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Dynamics of Ecological Communities Following Current Retreat of Glaciers

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► **To cite this version:**

Gentile Francesco Ficetola, Silvio Marta, Alessia Guerrieri, Mauro Gobbi, Roberto Ambrosini, et al.. Dynamics of Ecological Communities Following Current Retreat of Glaciers. Annual Review of Ecology, Evolution, and Systematics, 2021, 52 (1), pp.405-426. 10.1146/annurev-ecolsys-010521-040017. hal-03409533

HAL Id: hal-03409533

<https://hal.science/hal-03409533v1>

Submitted on 2 Feb 2024

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

3

4 **Manuscript accepted, *Annual Review Ecology Evolution and Systematics***

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26

27 **ABSTRACT**

28

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

43

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

46

47 **1. INTRODUCTION**

48

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

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

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

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

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

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

100

101 **2. PATTERNS OF COMMUNITY CHANGE**

102

103 **2.1 Patterns of colonization rate**

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

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

118 *Changes of colonization rate through time.* The rate of colonization is not
119 constant over time, with a rapid development of pioneer communities in the first 20-50
120 years, followed by a decrease in colonization rate at later successional stages (Kaufmann
121 2001; Gobbi et al. 2006a; Gobbi et al. 2010; Schlegel & Riesen 2012). The deceleration
122 of colonization rate is consistent with the predictions of the facilitation and inhibition
123 hypotheses (Connell & Slatyer 1977). Indeed, biotic interactions affect colonization rate
124 in multiple ways, with facilitation in the early colonization stages and an increasing
125 importance of competition, parasitism, or predation, decelerating colonization at later
126 stages (section 3.4; Koffel et al. 2018; Benavent-González et al. 2019). This change in the
127 type of biotic interactions can create complex patterns when glacier forelands are wide
128 and include multiple altitudinal zones (e.g. both areas above and below the tree line)
129 (Gobbi et al. 2007; Schlegel & Riesen 2012; Vater & Matthews 2015).

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

139 tardigrades), and several species of mosses, springtails, mites, spiders and insects, can
140 reach recently ice-free lands as "aeroplankton" (Coulson et al. 2003; Flø & Hågvar 2013;
141 Gobbi et al. 2017; Fontaneto 2019; Hågvar et al. 2020). Aerial transport is an effective
142 dispersal mechanism if the transported species are able to survive and reproduce on the
143 colonized substrate, and is also frequent for many non-flying organisms. These species
144 are capable of rapidly colonizing newly deglaciated terrains and, since they also have
145 specific traits (e.g. ability to perform ballooning, fast growth, short larval stages), they
146 determine the functional differences between early- and late-stage communities (Section
147 4).

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

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

168

169 **2.2 Patterns of community dynamics: additions, replacements, and tipping points.**

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

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

191 Distinguishing between these models can help identify the drivers of community
192 change for the different components of biodiversity (Fig. 3). Communities of plants often
193 follow the replacement model, suggesting a major role of competition (Connell & Slatyer
194 1977; Chapin et al. 1994). The observation of the replacement model for some
195 invertebrates suggested that biotic relations such as plant-animal interactions are major
196 drivers of community turnover (Kaufmann & Raffl 2002; Davey et al. 2015). Conversely,
197 the observation that invertebrate colonization more often follows an addition pattern
198 suggests that differences in colonization or tolerance play a larger role than competition
199 in determining community turnover for these groups (Gobbi et al. 2017). Although these
200 are sometimes described as "alternative" models (Vater 2012), their distinction is not
201 always clear-cut. In the real world, replacements and additions may jointly concur to
202 community changes over time, and their relative importance can be assessed by
203 partitioning beta-diversity into its dissimilarity and nestedness components for different
204 taxa or trophic groups (Dong et al. 2016; Ohlmann et al. 2019). The few studies assessing
205 the components of community changes suggest that, in the same chronosequence, both
206 nestedness and turnover can play a significant role (Nascimbene et al. 2017), but so far

