Chapter

Glacial Biodiversity: Lessons from Ground-dwelling and Aquatic Insects

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Abstract

At first glance, the ground surrounding the glacier front and the streams originated by melting glaciers seem to be too extreme to host life forms. They are instead ecosystems, colonized by bacteria, fungi, algae, mosses, plants and animals (called the "glacial biodiversity"). The best adapted animals to colonize glacier surface, the recently deglaciated terrains and glacial streams are insects, specifically the ground beetles (carabids) and the non-biting midges (chironomids). This chapter aims to overview the species colonizing these habitats, their adaptation strategies to face natural cold and anthropogenic heat and the extinction threats of glacial retreat and pollution by emerging contaminants. Notes on their role in the glacial-ecosystem functioning and related ecosystem services are also given.

Keywords: carabid beetles, chironomids, cold-adapted species, debris-covered glaciers, extinction risk, glacier forelands, rock glaciers

1. Introduction

Insects are the most diverse and abundant group of animals on Earth and are critical drivers of ecosystem function in terrestrial and aquatic systems.

Biodiversity of insects is threatened worldwide [1]; 40% of the world's insect species could go extinct within decades [2] with consequent loss of ecosystem functions and services.

Despite the attention from the media, and scientific community, it remains unclear whether such declines are widespread among habitats and geographic regions. Since most of the insects are providing services (e.g., pollination and decomposition) and disservices (e.g., damaging crops and spreading diseases), the efforts in insect conservation biology and population management have been mainly conveyed to highly impacted areas like, for instance, the lowlands.

On the other hand, around the world, mountain regions are changing at an unprecedented rate. Most of the evidences are based on the abiotic component (e.g., temperature increase and precipitation variations), but there are increasing evidences about changes in biological communities.

At high altitude in tropical and temperate mountains and at high latitude, habitat loss, pollution and climate change affect negatively cold-adapted insect species distribution and survival [3, 4]. It is unlikely that insect declines will be homogenous everywhere, but some general patterns can be identified. For example, at high altitude, the high frequency of extreme climatic events and the loss of ice-related landforms (e.g., glaciers and rock glaciers) are detrimental to cold-adapted insects, highly specialized to survive constantly at low temperature, high humidity, deep snow and ice cover. Most of the glaciers are strongly reducing their surface, some are disappearing, others are shifting in debris-covered glaciers and permafrost is melting [5]. The effects of climate change on high-altitude terrestrial and aquatic insect community composition and ecosystem functioning are partially unknown and still underconsidered [6].

Scattered studies on high-altitude and high-latitude insect communities are available for most of the glacialized areas of the world, but a synthesis paper merging the most recent advances on cold-adapted insect species living on and at the edge of ice-related landforms is still not available. To fill this gap, the purpose of this chapter is to (i) describe what insects live in glacialized areas, (ii) examine what are the flagship insects in terms of richness and adaptation to cold, (iii) identify threats and opportunities in the current warm-period and (iv) illustrate the role of insect communities in the glacial-ecosystem functioning and services.

2. Glacial biodiversity: glacial and periglacial landforms as habitat for cryophilous species

At first glance, the ground surrounding the glacier front, its surface and the streams originated by the melting glaciers seems to be too extreme to host any life forms. Conversely, there are many organisms that permanently colonize the cryosphere, from bacteria to vertebrates, the so-called glacial biodiversity [7].

From the quantitative point of view, the glacial biodiversity is mainly formed by little (less of 5 cm) or microscopic organisms linked to aquatic, semiaquatic, wet or terrestrial (mainly bare and rocky grounds) habitats.

The surface of glaciers is colonized by bacteria and algae [8, 9] and mosses, hosting in turn water bears (Tardigrade), roundworms (Nematoda) and potworms (Enchytraeidae) [10]. They can live also directly on the surface of the ice, in cryoconite holes and rivulets on ice. In addition, on the glaciers, it is possible to observe wandering several spiders (Araneae) during the day as well as some ground beetles (Coleoptera: Carabidae) during the night searching for preys. Many other invertebrates, mostly connected with aquatic/wet environments, such as springtails (Collembola), stoneflies (Plecoptera) and non-biting midges (Diptera: Chironomidae), can live directly on the surface of the ice [11]. Moreover, supraglacial cryoconite holes can be considered biodiversity hotspots for invertebrates such as Copepoda, worms (Annelida), water bears, roundworms and wheel animals (Rotifera) [11, 12].

Most of the invertebrates living on the glaciers can be found also along recently deglaciated terrains and in the uppermost reach of glacial streams. Thus, the glacial biodiversity living at the edge with the glacier front arrives from two different sinks: falling down from the glacier surface during the melting phases and shifting up along the glacier forelands, transported airborne or by walking. Typically, springtails and moss mites (Oribatida) are the first colonizers of recently deglaciated areas because they are easily transported by the wind, thanks to their lightweight. Some sheet weaver spiders (Linyphiidae) are as well colonizers transported by wind [13]. Thus, recently deglaciated terrains act as a source of glacial biodiversity characterized by species living on the ground but still linked to the presence of cold microclimate ensured by the presence of the glacier few meters far from them.

