Impacts of deglaciation on biodiversity and ecosystem function

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Abstract

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

[H1] Introduction

Global biodiversity is declining at rates faster than at any other time in human history[1–3], driven largely by changes in global land use and climate[4]. Emblematic of global change is the retreat and thinning of glaciers worldwide[5,6]. Despite global efforts to limit warming to 1.5 ºC by 2100, alpine glaciers are predicted to lose 34% of their mass by 2050, irrespective of future additional climate change[7,8]. Glacier–climate interactions create a positive feedback loop that accelerates further warming, leading to additional retreat and enhanced threats to highly-adapted biodiversity and ecosystem services that depend on glaciers, their runoff and adjacent post-glacial landscapes[9–11].

Glacier retreat has far-reaching consequences for diverse ecological functions, from nutrient cycling, energy flow and species interactions to connections between dependent ecosystems, such as the ice surface, downstream rivers and lakes, terrestrial proglacial **[G]** forefields, and marine environments[12–15]. On one hand, glacier retreat might benefit biodiversity because it exposes new terrain to weathering and sediment reworking[16,17], offering colonisation opportunities[18–20]. Ecological succession in these newly formed habitats typically leads to an initial increase in local species richness[21] in the short term. On the other hand, habitat homogenisation and competition leads to replacement of glacier-specialists by more generalist species, resulting in long-term biodiversity decline[22–24] and erosion of functional diversity[14,25,26]. However, whereas most empirical work on these dual forces has focused on describing taxonomic diversity, documenting colonisation and ecological succession patterns, and analysing biogeochemical properties[27], there has been limited focus on functional ecology and ecosystem functioning, particularly in terms of species interactions and how food webs assemble, develop and shift within and between glacier-dependent ecosystems on a global scale. Understanding how species interactions and cross-system linkages respond to glacier retreat is vital to fundamental ecological knowledge that can inform management practices and policies that could mitigate the detrimental effects of deglaciation on biodiversity and ecosystem services.

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

[H1] Glacier retreat and novel ecosystems

[H2] The glacial landscape and glacier retreat

Since the end of the Little Ice Age (ca. 1850), glaciers have been retreating globally but the rate of retreat has accelerated considerably over the past 30 years[10,28]. Between 1980 and 2015, global glacier area decreased by an average of 0.18% per year, and thinning rates have doubled in the past 20 years, 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 vary regionally, with glaciers in places such as the Tropical Andes retreating much faster than those at higher latitudes[7]. Even without any further temperature increase, an additional 41 ± 8% of global glacier mass will be lost by 2100 (refs[5,10,29]). In particular, many small glaciers are expected to vanish completely or to shrink into small ice–snow patches in coming decades[8,9]. The sensitivity of individual glaciers to mass loss is influenced by various factors, including temperature, precipitation, humidity and radiation, as well as their geophysical characteristics such as size, geometry, elevation and slope[30]. For example, in the Swiss Alps, smaller glaciers on gentle slopes at low elevations are likely to disappear first[31]. The timing and extent of glacier retreat will influence the availability and characteristics of the new habitats that form. More hospitable environments will emerge on shallower slopes and at lower latitudes, whereas extreme conditions might persist for longer at higher elevations and in colder regions, providing refuges for cold-adapted species[15,27,32–34].

As glaciers shrink and fragment, meltwater discharge initially increases but eventually declines dramatically[34], impacting downstream ecosystems. The concept of ‘peak water’[35] is based on evidence that annual glacier runoff continues to rise until a maximum is reached, beyond which runoff decreases because the reduced glacier volume provide less and less melt water from long-term storage[35]. This overall decrease in runoff impacts seasonal freshwater availability[6,30] and, consequently, biodiversity and ecosystem functions[13,15]. During the peak water phase, enhanced meltwater flux increases sediment transport, nutrient availability, and habitat connectivity in downstream, glacier-fed ecosystems. These changes can temporarily boost primary productivity and biodiversity, particularly in aquatic habitats. However, as water discharge declines after peak water, reduced meltwater leads to habitat desiccation, fragmentation of aquatic systems, and loss of species adapted to cold, glacier-fed waters[15,36–38]. The ecological impacts of peak water are not limited to aquatic systems, as altered hydrology in proglacial habitats exposes terrestrial habitats to reduced water availability and fluctuating groundwater levels, which can limit the establishment, growth and health of pioneer plants and microbial communities, ultimately slowing ecosystem development and nutrient cycling and favouring ecosystem aridification[39,40].

[H2] The emergence of novel post-glacial ecosystems

The type and structure of the habitats that emerge in place of ice depend on the region, the type of glacier, and local topography[9,11,12,19,31] (Figure 1a). The erosion, transport, and deposition of sediments by glaciers and meltwater streams generate diverse coastal, marine and inland habitats, freshwater systems and terrestrial landforms[16,41–43]. Glacial processes alter the biogeochemical properties of rivers, lakes, coastal marine environments, and sediments on land, leading to changes in matter and energy fluxes and, ultimately, biodiversity[22,44–47]. Supraglacial **[G]** , englacial **[G]** , subglacial **[G]** , terrestrial proglacial, and subaquatic proglacial habitats are inter-related habitats characteristics of glacial landscapes. These habitats are highly dynamic owing to paraglacial adjustment and sediment reworking (Figure 1b–f), and their biodiversity is adapted to environmental extremes such as low water temperature, high turbidity, frequent disturbances and low nutrient variability on land.