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

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

218

219 **3. THE PROCESSES DETERMINING COLONIZATION**

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

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

234

235 **3.1 Abiotic factors and processes: time, soil and disturbance**

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

247 Most abiotic features change rapidly over time, influencing biogeochemical
248 cycles, the rate of colonization, and the identity of colonizers (Chapin et al. 1994; Raffl
249 et al. 2006; Mori et al. 2017). Increasing age is related to higher surface stability and
250 related soil development (Erhart 1951; Raffl et al. 2006; Erschbamer et al. 2008),
251 including accumulation of organic matter, due to positive feedback loops between
252 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

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

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

292

293 **3.2 Abiotic factors and processes: the role of climate**

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

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

310 Temperature is not the only important climatic factor. Precipitation regimes and
311 climate continentality affect the water balance and may consequently alter the
312 successional trajectories (Vater & Matthews 2015). Additionally, season length and solar
313 irradiance vary with latitude and altitude, conditioning the time and energy available for
314 life processes (Körner 2000). Finally, climate interacts with other abiotic features.
315 Insolation and temperature influence snow cover persistence, melting-water discharge
316 and the length of growing season (Tampucci et al. 2015). This, in turn, may have
317 additional effects on decomposition rate, C and N mineralization, CO₂ and NO₂ fluxes
318 and net nitrification (Williams et al. 1998; Khedim et al. 2021). Microclimate, soil texture
319 and aspect also influence soil moisture, affecting the development of plant communities
320 and nitrogen mineralization (Raffl et al. 2006; Rydgren et al. 2014; Schumann et al.
321 2016).

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

333

334 **3.3 The role of dispersal, spatial proximity, and landscape context**

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

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

347 While many studies have shown that, within regional meta-communities, nearby
348 sites have communities more similar than expected by chance (Brown & Jumpponen
349 2014; Rime et al. 2015; Gobbi & Brambilla 2016; Wietrzyk et al. 2018), the actual
350 importance of dispersal remains controversial (Makoto & Wilson 2019). Spatial
351 autocorrelation can arise both because of connectivity/ dispersal limitation (intrinsic
352 autocorrelation), and because species are constrained by environmental features (e.g. soil,
353 temperature...) that, in turn, are spatially autocorrelated (extrinsic autocorrelation) (Beale
354 et al. 2010). Glacier forelands often include sequences of habitats where adjacent sites
355 share similar age and altitude (Fig. 1). In addition, glaciers influence the microclimate of
356 nearby areas and determine gradients of wind, moisture and temperature with spatially
357 autocorrelated structure (Matthews 1992; Gentili et al. 2015). As a consequence,
358 separating the role of environmental modifications vs. dispersal is challenging.

359 Available evidence suggests that dispersal is particularly important at early stages
360 of successions, but data remain scanty and heavily biased, with almost no information for
361 tropical areas (Makoto & Wilson 2019). At early stages, the impact of dispersal can be
362 assessed through experimental analyses, or by evaluating the abundance of species with
363 particular traits (Hodkinson et al. 2004; Erschbamer et al. 2008; Brambilla & Gobbi
364 2014; Erschbamer & Caccianiga 2016). Documenting the importance of dispersal in later
365 stages is more complex, but at least two approaches exist. First, spatially-explicit
366 analytical frameworks can be integrated with ecological theory and a-priori hypotheses to
367 tease apart the role of environmental and spatial factors (McIntire & Fajardo 2009;

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

377

378 **3.4 Biotic drivers of colonization: facilitation and competition**

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

382 The *facilitation model* has successfully described many patterns of early
383 community development, particularly for plants (Connell & Slatyer 1977; Koffel et al.
384 2018). In the early stages of succession, for example, nitrogen-fixing organisms (e.g.
385 actinorhizal plants) dominate due to the initial lack of available nitrogen (N) (Walker &
386 del Moral 2003; Koffel et al. 2018). Fixed N accumulates in the soil through biomass
387 turnover and recycling, becoming available to other organisms and promoting their
388 colonization (Chapin et al. 1994; Walker & del Moral 2003; Koffel et al. 2018;
389 Benavent-González et al. 2019). The presence of taxa with efficient N-fixation can lead
390 to very rapid successions. For instance, herbaceous plants in the foreland of the Pia