Aquatic fauna in rivulets on ice (= eukryal) and uppermost reaches of glacier-fed streams (=metakryal) is represented mainly by cold hardy non-biting midges that have resistant forms to survive freezing and desiccation. Other guests of such habitats are worms (e.g., Naididae and Enchytraeidae) and free-living and parasite roundworms.

Similar to recently deglaciated terrains, also rock glaciers—which are the best expression of the periglacial environment in alpine areas—can sustain glacial biodiversity, also in the places where there are no glaciers or they disappeared. Currently, the state of knowledge about the animals living on this kind of landform is still very limited; just few sites in Sierra Nevada and on the Alps were investigated [14–16]. Both studies highlighted the presence of microbes, arthropods and small rodent fauna linked to the cold and wet habitat ensured by the presence of interstitial ice. Given the known thermal and hydrologic capacity of rock glaciers to resist warming, this distinct landform has been suggested as potential climatic refugia for glacial biodiversity in the current warm stage period.

It is therefore evident that glacial biodiversity is characterized by species living in ice-related landforms, thus landforms ensuring, at the ground as well as on the water, average annual temperatures around 0°C [17, 18]. Thus, the species living on and around ice-related landforms can be defined as cryophilous (which means "loving the ice") or cold-adapted species. Among these, the best adapted to survive such extreme habitats are ground beetles (carabids) and non-biting midges (chironomids).

3. Ground beetles and non-biting midges as flagship organisms: richness and adaptation

Ground beetles (**Figure 1**) occur in almost all terrestrial environments and geographical areas and have different trophic requirements (e.g., predators, seed eaters and phytophagous), it is easy to collect them and their sensitivity to environmental and climate changes is known [19]. In addition, they can be considered among the most important meso- and macrofauna living on recently deglaciated terrains and on the glaciers in terms of species richness and abundance of individuals [13]. Last but not least, there is an ongoing awareness about the extinction risk for some endemic cryophilous species due to the habitat destruction (e.g., glacier

Figure 1.
The ground beetle Nebria germari *(approx. body length = 1 cm) walking on the Presena Glacier (2700 m a.s.l.) (Adamello-Presanella Mts., Italian Alps) (photo by F. Pupin/archive MUSE).*

disappearing) or changes in microhabitat conditions (e.g., permafrost melt). Most of the species living at high altitudes and latitudes have low dispersal abilities due to the lack of wings and are walking colonizers, ground hunters and small-sized, which are traits typical of species living in cold, wet and gravelly habitats [17]. To date, about 40,000 species are known in the world [20] and most of them are endemic to specific areas [21–23]; for instance, about 28% of the total species belonging to the Italian carabid fauna are endemic.

Non-biting midges (**Figure 2**) are the freshwater insect family that comprises the highest number of species, both in lentic and lotic habitats [24]. They are the most widespread of all aquatic insect families, with individual species occurring from Antarctica to the equator lands and the Arctic, from lowlands to thousands of meters of altitudes. There are species that thrive in almost every conceivable freshwater environment. Ice-cold glacial trickles, hot springs, thin films, minute containers of water in the leaf axils of plants and the depths of great lakes all have their characteristic species or communities. There are semiaquatic species, living in moist soil or vegetation and others that are truly terrestrial with few species occurring in marine water. Some species tolerate brackish water, others thrive in intertidal pools and, unusually among the insects, and a few are truly marine. Survival in harsh environments is due to a series of adaptations. Among these are the production of melanin, their small size, capacity for mating on the ground instead of in flight (they therefore have small or totally absent wings), the building of cocoons, diapause and resistance to cold [25]. To date, about 6500 species are known in the world; one tenth of which are in Italy and one thousandth in Alpine streams, springs and lakes.

Thanks to their species richness, adaptation to cold environments, key role in the ecological network structure and robustness and sensitivity to short-term and long-term climate changes, ground beetles and non-biting midges might be considered flagship organisms of the glacial biodiversity.

