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Impacts of deglaciation on biodiversity and ecosystem function

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32 Abstract

33 Glaciers and glacially influenced ecosystems host unique biodiversity spanning all kingdoms of life,
34 but glaciers are retreating as the global climate warms, threatening specialist species, ecosystem
35 functions and stability. We outline the impacts and consequences of glacier retreat, identifying key
36 drivers and mechanisms of change, focusing on biodiversity and interactions among glacier,
37 terrestrial, freshwater and marine ecosystems. We identify global glacial biodiversity patterns and
38 local nuances, highlighting taxa that are likely to thrive or decline with the loss of glaciers. Following
39 glacier retreat, the availability and size of ice-free areas initially increase, leading to a ‘biodiversity
40 peak’. However, as glaciers disappear, the formation of novel habitats decreases while communities
41 become more homogeneous and competition increases, leading to local-to-regional biodiversity
42 decline. Glacier loss impacts multiple ecosystem functions that contribute to climate regulation,
43 freshwater resources, carbon and nutrient cycling, soil development, primary productivity, and food
44 web stability. Key challenges in glacier ecosystem science include advancing knowledge of the
45 relationships between biodiversity and ecosystem functions and quantifying species interactions at
46 local-to-global scales to improve mechanistic understanding. Such advances will enhance prediction
47 of how biodiversity will change with the loss of glaciers, enabling informed and effective
48 conservation and management.

49 [H1] Introduction

50 Global biodiversity is declining at rates faster than at any other time in human history¹⁻³, driven
51 largely by changes in global land use and climate⁴. Emblematic of global change is the retreat and
52 thinning of glaciers worldwide^{5,6}. Despite global efforts to limit warming to 1.5 °C by 2100, alpine
53 glaciers are predicted to lose 34% of their mass by 2050, irrespective of future additional climate
54 change^{7,8}. Glacier–climate interactions create a positive feedback loop that accelerates further
55 warming, leading to additional retreat and enhanced threats to highly-adapted biodiversity and
56 ecosystem services that depend on glaciers, their runoff and adjacent post-glacial landscapes⁹⁻¹¹.

57 Glacier retreat has far-reaching consequences for diverse ecological functions, from nutrient cycling,
58 energy flow and species interactions to connections between dependent ecosystems, such as the ice
59 surface, downstream rivers and lakes, terrestrial **proglacial [G]** forefields, and marine environments¹²⁻
60 ¹⁵. On one hand, glacier retreat might benefit biodiversity because it exposes new terrain to
61 weathering and sediment reworking^{16,17}, offering colonisation opportunities¹⁸⁻²⁰. Ecological
62 succession in these newly formed habitats typically leads to an initial increase in local species
63 richness²¹ in the short term. On the other hand, habitat homogenisation and competition leads to
64 replacement of glacier-specialists by more generalist species, resulting in long-term biodiversity
65 decline²²⁻²⁴ and erosion of functional diversity^{14,25,26}. However, whereas most empirical work on these
66 dual forces has focused on describing taxonomic diversity, documenting colonisation and ecological
67 succession patterns, and analysing biogeochemical properties²⁷, there has been limited focus on
68 functional ecology and ecosystem functioning, particularly in terms of species interactions and how
69 food webs assemble, develop and shift within and between glacier-dependent ecosystems on a global
70 scale. Understanding how species interactions and cross-system linkages respond to glacier retreat is
71 vital to fundamental ecological knowledge that can inform management practices and policies that
72 could mitigate the detrimental effects of deglaciation on biodiversity and ecosystem services.

73 In this Review, we examine how glacier retreat affects global biodiversity across polar and mountain
74 regions, focusing on the key links between ice, water and land (Figure 1). We identify the drivers and
75 mechanisms that underlie biodiversity change, species interactions and functional process linkages
76 between ecosystems. In addition, we consider the structure and dynamics of ecological networks and
77 food webs, as these are the conduits through which flows of nutrients, matter and energy occur
78 between glacial, coastal and marine, freshwater, and terrestrial systems. Finally, we provide
79 recommendations for future research and discuss the implications of glacier retreat for conservation
80 strategies, emphasising the importance of managing biodiversity in the face of glacier extinction.

81 **[H1] Glacier retreat and novel ecosystems**

82 ***[H2] The glacial landscape and glacier retreat***

83 Since the end of the Little Ice Age (ca. 1850), glaciers have been retreating globally but the rate of
84 retreat has accelerated considerably over the past 30 years^{10,28}. Between 1980 and 2015, global glacier
85 area decreased by an average of 0.18% per year, and thinning rates have doubled in the past 20 years,
86 from 0.36 ± 0.21 m per year in 2000 to 0.69 ± 0.15 m in 2019 (ref.⁶). However, rates of glacier retreat
87 vary regionally, with glaciers in places such as the Tropical Andes retreating much faster than those at
88 higher latitudes⁷. Even without any further temperature increase, an additional $41 \pm 8\%$ of global
89 glacier mass will be lost by 2100 (refs^{5,10,29}). In particular, many small glaciers are expected to vanish
90 completely or to shrink into small ice–snow patches in coming decades^{8,9}. The sensitivity of
91 individual glaciers to mass loss is influenced by various factors, including temperature, precipitation,
92 humidity and radiation, as well as their geophysical characteristics such as size, geometry, elevation
93 and slope³⁰. For example, in the Swiss Alps, smaller glaciers on gentle slopes at low elevations are
94 likely to disappear first³¹. The timing and extent of glacier retreat will influence the availability and
95 characteristics of the new habitats that form. More hospitable environments will emerge on shallower
96 slopes and at lower latitudes, whereas extreme conditions might persist for longer at higher elevations
97 and in colder regions, providing refuges for cold-adapted species^{15,27,32–34}.

98 As glaciers shrink and fragment, meltwater discharge initially increases but eventually declines
99 dramatically³⁴, impacting downstream ecosystems. The concept of ‘peak water’³⁵ is based on evidence
100 that annual glacier runoff continues to rise until a maximum is reached, beyond which runoff
101 decreases because the reduced glacier volume provide less and less melt water from long-term
102 storage³⁵. This overall decrease in runoff impacts seasonal freshwater availability^{6,30} and,
103 consequently, biodiversity and ecosystem functions^{13,15}. During the peak water phase, enhanced
104 meltwater flux increases sediment transport, nutrient availability, and habitat connectivity in
105 downstream, glacier-fed ecosystems. These changes can temporarily boost primary productivity and
106 biodiversity, particularly in aquatic habitats. However, as water discharge declines after peak water,
107 reduced meltwater leads to habitat desiccation, fragmentation of aquatic systems, and loss of species
108 adapted to cold, glacier-fed waters^{15,36–38}. The ecological impacts of peak water are not limited to
109 aquatic systems, as altered hydrology in proglacial habitats exposes terrestrial habitats to reduced
110 water availability and fluctuating groundwater levels, which can limit the establishment, growth and
111 health of pioneer plants and microbial communities, ultimately slowing ecosystem development and
112 nutrient cycling and favouring ecosystem aridification^{39,40}.

113 ***[H2] The emergence of novel post-glacial ecosystems***

114 The type and structure of the habitats that emerge in place of ice depend on the region, the type of
115 glacier, and local topography^{9,11,12,19,31} (Figure 1a). The erosion, transport, and deposition of sediments
116 by glaciers and meltwater streams generate diverse coastal, marine and inland habitats, freshwater

117 systems and terrestrial landforms^{16,41–43}. Glacial processes alter the biogeochemical properties of
118 rivers, lakes, coastal marine environments, and sediments on land, leading to changes in matter and
119 energy fluxes and, ultimately, biodiversity^{22,44–47}. **Supraglacial [G]**, **englacial [G]**, **subglacial [G]**,
120 terrestrial proglacial, and subaquatic proglacial habitats are inter-related habitats characteristics of
121 glacial landscapes. These habitats are highly dynamic owing to paraglacial adjustment and sediment
122 reworking (Figure 1b–f), and their biodiversity is adapted to environmental extremes such as low
123 water temperature, high turbidity, frequent disturbances and low nutrient variability on land.