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

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

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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

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

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

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

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

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480 **4.2. From species identity to functional diversity**

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

483 interactions that occur in a community is prohibitive. Instead, traits are common
484 currencies, allowing comparisons across communities, even with different regional pools
485 (Gravel et al. 2016). Trait-based approaches can allow for generalization on the structure
486 and dynamics of ecological communities (Gravel et al. 2016; Moretti et al. 2016), and
487 have been used to approximate some aspects of ecosystem functioning (Naeem et al.
488 2012; Gravel et al. 2016). Early analyses of functional traits on deglaciated grounds
489 mostly focused on plants (e.g. Chapin et al. 1994), but we can now analyze traits for a
490 broad range of taxa, from bacteria to animals (Brbić et al. 2016; Moretti et al. 2016). A
491 growing number of studies has revealed the functional variation during successions after
492 glacier retreat, showing that the increase of species richness along chronosequences also
493 results in higher functional diversity and, sometimes, redundancy, with consistent
494 patterns across multiple taxa, including plants, arthropods and nematodes (Losapio et al.
495 2016; Ricotta et al. 2016; Brown et al. 2017; Guerrieri et al. unpublished; Cauvy-Fraunié
496 & Dangles 2019). Understanding which traits prevail in the early stages of community
497 formation and how they change during successions helps assessing how species
498 characteristics determine assembly rules and community dynamics (Chang & Turner
499 2019). Trait variation can also be used to discriminate the potential processes that explain
500 colonization, and to measure the trajectories of functional diversity and ecosystem
501 functioning (Fig. 3; Naeem et al. 2012; Gravel et al. 2016).

502

503 **4.3 Testing processes using patterns of functional traits**

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

506 that limited dispersal determines the rate of colonization is confirmed by the prevalence
507 of taxa with traits favoring dispersal immediately after glacier retreat, while a lag time is
508 often observed for poor dispersers (Section 2.1). Similarly, the tolerance model predicts
509 that early colonizers are replaced by species with better competitive ability, and has been
510 confirmed by the observation of ruderal, fast growing species in recently deglaciated
511 areas, while later stages host stress tolerant species with slower growth and denser and
512 smaller leaves (Erschbamer & Caccianiga 2016; Ricotta et al. 2020). The analysis of
513 traits can thus provide efficient tests of ongoing processes. Importantly, the proposed
514 processes are often non-exclusive, and some can prevail at early stages while becoming
515 less important subsequently. The rate of turnover of functional traits could be used to
516 evaluate how the importance of different processes changes through time (Brown et al.
517 2017). For instance, we could imagine strong turnover in dispersal-related traits during
518 the first decades after glacier retreat. Then, after a given age, poor dispersers can become
519 more frequent, and trends in competitive ability could emerge. Functional traits
520 representing growth, dispersal or competition can be obtained for most of the components
521 of communities, enabling to compare the importance of different processes across
522 functional levels, and might even be used to assess at which stage of the succession
523 communities are, predicting their stability and future development (Erschbamer & Mayer
524 2011; Ricotta et al. 2020). Traits can also be combined with prior information to build
525 trophic groups and analyze the changes in trophic richness and diversity (Potapov et al.
526 2016), given that trophic diversity (e.g. the number of trophic groups) could increase
527 substantially over the course of succession, with more competition within trophic groups.
528 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