3.1 Ground beetles on glaciers

Clean glaciers and debris-covered glaciers can host permanent populations of ground beetles, at least on the European glaciers since, to our knowledge, there are no data from other extra-European mountain chains. All the species found on the European glaciers belong to the genera *Nebria* and *Oreonebria*. The *Nebria*/

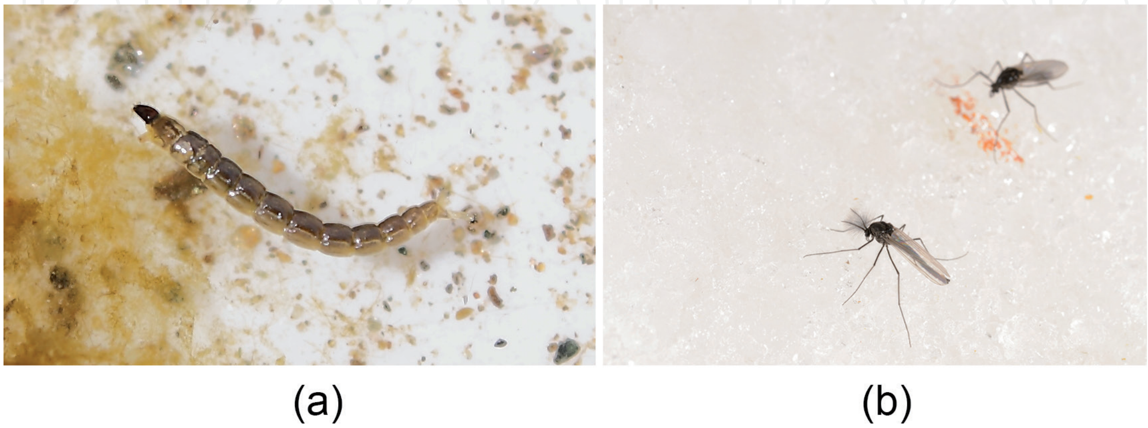

Figure 2.
The non-biting midge Diamesa zernyi *larva (a) from the Amola glacial stream (2540 m a.s.l.) and a couple of adults (male on the left, female on the right) (b) walking on the Presena Glacier (2700 m a.s.l.) (Adamello-Presanella Mts., Italian Alps) (photo by V. Lencioni) (a) and F. Pupin/archive MUSE (b). Animal sizes ca 1 cm.*

Oreonebria species living on clean glaciers are with reduced and not functional wings and wander on the glacier mainly during the night searching for preys (mainly springtails, spiders, non-biting midges and died insects). During the day, they find refuge under the rocks on glacier surface and within the moraines. Their legs are longer with respect to those closely-related species living at lower altitudes and in different habitats, in order to maintain the body to a higher distance from the frozen ground [26].

In addition, debris-covered glaciers are able to host permanent population of *Nebria/Oreonebria* species (**Figure 3**). Currently, data are available for five debris-covered glaciers of the Italian Alps [17, 18, 27, 28].

Nebria/Oreonebria are olfactory-tactile predators; it means that they use the chemoreceptors located on the antenna as instrument to find preys on the glacier surface or between the stony debris. Therefore, these organisms are well adapted to move between the stony debris covering the glaciers, thus across a three-dimensional space. The sex ratio on the glacier is female-biased [29], and the colonization of the glacier from the neighboring habitat seems be done by females that have a higher propensity to disperse than males [29].

3.2 Ground beetles along glacier forelands

The gradual melting of glaciers leave in front of them large areas of barren, pristine ground open for colonization of various life forms. Among these, ground beetles can be found along the entire glacier foreland. Ground beetles can colonize entire glacier forelands, from sites deglaciated since more than one-hundred years to sites deglaciated since one year (**Figure 4**).

The colonization of a glacier foreland by ground beetles is triggered mainly by time since glaciation, distance to glacier and vegetation cover, as highlighted by studies carried out in Northern Europe (e.g., [30–32]), Alps (e.g., [27, 33–36]) and more recently Andes [37]. The colonization of a glacier foreland by ground beetles can follow two different models: the “addition and persistence” and “replacement-change” models [31]. The former was mainly observed in Northern-Europe and on Andes [31, 37], with an exception in the peripheral mountain range of the Southern Alps [38]. It consists in the persistence of pioneer species (i.e., the initial colonizers, e.g., *Nebria* spp. in Europe; *Dyscolus* spp. on the Andes [37]) from the sites deglaciated few years ago (early successional stages) to sites deglaciated more than 100 years ago (late successional stages)—in this case, there is no species turnover along the chronosequence of glacier retreat. The “replacement-change” model, mainly observed on the Alps (e.g., [17, 36]), consists in a group of initial colonizers (the pioneer community) progressively replaced over time by one or more other species assemblages; thus, in this case, there is a clear species turnover. Notwithstanding these different models of colonization, Northern Europe and Alps share ground beetles belonging to common genera and exhibiting the same patterns of colonization. For instance, the species belonging to the genus *Nebria* are surface active predators able to immediately colonize deglaciated terrains of the European glacier forelands. The species belonging to the genus *Amara* and *Carabus*, the former omnivorous and the latter specialized predators, arrived on a deglaciated terrain after more than 20 years [30, 33]. A quite common pattern observed along the European glacier forelands is that the number of species increases with the time since deglaciation, with a more diversified community on terrains deglaciated 100 years ago.