124 Once glaciers retreat, biotic processes gradually become more important than geophysical processes
125 in shaping new ecosystems, but this transition can take many decades⁴⁸. On land, glacier retreat
126 exposes a mixture of bare rock and fine sediments that are unstable and undergo chemical and
127 biological weathering. Minerals and propagules from local and remote sources can be exchanged
128 between glaciers and newly exposed terrains⁴². These propagules provide the substrate for the first
129 phase of primary succession by pioneer organisms such as cyanobacteria, algae, fungi, bryophytes,
130 cushion plants, nematodes, and invertebrates^{20,49–51}. **Subglacial legacies [G]** influence the physical and
131 ecological characteristics of emerging habitats⁵², serving as precursors to ecosystem development in
132 deglaciated areas via inputs of nutrients, ancient organic matter, and propagules⁵³. Deposited fine
133 subglacial sediments, together with englacial material, provide a first substrate for early colonizers,
134 while some microbial communities adapted to subglacial conditions, such as chemolithoautotrophic
135 bacteria, often persist in the early stages of soil development^{54,55} and are therefore crucial in
136 establishing nutrient pathways that support subsequent colonisation by animals, plants, and symbiotic
137 microorganisms. The importance of the subglacial legacy and propagules or organic biomass released
138 from glacier ice decreases sharply over time, to be replaced by **autochthonous [G]** energy production
139 and matter recycling.

140 Over time, biotic processes such as vegetation growth, productivity, competition, and facilitation
141 become increasingly important in determining ecosystem structure on land. For example, plants such
142 as the mountain avens (*Dryas octopetala*), willows (*Salix* spp.) or the dwarf birch (*Betula nana*),
143 which are widespread in Arctic or alpine systems, and their nitrogen-fixing symbiotic microorganisms
144 stabilize and enrich soils, thereby facilitating the establishment of other species and ultimately
145 increasing biodiversity locally^{42,48,56}. Freshwater ecosystems can also be enriched by nutrient inputs
146 from aquatic invertebrates, fish straying into newly formed rivers and ice-free lands and, in the case of
147 Antarctica, even penguin colonies^{12,57}. Within 10–50 years after glacier retreat, pioneer communities
148 drive soil development through the accumulation of organic matter, while changes in sediment
149 stability, soil pH, and nutrients facilitate the establishment of diverse grasses, forbs, and dwarf shrubs
150 on older terrain^{19,21,23,49}. The interplay between newly formed terrestrial habitats and glaciofluvial
151 systems demonstrates the interconnected nature of these ecosystems. Although nutrient enrichment
152 from glacial runoff supports primary production downstream, the establishment of pioneer vegetation
153 in **glacier forelands [G]** aids sediment stabilization and water quality.

154 Post-glacial landscapes, including lateral moraines and glacier forelands, often develop into complex
155 mosaics of habitats^{11,27} that support diverse microclimates and ecosystems such as shrublands, forests,
156 grasslands, wetlands, ponds, lakes, and glacier-fed streams, which act as ecological corridors or
157 climate refugia^{15,58–60}. As many mountain glaciers are likely to disappear within the 21st century^{8,10,19},
158 ecological communities are experiencing tremendous alterations of hydrological and microclimate
159 conditions, with cascading effects on composition, both within and across ecosystem boundaries^{61–64}.

160 Sediment input and flow stability influence the development of near-shore marine environments,
161 streams and lakes formed by glacial meltwater, which are initially turbid due to the deposition of
162 glacial silts and clays⁶⁵⁻⁶⁷. Stable flow from glacier meltwater streams is an important recharge in
163 alpine aquatic ecosystems, which are prone to changes and instability when glaciers disappear. In
164 glacier-influenced fjords, glacier retreat and changing discharge rate can influence salinity,
165 circulation, upwelling rates and resource availability^{61,67}. For example, icebergs from marine-
166 terminating glaciers trigger increased productivity by delivery of nutrients in Arctic food webs,
167 whereas delivery of subglacial waters inhibits photosynthesis when turbidity increases⁶⁸⁻⁷⁰. **Benthic**
168 **[G]** organisms such as bryozoans, barnacles, copepods and algae are the first colonisers of newly ice-
169 freed substrates. Gradually, physical stressors decrease while biotic processes such as the retention of
170 organic material and decomposition become more pronounced, aiding nutrient cycling and supporting
171 biodiversity at higher trophic levels and food web complexity^{45,57,71,72}. Upstream glacier meltwaters
172 and proglacial terrestrial ecosystems transfer nutrients and organic matter into these aquatic
173 ecosystems whereas fluvial dynamics influence terrestrial ecosystems via erosion and sediment
174 deposition⁴². These aquatic ecosystems are strongly linked not only to nearby upstream glaciers but
175 also to proglacial terrestrial ecosystems through nutrient and organic matter transfer, mainly via food
176 webs⁷³.

177 **[H2] Irreversible changes and unique habitat loss**

178 On the surface of glaciers, the supraglacial ecosystem includes unique microhabitats such as snow
179 patches, **firm fields [G]**, **cryoconite [G]** holes, supraglacial cones, **glacier mice [G]**, surface meltwater
180 streams and pools, supraglacial debris, surface ice of the weathering crusts, **moulins [G]** and **crevasses**
181 **[G]**¹⁻⁶. These habitats are characterized by a diverse consortium of microorganisms, including
182 bacteria, algae, phytoflagellates, fungi and viruses, and higher trophic level consumers, such as
183 invertebrates^{11,22,44}. These organisms perform crucial roles in nutrient cycling and carbon fixation and
184 are an integral part of glacier-linked food webs, transferring energy and matter to downstream
185 ecosystems^{25,76}. Cryoconite holes are the most studied supraglacial microhabitat and form biodiversity
186 hotspots that support cyanobacteria, diatoms, rotifers, tardigrades, and diverse arthropods^{22,63,77}. In
187 rare cases, such as on debris-covered glaciers, supraglacial habitats also host mosses, flowering plants
188 and their pollinators, spiders, and trees^{60,78,79}. In addition, organisms transported from non-glacial
189 surroundings via atmospheric fallout or geomorphic processes are commonly found to be a source of
190 microorganisms and **allochthonous [G]** organic matter on the ice surfaces⁴⁸. However, many of these
191 organisms, which are considered to be glacier specialists, are unlikely to cope with habitat loss
192 associated with the disappearance of glaciers²².

193 Englacial ecosystems, such as englacial streams, veins, and reservoirs, are habitats for microbial
194 communities, both active and inactive; however, the role of these ecosystems is still not
195 understood^{80,81}. Beneath glaciers, subglacial habitats include wetlands, lakes, debris, and geothermal
196 caves^{11,41,82}, which are highly susceptible to glacial retreat but are often overlooked in biological
197 studies. Subglacial habitats are characterized by no light, high pressure and extremely low nutrient
198 availability. At the glacier bed, rock-till-ice interactions determine hydraulic conditions, which in
199 turn influence microbial activity and biogeochemistry⁵⁵. **Redox potential [G]** is determined by
200 hydrology, chemical weathering, and oxygen and controls community composition, which ranges
201 from aerobes to anaerobes or chemoautotrophic to heterotrophic bacteria. Members of the
202 Proteobacteria, Bacteroidetes, and Actinobacteria, which have general metabolic capabilities to
203 degrade organic carbon, are commonly recovered from subglacial sediments and water columns. The
204 presence and abundance of specialist taxa that are capable of cycling iron, sulphur, nitrogen, or

205 methane vary among glaciers depending on meltwater and bedrock characteristics^{45,52}. Generally,
206 these subglacial microbial communities rely on chemosynthesis⁵³. Some of these unique environments
207 can support eukaryotic organisms such as mosses, algae, nematodes, earthworms and arthropods^{82,83}.
208 Collectively, subglacial ecosystems contribute to carbon cycling within and across glacier
209 environments through their emission of methane and carbon dioxide⁸⁴.

