvar & Ohlson 2013; Raso et al. 2014; Azzoni et al. 2016; Sint et al. 2019). Subsequently, the colonization by arthropods can be an important catalyst for plant colonization, by providing additional nutrients on recently exposed terrains, thus accelerating the transition from heterotrophic to productive communities capable of supporting more complex food webs, and to stock large amount of organic matter (König et al. 2011; Mori et al. 2017; Benavent-González et al. 2019). At late successional stages, intraguild predation remains present, but the availability of prey at low trophic levels increases (e.g. increased frequency and diversity of herbivores), thus predators have a broader prey spectrum and show increased specialization and niche differentiation, enabling the emergence of more complex food webs (Raso et al. 2014; Sint et al. 2019; Hågvar et al. 2020). Complex feedbacks also occur for herbivorous vertebrates that exploit environments. Several mammals and birds can attain high biomass nearby glaciers; their feces increase the availability of nutrients and dissolved organic matter, thus influencing both bacterial and plant communities (Rosvold 2016; Vega et al. 2020).

Interactions between plants and animals are not limited to consumption. Analyses assessing taxonomic and functional diversity of plants and interacting insects showed that, in recently deglaciated areas, communities host a limited number of species and only a few functional groups, the flowers being mainly visited by pollinators. In late successional stages, the same flower species are visited by a larger number of insects belonging to more functional groups, including predators, parasitoids and phytophagous (Losapio et al. 2015). The increase of species richness along chronosequences also results in increased levels of functional and trophic diversity and, sometimes,

redundancy, with plants and their pollinating insects forming increasingly complex networks at late successional stages. In turn, the growing complexity of these networks probably confers stability and robustness to the entire food web (Albrecht et al. 2010; Losapio et al. 2015; Losapio et al. 2016; Ricotta et al. 2016).

Some colonizing animals can even act as ecosystem engineers, with cascading effects on multiple components of communities. For example, mammals that feed on fungi frequently have spores in their fecal pellets, thus providing inoculum to accelerate the spread and diversify populations of mycorrhizal fungi for early successional plants, with potential feedbacks on the whole community (Cázares & Trappe 1994). Second, burrowing animals such as marmots and gophers can disturb large areas of forelands. Soils disturbed by these animals have lower compactness and higher nutrient contents, and in these soils conifers have better germination and establishments (Whitesides & Butler 2016). Despite these advances, most studies have so far focused on a few components of ecological networks (e.g. arthropod predators vs prey; mammals vs plants), calling for more integrative studies analyzing a broader set of guilds. For instance, the increased taxonomic and functional diversity along chronosequences is probably paralleled by a growth of parasitic interactions (see Lei et al. 2015 for an example with nematodes), but very few studies addressed variation of parasites in these environments.

#### **4.2. From species identity to functional diversity**

Multitrophic studies enable a more complete understanding of community patterns, but also increase the complexity of analyses. Documenting all the potential pairwise

interactions that occur in a community is prohibitive. Instead, traits are common currencies, allowing comparisons across communities, even with different regional pools (Gravel et al. 2016). Trait-based approaches can allow for generalization on the structure and dynamics of ecological communities (Gravel et al. 2016; Moretti et al. 2016), and have been used to approximate some aspects of ecosystem functioning (Naeem et al. 2012; Gravel et al. 2016). Early analyses of functional traits on deglaciated grounds mostly focused on plants (e.g. Chapin et al. 1994), but we can now analyze traits for a broad range of taxa, from bacteria to animals (Brbić et al. 2016; Moretti et al. 2016). A growing number of studies has revealed the functional variation during successions after glacier retreat, showing that the increase of species richness along chronosequences also results in higher functional diversity and, sometimes, redundancy, with consistent patterns across multiple taxa, including plants, arthropods and nematodes (Losapio et al. 2016; Ricotta et al. 2016; Brown et al. 2017; Guerrieri et al. unpublished; Cauvy-Fraunié & Dangles 2019). Understanding which traits prevail in the early stages of community formation and how they change during successions helps assessing how species characteristics determine assembly rules and community dynamics (Chang & Turner 2019). Trait variation can also be used to discriminate the potential processes that explain colonization, and to measure the trajectories of functional diversity and ecosystem functioning (Fig. 3; Naeem et al. 2012; Gravel et al. 2016).