Once glaciers retreat, biotic processes gradually become more important than geophysical processes in shaping new ecosystems, but this transition can take many decades[48]. On land, glacier retreat exposes a mixture of bare rock and fine sediments that are unstable and undergo chemical and biological weathering. Minerals and propagules from local and remote sources can be exchanged between glaciers and newly exposed terrains[42]. These propagules provide the substrate for the first phase of primary succession by pioneer organisms such as cyanobacteria, algae, fungi, bryophytes, cushion plants, nematodes, and invertebrates[20,49–51]. Subglacial legacies **[G]** influence the physical and ecological characteristics of emerging habitats[52], serving as precursors to ecosystem development in deglaciated areas via inputs of nutrients, ancient organic matter, and propagules[53]. Deposited fine subglacial sediments, together with englacial material, provide a first substrate for early colonizers, while some microbial communities adapted to subglacial conditions, such as chemolithoautotrophic bacteria, often persist in the early stages of soil development[54,55] and are therefore crucial in establishing nutrient pathways that support subsequent colonisation by animals, plants, and symbiotic microorganisms. The importance of the subglacial legacy and propagules or organic biomass released from glacier ice decreases sharply over time, to be replaced by autochthonous **[G]** energy production and matter recycling.

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

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

Sediment input and flow stability influence the development of near-shore marine environments, streams and lakes formed by glacial meltwater, which are initially turbid due to the deposition of glacial silts and clays[65–67]. Stable flow from glacier meltwater streams is an important recharge in alpine aquatic ecosystems, which are prone to changes and instability when glaciers disappear. In glacier-influenced fjords, glacier retreat and changing discharge rate can influence salinity, circulation, upwelling rates and resource availability[61,67]. For example, icebergs from marine-terminating glaciers trigger increased productivity by delivery of nutrients in Arctic food webs, whereas delivery of subglacial waters inhibits photosynthesis when turbidity increases[68–70]. Benthic **[G]** organisms such as bryozoans, barnacles, copepods and algae are the first colonisers of newly ice-freed substrates. Gradually, physical stressors decrease while biotic processes such as the retention of organic material and decomposition become more pronounced, aiding nutrient cycling and supporting biodiversity at higher trophic levels and food web complexity[45,57,71,72]. Upstream glacier meltwaters and proglacial terrestrial ecosystems transfer nutrients and organic matter into these aquatic ecosystems whereas fluvial dynamics influence terrestrial ecosystems via erosion and sediment deposition[42]. These aquatic ecosystems are strongly linked not only to nearby upstream glaciers but also to proglacial terrestrial ecosystems through nutrient and organic matter transfer, mainly via food webs[73].

[H2] Irreversible changes and unique habitat loss

On the surface of glaciers, the supraglacial ecosystem includes unique microhabitats such as snow patches, firn fields **[G]**, cryoconite **[G]** holes, supraglacial cones, glacier mice **[G]** , surface meltwater streams and pools, supraglacial debris, surface ice of the weathering crusts, moulins **[G]** and crevasses **[G]** [1–6] . These habitats are characterized by a diverse consortium of microorganisms, including bacteria, algae, phytoflagellates, fungi and viruses, and higher trophic level consumers, such as invertebrates[11,22,44]. These organisms perform crucial roles in nutrient cycling and carbon fixation and are an integral part of glacier-linked food webs, transferring energy and matter to downstream ecosystems[25,76]. Cryoconite holes are the most studied supraglacial microhabitat and form biodiversity hotspots that support cyanobacteria, diatoms, rotifers, tardigrades, and diverse arthropods[22,63,77]. In rare cases, such as on debris-covered glaciers, supraglacial habitats also host mosses, flowering plants and their pollinators, spiders, and trees[60,78,79]. In addition, organisms transported from non-glacial surroundings via atmospheric fallout or geomorphic processes are commonly found to be a source of microorganisms and allochthonous **[G]** organic matter on the ice surfaces[48]. However, many of these organisms, which are considered to be glacier specialists, are unlikely to cope with habitat loss associated with the disappearance of glaciers[22].

Englacial ecosystems, such as englacial streams, veins, and reservoirs, are habitats for microbial communities, both active and inactive; however, the role of these ecosystems is still not understood[80,81]. Beneath glaciers, subglacial habitats include wetlands, lakes, debris, and geothermal caves[11,41,82], which are highly susceptible to glacial retreat but are often overlooked in biological studies. Subglacial habitats are characterized by no light, high pressure and extremely low nutrient availability. At the glacier bed, rock–till–ice interactions determine hydraulic conditions, which in turn influence microbial activity and biogeochemistry[55]. Redox potential **[G]** is determined by hydrology, chemical weathering, and oxygen and controls community composition, which ranges from aerobes to anaerobes or chemoautotrophic to heterotrophic bacteria. Members of the Proteobacteria, Bacteroidetes, and Actinobacteria, which have general metabolic capabilities to degrade organic carbon, are commonly recovered from subglacial sediments and water columns. The presence and abundance of specialist taxa that are capable of cycling iron, sulphur, nitrogen, or methane vary among glaciers depending on meltwater and bedrock characteristics[45,52]. Generally, these subglacial microbial communities rely on chemosynthesis[53]. Some of these unique environments can support eukaryotic organisms such as mosses, algae, nematodes, earthworms and arthropods[82,83]. Collectively, subglacial ecosystems contribute to carbon cycling within and across glacier environments through their emission of methane and carbon dioxide[84].