210 With deglaciation, supraglacial, englacial and subglacial habitats transition into proglacial ecosystems
211 (Figure 1). Although these areas provide opportunities for biotic colonisation, they are also vulnerable
212 to biodiversity loss, nutrient depletion and hydrological changes associated with continued ice loss.
213 Inputs of nutrients and organic matter from glacier ecosystems to proglacial streams, ponds, lakes,
214 terrestrial forelands and near-shore marine environments will also be reduced or lost with glacier loss
215 ^{61,67,85}, impacting resident and transient species and their functioning in ways that remain poorly
216 understood. Of note, the loss of glaciers removes habitat features and biological processes that act as
217 barriers to species colonisation, leading to an influx of generalist and competitive species and
218 potentially to biotic homogenization^{18,23,26,32}. However, the rates and timescale of colonisation and loss
219 of pioneer habitats characterized by soil instability can be strongly dependent on climate. For
220 example, pioneer habitats in New Zealand glacier forelands can persist over millennia, as high rainfall
221 keeps sediments unstable⁸⁶. With climate change and glacier retreat, habitat loss is expected for a
222 diverse set of organisms^{22,27,70} (discussed later). Of note, local biodiversity loss in both subglacial and
223 supraglacial habitats has cascading effects across ecosystems, as nutrients, organic matter and
224 organisms are redistributed to downstream terrestrial and aquatic habitats, influencing ecological
225 succession and carbon dynamics.

226 Analogous to the ‘peak water’ concept that offers a crucial framework for understanding the
227 hydrological and ecological consequences of glacier retreat and glacier extinction³⁵, here we propose
228 the ‘peak biodiversity’ concept, which includes species and habitat diversity. Following glacier
229 retreat, the availability and size of ice-free areas initially increase^{15,32,85}, leading to a peak in habitat
230 availability, heterogeneity and local species diversity — a phase referred to as peak biodiversity.
231 Beyond this peak, as glaciers continue to shrink and finally disappear, glacial habitats and their
232 associated organisms, as well as the formation of novel habitats, decreases progressively, while
233 former communities become more homogeneous²⁴ and biodiversity at the local-to-landscape scale
234 declines^{19,23,87,88}. Of note, pioneer habitats formed by glacier retreat can continue to exist only in the
235 presence of glaciers. In the absence of glaciers, no new habitats will emerge, whereas pioneer and
236 intermediate habitats will undergo succession (discussed later), with inherent habitat and species loss
237 and homogenization^{89,90}.

238 **[H1] Drivers and mechanisms of biodiversity change**

239 Although much research has focused on documenting the spatiotemporal changes in biodiversity after
240 glacier retreat, a better understanding of the eco-evolutionary mechanisms governing these changes is
241 needed to predict the implications for ecosystem functioning and stability (Figure 2). In this section,
242 we describe the spatiotemporal changes in ecological processes that occur during glacial retreat.

243 ***[H2] Ecological succession: from ice to water and land***

244 The hierarchical successional framework^{89,91} offers a comprehensive approach to understanding
245 community replacement in glacier and glacier-associated ecosystems, by incorporating facilitation,
246 tolerance, and inhibition mechanisms. This framework spans different spatial scales, from plant

247 neighbourhoods to landscapes and biogeographic regions, enabling a nuanced understanding of how
248 glacier retreat affects habitat availability, species availability, and species performance. We integrate
249 this framework with the concept of **paraglacial adjustment [G]**¹⁶ and **biogeomorphic feedbacks [G]**¹⁷
250 after glacier retreat.

251 Habitat availability in terrestrial, freshwater, and marine systems increases with glacier retreat, at the
252 expense of glacial habitats in the long term. In glacier forelands, new ice-free terrains offer unique
253 opportunities for early successional species, but these habitats diminish as glaciers ultimately
254 disappear according to ‘peak biodiversity’ patterns. That is, the response of habitat availability to
255 glacier retreat is non-linear but changes over space and time, depending also on local conditions such
256 as microclimate and bedrock. Furthermore, disturbance regimes, such as sediment deposition, erosion,
257 and hydrological changes continue to have crucial roles in shaping habitat availability at the landscape
258 scale^{42,48,61}. Sediment instability associated with paraglacial adjustment¹⁶, including debris flows and
259 erosion, limits successional rates^{86,92}. Pioneer plants such as cushion plants play a key part in early-
260 successional development facilitating biogeomorphic feedbacks⁸⁶, increasing the size of areas that are
261 suitable for growth and diversifying microtopography. Such increased stability in turn creates more
262 favourable conditions for biodiversity development and influences the rate of colonisation and
263 succession⁹³.

264 Species availability is a key factor in the successional process. In glacier and glacier-associated
265 ecosystems, connectivity to colonisation sources is often limited by topographic barriers in
266 mountainous and marine environments^{88,94,95}. However, glacial retreat leads to the emergence of
267 dispersal corridors and alters habitat connectivity, increasing rates of species immigration and
268 extirpation¹⁵. Rivers fed by glacial meltwater serve as crucial pathways for the migration of fish and
269 invertebrates and for the transportation of plant seeds over long distances^{14,96}. Wind and slope
270 processes such as avalanches and landslides can also transport propagules into newly deglaciated
271 areas^{19,97}. In coastal zones where tidewater glaciers retreat, marine currents help to carry species to
272 newly exposed **benthic [G]** and **pelagic [G]** zones, thereby facilitating colonisation^{61,98,99}.

273 Species performance is shaped by environmental constraints, functional traits, and biotic
274 interactions^{23,26,92,93}. Environmental constraints in glacier-associated ecosystems, such as light
275 intensity that is too low or too high, poor soil nutrients, unstable substrates, low temperatures, and
276 freeze–thaw cycles, limit the growth and establishment of species⁸⁹. Autecological factors such as
277 fecundity, growth rates, and survival strategies are also key in determining which species succeed. In
278 early stages of succession, biotic interactions are influenced by the identity of neighbouring species,
279 soil microbial communities, and the spatial distribution of populations^{13,62}. Integrating these factors is
280 a necessary next step to providing a coherent picture of the mechanisms underlying successional
281 changes after glacier retreat, as well as identifying potential new mechanisms underlying biodiversity
282 maintenance once glaciers vanish.

283 Functional traits are pivotal in shaping species response, community assembly, and ecosystem
284 development after glacier retreat^{23,100–102}. Animal traits such as physiological capability, body size,
285 dispersal ability, and dietary requirements contribute to the capacity of species to colonize and persist
286 in glacial habitats¹⁰³. Plant traits such as specific leaf area (SLA), leaf dry matter content (LDMC),
287 flowering strategy, and canopy height are crucial for understanding plant strategies in resource
288 acquisition, stress tolerance, and competition^{26,100}. Early successional stages are often dominated by

289 species that are adapted to nutrient-poor conditions and acquire resources effectively^{46,104}. Over time,
290 these species are replaced by competitive species with denser leaves, reflecting a shift towards
291 resource conservation strategies that limit nutrient dynamics^{92,93}. The role of functional traits extends
292 beyond colonisation, as plant traits influence succession through biogeomorphic feedbacks^{42,105}. For
293 example, traits associated with ecosystem engineers such as *Dryas octopetala* or *Saxifraga*
294 *oppositifolia* contribute to reducing erosion and enhancing soil development rates. This biotic–abiotic
295 interplay promotes habitat creation, enabling the establishment of more diverse communities over
296 space and time.

297 **[H2] Species interactions and food webs: the flow of matter and energy**

298 Understanding how species interactions evolve after glacier retreat is crucial for predicting the
299 responses of biodiversity to climate change, but interactions are still poorly understood within specific
300 ecosystem types, let alone between ecosystems. One of the most comprehensive studies focused on
301 interactions and links among river, lake, terrestrial and marine intertidal ecosystems during glacier
302 retreat at Glacier Bay, Alaska^{57,102,106}. The nature and strength of physical and biological interactions
303 between these systems changed non-uniformly over space and time. This approach needs to be
304 expanded to other regions of the world to identify general patterns.