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

553 Stable isotope analysis is another approach that can greatly expand our
554 understanding of multi-trophic linkages, by measuring flows of biomass between multiple
555 components of food webs. This approach has only rarely been applied into pro-glacial
556 ecosystems (Niedrist & Fureder 2017), but the few available studies have revealed
557 intriguing and unexpected patterns of intraguild predation, helping to understand the
558 formation of food webs (König et al. 2011; Raso et al. 2014). Furthermore, advances in
559 remote sensing allow fast and broad-scale assessment of functional traits, particularly for
560 plants. Although seldom applied to high-mountain environments, remote sensing can help
561 measuring ecosystem functioning and responses to environmental changes, particularly in
562 remote regions (Asner et al. 2017). Finally, we can learn a lot from simulation analyses
563 integrating scenarios of climate change, and from manipulative experiments performed in
564 the field or in mesocosms, assessing the functional impacts of specific components of
565 biodiversity (Whitesides & Butler 2016; Donhauser & Frey 2018; Makoto & Wilson
566 2019; Vega et al. 2020). Importantly, manipulative experiments can now be combined
567 with other approaches (e.g. metabarcoding, isotope analyses) that allow evaluating the
568 impact of manipulation on the whole food web, including microbes (Rillig et al. 2019).

569

570 **5. CONCLUSIONS**

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

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

587

588 Acknowledgments

589 We thank J. Hille Ris Lambers for constructive suggestions. This study was supported by
590 the European Research Council under the European Community's Horizon 2020
591 Programme, Grant Agreement no. 772284 (IceCommunities).

592

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928

929

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

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

951

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

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

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

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

978

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

980 Community assembly after glacier retreat is often described as the "ideal example" of primary
981 succession. However, glaciers are not lifeless environments, as they are ecosystems teeming with
982 microbial and eukaryotic life and supporting active ecological processes (Hodson et al. 2008;
983 Hotaling et al. 2017; Gobbi et al. 2021). Glaciers host rich communities, which are connected by
984 the flow of meltwater from the glacier through the ice fractures to the subglacial sediments
985 (Hotaling et al. 2017). Glacier meltdown exposes subglacial sediments; moreover, supraglacial
986 sediments, together with the communities they host, are added to subglacial till. Bacterial
987 communities in recently deglaciated terrains can be more similar to those of supra- and
988 subglacial sediments than to those found in atmospheric deposition (snow, rain and wind-
989 dispersed dust). This indicates that bacteria inherited from the glacier are important starting
990 points of communities in newly deglaciated surfaces (Rime et al. 2016). Similar processes have
991 been proposed for other glacier-dwelling organisms, such as invertebrates and algae (Stibal et al.
992 2020; Rosero et al. 2021). Thus, even the most recently deglaciated areas are not devoid of life,
993 as they host many life forms from glacier environments. In addition, melting glaciers release a
994 substantial amount of ancient organic matter, which pioneer species can feed on. As this ancient
995 carbon can be the basis of food webs in recently deglaciated grounds, the term "primary
996 succession" is questionable (Hågvar & Ohlson 2013). Complex feedbacks between glaciers and
997 their forelands are also possible, as communities in environments close to glaciers are sources of
998 colonization of supraglacial environments (Franzetti et al. 2017; Gobbi et al. 2017). Hence,
999 glacier and near-glacier ecosystems cannot be disentangled; rather, they must be considered
1000 together for a comprehensive understanding of ecological responses to glacier retreat (Stibal et
1001 al. 2020).

1002

1003 ***BOX 4. Environmental DNA and metabarcoding for the reconstruction of communities and***
1004 ***food webs***

1005 Increasing evidence that all trophic levels contribute to the development of biodiversity in
1006 deglaciaded terrains has led to an increase in studies targeting a broad range of taxa and trophic
1007 levels (Fig. 2). However, the morphological identification of species is often laborious and time-
1008 consuming. Metabarcoding of environmental DNA (eDNA) is increasingly used to reconstruct
1009 communities of soil and water organisms, and can provide a more complete understanding of
1010 community dynamics. eDNA is the DNA that can be extracted from environmental samples
1011 (e.g., water, sediments, soil...) without isolating the macroscopic remains of the organisms
1012 (Taberlet et al. 2018). A given environmental sample generally contains the eDNA of many
1013 organisms. Multiple species of a given taxonomic group (e.g. insects, annelids, bacteria...) can
1014 be amplified using "universal primers", compared with reference databases and eventually
1015 identified in a procedure called eDNA metabarcoding (Taberlet et al. 2018).