#### **4.3 Testing processes using patterns of functional traits**

Many mechanisms proposed to explain community dynamics in deglaciated terrains provide clear predictions on trait variation over time (Fig. 3). For instance, the hypothesis

that limited dispersal determines the rate of colonization is confirmed by the prevalence of taxa with traits favoring dispersal immediately after glacier retreat, while a lag time is often observed for poor dispersers (Section 2.1). Similarly, the tolerance model predicts that early colonizers are replaced by species with better competitive ability, and has been confirmed by the observation of ruderal, fast growing species in recently deglaciated areas, while later stages host stress tolerant species with slower growth and denser and smaller leaves (Erschbamer & Caccianiga 2016; Ricotta et al. 2020). The analysis of traits can thus provide efficient tests of ongoing processes. Importantly, the proposed processes are often non-exclusive, and some can prevail at early stages while becoming less important subsequently. The rate of turnover of functional traits could be used to evaluate how the importance of different processes changes through time (Brown et al. 2017). For instance, we could imagine strong turnover in dispersal-related traits during the first decades after glacier retreat. Then, after a given age, poor dispersers can become more frequent, and trends in competitive ability could emerge. Functional traits representing growth, dispersal or competition can be obtained for most of the components of communities, enabling to compare the importance of different processes across functional levels, and might even be used to assess at which stage of the succession communities are, predicting their stability and future development (Erschbamer & Mayer 2011; Ricotta et al. 2020). Traits can also be combined with prior information to build trophic groups and analyze the changes in trophic richness and diversity (Potapov et al. 2016), given that trophic diversity (e.g. the number of trophic groups) could increase substantially over the course of succession, with more competition within trophic groups. Analyzing and testing how patterns of trophic diversity (within and between well-defined



529 trophic groups) change along glacier forelands might therefore provide rich insights on  
530 community formation, as it has been shown along post-fire chronosequences (Gongalsky  
531 et al. 2021).

#### 532 533 **4.4 Emerging approaches for multitrophic and functional analyses**

534 Several approaches can boost our understanding of multitrophic dynamics and  
535 functional diversity. First, metabarcoding is the only practical way for broad-scale  
536 quantification of several important taxa (e.g. microbes), and has excellent performance  
537 also for rapid assessment of animals and plants (Taberlet et al. 2018). The possibility of  
538 analyzing multiple, very distant trophic groups within the same framework offers unique  
539 opportunities for multi-trophic analyses (Rosero et al. 2021), and to evaluate the links  
540 between animals, plants and the components of the microbiota (bacteria, fungi and  
541 protists). Nevertheless, we are at the beginning of these analyses in deglaciated terrains,  
542 and general patterns are yet to emerge. Some metabarcoding studies suggested that plants  
543 are more important for structuring bacterial communities at the beginning of primary  
544 succession than they are for fungal communities (Brown & Jumpponen 2014), while  
545 others observed tight linkages between plant and fungal successions (Davey et al. 2015).  
546 It is likely that symbiotic micro-organisms, such as root-associated fungi, follow different  
547 trends from the general community (Dong et al. 2016), although complex interactions are  
548 extremely important also for non-symbiotic taxa. As for plants, competition between  
549 fungal or bacterial taxa is probably more intense in nutrient-rich environments, such as  
550 late colonization stages, and could play a role in the disappearance of some taxa (i.e. the

replacement model) and in the non-linear trends observed for the dynamics of species richness (Davey et al. 2015; Koffel et al. 2018).