305 Cryoconite holes, supraglacial streams, ponds, weathering crusts and snow patches on glacier surfaces
306 are key glacial microhabitats that support highly specialised and at-risk food webs^{22,75,76,107}. These
307 food webs are fairly simple, characterized by short trophic chains. Autotrophic, photosynthetic
308 microorganisms such as cyanobacteria and green algae capture solar energy and use glacial meltwater
309 to fix carbon and nitrogen⁹⁹. As expected, they are the first colonizers of these habitats, followed by
310 heterotrophic bacteria, fungi, and protozoa that recycle nutrients within the food web for consumers at
311 higher trophic levels, such as rotifers, tardigrades, ice worms, springtails, copepods and chironomid
312 midges. Extended glacier food webs can incorporate vertebrate consumers, such as rosy finches
313 (*Leucosticte tephrocotis*) that feed on ice worms (*Mesenchytraeus solifugus*) in Paradise Glacier
314 (Washington, USA)¹⁰⁷. Debris-covered glaciers hosting herbaceous plants also harbour their
315 associated pollinators and herbivores⁷⁸. These food webs provide resources for downstream, aquatic
316 and terrestrial ecosystem development^{71,108}.

317 As in supraglacial systems, pioneer microbial communities, including cyanobacteria, fungi, algae, and
318 protists, are also the first colonizers in proglacial aquatic and terrestrial ecosystems^{99,109,110}. These
319 microbial communities produce and stabilize organic matter from mineral and organic resources from
320 glacier meltwater, sediments, terrestrial detritus, and airborne inputs^{36,38,69}. They support omnivorous
321 (herbivore and detritivore) communities that feed on microorganisms, algae and detritus, serving as
322 prey for larger invertebrate herbivores and predators. In marine-terminating (tidewater) glacier
323 ecosystems, buoyant plumes and subsequent upwelling of deep nutrient-rich meltwater promote
324 higher biodiversity and productivity compared with land-terminating systems^{68,69}. Polar marine food
325 webs benefit from marine-terminating glacial meltwater that delivers essential nutrients such as iron
326 and silica to the photic zone, stimulating phytoplankton blooms and primary production^{66,67,69,108},
327 which form the food base for key marine herbivores such as Arctic copepods and Antarctic krill. In
328 turn, these primary consumers transfer energy and nutrients from phytoplankton to higher trophic
329 levels, which are first characterised by planktivorous seabirds such as little auks (*Alle alle*), forage
330 fish such as capelin (*Mallotus villosus*), and baleen whales (for example, blue whales *Balaenoptera*
331 *musculus*), and then by salmon (*Oncorhynchus* spp.), seabirds such as Kittlitz's murrelet
332 (*Brachyramphus brevirostris*) in Alaska, and blue-eyed shags (*Phalacrocorax atriceps*) in Antarctica,

333 and ultimately by marine mammals such as beluga whales (*Delphinapterus leucas*), ringed seals
334 (*Pusa hispida*), and leopard seals (*Hydrurga leptonyx*)^{68,111}. As a consequence of glacier retreat,
335 reduced meltwater flow can limit nutrient availability and disrupt trophic interactions⁶⁹.

336 In terrestrial glacier foreland ecosystems, microbial communities are similarly crucial in establishing
337 early trophic interactions, thereby supporting detritivore communities and larger invertebrate
338 herbivores and predators such as beetles, spiders and flies^{56,72,109,112–114}. Besides trophic interactions,
339 mutualistic interactions between pioneer plants and nitrogen-fixing symbiotic bacteria are crucial for
340 facilitating the establishment of less-specialised plant and animal species by stabilizing sediments,
341 retaining water, increasing organic matter and nutrients, and providing food resources and habitat for
342 invertebrates^{73,78,90,115}, ultimately increasing biodiversity. Furthermore, plant litter inputs to rivers and
343 lakes increase detritivores and thus secondary production. With succession, plant facilitation and
344 mutualistic and antagonistic interactions such as pollination, mycorrhization, herbivory and parasitism
345 add further interaction diversity, and decentralized nested networks become more prominent^{78,116,117}.
346 Competitive interactions begin to dominate over facilitative ones as key resources such as
347 phosphorus, light, and space become a limiting factor. This shift in interactions from facilitation to
348 competition influences species turnover, with key pioneer communities being replaced by later
349 successional communities that are characterised by lower levels of biodiversity^{93,118,119}.

350 **[H2] Biogeographical and evolutionary processes**

351 The glacial history of Earth has shaped biodiversity and ecosystem development since the
352 Precambrian era²². Glaciated regions with ice-free refugia and glacier fluctuations during the
353 Pleistocene influenced gene flow⁷⁰ and speciation by isolation and divergence^{120,121}, reshuffling
354 population connectivity^{94,95} and diversifying phylogenetic lineages¹²². Owing to the similarities in
355 physical conditions across distant regions, such as the Alpine and Arctic regions, glaciers provide
356 unique habitats for the dispersal, refugium, and evolution of extreme cold-adapted organisms^{34,58–60,123}.
357 For example, many groups of organisms in these disparate regions share convergent traits, such as
358 pigmentation in algal taxa and short reproductive cycles in invertebrate taxa¹²², despite being
359 separated by vast geographic distances¹²¹. Although glacier habitats often support endemic species,
360 long-distance dispersal is not uncommon^{94,120,124}.

361 In the current deglaciation phase, glacial habitats are also climate refugia^{58,59,121,125}. With the loss of
362 glacial habitats in polar and mountain regions, glacial organisms have three possible fates: the
363 extinction of unique populations and endemic, glacial specialist species; survival in cold refugia, such
364 as debris-covered glaciers, rock glaciers, snow fields, cold lakes and cold seeps; or adaptation to new,
365 ice-free habitats with heterogeneous environmental conditions. Long-range dispersal from small,
366 disappearing ice patches to larger ice masses might offer opportunities for survival if the
367 characteristics of new glacier habitats are suitable. In addition, glaciers and adjacent environments can
368 act as ‘time capsules’ that preserve microorganisms¹²⁶ and plants⁶⁴ that later regenerate with melting.
369 However, the loss of glaciers and glacial habitats poses a survival challenge for organisms that inhabit
370 ice, water, and terrestrial glacial ecosystems.

371 **[H1] Winners and losers of deglaciation**

372 The retreat of glaciers is leading to large shifts in biodiversity, with some species emerging as
373 ‘winners’ (thriving long term) and others as ‘losers’ (facing range and population contractions and
374 increased risk of extinction)^{15,23,46,92}. Generally, glacial specialists face severe threats to their

375 persistence: the higher the degree of specialisation and dependence on glacial environments, the
376 higher the extinction risk (**Figure 3**). The persistence of populations restricted to glacial ecosystems
377 depends also on their geographic distribution and the geophysical characteristics of the glacier: the
378 faster the retreat and the smaller the glacier, the higher the risk. In this section, we explore how glacier
379 retreat is reshuffling biodiversity, including microorganisms, animals, and plants, across ice, glacial
380 waters, and deglaciated lands.

381 **[H2] Glacial biodiversity**

382 Current models project continued ice occurrence globally by the end of this century^{8,10}, but with
383 substantially reduced areas of supraglacial habitats²⁷. There are few winner species that thrive in
384 supraglacial ecosystems and are likely to persist; those species are rather generalist such as surface
385 snow algae; Chlorophyta species, such as *Sanguina* and *Chlamydomonas*, which mainly thrive in
386 accumulation areas; and glacier algae *Ancylonema* spp. which is prominent in the ablation zone^{25,44,63}.
387 Cryophilic fungi that parasitize algae and heterotrophic bacteria that are consumed by microscopic
388 invertebrates such as springtails, rotifers, and tardigrades might also thrive, as long as glaciers
389 persist¹²⁷. Generalist communities characterized by Proteobacteria, Actinobacteria, Bacteroidota,
390 Chloroflexi, and Cyanobacteria^{63,99}, as well as invertebrates (Nematoda, Tardigrada, Rotifera,
391 Collembola, Chironomidae)^{75,128} that occur non-exclusively in sediments of supraglacial water bodies,
392 might persist in nearby microhabitat sediments.