1016 Recent metabarcoding analyses have revealed the complex patterns of microbial diversity in
1017 deglaciaded terrains (e.g. Schmidt et al. 2008; Blaalid et al. 2012; Rime et al. 2015; Dong et al.
1018 2016; Matsuoka et al. 2019). Although fewer studies have thus far used metabarcoding to study
1019 macro-organisms in deglaciaded terrains, the application of these approaches to a wide range of
1020 taxa could improve our understanding of biodiversity dynamics and of multitrophic relationships
1021 (Rosero et al. 2021). Metabarcoding can also be used to analyze the gut content of organisms,
1022 assess their diet and the variation of food webs. For instance, molecular analyses have been used
1023 to identify the food sources of predators that dominate at the early stage of colonization (Sint et
1024 al. 2019).

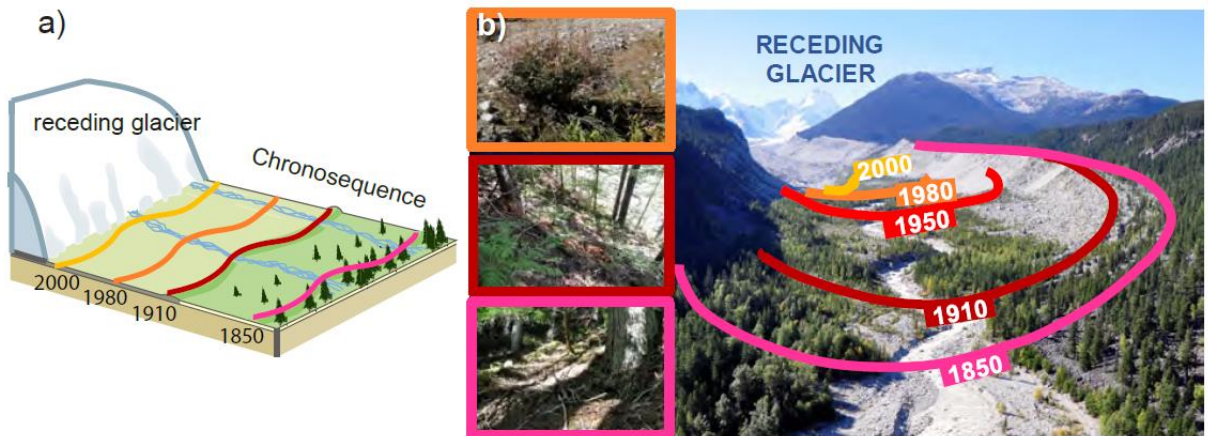
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1027 Figure legends

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1029 Figure 1. a) In a glacier foreland, a "chronosequence" is a sequence of dated sites for which time
1030 after retreat has been measured using a wide range of approaches (e.g. photographs,
1031 radionuclides...). b) The Tiedemann Glacier chronosequence (Canada), with strongly different
1032 communities between early and late development stages.