Stable isotope analysis is another approach that can greatly expand our understanding of multi-trophic linkages, by measuring flows of biomass between multiple components of food webs. This approach has only rarely been applied into pro-glacial ecosystems (Niedrist & Fureder 2017), but the few available studies have revealed intriguing and unexpected patterns of intraguild predation, helping to understand the formation of food webs (König et al. 2011; Raso et al. 2014). Furthermore, advances in remote sensing allow fast and broad-scale assessment of functional traits, particularly for plants. Although seldom applied to high-mountain environments, remote sensing can help measuring ecosystem functioning and responses to environmental changes, particularly in remote regions (Asner et al. 2017). Finally, we can learn a lot from simulation analyses integrating scenarios of climate change, and from manipulative experiments performed in the field or in mesocosms, assessing the functional impacts of specific components of biodiversity (Whitesides & Butler 2016; Donhauser & Frey 2018; Makoto & Wilson 2019; Vega et al. 2020). Importantly, manipulative experiments can now be combined with other approaches (e.g. metabarcoding, isotope analyses) that allow evaluating the impact of manipulation on the whole food web, including microbes (Rillig et al. 2019).

## **5. CONCLUSIONS**

Despite recent advances in our understanding of the drivers and rates of community assembly, many important questions remain unanswered (Fig. 4). Scientists can benefit from a growing range of laboratory and statistical approaches that were not available a

few decades ago and promise unprecedented details on the dynamics of these environments. Most of the studies performed so far have limited geographic focus, often considering just one or a few nearby forelands. Consequently, it is unclear to what extent the results of a specific study are generalizable to disparate geographic areas or can help to forecast future dynamics. Combining experimental manipulation with broad-scale and long-term correlative analyses can provide key insight into the mechanisms that drive the modifications of these environments, enabling the advancement of a more complete theory of ecosystem dynamics (Chang & Turner 2019). Global change scenarios forecast an acceleration of glacier retreat during the next decades (Hock et al. 2019); thus, deglaciated terrains will constitute a critical component of high-mountain ecosystems. Sound ecological knowledge is crucial to understand the consequences of ongoing climate change, and to define effective strategies for the management and adaptation in these highly dynamic environments.

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***BOX 1. Early models of succession in deglaciated terrains***

The study of communities developing in deglaciated areas (i.e. the areas that were until recently occupied by glaciers) provided a major basis for the development of ecological succession theory, which has had a dominant role since the beginning of the 20<sup>th</sup> Century (Clements 1916; Robbins 1918; Cooper 1923; Connell & Slatyer 1977; Box 1). Seminal analyses have proposed three alternative models to describe how communities change during colonization (Connell & Slatyer 1977). First, early colonizers can modify the environment to increase the suitability for species living in later successions (**facilitation model**). The facilitation model emphasizes the importance of biotic interactions for colonization. Second, species that emerge in later successional stages have traits that limit their success at early colonization stages (e.g. limited dispersal or slow growth rate), and / or have a better tolerance (e.g. tolerance to shade) (**tolerance model**). In the tolerance model, life history and ecological traits have a key role in determining the sequence of species. Third, the first colonizers can secure resources or space, thus limiting the colonization by subsequent species. Thus, other species can only colonize the community after the death of colonizers and the subsequent release of resources (**inhibition model**). Although the facilitation model was assumed to be particularly important for primary successions (Connell & Slatyer 1977), all these models received support from the colonization of glacier forelands, and they remain pivotal for the interpretation of data collected over the last decades. Building on these models, recent advances enrich our understanding of ongoing processes, showing that them all can jointly contribute to the development of communities over time.

***BOX 2 Recent research on biotic colonization after the retreat of glaciers***

To identify research topics and trends, we conducted a literature search in the ISI Web of Science (April 2020), using the search terms TS=(glacier\* AND (succession OR colonization OR biotic OR (ecosystem dynamic\*))) without temporal constraints. The search returned 1776 articles, which were individually checked to identify those using empirical data to describe biotic colonization after glacier retreat. We retained 748 studies, which were assessed to identify geographical biases, taxonomic targets and the frequency of multitrophic research. The number of papers on this topic showed an impressive growth during the last 20 years (Fig. 2). Many papers focused on Europe and North America, still studies covered most mountain ranges worldwide, and the major mountain ranges have benefited from a considerable study effort even if they were in remote regions (e.g. Central Asia and the Southern Andes; Fig. 2a).