The speed of colonization along the glacier forelands varies with the time since deglaciation. Specifically it is high in the first years after the glacier retire due to the low competition in colonizing pristine terrains, while it is low in terrains located far from the glacier front because more competitive in terms of microhabitat and resource availability [35]. In the contest of the ongoing climate warming, it is interesting to highlight that an increase of 0.6°C in summer temperatures approximately doubled the speed of initial colonization, whereas later successional stages were less sensitive to climate change [39].

Figure 3.
Stony debris covering the surface of the Sorapiss Centrale glacier (45°N, 12°E, Ampezzo Dolomites, Italian Alps); it hosts permanent populations of cold-adapted ground beetles, spiders and springtails (photo by M. Gobbi).

Figure 4.
Pitfall trap near the front of the Agola Glacier (46°N, 10°E, Brenta Dolomites, Italy). Pitfall trapping is one of the most successful methods to collect ground-dwelling invertebrates at high altitudes during the snow free period (photo by M. Gobbi).

3.3 Ground beetles on rock glaciers

Currently, data on ground beetles found on rock glaciers are available only for the Italian Alps [16, 40 41]. Active rock glaciers are a unique landform: the occurrence of permafrost and the size of the stones differentiate them from the surrounding landforms (e.g., scree slopes) in terms of temperature regime and depth of the substrate. Active rock glaciers show occurrences of cold-adapted species. Even though ground beetle communities of active rock glaciers show few differences in terms of species richness and abundance with respect to scree slopes, some characteristic species of each of the two landforms can be identified. The ground beetle community observed on the rock glaciers is exclusive of this landform because it is composed of large populations of species belonging to the genera *Oreonebria*, *Nebria* and *Trechus* [16, 40]. To these genera belong species (e.g., *Nebria germari*, *Oreonebria soror* and *Trechus tristiculus*) typical of cold and wet high-altitude environments. These species have two kinds of life style: epigeic (they move on the surface of the rock glacier where the rocky detritus is fine) and endogeic (they reach the depth of the stony detritus moving between the interstitial space between stones). Conversely, the surrounding ice-free landforms (e.g., scree slopes) host species assemblages characterized by the presence of species typical of alpine grasslands (e.g., *Carabus* spp. and *Cymindis vaporariorum*). Therefore, an active rock glacier can be defined as a superficial subterranean habitat [16] represented by fissure network among boulders, human-sized caves included.

Unlike other superficial subterranean habitats like scree slopes, where temperatures could reach relatively high values in summer [16, 42], rock glaciers are selected by cold-adapted species, which avoid scree slopes as they do not offer constantly low temperatures during summer.

3.4 Non-biting midges on the glacier

To our knowledge, the only aquatic insects found permanently colonizing the ice are non-biting midges of the genus *Diamesa* in temperate zones and the stonefly *Andiperla willinki* (family Gripopterygiidae) in South America [43]. Larvae of *Diamesa steinboecki* and *Diamesa latitarsis* were collected on one Alpine glacier (2625–2650 m a.s.l., Agola, Brenta Dolomites, Italy), surviving a summer temperature ranging for 0.07 to 0.19°C. Larvae of *Diamesa* were collected also on Yala glacier (5100–5700 m a.s.l., Nepal, Himalayas [44, 45]), growing in melt-water drainage channels under the ice and feeding on blue-green algae and bacteria. They eat the scares allochthonous detritus transported by the wind and left by the glacier in the ice melt waters. Typically, primary food resources in eukryal consist of dust (allochthonous particles or airborne detritus) and algae (various species of cyanophytes and green algae), and fungi and bacteria associated with algae and detritus [46]. Adults were brachypterous (characterized by reduced wings), unable to fly, walking at temperatures as low as −16°C on the surface of the glacier and in small cavities beneath it.

3.5 Non-biting midges in proglacial ponds

Non-biting midges are first colonizers of ephemeral ponds in the proximity of glacier snout. The appearance of new ponds is usually followed by their rapid disappearance and by a concomitant appearance of new ones, frequently observed in the Alps above the tree line [47]. Most of them are relatively small (surface <2 ha) [48], unproductive due to their sparse soil development and small catchments. Ponds are especially susceptible to the effects of climatic changes because of their relatively low water volumes and high surface area-to-depth ratios. Therefore, they act as early indicators of the impacts of climate change. During the ice-free months, typically, they undergo high-level fluctuations due to ice-snow melt rate and rainfall pattern. In winter, they freeze, totally if shallow [48]. Water temperature can be highly variable as well, ranging from 0 to 15°C during summer.