With deglaciation, supraglacial, englacial and subglacial habitats transition into proglacial ecosystems (Figure 1). Although these areas provide opportunities for biotic colonisation, they are also vulnerable to biodiversity loss, nutrient depletion and hydrological changes associated with continued ice loss. Inputs of nutrients and organic matter from glacier ecosystems to proglacial streams, ponds, lakes, terrestrial forelands and near-shore marine environments will also be reduced or lost with glacier loss [61,67,85], impacting resident and transient species and their functioning in ways that remain poorly understood. Of note, the loss of glaciers removes habitat features and biological processes that act as barriers to species colonisation, leading to an influx of generalist and competitive species and potentially to biotic homogenization[18,23,26,32]. However, the rates and timescale of colonisation and loss of pioneer habitats characterized by soil instability can be strongly dependent on climate. For example, pioneer habitats in New Zealand glacier forelands can persist over millennia, as high rainfall keeps sediments unstable[86]. With climate change and glacier retreat, habitat loss is expected for a diverse set of organisms[22,27,70] (discussed later). Of note, local biodiversity loss in both subglacial and supraglacial habitats has cascading effects across ecosystems, as nutrients, organic matter and organisms are redistributed to downstream terrestrial and aquatic habitats, influencing ecological succession and carbon dynamics.

Analogous to the ‘peak water’ concept that offers a crucial framework for understanding the hydrological and ecological consequences of glacier retreat and glacier extinction[35], here we propose the ‘peak biodiversity’ concept, which includes species and habitat diversity. Following glacier retreat, the availability and size of ice-free areas initially increase[15,32,85], leading to a peak in habitat availability, heterogeneity and local species diversity — a phase referred to as peak biodiversity. Beyond this peak, as glaciers continue to shrink and finally disappear, glacial habitats and their associated organisms, as well as the formation of novel habitats, decreases progressively, while former communities become more homogeneous[24] and biodiversity at the local-to-landscape scale declines[19,23,87,88]. Of note, pioneer habitats formed by glacier retreat can continue to exist only in the presence of glaciers. In the absence of glaciers, no new habitats will emerge, whereas pioneer and intermediate habitats will undergo succession (discussed later), with inherent habitat and species loss and homogenization[89,90].

[H1] Drivers and mechanisms of biodiversity change

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

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

The hierarchical successional framework[89,91] offers a comprehensive approach to understanding community replacement in glacier and glacier-associated ecosystems, by incorporating facilitation, tolerance, and inhibition mechanisms. This framework spans different spatial scales, from plant neighbourhoods to landscapes and biogeographic regions, enabling a nuanced understanding of how glacier retreat affects habitat availability, species availability, and species performance. We integrate this framework with the concept of paraglacial adjustment **[G]** [16] and biogeomorphic feedbacks **[G]** [17] after glacier retreat.

Habitat availability in terrestrial, freshwater, and marine systems increases with glacier retreat, at the expense of glacial habitats in the long term. In glacier forelands, new ice-free terrains offer unique opportunities for early successional species, but these habitats diminish as glaciers ultimately disappear according to 'peak biodiversity' patterns. That is, the response of habitat availability to glacier retreat is non-linear but changes over space and time, depending also on local conditions such as microclimate and bedrock. Furthermore, disturbance regimes, such as sediment deposition, erosion, and hydrological changes continue to have crucial roles in shaping habitat availability at the landscape scale[42,48,61]. Sediment instability associated with paraglacial adjustment[16], including debris flows and erosion, limits successional rates[86,92]. Pioneer plants such as cushion plants play a key part in early-successional development facilitating biogeomorphic feedbacks[86], increasing the size of areas that are suitable for growth and diversifying microtopography. Such increased stability in turn creates more favourable conditions for biodiversity development and influences the rate of colonisation and succession[93].

Species availability is a key factor in the successional process. In glacier and glacier-associated ecosystems, connectivity to colonisation sources is often limited by topographic barriers in mountainous and marine environments[88,94,95]. However, glacial retreat leads to the emergence of dispersal corridors and alters habitat connectivity, increasing rates of species immigration and extirpation[15]. Rivers fed by glacial meltwater serve as crucial pathways for the migration of fish and invertebrates and for the transportation of plant seeds over long distances[14,96]. Wind and slope processes such as avalanches and landslides can also transport propagules into newly deglaciated areas[19,97]. In coastal zones where tidewater glaciers retreat, marine currents help to carry species to newly exposed benthic **[G]** and pelagic **[G]** zones, thereby facilitating colonisation[61,98,99].