Although early research focused mainly on plants, recent years have seen an expansion of taxonomic coverage. Plants are still the subject of >50% of articles, but a growing number of studies now consider soil microbiota (e.g. bacteria, fungi). Surprisingly, while many animal taxa (e.g. arthropods) reach a high diversity in these environments, they were the focus of fewer studies. This reflects the complexity of their identification using traditional approaches (Zawierucha et al. 2021) and the lack of experienced taxonomists. The increasing availability of innovative approaches for species identification (e.g. environmental DNA metabarcoding, camera-traps) should reduce this gap in the coming years.

A broad taxonomic focus does not only mean obtaining information on many species. Studies combining data from multiple trophic levels, such as producers, consumers, parasites and decomposers (hereafter multitrophic studies) also provide a more complete understanding of the functioning of these ecosystems. Multitrophic studies were rare in the 1990s, but are now increasingly important, often combining information from plant and microbial communities (e.g. fungi). This allows drawing more comprehensive conclusions about the functioning of ecosystems and the complex role of interspecific interactions.

***BOX 3. Are glacier forelands an example of primary succession?***

Community assembly after glacier retreat is often described as the "ideal example" of primary succession. However, glaciers are not lifeless environments, as they are ecosystems teeming with microbial and eukaryotic life and supporting active ecological processes (Hodson et al. 2008; Hotaling et al. 2017; Gobbi et al. 2021). Glaciers host rich communities, which are connected by the flow of meltwater from the glacier through the ice fractures to the subglacial sediments (Hotaling et al. 2017). Glacier meltdown exposes subglacial sediments; moreover, supraglacial sediments, together with the communities they host, are added to subglacial till. Bacterial communities in recently deglaciated terrains can be more similar to those of supra- and subglacial sediments than to those found in atmospheric deposition (snow, rain and wind-dispersed dust). This indicates that bacteria inherited from the glacier are important starting points of communities in newly deglaciated surfaces (Rime et al. 2016). Similar processes have been proposed for other glacier-dwelling organisms, such as invertebrates and algae (Stibal et al. 2020; Rosero et al. 2021). Thus, even the most recently deglaciated areas are not devoid of life, as they host many life forms from glacier environments. In addition, melting glaciers release a substantial amount of ancient organic matter, which pioneer species can feed on. As this ancient carbon can be the basis of food webs in recently deglaciated grounds, the term "primary succession" is questionable (Hågvar & Ohlson 2013). Complex feedbacks between glaciers and their forelands are also possible, as communities in environments close to glaciers are sources of colonization of supraglacial environments (Franzetti et al. 2017; Gobbi et al. 2017). Hence, glacier and near-glacier ecosystems cannot be disentangled; rather, they must be considered together for a comprehensive understanding of ecological responses to glacier retreat (Stibal et al. 2020).

***BOX 4. Environmental DNA and metabarcoding for the reconstruction of communities and food webs***

Increasing evidence that all trophic levels contribute to the development of biodiversity in deglaciated terrains has led to an increase in studies targeting a broad range of taxa and trophic levels (Fig. 2). However, the morphological identification of species is often laborious and time-consuming. Metabarcoding of environmental DNA (eDNA) is increasingly used to reconstruct communities of soil and water organisms, and can provide a more complete understanding of community dynamics. eDNA is the DNA that can be extracted from environmental samples (e.g., water, sediments, soil...) without isolating the macroscopic remains of the organisms (Taberlet et al. 2018). A given environmental sample generally contains the eDNA of many organisms. Multiple species of a given taxonomic group (e.g. insects, annelids, bacteria...) can be amplified using "universal primers", compared with reference databases and eventually identified in a procedure called eDNA metabarcoding (Taberlet et al. 2018).

Recent metabarcoding analyses have revealed the complex patterns of microbial diversity in deglaciated terrains (e.g. Schmidt et al. 2008; Blaailid et al. 2012; Rime et al. 2015; Dong et al. 2016; Matsuoka et al. 2019). Although fewer studies have thus far used metabarcoding to study macro-organisms in deglaciated terrains, the application of these approaches to a wide range of taxa could improve our understanding of biodiversity dynamics and of multitrophic relationships (Rosero et al. 2021). Metabarcoding can also be used to analyze the gut content of organisms, assess their diet and the variation of food webs. For instance, molecular analyses have been used to identify the food sources of predators that dominate at the early stage of colonization (Sint et al. 2019).