The zoobenthic community of Alpine proglacial ponds is dominated by chironomid Orthocladiinae (generally representing >70% of the community) followed by Diamesinae (*Pseudokiefferiella parva* and *Diamesa* spp.). Aquatic beetles (e.g., Elmidae, Dytiscidae and Hydrophilidae), Oligochaeta (e.g., Enchytraeidae) and Hydracarina frequently represent the remaining fauna. Overall, the richness is low, with few dozens of species colonizing the same pond. Few taxa might be found with high density, up to >1000 individuals/m^2 in ponds >2 ha and less than 2 m deep. Among orthoclads, semiterrestrial genera are frequent (e.g., *Metriocnemus*, *Smittia* and *Parasmittia*), being environments that undergo high water level fluctuations during the ice-free period [49] (**Figure 5**). There are evidence of colonization by up to 4–5 congeneric species of *Metriocnemus* in

Figure 5.
Catching Metriocnemus *adults (non-biting midges) with tweezers on the shoreline of the Agola proglacial pond (2596 m a.s.l., 46°N, 10°E, Brenta Dolomites Mts., Italian Alps) (photo by D. Debiasi/archive MUSE).*

single Alpine ponds (Agola glacier, 2596 m a.s.l., Brenta Dolomites, Italy), with *M. fuscipes* and *M. eurynotus* as dominant species. The genus is considered semiterrestrial, found in mosses, phytotelmata, springs, ditches, streams and occasionally in the middle of lakes and rock pools [50]. Some ability to survive desiccation and hibernation often in combination with cocoon building and migration of larvae into the sediment [51] has been recorded for several *Metriocnemus* species dwelling in ephemeral habitats that seasonally dry or freeze out. The colonization of these ponds by *Metriocnemus* might be due more to these physiological adaptations than to repeated recolonization as observed for other chironomids colonizing ephemeral ponds [52]. In fact, due to the high geographical isolation of the pond and scarce connectivity with other suitable habitats in the catchment, we can suppose that these species persist by activating a physiological response to physical stress. Most of these species are univoltine, entering diapause in a desiccated-frozen state until spring thawing.

3.6 Non-biting midges in glacier-fed streams

Non-biting midges are the main colonizers of glacier-fed streams around the world. Glacially dominated rivers are characterized by a deterministic nature of benthic communities due to the overriding conditions of low water temperature, low channel stability, low food availability and strong daily discharge fluctuations associated to glacier runoff (**Figure 6**). A predictable longitudinal pattern of taxa richness and diversity increasing with distance from the glacier has been described for many European glacier-fed streams, starting from the kryal sector (where maximum water temperature is below 4°C), typically colonized almost exclusively by *Diamesa* species in the temperate regions [53]. *D. steinboecki*, *D. goetghebueri*, *D. tonsa*, *D. zernyi* and *D. bohemani* are the species more frequent and abundant in kryal sites in the Palearctic regions, followed by *D. bertrami*, *D. latitarsis*, *D. modesta*, *D. hamaticornis* and *D. cinerella*. Less frequent are *D. martae*, *D. nowickiana*, *D. longipes*, *D. wuelkeri* and *D. aberrata*; *D. insignipes*, *D. dampfi*, *D. permacra* and

Figure 6.
Dubani glacial stream at the glacier snout (3232 m a.s.l., 36°N, 74°E; Bagrote Valley, Karakoram range of northern Pakistan) (photo by L. Latella).

D. incallida are rare, being more frequent in glacio-rhithral and krenal habitats, characterized by a lower glacial influence. *D. arctica* is typical of the Arctic regions, and *D. akhrorovi*, *D. alibaevae*, *D. planistyla, D. solhoyi*, *D. aculeate*, *D. praecipua* and *D. khumbugelida* are among the *Diamesa* species typical of Pamir and Tibet mountains. In tropical streams, mainly Podonominae colonize the uppermost glacier-fed stream reaches, while Diamesinae appear more downstream [54]. In glacier-fed streams of New Zealand, [55] reported the mayflies (Ephemeroptera) *Deleatidium cornutum* and *Nesameletus* dominated at the upper sites of glacier-fed streams, with the chironomids *Eukiefferiella* and *Maoridiamesa*. Biodiversity naturally increases with decreasing altitude and increasing distance from the glacier terminus, with a more diversified community downstream of the confluence with tributaries fed by groundwater and rainfall (= krenal and kreno-rhithral). Orthocladiinae and Tanypodinae (e.g., *Zavrelimyia*) become more abundant, followed by Tanytarsini (e.g., *Micropsectra* spp.) in slow-flowing waters where mosses are abundant.

4. Threats and opportunities for ground beetles and non-biting midges in relation to climate warming

Glaciers and permafrost are disappearing all over the world, and with them, we are risking to lose also the associated glacial biodiversity. Therefore, it is mandatory to describe the temporal and spatial biological fingerprint of climate change impacts to deeply understand trends and patterns.

The available literature on ground beetles and non-biting midges is able to give us insights about the threats and opportunities they have in relation to the ongoing climate and, consequently, landscape changes.