Species performance is shaped by environmental constraints, functional traits, and biotic interactions[23,26,92,93]. Environmental constraints in glacier-associated ecosystems, such as light intensity that is too low or too high, poor soil nutrients, unstable substrates, low temperatures, and freeze–thaw cycles, limit the growth and establishment of species[89]. Autecological factors such as fecundity, growth rates, and survival strategies are also key in determining which species succeed. In early stages of succession, biotic interactions are influenced by the identity of neighbouring species, soil microbial communities, and the spatial distribution of populations[13,62]. Integrating these factors is a necessary next step to providing a coherent picture of the mechanisms underlying successional changes after glacier retreat, as well as identifying potential new mechanisms underlying biodiversity maintenance once glaciers vanish.

Functional traits are pivotal in shaping species response, community assembly, and ecosystem development after glacier retreat[23,100–102]. Animal traits such as physiological capability, body size, dispersal ability, and dietary requirements contribute to the capacity of species to colonize and persist in glacial habitats[103]. Plant traits such as specific leaf area (SLA), leaf dry matter content (LDMC), flowering strategy, and canopy height are crucial for understanding plant strategies in resource acquisition, stress tolerance, and competition[26,100]. Early successional stages are often dominated by species that are adapted to nutrient-poor conditions and acquire resources effectively[46,104]. Over time, these species are replaced by competitive species with denser leaves, reflecting a shift towards resource conservation strategies that limit nutrient dynamics[92,93]. The role of functional traits extends beyond colonisation, as plant traits influence succession through biogeomorphic feedbacks[42,105]. For example, traits associated with ecosystem engineers such as *Dryas octopetala* or *Saxifraga oppositifolia* contribute to reducing erosion and enhancing soil development rates. This biotic–abiotic interplay promotes habitat creation, enabling the establishment of more diverse communities over space and time.

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

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

Cryoconite holes, supraglacial streams, ponds, weathering crusts and snow patches on glacier surfaces are key glacial microhabitats that support highly specialised and at-risk food webs[22,75,76,107]. These food webs are fairly simple, characterized by short trophic chains. Autotrophic, photosynthetic microorganisms such as cyanobacteria and green algae capture solar energy and use glacial meltwater to fix carbon and nitrogen[99]. As expected, they are the first colonizers of these habitats, followed by heterotrophic bacteria, fungi, and protozoa that recycle nutrients within the food web for consumers at higher trophic levels, such as rotifers, tardigrades, ice worms, springtails, copepods and chironomid midges. Extended glacier food webs can incorporate vertebrate consumers, such as rosy finches (*Leucosticte tephrocotis*) that feed on ice worms (*Mesenchytraeus solifugus*) in Paradise Glacier (Washington, USA)[107]. Debris-covered glaciers hosting herbaceous plants also harbour their associated pollinators and herbivores[78]. These food webs provide resources for downstream, aquatic and terrestrial ecosystem development[71,108].

As in supraglacial systems, pioneer microbial communities, including cyanobacteria, fungi, algae, and protists, are also the first colonizers in proglacial aquatic and terrestrial ecosystems[99,109,110]. These microbial communities produce and stabilize organic matter from mineral and organic resources from glacier meltwater, sediments, terrestrial detritus, and airborne inputs[36,38,69]. They support omnivorous (herbivore and detritivore) communities that feed on microorganisms, algae and detritus, serving as prey for larger invertebrate herbivores and predators. In marine-terminating (tidewater) glacier ecosystems, buoyant plumes and subsequent upwelling of deep nutrient-rich meltwater promote higher biodiversity and productivity compared with land-terminating systems[68,69]. Polar marine food webs benefit from marine-terminating glacial meltwater that delivers essential nutrients such as iron and silica to the photic zone, stimulating phytoplankton blooms and primary production[66,67,69,108], which form the food base for key marine herbivores such as Arctic copepods and Antarctic krill. In turn, these primary consumers transfer energy and nutrients from phytoplankton to higher trophic levels, which are first characterised by planktivorous seabirds such as little auks (*Alle alle*), forage fish such as capelin (*Mallotus villosus*), and baleen whales (for example, blue whales *Balaenoptera musculus*), and then by salmon (*Oncorhynchus* spp.), seabirds such as Kittlitz's murrelet (*Brachyramphus brevirostris*) in Alaska, and blue-eyed shags (*Phalacrocorax atriceps*) in Antarctica, and ultimately by marine mammals such as beluga whales (*Delphinapterus leucas*), ringed seals (*Pusa hispida*), and leopard seals (*Hydrurga leptonyx*)[68,111]. As a consequence of glacier retreat, reduced meltwater flow can limit nutrient availability and disrupt trophic interactions[69].