Figure legends

Figure 1. a) In a glacier foreland, a "chronosequence" is a sequence of dated sites for which time after retreat has been measured using a wide range of approaches (e.g. photographs, radionuclides...). b) The Tiedemann Glacier chronosequence (Canada), with strongly different communities between early and late development stages.

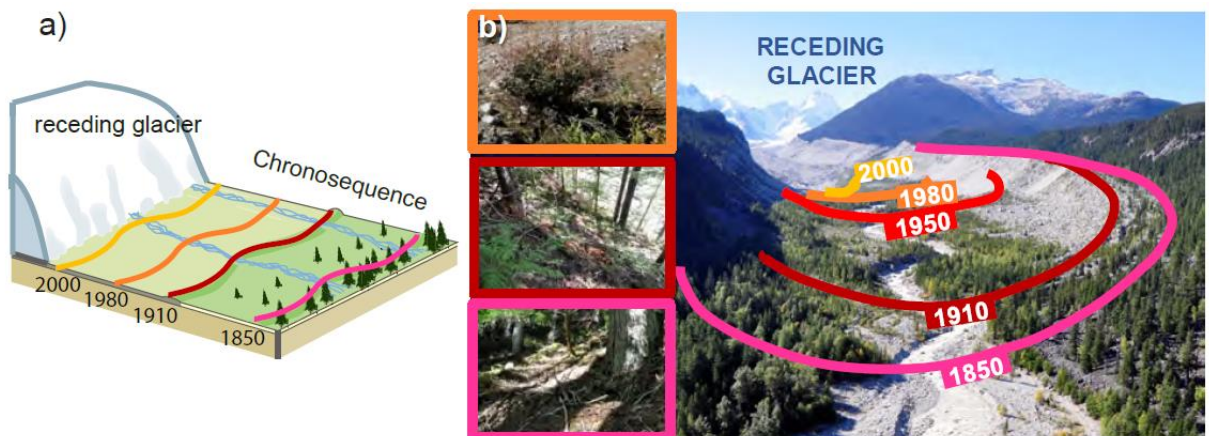




Figure 2. Temporal and spatial trends in research on community dynamics after glacier retreat. a) Number of papers published on the different glaciated areas of the world, compared to the number of extant glaciers; b) variation in the number of studies during the last 30 years; c) frequency of studies on plants (green), animals (orange) and microbes (blue). The sum can be >100 because several studies considered multiple trophic levels (e.g. plants+animals); d) frequency of multitrophic studies.