393 Beneath glacier surfaces, in the englacial zone, and beneath the body of the glacier, diverse
394 assemblages of microorganisms are found in subglacial streams and lakes where ice, rock and water
395 interact^{53,83}. These systems contribute unique taxa to local species pools compared with supraglacial
396 and proglacial streams¹²⁹, suggesting that they might not persist in the absence of glaciers. Ice loss
397 further imperils specialised cryoconite inhabitants, such as the tardigrades *Cryobiotus klebelsbergi* in
398 the Alps and *Fontourion glaciale* in the Arctic, or ice inhabitants such as the annelid *Mesenchytraeus*
399 *solifugus* that exclusively occur in glacial environments¹³⁰. The future is also uncertain for mammals
400 that use glaciers as refuges during warmer seasons¹³¹ or birds such as the white-tailed ptarmigan
401 (*Lagopus leucura*) that can nest on ice surfaces. Glacial-obligate organisms that are endemic to
402 smaller regions are at the highest risk, as the chances to find adequate climate refugia or to adapt
403 locally are reduced^{34,123}. The risk is lower for species with a broad geographic distribution or those
404 that are only randomly or sporadically associated with glacial habitats, which might face a reduction
405 in population size but might continue to persist within the landscape or in adjacent microhabitats, such
406 as rock glaciers or snow fields.

407 **[H2] Biodiversity in glacial waters**

408 Given that three-quarters of the Earth's freshwater is stored in glaciers and in light of accelerating
409 glacier retreat, many unique aquatic ecosystems will disappear or change considerably, affecting the
410 organisms that depend on them^{14,15,96}. This loss of water is also key for the health of terrestrial
411 communities⁵¹. Ice-associated vertebrates such as the ivory gull (*Pagophila eburnea*) and fish such as
412 Arctic cod (*Boreogadus saida*) might face reductions in foraging areas, food supply, and availability
413 of stable glaciers and sea ice for birthing and nursing¹³²⁻¹³⁴, while facing increased competition for
414 scarce resources and increased risks from predation in the long term¹³⁵. For example, retreat of
415 glaciers in the Arctic is impacting ice-dependent vertebrates that rely on cold-water, such as the little
416 auk (*Alle alle*), as their primary food source, the copepod *Calanus glacialis*, is declining with
417 increasing temperatures in glacier habitats^{136,137}. The population declines of ice-associated vertebrates
418 will have cascading effects on biodiversity at multiple trophic levels¹³⁵. In the Antarctic, generalist

419 vertebrates such as gentoo penguins (*Pygoscelis papua*) and herbivores that thrive in newly available
420 habitats might benefit from glacier retreat, as do some Antarctic pinniped species such as the southern
421 elephant seal (*Mirounga leonina*) which are attracted to large patches of the grass *Deschampsia*
422 *antarctica*⁶⁸.

423 Although increasing rates of glacier retreat threaten the persistence of extremophiles and specialist
424 species⁷⁰, it also creates opportunities for generalist species to thrive¹⁸. Increasing input of glacial
425 meltwaters can enhance nutrient availability such that, if disturbance and turbidity remain low,
426 phytoplankton primary producers such as diatoms will flourish, increasing local productivity as the
427 glacier continues to melt¹³⁸. Consequently, primary consumers can thrive, in turn supporting the
428 growth of fish populations that feed on them, such as Atlantic herring (*Clupea harengus*) and capelin
429 (*Mallotus villosus*)¹³⁹. These increasing populations can support biodiversity across trophic levels,
430 ultimately supporting top predators such as seabirds, marine mammals and sharks¹³⁵. Retreating
431 glaciers also create new territory for colonisation and succession processes in marine environments at
432 glacial margins, whereas calving glaciers can disturb benthic communities¹³⁴. For example, scouring
433 from icebergs calved from glaciers in the Antarctic can extirpate large areas of benthos, initiating new
434 succession processes and carbon cycling⁶⁹.

435 Organismal transport by glacial runoff forms a crucial linkage between terrestrial and marine systems,
436 enabling connectivity and sustaining biodiversity across these ecosystems. The composition and
437 functioning of bacterial communities in glacier-fed rivers are distinct from those of ice, snow,
438 permafrost and terrestrial communities, and many bacteria in glacier-fed rivers are endemic to
439 individual mountain ranges^{38,110}. Although microorganism α -diversity [G] increases locally with
440 decreasing influence of glacier meltwater^{12,18,20,127}, glacier retreat also leads to decreasing β -diversity
441 [G] and to the homogenization of microbial communities¹⁴⁰, which increasingly resemble those in
442 non-glacial rivers⁶², consequently leading to γ -diversity [G] decline¹¹⁰. Invertebrates in glacier-fed
443 rivers show strong biodiversity gradients from the glacier terminus downstream, as habitat properties
444 such as water temperature, stability, and resources become less harsh^{13,37,57}.

445 With increasing glacier retreat, invertebrate species that are typical of glacier terminuses, such as
446 *Diamesa* spp. chironomids (Diamesinae) in European and North American rivers³⁶, *Paraheptagyia*
447 spp. chironomids (Diamesinae) and *Anomalocosmoecus* sp. caddisflies (Limnephilidae) in South
448 America⁸⁷ or the mayflies (Ephemeroptera) *Deleatidium cornutum* and *Nesameletus* spp. in New
449 Zealand¹⁴¹ might face large population declines. Endemic, cold-water obligate invertebrates such as
450 the glacier stonefly (*Zapada glacier*) and meltwater stonefly (*Lednia tumana*) are expected to
451 experience population declines or even local extinctions as glaciers disappear¹⁴². This biotic
452 replacement of cold-adapted taxa leads to communities that increasingly include more generalist
453 blackflies (Simuliidae), craneflies (Tipulidae), worms (Oligochaeta) and river flies (mayflies,
454 stoneflies, and caddisflies) across European rivers^{15,37}.

455 [H2] Biodiversity in deglaciated lands

456 Although the retreat of glaciers creates new terrestrial habitats, allowing species to colonise and thrive
457 in the short term, the conditions in these deglaciated areas are often challenging for many plant and
458 animal species owing to low temperatures, permafrost, and poor soil development^{19,46}. Many
459 microorganisms that occur on glacier surfaces are well-suited to the transition into foreland
460 environments and consequently persist in the newly exposed terrains¹⁴³. However, as succession

461 progresses, microbial communities shift, with generalist species replacing specialised, cold-adapted
462 taxa that struggle to persist in the warmer and drier conditions of glacier forelands^{99,144}. Generalist
463 microorganisms, particularly ectomycorrhizal fungi, replace bacteria and arbuscular mycorrhizal
464 fungi, and dominate later stages of succession¹⁴⁵.

465 There is evidence of vegetation expansion in the Alps¹⁴⁶, polar greening and browning⁵¹, and
466 population range expansion for the grass *Deschampsia antarctica* and the cushion-plant *Colobanthus*
467 *quitensis* in Antarctica¹⁴⁷. However, the future is uncertain for many pioneer, cold-adapted, slow-
468 growing plant species, which might decline with increasing glacier retreat owing to a lack of habitat
469 availability and increasing competition with later colonisers such as trees and shrubs^{23,92,93,119}. In the
470 Alps, stress-tolerant pioneer species such as *Saxifraga bryoides*, *Saxifraga oppositifolia*, *Dryas*
471 *octopetala*, *Ranunculus glacialis*, and *Geum reptans* are increasingly being replaced by faster-
472 growing competitive species¹⁴⁸. In Andean glacier forelands, tropical alpine specialists are being
473 outcompeted by rapidly colonising non-native plant species^{92,149}. Similar to freshwater ecosystems,
474 the loss of glaciers increases the risk of biotic homogenization and reduced **ecological niche**
475 **availability [G]**^{24,26}, which can facilitate colonization by invasive species. For example, the grass *Poa*
476 *annua* is rapidly colonising newly deglaciated habitats in Antarctica¹⁴⁷. Encroachment or invasion by
477 woody plants can have negative effects on functional diversity and resilience in post-glacial
478 ecosystems in the long term.