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

[H2] Biogeographical and evolutionary processes

The glacial history of Earth has shaped biodiversity and ecosystem development since the Precambrian era[22]. Glaciated regions with ice-free refugia and glacier fluctuations during the Pleistocene influenced gene flow[70] and speciation by isolation and divergence[120,121], reshuffling population connectivity[94,95] and diversifying phylogenetic lineages[122]. Owing to the similarities in physical conditions across distant regions, such as the Alpine and Arctic regions, glaciers provide unique habitats for the dispersal, refugium, and evolution of extreme cold-adapted organisms[34,58–60,123]. For example, many groups of organisms in these disparate regions share convergent traits, such as pigmentation in algal taxa and short reproductive cycles in invertebrate taxa[122], despite being separated by vast geographic distances[121]. Although glacier habitats often support endemic species, long-distance dispersal is not uncommon[94,120,124].

In the current deglaciation phase, glacial habitats are also climate refugia[58,59,121,125]. With the loss of glacial habitats in polar and mountain regions, glacial organisms have three possible fates: the extinction of unique populations and endemic, glacial specialist species; survival in cold refugia, such as debris-covered glaciers, rock glaciers, snow fields, cold lakes and cold seeps; or adaptation to new, ice-free habitats with heterogeneous environmental conditions. Long-range dispersal from small, disappearing ice patches to larger ice masses might offer opportunities for survival if the characteristics of new glacier habitats are suitable. In addition, glaciers and adjacent environments can act as 'time capsules' that preserve microorganisms[126] and plants[64] that later regenerate with melting. However, the loss of glaciers and glacial habitats poses a survival challenge for organisms that inhabit ice, water, and terrestrial glacial ecosystems.

[H1] Winners and losers of deglaciation

The retreat of glaciers is leading to large shifts in biodiversity, with some species emerging as 'winners' (thriving long term) and others as 'losers' (facing range and population contractions and increased risk of extinction)[15,23,46,92]. Generally, glacial specialists face severe threats to their persistence: the higher the degree of specialisation and dependence on glacial environments, the higher the extinction risk (**Figure 3**). The persistence of populations restricted to glacial ecosystems depends also on their geographic distribution and the geophysical characteristics of the glacier: the faster the retreat and the smaller the glacier, the higher the risk. In this section, we explore how glacier retreat is reshuffling biodiversity, including microorganisms, animals, and plants, across ice, glacial waters, and deglaciated lands.

[H2] Glacial biodiversity

Current models project continued ice occurrence globally by the end of this century[8,10], but with substantially reduced areas of supraglacial habitats[27]. There are few winner species that thrive in supraglacial ecosystems and are likely to persist; those species are rather generalist such as surface snow algae; Chlorophyta species, such as *Sanguina* and *Chlamydomonas*, which mainly thrive in accumulation areas; and glacier algae *Ancylonema* spp. which is prominent in the ablation zone[25,44,63]. Cryophilic fungi that parasitize algae and heterotrophic bacteria that are consumed by microscopic invertebrates such as springtails, rotifers, and tardigrades might also thrive, as long as glaciers persist[127]. Generalist communities characterized by Proteobacteria, Actinobacteria, Bacteroidota, Chloroflexi, and Cyanobacteria[63,99], as well as invertebrates (Nematoda, Tardigrada, Rotifera, Collembola, Chironomidae)[75,128] that occur non-exclusively in sediments of supraglacial water bodies, might persist in nearby microhabitat sediments.

Beneath glacier surfaces, in the englacial zone, and beneath the body of the glacier, diverse assemblages of microorganisms are found in subglacial streams and lakes where ice, rock and water interact[53,83]. These systems contribute unique taxa to local species pools compared with supraglacial and proglacial streams[129], suggesting that they might not persist in the absence of glaciers. Ice loss further imperils specialised cryoconite inhabitants, such as the tardigrades *Cryobiotus klebelsbergi* in the Alps and *Fontourion glaciale* in the Arctic, or ice inhabitants such as the annelid *Mesenchytraeus solifugus* that exclusively occur in glacial environments[130]. The future is also uncertain for mammals that use glaciers as refuges during warmer seasons[131] or birds such as the white-tailed ptarmigan (*Lagopus leucura*) that can nest on ice surfaces. Glacial-obligate organisms that are endemic to smaller regions are at the highest risk, as the chances to find adequate climate refugia or to adapt locally are reduced[34,123]. The risk is lower for species with a broad geographic distribution or those that are only randomly or sporadically associated with glacial habitats, which might face a reduction in population size but might continue to persist within the landscape or in adjacent microhabitats, such as rock glaciers or snow fields.

[H2] Biodiversity in glacial waters

Given that three-quarters of the Earth's freshwater is stored in glaciers and in light of accelerating glacier retreat, many unique aquatic ecosystems will disappear or change considerably, affecting the organisms that depend on them[14,15,96]. This loss of water is also key for the health of terrestrial communities[51]. Ice-associated vertebrates such as the ivory gull (*Pagophila eburnea*) and fish such as Arctic cod (*Boreogadus saida*) might face reductions in foraging areas, food supply, and availability of stable glaciers and sea ice for birthing and nursing[132–134], while facing increased competition for scarce resources and increased risks from predation in the long term[135]. For example, retreat of glaciers in the Arctic is impacting ice-dependent vertebrates that rely on cold-water, such as the little auk (*Alle alle*), as their primary food source, the copepod *Calanus glacialis*, is declining with increasing temperatures in glacier habitats[136,137]. The population declines of ice-associated vertebrates will have cascading effects on biodiversity at multiple trophic levels[135]. In the Antarctic, generalist vertebrates such as gentoo penguins (*Pygoscelis papua*) and herbivores that thrive in newly available habitats might benefit from glacier retreat, as do some Antarctic pinniped species such as the southern elephant seal (*Mirounga leonina*) which are attracted to large patches of the grass *Deschampsia antarctica*[68].