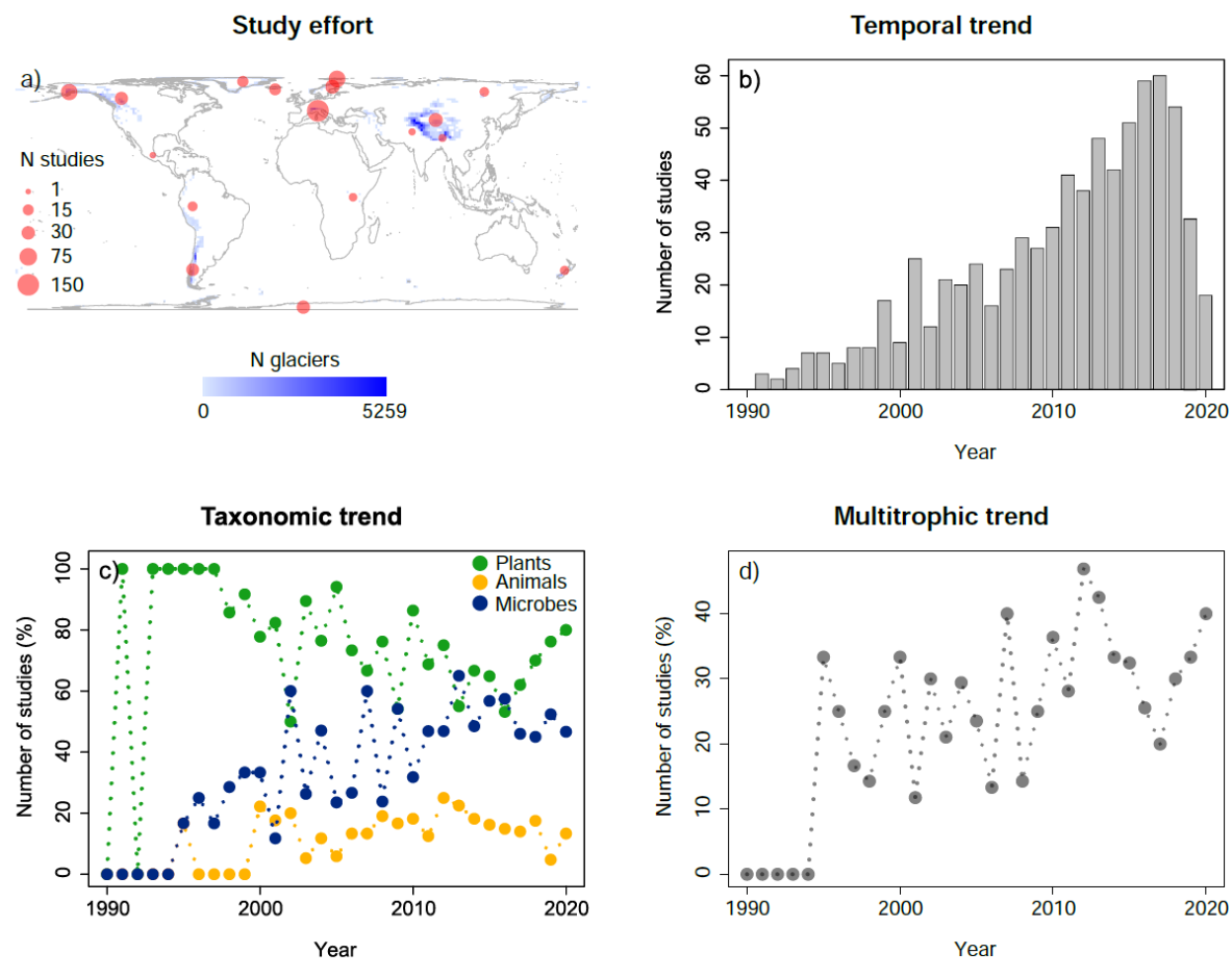


Figure 3. Examples on how analyses on abiotic factors, biotic interactions and functional traits can help to understand the dynamics of colonization after glacier retreats.