479 Invertebrate colonisation and succession are associated with changes in plant
480 communities^{21,90,118,150,151}. Opportunistic open-habitat specialists, which are associated with the
481 pioneer invertebrate community, disappear rapidly with increasing vegetation cover and are
482 vulnerable to population contractions when glacier loss occurs. This is particularly the case for cold-
483 adapted, specialized wingless carabid beetles and Linyphiidae spiders, which face severe limitations
484 in dispersal that lead to delayed colonisation or even local extirpation¹¹⁸. By contrast, generalist
485 organisms such as the springtails *Agrenia bidenticulata*⁷³ might thrive with glacier retreat, given their
486 aerial dispersal over large distances and broad ecological niche. Similarly, the future for mutualistic
487 and antagonistic insects such as pollinators and herbivores varies between taxonomic groups¹⁵¹.
488 Specialised pollinators, such as the drone fly *Platycheirus alpina* and the sweat bee *Dufourea alpina*,
489 which feed on a few pioneer plant species in the Alps, are at risk as open grassland habitats shrink,
490 plant diversity declines, and competition increases⁹⁰. By contrast, generalist and opportunistic
491 Staphylinid beetles (for example, *Aleochara bilineata* and *Eusphalerum alpinum*) and pollinators (for
492 example, *Syrphus vitripennis* and *Apis mellifera*) are well-adapted to changing conditions⁷⁸ and are
493 likely to thrive in the absence of glaciers.

494 The retreat of glaciers poses considerable challenges for conservation efforts, as many of the species
495 that currently thrive in glacier ecosystems are not well-adapted to the warming and drying conditions
496 in deglaciated landscapes. Supporting glacial biodiversity requires understanding the dynamic
497 processes of glacial ecosystems¹¹³ and the need to manage both the winners and losers of glacier
498 retreat. For example, conserving rare pioneer plants might require active interventions to decrease the
499 competitive impacts of late-successional species.

500 **[H1] Consequences for ecosystem functions**

501 Biodiversity has an essential role in maintaining ecosystem functions, services, and stability. In this
502 section, we examine how biodiversity mediates the impacts of glacier retreat on key ecosystem
503 functions such as climate regulation, nutrient cycling, and habitat maintenance, and highlight how
504 biodiversity change affects ecosystem processes (Figure 4).

505 **[H2] Climate regulation, nutrient dynamics, and productivity**

506 Glacier retreat has major consequences for climate regulation, influencing both physical and
507 biological feedback mechanisms. In both aquatic and terrestrial systems, exposed ice-free areas
508 absorb more solar radiation, reducing albedo [G] and creating a positive feedback loop that intensifies
509 warming and further melting¹⁵². On glacier surfaces, microorganisms such as red pigmented snow
510 algae (*Sanguina nivaloides*, Chlamydomonadaceae) cause a substantial reduction in albedo and
511 increase snow melt by changing the snow colour to red as algae bloom⁷⁷. The resulting increased
512 snow melt exposes underlying grey ice, which hosts brown–black pigmented glacier algae
513 (*Zygnematophyceae*), leading to further glacier melting⁴⁴.

514 Biologically, glacier retreat alters biodiversity, which can either enhance or diminish energy fluxes
515 and alter carbon sink–source dynamics^{49,51,67,153}. Expanding vegetation cover and soil microorganism
516 populations in newly exposed areas can act as carbon sinks, contributing to climate regulation.
517 However, the long-term efficacy of these processes is uncertain, as carbon storage capacity in soil can
518 become saturated in late stages of glacier retreat, such that carbon sinks might become carbon
519 sources^{47,112,153}. On a regional scale, changes in vegetation cover can exacerbate warming by reducing
520 albedo, whereas on a local scale, biodiversity shifts might enhance carbon sequestration and increase
521 evapotranspiration. For example, vegetation greening in the Arctic might reduce land surface albedo
522 and might represent increased biomass and primary production and enhanced soil respiration through
523 increased organic matter decomposition^{154,155}. However, the net effects of vegetation expansion in
524 post-glacial landscapes on climate regulation is complex and remains unclear.

525 In aquatic systems, the meltwater released from glaciers alters the biogeochemical properties of rivers,
526 lakes, and coastal marine environments, leading to changes in matter and energy fluxes that can spill
527 over into terrestrial communities^{36,99}. Glacier retreat leads to the expansion of ice-free areas, exposing
528 new aquatic habitats to colonisation⁹⁴, with the potential to sequester carbon dioxide from the
529 atmosphere⁶¹ as producers colonise these systems⁷¹. Glacier retreat also enhances the processing of
530 terrestrial organic matter that enters aquatic systems, increasing decomposition¹³, respiration and CO₂
531 release back to the atmosphere¹⁵⁵. Shifts in phytoplankton communities affect herbivory and
532 predation, influencing the biological carbon pump that transports carbon from the surface to the deep
533 ocean, thereby altering carbon cycling locally and regionally⁶⁷. As in terrestrial systems, the long-term
534 impacts of glacier retreat on aquatic ecosystems are complex, as the reduction in albedo owing to
535 glacier loss contributes to regional warming, creating feedback that accelerates warming and further
536 glacier loss. For example, streams in four catchments in Switzerland transitioned from CO₂ sinks to
537 sources as glacier cover decreased and vegetation expanded⁴⁷.

538 Nutrient availability in glacial ecosystems is context-dependent and varies across different habitats
539 and spatiotemporal scales. In supraglacial habitats and pioneer terrestrial habitats, nutrient availability
540 is generally low owing to the limited organic matter and primary productivity, although glaciers can
541 also supply ancient organic matter transported by the glacier as nutrient sources to pioneer
542 colonisers^{156,157}. Glaciers transport dissolved and particulate nutrients (for example, nitrogen,
543 phosphorus and iron) from supraglacial habitats to downstream aquatic systems^{45,57}, increasing
544 nutrient availability and supporting biodiversity and productivity of glacier-fed rivers and lakes^{158,159}.
545 Similarly, in coastal marine environments, glacial runoff can deliver nutrients (such as nitrogen,
546 phosphorus, potassium and iron) that promote phytoplankton blooms, fuelling primary production and
547 supporting marine food webs^{141,160}. Furthermore, ancient carbon from subglacial systems can be
548 utilised by subsurface microorganisms in Arctic fjords and so become a carbon source¹⁶¹. However,
549 meltwater influx can alter water properties, mainly temperature and turbidity, which can negatively
550 affect productivity, trophic interactions and biodiversity³⁵. Although understanding the temporal
551 dynamics of changes in nutrients, biodiversity, and food webs across different glacial habitats is

552 crucial for predicting shifts in ecosystem structure and function, a comprehensive model for making
553 accurate projections is lacking.

554

555 In terrestrial ecosystems, nutrient cycling is closely linked to plant–soil interactions. Plant
556 productivity, litter deposition, and root exudation are the main inputs of organic matter into the
557 system^{47,66}. These processes enrich nutrient-poor soils, facilitating the establishment of more diverse
558 plant communities and fostering microbial activity and energy fluxes. However, species replacement
559 could result in poorer interactions, as the remaining species might not fulfil all the ecological
560 functions and services previously provided by the lost species, where the functional diversity of traits
561 such as leaf nitrogen content or carbon/nitrogen ratios influence biogeochemical cycles, such as
562 carbon and nitrogen cycling. This reduced cycling can also lead to nutrient limitations in the
563 ecosystem, decreasing productivity and the overall health of the ecosystem.