Although increasing rates of glacier retreat threaten the persistence of extremophiles and specialist species[70], it also creates opportunities for generalist species to thrive[18]. Increasing input of glacial meltwaters can enhance nutrient availability such that, if disturbance and turbidity remain low, phytoplankton primary producers such as diatoms will flourish, increasing local productivity as the glacier continues to melt[138]. Consequently, primary consumers can thrive, in turn supporting the growth of fish populations that feed on them, such as Atlantic herring (*Clupea harengus*) and capelin (*Mallotus villosus*)[139]. These increasing populations can support biodiversity across trophic levels, ultimately supporting top predators such as seabirds, marine mammals and sharks[135]. Retreating glaciers also create new territory for colonisation and succession processes in marine environments at glacial margins, whereas calving glaciers can disturb benthic communities[134]. For example, scouring from icebergs calved from glaciers in the Antarctic can extirpate large areas of benthos, initiating new succession processes and carbon cycling[69].

Organismal transport by glacial runoff forms a crucial linkage between terrestrial and marine systems, enabling connectivity and sustaining biodiversity across these ecosystems. The composition and functioning of bacterial communities in glacier-fed rivers are distinct from those of ice, snow, permafrost and terrestrial communities, and many bacteria in glacier-fed rivers are endemic to individual mountain ranges[38,110]. Although microorganism α-diversity **[G]** increases locally with decreasing influence of glacier meltwater[12,18,20,127], glacier retreat also leads to decreasing β-diversity **[G]** and to the homogenization of microbial communities[140], which increasingly resemble those in non-glacial rivers[62], consequently leading to γ-diversity **[G]** decline[110]. Invertebrates in glacier-fed rivers show strong biodiversity gradients from the glacier terminus downstream, as habitat properties such as water temperature, stability, and resources become less harsh[13,37,57].

With increasing glacier retreat, invertebrate species that are typical of glacier terminuses, such as *Diamesa* spp. chironomids (Diamesinae) in European and North American rivers[36], *Paraheptagyia* spp. chironomids (Diamesinae) and *Anomalocosmoecus* sp. caddisflies (Limnephilidae) in South America[87] or the mayflies (Ephemeropetera) *Deleatidium cornutum* and *Nesameletus* spp. in New Zealand[141] might face large population declines. Endemic, cold-water obligate invertebrates such as the glacier stonefly (*Zapada glacier*) and meltwater stonefly (*Lednia tumana*) are expected to experience population declines or even local extinctions as glaciers disappear[142]. This biotic replacement of cold-adapted taxa leads to communities that increasingly include more generalist blackflies (Simuliidae), craneflies (Tipulidae), worms (Oligochaeta) and river flies (mayflies, stoneflies, and caddisflies) across European rivers[15,37].

[H2] Biodiversity in deglaciated lands

Although the retreat of glaciers creates new terrestrial habitats, allowing species to colonise and thrive in the short term, the conditions in these deglaciated areas are often challenging for many plant and animal species owing to low temperatures, permafrost, and poor soil development[19,46]. Many microorganisms that occur on glacier surfaces are well-suited to the transition into foreland environments and consequently persist in the newly exposed terrains[143]. However, as succession progresses, microbial communities shift, with generalist species replacing specialised, cold-adapted taxa that struggle to persist in the warmer and drier conditions of glacier forelands[99,144]. Generalist microorganisms, particularly ectomycorrhizal fungi, replace bacteria and arbuscular mycorrhizal fungi, and dominate later stages of succession[145].

There is evidence of vegetation expansion in the Alps[146], polar greening and browning[51], and population range expansion for the grass *Deschampsia antarctica* and the cushion-plant *Colobanthus quitensis* in Antarctica[147]. However, the future is uncertain for many pioneer, cold-adapted, slow-growing plant species, which might decline with increasing glacier retreat owing to a lack of habitat availability and increasing competition with later colonisers such as trees and shrubs[23,92,93,119]. In the Alps, stress-tolerant pioneer species such as *Saxifraga bryoides, Saxifraga oppositifolia, Dryas octopetala*, *Ranunculus glacialis*, and *Geum reptans* are increasingly being replaced by faster-growing competitive species[148]. In Andean glacier forelands, tropical alpine specialists are being outcompeted by rapidly colonising non-native plant species[92,149]. Similar to freshwater ecosystems, the loss of glaciers increases the risk of biotic homogenization and reduced ecological niche availability **[G]** [24,26], which can facilitate colonization by invasive species. For example, the grass *Poa annua* is rapidly colonising newly deglaciated habitats in Antarctica[147]. Encroachment or invasion by woody plants can have negative effects on functional diversity and resilience in post-glacial ecosystems in the long term.