1033



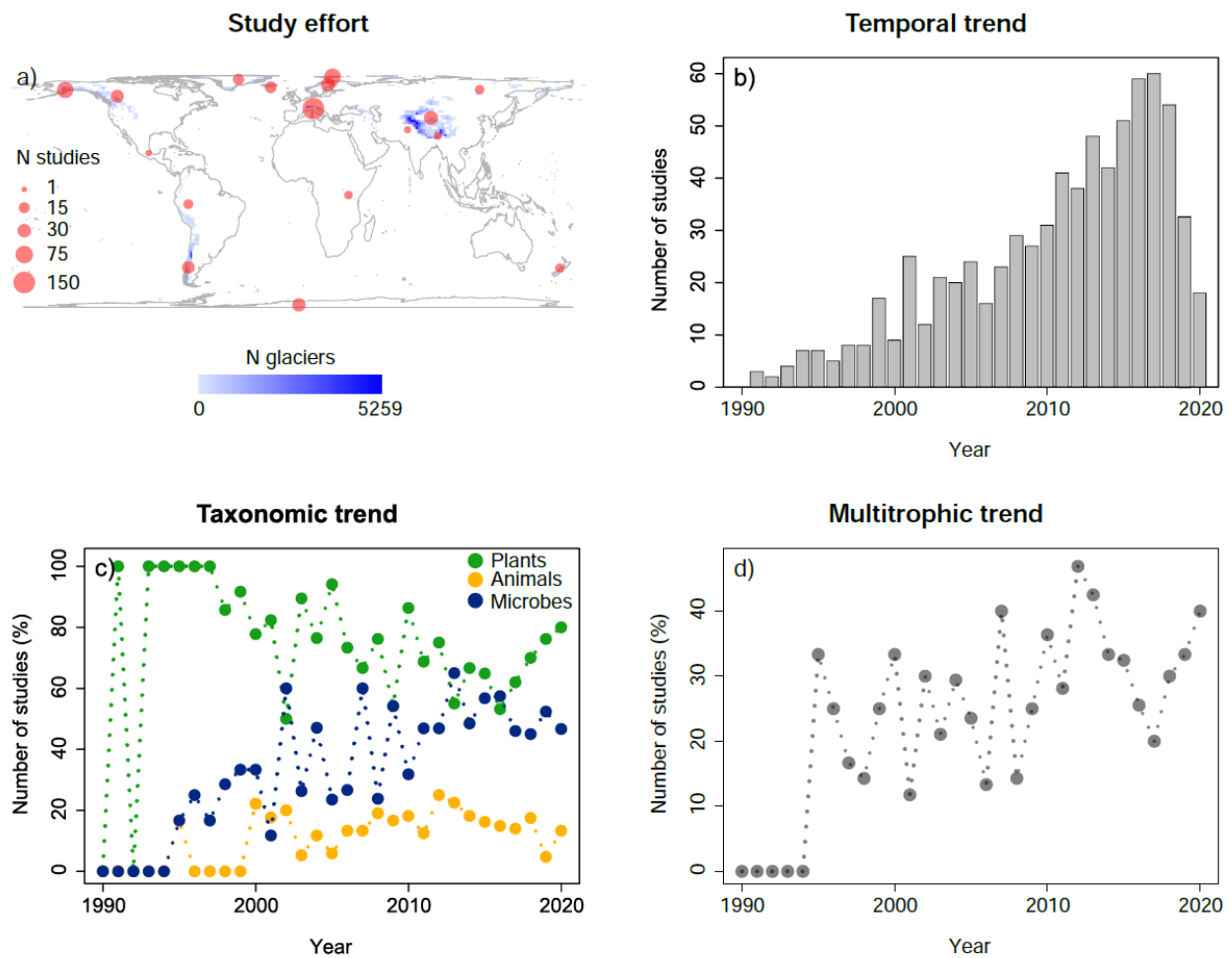
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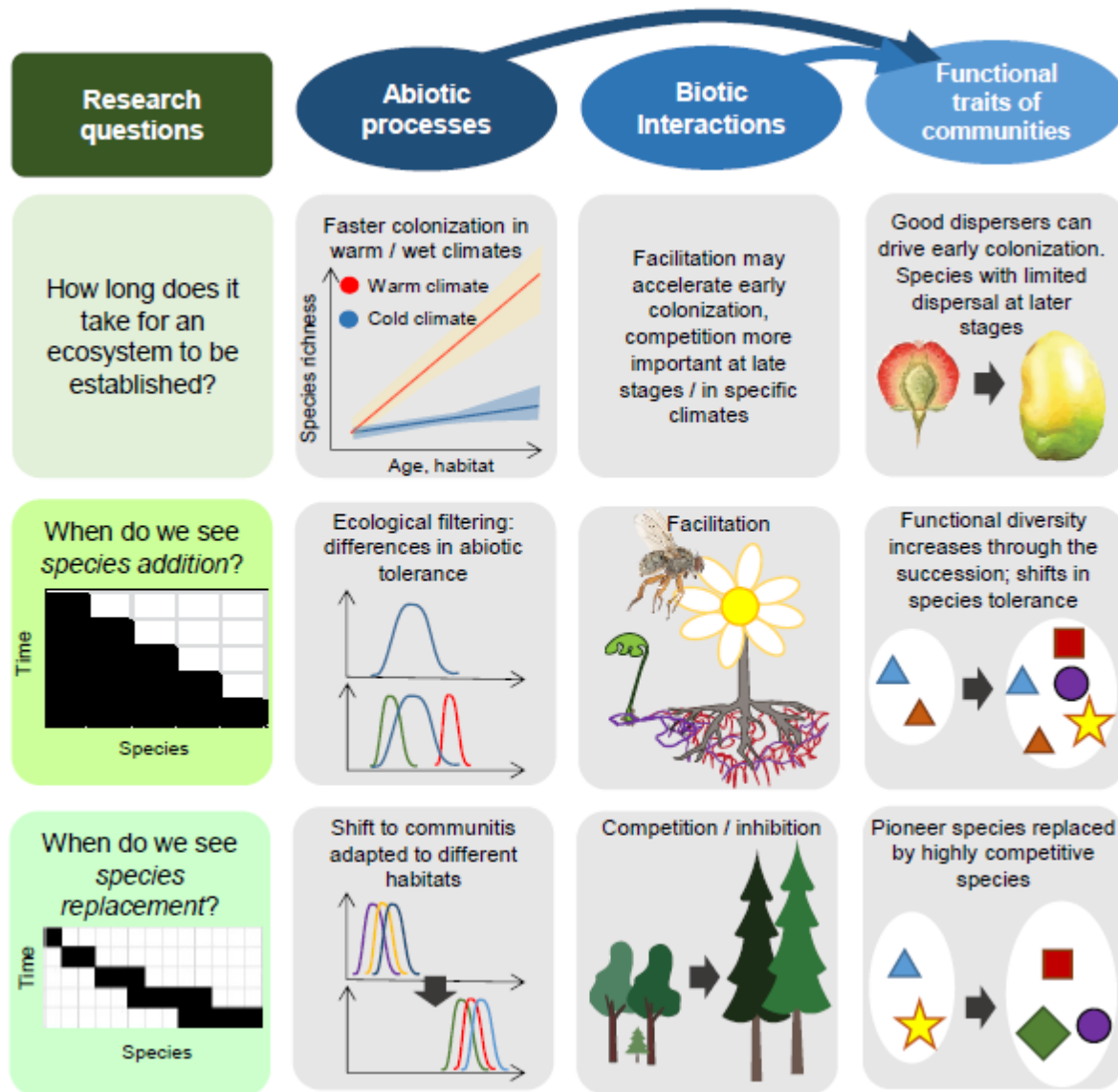
1038 Figure 2. Temporal and spatial trends in research on community dynamics after glacier retreat. a)
 1039 Number of papers published on the different glaciated areas of the world, compared to the
 1040 number of extant glaciers; b) variation in the number of studies during the last 30 years; c)
 1041 frequency of studies on plants (green), animals (orange) and microbes (blue). The sum can be
 1042 >100 because several studies considered multiple trophic levels (e.g. plants+animals); d)
 1043 frequency of multitrophic studies.