4.1 Extinction

Currently, no ground beetles living on glacial and periglacial landforms have been declared extinct. On the other hand, the temporal reduction in population size of two high-altitude species (*Nebria germari* and *Trechus dolomitanus*) of the Dolomites (Italy) in 30 years was documented [56]. Specifically, local extinction of *Nebria germari* populations was documented in some high-altitude prairies of the Dolomites, and now the species maintain large populations only on glacial and periglacial landforms; thus, it has become an ice-related species.

As observed for ground beetles, also for non-biting midges from kryal habitats, there is no evidence of global extinction of single species, rather of local extinction caused by the retreat of glaciers. The consequence of the glacial retreat is the further isolation of the populations in the short-term and, in the long-term, their possible disappearance due to very restricted habitat preference and limited dispersal abilities of midges. Glacier shrinking favors an upstream shift of lowland euriecious species of chironomid and other invertebrates, associated with an initial decrease in abundance and finally local extinction of kryal *Diamesa* species and other Diamesinae [57]. *Diamesa longipes* and *Syndiamesa nigra* have not been collected in recent years in Alpine running water [53], and the ice fly *Diamesa steinboecki* has disappeared in some glacier-fed streams in the Southern Alps [58]. The strong cold hardiness of *Diamesa* species [59] and the scarcity of potential refuge areas in glacial and periglacial area threaten these species seriously with extinction. Thus, *Diamesa* species have been suggested to be used as sentinels for climate change, especially in relation to glacier retreat. Recent studies found a direct relationship between the loss of *Diamesa* species in alpine riverine environments and the consequences of the changing climate [58].

4.2 Uphill and upstream shift

Higher temperatures and increased drought are leading to an upward shift of stenothermal species that depend on low temperatures and therefore to the fragmentation and progressive reduction in their habitat. Any endemic species, like several high-altitude ground beetles, that is restricted to summit areas and has a low dispersion ability is forced to move upward searching for microclimates suitable for its survivor. Data on ground beetles resampled in the same places after decades suggest common trend in cryophilous species. For instance, on the Andes, from 1880 to 1985, the species *Dyscolus diopsis* has shifted approximately 300 m upward, with the resulting area reduction of more than 90% from >12 km^2 to <1 km^2 [60]. The same altitudinal shift was observed on the Dolomites for the species *Nebria germari* [27] from 1950 to 2019; the habitat preference for this species was alpine prairies [61], N-exposed scree slopes and recently deglaciated terrains, and currently, it seems to be restricted only to ice-related landforms and scree slopes with high snow cover temporal extent.

Shrinking glaciers are resulting in the lengthening of glacial streams, with consequent upstream migration of specialist species to colonize the "new" stream reach, still harsh, in front of the glacier terminus. Downstream generalist species also migrate upstream, to conquer sites with ameliorated environmental conditions associated to a reduced glacial runoff and increased temperature and channel stability [62, 63]. For example, in the Alps, as first colonizers upstream were observed grazer (chironomid Orthocladiinae among which *Eukiefferiella* spp., *Heleniella* spp., *Orthocladius frigidus* and *Chaetocladius* spp.) and shredder insects (Nemouridae), covering distances from 300 m to about 2 km and a difference in altitude up to 600 m probably favored by higher amount of debris from the banks [58].

4.3 Adaptation

To the best of our knowledge, there is no evidence of physiological or morphological adaptation of carabid beetles in relation to the climate change at high altitudes, and it seems that limits to species distributions reflect present environmental tolerance limits rather than simply an historical lack of opportunity for range expansion [64]. Some studies on thermal tolerance highlighted that temperature gradients and acute thermal tolerance do not support the hypothesis that physiological constraints drive species turnover with elevation [65].

Cold stenothermal non-biting midges that adapted to live at temperatures close to their physiological limits like *Diamesa* spp. might only survive and reproduce if they can adapt to new environmental conditions or if they are able to avoid the stressor adopting specific behaviors. Barring these abilities, they are expected to disappear. There are evidences of physiological adaptation in Diamesinae to increasing water temperature in glacier-fed streams. For example, *Diamesa zernyi*, *Diamesa tonsa* and *Pseudodiamesa branickii* are cold hardy with a thermal optimum below 6°C but survive short-term heat shock by developing a heat shock response based on the synthesis of heat shock proteins [66]. It is clearly not sufficient to preserve the species considering the observed cases of local extinction. Decreasing glacier cover disadvantages Diamesinae and other cold stenothermal taxa but favors organisms with long life cycles (univoltine) or more (semivoltine) due to continuous growth around the year (life cycle shifts suggest that where glacier cover is high, nondiapausal organisms typically develop rapidly in the spring/summer melt seasons before rivers dry up or freeze through winter) [67]. Furthermore, decreasing glacier cover favors insects that undergo incomplete metamorphosis, such as Plecoptera (stoneflies) and Ephemeroptera (mayflies), and noninsect taxa such as Oligochaeta (worms), burrowing and using interstitial habitat. Dietary shifts reflect terrestrial vegetation succession with decreasing glacier cover supplying plant litter to rivers resulting in higher amount of organic material for detritivores. These shifts were observed in glacialized systems in European Alps (Austria and Italy), French Pyrénées, Greenland, Iceland, New Zealand Alps, Norway Western Fjords, US Rockies, Alaska and Svalbard [67].