Invertebrate colonisation and succession are associated with changes in plant communities[21,90,118,150,151]. Opportunistic open-habitat specialists, which are associated with the pioneer invertebrate community, disappear rapidly with increasing vegetation cover and are vulnerable to population contractions when glacier loss occurs. This is particularly the case for cold-adapted, specialized wingless carabid beetles and Linyphiidae spiders, which face severe limitations in dispersal that lead to delayed colonisation or even local extirpation[118]. By contrast, generalist organisms such as the springtails *Agrenia bidenticulata*[73] might thrive with glacier retreat, given their aerial dispersal over large distances and broad ecological niche. Similarly, the future for mutualistic and antagonistic insects such as pollinators and herbivores varies between taxonomic groups[151]. Specialised pollinators, such as the drone fly *Platycheirus alpina* and the sweat bee *Dufourea alpina*, which feed on a few pioneer plant species in the Alps, are at risk as open grassland habitats shrink, plant diversity declines, and competition increases[90]. By contrast, generalist and opportunistic Staphylinid beetles (for example, *Aleochara bilineata* and *Eusphalerum alpinum*) and pollinators (for example, S*yrphus vitripennis* and *Apis mellifera*) are well-adapted to changing conditions[78] and are likely to thrive in the absence of glaciers.

The retreat of glaciers poses considerable challenges for conservation efforts, as many of the species that currently thrive in glacier ecosystems are not well-adapted to the warming and drying conditions in deglaciated landscapes. Supporting glacial biodiversity requires understanding the dynamic processes of glacial ecosystems[113] and the need to manage both the winners and losers of glacier retreat. For example, conserving rare pioneer plants might require active interventions to decrease the competitive impacts of late-successional species.

[H1] Consequences for ecosystem functions

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

[H2] Climate regulation, nutrient dynamics, and productivity

Glacier retreat has major consequences for climate regulation, influencing both physical and biological feedback mechanisms. In both aquatic and terrestrial systems, exposed ice-free areas absorb more solar radiation, reducing albedo **[G]** and creating a positive feedback loop that intensifies warming and further melting[152]. On glacier surfaces, microorganisms such as red pigmented snow algae (*Sanguina nivaloides*, Chlamydomonadaceae) cause a substantial reduction in albedo and increase snow melt by changing the snow colour to red as algae bloom[77]. The resulting increased snow melt exposes underlying grey ice, which hosts brown–black pigmented glacier algae (Zygnematophyceae), leading to further glacier melting[44].

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

In aquatic systems, the meltwater released from glaciers alters the biogeochemical properties of rivers, lakes, and coastal marine environments, leading to changes in matter and energy fluxes that can spill over into terrestrial communities[36,99]. Glacier retreat leads to the expansion of ice-free areas, exposing new aquatic habitats to colonisation[94], with the potential to sequester carbon dioxide from the atmosphere[61] as producers colonise these systems[71]. Glacier retreat also enhances the processing of terrestrial organic matter that enters aquatic systems, increasing decomposition[13], respiration and CO_2 release back to the atmosphere[155]. Shifts in phytoplankton communities affect herbivory and predation, influencing the biological carbon pump that transports carbon from the surface to the deep ocean, thereby altering carbon cycling locally and regionally[67]. As in terrestrial systems, the long-term impacts of glacier retreat on aquatic ecosystems are complex, as the reduction in albedo owing to glacier loss contributes to regional warming, creating feedback that accelerates warming and further glacier loss. For example, streams in four catchments in Switzerland transitioned from CO_2 sinks to sources as glacier cover decreased and vegetation expanded[47].

Nutrient availability in glacial ecosystems is context-dependent and varies across different habitats and spatiotemporal scales. In supraglacial habitats and pioneer terrestrial habitats, nutrient availability is generally low owing to the limited organic matter and primary productivity, although glaciers can also supply ancient organic matter transported by the glacier as nutrient sources to pioneer colonisers[156,157]. Glaciers transport dissolved and particulate nutrients (for example, nitrogen, phosphorus and iron) from supraglacial habitats to downstream aquatic systems[45,57], increasing nutrient availability and supporting biodiversity and productivity of glacier-fed rivers and lakes[158,159]. Similarly, in coastal marine environments, glacial runoff can deliver nutrients (such as nitrogen, phosphorus, potassium and iron) that promote phytoplankton blooms, fuelling primary production and supporting marine food webs[141,160]. Furthermore, ancient carbon from subglacial systems can be utilised by subsurface microorganisms in Arctic fjords and so become a carbon source[161]. However, meltwater influx can alter water properties, mainly temperature and turbidity, which can negatively affect productivity, trophic interactions and biodiversity[35]. Although understanding the temporal dynamics of changes in nutrients, biodiversity, and food webs across different glacial habitats is crucial for predicting shifts in ecosystem structure and function, a comprehensive model for making accurate projections is lacking.