1044

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1046 Figure 3. Examples on how analyses on abiotic factors, biotic interactions and functional traits
 1047 can help to understand the dynamics of colonization after glacier retreats.



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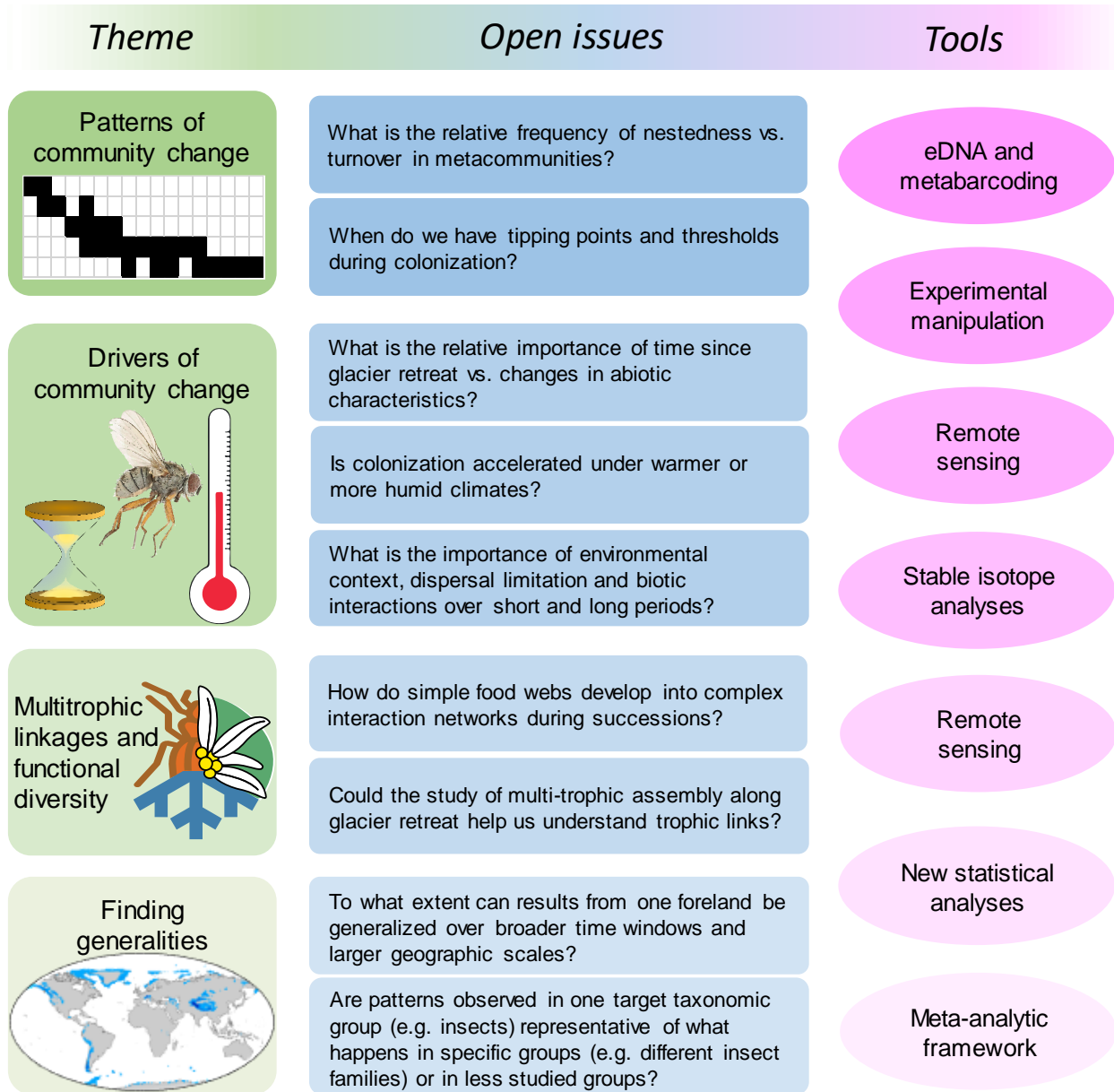
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1052 Figure 4. Non-exhaustive list of emerging questions. Each question can benefit from multiple
 1053 traditional and emerging tools.

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