564 **[H2] Habitat creation and maintenance**

565 Although the environment influences the ecology and evolution of species, organisms can also modify
566 their environment¹⁶². The process of ecosystem engineering includes creating new habitats, increasing
567 resource availability, and providing new niches for other species by physico-chemical and biotic
568 modification of the environment^{17,56}. This process results in the creation of diverse microhabitats that
569 support local and regional biodiversity and increase heterogeneity and functional diversity^{163,164}. For
570 example, the activity of cyanobacteria on the ice surface results in the formation of bioaggregates,
571 which then act as biogeochemical factories in the nutrient-poor supraglacial environment^{163,165,166}.

572 In aquatic systems, particularly in glacial floodplains and lakes, **biofilms [G]** and **periphyton [G]**
573 communities composed of bacteria, fungi, and algae are the first colonisers of newly exposed glacial
574 sediments and streambeds¹⁶⁴. Biofilms stabilise sediments through the production of extracellular
575 polymeric substances that bind mineral particles. This binding process reduces vertical infiltration in
576 sediments, thereby increasing sediment cohesion and water retention and reducing erosion. The new
577 stable habitats act as hotspots for microbial activity, enhancing biogeochemical cycling as sediments
578 are enriched with carbon, nitrogen and phosphorus⁹⁹, thereby providing primary production for
579 decomposers and grazing invertebrates^{14,87}. The activity of biofilms is also crucial for the
580 establishment of aquatic vegetation and the development of complex food webs, where energy and
581 matter are eventually transferred from these microorganisms to fish predators and parasites as well as
582 to terrestrial habitats¹⁶⁷.

583 Glacier recession in the Pacific northwest of North America is opening up new river systems for
584 colonisation by migratory salmonids¹⁴⁹, creating considerable disturbances as fish move from the
585 oceans up rivers, and redd (nest) building and spawning activity drive substantial decreases in algal
586 and invertebrate biomass. In glacier-fed fjords, coastal, benthic and pelagic habitats, invertebrates
587 such as polychaetes and molluscs act as ecosystem engineers by sediment bioturbation^{34,160} (mixing
588 by living organisms). In doing so, burrowing organisms create tunnels that serve as microhabitats for
589 smaller species, increasing habitat heterogeneity. Furthermore, they increase oxygen infiltration into
590 sediments, further stimulating microbial activity and nutrient cycling.

591 In terrestrial systems, the interactions between developing communities and geomorphic processes,
592 such as sediment deposition and erosion, create biogeomorphic feedbacks that shape the habitat
593 mosaic in deglaciated landscapes^{17,27,89}. The establishment of pioneer organisms is crucial for the
594 initial transition from barren, newly exposed terrains to complex ecosystems. Stress-tolerant plants,
595 such as *Lupinus nootkatensis*, *Saxifraga cespitosa*, and *Dryas octopetala* in the Arctic, *Saxifraga*
596 *oppositifolia* and *Poa alpina* in the Alps, or *Colobanthus quitensis* in Antarctica, create novel habitats

597 by stabilising sediments, fixing nitrogen through symbiotic interactions with bacteria, and increasing
598 organic matter. Furthermore, these plants also host symbiotic mycorrhizal fungi, provide resources for
599 pollinators, and create microhabitats for predators, ultimately increasing biodiversity across trophic
600 levels. In addition to vascular plants, cryptogamic soil crusts consisting of bryophytes, diatom algae,
601 cyanobacteria, and lichens support habitat creation by retaining water, increasing organic matter,
602 trapping fine mineral material, fixing nitrogen, and providing food resources for detritivores and
603 herbivores¹⁶⁸.

604 **[H1] Summary and future directions**

605 In this review, we discuss how glacier retreat drives changes in biodiversity and ecosystem functions
606 across different habitats, from supraglacial environments to newly exposed terrestrial and marine
607 ecosystems, highlighting the connections among systems via fluxes of matter and energy. Glacial
608 ecosystems worldwide contain several thousand taxa, including microorganisms, plants, invertebrates
609 and vertebrates. A consistent pattern across these systems is the concept of peak biodiversity,
610 according to which glacier retreat initially creates space for colonisation by pioneer species, driving
611 early stages of primary succession and ecosystem development and increasing biodiversity locally.
612 However, with the loss of glaciers, this dynamic ‘engine’ that creates novel habitats also disappears,
613 leading to eventual biotic homogenisation and biodiversity loss both locally and regionally. Once
614 glacier-free landscapes mature, biodiversity change stabilises, competition increases and generalist
615 species dominate, but the unique functions performed by glacial specialists might be eroded, leading
616 to potential long-term losses in ecosystem functioning.

617 We identify key shared processes across glacial ecosystems, including habitat creation, species
618 turnover, and nutrient cycling. These processes not only shape individual systems but also create vital
619 linkages between them. Across diverse habitats, three recurring patterns emerge. First, all
620 communities are sensitive to the cascading effects of glacier retreat. The loss of ice diminishes habitat
621 availability for specialists and simultaneously creates novel habitats for pioneer colonizers. However,
622 based on the ‘peak biodiversity’ pattern, we predict a net biodiversity decline in the long-term,
623 especially in arid regions. Second, glacier retreat initiates a sequence of habitat transformations and
624 reshuffles species interactions. Glacial habitats are the most at risk, while providing a legacy to
625 proglacial habitat development. Both glacier forelands and glacier-fed rivers and lakes witness a
626 development from simple ecosystems that host specialised species to complex ecosystems that finally
627 host opportunistic and competitive species. Third, all ecosystems depend on the movement of water
628 and nutrients. Glacier meltwater and biotic interactions act as conduits for nutrient and organismal
629 exchange from glacial habitats to downstream terrestrial and marine environments, playing a crucial
630 part in ecosystem productivity and stability.

631 Given these commonalities, the disappearance of glaciers clearly presents both challenges and
632 opportunities for biodiversity and ecosystem functioning. To fully understand how biodiversity
633 responds to glacier retreat, several key knowledge gaps need to be addressed. Given the limited
634 understanding of the structural and functional roles of species within and across glacier systems, a
635 better grasp of **functional diversity [G]** is essential to elucidate the roles of species in ecosystem
636 processes including climate mitigation, biogeochemical cycling, productivity, and biotic resistance
637 (the ability of communities to resist invasion by exotic species). Future research should focus on
638 functional approaches to understand how species interactions contribute to ecosystem processes¹⁶² and
639 eco-evolutionary mechanisms¹⁶⁹. Integrating functional traits into models of glacier ecosystem
640 dynamics will improve predictions of the responses of biodiversity and ecosystem functioning to
641 glacier loss²⁶. This information is crucial for identifying species at the highest risk of extinction and

642 for developing conservation strategies aimed at preserving functional diversity and ecosystem
643 services.

644 Research on species interactions within glacier ecosystems is still in its infancy. Understanding the
645 complexity of trophic, mutualistic, antagonistic, and neutral interactions is essential to predict how
646 populations and communities will respond to the cascading effects of glacial retreat. However, limited
647 interaction data are available for most species in glacier ecosystems, which hinders accurate
648 assessments of their extinction risk. Future studies should focus on mapping food webs and ecological
649 networks to identify keystone species and key interactions that stabilise ecosystems after glacier
650 retreat. Understanding **interaction diversity [G]** can provide a novel dimension of ecosystem health
651 that species richness alone cannot capture. Future research should address how variation in the net
652 effects of species interactions influences relevant ecological outcomes. Similarly, mechanisms driving
653 the erosion and loss of ecosystem functions, and the role biodiversity plays in stabilising these
654 functions, remain poorly understood. Experimental and modelling approaches should focus on
655 unravelling the biodiversity–function–stability relationships in deglaciating regions to guide
656 ecosystem management strategies effectively.