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

[H2] Habitat creation and maintenance

Although the environment influences the ecology and evolution of species, organisms can also modify their environment[162]. The process of ecosystem engineering includes creating new habitats, increasing resource availability, and providing new niches for other species by physico-chemical and biotic modification of the environment[17,56]. This process results in the creation of diverse microhabitats that support local and regional biodiversity and increase heterogeneity and functional diversity[163,164]. For example, the activity of cyanobacteria on the ice surface results in the formation of bioaggregates, which then act as biogeochemical factories in the nutrient-poor supraglacial environment[163,165,166].

In aquatic systems, particularly in glacial floodplains and lakes, biofilms **[G]** and periphyton **[G]** communities composed of bacteria, fungi, and algae are the first colonisers of newly exposed glacial sediments and streambeds[164]. Biofilms stabilise sediments through the production of extracellular polymeric substances that bind mineral particles. This binding process reduces vertical infiltration in sediments, thereby increasing sediment cohesion and water retention and reducing erosion. The new stable habitats act as hotspots for microbial activity, enhancing biogeochemical cycling as sediments are enriched with carbon, nitrogen and phosphorus[99], thereby providing primary production for decomposers and grazing invertebrates[14,87]. The activity of biofilms is also crucial for the establishment of aquatic vegetation and the development of complex food webs, where energy and matter are eventually transferred from these microorganisms to fish predators and parasites as well as to terrestrial habitats[167].

Glacier recession in the Pacific northwest of North America is opening up new river systems for colonisation by migratory salmonids[149], creating considerable disturbances as fish move from the oceans up rivers, and redd (nest) building and spawning activity drive substantial decreases in algal and invertebrate biomass. In glacier-fed fjords, coastal, benthic and pelagic habitats, invertebrates such as polychaetes and molluscs act as ecosystem engineers by sediment bioturbation[34,160] (mixing by living organisms). In doing so, burrowing organisms create tunnels that serve as microhabitats for smaller species, increasing habitat heterogeneity. Furthermore, they increase oxygen infiltration into sediments, further stimulating microbial activity and nutrient cycling.

In terrestrial systems, the interactions between developing communities and geomorphic processes, such as sediment deposition and erosion, create biogeomorphic feedbacks that shape the habitat mosaic in deglaciated landscapes[17,27,89]. The establishment of pioneer organisms is crucial for the initial transition from barren, newly exposed terrains to complex ecosystems. Stress-tolerant plants, such as *Lupinus nootkatensis*, *Saxifraga cespitosa*, and *Dryas octopetala* in the Arctic, *Saxifraga oppositifolia* and *Poa alpina* in the Alps, or *Colobanthus quitensis* in Antarctica, create novel habitats by stabilising sediments, fixing nitrogen through symbiotic interactions with bacteria, and increasing organic matter. Furthermore, these plants also host symbiotic mycorrhizal fungi, provide resources for pollinators, and create microhabitats for predators, ultimately increasing biodiversity across trophic levels. In addition to vascular plants, cryptogamic soil crusts consisting of bryophytes, diatom algae, cyanobacteria, and lichens support habitat creation by retaining water, increasing organic matter, trapping fine mineral material, fixing nitrogen, and providing food resources for detritivores and herbivores[168].

[H1] Summary and future directions

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

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

Given these commonalities, the disappearance of glaciers clearly presents both challenges and opportunities for biodiversity and ecosystem functioning. To fully understand how biodiversity responds to glacier retreat, several key knowledge gaps need to be addressed. Given the limited understanding of the structural and functional roles of species within and across glacier systems, a better grasp of functional diversity **[G]** is essential to elucidate the roles of species in ecosystem processes including climate mitigation, biogeochemical cycling, productivity, and biotic resistance (the ability of communities to resist invasion by exotic species). Future research should focus on functional approaches to understand how species interactions contribute to ecosystem processes[162] and eco-evolutionary mechanisms[169]. Integrating functional traits into models of glacier ecosystem dynamics will improve predictions of the responses of biodiversity and ecosystem functioning to glacier loss[26]. This information is crucial for identifying species at the highest risk of extinction and for developing conservation strategies aimed at preserving functional diversity and ecosystem services.

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

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

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

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

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G.L. conceived of the article and wrote the first manuscript draft. All authors contributed to literature research and provided a substantial contribution to the discussion of content and writing.

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Figures

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

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

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

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

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

Boxes

Box 1. Glossary

Albedo

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

Allochthonous

Introduced from a different (distant) location.

Autochthonous

Originating or formed in its present location.

Biotic homogenisation

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

Firn field

Layer of snow that is transforming into glacial ice.

Moulin

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

Crevasse

Fissure or crack in the surface of a glacier.

Cryoconite

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

Glacier mice

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

Supraglacial

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

Englacial

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

Subglacial

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

Proglacial

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

Glacier foreland

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

Benthic

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

Pelagic

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

Ecological niche

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

Redox potential

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

Periphyton

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

Biofilm

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

Cryptogamic soil crust

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

Biogeomorphic feedback

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

Subglacial legacy

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

Paraglacial adjustment

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

Dimensions of diversity:

α-Diversity

Mean species richness in a site (local diversity)

β-Diversity

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

γ-Diversity

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

Functional diversity

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

Interaction diversity

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