4.4 Refuge areas

If the speed of adaptive capacity—when possible—is not temporally synchronous with the speed of the glacier retreat, the only way to survive for cryophilous species is to find refuge areas. A refuge can be defined as sites able to preserve suitable climate conditions for cold-adapted species in spite of the climate warming [68]. The role of active rock glaciers and debris-covered glaciers as potential warm-stage refugia for cold-adapted ground beetle species is supported by data collected on the Italian Alps [16, 28, 40]. The thermal profile observed on some alpine active rock glaciers supports this view indicating decoupling of the local topoclimate from the regional climate, a key factor for a site to serve as a refugium. Specifically, active rock glaciers differ from the surrounding landforms (e.g., scree slopes) by overall lower ground surface temperature (average annual temperatures around or below 0°C). During postglacial periods, cold-adapted species found refuge in cooler habitats, such as subterranean environments (e.g., caves), where they could find cold and stable microclimatic conditions [69]. Thus, we cannot exclude that the same pattern is acting till now for ground beetles on active rock glaciers and debris-covered glaciers, because only these landforms are still able to support large-size populations of cold-adapted species.

In streams, the majority of invertebrates avoid the hazards of freezing or desiccation (due to freezing of the substrate or due to drought caused by increasing temperature) by migrating to unfrozen habitats (e.g., springs fed by groundwater inputs and hyporheic zone), where they remain active [70]. This is a temporary adaptation, to escape daily or seasonal risk of freezing or desiccation. On long time scale, these refugia cannot preserve cold stenothermal *Diamesa steinboecki* and similar species, never found in springs and not confined to the hyporheic having the terrestrial adult. Rock glacier outflows might act as a cold refuge areas after the glacier loss also for aquatic insects due to their constantly cold waters [71]. Ref. [72] investigated five streams fed by rock glaciers in South Tyrol (Italy) and found a dominance of Diamesinae and Orthocladiinae chironomids, besides Plecoptera, Ephemeroptera and Trichoptera (EPT). The authors reported the presence of cold-stenothermal species (*Diamesa* spp.), which suggests that rock glacial streams can act as refuge areas after the glacier loss [73]. However, further studies are necessary to demonstrate that cold-hardy *D. steinboecki* and other *Diamesa* species restricted to kryal habitat might survive competition with spring fauna (EPT) in rock glacier outflows.

4.5 Chemical pollution

Among the stressors that threaten the glacial biodiversity, there are also chemicals, i.e., persistent organics pollutants (POPs) deriving from long-range atmospheric transport and pesticides and emerging contaminants (e.g., personal care products as fragrances and polybrominated diphenyl ethers (PBDEs) widely used as flame retardants) carried to the glaciers by short-medium range atmospheric transport. These pollutants undergo cold condensation and accumulate in the glacier ice until their release in melt waters and ice-free soil [74, 75]. Among organic contaminants detected in glacier-fed streams, attention was paid to the insecticide chlorpyrifos, since high toxicity to insects and peak release by glacier melting occur concurrently with the period in which the streams are more densely populated by macroinvertebrates [76]. Chlorpyrifos and other organophosphate insecticides are known to exhibit increased toxicity in invertebrates at elevated temperatures [77]. Specifically, warming influences chlorpyrifos uptake in aquatic insects magnifying its negative effect on fauna. Other contaminants are heavy metals released by remains of the Great War, such as bombs, bullets, cannon parts and barbed wire buried in the ice 100 years ago, that are emerging due to glaciers retreating. These new sources of contamination have been recently documented for ice melt waters in the Italian Alps (mainly by nickel, arsenic and lead, unpublished data). Contamination of soils of the 1914–1918 Western Front zone, in Belgium and France by copper, lead and zinc was previously detected by [78]. Pesticides, fragrances and heavy metals affect swimming behavior and metabolism of *Diamesa* species from glacier-fed streams [79] at trace concentration (in order of ng/L), with still unknown effects on aquatic food web and on terrestrial fauna (*via* food web). To our knowledge, the understanding of final environmental fate of such pollutants is still scarce and fragmentary. Recently, evidences of microplastic bioaccumulation are given for freshwater amphipods from Svalbard glacier-fed streams [80] and for *Diamesa zernyi* larvae from the Amola Glacier-fed stream (Italy). No information is now available on their effects on ground beetle fauna.