657 Research efforts should also prioritise biodiversity monitoring in conjunction with glacier monitoring.
658 Although local and global glacier monitoring programmes are well established, similar initiatives are
659 currently lacking for biodiversity. Strengthening collaborations between glaciologists,
660 geomorphologists, and biologists is crucial for establishing integrated monitoring programmes that
661 track biodiversity response to glacier dynamics. Such interdisciplinary efforts will help to link
662 geophysical changes in glaciers with biological changes, providing a more complete picture of how
663 ecosystems are transitioning in response to deglaciation. Remote sensing, environmental DNA or
664 RNA sequencing, and proximate sensing using automated monitoring technologies could be
665 employed to capture seasonal variability and long-term changes in both abiotic and biotic components
666 of glacier systems.

667 A major challenge moving forward is conserving biodiversity associated with glacial habitats.
668 Although compiling species lists might help to document biological diversity, it will not provide
669 fundamental understanding of ecological and evolutionary mechanisms or help to inform sustainable
670 management strategies that ensure ecosystems retain the functions and services that glacier-associated
671 biodiversity provides. Conservation efforts will need to consider novel strategies, informed by filling
672 the aforementioned knowledge gaps, if there is any chance of conserving glacial habitats and species
673 specialists into the future. Such strategies could include translocations and artificial habitat
674 engineering and limiting tourism activities and built infrastructure^{113,149}. However, ultimately what is
675 needed is global action on climate change to limit further glacial retreat and preserve the remaining
676 glacier systems.

677 Understanding and anticipating the future of biodiversity in deglaciating regions hinges on integrating
678 research across disciplines and moving beyond descriptive studies towards understanding the
679 mechanisms and factors that are responsible for biodiversity maintenance. Research efforts should
680 prioritize understanding the diverse functions of species in the development and evolution of
681 ecosystems following glacier retreat. To mitigate biodiversity loss and erosion of species and
682 ecosystem functions, future research should focus on filling key knowledge gaps related to functional
683 diversity, species interactions, and cross-system linkages. Monitoring and managing these rapidly
684 changing ecosystems are essential to ensure that novel landscapes formed after glacier retreat will
685 continue to support biodiversity and crucial ecological processes.

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1124 **Figures**

1125 **Figure 1. The various habitats comprising glacial landscapes.** Glacial landscapes are built on
1126 interactions between ice, water, and land. **a** | Proglacial habitats in mountain environments include
1127 diverse ecosystems, ranging from grasslands to forests. **b** | Aquatic proglacial habitats include glacier-
1128 fed rivers and lakes. **c** | Marine-terminating glaciers create vast marine proglacial habitats in polar
1129 regions. **d** | Glacier surfaces provide key habitats for diverse microorganisms and invertebrates. Panel
1130 a provided courtesy of Bao Ngan Tu.

1131 **Figure 2. Mechanisms underlying biodiversity changes in response to glacier retreat.** Glacier
1132 retreat is a direct result of global warming. Glacier retreat affects biodiversity through various
1133 mechanisms, including ecological succession, biogeographical and evolutionary processes, and
1134 species interactions.

1135 **Figure 3. Winners and losers of deglaciation.** Glacier retreat makes space for generalist species but
1136 threatens specialized species. **a** | Glacial obligates that live exclusively on ice, such as the tardigrade
1137 *Cryobiotus klebelsbergi*, face the highest risk of decline or extirpation with loss of glaciers. **b** |
1138 Specialists that thrive in glacial habitats such as the pioneer plant *Ranunculus glacialis* benefit from

1139 glacier retreat in the short term but face decline a few decades after deglaciation owing to
1140 successional changes. c | Generalists and opportunistic species that occur in glacial habitats and
1141 elsewhere, such as the hoverfly *Syrphus vitripennis*, are expected to expand their range and increase
1142 population size.

1143 **Figure 4. Glacier retreat alters biodiversity and affects ecosystem functions.** Through changes in
1144 biodiversity, glacier retreat influences a diverse set of ecosystem functions, including albedo, carbon
1145 and nutrient cycling, and productivity. Some functions increase (blue) whereas others decrease (red)
1146 with vegetation succession as ecosystems transition from open habitats to closed forests.

1147 **Boxes**

1148 **Box 1. Glossary**

1149 **Albedo**

1150 The fraction of incident sunlight that is reflected by a given surface.

1151 **Allochthonous**

1152 Introduced from a different (distant) location.

1153 **Autochthonous**

1154 Originating or formed in its present location.

1155 **Biotic homogenisation**

1156 The process by which (spatially) distinct ecological communities become increasingly similar over
1157 time

1158 **Firn field**

1159 Layer of snow that is transforming into glacial ice.

1160 **Moulin**

1161 Vertical shaft that carries meltwater from glacier surface to the bedrock under glacial ice.

1162 **Crevasse**

1163 Fissure or crack in the surface of a glacier.

1164 **Cryoconite**

1165 A mixture of mineral and organic material accumulated on the glacier surface, which owing to being a
1166 darker colour than surrounding ice and having higher heat absorption, often melts to form cryoconite
1167 holes.

1168 **Glacier mice**

1169 Supraglacial, unattached balls of moss (taxonomically nonspecific) and sediment that harbour an
1170 invertebrate fauna and can move along the glacier surface

1171 **Supraglacial**

1172 The zone on the glacier surface, encompassing fresh snow, firn, pure ice, meltwater streams, ice
1173 caves, and crevasses

1174 **Englacial**

1175 The zone within a glacier situated between supraglacial and subglacial zones which harbour meltwater
1176 streams or caverns

1177 **Subglacial**

1178 The zone below a glacier in the liquid interface between glacier, sediment and bedrock

1179 **Proglacial**

1180 The zone in front of an active glacier, which is subject to frequent changes owing to meltwater
1181 dynamics and movement of unconsolidated sediment

1182 **Glacier foreland**

1183 The young ice-free terrain around and in front of a glacier that has deglaciated since the end of the
1184 Little Ice Age (the cold period that terminated around 1850)

1185 **Benthic**

1186 The zone on the bottom of an aquatic body (for example, a river, lake or ocean)

1187 **Pelagic**

1188 The zone near the water surface or within the water column in an aquatic body

1189 **Ecological niche**

1190 Set of environmental conditions required by an organism or the functions it performs, encompassing
1191 all environmental factors influencing the establishment, growth and reproduction of a species.

1192 **Redox potential**

1193 Oxidation (loss of electrons) or reduction (acquisition of electrons) potential is a key physicochemical
1194 parameter driving microbial activity

1195 **Periphyton**

1196 Microorganism assemblages dominated by microalgae and including heterotrophic bacteria,
1197 cyanobacteria and fungi that grow on the surface of submerged sediments, rocks, plants, and
1198 suspended particles in aquatic ecosystems.

1199 **Biofilm**

1200 A thin layer that covers surfaces, consisting of bacteria and other microorganisms

1201 **Cryptogamic soil crust**

1202 An intimate association between soil particles and variable proportions of photoautotrophic and
1203 heterotrophic organisms, living within or immediately on top of the soil surface as a coherent layer

1204 **Biogeomorphic feedback**

1205 The interplay of geomorphic disturbances and their feedback with vegetation and microbial
1206 succession, which results in gradual ground stabilization from plant scale to slope scale

1207 **Subglacial legacy**

1208 Subglacial sediments and organic matter substrates that originated from past biogeochemical
1209 processes and have been reworked by subglacial microbial communities and that are exposed at
1210 receding glacier fronts

1211 **Paraglacial adjustment**

1212 (Geomorphological) responses in slopes in glacially steepened rockwalls to alteration of stress within
1213 the rock owing to deglaciation (often associated with rock-slope failures)

1214 **Dimensions of diversity:**

1215 **α -Diversity**

1216 Mean species richness in a site (local diversity)

1217 **β -Diversity**

1218 Ratio between regional and local species diversity indicating heterogeneity or species dissimilarity
1219 between sites

1220 **γ -Diversity**

1221 Total species diversity in a landscape (regional diversity or species pool)

1222 **Functional diversity**

1223 The value, range, relative abundance or variation of functional traits

1224 **Interaction diversity**

1225 The number and type of biotic interactions that link species together into communities