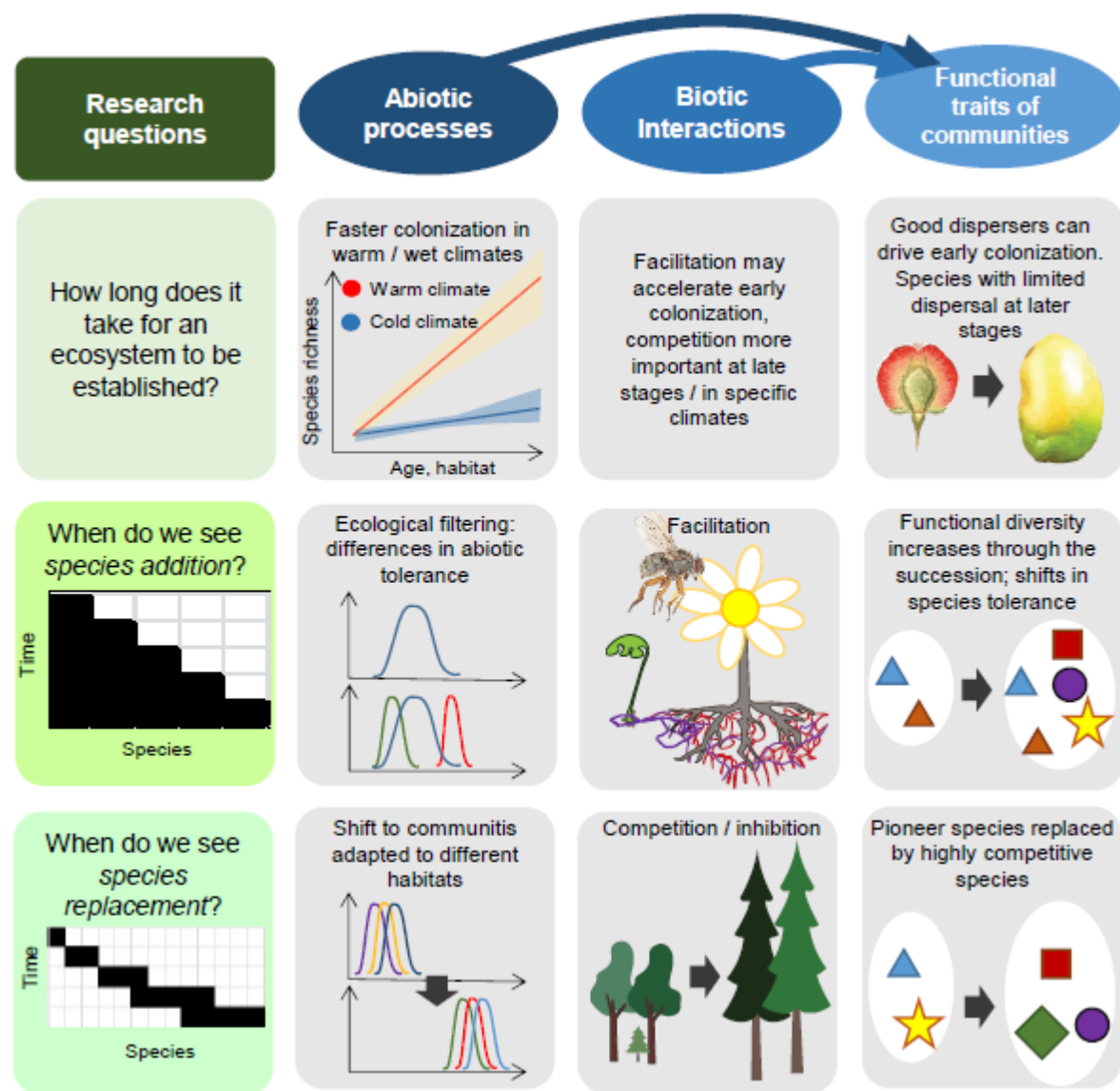
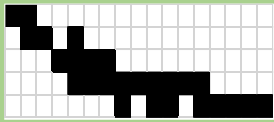
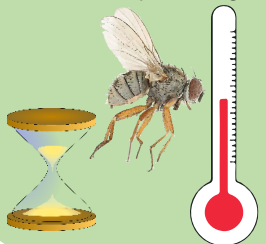




Figure 4. Non-exhaustive list of emerging questions. Each question can benefit from multiple traditional and emerging tools.

Theme	Open issues	Tools
<b>Patterns of community change</b> 	<p>What is the relative frequency of nestedness vs. turnover in metacommunities?</p> <p>When do we have tipping points and thresholds during colonization?</p>	<p>eDNA and metabarcoding</p> <p>Experimental manipulation</p>
<b>Drivers of community change</b> 	<p>What is the relative importance of time since glacier retreat vs. changes in abiotic characteristics?</p> <p>Is colonization accelerated under warmer or more humid climates?</p> <p>What is the importance of environmental context, dispersal limitation and biotic interactions over short and long periods?</p>	<p>Remote sensing</p> <p>Stable isotope analyses</p>
<b>Multitrophic linkages and functional diversity</b> 	<p>How do simple food webs develop into complex interaction networks during successions?</p> <p>Could the study of multi-trophic assembly along glacier retreat help us understand trophic links?</p>	<p>Remote sensing</p> <p>New statistical analyses</p>
<b>Finding generalities</b> 	<p>To what extent can results from one foreland be generalized over broader time windows and larger geographic scales?</p> <p>Are patterns observed in one target taxonomic group (e.g. insects) representative of what happens in specific groups (e.g. different insect families) or in less studied groups?</p>	<p>Meta-analytic framework</p>