5. Role of glacial biodiversity in the glacial-ecosystem functioning and services

Given the global change scenarios, it is opportune to analyze the role of glaciated areas in the context of persistent change from the physiographic point of view as well as the glacial biodiversity they host.

Standardized long-term monitoring, additional high-quality empirical studies on key organisms and landforms, and further development of analytical methods are of extreme importance in helping to quantify the extinction debt better and to more successfully enhance and protect glacial biodiversity.

Glacier shrinkage will alter hydrological regimes, sediment transport, and biogeochemical and contaminant fluxes from rivers to oceans, which will profoundly influence the natural environment and the ecosystem services that glacier-fed rivers provide to humans, particularly provision of water for agriculture, hydropower and consumption [4]. Biodiversity influences ecosystem functioning through changes in the amount of resource use or water self-depuration processes (regulating services) but is also a source of scientific and tourist attraction (cultural service).

Glacial biodiversity has an intrinsic value; most of the species are highly specialized to live in harsh environments, thus highly vulnerable to changes also of low intensity, have low dispersal ability and in most of the glacialized area of the world are endemic. Therefore, glaciated areas become territories with a collection of communities and species that mostly differ from those dominant in middle and low altitudes as well as differ between geographic areas. In addition, insects and other arthropods (e.g., spiders) living on the moraines, on the glaciers or flying on the glaciers (e.g., chironomids and stoneflies) act as additional source of food for some high-altitude mammals and bird species living at the edge of ice-related landforms [81, 82]. Therefore, glacial biodiversity is able to furnish an additional important naturalistic value of glacialized mountain regions.

Aquatic and terrestrial insects living in glacialized areas are trophically connected [83, 84], but not all insect groups react in the same way to the ongoing glacier retreat. Increasing glacial retreat differently affects ground-dwelling and aquatic insect taxa: ground beetles respond faster to glacier retreat than do non-biting midges, at least in species richness and species turnover patterns [84]. It depends on how fast habitat conditions change in relation to glacier retreat: the terrestrial environment changes faster than the aquatic environment. For instance, an increase of 0.6°C in summer temperatures approximately doubled the speed of colonization of the recently deglaciated terrains by ground-dwelling invertebrates [39]. The glacial stream lengthens but the physicochemical features and hydrological regime may not change for a long time, until the surface of the glacier is reduced to a few hectares and finally the environment becomes less extreme for life. As a result, as long as the environmental conditions remain extreme, the community in the glacier-fed stream is not affected.

Because even small ecosystem fragments like glaciers or other ice-related landforms have conservation value for insect biodiversity and ecosystem services, a better understanding and delineation of the species that need to be protected is also important. Funding of long-term research activities on habitat conservation in general, and specifically on insect science and taxonomy, is especially important to evaluate and mitigate future changes in insect communities, obtain reliable insect time series and discover species before they go extinct.

6. Conclusions

A recent large-scale study aimed to investigate trends in insect abundances over space and time has brought evidences about an average decline of terrestrial insect abundance (ca. 9%) per decade and an increase of freshwater insect abundance (ca. 11%) per decade. Both patterns were particularly strong in North America and some European regions [85], and the hypothesized drivers are land-use change and climate change.

Ground beetles and non-biting midges are among the animals best adapted to live at high altitudes, specifically to colonize the glaciers and surrounding terrestrial and aquatic habitats. They are present with few species adapted to low temperatures and food scarcity, factors that make these habitats extreme for life.

Spatio-temporal shift in insect communities in relation to the ongoing climate change is one of the most common patterns in mountain regions, but it is important to highlight that it will not affect all species equally [85, 86]. Aquatic and terrestrial insect communities seem to be differently affected by climate change. Firstly, because temperature variability is stronger on the ground with respect to water, aquatic insects are required to make smaller behavioral or physiological adjustments than terrestrial insects and aquatic habitats will be more buffered from climate warming [86]. In addition, terrestrial insects may have wider opportunities to survive in appropriate microclimate colonizing or surviving in ice-related microhabitat, thanks to the higher microhabitat heterogeneity on the ground with respect to the aquatic habitat.

The chapter provides a synthesis about the fascinating adaptations in morphology, behavior and physiology in terrestrial and aquatic species, on the species distribution in relation to the ice-related landform heterogeneity and on which species are threatened with extinction due to climate change and pollution. The future challenge will be to try to improve the knowledge of the glacial biodiversity in high-altitude and high-latitude areas notwithstanding the difficulty of accessing most of these areas.

Three research goals should be addressed in the near future: (i) increase the studies aimed at describing the glacial biodiversity; (ii) plan long-term monitoring projects in key areas and (iii) improve the scientific communication about the threats on high-altitude habitats. Thus, with this chapter, we are confident to inspire young researches to investigate the life in glacial ecosystems of the world before its possible disappearance.

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Conflict of interest

The authors declare no conflict of interest.

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